Ministry for Primary Industries
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Changes to the food-web of the Hauraki Gulf during the period of human occupation: a mass-balance model approach

New Zealand Aquatic Environment and Biodiversity Report No. 160

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ISSN 1179-6480 (online)
ISBN 978-1-77665-051-4 (online)
September 2015

New Zealand Government

Growing and Protecting New Zealand

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EXECUTIVE SUMMARY

Pinkerton, M.H.; MacDiarmid, A.; Beaumont, J.; Bradford-Grieve, J.; Francis, M.P.; Jones, E.; Lalas, C.; Lundquist, C.J.; McKenzie, A.; Nodder, S.D.; Paul, L.; Stenton-Dozey, J.; Thompson, D.; Zeldis, J. (2015). Changes to the food-web of the Hauraki Gulf during the period of human occupation: a mass-balance model approach.
***New Zealand Aquatic Environment and Biodiversity Report No. 160.* 346 p.**

The multi-disciplinary *Taking Stock* project aimed to describe how the structure and functioning of New Zealand shelf ecosystems have changed during human occupation (the last thousand years) in response to climate variation and human activity. This report concerns ecosystem modelling of the Hauraki Gulf.

We developed five food-web models of the Hauraki Gulf region representing distinct phases of human marine resource exploitation over the last thousand years: (1) present day; (2) 1950, just prior to onset of industrial-scale fishing; (3) 1790, late Māori phase before European whaling and sealing; (4) 1500, early to middle pre-European Māori phase; (5) 1000, before human settlement in New Zealand. Each model represents all the major biota of the Hauraki Gulf, from bacteria to whales and was developed using information provided by ten teams of experts.

The first model to be developed was that representing the present day ecosystem of the Hauraki Gulf, as there is much more data to inform this than historical models. Stable isotope measurements were successfully used to validate the trophic levels of organisms in the present day model. Sensitivity analysis showed that the present day model was robust to uncertainties in the initial parameter estimates of up to a factor of three. Historical models were then developed working backwards in time from the present day. Biomass and catch parameters were altered using information from historical reconstructions of catch histories, fisheries stock modelling, historical and archaeological information (middens), reconstructions of past climate, and evidence from narratives. Historical diets were estimated assuming that prey preferences had not changed from the present day. Food-web parameters were then adjusted to achieve balance, with greater variation allowed in parameters for which we had no prior information. Alternative methods of balancing historical models could be explored in the future and used to test the sensitivity of our conclusions to these assumptions.

We investigated changes to the structure of the food-web by estimating “trophic importance”. The trophic importance of a group describes how important it may be to the dynamics of the ecosystem (which is related to stability and resilience). Groups with high trophic importance are considered as more likely to be keystone or foundation groups i.e. ones with higher importance in maintaining the structure and function of the food-web as a whole.

Key conclusions are given below.

1. In the present day model, the five groups in the Hauraki Gulf ecosystem with highest trophic importance were (in decreasing order): phytoplankton; macrobenthos (small benthic crustaceans and worms); mesozooplankton; bivalves; snapper (which is the highest trophic importance fish group). Management of the Hauraki Gulf should take into account the larger ecosystem effects that may result from further impacting these groups either directly (target species) or indirectly (impacts of bottom gear). Management action which may be considered appropriate could include additional data collection to understand or monitor these groups, modelling to investigate how these groups affect resilience, or reducing direct and indirect human impacts on these groups.
2. According to the model, carbon is estimated to be accumulating in the Hauraki Gulf ecosystem at the rate of 0.3 Mty^{-1} which implies a value of ecosystem services in terms of carbon burial of about NZ$6.5 million per year (assuming a “carbon-tax” value of $25/tC).

3. Some higher trophic level parts of the ecosystem of the Hauraki Gulf have changed substantially since human arrival, largely as a result of harvesting and introduced land-based predators. Fur seals and sea-lions were extirpated (made locally absent) from the Hauraki Gulf ecosystem before 1790 as a result of hunting by Māori. The abundance of cetaceans is estimated to have declined by 97% since 1000. The abundance of seabirds was estimated to have declined by 69% since 1000, largely due to the introduction of rats and other predators of eggs and chicks. Reductions in the biomass of fish groups over the period of human occupation due to fishing were estimated to be: sharks, 86%; snapper, 83%; rock lobster, 76%; other key fish stocks (jack mackerels, blue mackerel, gurnard, leatherjacket, tarakihi, kahawai, rig, flatfish, trevally, barracouta, skipjack tuna), average of 57%; "other demersal fish", 59%.

4. Cetaceans and seals were some of the groups with highest trophic importance (third and fifth respectively out of 46 groups) in the Hauraki Gulf system in the pre-human model. Reductions in the biomass of upper trophic levels over time led to substantial declines (or complete removal for seals) in their trophic importance (to twenty-first for cetaceans in the present day model). Sharks and rock lobster also had much higher trophic importance in 1000 than in the present day due to reductions in their biomasses over time.

5. The biomasses of many middle trophic level groups (such as small and large pelagic fishes, macrobenthos, squid, macrozooplankton, and gelatinous zooplankton) changed substantially (11–44%) over time in the models while others did not (especially benthic invertebrate epifauna). The groups that changed in biomass in the models were generally those that are important prey items for middle and upper level predators. We recommend establishing monitoring for changes in these middle trophic level groups in the Hauraki Gulf due to their likely important role in maintaining ecosystem resilience.

6. Despite large reduction to the biomasses of many upper and middle trophic level groups, some of which had high trophic importance, according to the trophic modelling, the rank trophic importance of about half the groups in the Hauraki Gulf did not change substantially over the period of human occupation; the rank trophic importance of 24 of 46 non-detrital groups changed by fewer than four places between 1000 and the present day. The groups with little change in their rank trophic importance include some commercially-important fish groups (snapper, gurnard, leatherjacket, tarakihi, flatfish, and barracouta), large and small pelagic fishes, small reef fish, many groups of benthic epifauna (urchins, bivalves, sponges, macrobenthos), squid, all groups of zooplankton, phytoplankton and macroalgae.

7. The biomasses of the lower food-web of the Hauraki Gulf (primary producers, bacteria, detrital pathways, microbial function) were little affected in the ecosystem models by quite substantial changes over time to the biomass of fish and higher trophic levels. Our modelling suggests that the functioning of the lower food-web of the Hauraki Gulf is somewhat decoupled from changes at higher trophic levels, probably by the "buffering" or stabilizing effect of middle trophic level organisms.

8. If the biomass of some higher predator groups recover towards former levels it is likely to change the pattern of trophic importance in the region. For example, after an absence of nearly 500 years New Zealand fur seals have reappeared in the Hauraki Gulf although their biomass is still negligible. Management of the region should be aware of the potential for large-scale trophic and system-level effects to arise from the re-establishment and recovery of marine mammal populations towards historical levels.

1. INTRODUCTION

New Zealand was the last major land mass in the world to be settled by humans, occurring sometime between 1230 and 1280 (Wilmshurst et al. 2010). Consequently, New Zealand has a short and reasonably complete archaeological, historical and contemporary record of human exploitation of marine resources (MacDiarmid 2011). The collaborative multi-disciplinary Taking Stock project (ZBD200505), had the overall objective of determining the effects of climate variation and human impact on the structure and functioning of New Zealand shelf ecosystems over the timescale of human occupation.

Overall objective:	To determine the effects of climate variation and human impact on the structure and functioning of New Zealand shelf ecosystems
Specific objective 4:	To build mass-balance ecosystem models (e.g. Ecopath) of the coastal and shelf ecosystem in each area for five critical time periods: now, 60 years BP (before modern industrial fishing), 250 years BP (before European whaling and sealing), 600 y BP (early Maori phase) and 1000 years BP (before human settlement).

The Hauraki Gulf (Figure 1) was chosen as the first case study as it is important in terms of economics, ecology, social structure and culture; it was one of the first areas settled by Māori and now borders the largest urban centre in New Zealand, Auckland. The region has been intensively studied for decades, and there is sufficient prehistoric, historic and modern information about marine resource use and present day ecology to indicate the pattern and magnitude of human impacts on the marine environment in this region (Smith 2011, MacDiarmid 2011). The model area includes the area from mean high water to the 250 m depth contour.

This project developed five food-web models of the Hauraki Gulf region: (1) present day; (2) 1950, just prior to onset of industrial-scale fishing; (3) 1790, before European whaling and sealing; (4) 1500, early Maori settlement phase; (5) 1000, before human settlement in New Zealand. Each model quantifies the flow of energy or organic matter through the marine food-web over an annual period representing the typical conditions at that point in history. Each model includes all the major biota of the Hauraki Gulf, from bacteria to whales. As part of this project, ten teams of experts provided information to estimate the initial set of parameters describing the annual average abundance, energetics (growth, reproduction, consumption), and trophic linkages (diets) for all biota. Summaries of the derivation of parameters for the model are given in Appendices 1–10 of this report.

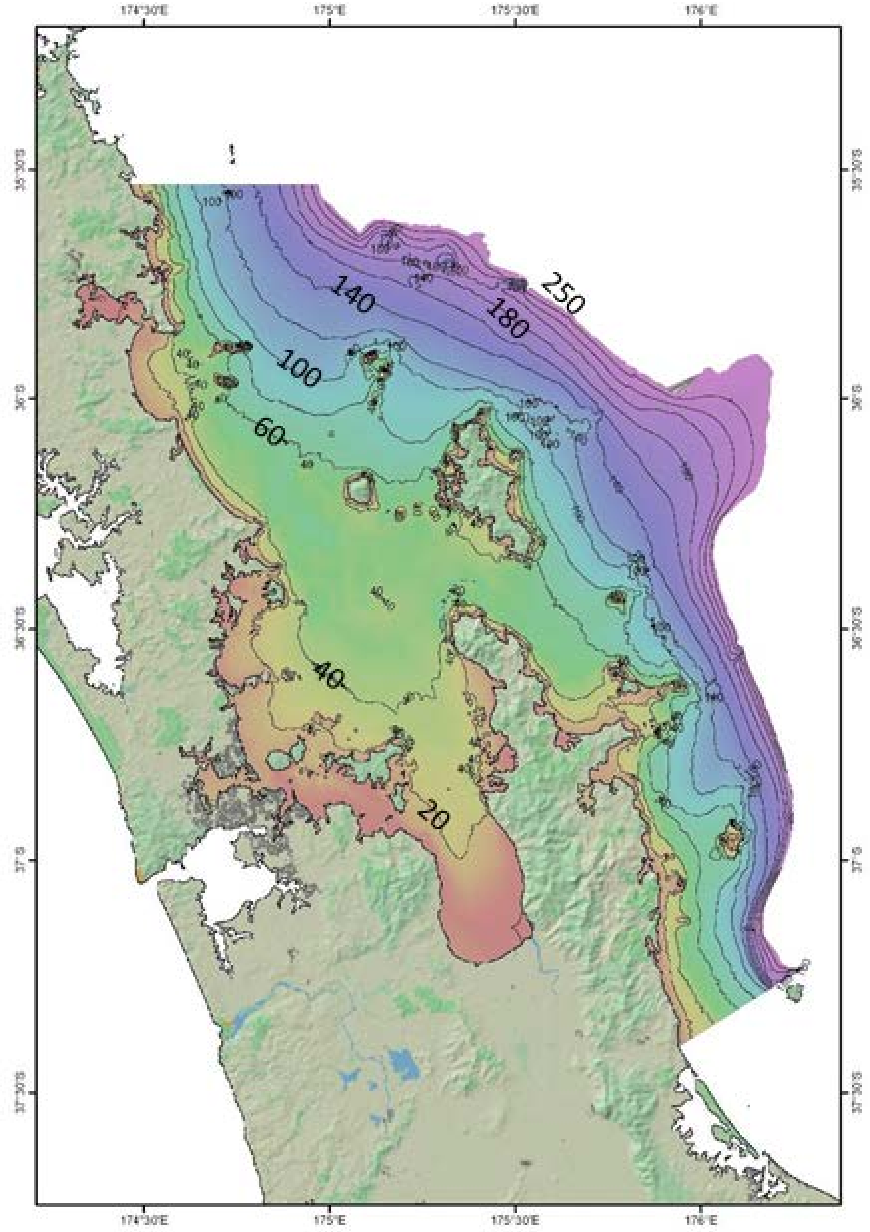


Figure 1: The Hauraki Gulf study area. Contours (labelled by depth in metres) representing bathymetry are drawn at 20 m intervals, with red/orange indicating shallow water (less than 40 m) and purple representing deep water (more than 200 m). The study area is constrained by the 250 m depth contour.

2. METHODS

2.1 Model structure

The trophic model developed here is based on the approach described by Pinkerton et al. (2008, 2010), and Pinkerton (2011). The model quantifies the transfer of organic carbon through a food web based on the widely used mass-balance identities of the Ecopath trophic model (Christensen & Walters 2004; Christensen et al. 2008). Biomass is presented in units of organic carbon density (gm^{-2}) and trophic flows in units of gm^{-2} y^{-1}. In quantifying the trophic structure of the ecosystem, the fundamental information includes the species present, estimated abundance in terms of weight, the energetics of species (i.e. production, consumption, growth efficiency, respiration), and trophic interconnections between species through information on diets of predators. The model developed here also includes non-trophic transfers of organic carbon between groups of organisms in the model ("trophic groups"). These transfers include: (1) unassimilated consumption (excreted material); (2) loss of material through exudates (e.g. primarily phytoplankton); (3) non-predation mortality (e.g. due to age, disease, starvation); (4) "messy eating" i.e. when an organism is killed, some organic material is not consumed by the predator; (5) ontogenic growth resulting in a transfer from one group (younger/smaller individuals) to another group (older/larger individuals); (6) vertical sinking flux of detritus from the water column to the benthos; (7) long-term burial of organic material in the benthic sediments, including deposition of shells. Note that (2) + (3) + (4) are often described by an ecotrophic efficiency parameter.

There is no assumption that the system is closed; transfers between the study area and the surrounding area are parameterised as imports and exports for each group. Furthermore, there is no necessity to assume that any of the groups individually or the system as a whole is in steady state; long-term accumulations can be (and are) included for all groups where information supports this. Primary production of producer groups represent the main source of organic matter into the system. The main losses of organic matter are from respiration of all living trophic groups (organic carbon is converted to carbon dioxide). Respiration loss is parameterised via production/consumption efficiency parameters for each living group. Flows relevant to non-living groups ("detritus") include imports from outside the system (e.g. riverine run-off) and exports (e.g. long-term burial or organic matter and calcified shells). Production is defined according to Equation 1. For non-detrital groups, production represents the intrinsic rate of growth of all individuals in the population. For detrital groups, production is the total net flow of organic matter into the group, including faecal material (unassimilated consumption) from consumers, dead organisms, non-consumed predation ("messy eating"), planktonic exudants and transfers between groups. These latter transfers include, for example, the release of organic material into the water column through the ablation of macro-algal blades, and the sinking of detrital/ungrazed material to the benthos. Carbon flow through each trophic group per year is balanced according to equation 2 under the assumption that all parts of the ecosystem will be in balance in an average year. These balance equations provide a number of equality constraints to the system. Another set of equality constraints are provided by the fact that diet fractions of each predator are defined to sum to unity.

$$P_i = B_i \left(\frac{P}{B} \right)_i \qquad \text{Non-detrital groups (1a)}$$

$$P_j = \sum_{i=1}^{n} P_i \left[T_{ij}^{1-E} + U_{ij} \left(\frac{Q}{P} \right)_i + T_{ij}^{s} \right] \qquad \text{Detrital groups (1b)}$$

$$P_i \left[1 - \sum_{j=1}^{n} (T_{ij}^{1-E} + T_{ij}^{g} + T_{ij}^{s}) - X_i - A_i \right] - \sum_{j=1}^{n} P_j \left(\frac{Q}{P} \right)_j D_{ij} - F_i = 0 \qquad \text{All groups (2)}$$

In these and other equations in this paper, for trophic group *i*:

B_i	annual average biomass (gC m^{-2})
P_i	annual production (gC m^{-2} y^{-1}). Autotrophic production rate is net of respiration but includes production of phytoplankton exudants.
Q_i	annual consumption (gC m^{-2} y^{-1}). Note that autotrophs and detritus have Q_i=0.

$(P/B)_i$	production/biomass ratio (y^{-1})
$(Q/P)_i$	reciprocal of the growth efficiency (dimensionless)
D_{ij}	average fraction of prey *i* in the diet of predator *j* by weight (dimensionless)
X_i	fraction of production exported over year due to advection and migration (dimensionless)
A_i	fraction of production accumulated over a year (dimensionless)
F_i	fishing removals (gC m^{-2} y^{-1}).
T_{ij}^{1-E}	detrital transfer: fraction of production transferred from group *i* to detrital group *j* as non-living material, i.e. excluding direct predation but including phytoplankton exudants, parts of organisms (e.g. due to "messy eating"), whole dead organisms and carcasses (dimensionless)
T_{ij}^{g}	growth transfer: fraction of production transferred from group *i* to group *j* due to growth, i.e. as an organism gets older and/or larger it changes from one group to another (dimensionless)
T_{ij}^{s}	seasonal transfer: fraction of production transferred from group *i* to group *j* by non-trophic, seasonal processes, e.g. due to vertical flux of material (dimensionless)
U_{ij}	fraction of food that has been consumed by component *i* but which is not assimilated, instead being passed to detrital group *j*, (dimensionless)
n	total number of groups in the model
R_i	loss of organic carbon from the system due to respiration (gC m^{-2} y^{-1}). Respiration can be calculated as $R_i=Q_i{\cdot}(1-U_i)-P_i$

Equations 1 and 2 differ from the standard Ecopath equations (Christensen & Walters 2004; Christensen et al. 2008) as follows. First, consumption is parameterised based on production (*P*) and *Q*/*P*, the reciprocal of the growth efficiency, rather than being based on biomass (*B)* and *Q*/*B*. This is done so that during model balancing, *P*/*B* and *Q*/*B* cannot vary independently and give unrealistic growth efficiencies. Second, the factor T_{ij}^{1-E} is used instead of the Ecopath ecotrophic efficiency parameter, EE_i, and is defined such that $T_{ij}^{1-E}=(1-EE_i)$. This factor quantifies the fraction of production which is transferred from a living to detrital group(s) by processes other than unassimilated consumption. For example, it is known that a substantial part of primary produced organic matter is not directly consumed but enters the detrital pool where it is decomposed by bacterial action. The proportion of net primary production undergoing these fates is given by the $P{\cdot}T^{1-E}$ term for the phytoplankton group. Third, two new non-trophic transfer parameters are included: growth and seasonal transfers (T_{ij}^{g}, T_{ij}^{s}). Growth transfer allows organisms to move between model groups as they grow (e.g. small fish becoming medium sized fish). Seasonal transfers include physical movement of material between groups, for example, settling of water column detritus to form benthic detritus. Neither seasonal or growth transfer processes can easily be represented in standard Ecopath equations.

2.2 Model groups

We assume that living organisms in a marine ecosystem can be grouped usefully into relatively few functional groups with distinct and stable characteristics. Too few groups will not allow the model to describe the trophic structure with sufficient subtlety, whereas too many groups can lead to spurious results because of lack of information to provide good parameterisation. Here, we use 49 trophic groups which is similar to, but towards the higher end, of the number of trophic groups used in Ecopath models (typically 25–50 groups). This approximate number of groups is generally believed to be sufficiently resolved that the characteristics of the system can be ascertained from the food-web model, yet be simple enough that it is not compromised by lack of information to estimate the parameters (Christensen & Walters 2004; Christensen et al. 2008). The divisions we use include taxonomy (species or groups of species), function (e.g. water column primary producers), habitat, and sampling methodology (e.g. benthic organisms by size). Ideally, groups would be chosen so that organisms combined into groups have similar characteristics such as size, energetics (growth rates, respiration rates, etc.), and similar trophic links (similar prey items, predators). In reality, choice of groups is often constrained by the available information. It is generally assumed that the choice of groups does not affect the fundamental characteristics of ecosystem models, and, although this has not yet been exhaustively tested, we follow best scientific practice that: “within the context of ecosystem models…aggregating species to the level of functional groups is acceptable” (Fulton et al. 2003). Although the order is not strictly important, groups in mass balance models tend to be ordered approximately from higher trophic levels group to lower trophic level groups, with groups in similar habitats close together. The 49 groups selected for this study are as follows (the order does not imply priority):

- Air-breathing predators (3 groups): seabirds, cetaceans, seals and sea-lions (note that the seal and sea lion group is only in models of 1500 and 1000);
- Benthic invertebrate fauna (12 groups): crayfish (red rock lobster), crabs, seastars, urchins, carnivorous gastropods and sea slugs, herbivorous/detrivores gastropods and chiton, sea cucumbers, bivalves, sponges, other encrusting invertebrates, benthic macrofauna, benthic meiofauna;
- Individual species or groups of species of fish (12 groups): snapper, jack mackerels, blue mackerel, gurnard, leatherjacket, tarakihi, kahawai, rig, flatfish, trevally, barracouta, skipjack tuna;
- Groups of fishes (6 groups): small reef fishes, large reef fishes, demersal fishes, small pelagic/mesopelagic fishes, large pelagic/mesopelagic fishes (including juvenile fishes), sharks;
- Cephalopods (2 groups): squids, octopus;
- Zooplankton (5 groups): gelatinous zooplankton (including salps), macrozooplankton, mesozooplankton, heterotrophic microplankton (ciliates), heterotrophic nanoplankton (flagellates);
- Primary producers (4 groups): phytoplankton, macroalgae, microphtyes, and a group which includes mangrove, seagrass and saltmarsh;
- Bacteria (2 groups): water column bacteria, benthic bacteria;
- Detritus (3 groups): particulate and dissolved water column detritus, benthic detritus, carcasses.

2.3 Ecotrophic efficiency

A substantial part of organic material (especially at lower trophic levels) is not directly consumed but enters the detrital pool where it is decomposed by bacterial action (Parsons et al., 1984; Kirchman, 2001). This material is typically accounted for in an ecotrophic model using an “ecotrophic efficiency” parameter. Ecotrophic efficiency is defined as the fraction of production that is consumed by other organisms, exported, fished or accumulated. The remainder of production (the fraction 1-EE of production) in the trophic models developed here is directed to a detrital group. Whereas small organisms that die from reasons other than direct predation (e.g., disease, parasites, injury) are likely to be decomposed by bacterial action, we suggest that larger organisms that die in the sea are more likely to be consumed by scavenging fauna. Remains of small dead organisms are transferred to the water column or benthic detrital group. Remains of larger organisms are transferred to the “carcass” group. There is also a flow of material to the water column and benthic detritus groups in the model because of “unassimilated consumption” from each consumer. Unassimilated consumption includes faecal material and the results of “messy eating” at lower trophic levels. Some of the smaller detritus will be in the form of particulate material in the water column, some as dissolved organic matter (e.g. phytoplankton exude transparent exopolymers), and some will be deposited to the sea bed in intense sedimentation events (e.g. rapid sinking of “marine snow”).

2.4 Parameter estimation

There is a large amount of information on the physical environment of the study region, and its flora and fauna, including physiology, life histories, energetics, and ecology. Detailed information on the estimation of the biomass, energetic parameters, and diets for each trophic group is given in Appendices 1–10 of this report, namely: (1) Seals and sea-lions; (2) Birds; (3) Cetaceans; (4) Benthic invertebrates; (5) Fishes; (6) Cephalopods; (7) Zooplankton; (8) Phytoplankton; (9) Mangrove, macroalgae, seagrass and saltmarsh; (10) Detritus and bacteria.

Diet fractions in trophic mass balance models are the proportion by weight (in terms of organic carbon) of various prey items in the diet of a consumer averaged over a typical year. Where possible, we used recent quantitative measurements of diet from the study area. Where this was not possible, we used values of diet from the literature. Diet fractions developed from stomach analyses in general have quite high uncertainty for a number of reasons (Hyslop (1980) and Cortés (1997) and references therein for more details). First, diets vary with the relative abundances/availabilities of prey items which are generally not measured independently of the diet sampling. Second, studies of consumer diets are often based on relatively few samples and are unlikely to allow good estimates of the spatial and temporal variability in diets. There may also be significant variation in diets between individuals in a population in a given area at a given time which will only be recognised if the sample sizes used in the diet study are sufficiently large. Third, studies of consumer diets are often only semi-quantitative, with prey abundance often being measured in terms of presence/absence, percent occurrence in diet, or by wet weight. Finally, methods used to correct for the relative rates of digestion of different organisms are uncertain, so that there may be a bias in diet studies towards prey items that are slowly digested, or contain hard parts that are readily identified in stomach analysis. Some particularly digestible prey items may be missed by diet studies altogether.

2.5 Balancing methodology

We used the semi-objective balancing method described in the peer-reviewed publications Pinkerton et al. (2008) and Pinkerton et al. (2010). Most studies of this kind do use semi-objective balancing of parameters (Kavanagh et al. 2004), but instead generally assume most parameters are correct, address gross inconsistencies using ad-hoc adjustments, and then use other factors (especially ecotrophic efficiency) to coerce models to balance. The semi-objective approach used here is believed to be more rigorous and likely to give more plausible (and useful) results than most ecosystem modelling studies elsewhere.

Each of the model parameters initially estimated has an associated uncertainty because the values are imperfectly and incompletely observed, and because the parameters vary between years. Initial estimates of all parameters are adjusted to obtain a model where all the equality constraints are fulfilled. Such solutions are henceforth referred to as balance points. We allow all parameters to vary except fishing removals (*F*). Models such as this are highly under-constrained, often with more than three times more parameters to fit than constraints (Pinkerton et al. 2010), so there is a large family of possible solutions all of which are feasible according to the conceptual model. We want to find the solution that is “closest” to our initial set of estimated parameters as defined below. The system is first linearised and then Singular Value Decomposition (SVD: Press et al. 1992) is applied to find the adjustment vector which minimises the cost function, Δ (Equation 3). This balance point is the closest one to our initial parameter set taking into account relative uncertainties between parameters.

$$\Delta^2 = \sum_{\text{all}\, i}\left[\delta B_i{}^2 + \delta\left(\tfrac{P}{B}\right)_i^2 + \delta\left(\tfrac{Q}{P}\right)_i^2 + \delta X_i{}^2 + \delta A_i{}^2 + \delta U_{ij}{}^2\right] + \sum_{\text{all}\, i,j}\left[\delta D_{ij}{}^2 + \delta T_{ij}^{1-E\,2} + \delta T_{ij}^{G\,2} + \delta T_{ij}^{s\,2}\right] \quad (3)$$

Where the parameters δB_i, $\delta(P/B)_i$ etc. represent the changes to the parameter needed to achieve model balance. These changes are defined below. In equations 4–13, using export as an example, X_i’ is the value of export that causes the model to balance, and X_i is the starting value (initial estimate of value from the literature and data). The family of dimensionless K parameters represents the relative uncertainty between parameters, with high K values representing greater uncertainty.

Biomass
$$B_i' = B_i + B_i^s \cdot K_i^B \cdot \delta B_i \tag{4}$$

Production
$$\left(P/B\right)_i' = \left(P/B\right)_i + \left(P/B\right)_i^s \cdot K_i^P \cdot \delta\left(P/B\right)_i \tag{5}$$

Growth efficiency^{-1}
$$\left(Q/P\right)_i' = \left(Q/P\right)_i + \left(Q/P\right)_i^s \cdot K_i^{QP} \cdot \delta\left(Q/P\right)_i \tag{6}$$

Export fraction
$$X_i' = X_i + K_i^X \cdot \delta X_i \tag{7}$$

Accumulation fraction
$$A_i' = A_i + K_i^A \cdot \delta A_i \tag{8}$$

Unassimilated consumption
$$U_{ij}' = U_{ij} + K_{ij}^U \cdot \delta U_{ij} \tag{9}$$

Diet fraction
$$D_{ij}' = D_{ij} + K_{ij}^D \cdot \delta D_{ij} \tag{10}$$

Transfer to detritus
$$T_{ij}^{1-E\,'} = T_{ij}^{1-E} + K_{ij}^{1-E} \cdot \delta T_{ij}^{1-E} \tag{11}$$

Transfer by growth
$$T_{ij}^{G\,'} = T_{ij}^G + K_{ij}^G \cdot \delta T_{ij}^G \tag{12}$$

Seasonal transfer
$$T_{ij}^{s\,'} = T_{ij}^s + K_{ij}^s \cdot \delta T_{ij}^s \tag{13}$$

For changes to three model parameters (B, P/B, Q/P) the changes were applied relative to scale values, B^s, $(P/B)^s$, $(Q/P)^s$ which are initially set to the estimated starting parameter values. Using the parameter values themselves to scale the adjustments appropriately handles the large range in magnitudes of these parameters across the food web. The parameter changes were not scaled for diet and transfer fractions because these parameters are of similar magnitudes (between 0 and 1) as they are scaled by P to obtain the actual flows of carbon (Equation 2). After adjustment in this way by SVD, the set of equality constraints will not be satisfied exactly because the minimisation works on a linearised version of the constraints assuming small changes. We hence iterate until the equality constraints are satisfied within a given tolerance. On each iteration, we update the three scale parameters B^s, $(P/B)^s$, $(Q/P)^s$ by setting each to the lower of the current estimate or the initial estimate of that parameter. Updating scale values in this way means that logarithmically-equal increases and decreases of parameters over multiple iterations will lead to the same change to the cost function. For example, $K.\delta = +1$ will represent a doubling of the parameter and $K.\delta = -1$ will represent a halving of the parameter.

2.6 Uncertainty parameters

In order to use an objective balancing method, it is necessary to assign relative magnitudes to the uncertainties of all parameters in the model. The absolute magnitudes of K across all groups are not important, but their relative values will affect the balanced model obtained. In effect, there is an infinite set of balanced models and which of these is deemed the "best" balanced model (and presented here) depends on the balancing procedure and hence on the relative uncertainties between parameters specified.

Whereas it is possible to assign uncertainties to some parameters by using information on the variability associated with various parts of the data used in their derivations, an entirely objective approach is not possible for all parameters for all groups. As a solution to the problem of assigning uncertainties to parameters consistently, Kavanagh et al. (2004) suggested that a "data pedigree" approach was useful where parameters were assigned indices representing their relative uncertainties and these pedigree indices then mapped onto numerical uncertainty factors. There are four main sets of uncertainty parameters, those for biomass (K_B), production (K_P), growth efficiency (K_{PQ}), and diet (K_D). Each of these four parameters for each group was given a score (or pedigree) of 1–9, with higher values representing more reliable data. Four mappings were then used to translate pedigree values into relative uncertainty values. The mappings are given in Table 1. Uncertainty factors for other parameters (K_E, K_A, K_X, K_F, K_U, K_S, K_R, K_G) were estimated directly, without reference to pedigree. Relative uncertainty factors which were used in the balancing procedure are given in Table 2. Note that the uncertainty values in this table do not imply absolute limits on plausible parameters as actual changes are determined by K values and the required δ values for balance.

Diet uncertainty factors (K^D) were estimated by a two stage process. First, a base value of K^D was assigned to all diet fractions of a given predator based on an estimate of the quality of the available diet information for that predator in the Hauraki Gulf. This predator-wise K value is denoted as K_{0j}^D for all diet fractions of a predator j. These base values were then adjusted for each prey item in the diet of the predator, based on the actual values of the estimated diet fractions, as equation 14.

Diet fraction uncertainties
$$K_{ij}^D = K_{0j}^D \cdot \left[a - b \cdot \exp(-c \cdot D_{ij})\right] \qquad (14)$$

where the constants a=1.114, b=0.9143, c=4.159 were chosen so that $K_{ij}^D/K_{0j}^D=1$ at $D_{ij}=0.5$. For diet fractions of $D_{ij}\rightarrow 0$ and $D_{ij}=1$, $K_{ij}^D/K_{0j}^D=0.2$ and $K_{ij}^D/K_{0j}^D=1.1$ respectively. This means that changes to diet fractions will tend to be smaller for prey species that make up lower proportions of the diet, to prevent these minor prey fractions being overinflated during the balancing procedure.

Similarly, we estimated K factors for transfer fractions ($K^{1\text{-}E}$, K^S, K^G, K^R, K^A, K^X) using a two step methodology. First, we set base transfer parameter uncertainties for all groups in the model ($K_0^{1\text{-}E}$, K_0^S, K_0^G, K_0^R, K_0^A, K_0^X) and then adjusted these according to our estimates of the actual values of the parameters (equations 15–20).

Accumulation
$$K_i^A = K_0^A \cdot \left(a \cdot A_i^2 + b \cdot A_i + c\right) \qquad (15)$$

Export
$$K_i^X = K_0^X \cdot \left(a \cdot X_i^2 + b \cdot X_i + c\right) \qquad (16)$$

Transfer to detritus
$$K_{ij}^{1-E} = K_0^{1-E} \cdot \left[a \cdot \left(T_{ij}^{1-E}\right)^2 + b \cdot T_{ij}^{1-E} + c\right] \qquad (17)$$

Transfer by growth $$K_{ij}^{G} = K_{0}^{G} \cdot \left[a \cdot \left(T_{ij}^{G} \right)^{2} + b \cdot T_{ij}^{G} + c \right] \tag{18}$$

Seasonal transfer $$K_{ij}^{S} = K_{0}^{S} \cdot \left[a \cdot \left(T_{ij}^{S} \right)^{2} + b \cdot T_{ij}^{S} + c \right] \tag{19}$$

Reproductive transfer $$K_{ij}^{R} = K_{0}^{R} \cdot \left[a \cdot \left(T_{ij}^{R} \right)^{2} + b \cdot T_{ij}^{R} + c \right] \tag{20}$$

We use constants in equations 15–20 of a= -2.8, b= 2.8, c= 0.3. This formulation gives K_{ij}/K_{i0}=1 for T_{ij}=0.5, and K_{ij}/K_{i0}=0.3 for $T_{ij} \rightarrow 0$ and T_{ij}=1. This approach prevents excessive changes occurring during balancing when initial estimates are towards an extreme of the possible range. We used base values of K_0^A=0.3, $K_0^{1\text{-}E}$=0.3, for all groups in the model where initial estimates were non-zero. We used K_{ij}^U=0.1 for all groups. We set K_i^F=0 for all groups i.e. we do not allow the balancing to adjust fishing removals. We set K_i^Q=0 for all groups so that the balancing adjusts consumption rates only via adjusting P/Q values. Although still more arbitrary than ideal, this method of assigning relative uncertainties is certainly an improvement on other methods currently available, and leads to a plausible balanced model. The sensitivity of the balanced model to different K factors is an important issue and is discussed later.

Table 1: Mappings between pedigree values and relative uncertainties for four parameters.

Pedigree	Comment	K_B	K_P	K_{PQ}	K_D
1	Virtually no relevant information	9	4	2	9
2	Guesstimate; Very poor information	4	2	1	4
3	Approximate or indirect method	2	1	0.64	2
4	Order of magnitude information	1	0.5	0.32	1
5	Some information, but low precision/unreliable	0.5	0.3	0.16	0.5
6	Reasonable information	0.3	0.2	0.08	0.3
7	Good information from the study area	0.2	0.1	0.04	0.2
8	Very good information from the study area	0.1	0.05	0.02	0.1
9	Fixed	0	0	0	0

Table 2: Uncertainty factors for parameters for balancing the present day model. Seals are not included because they do not feature in the model of the present day food-web. See text for explanation of headings and symbols.

	Group	K_E	K_B	K_P	K_{PQ}	K_A	K_X	K_F	K_U	K_S	K_R	K_G	K_D
1	Birds	0.6	0.2	0.05	0	0	0	0	0	0	0	0	0.5
2	Cetaceans	0.6	0.2	0.05	0.02	0	0	0	0	0	0	0	0.5
3	Crayfish	0.3	0.3	0.3	0.08	0	0	0	0	0	0	0	0.5
4	Crabs	0.3	0.3	0.3	0.08	0	0	0	0	0	0	0	0.5
5	Seastars	0.3	0.3	0.3	0.08	0	0	0	0	0	0	0	0.5
6	Urchins	0.3	0.3	0.3	0.08	0	0	0	0	0	0	0	0.5
7	Gastropods_carn	0.3	0.3	0.3	0.08	0	0	0	0	0	0	0	0.5
8	Gastropods_graz	0.3	0.3	0.3	0.08	0	0	0	0	0	0	0	0.5
9	Sea_cucumbers	0.6	0.3	0.3	0.08	0	0	0	0	0	0	0	0.5
10	Bivalves	0.3	0.3	0.3	0.08	0	0	0	0	0	0	0	0.5
11	Sponges	0.3	0.3	0.3	0.08	0	0	0	0	0	0	0	0.5
12	Encrusting	0.3	0.3	0.3	0.08	0	0	0	0	0	0	0	0.5
13	Macrobenthos	0.3	1	0.3	0.08	0	0	0	0	0	0	0	1
14	Meiobenthos	0.3	1	0.3	0.08	0	0	0	0	0	0	0	1
15	Snapper	0.3	0.1	0.1	0.04	0	0	0	0	0	0	0	0.3
16	Jack_mackerels	0.3	0.2	0.1	0.04	0	0	0	0	0	0	0	0.3
17	Blue_mackerel	0.3	0.2	0.1	0.04	0	0	0	0	0	0	0	0.3
18	Gurnard	0.3	0.1	0.1	0.04	0	0	0	0	0	0	0	0.3
19	Leatherjacket	0.3	0.3	0.1	0.04	0	0	0	0	0	0	0	0.3
20	Tarakihi	0.3	0.2	0.1	0.04	0	0	0	0	0	0	0	0.3
21	Kahawai	0.3	0.1	0.1	0.04	0	0	0	0	0	0	0	0.3
22	Rig	0.3	0.2	0.1	0.04	0	0	0	0	0	0	0	0.3
23	Flatfish	0.3	0.2	0.1	0.04	0	0	0	0	0	0	0	0.3
24	Trevally	0.3	0.1	0.1	0.04	0	0	0	0	0	0	0	0.3
25	Barracouta	0.3	0.2	0.1	0.04	0	0	0	0	0	0	0	0.3
26	Skipjack	0.3	0.5	0.1	0.04	0	0	0	0	0	0	0	0.3
27	Reef_fish_large	0.3	0.3	0.1	0.04	0	0	0	0	0	0	0	0.5
28	Reef_fish_small	0.3	0.3	0.1	0.04	0	0	0	0	0	0	0	0.5
29	Demersal_fish	0.3	0.3	0.1	0.04	0	0	0	0	0	0	0	0.5
30	Sharks	0.3	0.5	0.1	0.04	0	0	0	0	0	0	0	0.5
31	Pelagic_fish_large	0.3	0.3	0.1	0.04	0	0	0	0	0	0	0	0.5
32	Pelagic_fish_small	0.3	0.5	0.1	0.04	0	0	0	0	0	0	0	0.5
33	Squid	0.3	0.5	0.3	0.08	0	0	0	0	0	0	0	0.3
34	Octopus	0.3	1	0.3	0.08	0	0	0	0	0	0	0	0.3
35	Gelatinous	0.3	0.5	0.2	0.04	0	0	0	0	0	0	0	0.5
36	Macrozoo	0.3	1	0.2	0.04	0	0	0	0	0	0	0	0.5
37	Mesozoo	0.3	0.3	0.2	0.04	0	0	0	0	0	0	0	0.5
38	Microzoo	0.3	0.3	0.3	0.04	0	0	0	0	0	0	0	0.5
39	Nanozoo	0.3	1	0.3	0.04	0	0	0	0	0	0	0	0.5
40	Phytoplankton	0.6	0.2	0.1	0	0	0	0	0	0	0	0	0
41	Macroalgae	0.6	0.3	0.2	0	0	0	0	0	0	0	0	0
42	Mangrove_seagrass	0.6	0.3	0.2	0	0	0	0	0	0	0	0	0
43	Microphtyes	0.6	0.3	0.2	0	0	0	0	0	0	0	0	0
44	Bacteria_water	1	2	1	0.64	0	0	0	0	0	0	0	1
45	Bacteria_benthic	1	2	1	0.64	0	0	0	0	0	0	0	1
46	Carcasses	0	0	0	0	0	0	0	0	0	0	0	0
47	Detritus_water	0	0	0	0	0	0	0	0	2	0	0	0
48	Detritus_benthic	0	0	0	0	0.5	0	0	0	0	0	0	0

2.7 Trophic levels

We calculated trophic levels (Lindeman 1942, Christensen & Pauly 1992) in the balanced model using matrix inversion based on three rules. First, primary producers, detritus and bacteria are defined as having a trophic level (TrL) of 1. Bacteria, despite being "consumers" are defined as being at the same TrL as primary producers. This is assumed for consistency with other ecosystem models that tend not to model bacteria explicitly, and instead define the detritus-bacteria complex as having TrL=1 (e.g. Jarre-Teichman et al. 1998, Arreguin-Sanchez et al. 2002, Jiang & Gibbs 2005). Second, a consumer's trophic level is the sum of the trophic levels of their prey items, weighted by diet fraction, plus one. Third, carcasses are defined as having a trophic level equal to the weighted average of material flowing into the group.

Two other estimates of trophic level of groups in the study area were obtained in order to validate the trophic model representing the present day. First, trophic levels for 12 key fish groups in the trophic model (namely snapper, jack mackerels, blue mackerel, gurnard, leatherjacket, tarakihi, kahawai, rig, flatfish, trevally, barracouta, and skipjack tuna) were obtained from FishBase (Froese & Pauly 2009) and references therein (Table 3).

Table 3: Trophic levels (TrL) obtained from FishBase and references (with region of study in brackets) applicable to fish species/groups for the Hauraki Gulf model representing the present day conditions.

Group	Species	TrL	Reference
Snapper	*Pagrus auratus*	3.4 (3.3–3.5)	Russell 1983 (NZ)
Jack_mackerels	*Trachurus declivis; T. novaezelandiae; T. murphyi*	3.5 (3.2–3.9)	Maxwell 1979 (Australia); Godfriaux 1970 (NZ); Konchina 1992 (Peru)
Blue_mackerel	*Scomber australasicus*	4.2	Fujita et al. 1995 (Japan)
Gurnard	*Chelidonichthys kumu*	3.7	Godfriaux 1970 (NZ)
Leatherjacket	*Parika scaber*	3.0	Russell 1983 (NZ)
Tarakihi	*Nemadactylus macropterus*	3.4	Godfriaux 1970 (NZ)
Kahawai	*Arripis trutta*	4.1	Russell 1983 (NZ)
Rig	*Mustelus lenticulatus*	3.5	Cortés 1999 (not given)
Flatfish	*Rhombosolea leporina; R. plebeia*	3.05	Froese & Pauly (2009) (not given)
Trevally	*Pseudocaranx dentex*	3.4 (3.1–3.9)	Hindell et al. 2000 (Australia); Russell 1983 (NZ); Kulbicki et al. 2005 (New Caledonia)
Barracouta	*Thyrsites atun*	3.8 (3.2–4.5)	O'Driscoll 1998 (NZ); Russell 1983 (NZ)
Skipjack tuna	*Katsuwonus pelamis*	4.2 (3.8–4.5)	Cox et al. 2002 (Pacific); Sierra et al. 1994 (Cuba); Roger 1993 (Indian Ocean)

Second, stable isotope data of a variety of organisms from the Hauraki Gulf were used to estimate trophic levels. Carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) can track trophic connections within ecosystems and provide information on the structure of food-webs. Carbon isotopes are a powerful tool for identifying primary sources of organic material within ecosystems and showing benthic reworking (Fry & Sherr, 1984; Peterson & Fry, 1987). In a relatively small area like the Hauraki Gulf, variations in $\delta^{13}C$ tend to be low compared to $\delta^{15}N$ variations and may be of limited value except for highly mobile organisms, or those with a mixture of benthic and pelagic feeding. Nitrogen isotope ratios often show distinct enrichments per successive trophic level and have strong applications in food web and dietary studies (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; van der Zanden & Rasmussen, 2001). The isotope data were collected for the MPI biodiversity project ZBD2005-09, and summarised in Beaumont et al. (2009). This study covered a number of sites, including Goat Island, Great Barrier Island, Kawau Island, Leigh, Long Bay, Mokohinau Islands, Poor Knights Islands, Tawharanui, Tiritiri Matangi Island, and Torbay. There are 1350 measurements available, covering 22 organisms/groups of organisms (Table

4). Because of the lack of nitrogen isotope measurements for phytoplankton in most sites and the variability of δ^{15}N for phytoplankton and macroalgae across sites in this study, we re-calculated a nitrogen isotope baseline value using grazers. We used an average of the δ^{15}N values for the three groups "Isopod", "Asterocarpa", and "Sponge", assumed that these groups have a trophic level of 2, and used a standard δ^{15}N enrichment per trophic level of 3.4 (Post, 2002). These groups were chosen because the study measured δ^{15}N values for all of these biota at most sites in the Hauraki Gulf and because these are known to be entirely herbivorous.

Table 4: Stable isotope data for organisms in the Hauraki Gulf collected for the Ministry for Primary Industries biodiversity project ZBD2005-09 and summarised in Beaumont et al. (2009). Data were recalculated using grazers to establish the baseline as described in Section 2.7 and used to estimate trophic level (TrL).

	Group	N	δ^{15}N ($^{0}/_{00}$)	TrL	sd(TrL)
1	Ascidian	19	12.1	3.5	0.1
2	Asterocarpa	133	10.0	2.2	0.2
3	Blue maomao	23	11.9	3.3	0.1
4	Butterfish	61	10.9	2.7	0.2
5	Cookia	86	9.1	2.0	0.2
6	Crayfish	18	13.7	3.6	0.1
7	Ecklonia	10	8.2	1.7	0.3
8	Goby	8	10.4	2.6	0.3
9	Hermit crab	28	11.1	2.9	0.2
10	Isopod	70	8.0	1.7	0.4
11	Kina	104	10.0	2.2	0.2
12	Lobster	87	14.0	3.4	0.2
13	Parore	97	13.6	3.2	0.2
14	Red Alga	13	7.9	1.3	0.3
15	Red Moki	39	13.9	3.5	0.2
16	Sea Cucumber	44	13.1	3.1	0.3
17	Snapper	175	14.7	3.6	0.3
18	Sponge	160	9.5	2.1	0.2
19	Spotty	48	14.3	3.4	0.2
20	Sweep	66	13.4	3.2	0.2
21	Triplefin	26	12.2	3.3	0.3
22	Turbo[1]	35	11.2	2.0	0.2
	ALL	1 350			

Notes

[1] *Lunella (Turbo) smaragdus*

2.8 Trophic importance

Based on a balanced food-web model, the "Mixed Trophic Impact" (MTI) method can be used to estimate the trophic interconnectedness between pairs of species or species groups in the model (Ulanowicz & Puccia 1990; Libralato et al. 2006). The elements of the MTI matrix, $\mathbf{M}$ (m_{ij}) can be interpreted as the potential change in the biomass of one group (the "impacted" group, j) due to a small (infinitesimal) change in the biomass in another group (the "impacting" group, i) due to trophic effects alone (e.g. Libralato et al. 2006). These mixed trophic impacts can be positive or negative, and may be estimated to be strong (higher absolute values) or weak (closer to zero). The trophic importance (TI) of a model group is defined as the average of the absolute values of its impact on all other groups in the model. Trophic importance is a measure of how much changes to the biomass of a group may affect the dynamics of the whole ecosystem about the current balance point – this is related to ecosystem stability and resilience. Mixed trophic impacts and trophic importance should not be interpreted as showing the extent to which large changes to the biomass of one group will affect the biomasses of other groups. This is because MTI analysis includes no knowledge of the factors controlling the abundances of different groups and no allowance for changes to ecosystem structure over time.

Trophic importance is preferred over ‘keystone-ness’ since the meaning of the latter has never been adequately defined. Keystone-ness was defined by Power et al. (1996) as the amount by which the trophic importance of a species exceeds that “expected on the basis of abundance alone”. Unfortunately, there is no accepted measure of the trophic importance expected based on abundance alone. Some interpretations of keystone-ness essentially equate it to trophic importance (Libralato et al. 2006) whereas others weight trophic importance by the reciprocal of biomass (Power et al. 1996). In any case, trophic importance is the relevant measure in terms of assessing by how much changes to one species or group could affect the dynamic properties of the food-web, irrespective of whether the group has high or low biomass in the ecosystem.

The Mixed Trophic Impact (MTI) matrix, **M** is calculated as follows (Ulanowicz & Puccia 1990). First, a measure of the direct (one-step) trophic impact of species i on species j is written as element q_{ij} in the matrix **Q**, and defined as the difference between bottom-up (g_{ij}) and top-down effects (f_{ij}) (equation 21, Ulanowicz & Puccia 1990).

$$q_{ij} = g_{ij} - f_{ij} \qquad (21)$$

Here, g_{ij} is the proportion of prey item i in the diet of predator j, and f_{ij} is the fraction of the net production of prey item j that is consumed by predator i (Ulanowicz & Puccia 1990). “Net production” excludes respiratory output which is equal to “production” (P) in Ecopath and Ecosim models (Christensen & Walters, 2004; Christensen et al. 2008). The MTI matrix **M** is calculated as equation 22 to take into account indirect food-web effects, that is, impacts of one species on another via multiple steps through the food-web (Ulanowicz & Puccia 1990). Here, **I** is the identity matrix of size n by n where n is the number of groups in the model.

$$\mathbf{M}^t = (\mathbf{I} - \mathbf{Q}^t)^{-1} - \mathbf{I} \qquad (22)$$

We define the trophic importance of group i, $TI(i)$, as equation 23. We use absolute rather than squared values (Libralato et al. 2006) to give weak links more appropriate importance (McCann et al. 1998; Pinnegar et al. 2005; Pinkerton & Bradford-Grieve, 2014).

$$TI(i) = \textstyle\sum_{j=1}^{n} |m_{ij}| \qquad (23)$$

2.9 Omnivory index

Omnivory index (OI) is a measure of the breadth of a consumer’s diet and is calculated from the square of the difference in trophic level between predator and prey, as equation 24 (Christensen & Walters, 2004; Christensen et al. 2008).

$$OI_i = \sum_{j=1}^{n} (TL_j - (TL_i - 1))^2 \cdot D_{ij} \qquad (24)$$

Here, TL_j is the trophic level of prey j, TL_i is the trophic level of predator i, and D_{ij} is the proportion prey j contributes to the diet of predator i.

2.10 Sensitivity analysis

A sensitivity analysis of the present-day model was carried out by randomly perturbing key input parameters, rebalancing the model, and recalculating the trophic importances of all groups. This tests for the consequence of having incorrect initial estimates of key parameters before the model was balanced. Biomass, productivity (P/B) and diets were perturbed as these are likely to be the key drivers of model structure. Initial estimates of these parameters were multiplied by a random factor representing changes of up to a factor of 3 (Figure 2), with decreases and increases of all sizes (within the limit) equally likely. Diet fractions were normalised to sum to unity. The model was then balanced, mixed trophic impact analysis carried out, the result stored and the process repeated 2000 times. The distribution of properties across all stored models was then used to investigate the robustness of the model to parameter uncertainty.

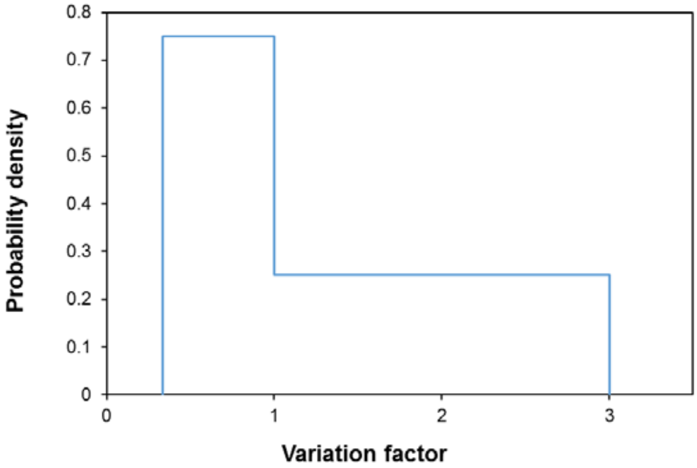


Figure 2: Probability density distribution of random variations to parameters, with up to a factor of 3 variation (changes between factor of $^1/_3$ and 3) and increases as likely as decreases.

2.11 Historical models

Trophic models were developed for the present day and for four historical time periods:

- 1950 – just prior to the onset of industrial-scale fishing
- 1790 – before European whaling and sealing
- 1500 – early Maori settlement phase
- 1000 – before human settlement in New Zealand

These periods were chosen to focus on periods or time between expected major perturbations caused by human activity (MacDiarmid, 2011). We estimated an initial set of parameters for each historical model using three methods. First, some key parameters in the historical models were specified as being different to the present day model. Evidence used includes historical data, archaeological information, dynamic “backward-projection” models (such as stock assessment models for particular species), changes based on reconstructions of past climate, or evidence gleaned from eye-witness narratives.

Natural drivers of environmental change in New Zealand during the last millennium were examined by Lorrey et al. (2013). The collection of palaeoclimate precipitation and temperature data were interpreted using a regional climate regime classification to reconstruct circulation patterns. Lorrey et al. (2013) concluded that: “The progression of temperature changes observed in New Zealand proxies that cover the last 1000 years that are hypothesized as a result of a shift from more equatorial climate influences on regional circulation to one with more polar influences include:

(a) early warm interval that began prior to 1000 through ~1300;

(b) gradual temperature decline through the early warm interval that subsequently continued through ~1450;
(c) dramatic temperature decline [around 1450];
(d) cooler than present temperatures [between 1500–1900], with multi-decadal to centennial variability that was superposed on a low frequency warming trend evident since the mid 1500s;
(e) marked temperature increase since the 1950s."

The authors also state that: "Propagation of downstream changes to coastal environments via sedimentary and geomorphic processes would have undoubtedly affected nearshore aquatic ecosystems" (Lorrey et al. 2013).

Information to constrain the historical models includes biomass for seals (which do not exist in the model representing present day conditions), birds, cetaceans, crayfish (red rock lobster), fishes, phytoplankton, and mangrove/seagrass/saltmarsh and is shown by grey shading in the tables summarising the parameters for the historical models (Section 3.2). Second, initial estimates of diet fractions for all groups were estimated as described in Section 2.12. Briefly, we assumed that diets in the present day include all prey items consumed since before humans arrived in New Zealand and that electivities (preferences) for every predator-prey link were constant through time (see Section 2.12 for details). Third, all other parameters were set to the value in the balanced model just after that being developed - we worked backwards from the present day model to the 1950 model, and so on until balancing the 1000 model last. It is likely that uncertainty in the models hence increases as the time is wound back.

For each historical model separately, the initial parameter set was then adjusted to achieve balance using the semi-objective balancing procedure described in Section 2.5. Uncertainty parameters used to balance the historical models were the same for 1950, 1790, 1500 and 1000 models and are shown in Table 5. Changes to non-specified (unconstrained) parameters were generally allowed to vary by more than specified parameters during balancing of the historical models reflecting the view that non-specified parameters in the historical models are more poorly known than those which can be estimated before balancing. This approach reconciles limited historical information on a few parts of the system into a balanced ecosystem by allowing the less well known parts of the system to vary most. We do not propose ecological mechanisms by which this adjustment occurs, but simply allow key parameters (especially ecotrophic efficiencies, biomasses and diets) to vary to achieve balance in the historical models. Alternative methods of balancing historical models should be explored in the future using different assumptions about the mechanisms by which changes to one group affects others, and assumptions about the factors controlling the biomass of each group in the model at each time. Given that these mechanisms and controlling factors are poorly known, the method used here is an appropriate way to start exploring what the structure of the Hauraki Gulf food-web could have looked like at different times in history.

Table 5: Uncertainty factors for parameters in the historical models. Note that seals are only in models for 1500 and 1000.

	Group	K_E	K_B	K_P	K_{PQ}	K_A	K_X	K_F	K_U	K_S	K_R	K_G	K_D
1	Seals	1	0	0	0	0	0	0	0	0	0	0	0.2
2	Birds	0.5	0	0.05	0	0	0	0	0	0	0	0	0.5
3	Cetaceans	0.5	0	0.05	0	0	0	0	0	0	0	0	0.5
4	Crayfish	0.5	0.3	0.05	0	0	0	0	0	0	0	0	0.5
5	Crabs	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
6	Seastars	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
7	Urchins	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
8	Gastropods_carn	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
9	Gastropods_graz	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
10	Sea_cucumbers	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
11	Bivalves	0.5	0.3	0.05	0	0	0	0	0	0	0	0	0.5
12	Sponges	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
13	Encrusting	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
14	Macrobenthos	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
15	Meiobenthos	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
16	Snapper	0.5	0.1	0.05	0	0	0	0	0	0	0	0	0.5
17	Jack_mackerels	0.5	0.1	0.05	0	0	0	0	0	0	0	0	0.5
18	Blue_mackerel	0.5	0.1	0.05	0	0	0	0	0	0	0	0	0.5
19	Gurnard	0.5	0.1	0.05	0	0	0	0	0	0	0	0	0.5
20	Leatherjacket	0.5	0.3	0.05	0	0	0	0	0	0	0	0	0.5
21	Tarakihi	0.5	0.1	0.05	0	0	0	0	0	0	0	0	0.5
22	Kahawai	0.5	0.1	0.05	0	0	0	0	0	0	0	0	0.5
23	Rig	0.5	0.1	0.05	0	0	0	0	0	0	0	0	0.5
24	Flatfish	0.5	0.1	0.05	0	0	0	0	0	0	0	0	0.5
25	Trevally	0.5	0.1	0.05	0	0	0	0	0	0	0	0	0.5
26	Barracouta	0.5	0.1	0.05	0	0	0	0	0	0	0	0	0.5
27	Skipjack	0.5	0.3	0.05	0	0	0	0	0	0	0	0	0.5
28	Reef_fish_large	0.5	0.3	0.05	0	0	0	0	0	0	0	0	0.5
29	Reef_fish_small	0.5	0.3	0.05	0	0	0	0	0	0	0	0	0.5
30	Demersal_fish	0.5	0.3	0.05	0	0	0	0	0	0	0	0	0.5
31	Sharks	0.5	0.3	0.05	0	0	0	0	0	0	0	0	0.5
32	Pelagic_fish_large	0.5	0.3	0.05	0	0	0	0	0	0	0	0	0.5
33	Pelagic_fish_small	0.5	0.3	0.05	0	0	0	0	0	0	0	0	0.5
34	Squid	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
35	Octopus	0.5	1	0.05	0	0	0	0	0	0	0	0	0.5
36	Gelatinous	0.5	1	0.1	0	0	0	0	0	0	0	0	0.5
37	Macrozoo	0.5	1	0.1	0	0	0	0	0	0	0	0	0.5
38	Mesozoo	0.5	1	0.1	0	0	0	0	0	0	0	0	0.5
39	Microzoo	0.5	1	0.3	0	0	0	0	0	0	0	0	0.5
40	Nanozoo	0.5	1	0.3	0	0	0	0	0	0	0	0	0.5
41	Phytoplankton	0.5	0	0.05	0	0	0	0	0	0	0	0	0
42	Macroalgae	0.5	0	0.05	0	0	0	0	0	0	0	0	0
43	Mangrove_seagrass	0.5	0	0.05	0	0	0	0	0	0	0	0	0
44	Microphtyes	0.5	0	0.05	0	0	0	0	0	0	0	0	0
45	Bacteria_water	0.5	2	1	0.5	0	0	0	0	0	0	0	0.5
46	Bacteria_benthic	0.5	2	1	0.5	0	0	0	0	0	0	0	0.5
47	Carcasses	0	0	0	0	0	0	0	0	0	0	0	0
48	Detritus_water	0	0	0	0	0	0	0	0	2	0	0	0
49	Detritus_benthic	0	0	0	0	0	1	0	0	0	0	0	0

2.12 Adjustment of historical diet parameters

Diets of animals may change historically as the abundance and/or availability of prey items varies, especially as many predators may change their diets in response to changes in prey abundance. We had no empirical information on these historical changes in diet and instead past diets were estimated following guidelines from similar studies elsewhere (Link & Garrison 2004; Pitcher, 2004; Heymans & Pitcher, 2004). We obtained an initial estimate of historical diets under three assumptions. First, we assume that all potential prey items for each predator are the same historically as observed now. It is possible that a predator consumed a prey item in the past which is now not consumed at all and does not appear in diet studies for that predator. We have no information on whether this occurred and assume instead that predators consume the same types of organism today as they always have, albeit in different proportions. Second, we assume that the proportions of prey items in the diet of a predator depend on the preference of the predator for different potential prey items and the abundance of the prey item to the predator (equation 26, Lundquist & Pinkerton, 2008 following a Type I Holling function, Holling, 1959). A predator's optimum foraging strategy may be to actively seek and consume a high proportion of a non-abundant prey item (higher electivities for lower abundance prey items), or to consume the most abundant prey items (uniform electivities). Third, we assume that "abundance" of prey items can be estimated using their biomass and annual productivities as equation 25.

$$D_{ij} = \frac{E_{ij} \cdot \Phi_j}{\sum_{\text{all } j} (E_{ij} \cdot \Phi_j)} \qquad (25)$$

Here, D_{ij} is the diet fraction of prey j in the diet of predator i. Electivities, E_{ij} are the proportions consumed by predator i if all prey items (j) have equal abundances (Φ_j). For example, if a predator had an electivity of 0.6 for prey A and 0.4 for prey B, if prey A and B were equally abundant the predator would consume 60% A and 40% B. However, if prey B is twice as abundant as prey A then the predator would consume 43% A and 57% B. This reflects the assumption that the predator would rather consume A than B, but that B is more abundant.

$$\Phi_j = B_j \cdot [1 + 0.5 \tfrac{P}{B}_j (1 - X_j - A_j - T_j^S - T_j^G - T_j^R)] \qquad (26)$$

For the purposes of estimating diets (equation 26), "abundance" Φ_j of prey item j is defined as equation 26. Here, P/B_j (y^{-1}) is the intrinsic annual production rate of prey j. Other symbols are as defined before. This formulation means that the "abundance" of prey items with low productivities will be dominated by their standing stock, whereas prey items with high productivities will have elevated abundances since the biomass will get replaced several times over the year.

Note that this formulation for abundance does not take into account the degree to which different prey species may be cryptic, or foraging/predator avoidance strategies – this is taken into account by electivities. If a prey item is abundant but is cryptic, electivities for that predator-prey combination will be low reflecting the fact that the predator does not consume much of it even though it is abundant. In contrast, a different predator may be able to overcome the cryptic nature of the prey or may be prepared to put more effort into seeking it out, in which case electivity for that predator-prey combination will be higher. Electivities for all predator-prey combinations were calculated from the balanced present day model and these were used to estimate starting diet fractions in each historical model, based on biomass, production, and transfer parameters specific to each historical model.

3. RESULTS

3.1 Present day model

1.1.1 Summary of initial parameter set

Biomass, energetic, transfer and diet parameters obtained from the literature are shown in Table 6 and Table 7.

Table 6: Present day model; parameters from the initial estimation phase. EE=Ecotrophic efficiency; B=Biomass; P/B= production ratio; Q/B= consumption ratio; P/Q=growth efficiency; Acc=Accumulation as a fraction of annual production; Export=X; U=Unassimilated consumption; T=Transfers, as a fraction of annual production; T_S=seasonal transfers; T_R=Reproductive transfers; T_G=Growth transfers.

	Group	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Acc A/P	Export X/P	Fishery gC m^{-2} y^{-1}	U	Seasonal T_S/P	Spawn T_R/P	Growth T_G/P	Detritus Fate	Carcass Fate	Seas. Fate	Spawn Fate	Growth Fate
1	Birds	2.47E-03	0.26	117	0.33	0.0022	0	0.33	0	0.30	0	0	0	47	46	0	0	0
2	Cetaceans	1.73E-03	0.053	9.1	0.10	0.0058	0	0	0	0.20	0	0	0	47	46	0	0	0
3	Crayfish	6.73E-03	1.2	6.8	0.95	0.18	0	0.24	1.5E-03	0.30	0	0.06	0	48	46	0	37	0
4	Crabs	0.67	6.2	30	0.95	0.20	0	0.42	3.8E-04	0.30	0	0.05	0	48	46	0	37	0
5	Seastars	0.20	1.4	5.7	0.95	0.25	0	0	0	0.30	0	0.59	0	48	48	0	37	0
6	Urchins	0.16	0.83	5.5	0.95	0.15	0	0.22	5.3E-04	0.30	0	0.54	0	48	48	0	37	0
7	Gastropods_carn	0.98	4.3	17	0.95	0.25	0	0.43	4.3E-07	0.30	0	0.14	0	48	46	0	37	0
8	Gastropods_graz	0.47	3.3	18	0.95	0.18	0	0.42	7.8E-04	0.30	0	0.18	0	48	46	0	37	0
9	Sea_cucumbers	1.2	0.6	3.4	0.11	0.18	0	0	0	0.30	0	0.10	0	48	48	0	37	0
10	Bivalves	1.4	4.7	24	0.95	0.20	0	0.73	3.2E-02	0.20	0	0.03	0	48	46	0	37	0
11	Sponges	0.54	0.2	0.8	0.95	0.25	0	0	0	0.30	0	0.10	0	48	48	0	37	0
12	Encrusting	0.22	3.3	13	0.75	0.25	0	0.52	0	0.30	0	0.07	0	48	48	0	37	0
13	Macrobenthos	0.25	5.4	22	0.95	0.24	0	0	0	0.30	0	0.10	0	48	48	0	37	0
14	Meiobenthos	0.11	7	23	0.95	0.31	0	0	0	0.30	0	0.10	0	48	48	0	37	0
15	Snapper	0.24	0.45	5.3	0.94	0.09	0	0	2.6E-02	0.27	0	0.15	-0.014	47	46	0	37	32
16	Jack_mackerels	0.19	0.54	5.3	0.93	0.10	0	0	1.7E-02	0.27	0	0.12	-0.038	47	46	0	37	32
17	Blue_mackerel	0.16	0.45	4.6	0.95	0.10	0	0	1.2E-02	0.27	0	0.15	-0.023	47	46	0	37	32
18	Gurnard	0.088	0.56	5.0	0.94	0.11	0	0	1.9E-03	0.27	0	0.12	-0.090	47	46	0	13	32
19	Leatherjacket	0.020	0.44	4.4	0.92	0.10	0	0	7.3E-04	0.27	0	0.15	-0.026	47	46	0	13	32
20	Tarakihi	0.049	0.43	5.3	0.95	0.08	0	0	1.7E-03	0.27	0	0.15	-0.009	47	46	0	37	32
21	Kahawai	0.035	0.40	5.1	0.90	0.08	0	0	3.7E-03	0.27	0	0.16	-0.018	47	46	0	37	32
22	Rig	0.022	0.32	3.1	0.89	0.10	0	0	3.8E-04	0.27	0	0.21	-0.009	47	46	0	32	32
23	Flatfish	0.022	0.48	4.2	0.94	0.11	0	0	2.3E-03	0.27	0	0.14	-0.106	47	46	0	13	32
24	Trevally	0.017	0.41	5.0	0.94	0.08	0	0	2.1E-03	0.27	0	0.16	-0.014	47	46	0	37	32
25	Barracouta	0.014	0.36	3.8	0.94	0.10	0	0	4.7E-04	0.27	0	0.18	-0.014	47	46	0	37	32
26	Skipjack	0.012	0.25	3.8	0.95	0.07	0	0	1.2E-03	0.27	0	0.26	-0.007	47	46	0	37	32
27	Reef_fish_large	0.096	0.44	5.3	0.94	0.08	0	0	2.4E-03	0.27	0	0.15	-0.050	47	46	0	13	28
28	Reef_fish_small	0.006	0.90	7.4	0.95	0.12	0	0	2.1E-05	0.27	0	0.07	-0.291	47	46	0	13	32
29	Demersal_fish	0.039	0.40	4.4	0.93	0.09	0	0	1.8E-03	0.27	0	0.16	-0.042	47	46	0	37	32
30	Sharks	0.011	0.19	2.6	0.73	0.08	0	0	6.1E-04	0.27	0	0.26	-0.005	47	46	0	32	32
31	Pelagic_fish_large	0.025	0.41	5.6	0.93	0.07	0	0	5.7E-04	0.27	0	0.16	-0.060	47	46	0	37	32
32	Pelagic_fish_small	0.074	1.7	11	0.95	0.16	0	0	3.1E-03	0.27	0	0.01	0	47	46	0	37	0
33	Squid	0.025	2.8	11	0.99	0.25	0	0	1.4E-04	0.13	0	0.07	0	47	46	0	37	0
34	Octopus	0.021	5.1	12	0.98	0.42	0	0	3.6E-05	0.12	0	0.04	0	47	46	0	37	0
35	Gelatinous	0.022	10	34	0.95	0.29	0	0	0	0.20	0	0	0	47	47	0	0	0
36	Macrozoo	0.077	7	23	0.95	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
37	Mesozoo	0.41	25	83	0.95	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
38	Microzoo	0.12	75	250	0.95	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
39	Nanozoo	0.15	150	429	0.95	0.35	0	0	0	0.20	0	0	0	47	47	0	0	0
40	Phytoplankton	1.1	190	0	0.91	0	0	0	0	0	0	0	0	47	47	0	0	0
41	Macroalgae	2.9	5.2	0	0.40	0	0	0.25	0	0	0	0	0	47	47	0	0	0
42	Mangrove_seagrass	8.7	0.17	0	0.40	0	0.24	0	0	0	0	0	0	47	47	0	0	0
43	Microphtyes	0.27	21	0	0.80	0	0	0	0	0	0	0	0	47	47	0	0	0

	Group	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Acc A/P	Export X/P	Fishery gC m^{-2} y^{-1}	U	Seasonal T_S/P	Spawn T_R/P	Growth T_G/P	Detritus Fate	Carcass Fate	Seas. Fate	Spawn Fate	Growth Fate
44	Bacteria_water	0.61	82	272	0.50	0.30	0	0	0	0	0	0	0	47	47	0	0	0
45	Bacteria_benthic	2.0	10	33	0.50	0.30	0	0	0	0	0	0	0	48	48	0	0	0
46	Carcasses	0	0	0	1.00	0	0	0	0	0	0	0	0	0	0	0	0	0
47	Detritus_water	0	0	0	1.00	0	0	0.00	0	0	0.29	0	0	0	0	48	0	0
48	Detritus_benthic	0	0	0	1.00	0	0.16	0	0	0	0	0	0	0	0	0	0	0

Table 7a: Present day model; diet from the parameter estimation phase for the present day model, showing predators 1-21. Figures are the proportions of prey by weight in diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of "0.00" indicate that the diet fraction is >0% and <0.5%.

		Predators																				
	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Birds																					
2	Cetaceans		0.00																			
3	Crayfish																					
4	Crabs	0.00		0.20	0.02	0.02										0.36			0.43		0.25	0.07
5	Seastars							0.02								0.03					0.25	
6	Urchins			0.10	0.05	0.05										0.15						
7	Gastropods_carn	0.01		0.05	0.10	0.05		0.10								0.02					0.09	0.02
8	Gastropods_graz	0.00		0.15	0.15	0.08		0.30								0.08					0.04	0.01
9	Sea_cucumbers					0.05																
10	Bivalves	0.01		0.17	0.17	0.08		0.30								0.08					0.13	0.03
11	Sponges						0.03													0.49		
12	Encrusting			0.03	0.05		0.03	0.15	0.02											0.38		
13	Macrobenthos	0.01		0.20	0.30	0.10		0.10						0.01		0.08	0.05		0.50		0.25	0.07
14	Meiobenthos					0.10				0.90				0.06	0.10							
15	Snapper	0.01	0.09																			
16	Jack_mackerels	0.03	0.09																			
17	Blue_mackerel		0.08																			
18	Gurnard																					
19	Leatherjacket															0.01			0.01			
20	Tarakihi																					
21	Kahawai																					
22	Rig		0.01																			
23	Flatfish		0.01																			
24	Trevally		0.01																			
25	Barracouta		0.01														0.03					0.03
26	Skipjack		0.01														0.02					0.03
27	Reef_fish_large															0.03			0.06			
28	Reef_fish_small	0.03		0.03												0.10			0.00			
29	Demersal_fish		0.17													0.03						
30	Sharks		0.13																			
31	Pelagic_fish_large		0.01													0.01	0.05					0.06
32	Pelagic_fish_small	0.44	0.06													0.02	0.22					0.27
33	Squid	0.11	0.15																			
34	Octopus				0.02																	
35	Gelatinous	0.01	0.02														0.32					

Predators

36	Macrozoo	0.28	0.11														0.02	0.06				0.02
37	Mesozoo	0.05	0.06														0.30	0.94				0.39
38	Microzoo										0.15		0.10									
39	Nanozoo										0.05	0.10	0.30									
40	Phytoplankton										0.50	0.20	0.30	0.15								
41	Macroalgae			0.05	0.03		0.43		0.27					0.15						0.13		
42	Mangrove_seagrass				0.01				0.02					0.03								
43	Microphtyes					0.05	0.03		0.18					0.15								
44	Bacteria_water										0.20	0.70	0.30	0.06								
45	Bacteria_benthic						0.25		0.10	0.10				0.32	0.90							
46	Carcasses	0.01		0.02	0.10	0.05		0.03														
47	Detritus_water					0.07					0.10											
48	Detritus_benthic					0.30	0.25		0.41					0.08								

Table 7b: Present day model; as in Table 7a but for predators 22–45 (primary producers and detritus are not shown).

Predator

	Prey	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	44	45
1	Birds																				
2	Cetaceans																				
3	Crayfish													0.01							
4	Crabs	0.33	0.20	0.05			0.20	0.09	0.11	0.13	0.05			0.35							
5	Seastars		0.20					0.05	0.02	0.03	0.03										
6	Urchins						0.01		0.01	0.03	0.01			0.11							
7	Gastropods_carn		0.07	0.02			0.01	0.03	0.03	0.04	0.01			0.13							
8	Gastropods_graz		0.03	0.03			0.00	0.01	0.01	0.02	0.00			0.13							
9	Sea_cucumbers																				
10	Bivalves		0.10	0.05			0.01	0.05	0.05	0.06	0.01			0.25							
11	Sponges																				
12	Encrusting						0.02														
13	Macrobenthos	0.67	0.40	0.45	0.05		0.24	0.22	0.23	0.18	0.09	0.05									
14	Meiobenthos																				
15	Snapper						0.01	0.03	0.02	0.06											
16	Jack_mackerels						0.01		0.01	0.05											
17	Blue_mackerel						0.01		0.01	0.04											
18	Gurnard								0.01	0.02											
19	Leatherjacket						0.01	0.01	0.01	0.01	0.00										
20	Tarakihi									0.01											
21	Kahawai									0.01											
22	Rig																				
23	Flatfish									0.01											
24	Trevally																				
25	Barracouta					0.03		0.00	0.01	0.01	0.01										
26	Skipjack				0.01			0.00	0.01	0.01	0.01										
27	Reef_fish_large						0.02	0.04	0.05	0.05											
28	Reef_fish_small						0.00	0.00	0.00	0.00	0.01			0.02							
29	Demersal_fish												0.02								

																			Predator
30	Sharks																		
31	Pelagic_fish_large		0.05	0.05		0.01	0.01	0.02	0.02		0.04								
32	Pelagic_fish_small		0.20	0.24		0.03	0.06	0.10	0.11		0.20								
33	Squid		0.05	0.34	0.01		0.11	0.03	0.09		0.06								
34	Octopus							0.02											
35	Gelatinous				0.06	0.01	0.03		0.09										
36	Macrozoo	0.02	0.04	0.02	0.02	0.02	0.01	0.00	0.02	0.05	0.40			0.04					
37	Mesozoo	0.38	0.60	0.32	0.28	0.37	0.12	0.05	0.39	0.78	0.28		0.10	0.41	0.10				
38	Microzoo												0.25	0.05	0.20				
39	Nanozoo												0.25	0.05	0.15	0.10	0.10		
40	Phytoplankton												0.20	0.32	0.45	0.30	0.70		
41	Macroalgae				0.08	0.01	0.02		0.04	0.07									
42	Mangrove_seagrass																		
43	Microphtyes																		
44	Bacteria_water												0.10			0.30	0.20		
45	Bacteria_benthic																		
46	Carcasses																		0.01
47	Detritus_water												0.10	0.13	0.10	0.30		1.00	
48	Detritus_benthic						0.03			0.04									0.99

1.1.2 Model balancing

The present day model had 747 non-zero variables and 88 constraints, implying a highly under-constrained system as expected. Variation in production (defined as the intrinsic rate of growth of all individuals in the population plus reproductive output) varied by 6.3 orders of magnitude between groups. Total primary production in the initial parameter set was 222 gC m^{-2} y^{-1}. Total system production plus unassimilated consumption flows to detritus (a measure of available energy in the system) was P_0=416 gC m^{-2} y^{-1} and total system consumption (i.e. consumption of all groups in the model) was Q_0=467 gC m^{-2} y^{-1}. The ratio of total system consumption to total system production (Q_0/P_0) was 1.12. This ratio must be less than 1 for a balanced system, so we have over-estimated consumption or under-estimated production in the initial parameter set.

Seven iterations of SVD gave a steady solution with residuals of less than 0.3%, and generally less than 0.02%. The balancing procedure changed many of the initial parameters extensively (Table 8), but the median absolute adjustment of biomass was 4.7% and changes to other sets of parameters were smaller. Changes were of similar magnitudes as seen in Pinkerton et al. (2008) and Pinkerton et al. (2010) to which an international reviewer remarked: “I would in fact argue that even changes in the range 10–20% or even 40% are fairly small”. Considering the three parameters of biomass, P/B, P/Q, changes to the initial set of parameters were between zero and 77% (biomass of macrobenthos), with a median absolute change during balancing of 2.3%. Excluding bacteria, within the 10 groups estimated to have the highest ecological importance (see later), only biomass of macrofauna (changed by +77%) and crabs (changed by -51%) changed by more than 8%. Median changes by parameter type were 4.7% (biomass), 3.8% (P/B), and 0.6% (P/Q). Ecotrophic efficiencies changed by between zero and 22% during balancing (median absolute change of 1.7%). Diet fractions changed by between zero and 36% during balancing (median absolute change of 1.5%). The relative sizes of the changes between types of parameter (biomass versus P/B versus diets etc.) and between trophic groups are determined by a combination of the uncertainty factors and the changes required to balance the model.

Table 8: Present day model; changes to biomass (B), production (P/B), ecotrophic efficiency (EE), growth efficiency (P/Q) and diet fractions (D) during the SVD balancing process (from “initial” to “balanced”). Only changes with an absolute value of more than 10% are shown. Diets are shown: Predator ⟵ Prey.

Parameter	Group	Initial	Balanced	Change (%)
B	Macrobenthos	0.25	0.44	77
	Gastropods_carn	0.98	0.35	-64
	Meiobenthos	0.11	0.16	53
	Crabs	0.67	0.33	-51
	Octopus	0.02	0.01	-43
	Bacteria_water	0.61	0.41	-34
	Sea_cucumbers	1.16	0.80	-31
	Tarakihi	0.05	0.04	-27
	Bacteria_benthic	2.00	1.51	-24
	Nanozoo	0.15	0.19	24
	Bivalves	1.35	1.63	21
	Pelagic_fish_small	0.07	0.09	19
	Gelatinous	0.02	0.03	16
	Squid	0.02	0.02	-16
	Jack_mackerels	0.19	0.17	-13

Parameter	Group	Initial	Balanced	Change (%)
	Phytoplankton	1.05	0.92	-12
	Rig	0.02	0.02	-12
	Flatfish	0.02	0.02	-11
P/B	Gastropods_carn	4.27	1.54	-64
	Crabs	6.18	3.05	-51
	Sea_cucumbers	0.60	0.41	-31
	Macrobenthos	5.41	6.65	23
	Bivalves	4.74	5.73	21
	Meiobenthos	7.00	8.11	16
	Bacteria_water	81.51	68.79	-16
	Octopus	5.13	4.38	-15
	Tarakihi	0.43	0.37	-14
	Bacteria_benthic	10.00	8.93	-11
EE	Bacteria_benthic	0.50	0.72	22
	Macroalgae	0.40	0.61	21
	Bacteria_water	0.50	0.69	19
	Tarakihi	0.95	0.78	-17
	Rig	0.89	0.73	-16
	Kahawai	0.90	0.77	-13
	Phytoplankton	0.91	0.80	-11
	Mangrove_seagrass	0.40	0.51	11
P/Q	Bacteria_water	0.30	0.48	60
	Bacteria_benthic	0.30	0.42	39
	Crabs	0.20	0.28	35
	Gastropods_carn	0.25	0.31	25
	Snapper	0.09	0.10	14
	Sea_cucumbers	0.18	0.20	14
D	Birds ⟵Pelagic_fish_small	0.44	0.08	-36
	Jack_mackerels ⟵Mesozoo	0.30	0.56	26
	Birds ⟵Macrozoo	0.28	0.54	25
	Sea_cucumbers ⟵Bacteria_benthic	0.10	0.34	24
	Sea_cucumbers ⟵Meiobenthos	0.90	0.66	-24
	Jack_mackerels ⟵Pelagic_fish_small	0.22	0.00	-22
	Sharks ⟵Tarakihi	0.01	0.21	20
	Seastars ⟵Detritus_benthic	0.30	0.50	20
	Reef_fish_large ⟵Crabs	0.20	0.00	-20
	Demersal_fish ⟵Gurnard	0.01	0.20	19
	Crabs ⟵Macroalgae	0.03	0.22	19
	Nanozoo ⟵Bacteria_water	0.20	0.04	-16
	Cetaceans ⟵Rig	0.01	0.17	16
	Snapper ⟵Urchins	0.15	0.01	-14
	Cetaceans ⟵Trevally	0.01	0.15	14
	Crabs ⟵Gastropods_graz	0.15	0.01	-14

Parameter	Group	Initial	Balanced	Change (%)
	Mesozoo ⟵Mesozoo	0.10	0.23	13
	Gurnard ⟵Macrobenthos	0.50	0.63	13
	Pelagic_fish_large ⟵Mesozoo	0.39	0.51	13
	Sharks ⟵Kahawai	0.01	0.13	12
	Gastropods_carn ⟵Gastropods_graz	0.30	0.18	-12
	Snapper ⟵Macrobenthos	0.08	0.19	11
	Sharks ⟵Flatfish	0.01	0.12	11
	Gastropods_carn ⟵Bivalves	0.30	0.41	11
	Snapper ⟵Bivalves	0.08	0.19	11
	Nanozoo ⟵Phytoplankton	0.70	0.81	11
	Mesozoo ⟵Microzoo	0.20	0.09	-11
	Reef_fish_large ⟵Mesozoo	0.28	0.38	11
	Snapper ⟵Gastropods_graz	0.08	0.18	10

The biomasses of many of the benthic invertebrate groups were substantially reduced during balancing, including changes to the biomasses of carnivorous gastropods by -64%, crabs by -51%, octopus -43% and sea cucumbers by -31%. Biomasses of bacteria were changed substantially during balancing (water column bacteria by -34% and benthic bacteria biomass by -24%). The biomasses of macrobenthos and meiobenthos were increased during balancing (by +77% and +53% respectively), as was the biomass of bivalves (+21%). The production rates of some benthic groups were also reduced, including substantial changes in the P/B ratios for carnivorous gastropods (-64%), crabs (-51%), sea cucumbers (-31%) and octopus (-15%), but with increases in P/B for bivalves (+21%), macrobenthos (+23%) and meiobenthos (+16%). The ecotrophic efficiencies of many fish groups (rig, tarakihi, trevally, kahawai, gurnard, flatfish) were reduced from near unity to 73–87%, indicating that there was not enough consumption of these fish species estimated in the initial dataset. Direct predation is the greatest source of natural mortality for all fish groups, but the model suggests that a small amount of the natural mortality of these fish species is due to disease, starvation, effects of parasites or other causes of death other than direct predation. Increases in P/Q during balancing tend to indicate that there is too much consumption of a group in the initial dataset but that the group is also having an important effect on its prey. Groups where P/Q changes substantially hence tend to be those that are tightly woven into the structure of the food-web. Here, these groups are snapper, crabs, carnivorous gastropods and grazing gastropods.

Diet fractions changed throughout the food web during balancing of the present day model. Some of the largest changes to diet fractions were decreases in predation on small pelagic fishes by many of their consumers including birds and jack mackerels. The reduction in the fraction of crabs consumed by large reef fish implies that the reduction in the biomass of crabs during balancing was to reduce consumption of prey by crabs, not because there was insufficient predation on crabs according to the initial estimation. In contrast, consumptions of mesozooplankton, macrobenthos, meiobenthos and bivalves were generally increased during balancing because our initial estimate of production and/or capacity for elevation of production by these groups was able to accommodate more consumption by their predators.

The balanced model of the present day system is shown in Table 9, Table 10 and some key properties of the balanced model are shown in Table 11. A flow diagram of the present day model is shown in Figure 3 and the mixed trophic impact matrix is shown in Figure 4.

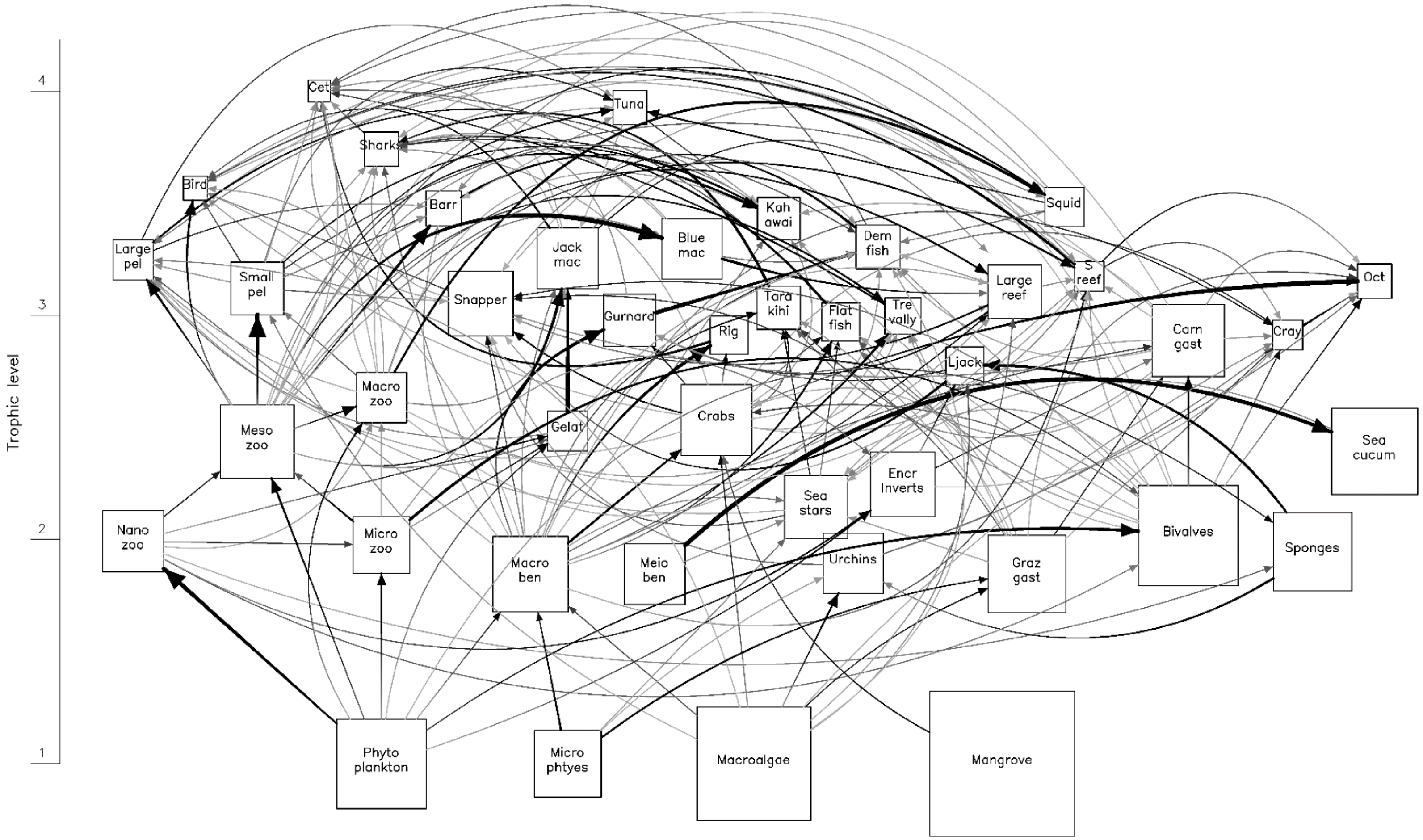


Figure 3: Present day model. Trophic model flow diagram, with arrows showing the direction of organic carbon flow. Larger boxes indicate higher biomass and are positioned vertically according to trophic level. Flows to detritus and respiration sinks are not shown for clarity. Darker and thicker lines leaving a box show higher importance of the trophic flow to the prey (i.e. more potential for top-down control). Darker and thicker lines arriving at a box show the importance of that predation link to the predator (i.e. the importance of the prey in the diet of the predator). Values less than 2% not shown.

Table 9: Present day model; biomass, energetic and transfer parameters in the balanced model. Column headings as in Table 6.

	Group	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Acc A/P	Export X/P	Fishery gC m^{-2} y^{-1}	U	Seasonal T_S/P	Spawn T_R/P	Growth T_G/P	Detritus Fate	Carcass Fate	Seas. Fate	Spawn Fate	Growth Fate
1	Birds	2.39E-03	0.26	116	0.33	0.00	0	0.33	0	0.30	0	0	0	47	46	0	0	0
2	Cetaceans	1.74E-03	0.05	9.2	0.10	0.01	0	0	0	0.20	0	0	0	47	46	0	0	0
3	Crayfish	6.59E-03	1.19	6.6	0.95	0.18	0	0.24	1.54E-03	0.30	0	0.06	0	48	46	0	37	0
4	Crabs	3.29E-01	3.05	11	1.00	0.28	0	0.42	3.79E-04	0.30	0	0.05	0	48	46	0	37	0
5	Seastars	1.97E-01	1.38	5.4	0.97	0.26	0	0	0	0.30	0	0.59	0	48	48	0	37	0
6	Urchins	1.59E-01	0.85	5.6	0.97	0.15	0	0.22	5.29E-04	0.30	0	0.54	0	48	48	0	37	0
7	Gastropods_carn	3.54E-01	1.54	4.9	0.97	0.31	0	0.43	4.30E-07	0.30	0	0.14	0	48	46	0	37	0
8	Gastropods_graz	5.08E-01	3.53	19	0.96	0.19	0	0.42	7.85E-04	0.30	0	0.18	0	48	46	0	37	0
9	Sea_cucumbers	8.02E-01	0.41	2.1	0.21	0.20	0	0	0	0.30	0	0.10	0	48	48	0	37	0
10	Bivalves	1.63E+00	5.73	29	0.93	0.20	0	0.73	3.20E-02	0.20	0	0.03	0	48	46	0	37	0
11	Sponges	5.37E-01	0.20	0.8	0.95	0.25	0	0	0	0.30	0	0.10	0	48	48	0	37	0
12	Encrusting	2.23E-01	3.40	14	0.83	0.25	0	0.52	0	0.30	0	0.07	0	48	48	0	37	0
13	Macrobenthos	4.41E-01	6.65	27	0.99	0.24	0	0	0	0.30	0	0.10	0	48	48	0	37	0
14	Meiobenthos	1.65E-01	8.11	26	0.97	0.31	0	0	0	0.30	0	0.10	0	48	48	0	37	0
15	Snapper	2.22E-01	0.42	4.3	0.93	0.10	0	0	2.64E-02	0.27	0	0.15	-0.014	47	46	0	37	32
16	Jack_mackerels	1.68E-01	0.51	4.6	0.92	0.11	0	0	1.74E-02	0.27	0	0.12	-0.038	47	46	0	37	32
17	Blue_mackerel	1.61E-01	0.45	4.5	0.93	0.10	0	0	1.25E-02	0.27	0	0.15	-0.023	47	46	0	37	32
18	Gurnard	8.32E-02	0.53	4.6	0.86	0.12	0	0	1.93E-03	0.27	0	0.12	-0.090	47	46	0	13	32
19	Leatherjacket	2.00E-02	0.44	4.4	0.92	0.10	0	0	7.26E-04	0.27	0	0.15	-0.026	47	46	0	13	32
20	Tarakihi	3.58E-02	0.37	4.5	0.78	0.08	0	0	1.71E-03	0.27	0	0.15	-0.009	47	46	0	37	32
21	Kahawai	3.34E-02	0.38	4.8	0.77	0.08	0	0	3.67E-03	0.27	0	0.16	-0.018	47	46	0	37	32
22	Rig	1.95E-02	0.30	2.9	0.73	0.10	0	0	3.78E-04	0.27	0	0.21	-0.009	47	46	0	32	32
23	Flatfish	1.94E-02	0.45	4.0	0.87	0.11	0	0	2.31E-03	0.27	0	0.14	-0.106	47	46	0	13	32
24	Trevally	1.62E-02	0.39	4.8	0.85	0.08	0	0	2.09E-03	0.27	0	0.16	-0.014	47	46	0	37	32
25	Barracouta	1.39E-02	0.36	3.8	0.94	0.10	0	0	4.68E-04	0.27	0	0.18	-0.014	47	46	0	37	32
26	Skipjack	1.27E-02	0.25	3.8	0.97	0.07	0	0	1.19E-03	0.27	0	0.26	-0.007	47	46	0	37	32
27	Reef_fish_large	9.36E-02	0.44	5.2	0.94	0.09	0	0	2.38E-03	0.27	0	0.15	-0.050	47	46	0	13	28
28	Reef_fish_small	6.36E-03	0.90	7.4	0.95	0.12	0	0	2.10E-05	0.27	0	0.07	-0.291	47	46	0	13	32
29	Demersal_fish	3.84E-02	0.40	4.3	0.93	0.09	0	0	1.75E-03	0.27	0	0.16	-0.042	47	46	0	37	32
30	Sharks	1.22E-02	0.20	2.6	0.73	0.07	0	0	6.06E-04	0.27	0	0.26	-0.005	47	46	0	32	32
31	Pelagic_fish_large	2.48E-02	0.41	5.5	0.94	0.07	0	0	5.71E-04	0.27	0	0.16	-0.060	47	46	0	37	32
32	Pelagic_fish_small	8.76E-02	1.81	11	0.97	0.16	0	0	3.13E-03	0.27	0	0.01	0	47	46	0	37	0
33	Squid	2.05E-02	2.68	11	0.99	0.25	0	0	1.37E-04	0.13	0	0.07	0	47	46	0	37	0
34	Octopus	1.20E-02	4.38	10	0.98	0.43	0	0	3.63E-05	0.12	0	0.04	0	47	46	0	37	0
35	Gelatinous	2.58E-02	10.7	37	0.97	0.29	0	0	0	0.20	0	0	0	47	47	0	0	0
36	Macrozoo	7.62E-02	6.99	23	0.95	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
37	Mesozoo	4.08E-01	24.9	83	0.94	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
38	Microzoo	1.22E-01	76.6	256	0.95	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
39	Nanozoo	1.92E-01	161	462	0.94	0.35	0	0	0	0.20	0	0	0	47	47	0	0	0
40	Phytoplankton	9.21E-01	178	NA	0.80	NA	0	0	0	0	0	0	0	47	47	0	0	0
41	Macroalgae	2.88E+00	5.19	NA	0.61	NA	0	0.25	0	0	0	0	0	47	47	0	0	0
42	Mangrove_seagrass	8.74E+00	0.17	NA	0.51	NA	0.24	0	0	0	0	0	0	47	47	0	0	0
43	Microphtyes	2.64E-01	21.3	NA	0.77	NA	0	0	0	0	0	0	0	47	47	0	0	0
44	Bacteria_water	4.06E-01	68.8	143	0.69	0.48	0	0	0	0	0	0	0	47	47	0	0	0
45	Bacteria_benthic	1.51E+00	8.93	21	0.72	0.42	0	0	0	0	0	0	0	48	48	0	0	0
46	Carcasses	NA	NA	NA	NA	NA	0	0	0	0	0	0	0	0	0	0	0	0
47	Detritus_water	NA	NA	NA	NA	NA	0	-0.005	0	0	0.28	0	0	0	0	48	0	0
48	Detritus_benthic	NA	NA	NA	NA	NA	0.15	0	0	0	0	0	0	0	0	0	0	0

Table 10a: Present day model; diet parameters in the balanced model for predators 1–21. Figures are the proportions of prey by weight of organic carbon in the diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of "0.00" indicate that the diet fraction is between 0 and 0.5%.

		Predators																				
	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Birds																					
2	Cetaceans		0.00																			
3	Crayfish																					
4	Crabs			0.18	0.00	0.00										0.27			0.33		0.21	0.07
5	Seastars							0.00								0.04					0.24	
6	Urchins			0.08	0.00	0.00										0.01						
7	Gastropods_carn	0.02		0.05	0.00	0.01		0.05								0.06					0.09	0.03
8	Gastropods_graz	0.02		0.16	0.01	0.03		0.18								0.18					0.04	0.01
9	Sea_cucumbers					0.03																
10	Bivalves	0.02		0.18	0.14	0.05		0.41								0.19					0.14	0.04
11	Sponges						0.05													0.50		
12	Encrusting			0.03	0.00		0.00	0.07	0.00											0.36		
13	Macrobenthos	0.02		0.21	0.38	0.08		0.16								0.19	0.09		0.63		0.28	0.08
14	Meiobenthos					0.06				0.66				0.00	0.00							
15	Snapper	0.05	0.07																			
16	Jack_mackerels	0.09	0.07																			
17	Blue_mackerel		0.07																			
18	Gurnard																					
19	Leatherjacket															0.00			0.00			
20	Tarakihi																					
21	Kahawai																					
22	Rig		0.17																			
23	Flatfish		0.08																			
24	Trevally		0.15																			
25	Barracouta																0.00					0.01
26	Skipjack																0.00					0.00
27	Reef_fish_large															0.01			0.04			
28	Reef_fish_small	0.00		0.02												0.00						
29	Demersal_fish		0.11													0.01						
30	Sharks		0.03																			
31	Pelagic_fish_large		0.00													0.00	0.00					0.01
32	Pelagic_fish_small	0.08	0.04													0.02	0.00					0.23
33	Squid	0.03	0.10																			
34	Octopus				0.01																	
35	Gelatinous	0.01	0.01														0.30					
36	Macrozoo	0.54	0.08														0.05	0.06				0.03
37	Mesozoo	0.09	0.04														0.56	0.94				0.48
38	Microzoo										0.11		0.10									
39	Nanozoo										0.07	0.10	0.31									
40	Phytoplankton										0.60	0.20	0.30	0.21								
41	Macroalgae			0.06	0.22		0.42		0.25					0.13						0.13		
42	Mangrove_seagrass				0.10				0.00					0.00								
43	Microphtyes					0.09	0.03		0.21					0.18								
44	Bacteria_water										0.14	0.70	0.29	0.07								
45	Bacteria_benthic						0.25		0.10	0.34				0.30	1.00							
46	Carcasses	0.02		0.02	0.13	0.03		0.13														
47	Detritus_water					0.12					0.08											
48	Detritus_benthic					0.50	0.25		0.43					0.10								

Table 10b: Present day; diet parameters in the balanced model for predators 22–45 (primary producers and detritus are not shown). Figures are the proportions of prey by weight of organic carbon in diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of "0.00" indicate that the diet fraction is between 0 and 0.5%.

Predator

	Prey	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	44	45
1	Birds																				
2	Cetaceans																				
3	Crayfish													0.03							
4	Crabs	0.32	0.18	0.04			0.00	0.07	0.04	0.06	0.03			0.30							
5	Seastars		0.19					0.05	0.01	0.01	0.02										
6	Urchins						0.00		0.00	0.01	0.00			0.08							
7	Gastropods_carn		0.07	0.02			0.01	0.03	0.03	0.02	0.01			0.14							
8	Gastropods_graz		0.03	0.03			0.00	0.01	0.01	0.01	0.01			0.15							
9	Sea_cucumbers																				
10	Bivalves		0.11	0.05			0.01	0.05	0.05	0.04	0.02			0.28							
11	Sponges																				
12	Encrusting						0.02														
13	Macrobenthos	0.68	0.41	0.45	0.05		0.24	0.23	0.24	0.11	0.11	0.01									
14	Meiobenthos																				
15	Snapper						0.05	0.04	0.04	0.04											
16	Jack_mackerels						0.04		0.03	0.03											
17	Blue_mackerel						0.07		0.04	0.03											
18	Gurnard								0.20	0.06											
19	Leatherjacket							0.01	0.00												
20	Tarakihi									0.21											
21	Kahawai									0.13											
22	Rig																				
23	Flatfish									0.12											
24	Trevally																				
25	Barracouta					0.02				0.00	0.00										
26	Skipjack										0.00										
27	Reef_fish_large						0.00	0.03	0.01	0.02											
28	Reef_fish_small							0.00			0.00			0.01							
29	Demersal_fish												0.01								
30	Sharks																				
31	Pelagic_fish_large				0.04	0.04			0.00	0.00	0.00		0.00								
33	Pelagic_fish_small				0.19	0.23		0.02	0.00	0.04	0.05		0.12								
34	Squid				0.05	0.34	0.00		0.03	0.01	0.05		0.04								
35	Octopus									0.01											
36	Gelatinous						0.02	0.01	0.02		0.09										
37	Macrozoo			0.02	0.04	0.02	0.03	0.03	0.01		0.04	0.05	0.48			0.05					
38	Mesozoo			0.39	0.63	0.35	0.38	0.40	0.14	0.03	0.51	0.82	0.34		0.10	0.42	0.23				
39	Microzoo														0.25	0.05	0.09				
40	Nanozoo														0.25	0.05	0.18	0.14	0.16		
41	Phytoplankton														0.20	0.31	0.45	0.37	0.81		
42	Macroalgae						0.11	0.01	0.03		0.06	0.08									
43	Mangrove_seagrass																				
44	Microphtyes																				
45	Bacteria_water														0.10			0.23	0.04		
46	Bacteria_benthic																				
47	Carcasses																				0.00
48	Detritus_water														0.10	0.12	0.05	0.26		1.00	
33	Detritus_benthic								0.04			0.04									1.00

Table 11: Present day model; key indices for the balanced model, showing respiration quotient (R/B, y^{-1}, shown as a percentage), trophic level (TrL), omnivory index (OI), trophic importance (TI), and the rank of TI, with 1 being most important.

	Group	R/B (%)	TrL	OI	TI	Rank TI
1	Birds	81	4.0	0.18	1.74	13
2	Cetaceans	7.3	4.4	0.12	1.25	21
3	Crayfish	3.4	3.2	0.26	0.31	42
4	Crabs	4.7	2.8	0.32	3.33	6
5	Seastars	2.4	2.4	0.33	0.87	26
6	Urchins	3.1	2.1	0.06	0.79	29
7	Gastropods_carnivorous	1.9	3.2	0.07	1.30	19
8	Gastropods_grazing	9.8	2.0	0.00	1.94	9
9	Sea_cucumbers	1.0	2.7	0.22	0.75	30
10	Bivalves	17	2.2	0.20	4.13	4
11	Sponges	0.36	2.1	0.13	0.49	36
12	Encrusting	6.1	2.5	0.34	0.73	32
13	Macrobenthos	12	2.0	0.00	4.49	2
14	Meiobenthos	10.1	2.0	0.00	0.82	28
15	Snapper	2.7	3.4	0.20	3.58	5
16	Jack_mackerels	2.9	3.7	0.05	1.41	16
17	Blue_mackerel	2.9	3.7	0.00	0.59	35
18	Gurnard	2.8	3.3	0.18	1.51	14
19	Leatherjacket	2.8	3.1	0.22	0.42	37
20	Tarakihi	2.9	3.4	0.15	0.64	33
21	Kahawai	3.1	3.9	0.22	0.96	25
22	Rig	1.8	3.2	0.13	0.34	40
23	Flatfish	2.5	3.3	0.14	0.41	38
24	Trevally	3.1	3.4	0.14	0.30	44
25	Barracouta	2.4	3.9	0.21	0.30	43
26	Skipjack	2.5	4.4	0.29	0.74	31
27	Reef_fish_large	3.3	3.5	0.56	1.91	11
28	Reef_fish_small	4.5	3.6	0.23	0.17	45
29	Demersal_fish	2.8	3.7	0.58	1.96	8
30	Sharks	1.7	4.2	0.33	1.48	15
31	Pelagic_fish_large	3.6	3.6	0.36	0.33	41
32	Pelagic_fish_small	6.4	3.5	0.32	0.97	24
33	Squid	6.7	4.0	0.11	1.02	23
34	Octopus	4.7	3.5	0.20	0.86	27
35	Gelatinous	19	2.8	0.41	0.63	34
36	Macrozoo	9.3	2.9	0.69	1.38	17
37	Mesozoo	33	2.7	0.54	4.48	3
38	Microzoo	102	2.2	0.17	1.33	18
39	Nanozoo	208	2.2	0.18	1.27	20
40	Phytoplankton	NA	1	NA	6.50	1
41	Macroalgae	NA	1	NA	2.15	7
42	Mangrove_seagrass	NA	1	NA	0.40	39
43	Microphtyes	NA	1	NA	1.24	22
44	Bacteria_water	74	1	NA	1.91	10
45	Bacteria_benthic	13	1	NA	1.87	12
46	Carcasses	NA	2.3	NA	NA	NA
47	Detritus_water	NA	1	NA	NA	NA
48	Detritus_benthic	NA	1	NA	NA	NA

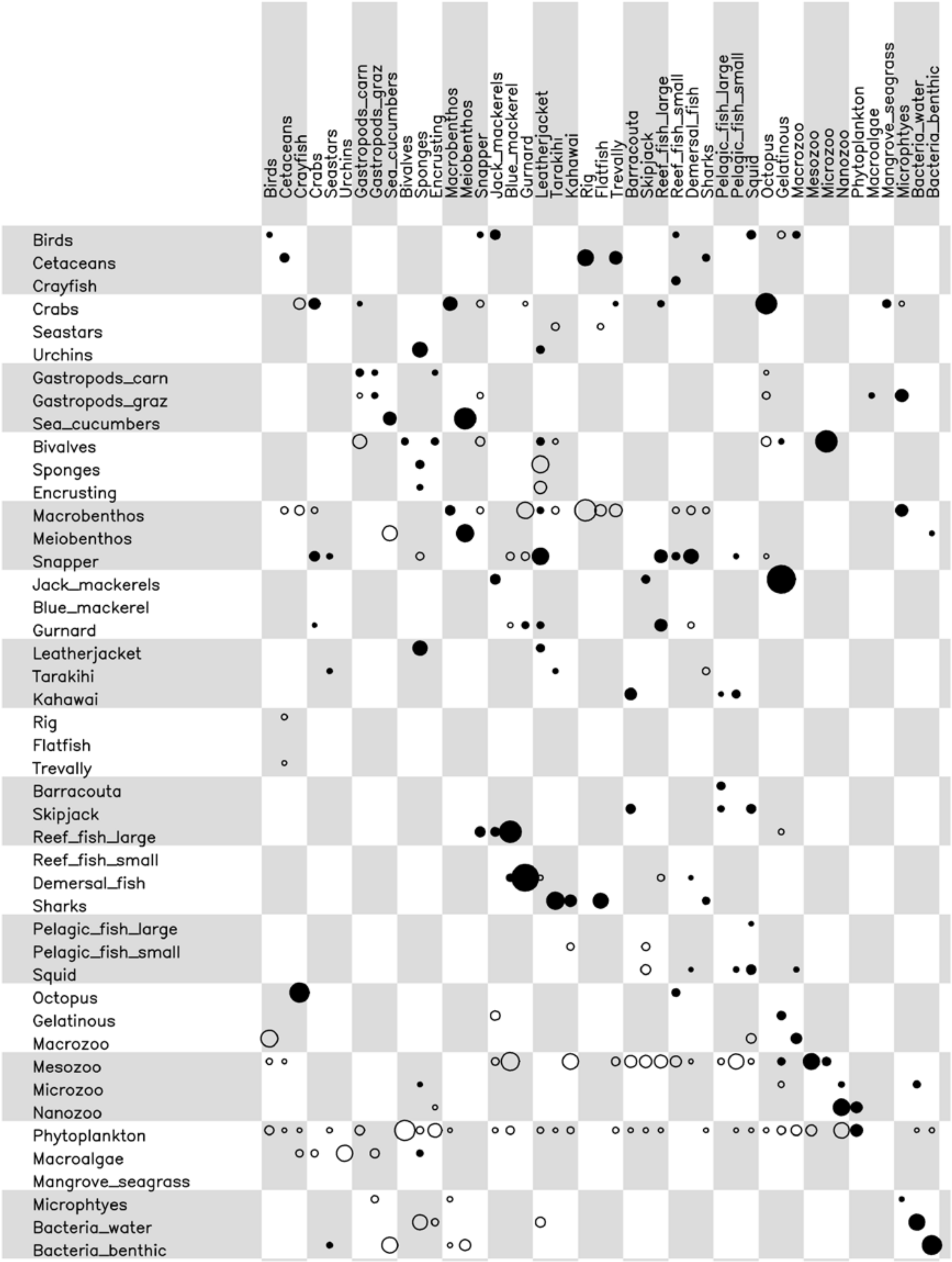


Figure 4: Mixed Trophic Impact Matrix for the present day model. Positive impacts are shown black and negative are white, with the diameter of the circle proportional to the magnitude of the effect.

1.1.3 Validation using trophic levels

Trophic levels for the groups in the balanced model agreed well (within about 0.3 of a trophic level generally) with those from trophic models elsewhere. For example, for birds in the present day model TrL=4.0 compared reasonably well with 3.8 (Arreguin-Sanchez et al. 2002) and 4.5 (Jarre-Teichman et al. 1998). Birds in the Hauraki Gulf tend to be coastal rather than open ocean foragers and were likely to more closely resemble the coastal invertebrate feeders as in the model by Arreguin-Sanchez et al. (2002) than the fish-eating birds of the open ocean Benguela system modelled by Jarre-Teichman et al. (1998). Trophic levels for crabs and lobsters (TrL=2.8, 3.2 respectively) compared well with values for crabs and predatory invertebrates: 3.3–3.4 (Wolff 1994) and 2.4–2.8 (Arreguin-Sanchez et al. 2002). Macrobenthos at TrL=2.0 agreed with value of 2.0–2.1 (Jiang & Gibbs 2005). Microzooplankton here had TrL=2.2 compared to values for "zooplankton" of 2.2–2.4 (Jarre-Teichman et al. 1998), 2.0 (Mendoza 1993, Jiang & Gibbs 2005) and 2.2 (Arreguin-Sanchez et al. 2002). Trophic levels for most demersal fish in the Hauraki Gulf model at 3.1–4.4 were similar to values given in other coastal ecosystem studies, for example, 3.3 (Jarre-Teichman et al. 1998), 2.7–3.5 (Wolff 1994), 3.2–3.9 (Mendoza 1993), 3.1–3.8 (Jiang & Gibbs 2005). Trophic levels for fish in the Hauraki Gulf model were comparable with open-ocean studies, e.g. 3.4–5.1 (Chilean upwelling system; Neira & Arancibia 2004), and for the Benguela system of 3.5–4.7 (Shannon et al. 2001).

Two other comparisons were also carried out as described in the methods section: with values obtained from stable isotopes (Beaumont et al. 2009), and with trophic levels for fishes from FishBase and references therein (Table 3). The agreement was very good (Figure 5). Least squares regression gave a slope of 0.988, a non-significant offset, $R^2=0.993$, $F(1, 25)=3338$, $p < 0.001$. The mean absolute difference in TrL was 0.22 and the root-mean-square (RMS) difference was 0.27. This comparison provided independent validation of the balanced trophic model of the present day in that trophic levels from the model are consistent with those estimated independently. We note several important features of this comparison. First, macroalgae and phytoplankton do not generally have the same $\delta^{15}N$ value so that calculating TrL by assuming all primary producers have TrL=1 led to differences between TrL estimated based on diet and calculated from nitrogen isotopes where there are multiple sources of primary organic material. The model gave too low a TrL for sea cucumbers (2.7 rather than 3.1) indicating that sea cucumbers are more predatorial and less herbivorous/detrivorous than estimated in the model. The TrL in the model was also too low for encrusting invertebrates (2.5 compared to 2.8), but we note that the range TrL of "encrusting invertebrates" in the isotope dataset was very wide, 2.1 to 3.5. This indicated that the feeding of biota in the encrusting invertebrates group was varied, including pure herbivores and also omnivorous feeding behaviour.

The trophic levels of both large and small reef fish were too high in the trophic model (3.5–3.6 versus the isotope value of TrL=3.1). This may arise because reef fishes in the study ecosystem spanned the trophic continuum from pure herbivores to pure carnivores. For example, the isotope data for large reef fish referred to three species, two of which are herbivores (butterfish, parore) and one of which is an invertebrate predator (red moki). Somewhat surprisingly we note that the model gave slightly higher TrL for small reef fish than large reef fish (3.57 versus 3.49) but this relative TrL was also suggested by the isotope data (TrL=3.12 for small reef fish compared to TrL=3.08 for large reef fish). This difference again may be explained by the large reef fish group including some obligate herbivores whereas the small reef fish were all predators of prey of various sizes and trophic levels. The issue of comparing a group of fishes with diverse feeding behaviour and diet in the model with isotope data on a few particular species was also relevant for the large pelagic fish group. For this group, the model suggested a higher trophic level than did the isotope data (3.7 versus 3.2) but the two fish for which isotope data exist (blue maomao and sweep) are planktivores and consume a mix of zooplankton and some macroalgal fragments (Beaumont et al. 2009), rather than piscivores or invertebrate feeders so a mixed group of fish will have a higher trophic level than planktivores alone.

We note that blue mackerel had a lower trophic level in the trophic model than in FishBase (3.7 versus 4.2). The trophic level of this species in FishBase was obtained from a study of the species in Japanese waters (Fujita et al. 1995) so it is possible that the ecosystem characteristics and/or diet of this species may be different in the two regions. Despite these issues, differences in trophic level of the 12 key fish groups in the trophic model presented here and data in FishBase were only 0.18 on average consistent with diets of fish in the Hauraki Gulf model being appropriate.

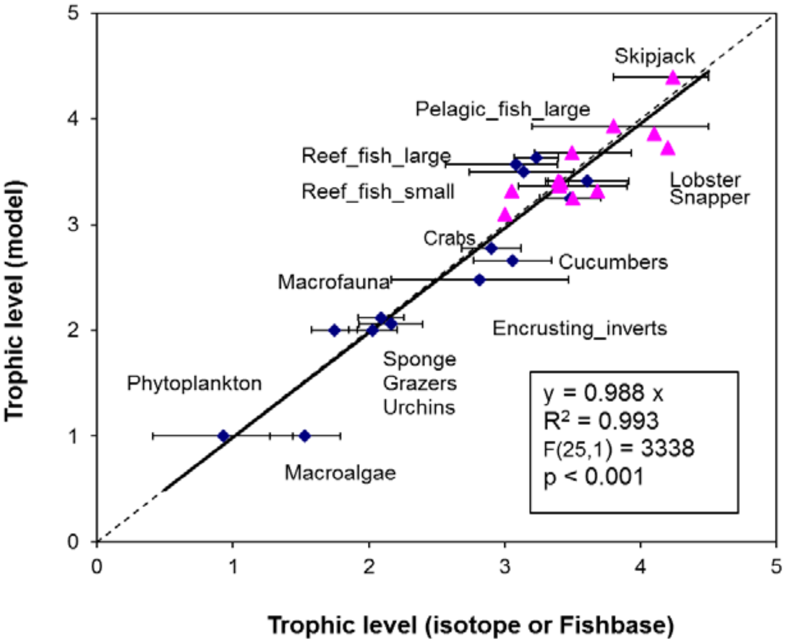


Figure 5: Comparison between trophic level (TrL) estimated from the balanced model representing the present day, and two sets of data. Blue diamonds: trophic levels from the stable isotope values obtained in the Ministry of Primary Industries biodiversity project ZBD2005-09. Pink triangles: trophic levels for 12 groups of fishes obtained from FishBase (Froese & Pauly 2009). All labels refer to blue diamonds, except for "Skipjack". The dashed line is the 1:1 comparison, and the solid line and text box gives the least-squares regression result based on all data (isotope and FishBase data combined).

1.1.4 Model summary

In the present day balanced model, total primary production (net of respiration) is 201 gC m^{-2} y^{-1}, with phytoplankton being responsible for 88% of this primary production, macroalgae 8.0%, microphytes 3.0% and mangrove/seagrass/saltmarsh only 0.8%. Phytoplankton production is equivalent to an average of 449 mgC m^{-2} d^{-1}. Mangrove and macroalgae have high biomass but low productivity, whereas phytoplankton have low biomass but very high productivity. The dominance of phytoplankton over other primary producers in terms of net primary production ratio contrasts with the comparison in terms of primary producer biomass, where mangrove/seagrass/saltmarsh dominate (68% total primary producer biomass), macroalgae (23%), phytoplankton (7.2%) and microphytes (2.1%).

Most net primary production in the model is directly consumed (76%). Nearly all phytoplankton and microphyte productions is grazed (80% and 77% respectively), and less than half of the primary production of macroalgae (36%) and mangrove/seagrass/saltmarsh (27%) is directly grazed. This result agrees qualitatively with a previous modeling study that suggested that only a fraction of macroalgae is directly consumed in New Zealand rocky reef ecosystems (Pinkerton et al. 2008). A higher fraction of the production is estimated to be consumed in the present study than for Pinkerton et al. (2008), 36%

compared to less than 10%. Reasons for this difference are not known but is likely to be due to different abundances of macroalgal grazers in different systems.

The sum of total system production plus unassimilated consumption flows to detritus (a measure of available energy in the system) is 358 gC m^{-2} y^{-1} and total system consumption is 339 gC m^{-2} y^{-1}, giving a ratio of total system consumption to total system production, $Q_0/P_0=0.95$. About 65% of the total consumption occurs in the water column with the other 35% of total consumption occurring in the benthic part of the system.

The system retains and recycles most primary production, with substantial energy flowing through detrital groups. Total material entering the detrital pool is 118 gC m^{-2} y^{-1}, equivalent to 64% of total primary production. Detrital flow as carcasses (dead bodies of larger organisms, including fishing discards and offal) is only 0.7% of the total detrital input. Most detritus (79%) is small particles from low trophic level biota (primary producers, bacteria, nanozooplankton, microzooplankton, mesozooplankton). Most detritus enters the water column (78%) with 21% entering the benthic detritus pool directly. In the model, the annual flux of detritus from sinking of "marine snow" from the water column to the benthos is estimated to be 20 gC m^{-2} y^{-1}, which is greater than estimated from limited trap measurements in the region (14 gC m^{-2} y^{-1}; Scott Nodder pers. com.). This discrepancy may be because sediment traps in shallow water can often underestimate flux rates as sedimentation can be episodic.

Flux of detritus from the water column to the benthos amounts to 22% of the annual flow of detritus into water column detritus so that 78% of small particle detritus entering the water column is remineralized. In the balanced model, organic carbon accumulates in the soft sediments at the rate of 7.0 gC m^{-2} y^{-1} equivalent to 3.7% of primary production. This is close to the mean accumulation rate of organic carbon in the sediments of 8.1 gC m^{-2} y^{-1} estimated from the literature. In the balanced model, this long term accumulation of organic matter in the sediments is equivalent to 34% of the vertical flux of detritus or 15% of the total inflow of detritus to the seabed implying that a substantial fraction of organic matter delivered to the sediments is not consumed by benthic detrivores or bacteria in the sediments. Carbon in the form of aragonite in shells and exoskeletons is exported from the ecosystem as inorganic carbon deposits on the sea-bed – a form of biological carbon pump. This accumulation of inorganic carbon in shells and exoskeletons is estimated to be 8.7 gC m^{-2} y^{-1}, with bivalves being responsible for 79% of this export of inorganic carbon. Long term burial of material from mangroves is estimated to be 0.35 gC m^{-2} y^{-1} in the model. The total export of carbon in the ecosystem is hence estimated to be 16.0 gC m^{-2} y^{-1} (i.e. 7.0+8.7+0.35) equivalent to 0.26 MtC y^{-1}. At a nominal cost per tonne of carbon in the New Zealand Emissions Trading Scheme of NZ$25 (MfE 2009) this means the Hauraki Gulf ecosystem services in terms of carbon burial are worth, according to the model, NZ$ 6.5 million per year.

Bacteria account for the largest proportion (27%) of the total consumption in the model and are estimated to comprise 21% of consumer biomass. Bacteria in the sediment dominate bacterial biomass (79% total bacterial biomass) but consumption by bacteria is higher in the water column (64% total consumption by bacteria).

In the balanced present day model, nano- and microzooplankton are the next largest consumers of material (together 35% total consumption) but account for only 3.4% of consumer biomass (average standing stock at a given time) in the ecosystem. Mesozooplankton account for 10% of all consumption and 4.4% of total consumer biomass. Macrozooplankton (crustacean and gelatinous together) are responsible for just 0.8% of consumption and 1.1% of consumer biomass in the system. Benthic invertebrates together account for 58% of total consumer biomass and 25% of total consumption in the initial dataset. Bivalves are the dominant benthic fauna in the balanced model in terms of biomass (31% total benthic invertebrate biomass) and consumption (55%). Bivalves account for 14% of all consumption in the model which is high. Sponges and sea cucumbers are important in terms of biomass in the benthic invertebrate community (10% and 15% of total benthic invertebrate biomass respectively), but unimportant in terms of consumption or production (0.5% and 1.9% of total benthic invertebrate consumption respectively). In contrast, macrobenthos and meiobenthos are more important to the benthic community in terms of production and consumption than in terms of biomass (14% and 5% of total benthic consumption; 8.2% and 3.1% of total benthic biomass respectively). Taylor (1998) estimated that in a northern New Zealand rocky reef ecosystem, grazing gastropods were 28% of the total (benthic) faunal biomass in the system and contributed roughly 12% of the total production. Here, we estimate that grazing gastropods constitute 9.5% of the benthic biomass and 11% of production of benthic invertebrates, so these results are quite consistent. The lower values in our model may arise because rocky reefs are only a fraction of the study area; most of our study region is deeper than studied by Taylor (1998) and composed of soft sediment which will have different benthic communities, including smaller (and hence more energetic in terms of P/B) biota.

All fish and cephalopods groups (hereafter, “nekton”) account for 12% of total consumer biomass in the ecosystem but only 1.6% of all consumption in the model. Within the nekton, snapper dominate in terms of biomass (20% total nekton biomass), but have similar consumption to jack and blue mackerels (17% compared to 14% and 13% of total nekton consumption, respectively), and lower consumption than small pelagic fish (17% total nekton consumption, 8.0% total nekton biomass). Large reef fish also have quite high biomass within the nekton group (8.5% total nekton biomass, 8.4% total nekton consumption). Cephalopods (squid and octopus together) account for 3.0% total nekton biomass but 6.0% of total nekton consumption.

Air-breathing predators (birds and cetaceans) in the balanced model account for only 0.04% of system consumer biomass and only 0.09% of consumption. Birds take 17 times more food than cetaceans.

Omnivory index (OI) ranges from zero to 0.69 in the balanced model, with a median OI=0.20 (Table 11). There is no variation in OI with trophic level (R^2=0.02). Amongst fish groups, perhaps not surprisingly, high OI tends to be associated with species groups which potentially have a diverse range of feeding behaviours and diets. Within the six species groups of fish (i.e. large and small reef fish, large and small pelagic fish, demersal fish, sharks), OI is between 0.23 and 0.58, with a median of 0.35. In contrast, the maximum OI for the 12 individual fish groups is 0.29 and the median is 0.17. Within the benthic invertebrate community, five groups (carnivorous and grazing gastropods, macrobenthos and meiobenthos, urchins) have low OI (less than or equal to 0.08) whereas other groups have higher OI in the range 0.13–0.34 (median OI=0.24). The omnivory index of air-breathing predators are in a narrower range (0.12–0.18).

Trophic importance was calculated using mixed trophic impact analysis. The MTI matrix for the present day model is shown in Figure 4. All groups (excluding the three detrital groups but including bacteria and primary producers) were ranked by TI (Table 11). Groups with highest trophic importance in the system were phytoplankton, macrobenthos, mesozooplankton, bivalves, and snapper (not including bacteria).

1.1.5 Results of the sensitivity analysis

The balancing and mixed trophic impact analysis completed successfully in 52% of the cases (1043 out of 2000) i.e. randomly varying all initial biomass, productivity and diet parameters by up to a factor of 3 from the “baseline” model (balanced present day model with no perturbation) led to a balanced model in about half the cases.

The pattern of trophic importance between groups in the model did not vary much with changes in the initial parameters (Figure 6) - note that the red dots (baseline model results) are usually very close to the medians of the cases using randomly-varied parameters (central lines in boxes). The trophic importance estimates from the baseline model were always within the 25th–75th percentiles of the randomly-perturbed models (red dots always within the grey boxes) except for rock lobster (crayfish) where the difference was small. The changes between the baseline model and the assemblage of balanced models in terms of their rank trophic importance were also generally small (Figure 7: the red dashed line passes through the 25th–75th percentile boxes of almost all groups). This implies that the rank trophic importance of a group was fairly robust to uncertainties in initial parameters. Overall, the differences to the estimates of trophic importance caused by varying the initial parameters by up to a factor of three were small, and this suggests that the present-day model is reasonably robust to parameter uncertainty.

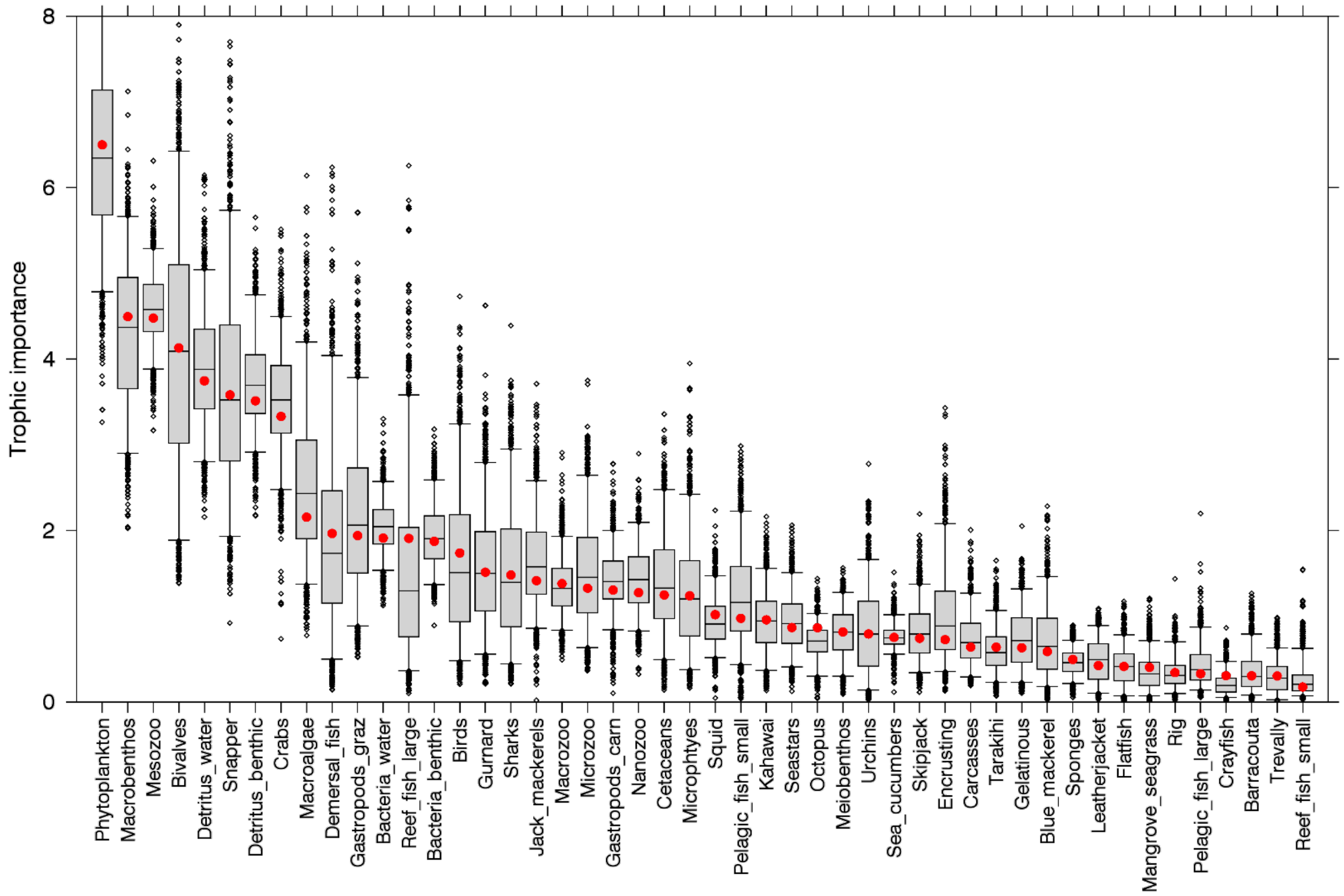


Figure 6: Sensitivity of trophic importance of model groups to uncertainties in the initial parameters. Groups are arranged according to decreasing trophic importance in the baseline model (red dots). Boxes show the effect of randomly varying the uncertainty parameters by up to a factor of 3, N=1042. Boxes show 25th–75th percentiles (with median line); whiskers show 5th–95th percentiles; individual outliers shown as black dots.

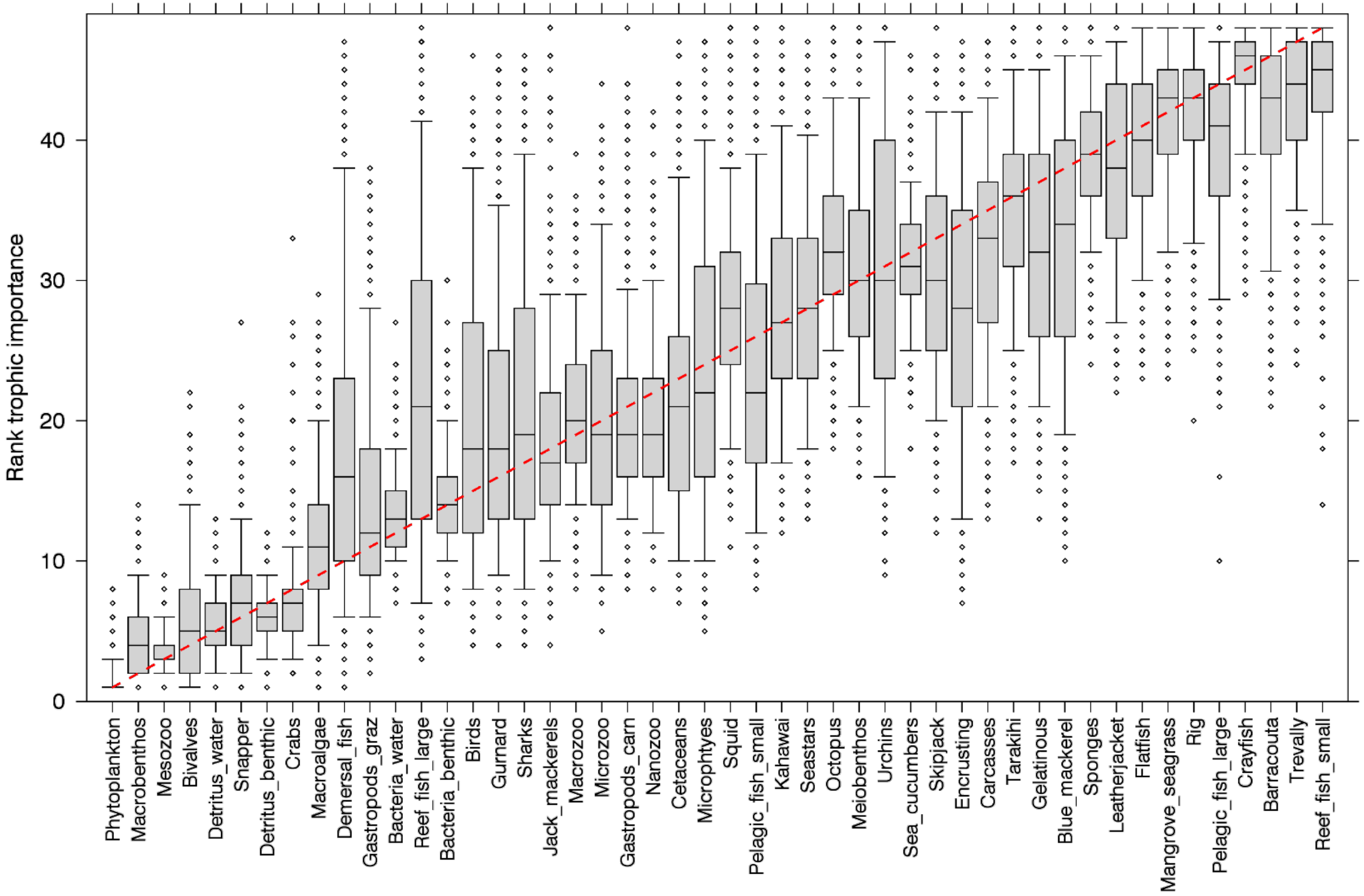


Figure 7: Sensitivity of rank trophic importance of model groups to parameter uncertainties of up to a factor of 3. Groups are arranged according to decreasing trophic importance in the baseline model (red dashed line). Boxes show the effect of randomly varying the parameters by up to a factor of 3 (changes between factor of 0.33 and 3 from baseline model). N=1042. Boxes show 25th–75th percentiles (with median line); whiskers show 5th–95th percentiles; individual outliers shown as black dots.

3.2 Historical models

1.1.6 Balancing of historical models

Median changes to parameters occurring during model balancing are shown in Figure 8. It can be seen that changes required to achieve model balance in the historical models are generally small, less than 1%. The only model where median changes were greater than 1% was in the present day model. Obtaining a balanced present-day model from field measurements and other data required more adjustments to parameters than moving from one historical period to the next. It seems that changes to parameters in historical models estimated from historical or archaeological data could be accommodated in balanced ecosystem models with relatively small changes of other parameters.

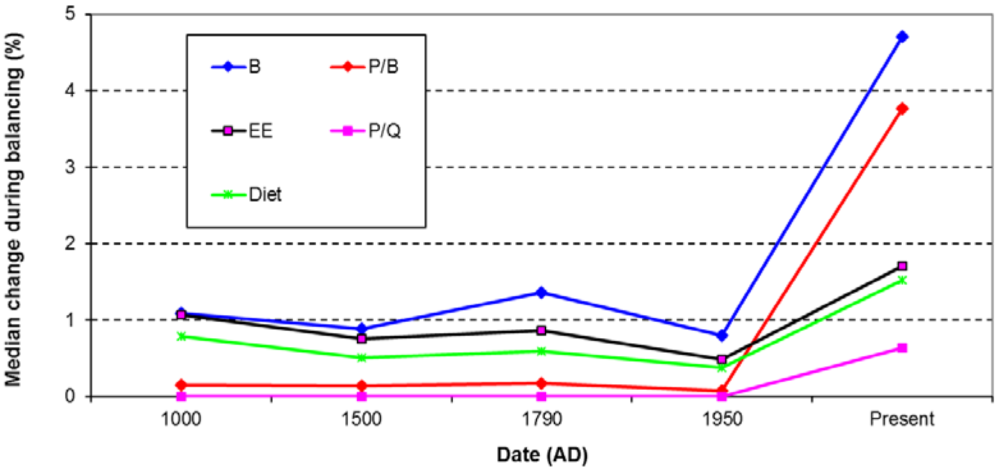


Figure 8: Median changes to parameters during model balancing.

1.1.7 Summary of balanced models

For each balanced historical model, four tables and one figure are shown:

1950 model: changes to parameters during balancing (Table 12); key parameters in the 1950 balanced model (Table 13); diet fractions in the 1950 balanced model (Table 14); key emergent properties of the balanced 1950 model (Table 15); flow diagram of the 1950 model is shown in Figure 9; Mixed Trophic Impact matrix for 1950 model (Figure 10).

1790 model: changes to parameters during balancing (Table 16); key parameters in the 1790 balanced model (Table 17); diet fractions in the 1790 balanced model (Table 18); key emergent properties of the balanced 1790 model (Table 19); flow diagram of the 1790 model is shown in Figure 11; Mixed Trophic Impact matrix for 1790 model (Figure 12).

1500 model: changes to parameters during balancing (Table 20); key parameters in the 1500 balanced model (Table 21); diet fractions in the 1500 balanced model (Table 22); key emergent properties of the balanced 1500 model (Table 23); flow diagram of the 1500 model is shown in Figure 13; Mixed Trophic Impact matrix for 1500 model (Figure 14).

1000 model: changes to parameters during balancing (Table 24); key parameters in the 1000 balanced model (Table 25); diet fractions in the 1000 balanced model (Table 26); key emergent properties of the balanced 1000 model (Table 27); flow diagram of the 1000 model is shown in Figure 15; .Mixed Trophic Impact matrix for 1000 model (Figure 16).

Table 12: 1950 model; changes to biomass (B), production (P/B), ecotrophic efficiency (EE), growth efficiency (P/Q) and diet fractions (D) during the SVD balancing process (from "initial" to "balanced"). Only changes with an absolute value of more than 10% are shown. Diets are shown: Predator ⟵ Prey.

Parameter	Group	Initial	Balanced	Change (%)
B	Macrobenthos	0.44	0.59	34
B	Gastropods_carn	0.35	0.26	-26
B	Gastropods_graz	0.51	0.60	18
B	Sharks	0.09	0.08	-11
B	Crabs	0.33	0.29	-11
P/B	None >5%			
EE	None >10%			
P/Q	None >1%			
D	Snapper⟵Crabs	0.28	0.05	-23
D	Snapper⟵Macrobenthos	0.20	0.38	18
D	Cetaceans⟵Sharks	0.11	0.28	17
D	Demersal_fish⟵Gurnard	0.32	0.17	-15
D	Sharks⟵Tarakihi	0.16	0.01	-15
D	Sharks⟵Kahawai	0.20	0.06	-15
D	Crabs⟵Macroalgae	0.23	0.36	13
D	Cetaceans⟵Trevally	0.36	0.24	-12
D	Snapper⟵Bivalves	0.16	0.28	12
D	Gurnard⟵Macrobenthos	0.62	0.73	11

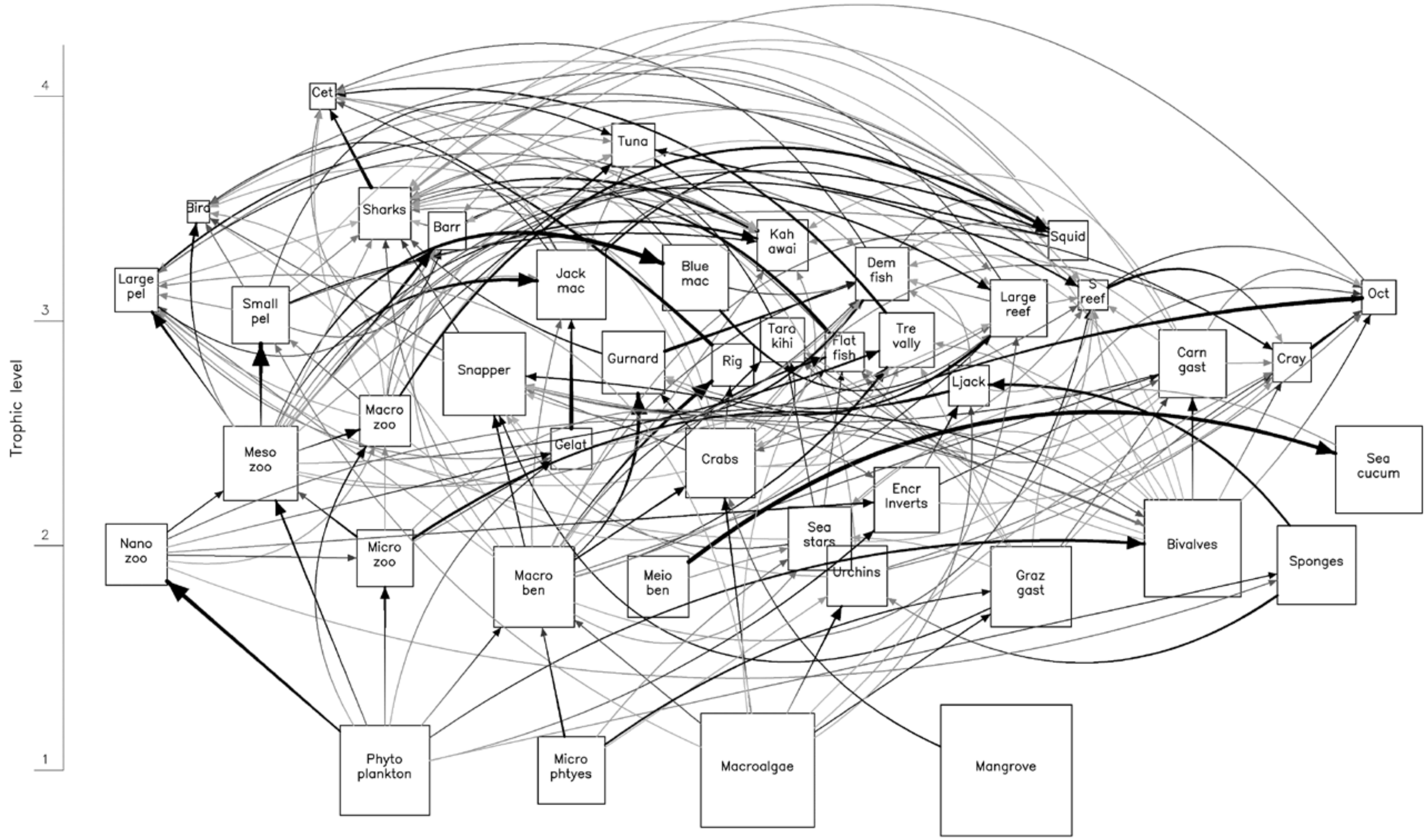


Figure 9: 1950 model: trophic model flow diagram (see Figure 3 caption for more information). Box sizes are consistent with those in Figure 3.

Table 13: 1950 model; biomass, energetic and transfer parameters in the balanced model. Column headings as Table 6. Grey cells indicate that data specific to this period were used to estimate the parameter.

	Group	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Acc A/P	Export X/P	Fishery gC m^{-2} y^{-1}	U	Seasonal T_S/P	Spawn T_R/P	Growth T_G/P	Detritus Fate	Carcass Fate	Seas. Fate	Spawn Fate	Growth Fate
1	Birds	1.7E-03	0.29	103	0.33	0.003	0	0.33	0	0.30	0	0	0	47	46	0	0	0
2	Cetaceans	3.5E-03	0.083	14	0.10	0.006	0	0	0	0.20	0	0	0	47	46	0	0	0
3	Crayfish	2.2E-02	1.2	6.6	0.94	0.18	0	0.24	9.2E-04	0.30	0	0.06	0	48	46	0	37	0
4	Crabs	2.9E-01	3.0	11	1.00	0.28	0	0.42	2.4E-04	0.30	0	0.048	0	48	46	0	37	0
5	Seastars	2.0E-01	1.4	5.4	0.98	0.26	0	0	0	0.30	0	0.59	0	48	48	0	37	0
6	Urchins	1.6E-01	0.85	5.6	0.98	0.15	0	0.22	6.0E-04	0.30	0	0.54	0	48	48	0	37	0
7	Gastropods_carn	2.6E-01	1.5	4.9	0.99	0.31	0	0.43	1.3E-05	0.30	0	0.14	0	48	46	0	37	0
8	Gastropods_graz	6.0E-01	3.6	19	0.98	0.19	0	0.42	1.4E-04	0.30	0	0.18	0	48	46	0	37	0
9	Sea_cucumbers	7.9E-01	0.41	2.1	0.21	0.20	0	0	0	0.30	0	0.10	0	48	48	0	37	0
10	Bivalves	1.4E+00	5.8	29	0.95	0.20	0	0.73	1.7E-03	0.20	0	0.031	0	48	46	0	37	0
11	Sponges	5.4E-01	0.20	0.79	0.95	0.25	0	0	0	0.30	0	0.10	0	48	48	0	37	0
12	Encrusting	2.3E-01	3.4	14	0.85	0.25	0	0.52	0	0.30	0	0.07	0	48	48	0	37	0
13	Macrobenthos	5.9E-01	6.8	28	1.00	0.24	0	0	0	0.30	0	0.10	0	48	48	0	37	0
14	Meiobenthos	1.6E-01	8.1	26	0.97	0.31	0	0	0	0.30	0	0.10	0	48	48	0	37	0
15	Snapper	6.6E-01	0.29	3.5	0.95	0.085	0	0	2.7E-02	0.27	0	0.15	-0.014	47	46	0	37	32
16	Jack_mackerels	3.0E-01	0.39	3.8	0.95	0.10	0	0	1.8E-07	0.27	0	0.12	-0.035	47	46	0	37	32
17	Blue_mackerel	2.4E-01	0.35	3.6	0.95	0.10	0	0	0	0.27	0	0.15	-0.022	47	46	0	37	32
18	Gurnard	1.9E-01	0.44	3.9	0.96	0.11	0	0	1.6E-03	0.27	0	0.12	-0.11	47	46	0	13	32
19	Leatherjacket	2.6E-02	0.32	3.2	0.95	0.10	0	0	4.3E-05	0.27	0	0.15	-0.030	47	46	0	13	32
20	Tarakihi	3.9E-02	0.28	3.4	0.95	0.082	0	0	6.2E-03	0.27	0	0.15	-0.020	47	46	0	37	32
21	Kahawai	7.5E-02	0.25	3.2	0.95	0.079	0	0	4.5E-04	0.27	0	0.16	-0.017	47	46	0	37	32
22	Rig	3.1E-02	0.26	2.6	0.89	0.10	0	0	1.6E-04	0.27	0	0.21	-0.010	47	46	0	32	32
23	Flatfish	2.2E-02	0.42	3.7	0.95	0.11	0	0	1.3E-03	0.27	0	0.14	-0.10	47	46	0	13	32
24	Trevally	1.0E-01	0.24	3.0	0.67	0.082	0	0	1.5E-03	0.27	0	0.16	-0.019	47	46	0	37	32
25	Barracouta	1.9E-02	0.30	3.2	0.95	0.10	0	0	4.2E-05	0.27	0	0.18	-0.015	47	46	0	37	32
26	Skipjack	3.5E-02	0.19	2.9	0.95	0.07	0	0	2.5E-06	0.27	0	0.26	-0.008	47	46	0	37	32
27	Reef_fish_large	1.2E-01	0.39	4.5	0.95	0.09	0	0	3.5E-04	0.27	0	0.17	-0.052	47	46	0	13	28
28	Reef_fish_small	6.5E-03	0.90	7.4	0.95	0.12	0	0	0	0.27	0	0.073	-0.29	47	46	0	13	32
29	Demersal_fish	8.9E-02	0.29	3.3	0.95	0.087	0	0	2.2E-04	0.27	0	0.23	-0.027	47	46	0	37	32
30	Sharks	8.0E-02	0.25	3.1	0.87	0.081	0	0	1.2E-04	0.27	0	0.19	-0.005	47	46	0	32	32
31	Pelagic_fish_large	3.6E-02	0.37	5.1	0.95	0.071	0	0	7.9E-05	0.27	0	0.18	-0.051	47	46	0	37	32
32	Pelagic_fish_small	1.2E-01	1.7	11	0.96	0.16	0	0	0	0.27	0	0.011	0	47	46	0	37	0
33	Squid	2.1E-02	2.7	11	1.00	0.25	0	0	0.0E+00	0.13	0	0.072	0	47	46	0	37	0
34	Octopus	1.2E-02	4.4	10	0.98	0.43	0	0	0.0E+00	0.12	0	0.040	0	47	46	0	37	0
35	Gelatinous	2.8E-02	11	37	0.97	0.29	0	0	0	0.20	0	0	0	47	47	0	0	0
36	Macrozoo	7.6E-02	7.0	23	0.95	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
37	Mesozoo	4.1E-01	25	84	0.94	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
38	Microzoo	1.2E-01	76	254	0.95	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
39	Nanozoo	1.9E-01	161	462	0.94	0.35	0	0	0	0.20	0	0	0	47	47	0	0	0
40	Phytoplankton	9.5E-01	171	0	0.79	0	0	0	0	0	0	0	0	47	47	0	0	0
41	Macroalgae	2.9E+00	5.2	0	0.68	0	0	0.25	0	0	0	0	0	47	47	0	0	0

	Group	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Acc A/P	Export X/P	Fishery gC m^{-2} y^{-1}	U	Seasonal T_S/P	Spawn T_R/P	Growth T_G/P	Detritus Fate	Carcass Fate	Seas. Fate	Spawn Fate	Growth Fate
42	Mangrove_seagrass	5.5E+00	0.17	0	0.54	0	0.24	0	0	0	0	0	0	47	47	0	0	0
43	Microphtyes	2.6E-01	21	0	0.81	0	0	0	0	0	0	0	0	47	47	0	0	0
44	Bacteria_water	3.9E-01	67	137	0.69	0.49	0	0	0	0	0	0	0	47	47	0	0	0
45	Bacteria_benthic	1.7E+00	9.4	22	0.74	0.43	0	0	0	0	0	0	0	48	48	0	0	0
46	Carcasses	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
47	Detritus_water	0	0	0	1	0	0	-0.005	0	0	0.37	0	0	0	0	48	0	0
48	Detritus_benthic	0	0	0	1	0	0.12	0	0	0	0	0	0	0	0	0	0	0

Table 14a: 1950 model; diet parameters in the balanced model for predators 1–21. Figures are the proportions of prey by weight of organic carbon in diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of “0.00” indicate that the diet fraction is between 0 and 0.5%.

		Predators																				
	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Birds																					
2	Cetaceans		0.00																			
3	Crayfish																					
4	Crabs			0.17												0.05			0.24		0.21	0.05
5	Seastars															0.02					0.24	
6	Urchins			0.08												0.00						
7	Gastropods_carn	0.02		0.05		0.00		0.01								0.03					0.09	0.02
8	Gastropods_graz	0.01		0.16	0.00	0.02		0.14								0.23					0.04	0.01
9	Sea_cucumbers					0.03																
10	Bivalves	0.02		0.16	0.08	0.03		0.39								0.28					0.12	0.03
11	Sponges						0.05													0.50		
12	Encrusting			0.04	0.01			0.11												0.36		
13	Macrobenthos	0.02		0.23	0.38	0.07		0.20								0.38	0.09		0.73		0.30	0.08
14	Meiobenthos					0.06				0.66				0.00	0.00							
15	Snapper	0.11	0.07																			
16	Jack_mackerels	0.14	0.05																			
17	Blue_mackerel		0.04																			
18	Gurnard																					
19	Leatherjacket															0.00			0.00			
20	Tarakihi																					
21	Kahawai																					
22	Rig		0.11																			
23	Flatfish		0.02																			
24	Trevally		0.24																			
25	Barracouta																					0.00
26	Skipjack																0.00					0.00
27	Reef_fish_large															0.00			0.03			

																						Predators
28	Reef_fish_small	0.00		0.02																		
29	Demersal_fish		0.10													0.00						
30	Sharks		0.28																			
31	Pelagic_fish_large																					0.01
32	Pelagic_fish_small	0.08	0.02													0.00						0.26
33	Squid	0.02	0.03																			
34	Octopus				0.01																	
35	Gelatinous	0.01	0.00														0.23					
36	Macrozoo	0.48	0.03														0.05	0.06				0.03
37	Mesozoo	0.09	0.02														0.63	0.94				0.49
38	Microzoo										0.11		0.10									
39	Nanozoo										0.07	0.10	0.31									
40	Phytoplankton										0.59	0.20	0.30	0.23								
41	Macroalgae			0.06	0.36		0.42		0.24					0.12						0.13		
42	Mangrove_seagrass				0.09																	
43	Microphtyes					0.10	0.03		0.18					0.14								
44	Bacteria_water										0.14	0.70	0.29	0.08								
45	Bacteria_benthic						0.25		0.11	0.34				0.32	1.00							
46	Carcasses	0.02		0.02	0.08	0.02		0.15														
47	Detritus_water					0.13					0.08											
48	Detritus_benthic					0.54	0.25		0.47					0.11								

Table 14b: 1950 model; diet parameters in the balanced model for predators 22–45 (primary producers and detritus are not shown). Figures are the proportions of prey by weight of organic carbon in diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of "0.00" indicate that the diet fraction is between 0 and 0.5%.

																					Predator
	Prey	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	44	45
1	Birds																				
2	Cetaceans																				
3	Crayfish													0.13							
4	Crabs	0.31	0.18	0.03				0.07	0.03	0.07	0.03			0.28							
5	Seastars		0.19					0.04	0.01	0.02	0.02										
6	Urchins								0.00	0.02				0.08							
7	Gastropods_carn		0.07	0.01			0.00	0.03	0.03	0.03	0.01			0.14							
8	Gastropods_graz		0.03	0.03			0.00	0.01	0.01	0.02	0.01			0.14							
9	Sea_cucumbers																				
10	Bivalves		0.09	0.04			0.01	0.04	0.04	0.04	0.01			0.23							
11	Sponges																				
12	Encrusting						0.02														
13	Macrobenthos	0.69	0.43	0.45	0.05		0.22	0.21	0.22	0.14	0.11	0.00									
14	Meiobenthos																				

Predator

15	Snapper						0.08	0.10	0.09	0.14											
16	Jack_mackerels						0.07		0.05	0.08											
17	Blue_mackerel						0.07		0.05	0.06											
18	Gurnard								0.17	0.10											
19	Leatherjacket							0.01	0.00												
20	Tarakihi									0.01											
21	Kahawai									0.06											
22	Rig																				
23	Flatfish									0.02											
24	Trevally																				
25	Barracouta					0.02				0.01											
26	Skipjack										0.00										
27	Reef_fish_large							0.04	0.01	0.03											
28	Reef_fish_small													0.01							
29	Demersal_fish												0.02								
30	Sharks																				
31	Pelagic_fish_large				0.04	0.05				0.01											
32	Pelagic_fish_small				0.23	0.28		0.02	0.01	0.06	0.05		0.13								
33	Squid				0.04	0.28			0.01	0.01	0.03		0.02								
34	Octopus									0.02											
35	Gelatinous						0.02	0.01	0.02		0.09										
36	Macrozoo			0.02	0.04	0.02	0.03	0.02	0.02		0.04	0.05	0.48			0.05					
37	Mesozoo			0.41	0.60	0.34	0.37	0.38	0.14	0.05	0.53	0.82	0.35		0.10	0.42	0.21				
38	Microzoo														0.25	0.05	0.10				
39	Nanozoo														0.25	0.05	0.18	0.14	0.16		
40	Phytoplankton														0.20	0.31	0.46	0.37	0.81		
41	Macroalgae						0.11	0.01	0.03		0.06	0.08									
42	Mangrove_seagrass																				
43	Microphtyes																				
44	Bacteria_water														0.10			0.23	0.03		
45	Bacteria_benthic																				
46	Carcasses																				
47	Detritus_water														0.10	0.12	0.05	0.26		1.00	
48	Detritus_benthic								0.04			0.04									1.00

Table 15: 1950 model; key indices for the balanced model, showing respiration quotient (R/B, y^{-1}, shown as a percentage), trophic level (TrL), omnivory index (OI), trophic importance (TI), and the rank of TI, with 1 being most important.

	Group	R/B (%)	TrL	OI	TI	Rank TI
1	Birds	72	4.0	0.16	1.00	24
2	Cetaceans	11	4.6	0.13	2.96	7
3	Crayfish	3	3.2	0.24	0.93	26
4	Crabs	5	2.6	0.35	2.77	8
5	Seastars	2	2.3	0.26	0.80	31
6	Urchins	3	2.1	0.06	0.84	29
7	Gastropods_carn	2	3.2	0.04	1.31	19
8	Gastropods_graz	10	2.0	0.00	1.89	16
9	Sea_cucumbers	1	2.7	0.23	0.73	34
10	Bivalves	18	2.2	0.21	3.66	4
11	Sponges	0	2.1	0.13	0.50	37
12	Encrusting	6	2.5	0.34	0.80	30
13	Macrobenthos	13	2.0	0.00	4.58	2
14	Meiobenthos	10	2.0	0.00	0.78	33
15	Snapper	2	3.1	0.08	3.01	6
16	Jack_mackerels	2	3.7	0.05	1.91	14
17	Blue_mackerel	2	3.7	0.00	0.72	35
18	Gurnard	2	3.2	0.13	2.33	10
19	Leatherjacket	2	3.1	0.22	0.40	39
20	Tarakihi	2	3.3	0.13	0.30	42
21	Kahawai	2	3.8	0.22	0.80	32
22	Rig	2	3.2	0.08	0.41	38
23	Flatfish	2	3.3	0.12	0.22	44
24	Trevally	2	3.3	0.13	0.87	27
25	Barracouta	2	3.9	0.21	0.35	41
26	Skipjack	2	4.3	0.27	1.38	18
27	Reef_fish_large	3	3.5	0.55	1.93	13
28	Reef_fish_small	5	3.6	0.23	0.20	45
29	Demersal_fish	2	3.7	0.54	2.32	11
30	Sharks	2	4.0	0.39	3.45	5
31	Pelagic_fish_large	3	3.6	0.34	0.40	40
32	Pelagic_fish_small	6	3.5	0.31	1.09	23
33	Squid	7	3.9	0.10	1.10	22
34	Octopus	5	3.6	0.21	0.84	28
35	Gelatinous	19	2.8	0.41	0.63	36
36	Macrozoo	9	2.9	0.67	1.17	21
37	Mesozoo	34	2.7	0.52	4.39	3
38	Microzoo	102	2.2	0.17	1.38	17
39	Nanozoo	209	2.2	0.19	1.28	20
40	Phytoplankton	NA	1	NA	6.63	1
41	Macroalgae	NA	1	NA	2.51	9
42	Mangrove_seagrass	NA	1	NA	0.30	43
43	Microphtyes	NA	1	NA	1.00	25
44	Bacteria_water	70	1	1.00	1.97	12
45	Bacteria_benthic	12	1	1.00	1.90	15
46	Carcasses	NA	2.4	NA	NA	NA
47	Detritus_water	NA	1	NA	NA	NA
48	Detritus_benthic	NA	1	NA	NA	NA

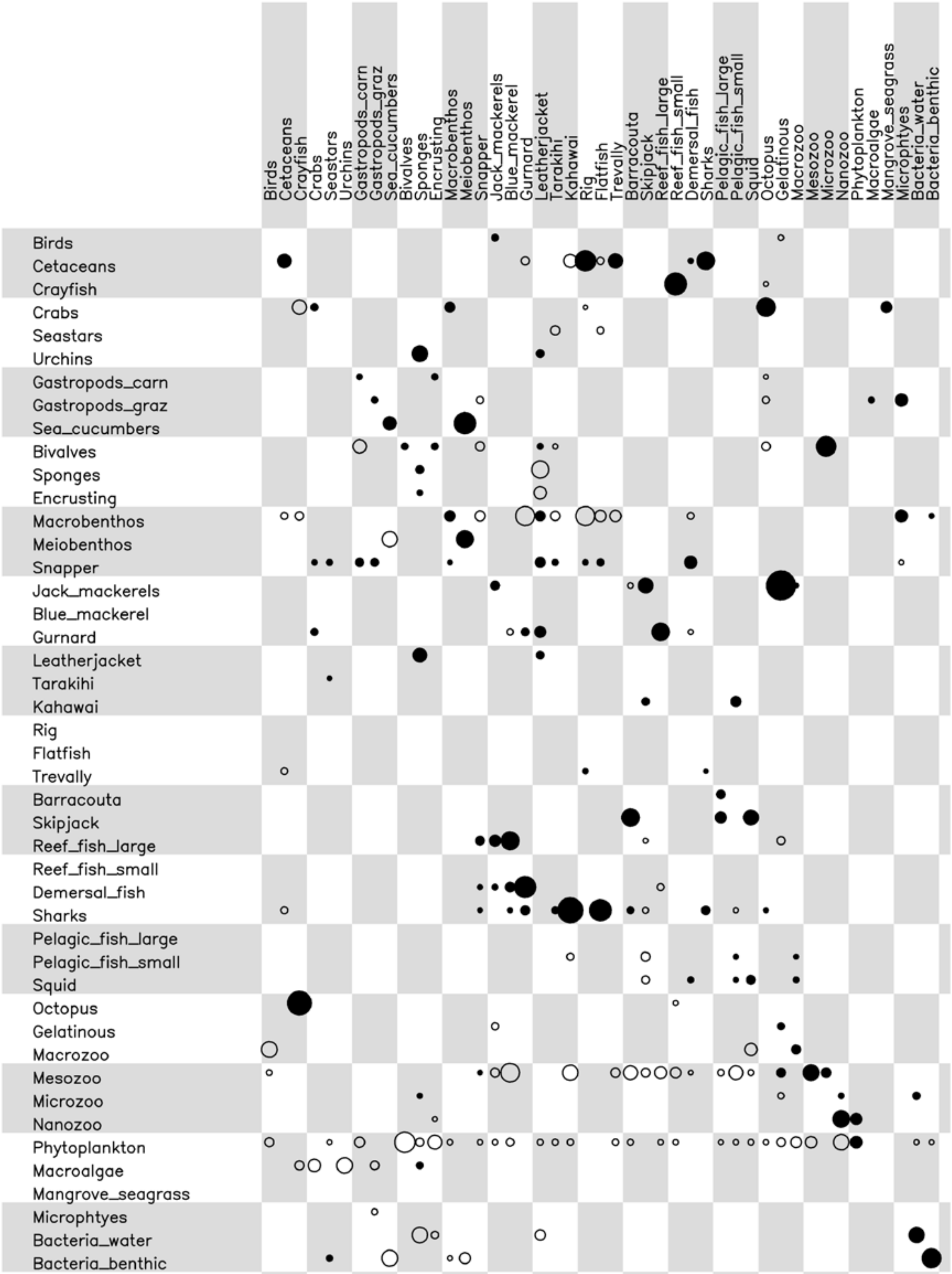


Figure 10: Mixed Trophic Impact Matrix for the 1950 model. Positive impacts are shown black and negative are white, with the diameter of the circle proportional to the magnitude of the effect (scaling consistent with Figure 4).

Table 16: 1790 model; changes to biomass (B), production (P/B), ecotrophic efficiency (EE), growth efficiency (P/Q) and diet fractions (D) during the SVD balancing process (from "initial" to "balanced"). Only changes with an absolute value of more than 10% are shown. Diets are shown: Predator ⟵ Prey.

Parameter	Group	Initial	Balanced	Change (%)
B	Macrobenthos	0.44	0.75	69
B	Gastropods_carn	0.35	0.19	-46
B	Gastropods_graz	0.51	0.67	32
B	Crabs	0.33	0.22	-32
B	Bacteria_benthic	1.51	1.73	14
B	Bacteria_water	0.41	0.36	-11
P/B	None > 10%			
EE	Birds	0.29	0.57	28
EE	Macroalgae	0.61	0.74	13
P/Q	None > 5%			
D	Snapper⟵Macrobenthos	0.20	0.54	34
D	Cetaceans⟵Trevally	0.37	0.08	-29
D	Snapper⟵Crabs	0.28	0.00	-28
D	Crabs⟵Macroalgae	0.24	0.46	23
D	Cetaceans⟵Snapper	0.15	0.33	18
D	Gurnard⟵Macrobenthos	0.62	0.78	16
D	Gurnard⟵Crabs	0.33	0.18	-15
D	Sharks⟵Tarakihi	0.27	0.14	-13
D	Snapper⟵Bivalves	0.16	0.27	11
D	Crabs⟵Bivalves	0.12	0.01	-11

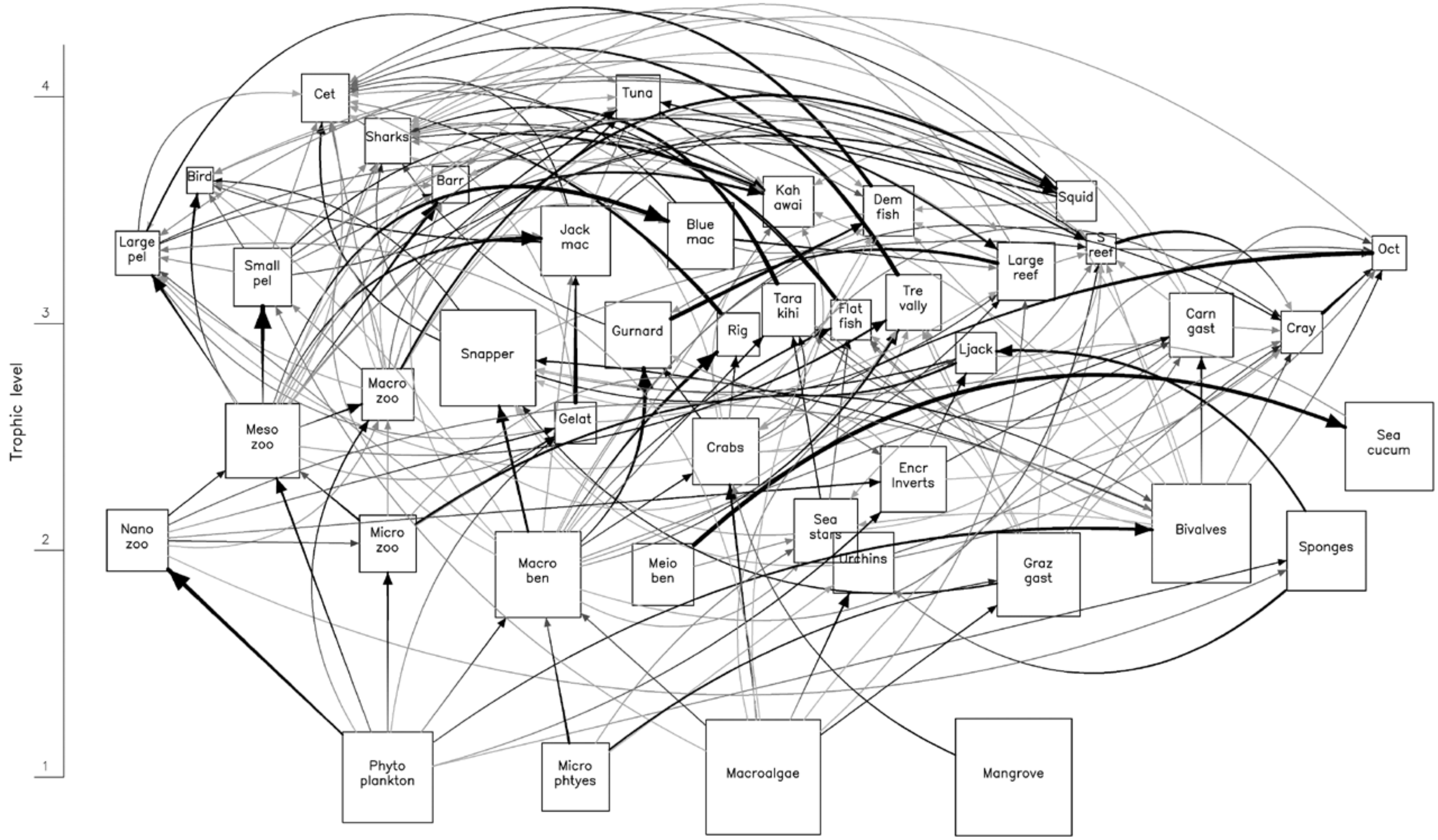


Figure 11: 1790 model; trophic model flow diagram (see Figure 3 caption for more information). Box sizes are consistent with those in Figure 3

Table 17: 1790 model; biomass, energetic and transfer parameters in the balanced model. Column headings as Table 6. Grey cells indicate that data specific to this period were used to estimate the parameter.

	Group	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Acc A/P	Export X/P	Fishery gC m^{-2} y^{-1}	U	Seasonal T_S/P	Spawn T_R/P	Growth T_G/P	Detritus Fate	Carcass Fate	Seas. Fate	Spawn Fate	Growth Fate
1	Birds	3.6E-03	0.33	100	0.57	0.003	0	0.28	0.0003473	0.30	0	0	0	47	46	0	0	0
2	Cetaceans	5.4E-02	0.017	5	0.10	0.004	0	0	1.317E-05	0.20	0	0	0	47	46	0	0	0
3	Crayfish	2.9E-02	1.2	6.5	0.94	0.18	0	0.24	9.2E-04	0.30	0	0.06	0	48	46	0	37	0
4	Crabs	2.2E-01	3.0	11	1.00	0.28	0	0.42	2.4E-04	0.30	0	0.048	0	48	46	0	37	0
5	Seastars	2.0E-01	1.4	5.4	0.99	0.26	0	0	0	0.30	0	0.59	0	48	48	0	37	0
6	Urchins	1.6E-01	0.85	5.6	0.98	0.15	0	0.22	6.0E-04	0.30	0	0.54	0	48	48	0	37	0
7	Gastropods_carn	1.9E-01	1.5	4.8	0.99	0.31	0	0.43	1.3E-05	0.30	0	0.14	0	48	46	0	37	0
8	Gastropods_graz	6.7E-01	3.6	19	0.98	0.19	0	0.42	1.4E-04	0.30	0	0.18	0	48	46	0	37	0
9	Sea_cucumbers	7.8E-01	0.41	2.1	0.22	0.20	0	0	0	0.30	0	0.10	0	48	48	0	37	0
10	Bivalves	1.5E+00	5.8	29	0.96	0.20	0	0.73	1.7E-03	0.20	0	0.031	0	48	46	0	37	0
11	Sponges	5.4E-01	0.20	0.79	0.95	0.25	0	0	0	0.30	0	0.10	0	48	48	0	37	0
12	Encrusting	2.3E-01	3.4	14	0.85	0.25	0	0.52	0	0.30	0	0.07	0	48	48	0	37	0
13	Macrobenthos	7.5E-01	6.9	28	1.00	0.24	0	0	0	0.30	0	0.10	0	48	48	0	37	0
14	Meiobenthos	1.6E-01	8.1	26	0.97	0.31	0	0	0	0.30	0	0.10	0	48	48	0	37	0
15	Snapper	1.2E+00	0.29	3.4	0.95	0.085	0	0	7.4E-06	0.27	0	0.15	-0.008	47	46	0	37	32
16	Jack_mackerels	2.9E-01	0.39	3.8	0.95	0.10	0	0	0.0E+00	0.27	0	0.12	-0.035	47	46	0	37	32
17	Blue_mackerel	2.4E-01	0.35	3.6	0.95	0.10	0	0	0	0.27	0	0.15	-0.022	47	46	0	37	32
18	Gurnard	2.3E-01	0.43	3.9	0.95	0.11	0	0	0.0E+00	0.27	0	0.12	-0.11	47	46	0	13	32
19	Leatherjacket	2.6E-02	0.32	3.2	0.94	0.10	0	0	0.0E+00	0.27	0	0.15	-0.031	47	46	0	13	32
20	Tarakihi	8.4E-02	0.28	3.4	0.96	0.082	0	0	0.0E+00	0.27	0	0.15	-0.011	47	46	0	37	32
21	Kahawai	6.8E-02	0.25	3.2	0.94	0.079	0	0	0.0E+00	0.27	0	0.16	-0.017	47	46	0	37	32
22	Rig	3.2E-02	0.26	2.6	0.96	0.10	0	0	0.0E+00	0.27	0	0.21	-0.009	47	46	0	32	32
23	Flatfish	2.4E-02	0.42	3.7	0.96	0.11	0	0	0.0E+00	0.27	0	0.14	-0.11	47	46	0	13	32
24	Trevally	1.1E-01	0.24	3.0	0.95	0.082	0	0	0.0E+00	0.27	0	0.16	-0.010	47	46	0	37	32
25	Barracouta	1.6E-02	0.30	3.2	0.90	0.10	0	0	0.0E+00	0.27	0	0.18	-0.016	47	46	0	37	32
26	Skipjack	3.5E-02	0.19	2.9	0.95	0.07	0	0	0.0E+00	0.27	0	0.26	-0.008	47	46	0	37	32
27	Reef_fish_large	1.2E-01	0.39	4.5	0.95	0.09	0	0	4.0E-04	0.27	0	0.17	-0.052	47	46	0	13	28
28	Reef_fish_small	6.5E-03	0.90	7.4	0.95	0.12	0	0	5.13E-07	0.27	0	0.073	-0.29	47	46	0	13	32
29	Demersal_fish	6.8E-02	0.29	3.3	0.95	0.087	0	0	1.8E-03	0.27	0	0.20	-0.035	47	46	0	37	32
30	Sharks	4.2E-02	0.26	3.2	0.89	0.081	0	0	5.6E-03	0.27	0	0.27	-0.011	47	46	0	32	32
31	Pelagic_fish_large	3.7E-02	0.37	5.1	0.95	0.071	0	0	0.0E+00	0.27	0	0.18	-0.051	47	46	0	37	32
32	Pelagic_fish_small	1.3E-01	1.7	11	0.96	0.16	0	0	0	0.27	0	0.039	0	47	46	0	37	0
33	Squid	2.2E-02	2.7	11	1.00	0.25	0	0	0.0E+00	0.13	0	0.072	0	47	46	0	37	0
34	Octopus	1.2E-02	4.4	10	0.98	0.43	0	0	0.0E+00	0.12	0	0.040	0	47	46	0	37	0
35	Gelatinous	2.8E-02	11	37	0.97	0.29	0	0	0	0.20	0	0	0	47	47	0	0	0
36	Macrozoo	8.2E-02	7.1	24	0.96	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
37	Mesozoo	4.0E-01	25	83	0.94	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
38	Microzoo	1.2E-01	76	252	0.95	0.30	0	0	0	0.30	0	0	0	47	47	0	0	0
39	Nanozoo	1.9E-01	159	457	0.94	0.35	0	0	0	0.20	0	0	0	47	47	0	0	0
40	Phytoplankton	9.0E-01	163	0	0.87	0	0	0	0	0	0	0	0	47	47	0	0	0
41	Macroalgae	2.9E+00	5.2	0	0.74	0	0	0.25	0	0	0	0	0	47	47	0	0	0

	Group	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Acc A/P	Export X/P	Fishery gC m^{-2} y^{-1}	U	Seasonal T_S/P	Spawn T_R/P	Growth T_G/P	Detritus Fate	Carcass Fate	Seas. Fate	Spawn Fate	Growth Fate
42	Mangrove_seagrass	3.1E+00	0.17	0	0.54	0	0.24	0	0	0	0	0	0	47	47	0	0	0
43	Microphtyes	2.6E-01	21	0	0.83	0	0	0	0	0	0	0	0	47	47	0	0	0
44	Bacteria_water	3.6E-01	65	115	0.73	0.57	0	0	0	0	0	0	0	47	47	0	0	0
45	Bacteria_benthic	1.7E+00	9.6	19	0.78	0.49	0	0	0	0	0	0	0	48	48	0	0	0
46	Carcasses	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
47	Detritus_water	0	0	0	1	0	0	-0.005	0	0	0.32	0	0	0	0	48	0	0
48	Detritus_benthic	0	0	0	1	0	0.03	0	0	0	0	0	0	0	0	0	0	0

Table 18a: 1790 model; diet parameters in the balanced model for predators 1–21. Figures are the proportions of prey by weight of organic carbon in diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of "0.00" indicate that the diet fraction is between 0 and 0.5%.

																						Predators
	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Birds																					
2	Cetaceans		0.00																			
3	Crayfish																					
4	Crabs			0.16												0.00			0.18		0.19	0.05
5	Seastars															0.00					0.23	
6	Urchins			0.08												0.00						
7	Gastropods_carn	0.01		0.05		0.00		0.01								0.01					0.09	0.02
8	Gastropods_graz	0.01		0.16	0.00	0.00		0.11								0.17					0.04	0.01
9	Sea_cucumbers					0.04																
10	Bivalves	0.02		0.16	0.01	0.02		0.35								0.27					0.13	0.03
11	Sponges						0.05													0.50		
12	Encrusting			0.04	0.01			0.13												0.36		
13	Macrobenthos	0.02		0.24	0.33	0.06		0.21								0.54	0.07		0.78		0.32	0.08
14	Meiobenthos					0.07				0.66					0.00							
15	Snapper	0.18	0.33																			
16	Jack_mackerels	0.10	0.11																			
17	Blue_mackerel		0.09																			
18	Gurnard																					
19	Leatherjacket															0.00			0.00			
20	Tarakihi																					
21	Kahawai																					
22	Rig		0.02																			
23	Flatfish		0.02																			
24	Trevally		0.08																			
25	Barracouta																					0.00
26	Skipjack																0.00					0.00

																						Predators
27	Reef_fish_large															0.00			0.03			
28	Reef_fish_small			0.02																		
29	Demersal_fish		0.04													0.00						
30	Sharks		0.00																			
31	Pelagic_fish_large		0.01																			0.00
32	Pelagic_fish_small	0.06	0.05													0.00						0.25
33	Squid	0.00	0.07																			
34	Octopus				0.02																	
35	Gelatinous	0.01	0.03														0.23					
36	Macrozoo	0.48	0.09														0.05	0.05				0.03
37	Mesozoo	0.09	0.06														0.65	0.95				0.50
38	Microzoo										0.11		0.10									
39	Nanozoo										0.07	0.10	0.32									
40	Phytoplankton										0.60	0.18	0.28	0.23								
41	Macroalgae			0.07	0.46		0.42		0.23					0.12						0.13		
42	Mangrove_seagrass				0.06																	
43	Microphtyes					0.10	0.02		0.16					0.12								
44	Bacteria_water										0.13	0.71	0.30	0.09								
45	Bacteria_benthic						0.25		0.11	0.34				0.32	1.00							
46	Carcasses	0.02		0.02	0.10	0.01		0.18														
47	Detritus_water					0.14					0.09											
48	Detritus_benthic					0.56	0.26		0.50					0.13								

Table 18b: 1790 model; diet parameters in the balanced model for predators 22–45 (primary producers and detritus are not shown). Figures are the proportions of prey by weight of organic carbon in diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of "0.00" indicate that the diet fraction is between 0 and 0.5%.

																					Predator
	Prey	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	44	45
1	Birds																				
2	Cetaceans																				
3	Crayfish													0.18							
4	Crabs	0.30	0.18	0.03				0.06	0.02	0.05	0.03			0.26							
5	Seastars		0.19					0.04	0.01	0.01	0.02										
6	Urchins									0.01				0.07							
7	Gastropods_carn		0.07	0.01			0.00	0.03	0.02	0.02	0.01			0.13							
8	Gastropods_graz		0.03	0.02			0.00	0.01	0.01	0.01	0.01			0.13							
9	Sea_cucumbers																				
10	Bivalves		0.09	0.04			0.01	0.04	0.03	0.03	0.01			0.22							
11	Sponges																				
12	Encrusting						0.02														
13	Macrobenthos	0.70	0.44	0.45	0.05		0.20	0.20	0.17	0.09	0.11										

																			Predator
14	Meiobenthos																		
15	Snapper				0.13	0.17	0.12	0.17											
16	Jack_mackerels				0.04		0.03	0.04											
17	Blue_mackerel				0.06		0.04	0.04											
18	Gurnard						0.34	0.13											
19	Leatherjacket					0.01	0.00												
20	Tarakihi							0.14											
21	Kahawai							0.10											
22	Rig																		
23	Flatfish							0.04											
24	Trevally																		
25	Barracouta			0.02				0.00											
26	Skipjack								0.00										
27	Reef_fish_large					0.04	0.01	0.02											
28	Reef_fish_small											0.01							
29	Demersal_fish										0.00								
30	Sharks																		
31	Pelagic_fish_large		0.04	0.05				0.00											
32	Pelagic_fish_small		0.23	0.29		0.02	0.00	0.04	0.05		0.12								
33	Squid		0.04	0.25			0.00	0.01	0.02		0.01								
34	Octopus							0.02											
35	Gelatinous				0.02	0.01	0.02		0.09										
36	Macrozoo	0.02	0.04	0.02	0.03	0.02	0.01		0.04	0.04	0.49			0.03					
37	Mesozoo	0.43	0.60	0.36	0.38	0.35	0.11	0.03	0.55	0.84	0.37		0.10	0.44	0.20				
38	Microzoo												0.25	0.05	0.10				
39	Nanozoo												0.26	0.05	0.19	0.15	0.15		
40	Phytoplankton												0.18	0.30	0.45	0.36	0.83		
41	Macroalgae				0.12	0.01	0.02		0.07	0.08									
42	Mangrove_seagrass																		
43	Microphtyes																		
44	Bacteria_water												0.10			0.22	0.02		
45	Bacteria_benthic																		
46	Carcasses																		0.00
47	Detritus_water												0.10	0.13	0.06	0.27		1.00	
48	Detritus_benthic						0.03			0.05									1.00

Table 19: 1790 model; key indices for the balanced model, showing respiration quotient (R/B, y^{-1}, shown as a percentage), trophic level (TrL), omnivory index (OI), trophic importance (TI), and the rank of TI, with 1 being most important.

	Group	R/B (%)	TrL	OI	TI	Rank TI
1	Birds	70	4.0	0.12	1.65	16
2	Cetaceans	3.9	4.3	0.13	3.66	6
3	Crayfish	3.4	3.2	0.23	1.09	24
4	Crabs	4.6	2.5	0.38	2.84	9
5	Seastars	2.4	2.2	0.23	0.77	33
6	Urchins	3.1	2.1	0.06	0.81	31
7	Gastropods_carn	1.9	3.2	0.04	1.09	23
8	Gastropods_graz	10	2.0	0.00	1.86	14
9	Sea_cucumbers	1.0	2.7	0.23	0.73	34
10	Bivalves	18	2.2	0.21	3.81	4
11	Sponges	0.36	2.1	0.13	0.50	37
12	Encrusting	6.1	2.5	0.34	0.87	27
13	Macrobenthos	13	2.0	0.00	4.48	3
14	Meiobenthos	10	2.0	0.00	0.78	32
15	Snapper	2.2	3.1	0.02	3.70	5
16	Jack_mackerels	2.4	3.7	0.04	1.79	15
17	Blue_mackerel	2.3	3.7	0.00	0.72	35
18	Gurnard	2.4	3.2	0.11	2.54	11
19	Leatherjacket	2.0	3.1	0.22	0.41	39
20	Tarakihi	2.2	3.3	0.12	0.89	25
21	Kahawai	2.1	3.8	0.22	0.84	29
22	Rig	1.6	3.2	0.06	0.21	44
23	Flatfish	2.3	3.2	0.11	0.30	41
24	Trevally	1.9	3.3	0.12	0.43	38
25	Barracouta	2.0	3.9	0.20	0.30	42
26	Skipjack	1.9	4.3	0.26	1.28	21
27	Reef_fish_large	2.9	3.5	0.50	1.55	17
28	Reef_fish_small	4.5	3.6	0.22	0.19	45
29	Demersal_fish	2.1	3.7	0.43	2.64	10
30	Sharks	2.1	4.1	0.29	2.95	7
31	Pelagic_fish_large	3.4	3.6	0.31	0.38	40
32	Pelagic_fish_small	6.0	3.5	0.31	1.11	22
33	Squid	7	3.9	0.07	0.82	30
34	Octopus	4.7	3.6	0.22	0.85	28
35	Gelatinous	19	2.8	0.40	0.64	36
36	Macrozoo	9.4	2.9	0.65	1.44	18
37	Mesozoo	33	2.7	0.51	4.56	2
38	Microzoo	101	2.2	0.17	1.35	20
39	Nanozoo	206	2.2	0.17	1.36	19
40	Phytoplankton	NA	1	NA	5.98	1
41	Macroalgae	NA	1	NA	2.87	8
42	Mangrove_seagrass	NA	1	NA	0.22	43
43	Microphtyes	NA	1	NA	0.88	26
44	Bacteria_water	50	1	1.00	1.89	13
45	Bacteria_benthic	9.8	1	1.00	1.94	12
46	Carcasses	NA	2.3	NA	NA	NA
47	Detritus_water	NA	1	NA	NA	NA
48	Detritus_benthic	NA	1	NA	NA	NA

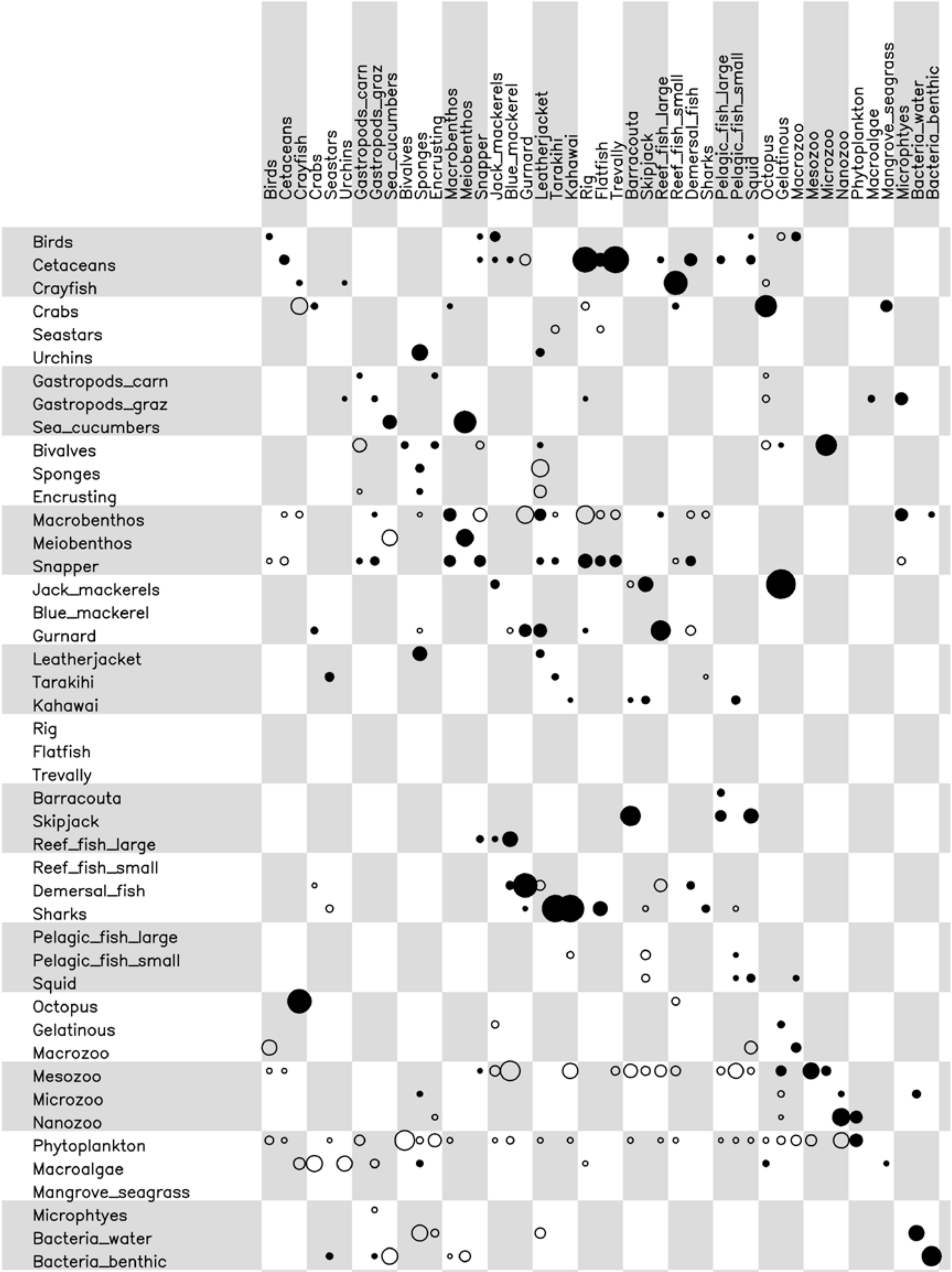


Figure 12: Mixed Trophic Impact Matrix for the 1790 model. Positive impacts are shown black and negative are white, with the diameter of the circle proportional to the magnitude of the effect (scaling consistent with Figure 4).

Table 20: 1500 model; changes to biomass (B), production (P/B), ecotrophic efficiency (EE), growth efficiency (P/Q) and diet fractions (D) during the SVD balancing process (from "initial" to "balanced"). Only changes with an absolute value of more than 10% are shown. Diets are shown: Predator ⟵ Prey.

Parameter	Group	Initial	Balanced	Change (%)
B	Macrobenthos	0.44	0.72	63
B	Gastropods_carn	0.35	0.19	-45
B	Crabs	0.33	0.22	-32
B	Gastropods_graz	0.51	0.66	30
B	Bacteria_water	0.41	0.32	-22
B	Macrozoo	0.08	0.09	14
P/B	None > 10%			
EE	Birds	0.23	0.43	20
EE	Macroalgae	0.61	0.72	12
P/Q	None > 5%			
D	Snapper⟵Macrobenthos	0.19	0.51	31
D	Snapper⟵Crabs	0.27	0.00	-27
D	Crabs⟵Macroalgae	0.22	0.44	22
D	Gurnard⟵Macrobenthos	0.63	0.81	18
D	Gurnard⟵Crabs	0.33	0.16	-17
D	Cetaceans⟵Rig	0.17	0.02	-15
D	Crabs⟵Bivalves	0.14	0.01	-13
D	Octopus⟵Crayfish	0.03	0.15	12
D	Cetaceans⟵Snapper	0.07	0.18	12

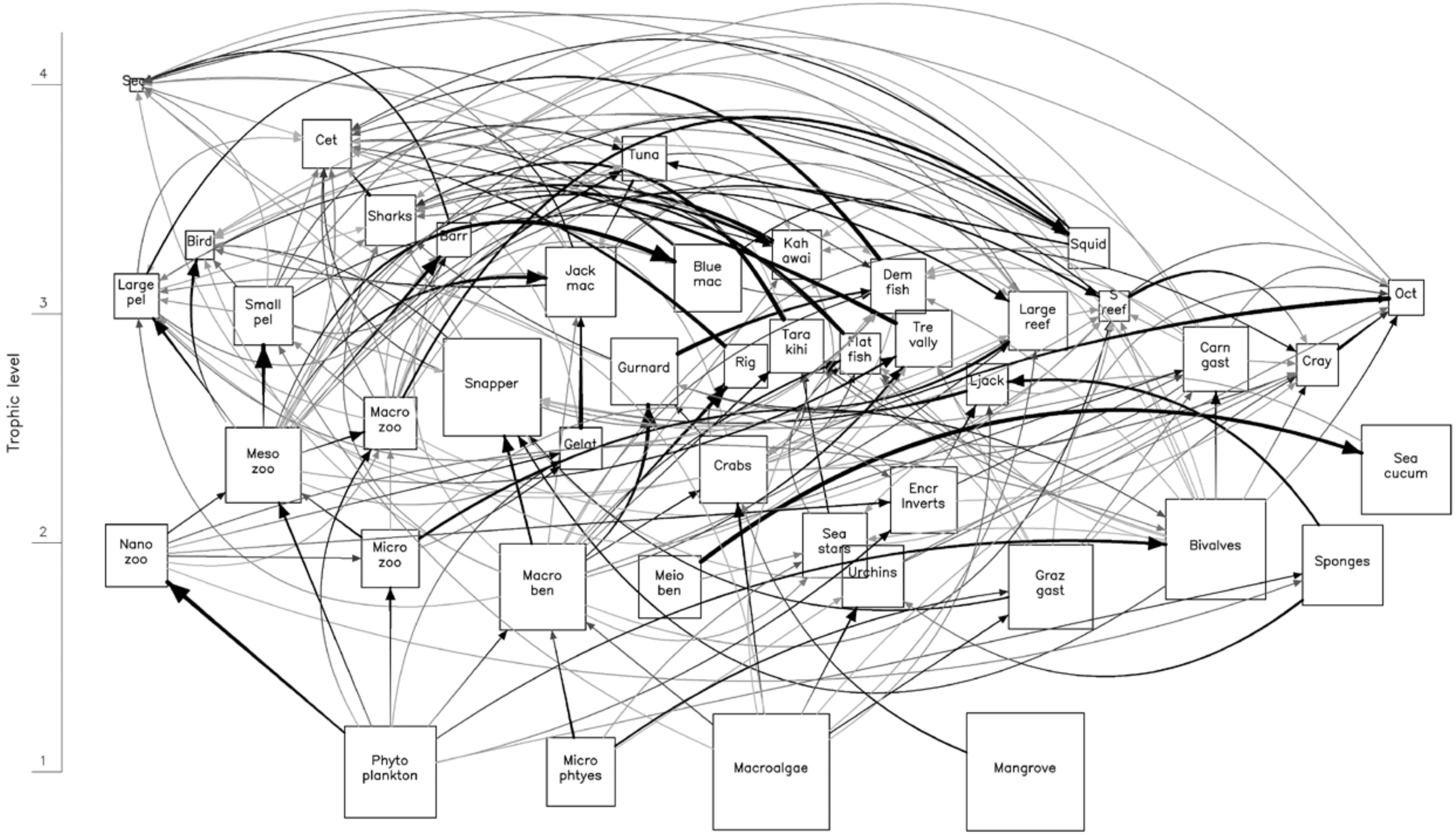


Figure 13: 1500 model; trophic model flow diagram (see Figure 3 caption for more information). Box sizes are consistent with those in Figure 3.

Table 21: 1500 model; biomass, energetic and transfer parameters in the balanced model. Column headings as Table 6. Grey cells indicate that data specific to this period were used to estimate the parameter.

	Group	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Acc A/P	Export X/P	Fishery gC m^{-2} y^{-1}	U	Seasonal T_S/P	Spawn T_R/P	Growth T_G/P	Detritus Fate	Carcass Fate	Seas. Fate	Spawn Fate	Growth Fate
1	Seals	1.2E-04	0.25	52	0.60	0.005	0	0	0	0.20	0	0	0	48	47	0	0	0
2	Birds	4.9E-03	0.33	96	0.43	0.003	0	0.33	1.6E-04	0.30	0	0	0	48	47	0	0	0
3	Cetaceans	5.5E-02	0.019	5.2	0.13	0.004	0	0	1.3E-04	0.20	0	0	0	48	47	0	0	0
4	Crayfish	2.8E-02	1.2	6.5	0.87	0.18	0	0.24	1.7E-04	0.30	0	0.06	0	49	47	0	38	0
5	Crabs	2.2E-01	3.0	11	1.00	0.28	0	0.42	8.0E-05	0.30	0	0.05	0	49	47	0	38	0
6	Seastars	2.0E-01	1.4	5.4	0.99	0.26	0	0	0	0.30	0	0.59	0	49	49	0	38	0
7	Urchins	1.6E-01	0.85	5.6	0.98	0.15	0	0.22	2.0E-04	0.30	0	0.54	0	49	49	0	38	0
8	Gastropods_carnivorous	1.9E-01	1.5	4.8	0.99	0.31	0	0.43	1.3E-05	0.30	0	0.14	0	49	47	0	38	0
9	Gastropods_grazing	6.6E-01	3.6	19	0.98	0.19	0	0.42	2.3E-04	0.30	0	0.18	0	49	47	0	38	0
10	Sea_cucumbers	7.8E-01	0.41	2.1	0.22	0.20	0	0	0	0.30	0	0.10	0	49	49	0	38	0
11	Bivalves	1.5E+00	5.8	29	0.96	0.20	0	0.73	1.6E-03	0.20	0	0.03	0	49	47	0	38	0
12	Sponges	5.4E-01	0.20	0.79	0.95	0.25	0	0	0	0.30	0	0.10	0	49	49	0	38	0
13	Encrusting	2.3E-01	3.4	14	0.85	0.25	0	0.52	0	0.30	0	0.07	0	49	49	0	38	0
14	Macrobenthos	7.2E-01	6.9	28	1.00	0.24	0	0	0	0.30	0	0.10	0	49	49	0	38	0
15	Meiobenthos	1.6E-01	8.1	26	0.98	0.31	0	0	0	0.30	0	0.10	0	49	49	0	38	0
16	Snapper	1.2E+00	0.26	3.0	0.87	0.085	0	0	3.6E-03	0.27	0	0.15	-0.008	48	47	0	38	33
17	Jack_mackerels	2.8E-01	0.37	3.6	0.95	0.10	0	0	1.2E-03	0.27	0	0.12	-0.036	48	47	0	38	33
18	Blue_mackerel	2.4E-01	0.34	3.5	0.95	0.10	0	0	1.1E-04	0.27	0	0.15	-0.022	48	47	0	38	33
19	Gurnard	2.3E-01	0.44	3.9	0.94	0.11	0	0	1.0E-05	0.27	0	0.12	-0.11	48	47	0	14	33
20	Leatherjacket	2.7E-02	0.32	3.2	0.95	0.10	0	0	2.1E-05	0.27	0	0.15	-0.031	48	47	0	14	33
21	Tarakihi	8.3E-02	0.38	4.6	0.96	0.082	0	0	4.0E-06	0.27	0	0.15	-0.011	48	47	0	38	33
22	Kahawai	5.7E-02	0.24	3.1	0.95	0.079	0	0	8.8E-04	0.27	0	0.16	-0.018	48	47	0	38	33
23	Rig	3.2E-02	0.27	2.6	0.95	0.10	0	0	0	0.27	0	0.21	-0.009	48	47	0	33	33
24	Flatfish	2.4E-02	0.46	4.0	0.95	0.11	0	0	4.6E-05	0.27	0	0.14	-0.11	48	47	0	14	33
25	Trevally	1.1E-01	0.24	2.9	0.96	0.082	0	0	2.0E-04	0.27	0	0.16	-0.010	48	47	0	38	33
26	Barracouta	1.1E-02	0.29	3.1	0.93	0.10	0	0	6.3E-04	0.27	0	0.18	-0.019	48	47	0	38	33
27	Skipjack	3.5E-02	0.19	2.9	0.95	0.066	0	0	0	0.27	0	0.26	-0.008	48	47	0	38	33
28	Reef_fish_large	1.3E-01	0.38	4.4	0.95	0.086	0	0	1.6E-04	0.27	0	0.17	-0.051	48	47	0	14	29
29	Reef_fish_small	6.5E-03	0.90	7.4	0.95	0.12	0	0	4.3E-07	0.27	0	0.07	-0.29	48	47	0	14	33
30	Demersal_fish	9.3E-02	0.29	3.3	0.96	0.087	0	0	8.1E-05	0.27	0	0.23	-0.029	48	47	0	38	33
31	Sharks	6.3E-02	0.23	2.8	0.94	0.081	0	0	1.9E-03	0.27	0	0.22	-0.006	48	47	0	33	33
32	Pelagic_fish_large	3.7E-02	0.36	5.0	0.95	0.071	0	0	6.2E-07	0.27	0	0.18	-0.051	48	47	0	38	33
33	Pelagic_fish_small	1.3E-01	1.7	11	0.96	0.16	0	0	0	0.27	0	0.01	0	48	47	0	38	0
34	Squid	2.2E-02	2.7	11	1.00	0.25	0	0	0.0E+00	0.13	0	0.07	0	48	47	0	38	0
35	Octopus	1.2E-02	4.4	10	0.98	0.43	0	0	0.0E+00	0.12	0	0.04	0	48	47	0	38	0
36	Gelatinous	2.8E-02	11	37	0.97	0.29	0	0	0	0.20	0	0	0	48	48	0	0	0
37	Macrozoo	8.7E-02	7.1	24	0.96	0.30	0	0	0	0.30	0	0	0	48	48	0	0	0
38	Mesozoo	4.0E-01	25	83	0.94	0.30	0	0	0	0.30	0	0	0	48	48	0	0	0
39	Microzoo	1.1E-01	75	251	0.95	0.30	0	0	0	0.30	0	0	0	48	48	0	0	0

	Group	B	P/B	Q/B	EE	P/Q	Acc	Export	Fishery	U	Seasonal	Spawn	Growth	Detritus	Carcass	Seas.	Spawn	Growth
		gC m^{-2}	y^{-1}	y^{-1}			A/P	X/P	gC m^{-2} y^{-1}		T_S/P	T_R/P	T_G/P	Fate	Fate	Fate	Fate	Fate
40	Nanozoo	1.8E-01	158	453	0.94	0.35	0	0	0	0.20	0	0	0	48	48	0	0	0
41	Phytoplankton	8.6E-01	156	NA	0.96	NA	0	0	0	0	0	0	0	48	48	0	0	0
42	Macroalgae	2.9E+00	5.2	NA	0.72	NA	0	0.25	0	0	0	0	0	48	48	0	0	0
43	Mangrove_seagrass	3.1E+00	0.17	NA	0.60	NA	0.24	0	0	0	0	0	0	48	48	0	0	0
44	Microphtyes	2.6E-01	21	NA	0.83	NA	0	0	0	0	0	0	0	48	48	0	0	0
45	Bacteria_water	3.2E-01	62	100	0.74	0.62	0	0	0	0	0	0	0	48	48	0	0	0
46	Bacteria_benthic	1.7E+00	9.4	18	0.79	0.52	0	0	0	0	0	0	0	49	49	0	0	0
47	Carcasses	NA	NA	NA	1	NA	0	0	0	0	0	0	0	0	0	0	0	0
48	Detritus_water	NA	NA	NA	1	NA	0	-0.005	0	0	0.29	0	0	0	0	49	0	0
49	Detritus_benthic	NA	NA	NA	1	NA	0.00	0	0	0	0	0	0	0	0	0	0	0

Table 22a: 1500 model; diet parameters in the balanced model for predators 1–21. Figures are the proportions of prey by weight of organic carbon in diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of “0.00” indicate that the diet fraction is between 0 and 0.5%.

		Predators																				
	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Seals	0.00		0.00																		
2	Birds																					
3	Cetaceans																					
4	Crayfish																					
5	Crabs	0.03			0.15												0.00			0.16		0.17
6	Seastars																0.00					0.21
7	Urchins				0.08												0.00					
8	Gastropods_carn		0.01		0.05		0.00		0.01								0.00					0.09
9	Gastropods_graz		0.01		0.16	0.00	0.01		0.11								0.19					0.04
10	Sea_cucumbers						0.03															
11	Bivalves		0.02		0.19	0.01	0.02		0.38								0.29					0.16
12	Sponges							0.05													0.50	
13	Encrusting				0.04	0.01			0.12												0.36	
14	Macrobenthos		0.02		0.23	0.34	0.06		0.20								0.51	0.07		0.81		0.33
15	Meiobenthos						0.07				0.66					0.00						
16	Snapper	0.04	0.13	0.18																		
17	Jack_mackerels	0.19	0.07	0.11																		
18	Blue_mackerel	0.07		0.10																		
19	Gurnard	0.04																				
20	Leatherjacket	0.00															0.00			0.00		
21	Tarakihi	0.02																				
22	Kahawai	0.01																				
23	Rig	0.01		0.02																		

																					Predators
24	Flatfish	0.02		0.01																	
25	Trevally	0.01		0.07																	
26	Barracouta	0.18																			
27	Skipjack																	0.00			
28	Reef_fish_large	0.02															0.00			0.03	
29	Reef_fish_small	0.00			0.02																
30	Demersal_fish	0.02		0.07																	
31	Sharks	0.01		0.03																	
32	Pelagic_fish_large	0.01		0.01																	
33	Pelagic_fish_small	0.07	0.06	0.06													0.01				
34	Squid	0.14	0.00	0.07																	
35	Octopus	0.10				0.02															
36	Gelatinous		0.01	0.03														0.24			
37	Macrozoo		0.54	0.14														0.04	0.04		
38	Mesozoo		0.11	0.08														0.64	0.96		
39	Microzoo											0.10		0.10							
40	Nanozoo											0.07	0.10	0.31							
41	Phytoplankton											0.63	0.20	0.31	0.25						
42	Macroalgae				0.06	0.44		0.42		0.24					0.12						0.13
43	Mangrove_seagrass					0.07															
44	Microphtyes						0.10	0.03		0.16					0.12						
45	Bacteria_water											0.11	0.70	0.29	0.08						
46	Bacteria_benthic							0.25		0.10	0.34				0.30	1.00					
47	Carcasses		0.02		0.02	0.10	0.01		0.17												
48	Detritus_water						0.14					0.08									
49	Detritus_benthic						0.56	0.26		0.50					0.12						

Table 22b: 1500 model; diet parameters in the balanced model for predators 22–45 (primary producers and detritus are not shown). Figures are the proportions of prey by weight of organic carbon in diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of "0.00" indicate that the diet fraction is between 0 and 0.5%.

																						Predator
	Prey	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	45	46
1	Seals																					
2	Birds																					
3	Cetaceans																					
4	Crayfish														0.15							
5	Crabs	0.05	0.30	0.17	0.03				0.07	0.02	0.07	0.03			0.25							
6	Seastars			0.19					0.05	0.00	0.02	0.02										
7	Urchins										0.01				0.07							
8	Gastropods_carnivorous	0.03		0.07	0.01				0.03	0.02	0.03	0.01			0.13							

																						Predator
9	Gastropods_grazing	0.01		0.03	0.02				0.01	0.01	0.01	0.01			0.13							
10	Sea_cucumbers																					
11	Bivalves	0.04		0.11	0.04			0.01	0.05	0.05	0.05	0.02			0.26							
12	Sponges																					
13	Encrusting							0.02														
14	Macrobenthos	0.08	0.70	0.43	0.45	0.05		0.21	0.23	0.23	0.15	0.12										
15	Meiobenthos																					
16	Snapper							0.13	0.04	0.08	0.08											
17	Jack_mackerels							0.02		0.02	0.04											
18	Blue_mackerel							0.03		0.03	0.04											
19	Gurnard									0.25	0.10											
20	Leatherjacket								0.00													
21	Tarakihi										0.14											
22	Kahawai										0.06											
23	Rig																					
24	Flatfish										0.04											
25	Trevally																					
26	Barracouta						0.01															
27	Skipjack	0.00										0.00										
28	Reef_fish_large								0.03	0.01	0.03											
29	Reef_fish_small														0.01							
30	Demersal_fish													0.00								
31	Sharks																					
32	Pelagic_fish_large	0.01				0.04	0.04				0.00											
33	Pelagic_fish_small	0.22				0.19	0.25		0.02	0.00	0.05	0.04		0.11								
34	Squid					0.04	0.27			0.00	0.00	0.02		0.01								
35	Octopus										0.02											
36	Gelatinous							0.02	0.01	0.02		0.09										
37	Macrozoo	0.03			0.02	0.04	0.03	0.03	0.03	0.01		0.04	0.03	0.50			0.01					
38	Mesozoo	0.52			0.43	0.64	0.40	0.41	0.41	0.16	0.05	0.55	0.85	0.38		0.10	0.44	0.20				
39	Microzoo															0.25	0.05	0.09				
40	Nanozoo															0.25	0.05	0.18	0.15	0.15		
41	Phytoplankton															0.20	0.32	0.47	0.40	0.84		
42	Macroalgae							0.12	0.01	0.03		0.07	0.08									
43	Mangrove_seagrass																					
44	Microphtyes																					
45	Bacteria_water															0.10			0.20	0.01		
46	Bacteria_benthic																					
47	Carcasses																					0.00
48	Detritus_water															0.10	0.13	0.05	0.26		1.00	
49	Detritus_benthic									0.04			0.05									1.00

Table 23: 1500 model; key indices for the balanced model, showing respiration quotient (R/B, y^{-1}, shown as a percentage), trophic level (TrL), omnivory index (OI), trophic importance (TI), and the rank of TI, with 1 being most important.

	Group	R/B (%)	TrL	OI	TI	Rank TI
1	Seals	41.5	4.58	0.09	0.32	40
2	Birds	66.5	3.90	0.11	1.77	17
3	Cetaceans	4.1	4.30	0.15	5.18	2
4	Crayfish	3.4	3.18	0.22	1.03	24
5	Crabs	4.6	2.57	0.39	2.74	9
6	Seastars	2.4	2.23	0.23	0.75	32
7	Urchins	3.1	2.06	0.06	0.81	30
8	Gastropods_carn	1.9	3.22	0.04	1.07	23
9	Gastropods_graz	9.9	2.00	0.00	1.88	14
10	Sea_cucumbers	1.0	2.66	0.23	0.73	33
11	Bivalves	17.7	2.21	0.20	3.96	5
12	Sponges	0.36	2.12	0.12	0.50	38
13	Encrusting	6.1	2.48	0.33	0.87	29
14	Macrobenthos	12.8	2.00	0.00	4.63	4
15	Meiobenthos	10.1	2.00	0.00	0.79	31
16	Snapper	1.9	3.08	0.03	3.07	7
17	Jack_mackerels	2.3	3.64	0.04	1.94	12
18	Blue_mackerel	2.2	3.66	0.00	0.72	34
19	Gurnard	2.4	3.14	0.10	2.35	11
20	Leatherjacket	2.0	3.10	0.21	0.42	39
21	Tarakihi	3.0	3.29	0.12	1.02	25
22	Kahawai	2.0	3.77	0.20	0.57	36
23	Rig	1.6	3.17	0.07	0.24	45
24	Flatfish	2.5	3.25	0.11	0.30	41
25	Trevally	1.9	3.34	0.11	0.52	37
26	Barracouta	2.0	3.86	0.19	0.27	43
27	Skipjack	1.9	4.23	0.26	1.17	22
28	Reef_fish_large	2.8	3.42	0.46	1.32	20
29	Reef_fish_small	4.5	3.51	0.19	0.15	46
30	Demersal_fish	2.1	3.58	0.46	2.54	10
31	Sharks	1.8	3.96	0.34	3.08	6
32	Pelagic_fish_large	3.3	3.53	0.29	0.29	42
33	Pelagic_fish_small	6.0	3.45	0.30	1.21	21
34	Squid	6.7	3.85	0.06	0.92	26
35	Octopus	4.7	3.54	0.21	0.90	28
36	Gelatinous	18.9	2.75	0.40	0.69	35
37	Macrozoo	9.5	2.86	0.63	1.80	15
38	Mesozoo	33.4	2.65	0.50	4.77	3
39	Microzoo	100.4	2.17	0.17	1.38	19
40	Nanozoo	204.5	2.17	0.17	1.64	18
41	Phytoplankton	NA	1	NA	5.77	1
42	Macroalgae	NA	1	NA	2.84	8
43	Mangrove_seagrass	NA	1	NA	0.25	44
44	Microphtyes	NA	1	NA	0.91	27
45	Bacteria_water	38.1	1	1.00	1.79	16
46	Bacteria_benthic	8.5	1	1.00	1.91	13
47	Carcasses	NA	2.39	NA	NA	NA
48	Detritus_water	NA	1	NA	NA	NA
49	Detritus_benthic	NA	1	NA	NA	NA

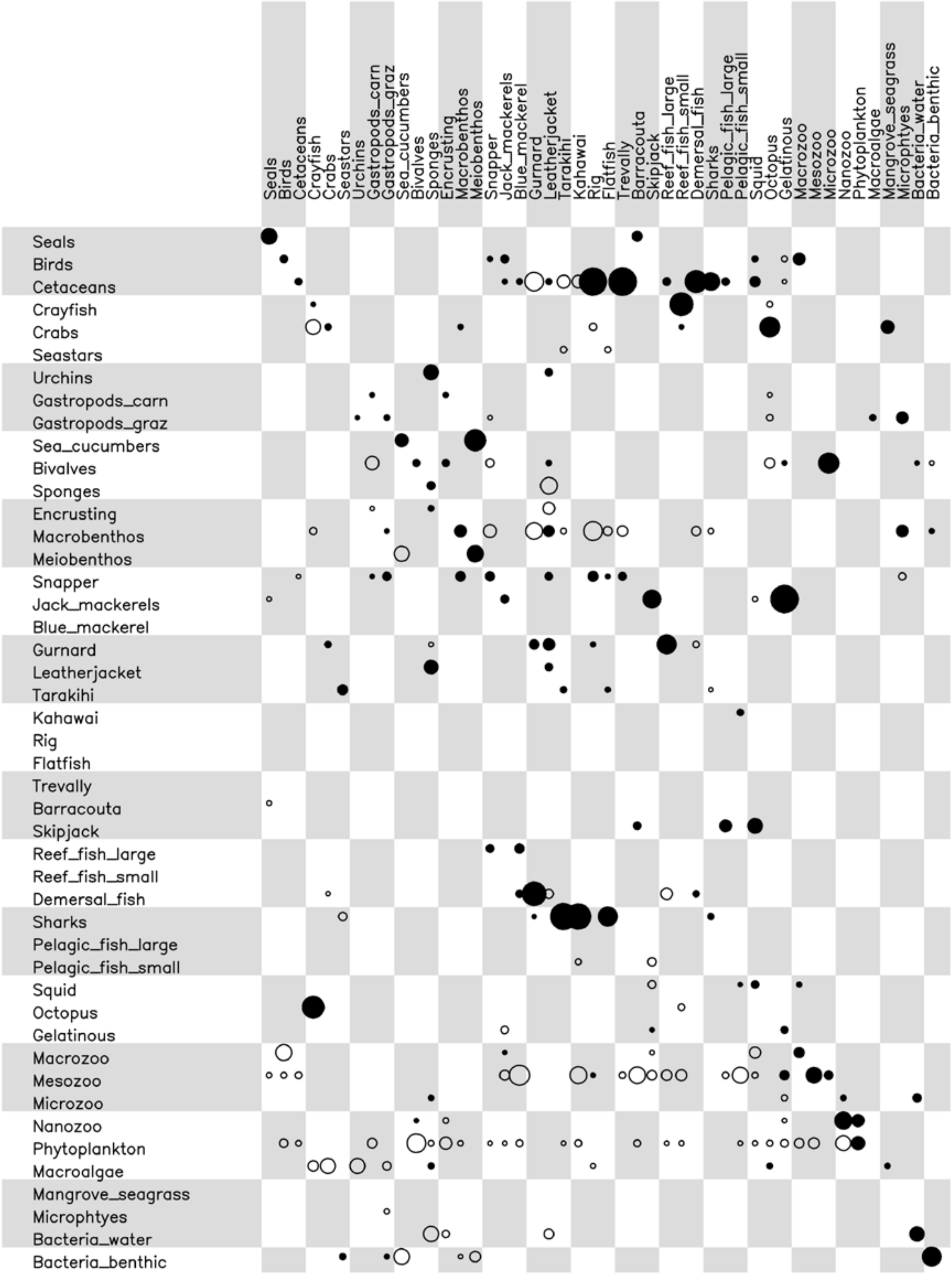


Figure 14: Mixed Trophic Impact Matrix for the 1500 model. Positive impacts are shown black and negative are white, with the diameter of the circle proportional to the magnitude of the effect (scaling consistent with Figure 4).

Table 24: 1000 model; changes to biomass (B), production (P/B), ecotrophic efficiency (EE), growth efficiency (P/Q) and diet fractions (D) during the SVD balancing process (from “initial” to “balanced”). Only changes with an absolute value of more than 10% are shown. Diets are shown: Predator ⟵ Prey.

Parameter	Group	Initial	Balanced	Change (%)
B	Macrobenthos	0.44	0.79	79
B	Gastropods_carn	0.35	0.18	-50
B	Gastropods_graz	0.51	0.69	36
B	Crabs	0.33	0.21	-36
B	Macrozoo	0.08	0.10	28
B	Bacteria_benthic	1.51	1.77	17
B	Squid	0.02	0.02	13
B	Gelatinous	0.03	0.03	13
B	Bivalves	1.34	1.48	11
P/B	None > 9%			
EE	Macroalgae	0.61	0.74	13
EE	Mangrove_seagrass	0.51	0.61	10
P/Q	Bacteria_benthic	0.42	0.48	15
P/Q	Bacteria_water	0.48	0.53	11
D	Snapper⟵Macrobenthos	0.19	0.56	37
D	Snapper⟵Crabs	0.27	0.00	-27
D	Crabs⟵Macroalgae	0.22	0.46	24
D	Gurnard⟵Macrobenthos	0.63	0.84	21
D	Gurnard⟵Crabs	0.33	0.13	-20
D	Cetaceans⟵Rig	0.17	0.01	-16
D	Sharks⟵Tarakihi	0.21	0.05	-16
D	Crabs⟵Bivalves	0.14	0.00	-14
D	Jack_mackerels⟵Mesozoo	0.56	0.68	13
D	Octopus⟵Crayfish	0.03	0.15	12
D	Seals⟵Barracouta	0.15	0.02	-12
D	Sharks⟵Flatfish	0.12	0.00	-12
D	Cetaceans⟵Snapper	0.07	0.18	11
D	Skipjack⟵Squid	0.34	0.24	-10

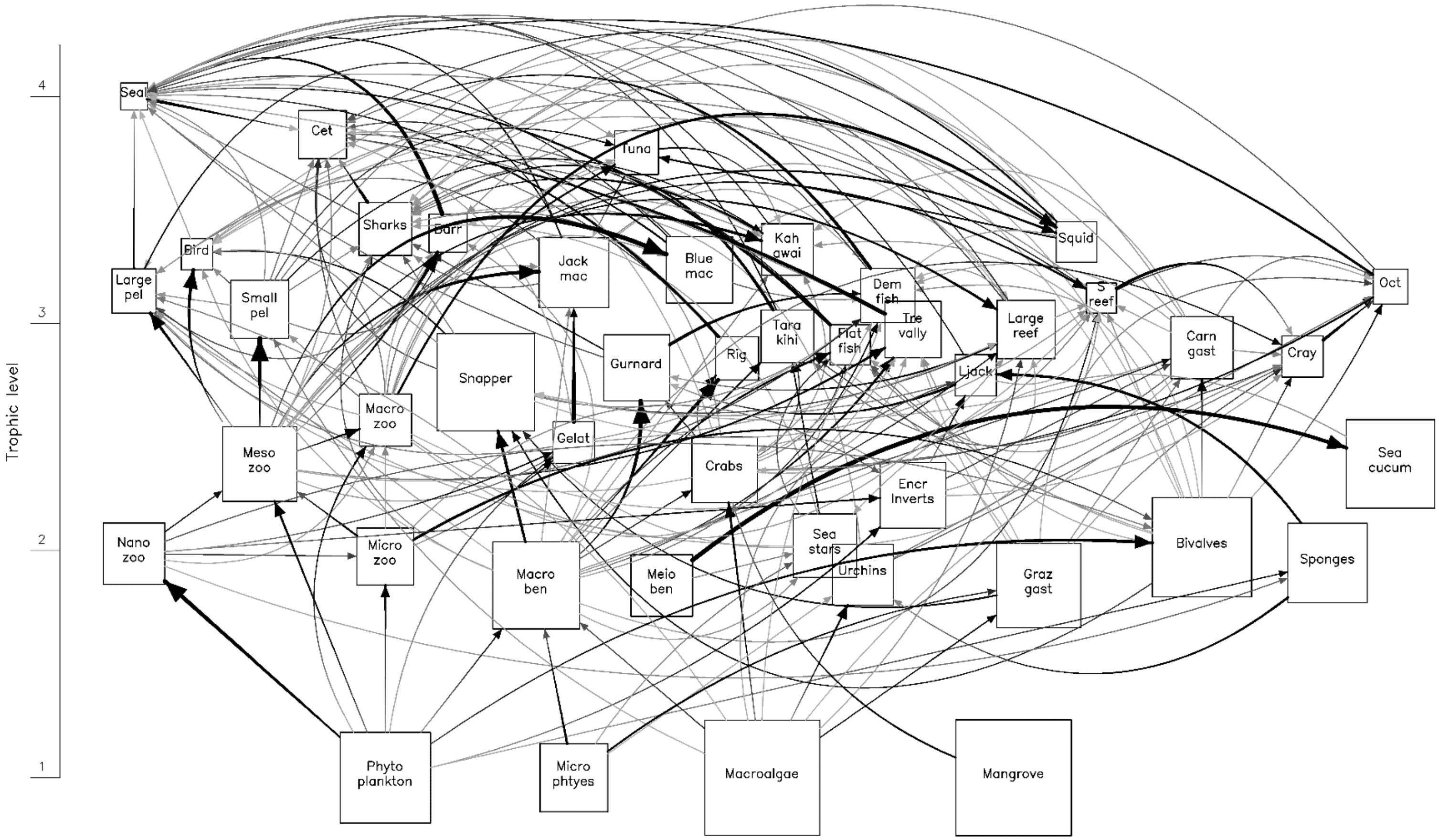


Figure 15: 1000 model; trophic model flow diagram (see Figure 3 caption for more information). Box sizes are consistent with those in Figure 3

Table 25: 1000 model; biomass, energetic and transfer parameters in the balanced model. Column headings as Table 6. Grey cells indicate that data specific to this period were used to estimate the parameter.

	Group	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Acc A/P	Export X/P	Fishery gC m^{-2} y^{-1}	U	Seasonal T_S/P	Spawn T_R/P	Growth T_G/P	Detritus Fate	Carcass Fate	Seas. Fate	Spawn Fate	Growth Fate
1	Seals	4.0E-03	0.25	50	0.61	0.005	0	0	0	0.20	0	0	0	48	47	0	0	0
2	Birds	7.7E-03	0.31	103	0.32	0.003	0	0.24	0.0E+00	0.30	0	0	0	48	47	0	0	0
3	Cetaceans	5.5E-02	0.019	5.2	0.10	0.004	0	0	0.0E+00	0.20	0	0	0	48	47	0	0	0
4	Crayfish	2.8E-02	1.2	6.5	0.87	0.18	0	0.24	0.0E+00	0.30	0	0.06	0	49	47	0	38	0
5	Crabs	2.1E-01	3.0	11	1.00	0.28	0	0.42	0.0E+00	0.30	0	0.05	0	49	47	0	38	0
6	Seastars	2.0E-01	1.4	5.4	0.99	0.26	0	0	0	0.30	0	0.59	0	49	49	0	38	0
7	Urchins	1.6E-01	0.85	5.6	0.98	0.15	0	0.22	0.0E+00	0.30	0	0.54	0	49	49	0	38	0
8	Gastropods_carnivorous	1.8E-01	1.5	4.8	0.99	0.31	0	0.43	0.0E+00	0.30	0	0.14	0	49	47	0	38	0
9	Gastropods_grazing	6.9E-01	3.6	19	0.98	0.19	0	0.42	0.0E+00	0.30	0	0.18	0	49	47	0	38	0
10	Sea_cucumbers	7.8E-01	0.41	2.1	0.22	0.20	0	0	0	0.30	0	0.10	0	49	49	0	38	0
11	Bivalves	1.5E+00	5.8	29	0.96	0.20	0	0.73	0.0E+00	0.20	0	0.03	0	49	47	0	38	0
12	Sponges	5.4E-01	0.20	0.79	0.95	0.25	0	0	0	0.30	0	0.10	0	49	49	0	38	0
13	Encrusting	2.3E-01	3.4	14	0.85	0.25	0	0.52	0	0.30	0	0.07	0	49	49	0	38	0
14	Macrobenthos	7.9E-01	6.9	28	1.00	0.24	0	0	0	0.30	0	0.10	0	49	49	0	38	0
15	Meiobenthos	1.6E-01	8.1	26	0.97	0.31	0	0	0	0.30	0	0.10	0	49	49	0	38	0
16	Snapper	1.3E+00	0.29	3.4	0.90	0.085	0	0	0.0E+00	0.27	0	0.15	-0.008	48	47	0	38	33
17	Jack_mackerels	3.0E-01	0.39	3.8	0.96	0.10	0	0	0.0E+00	0.27	0	0.12	-0.035	48	47	0	38	33
18	Blue_mackerel	2.4E-01	0.35	3.6	0.96	0.10	0	0	0.0E+00	0.27	0	0.15	-0.022	48	47	0	38	33
19	Gurnard	2.3E-01	0.43	3.9	0.95	0.11	0	0	0.0E+00	0.27	0	0.12	-0.11	48	47	0	14	33
20	Leatherjacket	2.7E-02	0.32	3.2	0.95	0.10	0	0	0.0E+00	0.27	0	0.15	-0.031	48	47	0	14	33
21	Tarakihi	8.4E-02	0.28	3.4	0.96	0.082	0	0	0.0E+00	0.27	0	0.15	-0.011	48	47	0	38	33
22	Kahawai	7.5E-02	0.25	3.2	0.96	0.079	0	0	0.0E+00	0.27	0	0.16	-0.017	48	47	0	38	33
23	Rig	3.2E-02	0.26	2.6	0.95	0.10	0	0	0	0.27	0	0.21	-0.009	48	47	0	33	33
24	Flatfish	2.4E-02	0.42	3.7	0.96	0.11	0	0	0.0E+00	0.27	0	0.14	-0.11	48	47	0	14	33
25	Trevally	1.1E-01	0.24	3.0	0.96	0.082	0	0	0.0E+00	0.27	0	0.16	-0.010	48	47	0	38	33
26	Barracouta	1.9E-02	0.30	3.2	0.96	0.10	0	0	0.0E+00	0.27	0	0.18	-0.015	48	47	0	38	33
27	Skipjack	3.5E-02	0.19	2.8	0.95	0.066	0	0	0	0.27	0	0.26	-0.008	48	47	0	38	33
28	Reef_fish_large	1.3E-01	0.38	4.4	0.95	0.086	0	0	0.0E+00	0.27	0	0.17	-0.051	48	47	0	14	29
29	Reef_fish_small	6.5E-03	0.90	7.4	0.95	0.12	0	0	0.0E+00	0.27	0	0.07	-0.29	48	47	0	14	33
30	Demersal_fish	9.3E-02	0.29	3.4	0.96	0.086	0	0	0.0E+00	0.27	0	0.23	-0.029	48	47	0	38	33
31	Sharks	8.5E-02	0.25	3.1	0.95	0.081	0	0	0.0E+00	0.27	0	0.20	-0.005	48	47	0	33	33
32	Pelagic_fish_large	3.7E-02	0.36	5.0	0.95	0.071	0	0	0.0E+00	0.27	0	0.18	-0.051	48	47	0	38	33
33	Pelagic_fish_small	1.3E-01	1.7	11	0.97	0.16	0	0	0	0.27	0	0.01	0	48	47	0	38	0
34	Squid	2.3E-02	2.7	11	1.00	0.25	0	0	0.0E+00	0.13	0	0.07	0	48	47	0	38	0
35	Octopus	1.2E-02	4.4	10	0.98	0.43	0	0	0.0E+00	0.12	0	0.04	0	48	47	0	38	0
36	Gelatinous	2.9E-02	11	37	0.98	0.29	0	0	0	0.20	0	0	0	48	48	0	0	0
37	Macrozoo	9.7E-02	7.2	24	0.98	0.30	0	0	0	0.30	0	0	0	48	48	0	0	0
38	Mesozoo	4.0E-01	25	83	0.94	0.30	0	0	0	0.30	0	0	0	48	48	0	0	0
39	Microzoo	1.2E-01	76	253	0.95	0.30	0	0	0	0.30	0	0	0	48	48	0	0	0

	Group	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Acc A/P	Export X/P	Fishery gC m^{-2} y^{-1}	U	Seasonal T_S/P	Spawn T_R/P	Growth T_G/P	Detritus Fate	Carcass Fate	Seas. Fate	Spawn Fate	Growth Fate
40	Nanozoo	1.8E-01	158	454	0.94	0.35	0	0	0	0.20	0	0	0	48	48	0	0	0
41	Phytoplankton	9.3E-01	168	NA	0.83	NA	0	0	0	0	0	0	0	48	48	0	0	0
42	Macroalgae	2.9E+00	5.2	NA	0.74	NA	0	0.25	0	0	0	0	0	48	48	0	0	0
43	Mangrove_seagrass	3.0E+00	0.17	NA	0.61	NA	0.24	0	0	0	0	0	0	48	48	0	0	0
44	Microphtyes	2.6E-01	21	NA	0.83	NA	0	0	0	0	0	0	0	48	48	0	0	0
45	Bacteria_water	3.7E-01	66	124	0.71	0.53	0	0	0	0	0	0	0	48	48	0	0	0
46	Bacteria_benthic	1.8E+00	9.7	20	0.78	0.48	0	0	0	0	0	0	0	49	49	0	0	0
47	Carcasses	NA	NA	NA	1	NA	0	0	0	0	0	0	0	0	0	0	0	0
48	Detritus_water	NA	NA	NA	1	NA	0	-0.005	0	0	0.36	0	0	0	0	49	0	0
49	Detritus_benthic	NA	NA	NA	1	NA	0.07	0	0	0	0	0	0	0	0	0	0	0

Table 26a: 1000 model; diet parameters in the balanced model for predators 1–21. Figures are the proportions of prey by weight of organic carbon in diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of "0.00" indicate that the diet fraction is between 0 and 0.5%.

		Predators																				
	Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Seals			0.00																		
2	Birds	0.00																				
3	Cetaceans			0.00																		
4	Crayfish																					
5	Crabs	0.04			0.15												0.00			0.13		0.17
6	Seastars																0.00					0.23
7	Urchins				0.08												0.00					
8	Gastropods_carn		0.01		0.05		0.00		0.01								0.00					0.09
9	Gastropods_graz		0.01		0.16	0.00	0.00		0.11								0.17					0.04
10	Sea_cucumbers						0.04															
11	Bivalves		0.02		0.19	0.00	0.01		0.37								0.26					0.15
12	Sponges							0.05													0.50	
13	Encrusting				0.04	0.02			0.13												0.36	
14	Macrobenthos		0.03		0.23	0.32	0.05		0.20								0.56	0.07		0.84		0.32
15	Meiobenthos						0.07				0.66					0.00						
16	Snapper	0.09	0.13	0.18																		
17	Jack_mackerels	0.17	0.02	0.12																		
18	Blue_mackerel	0.10		0.11																		
19	Gurnard	0.06																				
20	Leatherjacket	0.01															0.00			0.01		
21	Tarakihi	0.03																				
22	Kahawai	0.02																				
23	Rig	0.02		0.01																		
24	Flatfish	0.04		0.01																		

																					Predators
25	Trevally	0.01		0.07																	
26	Barracouta	0.02																			
27	Skipjack																	0.00			
28	Reef_fish_large	0.04															0.00			0.02	
29	Reef_fish_small	0.01			0.01																
30	Demersal_fish	0.02		0.06																	
31	Sharks	0.01		0.05																	
32	Pelagic_fish_large	0.02		0.00																	
33	Pelagic_fish_small	0.06	0.03	0.07													0.00				
34	Squid	0.10	0.00	0.04																	
35	Octopus	0.12				0.01															
36	Gelatinous		0.02	0.04														0.22			
37	Macrozoo		0.54	0.16														0.02	0.02		
38	Mesozoo		0.15	0.09														0.68	0.98		
39	Microzoo											0.11		0.10							
40	Nanozoo											0.07	0.10	0.31							
41	Phytoplankton											0.61	0.20	0.31	0.25						
42	Macroalgae				0.07	0.46		0.42		0.23					0.11						0.14
43	Mangrove_seagrass					0.08															
44	Microphtyes						0.10	0.02		0.16					0.11						
45	Bacteria_water											0.13	0.70	0.29	0.09						
46	Bacteria_benthic							0.25		0.11	0.34				0.31	1.00					
47	Carcasses		0.03		0.02	0.12	0.01		0.18												
48	Detritus_water						0.14					0.08									
49	Detritus_benthic						0.57	0.26		0.50					0.12						

Table 26b: 1000 model; diet parameters in the balanced model for predators 22–45 (primary producers and detritus are not shown). Figures are the proportions of prey by weight of organic carbon in diet of each predator. Predators are shown as columns and prey as rows. Columns sum to 1. Entries of “0.00” indicate that the diet fraction is between 0 and 0.5%.

																						Predator
	Prey	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	45	46
1	Seals																					
2	Birds																					
3	Cetaceans																					
4	Crayfish														0.15							
5	Crabs	0.05	0.30	0.17	0.02				0.07	0.03	0.09	0.02			0.25							
6	Seastars			0.19					0.05	0.01	0.02	0.02										
7	Urchins									0.00	0.02	0.00			0.07							
8	Gastropods_carnivorous	0.03		0.07	0.01				0.03	0.03	0.04	0.01			0.13							
9	Gastropods_grazing	0.01		0.03	0.02				0.01	0.01	0.02	0.01			0.13							
10	Sea_cucumbers																					

																						Predator
11	Bivalves	0.04		0.11	0.04			0.01	0.05	0.05	0.06	0.02			0.26							
12	Sponges																					
13	Encrusting							0.02														
14	Macrobenthos	0.09	0.70	0.43	0.45	0.06		0.23	0.23	0.26	0.18	0.12										
15	Meiobenthos																					
16	Snapper							0.10	0.04	0.07	0.10											
17	Jack_mackerels							0.00		0.02	0.05											
18	Blue_mackerel							0.00		0.02	0.04											
19	Gurnard									0.18	0.10											
20	Leatherjacket								0.00	0.00												
21	Tarakihi										0.05											
22	Kahawai										0.04											
23	Rig																					
24	Flatfish										0.00											
25	Trevally																					
26	Barracouta						0.00															
27	Skipjack	0.00										0.00										
28	Reef_fish_large								0.03	0.01	0.03											
29	Reef_fish_small														0.00							
30	Demersal_fish													0.00								
31	Sharks																					
32	Pelagic_fish_large	0.00				0.03	0.04															
33	Pelagic_fish_small	0.19				0.18	0.26		0.02	0.00	0.06	0.04		0.10								
34	Squid					0.03	0.24			0.00		0.00		0.00								
35	Octopus										0.03											
36	Gelatinous							0.02	0.01	0.03		0.09										
37	Macrozoo	0.03			0.02	0.04	0.03	0.02	0.03	0.01		0.04	0.00	0.49			0.00					
38	Mesozoo	0.55			0.44	0.66	0.43	0.46	0.41	0.18	0.06	0.57	0.87	0.41		0.10	0.44	0.19				
39	Microzoo															0.25	0.05	0.10				
40	Nanozoo															0.25	0.05	0.19	0.14	0.15		
41	Phytoplankton															0.20	0.33	0.47	0.38	0.83		
42	Macroalgae							0.14	0.01	0.04		0.07	0.08									
43	Mangrove_seagrass																					
44	Microphtyes																					
45	Bacteria_water															0.10			0.22	0.03		
46	Bacteria_benthic																					
47	Carcasses																					0.00
48	Detritus_water															0.10	0.13	0.06	0.26		1.00	
49	Detritus_benthic									0.05			0.05									1.00

Table 27: 1000 model; key indices for the balanced model, showing respiration quotient (R/B, y^{-1}, shown as a percentage), trophic level (TrL), omnivory index (OI), trophic importance (TI), and the rank of TI, with 1 being most important.

	Group	R/B (%)	TrL	OI	TI	Rank TI
1	Seals	39.6	4.44	0.09	4.60	5
2	Birds	71.6	3.81	0.08	1.74	16
3	Cetaceans	4.1	4.24	0.15	4.65	3
4	Crayfish	3.4	3.16	0.21	0.92	25
5	Crabs	4.6	2.53	0.35	2.11	10
6	Seastars	2.4	2.22	0.22	0.77	31
7	Urchins	3.1	2.06	0.06	0.82	29
8	Gastropods_carn	1.8	3.21	0.04	1.01	23
9	Gastropods_graz	10.0	2.00	0.00	1.85	15
10	Sea_cucumbers	1.0	2.66	0.23	0.72	35
11	Bivalves	17.7	2.21	0.20	3.91	6
12	Sponges	0.36	2.12	0.12	0.51	38
13	Encrusting	6.1	2.47	0.33	0.86	27
14	Macrobenthos	12.9	2.00	0.00	4.60	4
15	Meiobenthos	10.1	2.00	0.00	0.76	32
16	Snapper	2.2	3.06	0.01	2.83	7
17	Jack_mackerels	2.4	3.63	0.04	2.05	11
18	Blue_mackerel	2.3	3.64	0.00	0.78	30
19	Gurnard	2.4	3.10	0.07	2.01	12
20	Leatherjacket	2.0	3.10	0.21	0.45	39
21	Tarakihi	2.2	3.28	0.12	0.76	33
22	Kahawai	2.1	3.73	0.18	0.67	36
23	Rig	1.6	3.16	0.06	0.20	45
24	Flatfish	2.3	3.24	0.11	0.32	41
25	Trevally	1.9	3.33	0.11	0.43	40
26	Barracouta	2.0	3.82	0.17	0.30	42
27	Skipjack	1.9	4.16	0.25	0.90	26
28	Reef_fish_large	2.8	3.31	0.38	0.73	34
29	Reef_fish_small	4.5	3.49	0.18	0.14	46
30	Demersal_fish	2.2	3.47	0.44	1.73	17
31	Sharks	2.0	3.83	0.36	2.70	8
32	Pelagic_fish_large	3.3	3.49	0.26	0.30	43
33	Pelagic_fish_small	6.0	3.42	0.31	1.14	22
34	Squid	6.7	3.82	0.05	0.95	24
35	Octopus	4.7	3.53	0.21	1.24	21
36	Gelatinous	19.0	2.75	0.39	0.62	37
37	Macrozoo	9.6	2.84	0.62	1.71	18
38	Mesozoo	33.4	2.64	0.48	4.94	2
39	Microzoo	101.2	2.17	0.17	1.33	19
40	Nanozoo	204.8	2.17	0.17	1.30	20
41	Phytoplankton	NA	1	NA	6.71	1
42	Macroalgae	NA	1	NA	2.64	9
43	Mangrove_seagrass	NA	1	NA	0.21	44
44	Microphtyes	NA	1	NA	0.85	28
45	Bacteria_water	57.8	1	1.00	1.95	13
46	Bacteria_benthic	10.6	1	1.00	1.94	14
47	Carcasses	NA	2.35	NA	NA	NA
48	Detritus_water	NA	1	NA	NA	NA
49	Detritus_benthic	NA	1	NA	NA	NA

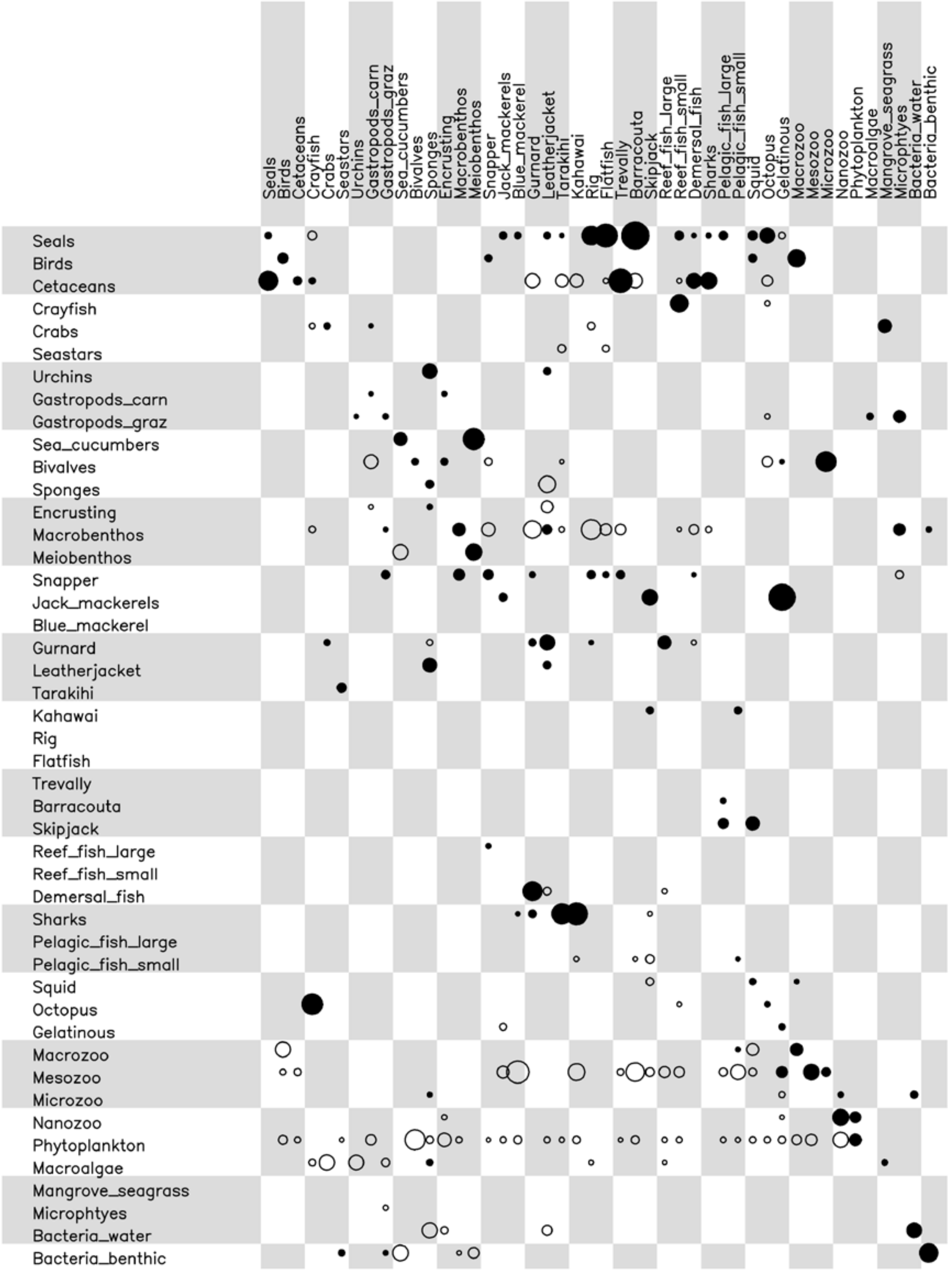


Figure 16: Mixed Trophic Impact Matrix for the 1000 model. Positive impacts are shown black and negative are white, with the diameter of the circle proportional to the magnitude of the effect (scaling consistent with Figure 4).

1.1.8 Changes to ecosystem flows over time

Changes in ecosystem properties over time in the models are shown in Table 28. Total net primary production, total system production and flows to detritus (P_0), total system consumption (Q_0), P_0/Q_0 and total detrital inflow did not change substantially over the period modeled. This is because these properties are largely dependent on the lower part of the food web (primary producers, micro- and nano-zooplankton and bacteria) which were estimated to have remained relatively constant between 1000 and the present day. There was a 16% decrease in the flux of detritus from the water column to the benthos between 1950 and the present day in the models, but this figure was poorly constrained by the available data. Similarly, changes in accumulation (long term sequestration) rates of carbon by the Hauraki Gulf ecosystem did not change substantially over the period modeled, but again, these results should be treated with caution as they were poorly constrained by the available data.

Table 28: Key properties of the system at different periods in history in the balanced trophic models. Q_0=All consumption in the model; P_0=all production and flows of material to detritus in the model.

Index	Units	1000	1500	1790	1950	Present
Primary production	gC m^{-2} y^{-1}	177	156	168	184	186
Q_0/P_0	…	0.96	0.96	0.96	0.95	0.95
Total detrital inflow	gC m^{-2} y^{-1}	110	84	101	118	118
Detrital flux from water column to benthos	gC m^{-2} y^{-1}	22	13	18	25	20
Accumulation of carbon						
By burial or organic carbon in sediments	gC m^{-2} y^{-1}	3.3	0.0	1.5	6.2	7.0
By accumulation of mangrove biomass	gC m^{-2} y^{-1}	0.1	0.1	0.1	0.2	0.3
Accumulation of inorganic C in shells/skeletons	gC m^{-2} y^{-1}	8.2	8.0	8.0	7.7	8.7
All accumulation carbon	MtC y^{-1}	0.19	0.13	0.16	0.23	0.26
Proportion of consumers by Biomass (B)						
Air-breathing predators	%	0.6	0.5	0.5	0.0	0.0
Benthic invertebrates	%	47.5	48.4	48.3	50.6	58.2
Fish	%	25.7	25.5	24.9	21.2	11.6
Cephalopods	%	0.3	0.3	0.3	0.3	0.4
Macrozooplankton	%	1.1	1.0	1.0	1.0	1.1
Mesozooplankton	%	3.5	3.6	3.6	4.0	4.4
Nano and micro zooplankton	%	2.6	2.7	2.7	3.0	3.4
Bacteria	%	18.7	17.9	18.8	19.8	20.8
Proportion of consumption (Q)						
Air breathing predators	%	0.4	0.2	0.2	0.1	0.1
Benthic invertebrates	%	27.8	29.1	27.8	24.8	25.3
Fish	%	3.3	3.3	3.3	2.6	1.6
Cephalopods	%	0.1	0.1	0.1	0.1	0.1
Macrozooplankton	%	1.0	1.0	0.9	0.8	0.8
Mesozooplankton	%	9.9	10.7	10.1	10.1	10.0
Nano and micro zooplankton	%	33.1	35.6	34.8	35.1	35.4
Bacteria	%	24.4	19.8	22.8	26.4	26.7
Mean Trophic level						
All		3.08	3.11	3.10	3.12	3.15
Fish (average by fish groups)		3.46	3.50	3.54	3.55	3.60
Fish (average weighted by biomass)		3.29	3.32	3.33	3.45	3.55

1.1.9 Changes of biomass over time

There are clear changes over time in the relative magnitudes of biomass and consumption in the ecosystem due to different types of biota (Figure 17). Air-breathing predators become much less abundant between 1000 and the present day (94% decline in biomass, 77% decline in consumption). Indeed, biomasses of air breathing predators changed by the greatest amount of any groups, with large changes taking place between 1000 and 1500 (seals) and between 1790 and 1950 (cetaceans).

Fishes in the models decreased by 64% (biomass) and 52% (consumption) between 1000 and the present day, consistent with fishing reducing stock sizes. The smaller reduction in consumption than biomass for fish is due to greater reductions of larger species of fish that have lower consumption rates per unit biomass. Most of the change in the fish biomass occurred between 1950 and the present day, consistent with the development of industrial-scale fisheries over this period and management to reduce biomass to a level that supports maximum sustainable yield (often assessed as 30–40% of unfished biomass in a single-species context). All fish groups declined in biomass between 1000 and the present (Figure 17), but the decline in biomass of some fish groups was greater than others. The highest decreases were for snapper (83% decrease), trevally (86% decrease), and sharks (86% decrease). Barracouta is the only fish group that had its lowest biomass in any period other than the present day (45% decrease from 1000 to 1500; 28% decrease from 1000 to present day) because of the estimated harvest of barracouta in the historical period (Smith, 2011). Changes to biomasses of fish stocks were estimated using population modelling based on catch histories assembled from recent and historical information (see Appendix 5).

Rock lobster also showed a substantial decline in biomass, between 1790 and 1950, and again to the present day. Present day biomass of rock lobster was estimated to have reduced by 76% between 1000 and the present day. Biomass of benthic megafauna (individuals larger than 2 mm) decreased by 6% on average between 1000 and the present in the models. Some groups of benthic mega-invertebrates increased in abundance in the models between 1000 and the present day, especially carnivorous gastropods (approximately doubled) and crabs (increase of 56%). The biomass of macrobenthic invertebrates decreased by 44% between 1000 and the present day in the models.

In the models, squid biomass decreased by 11% from 1000 to the present. Gelatinous zooplankton had small changes prior to 1950, but declined in biomass from 1950 to the present by 8%. There were no major changes in the biomasses of smaller zooplankton in the models, despite the changes to primary productivity. Primary production in the models increased by 18% in the period between 1500 (which had the lowest PP in the models) and the present day. This increase in PP to the present day was due to changes in phytoplankton production. The change in PP by phytoplankton between models was less than estimated *a priori* because phytoplankton PP in the present day model was reduced during model balancing to be consistent with estimated consumption rates of microbial grazers. The biomass of benthic bacteria in the models decreased by 15% and that of bacteria in the water column increased by 9% between 1000 and the present day.

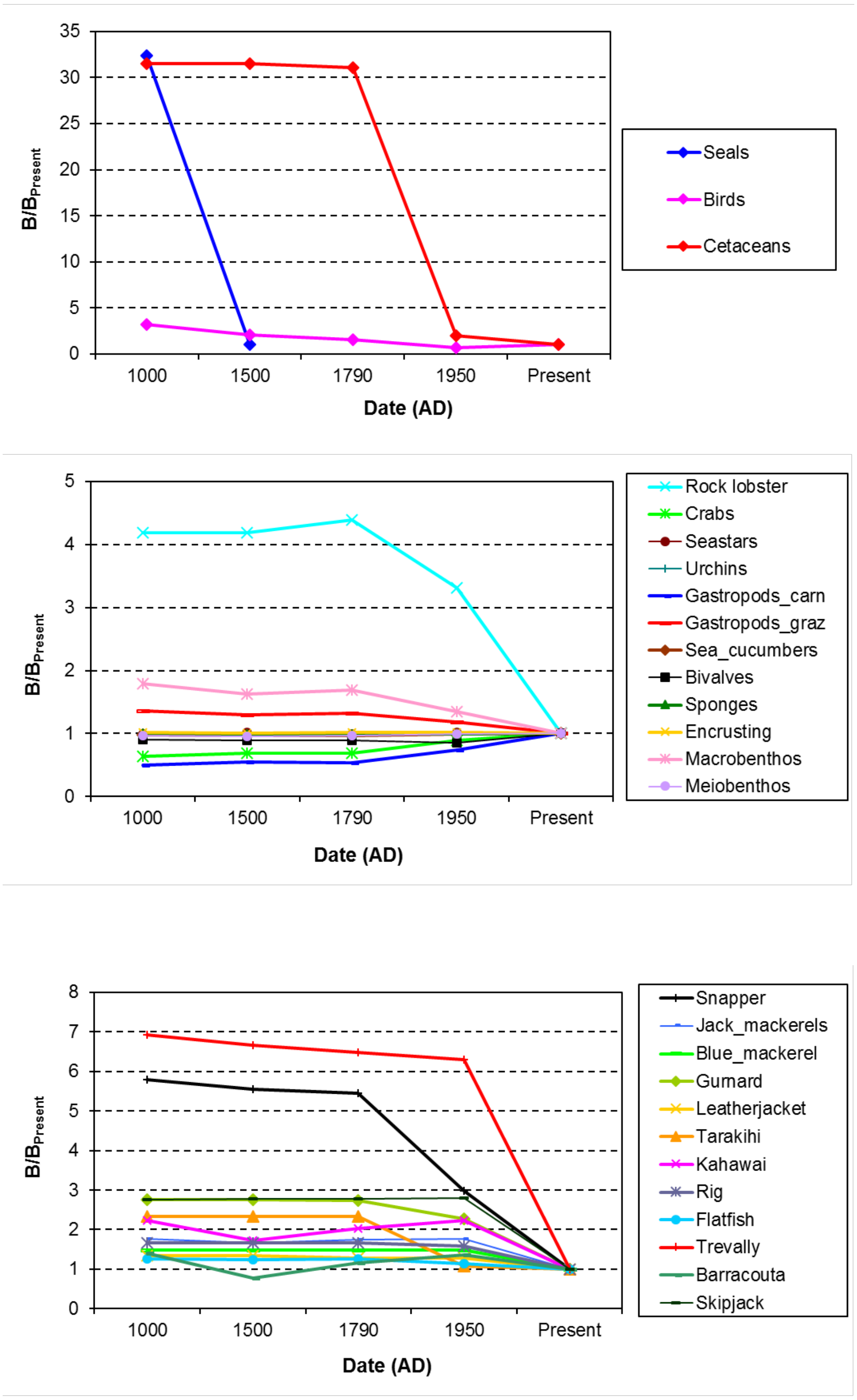


Figure 17a: Changes to biomass in the balanced trophic models. Except for seals, the y-axis shows the ratio of the biomass at a given point in history to that at the present day. For seals, the y-axis is the biomass at a given point in history to that in 1500 as there are no seals in any more recent models.

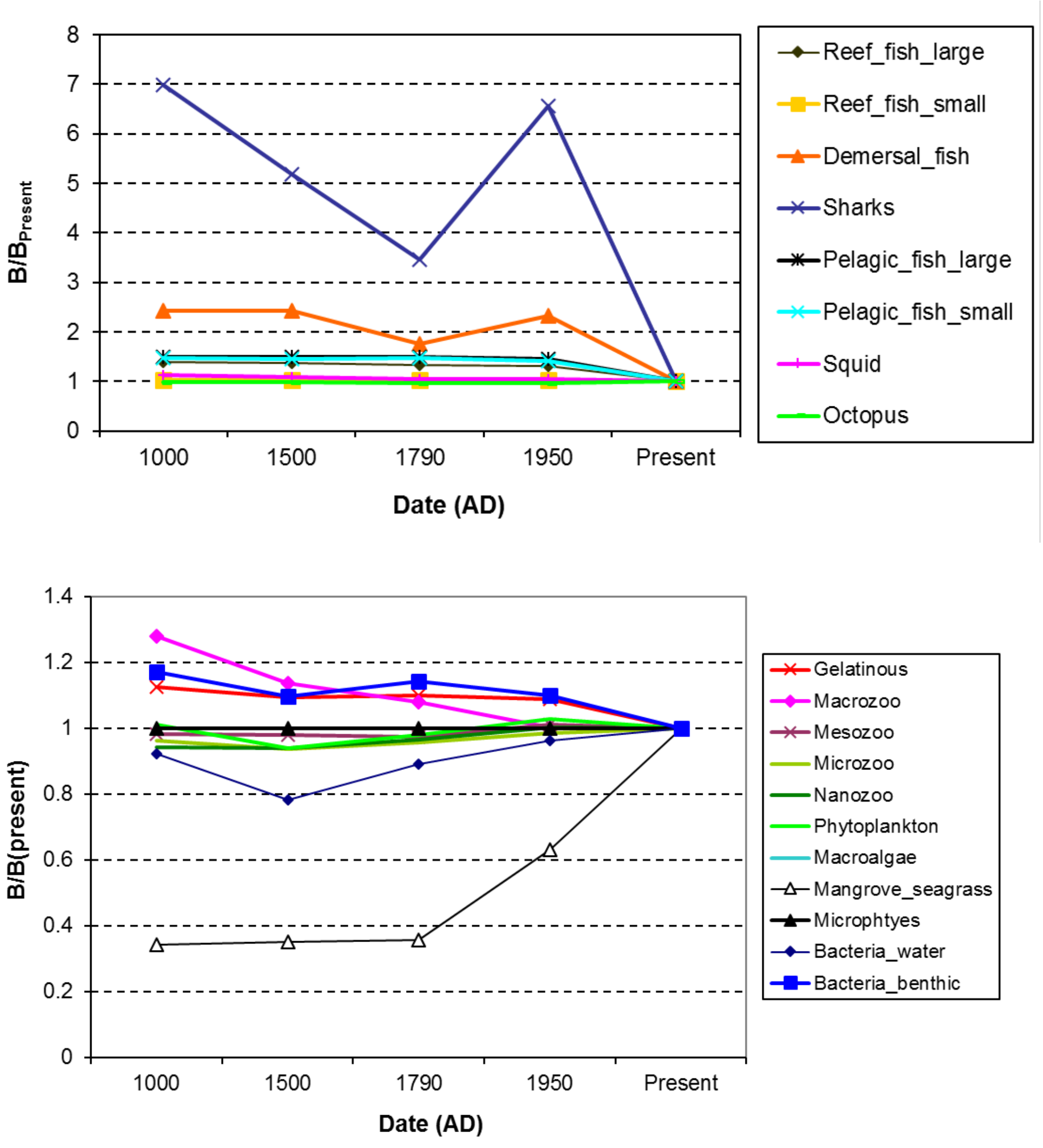


Figure 17b: Changes to biomass in the balanced trophic models continued. The y-axis shows the ratio of the biomass at a given point in history to that at the present day.

1.1.10 Changes of diet over time

In the models, 19 diet fractions changed by more than 10% from the present day in one or more of the historical models (Figure 18), and some of these changes are hard to interpret. Snapper became less important as a prey item for birds between 1000 and the present (being replaced by more consumption of squid). There was a negligible change (less than 1%) in the proportion of carcasses (which include fishing discards and offal) in the diet of birds between 1950 and the present day. Snapper was more important as a prey item for cetaceans historically than at the present day (especially in 1950 when cetacean biomass was low and snapper biomass relatively high). The models suggest that rig now makes up a larger proportion of the diet of cetaceans than historically. In the models, crabs have progressively consumed less macroalgae and more bivalves between 1000 and the present. The models suggested that the diet of snapper may have changed over the same period, with increasing consumption of crabs and decreasing consumption of macrobenthic invertebrates. Gurnard diet in the models changed similarly, with more consumption of crabs and less consumption of macrobenthos. The diet of jack mackerels in the more recent models had less consumption of mesozooplankton than historically. Consumption of squid by tuna increased over time in the models. The models suggest that sharks replaced snapper in their diet with flatfish and tarakihi, especially between 1950 and the present day. Consumption of rock lobster (crayfish) by octopus has reduced over time in the models as a result of lower biomass of lobster.

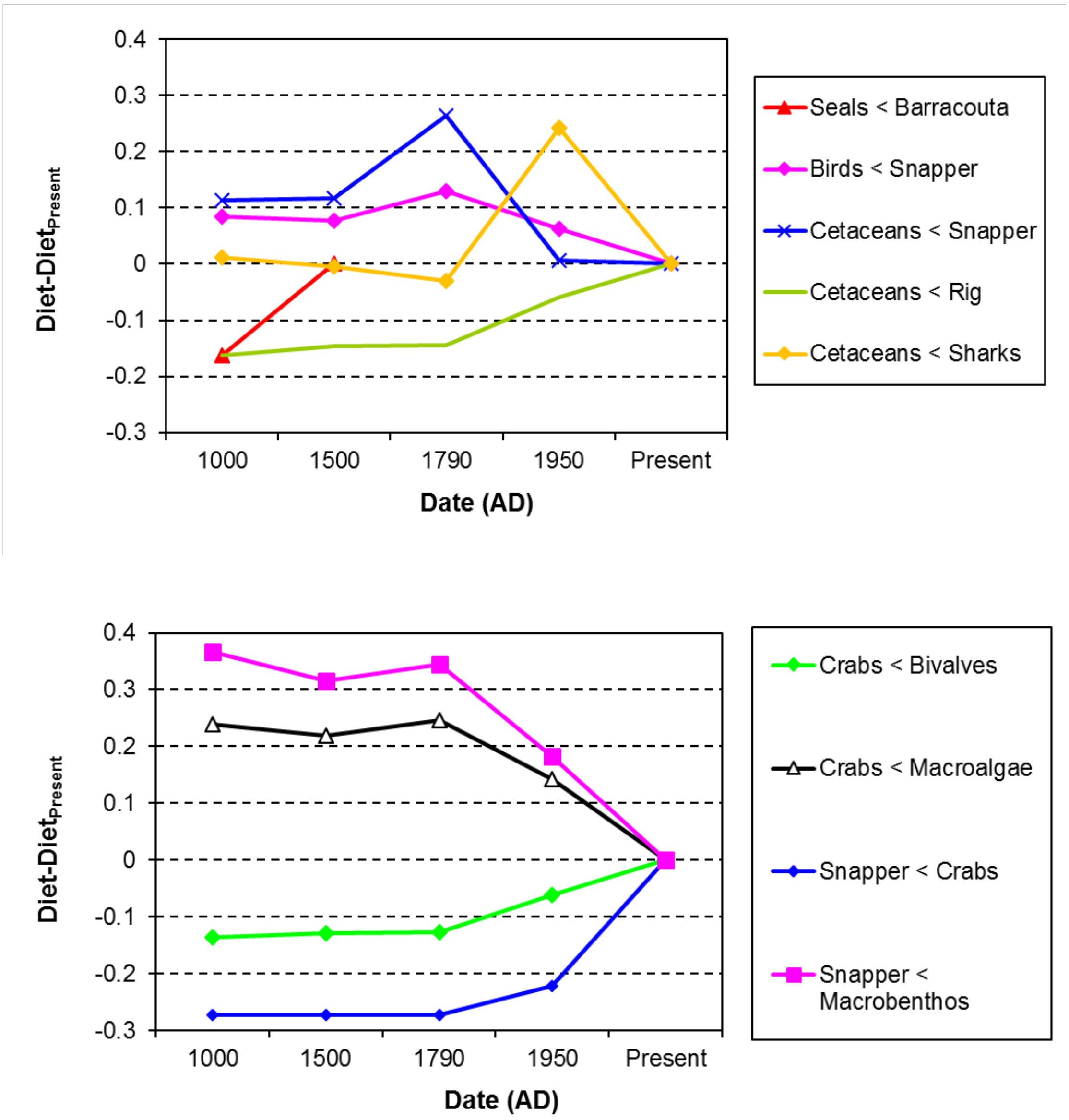
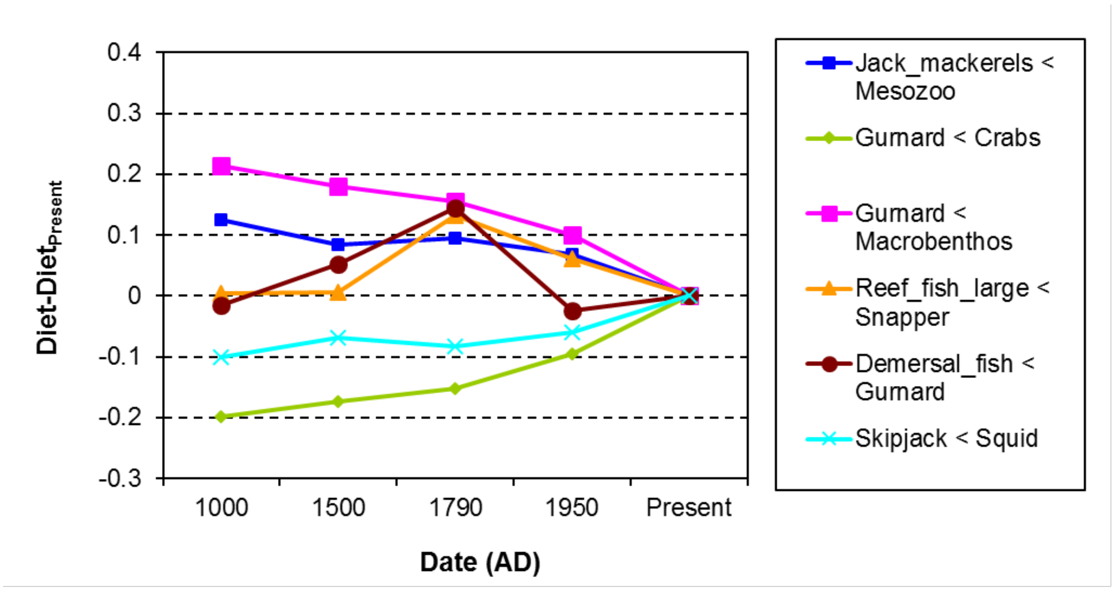


Figure 18a: Changes to diet fraction in the balanced trophic models. The y-axis shows the ratio of the diet fraction at a given point in history to that at the present day.



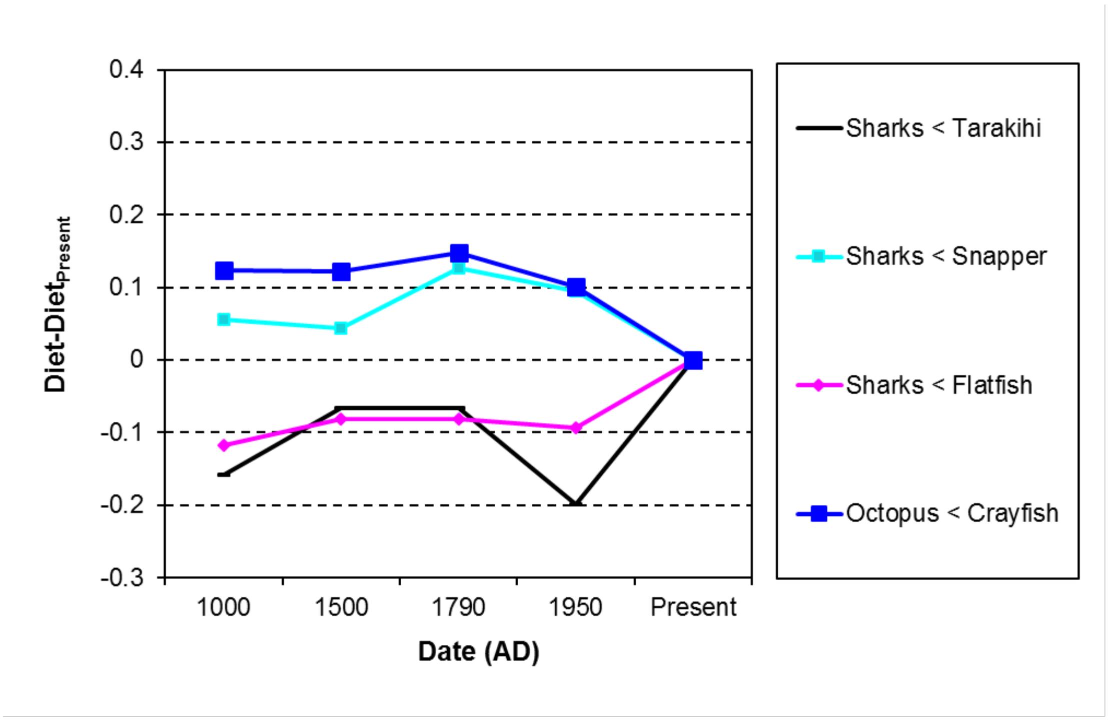


Figure 18b: Changes to diet fraction in the balanced trophic models (continued). The y-axis shows the ratio of the diet fraction at a given point in history to that at the present day.

1.1.11 Changes of trophic level over time

Figure 19 shows that trophic levels (TrL) of almost all organisms in the Hauraki Gulf models have increased from 1000 to the present, with larger increases tending to occur for higher trophic level organisms than lower trophic level organisms. Sharks and snapper showed the largest increase in TrL from 1000 to the present day, of 0.37 and 0.36 respectively. The models suggested that there was a similar total amount of food available in the past but because there were substantially more consumers in the past (especially air breathing predators and fish), most predators were likely to feed at a slightly lower trophic level historically than at the present day. Between 1000 and the present day, the same amount of primary production must be divided between progressively fewer high trophic level predators so that each predator can feed on slightly higher trophic level prey. We did not test the alternative hypothesis that diets (and hence trophic levels) are constant historically. This assumption would require there to be some “spare” (unconsumed) in the present day. The former explanation also has some empirical support; it seems that New Zealand sea lions may feed on smaller prey when predator population is at carrying capacity; average prey size (and hence trophic level) of teleost fishes by New Zealand sea lions at Otago (colonising population) is 0.5–1 kg, about a magnitude higher than at Auckland Islands where the population is at carrying capacity (Lalas 1997; Augé et al. 2012).

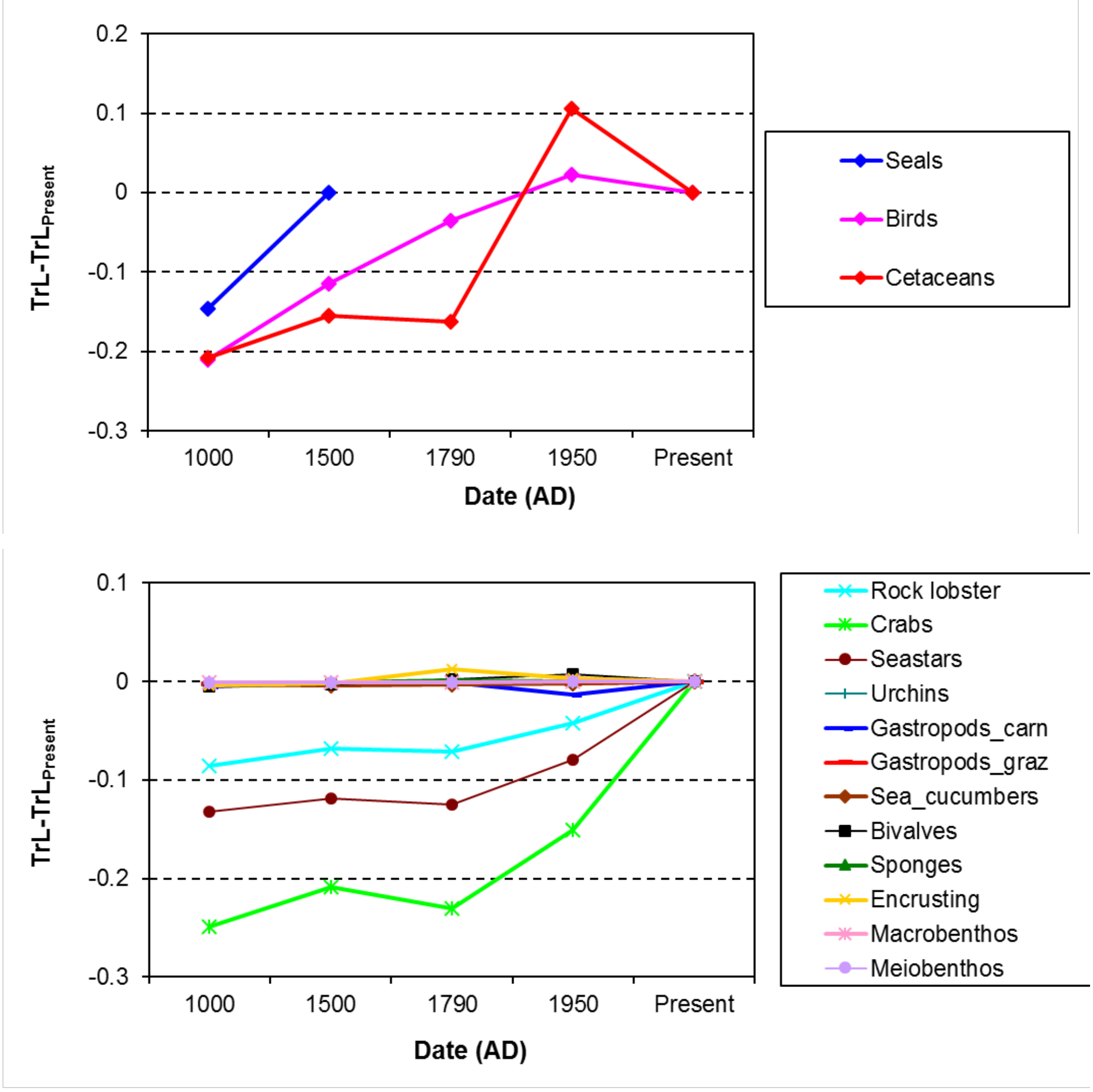


Figure 19a: Changes to Trophic Level (TrL) in the balanced trophic models. Except for seals, the y-axis shows the difference between TrL at a given point in history and that at the present day. For seals, the y-axis is the difference between the TrL at a given point in history and that in 1500 as there are no seals in any later models.

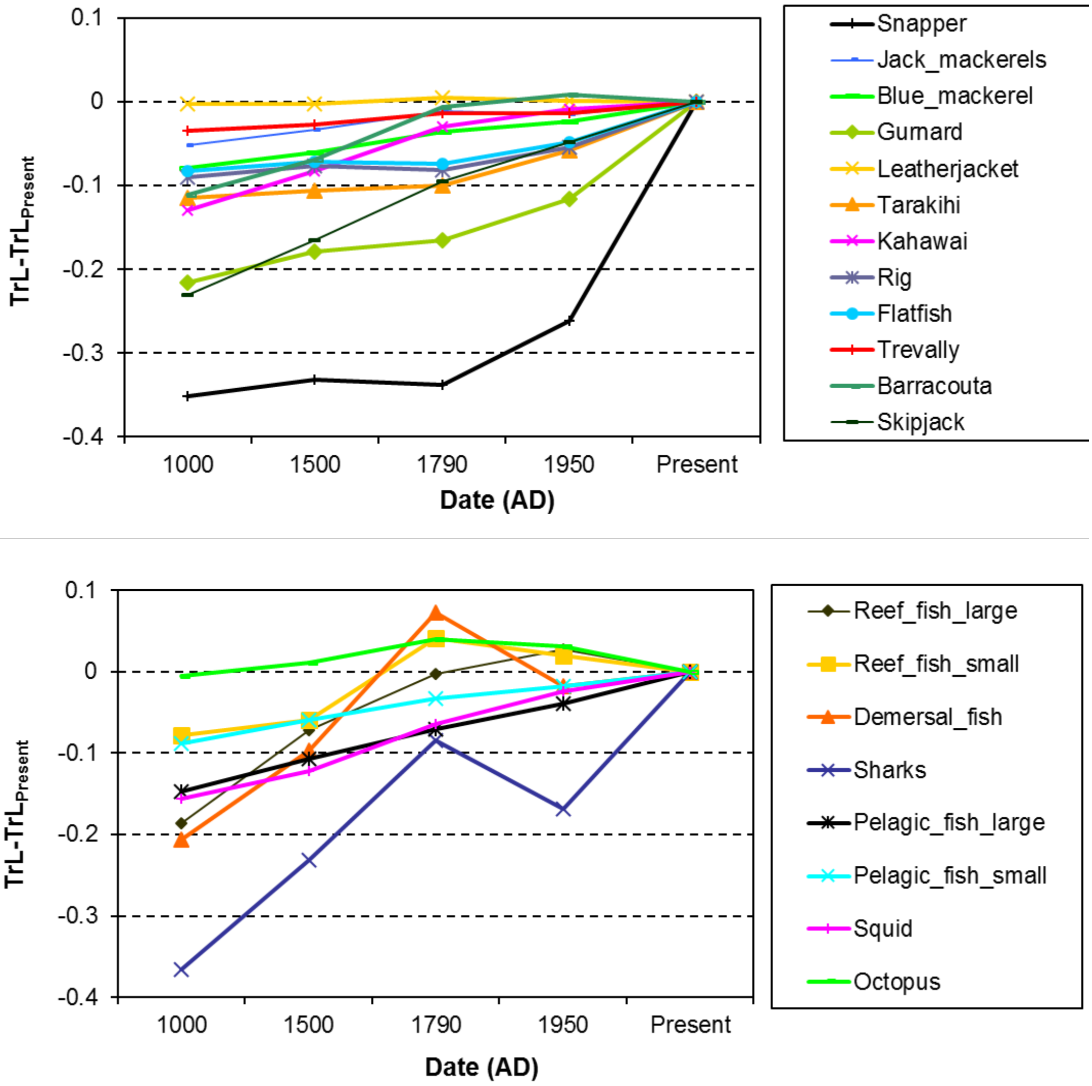


Figure 19b: Changes to Trophic Level (TrL) in the balanced trophic models (continued). The y-axis shows the difference between TrL at a given point in history and that at the present day. Changes in TrL of other groups were less than 0.1 over the whole period modelled.

1.1.12 Changes of trophic importance over time

The trophic importance (TI) of groups within an ecosystem depend on the structure of the whole ecosystem. Trophic importance is often interpreted as showing by how much changing the biomass of a group would affect the rest of the ecosystem (Libralato et al., 2006). Figure 20 shows changes to the rank of an average of the TI. In the balanced model for 1000, cetaceans have the 3rd highest TI, and seals and sea lions the 5th highest TI. The TI of seals and sea lions declines from 5th to 40th between 1000 and 1500 and this group of animals were extirpated from the study area by the time of the 1790 model (zero TI). With the decline in cetacean biomass between the 1790 and 1950 models due to whaling, the cetacean group declines from being between the 2nd and 6th most trophically important group in the three models for 1000, 1500 and 1790, to being 7th (1950) and 21st (present day) most trophically important group in the system.

The models suggest that the TI of birds increased from 24th (1950) to 13th (present day) and this seems to follow the increase in biomass of birds over the same period. However, even though they had much higher abundances in 1000 and 1500 than in the present day, birds in the models had slightly lower TI historically than in the present day. This may be because birds are now fulfilling an ecological role left absent by the reduction in marine mammals in the system. This change is unlikely to be related to the feeding of seabirds on fishing discards or offal which makes up a small (approximately 3%) and constant part of their diets.

The TI of rock lobster in the models decreased from 25th (1000), to 42nd out of 45 groups in the present day model. Crabs, macrobenthos and bivalves had the highest TI of the benthic groups, and increased in TI from 1000 to the present.

The “Sharks” group has the first or second highest TI of all fish between 1000 and 1950 (rank TI over this time were between 5th and 8th overall). The rank TI of sharks decreased to 15th overall in the present day model. Snapper had the first highest TI of all fishes in 1000 (7th overall) and this increased to 5th overall in the present day model, where it was the most trophically important fish The rank TI of snapper increased by a small amount (from 6th to 5th overall) between 1950 and the present day, a period over which its biomass declined by 67%. In the same period, the biomass of many target species also declined, by an average of 60%. Over this “fish down” period between 1950 and the present day, there were generally larger changes to the TI of fish groups than of other groups in the system. For example, rank TI decreased in skipjack (by -13 places), sharks (-10), trevally (-17), gurnard (-4) whereas rank TI increased in tarakihi (+9), kahawai (+7), flatfish (+6), and large reef fishes (+2) between 1950 and the present day. Changes in rank TI of most other groups in the models (excepting rock lobster, birds and cetaceans), were within ±4 over the same period.

Amongst the zooplankton, small benthic invertebrates and primary producers, changes in rank of TI over the period modelled were smaller than the changes to higher trophic level groups. Phytoplankton (1st), and mesozooplankton (2nd–3rd) had very high TI throughout. Phytoplankton production provides the majority of energy flow into the food web, and mesozooplankton are key to transferring this energy up through the pelagic food-web. In the models, the TI of macrobenthos increased from 4th overall in 1000 to 2nd in the present day model. Macrobenthic invertebrates are a key part of the Hauraki Gulf benthic ecosystem and as prey for pelagic organisms.

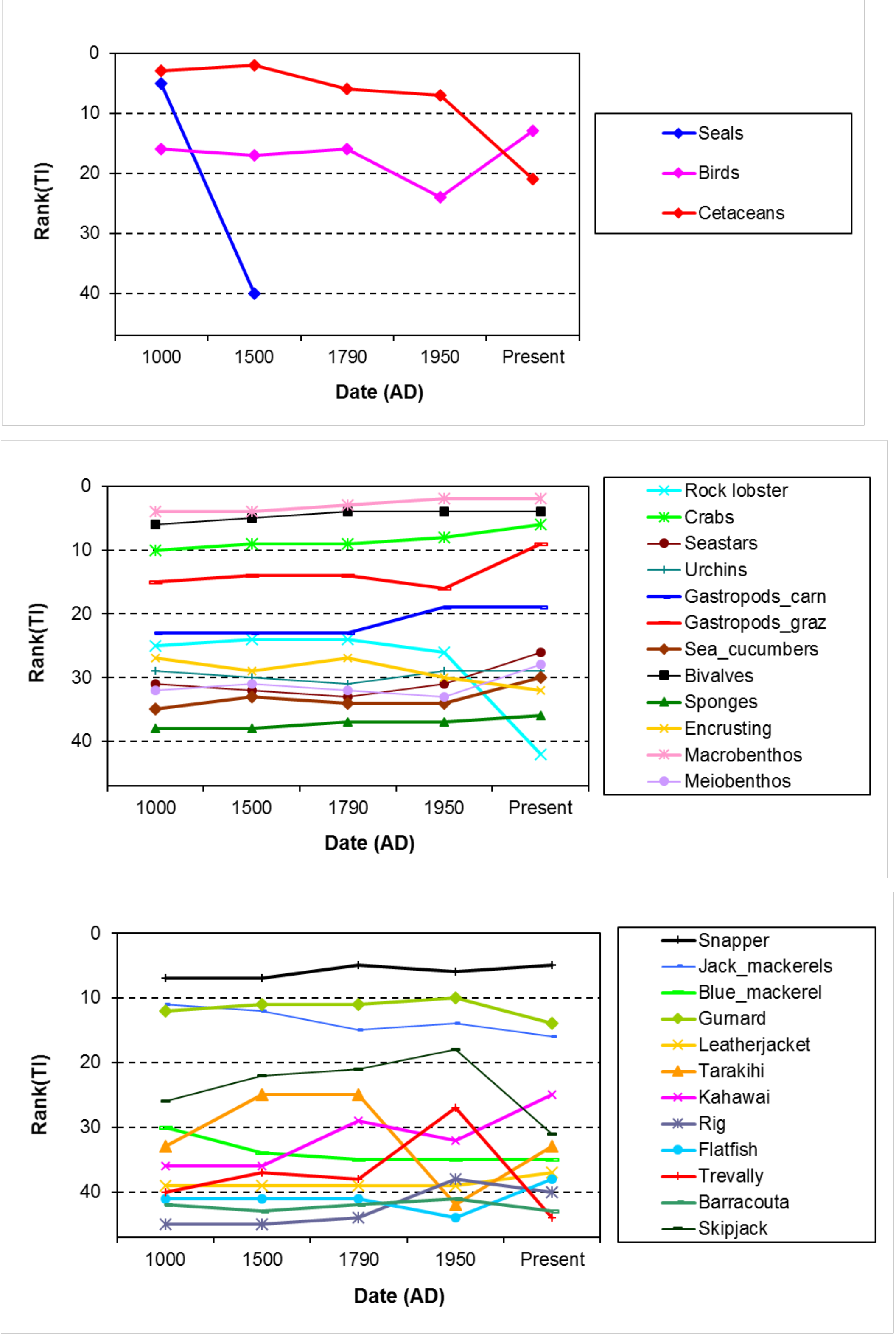


Figure 20a: Changes to the rank of Trophic Importance (TI) in the balanced trophic models (continued below). A rank of 1 means the group has the highest trophic importance in the ecosystem; a rank of 46 means the group has the lowest trophic importance in the ecosystem (the three detrital groups were not included in the ranking).

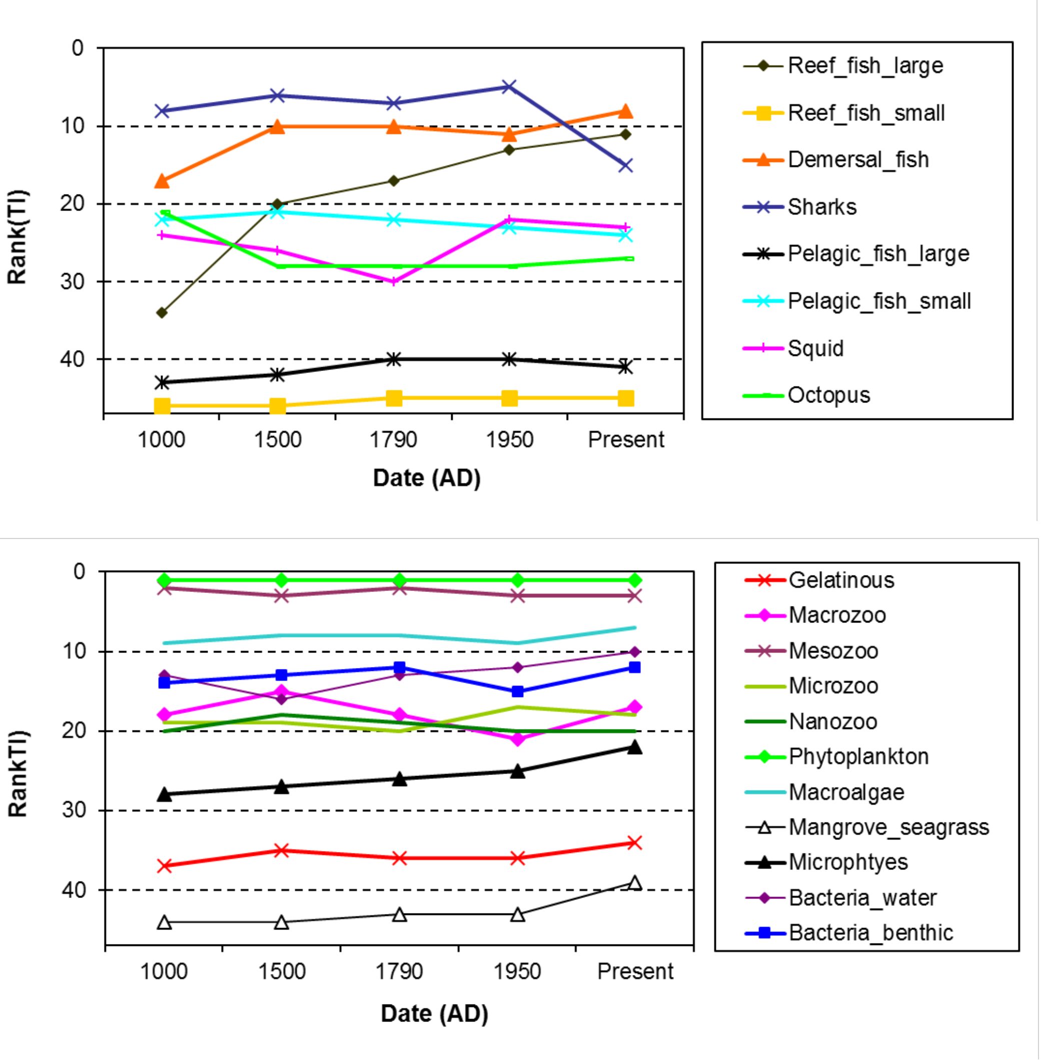


Figure 20b: Changes to the rank of Trophic Importance (TI) in the balanced trophic models (continued). A rank of 1 means the group has the highest trophic importance in the ecosystem.

4. DISCUSSION

4.1 Present-day ecosystem structure

Knowledge of how species are interrelated through feeding is an important step in understanding how an ecosystem is structured and provides insights into how the ecosystem may function. The Hauraki Gulf region has been intensively studied for decades, and is the best studied large coastal ecosystem in New Zealand. This study has shown that there is sufficient information on the present day ecology of the Hauraki Gulf to obtain a reasonable estimate of most parameters and hence develop an end-to-end mass balance of the ecosystem in its present day state.

Developing the initial parameter set and balancing the present day food-web model of the Hauraki Gulf representing present day conditions has been a long and involved undertaking which has drawn on decades of research experience across diverse areas of marine science in New Zealand and from around the world. Uniting this knowledge and coercing the disparate data into comparable forms has taken a number of years. The detail is given in the nearly 250 pages of appendices to this report. The potential future value of this dataset and model is high, for example as a starting point for developing dynamic models or generating hypotheses of ecosystem function.

Balancing the present-day model required some substantial changes to a few of the initial set of 747 parameters, with a maximum of 77% change in biomass of benthic macrofauna and a maximum 37% change in a diet fraction. However, overall, the adjustments were generally small and similar to those found in published studies using comparable balancing methods (Pinkerton et al. 2008; Pinkerton et al. 2010). The median change of biomass and energetic parameters (B, P/B, P/Q) was only 2.3%. Median values of the absolute changes to key parameters during balancing were 4.7% (biomass), 3.8% (productivity, P/B), 0.6% (growth efficiency, P/Q), 1.7% (ecotrophic efficiency), and 1.5% (diet fractions).

The biomasses of most benthic invertebrates through the Hauraki Gulf study area seem to be relatively poorly known in that changes to these parameters during balancing tended to be greater than average. Benthic invertebrates are difficult to represent appropriately in models because they are functionally and taxonomically diverse, often cryptic and/or hard to identify, have a very patchy spatial distribution, and have inconsistent energetic parameters (e.g. many vary their consumption and growth rates in response to local conditions). The amount of sampling of basic properties of benthic invertebrates (abundance, mean size, diet) is low even for a well-studied and accessible area like the Hauraki Gulf. To improve modelling such as this in the future, a habitat-stratified survey of benthic invertebrates in the study region is recommended. This kind of basic, baseline survey information is extremely valuable for developing models to understand ecosystem structure. Within each habitat stratum (which should be more detailed than used in the present study), randomly-located transects should measure key information including: identification of taxa (not necessarily to species level), abundance (number of individuals per square metre), and mean weight of individuals (blotted wet weight). There is a special paucity of data in deep strata (i.e. soft sediments between 40 and 250 m in depth) even though these habitats make up the majority (78%) of the study area.

Unfortunately, it was not possible to provided separate information in the model on different groups or species of bivalves (e.g. mussels versus scallops versus oysters) because the base data were not good enough to reliably estimate the biomasses of these groups separately. We did provide information on 12 groups of fish by species (snapper, blue mackerel, gurnard, leatherjacket, tarakihi, kahawai, rig, flatfish, trevally, barracouta, skipjack tuna) because reasonable quality information on the biomass of commercially important fish groups was available or could be developed. Information was also provided on jack mackerels as a species group.

Biomass and energetics of viable bacteria in the sediments and water column were poorly known. The annual flux rate of detritus from the water column to the benthos is a very useful parameter for modelling, and can be used to inform the relative productivities of the seabed ecosystem relative to the water column productivity.

It is recognised that the balanced model presented is but one solution of many possible solutions given that the conceptual model framework is highly under-constrained (747 non-zero variables; 88 constraints), and that there are significant uncertainties in many parameters. The balancing method used here is better than that used in many similar studies internationally in that it allows all key parameters and all diets to be varied simultaneously, taking into account the huge variation in the magnitude of flows between trophic groups (over more than six orders of magnitude for production). In similar studies, often only the ecotrophic efficient factor is varied to obtain model balance and the authors consider this untenable. Three key parameters (biomass, productivity and diet) for all groups in the model were allowed to randomly vary to test the sensitivity of the model to parameter uncertainty. This sensitivity analysis showed that the patterns of trophic importance shown in the balanced model were robust to parameter uncertainties of up to a factor of three. Such robustness to parameter uncertainty in this model follows from the fact that biomasses vary by up to six orders of magnitude across the ecosystem.

Stable isotope data taken in the study area obtained by the MPI biodiversity project ZBD2005-09 were combined with data from FishBase (Froese & Pauly 2009) to provide some independent validation of the trophic model. The agreement in trophic level between the model and isotope/FishBase data was good; the least squares regression had a slope only 2% from unity, and R^2=0.99 (N=26, and $p < 0.001$). The mean absolute difference in trophic level between the model and isotope/Fishbase was small (0.22).

Mixed trophic impact analysis was used to estimate relative trophic importance (TI) of different species or species groups in the Hauraki Gulf ecosystem. Trophic importance can be interpreted as the degree to which changing the biomass of one species (or species group) is likely to affect the biomass of other species in the ecosystem. Groups in the Hauraki Gulf ecosystem with the highest trophic importance in the present day were (in decreasing order of importance): (1) phytoplankton (which provides 88% of primary production in the system); (2) macrobenthos (mainly small benthic crustaceans and worms); (3) mesozooplankton (mainly copepods); (4) bivalves; and (5) snapper. Snapper are identified as being the most trophically important species of fish in the ecosystem.

According to the model, carbon is estimated to be accumulating in the Hauraki Gulf ecosystem at the rate of about 0.3 MtC y^{-1} which implies a value of ecosystem services in terms of carbon burial of about NZ$ 6.5 million per year (assuming $25/tC, as at 2009).

4.2 Changes to the ecosystem over time

We estimated initial parameter sets for four end-to-end models representing the Hauraki Gulf ecosystem in four historical periods: 1000, 1500, 1790 and 1950, working backwards from the present day model. These historical modes were balanced using a semi-objective method (Section 2.5) based on the previous model. Median changes in parameters required for balancing (from the present day balanced model) were less than 1% for biomass, energetic and diet parameters, indicating that the structure of the food-web was quite consistent between adjacent periods.

The models are unconstrained by the data – we do not have much information on how the ecosystem was structured before the present day. Hence, outputs from this modelling should be considered as working hypotheses. The models represent plausible scenarios of how the ecosystem could have been structured historically in a way that is consistent with all we know of organisms now and based on historical, archaeological and narrative evidence from the study region. It is recognised that there are other scenarios that also fit the available evidence and these should be explored in future work.

Changes to the biomasses of biota in the Hauraki Gulf ecosystem since 1000 to the present day show a pattern of large reductions at higher trophic level and smaller changes lower down the food web:

1. High trophic level groups (especially air-breathing predators) have become very much less abundant (97% reduction of cetacean biomass, 69% reduction of seabird biomass) or were extirpated (seals/sea-lions) between 1000 and the present day. Seals declined between 1000 and 1500, and cetaceans between 1790 and 1950. Seabird biomass declined to 1950 and has increased to the present day.
2. Biomass of fishes in the models have decreased by 60% on average, with the largest decreases by species/group being sharks (86% decrease), trevally (86% decrease), and snapper (83% decrease). Most of the change in the fish biomass occurred between 1950 and the present day during the “fish-down” phase of modern commercial fisheries.
3. The biomass of some benthic invertebrate groups has changed considerably between 1000 and the present day, with some groups increasing in abundance in the models (carnivorous gastropods +100%; crabs +56%) and some decreasing (macrobenthos -44%; rock lobster -76%).

4. The biomass of pelagic invertebrates (squid and zooplankton) have not changed substantially (under 11%) between 1000 and the present day.
5. The total primary production in the system is estimated to have increased by 15% between 1500 and the present day as a result of increased nutrient input from land-use changes and increasing human population in the Hauraki Gulf region.

There were substantial changes to the biomass of some important middle trophic level groups (small fish, cephalopods, benthic and pelagic invertebrates) in the historical models and it is notable that these changes arose from food-web rebalancings rather than being forced from historical data. For example, decreases in biomass between 1000 to the present day were estimated to have occurred for small and large pelagic fishes (32% and 33% respectively), macrobenthos (44%), squid (11%), macrozooplankton (22%), and gelatinous zooplankton (11%).

The historical ecosystem models of the Hauraki Gulf reveal substantial changes in the pattern of trophic importance (TI) during human occupation. The TI of cetaceans was the 3rd in the system in 1000, 7th highest in 1950 and declined to 21st (present day). Seals/sea lions had the 5th highest TI in 1000, but were extirpated from the Hauraki Gulf ecosystem by 1790. The reduction and losses of these apex predators in conjunction with their high historical levels of trophic importance suggests that the pattern of ecosystem control in the Hauraki Gulf ecosystem may have substantially changed during the period of human occupation, at least in the middle and upper trophic levels.

In the trophic models, sharks and snapper were the most trophically important fish in the Hauraki Gulf ecosystem between 1000 and 1950. Between 1950 and the present day the TI of sharks decreased substantially (from 5th to 15th in the system) due to reductions in their biomass. At the same time, the TI of snapper stayed approximately constant. In the present day model, snapper are the most trophically important fish (5th overall). Changes to the patterns of trophic importance in the models suggests that the "fishing-down" period between 1950 and the present day (when the total biomass of targeted fish species were reduced by 55% on average) led to a reorganisation of the relative trophic roles of many species of fish, but did not have major effects on the pattern of trophic interactions at lower trophic levels. The overall high importance of snapper in the food web was maintained and even slightly increased during the fish-down period between 1950 and the present day.

Rock lobster (crayfish) was a reasonably important benthic invertebrate group in the Hauraki Gulf before human arrival (6th out of 12 benthic groups) but with decreases in the biomass of rock lobster between 1000 and 1950 (76% decline), its TI declined to the least trophically important benthic invertebrate group and almost the lowest in the whole system (42nd out of 46 groups).

5. MANAGEMENT IMPLICATIONS

Management implications of this work are numbered for clarity (order does not imply importance):

1. The compilation of data and subsequent food-web modelling suggest that the relative trophic importance of upper trophic level organisms (fish, seabirds, marine mammals) in the Hauraki Gulf have changed over the period of human occupation, largely as a result of human harvesting (fishing, whaling, sealing) and the introduction of land-based predators. Patterns of trophic importance are indicative of the types of dynamics that may be expected in an ecosystem. Changes to trophic importance of upper trophic levels in the Hauraki Gulf hence suggest that the ecosystem dynamics we see in the present day may be different to those that operated in the past. Further work on what effect this may have on emergent properties of ecosystems which are of relevance to management (for example, ecosystem resilience) is recommended.

2. If the biomass of some groups recover towards former levels it is likely to change the balance of trophic importance in the region. For example, after an absence of nearly 500 years New Zealand fur seals have reappeared in the Hauraki Gulf although biomass is still negligible. Management and policy actions should take into account the effects of possible restablishment/recovery of marine mammals towards historical levels, and trophic modelling of future scenarios is recommended.

3. The structure of the lower food-web of the Hauraki Gulf (primary producers, bacteria, detrital pathways, microbial function) was little affected in the ecosystem models by quite substantial changes to fish and higher trophic levels. Our modelling suggests that the functioning of the lower food-web of the Hauraki Gulf is somewhat decoupled from changes at higher trophic levels.

4. Over the period of human occupation of the Hauraki Gulf the models predict that there have been quite large changes (11–44%) to the biomasses of middle trophic level groups such as small and large pelagic fishes, macrobenthos, squid, macrozooplankton, and gelatinous zooplankton. These are important prey items for a range of middle and upper level predators, especially fishes, and are likely to be affected by both top-down and bottom-up effects in ecosystems. We recommend establishing monitoring of changes in these middle trophic level groups in the Hauraki Gulf.

5. The present day food-web model suggests that snapper, benthic macrofauna (mainly small benthic crustaceans and worms) and mesozooplankton have high trophic importance (potentially a keystone role) in the ecosystem of the Hauraki Gulf. Fisheries management should take into account the larger ecosystem effects that may result from further impacting these groups either directly (target species) or indirectly (impacts of bottom gear). Management action which may be considered could include additional data collection to understand or monitor these groups, further modelling to investigate how these groups affect resilience, or reducing direct and indirect human impacts on these groups. Fisheries management should also be aware of the potential for changes to these groups (either directly through targeting of benthic species or indirectly for example, through impacts of bottom gear) to affect other groups of organisms in the ecosystem.

6. Recent changes in phytoplankton production resulting from agrarian and wastewater nutrient input to the region did not have a substantial effect on lower food web structure in the models. Given that mass-balance modelling such as that used here is functionally simplistic and does not include biogeochemical mechanisms, this result should be treated with caution. A biogeochemical model of the Hauraki Gulf would be useful to investigate this further.

7. Food-web and ecosystem modelling such as the present study can help to quantify the value of ecosystem services (for example, long-term burial rates of carbon; provision of food for fish targeted by commercial fisheries). Quantifying the value of ecosystem goods and services using food-web modelling may be useful to management in balancing economic and ecological use of marine ecosystems.

8. The biomass of most benthic invertebrates through the Hauraki Gulf study area were relatively poorly known. If management deems this kind of modelling useful, habitat-stratified survey(s) of benthic invertebrates in the study region are recommended to improve its quality. Within each habitat strata (which should be more detailed than used in the present study), randomly-located transects should measure key information including identification of taxa (not necessarily to species level), abundance (number individuals per square metre) and mean weight of individual (blotted wet weight).

There is a particular paucity of data in deep strata (i.e. soft sediments between 40 and 250 m in depth) and a lack of large-scale systematic mapping of invertebrates in shallow strata (intertidal zone).

6. ACKNOWLEDGMENTS

All authors are employed by the National Institute of Water and Atmospheric Research Ltd (NIWA) except Chris Lalas (Box 31 Portobello, Dunedin 9014) and Larry Paul (NIWA Researcher Emeritus). The trophic modelling research was funded by MPI project ZBD2005-05 “Long-term change in New Zealand coastal ecosystems”, Objective 4. The research was co-funded by NIWA under Coasts and Oceans Research Programme 4 (Structure and function of marine food-webs). We acknowledge Mary Livingston, Martin Cryer and Geoff Tingley (MPI) for reviews and comments. David Bowden (NIWA) provided useful insights that helped improve this work. Stable isotope data for validation was from MPI project ZBD2005-09, which relied on work by Sarah Bury and Julie Brown (both NIWA).

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8. APPENDICES

The appendices shown in Table 29 give detailed information about how the parameters were estimated.

Table 29: Appendices with detailed information on how parameters in the present day and historical models were estimated.

Appendix	Title	Authors	Pages
1	Seals	Pinkerton, M.H.; Lalas, C.	11
2	Birds	Pinkerton, M.H.; Thompson, D.; MacDiarmid, A.	14
3	Cetaceans	Pinkerton, M.H.; MacDiarmid, A.	31
4	Benthic invertebrates	Pinkerton, M.H.; Lundquist, C.J.; Jones, E.; MacDiarmid, A.	79
5	Fishes	Pinkerton, M.H.; McKenzie, A.; Francis, M.P.; Paul, L.	46
6	Cephalopods	Pinkerton, M.H.; Bradford-Grieve, J.	11
7	Zooplankton	Stenton-Dozey, J.; Pinkerton, M.H.; Zeldis, J.; Willis, K.	21
8	Phytoplankton	Pinkerton, M.H.; Zeldis, J.; Stenton-Dozey, J.	16
9	Macroalgae, mangrove, seagrass and saltmarsh	Pinkerton, M.H.; Lundquist, C.J.; Jones, E.; MacDiarmid, A.	22
10	Bacteria and detritus	Pinkerton, M.H.; Zeldis, J.; Nodder, S.D.	13

Appendix 1: Trophic modelling of Hauraki Gulf: Seals

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1 Background

This group includes eared (otariids) and earless (phocids) seals and will be referred to as "seals" for brevity. The New Zealand fur seal (*Arctocephalus forsteri*) and the New Zealand sea lion (*Phocarctos hookeri*) occurred in the study region in the past, but were extirpated from the system more than 500 years ago. Although still functionally absent from the region, a small number of New Zealand fur seals have recently reappeared in the region. Small amounts of remains of the southern elephant seal (*Mirounga leonina*) were found in Maori middens in the region around 1400 . These probably came from stray individuals and are not considered further.

2 New Zealand fur seal

Information on the New Zealand fur seal is based on research by Lalas & MacDiarmid (2011) as part of the Ministry of Fisheries biodiversity project on the long-term effects of climate variation and human impacts on the structure and functioning of New Zealand's shelf ecosystems (ZBD2005-5 MS12 Part E). New Zealand fur seals (*Arctocephalus forsteri*) are distributed around New Zealand, the southern coastline of Australia and Australasian temperate and subantarctic islands (Goldsworthy et al. 2003; Harcourt 2005). Numbers in New Zealand have increased and their breeding distribution has expanded northward through recent decades after extirpation attributable to Polynesian subsistence hunting (Smith 2005, 2011) followed by European commercial sealing in the late 18th and early 19th centuries (Lalas & Bradshaw 2001; Ling 2002; Richards 2003). Fur seals were last hunted commercially in New Zealand in 1946 and they did not receive full protection until the passing of the New Zealand Marine Mammals Protection Act in 1978 (Lalas & Bradshaw 2001). The most recent estimate for number in the New Zealand region is about 100 000 individuals in 1992 (Harcourt 2005).

The size of the historical population of fur seals in the Hauraki Gulf study region is not known. Ecosystem carrying capacity for fur seals is likely to depend on *inter alia* prey abundance and availability, breeding/haul out area, and foraging area. Satellite tracking of New Zealand fur seals shows that New Zealand fur seals may forage up to 200 km beyond the continental slope into water deeper than 1000 m, so carrying capacity is likely to depend to some extent on food availability outside the study area as well as factors intrinsic to the region itself.

Lalas & MacDiarmid (2011) report on the recent increase of the fur seal population in the Otago region of New Zealand, noting that the number of pups produced each year has now ceased to increase and that the plateau may be taken as an indicator of carrying capacity and can be used to estimate population size before human arrival. On this basis and taking into account the minimum population size capable of sustaining prehistoric catch of fur seals at the levels estimated by Smith (2011) until their regional extirpation around 1500, we estimate a Hauraki Gulf population of fur seals of 8000 (range 1500–15 000) in 1000 and 500 (0–1500) in 1500 (Table 30). The population is assumed to obtain half of its food from the study area on the basis of estimated foraging ranges, and reside there for the whole of the year. Present day biomass and that in years 1950 and 1790 are set to zero as it is highly likely that fur seals were extirpated from the study area before 1790 (Smith 2005, 2011).

New Zealand fur seals are sexually dimorphic, with males larger than females throughout life; respective average masses at birth are 3.9 kg and 3.3 kg, with respective recorded maxima for adults of 160 kg and 69 kg for males and females respectively (Harcourt 2005). Lalas et al. (2011a) estimated a mean individual weight of fur seals in a breeding population (excluding pups) of 41.3 kg, and we use this mean population value here.

3 New Zealand sea lion

Information on the New Zealand sea lion is based on Lalas et al. (2011b). The present distribution of New Zealand sea lions (*Phocarctos hookeri*) is restricted to southern New Zealand and subantarctic islands. The species population size was estimated at 12 000–14 000 individuals based on an annual production of about 2800 pups in 1995–96 (Gales & Fletcher 1999). Subsequent pup production at the Auckland Islands, the species population base, declined 40% from about 3000 pups in 1998 to about 1800 pups in 2010 (Robertson & Chilvers 2011). Auckland Islands accounted for 71% of pup production in 2010, and an increasing population at Campbell Island accounted for nearly all of the remainder (Robertson & Chilvers 2011). The pristine distribution was more widespread and included the entire coast of New Zealand where extirpation of the species was attributed mainly to Polynesian subsistence hunting (Childerhouse & Gales 1998; McConkey et al. 2002a, b). Recolonisation of New Zealand began in the 1980s (McConkey et al. 2002a,b), with currently 4–5 pups born annually at Otago Peninsula (Robertson & Chilvers 2011). In response to the restricted distribution and declining population size, the conservation status of New Zealand sea lions has been listed as 'nationally critical' under the New Zealand Threat Classification System (Baker et al. 2010). The possible causes for the recent population decline were reviewed by Robertson & Chilvers (2011) who concluded that the main threats to NZ sea lions were ongoing incidental mortality in a trawl fishery for arrow squid (*Nototodarus sloanii*) around the Auckland Islands, resource competition with subantarctic fisheries, and three epizootic disease events.

The historical populations of the New Zealand seal lion in the study region or New Zealand as a whole are not known. In this study we estimate that the Hauraki Gulf population of sea lions numbered 5000 (1000–24 000) in 1000 and 100 (0–1000) in 1500 based on the availability of haul-out beaches, prey availability and the ratio of New Zealand fur seals to New Zealand sea lion remains in early Maori middens. Present day biomass of sea lions in the study area and that in years 1950 and 1790 are set to zero as it is likely that this species was extirpated from the study area before 1790 (Smith 2005, 2011). The Hauraki Gulf population of sea lions is assumed to obtain 90% of its food from the study area on the basis of estimated foraging ranges, and reside there for the whole of the year.

New Zealand sea lions are sexually dimorphic with males larger than females throughout life; respective average masses at birth are 10.6 kg and 9.7 kg (Chilvers et al. 2006), with respective maxima for adults of 450 kg and 165 kg for males and females respectively (Harcourt 2005; Gales 2009). Lalas et al. (2011b) estimated a mean individual weight in a breeding population of sea lions (excluding pups) of 107 kg, and we use this mean population value here.

4 Consumption

We estimated food consumption requirements for the New Zealand fur seal and sea lion by four methods. First, Nagy (1987) estimated daily dry weight food consumption for eutherian mammals (with placenta) according to body weight as $Q_d=0.235W^{0.822}$, where Q_d is the daily consumption in g dry weight; W is the animal weight (g). Dry weight of prey items was converted to carbon using a ratio of 0.3 gC gDW^{-1} (Vinogradov 1953). This method gave Q/B=39, 33 y^{-1} (for fur seals, sea lions respectively). An estimate of oxygen consumption of a southern elephant seal by Hindell & Lea (1998) suggested that Nagy's (1994) equation may overestimate field metabolic rate. In the second and third methods, consumption of seals was estimated based on the amount of food they require to supply sufficient energy to satisfy their standard metabolic rate (SMR). There is conflicting evidence on whether the metabolic rate of seals is significantly greater than that of terrestrial mammals of a similar size in natural (i.e. non-captive) conditions (e.g., Riedman 1990, and references therein). We used the relation: SMR (kcal d^{-1}) = $71.3 \cdot W^{0.892}$, where W is the animal weight in kilograms which was developed for marine mammals in polar areas (Irving 1970). The third method used $SMR=70.5 \cdot W^{0.7325}$ (Lockyer 1981) In both cases, the average daily energy requirement of seals was taken as 2.8 times the standard metabolic rate (Lasiewski & Dawson 1967). An assimilation efficiency of 0.8 and energy/carbon ratio of about 10 kcal gC^{-1} were used to give carbon requirements (Croxall 1987; Lasiewski & Dawson 1967; Schneider & Hunt 1982). The latter figure is appropriate for fish, and we recognize that squid has a somewhat lower energy density relative to carbon than fish (e.g., van Franeker et al. 1997, and references therein). These methods led to Q/B=28, 26 y^{-1} and 33, 26 y^{-1} (fur seals, sea lions respectively). The averages of these three methods are Q/B=34, 28 y^{-1} (fur seals, sea lions). These are equivalent to an average feeding of 9.2, 7.7 % body weight per day (fur seals, sea lions).

In the fourth method, Lalas et al. (2011a,b) obtained sex- and age-specific estimates for daily consumption rates for New Zealand fur seals and sea lions following Winship et al. (2006) and applying transformations proportional to (body mass)$^{0.75}$ to the consumption model for Steller sea lions in Winship et al. (2002). Estimated consumption rates for New Zealand fur seals without pups were in the range of about 8–12% body weight per day (Figure 21a). Estimated consumption rates for New Zealand sea-lions without pups were in the range of about 7–10% body weight per day (Figure 21l). These values are very comparable to estimates given above. However, estimated consumption rates for females with pups are much higher. Lalas et al. (2011a) estimated an average daily consumption for all New Zealand fur seals in a breeding population of 6.4 kg, equivalent to 15% of mean body mass per day, or Q/B=56.6 y^{-1}. For New Zealand sea lions, Lalas et al. (2011b) estimated an average daily consumption per individual in a breeding population of 13.9 kg, equivalent to 13% of mean body mass per day, or Q/B=47.4 y^{-1}. In the trophic model, we use the population consumption estimates of Lalas et al. (2011a) for fur seals and that of Lalas et al. (2011b) for sea-lions, which are equivalent to Q/B=57, 47 y^{-1} (fur seals, sea lions).

Other work reports daily food intake for captive seals as 10% of body weight (Laws 1984), and 3.3% for harp seals (Nordoy et al. 1995). These imply Q/B values of between 12–37 y^{-1}, assuming that seals and their prey have the same carbon to wet weight ratio. If seals have a slightly higher C:WW ratio than their prey, these Q/B values will be lower. Jarre-Tiechmann et al. (1998) estimate that Cape fur seals have a Q/B ratio of 19 y^{-1}. Meynier (2010) estimated daily mass requirements of New Zealand sea lions in summer, autumn and winter as between 3% (adults) and 8–9% (juveniles) body mass per day. Bradford-Grieve et al. (2003) used Q/B=46 y^{-1} for New Zealand fur seals based on Laws (1984).

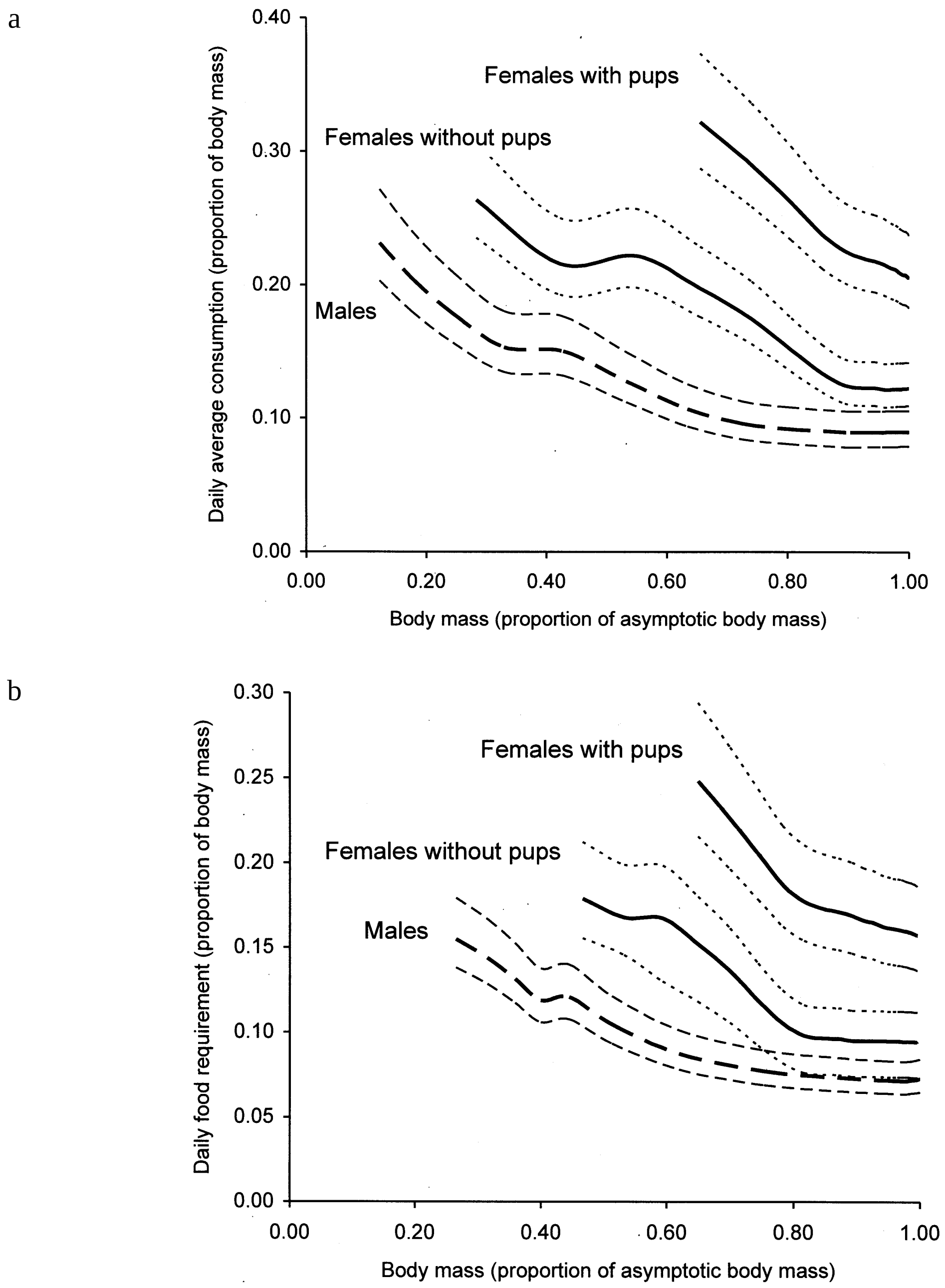

Figure 21: Daily food requirements of New Zealand fur seals (a) and sea lions (b) depicted relative to body mass, based on Lalas et al. (2011a,b) as described in the text. Best estimates and plausible ranges are plotted for females with pups and females without pups (thick solid lines flanked by thin dotted lines) and for males (thick dashed line flanked by thin dashed line).

5 Production

We estimated production of seals in two ways. First, we used the method of Banse & Mosher (1980) who related production to animal biomass as: P/B=12.9 $\cdot M_s^{-0.33}$ where M_s is the animal weight expressed as an energy equivalent (kcal), and P/B is the annual value (y^{-1}). Mammals are likely to have a higher energy content than fish (about 1 kcal gWW^{-1}: Schindler et al. 1993) as a result of their fat-rich blubber. Although the biochemical analysis of blubber of mammals varies, 60% lipid is likely (Koopman 2007) implying an energy content of about 9 kcal gWW^{-}

^{1}. Assuming such high-lipid tissues make up about 20% of body weight, we estimate a total energy density of 2.6 kcal g^{-1}. This method gives P/B=0.28 y^{-1} (fur seal) and P/B=0.21 y^{-1} (sea lion).

Second, we estimate production based on pup production and survival. We assume a mean adult weight of 41.3 kgWW (fur seal), 107 kg (sea lion), a mean pup weight of 3.6 kg (New Zealand fur seal) and 10.1 kg (New Zealand sea lion). Annual pup production is estimated to be 0.24 of total population for New Zealand fur seals (table 2 in Lalas et al. 2011a). Female adult fecundity (likelihood of a female aged giving birth in given year) is taken as 0.8 for New Zealand sea lions (Lalas et al. 2011b). Estimates of fur seal pup survival (Lalas 2008) range from about 0.60 (Mattlin, 1978) to about 0.80 (combination from Lalas & Harcourt 1995 and Bradshaw et al. 2003); McKenzie (2006) used 0.73 which we use here for New Zealand fur seals. Lalas et al. (2011b) suggests a pup survival of 0.68 for New Zealand sea lions. We hence estimate an annual production of P/B=0.19, 0.31 y^{-1} (fur seal, sea lion respectively). We use a mean value of P/B=0.24 y^{-1} for the New Zealand fur seal, and a mean value of P/B=0.26 y^{-1} for the New Zealand sea lion.

6 Harvesting removals

Smith (2011) estimated the magnitude of pre-European Maori marine harvest of fish, seabirds, invertebrates and mammals based on data preserved from middens, for years (actually, periods about nominal years) 1400 , 1550 and 1750 . No remains of seals are found after 1400 (Smith & James-Lee, 2009). Using linear interpolation by year, we estimate that removals of seals by humans in 1500 was 118 tWW y^{-1}. This was comprised of 81% fur seals, 18% sea lions and 1.3% southern elephant seals.

7 Diet (prey)

New Zealand fur seals in New Zealand typically forage offshore over the edge of the continental shelf and over the continental slope where they take cephalopods and teleost fishes, including species targeted by commercial fisheries (reviews by Harcourt 2005 and Boren 2010). The main prey species are arrow squid (*Nototodarus*, two spp.) and Maori octopus, (*Macroctopus maorum*) and a variety of pelagic and demersal teleost fishes ranging in size from lanternfish (Myctophidae) at 1–10 g to barracouta (*Thyrsites atun*) at 2–3 kg (Street 1964; Carey 1992; Fea et al. 1999; Harcourt et al. 2002; Lalas 2009). Although the diversity of prey is well documented, composition of the diet by mass remains unknown. Reports of species of large teleost fishes taken by New Zealand fur seals indicate that barracouta are important, supplemented mainly by hoki and jack mackerel (Carey, 1992; Boren, 2010). Here, we assume a diet for New Zealand fur seals as in Table 31.

New Zealand sea lions at the Auckland Islands forage across the continental shelf and continental slope (Geschke & Chilvers 2009; Chilvers et al. 2011). In this area, they target cephalopods and teleost fishes, with current knowledge of their diet derived from different sources and analyses. A numerical analysis of the contents of scats and regurgitates by Childerhouse et al. (2001) found that the most abundant prey were octopus (*Enteroctopus zelandicus*) and opalfish (*Hemerocoetes* spp.). Hoki (*Macruronus novaezelandiae*) and rattails (Macrouridae) also were numerous but there were few arrow squid (Childerhouse et al. 2001). A more comprehensive analysis of the digested fraction of the stomach contents of New Zealand sea lions killed in the squid fishery by Meynier et al. (2009) found that the most important prey were octopus (28% by mass) and arrow squid (18% by mass), with no other species contributing more than 5% by mass. Although opalfish were the most numerous prey, they contributed only 2% by mass (Meynier et al. 2009). Fatty acid signature analyses of blubber of New Zealand sea lions killed in the squid fishery (Meynier et al. 2008, 2010) found that the greatest contributions to the diet by mass were by arrow squid, hoki and rattails. As these stomach samples came from seals killed by fishing operations it is possible that their diets are not representative of the population as a whole. Males probably take more deep-benthic prey than females (Meynier et al. 2008) but no distinct differences in diet have been recorded between the sexes (Meynier et al. 2009). There is also evidence of feeding by sea lions on fur seal pups in areas where both occur and breed (Childerhouse et al. 2001; Lalas 1997). Here, we assume a diet for New Zealand sea lions as in Table 31.

It seems that New Zealand sea lions may feed on smaller prey (either smaller individuals of the same species or smaller species of fish) when the sea lion population is at carrying capacity; average prey size of teleost fishes by New Zealand sea lions at Otago (colonising population) is 0.5–1 kg, about a magnitude higher than at Auckland Islands (population at carrying capacity) (Lalas 1997; Augé et al. 2012).

8 Other information: P/Q, EE, U, accumulation, imports, exports, transfers

The values for production and consumption given by the methods explained above lead to gross transfer efficiencies (P/Q) of 0.41%. This range is of a similar magnitude to that used in other models (e.g. Pinkerton et al. 2010, P/Q for seals of 0.42–0.54%).

Ecotrophic efficiency measures the proportion of the annual production that is available for predation as well as exported (including as harvest and fishery landings, migration, spawning output, growth) or accumulated. The remainder of the production (a fraction of 1-E) is transferred to a detrital group. Generally, few fur seals are likely to be actively killed by other marine consumers, here, assumed to be 10% of annual production. It is likely that most seal production will end up within the marine system as carcasses, which will be scavenged by other marine biota.

Export and import of material can occur from a number of sources: (1) export from the system due to seals on average having a different weight when leaving the study area than when entering; (2) mortality of seals occurring over terrestrial habitat or over marine habitat outside of the study area; (3) different numbers of seals entering the study area than leaving it over a year, corrected for differences in their weight. Export by changes in weights of seals was assumed to be close to zero since there is not likely to be large scale seasonal migration of seals (Lalas, unpubl. data). Most mortality is likely to occur in the sea, so export to the land will be small. The proportion of mortality in the populations as a whole that occurs outside the study region is unknown but based on foraging ranges is estimated to be 50% for fur seals and 10% for sea lions, but this is already accounted for by adjusting the biomass in the study area by the fraction of the time spent in the area. Hence, we set X/P=0.

We assumed an unassimilated consumption ratio for fur seals of U=0.2 (Furness, 1984; Lavigne et al. 1982).

Measurements of the body composition of Antarctic fur seals (Arnould et al. 1996), showed that ash-free dry weight is approximately 35% of wet-weight. Assuming that ash-free dry weight is composed of material in approximately carbohydrate proportions ($C_6H_{12}O_6$) gives 0.15 gC gWW^{-1}. Other authors have used 0.1 gC gWW^{-1} for seals that we use here (e.g. Vinogradov 1953; Bradford-Grieve et al. 2003; Pinkerton et al. 2010).

9 Summary of parameters

Table 30: Summary of parameters for seals in the trophic model. The top four rows are for fur seals and sea-lions individually. The bottom 5 rows of the table give the values for the combined "seals" group in the trophic model. Grey cells indicate no data required or not applicable.

Model	N	Prop in area	B	P/B	Q/B	P/Q	U	EE	Export X/P	Fishery
			gC m^{-2}	y^{-1}	y^{-1}	%				tWW y^{-1}
Fur seals (1500)	500	0.5	6.4E-05	0.23	57	0.42	0.2	0.6	0	95
Fur seals (1000)	8000	0.5	1.0E-03	0.23	57	0.42	0.2	0.6	0	0
Sea lions (1500)	100	0.9	5.9E-05	0.26	47	0.54	0.2	0.6	0	21
Sea lions (1000)	5000	0.9	3.0E-03	0.26	47	0.54	0.2	0.6	0	0
Present	NA	NA	0	NA	NA	NA	NA	NA	NA	NA
1950	NA	NA	0	NA	NA	NA	NA	NA	NA	NA
1790	NA	NA	0	NA	NA	NA	NA	NA	NA	NA
1500	NA	NA	1.2E-04	0.21	52	0.41	0.2	0.6	0	7.3E-04
1000	NA	NA	4.0E-03	0.20	50	0.41	0.2	0.6	0	0

Table 31: Summary of diets for seals in the trophic model. Proportions are by weight (organic carbon) averaged over a year and over the whole population. Note that the last two columns give values for the "seal" group, obtained by combining diets of fur seals and sea-lions in proportion to their estimated consumptions.

Prey				Proportions in diet
	Fur seal	Sea lion	Group 1500	Group 1000
Seals	0	0.05	0.002	0.000
Birds	0	0.02	0.009	0.015
Crabs	0	0.05	0.030	0.037
Snapper	0	0.1	0.045	0.074
Jack_mackerels	0.25	0.1	0.187	0.149
Barracouta	0.25	0.1	0.187	0.149
Flatfish	0	0.05	0.022	0.037
Other demersal fish	0.1	0.25	0.183	0.245
Reef_fish_large	0	0.05	0.018	0.030
Sharks	0	0.05	0.007	0.012
Squid	0.2	0.05	0.136	0.097
Octopus	0.1	0.1	0.102	0.104
Pelagic_fish_small	0.1	0.03	0.070	0.052
Total	1	1	1	1

10 Acknowledgements

This research was funded by Ministry of Fisheries project ZBD200505 ("Long-term change in New Zealand coastal ecosystems") and by the New Zealand Foundation for Research, Science and Technology project C01X0501 (Coasts & Oceans OBI). We acknowledge Dr Mary Livingston and Dr Martin Cryer and the Ministry for Primary Industries for supporting this project and Alison MacDiarmid (NIWA) for project leadership and reviewing this research.

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Appendix 2: Trophic modelling of Hauraki Gulf: Birds

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1 General information

For the avian component of the Hauraki Gulf trophic model, 37 species of seabirds were considered (Table 32). We worked at species level for all parameters and then combined into a single group. Bird species were divided into those which breed in the study region (26 species) and those that do not breed in the study area. Non-breeding visitors either breed in New Zealand but outside the area, or visit New Zealand as breeders from elsewhere (11 species).

2 Biomass

For birds which breed in the study area and have breeding colonies accessible to study, we used censuses of the breeding colonies to estimate breeding pairs (Taylor 2000a, b). There is some variability in the level of accuracy in these estimates of the numbers of breeding pairs and some variability from year to year, but the best available data were used in each case. In order to estimate the total population size from breeding numbers it is necessary to estimate the number of non-breeding adults and juveniles typically absent from the breeding colony but present in the study area. This factor is typically not well known, and, after taking into account information on chick and adullt mortality in a number of seabird species and in discussion with seabird experts, we assumed that two-thirds of the population breeds in any year (e.g. Lundquist & Pinkerton 2008; Pinkerton et al. 2008).

For birds that do not breed in the Hauraki Gulf, or birds which are widely dispersed, we took numbers of birds from at-sea sighting surveys and other sources and, where necessary (7 species) estimated breeding numbers from the estimate of total population using an estimate of the breeding number to total population number as described above (Taylor 2000a, b).

We used two factors to correct the abundances of each bird species as estimated above to obtain an annual average abundance (Equation 1.1). First, we estimated the proportion of the year that the number of birds observed is likely to present in the study region. Some birds (e.g. fluttering shearwater) spend the whole year in the study region, whereas other species (e.g., Wilson’s Australasian gannet) are present in the region for some of the year. Second, we estimate, how much of their foraging occurs in the Hauraki Gulf study region compared to the surrounding area. Some species breed in the area but feed almost exclusively outside the area - Cook's petrel is a good example. This factor also includes an estimate of the proportion of non-marine food. Some species (e.g. shags and herons) feed in other non-marine habitats and the model is only concerned with feeding from the marine environment. Our estimates of these factors were based on tracking and other data by avian experts (Table 32).

$$B = \frac{N \cdot W \cdot C}{A} \cdot \left(\frac{S}{100} \right) \cdot \left(\frac{M}{12} \right) \qquad [1]$$

B = average annual biomass density (gC m^{-2})
N = number of birds in the study area
W = average weight of bird (gWW [wet-weight])
C = carbon:wet weight ratio (gC/gWW)

A = area of study region (m^2)
S = proportion of foraging area covered by the study region
M = months spent in the Ross Sea modelling area per year

Average fresh weights of birds were taken from Heather & Robertson (1986). Common seabirds found in the Hauraki Gulf have asymptotic adult weights between 30–2300 g, the smallest bird being the red-necked stint (*Calidris ruficollis*) and the largest being the Australasian gannet (*Morus serrator*). The median weight is 400 g. The mass in equation 1 is an average value for males and females as some species have sex-specific mass. Carbon to wet weight ratios for seabirds were taken as 10%, the same carbon content as fish (Vinogradov 1953), following previous trophic modelling work (e.g., Bradford-Grieve et al. 2003). The overall biomass of birds is estimated to be equivalent to an annual average of 401 metric tonnes.

3 Production

Production of marine birds is generally not one of the most important parameters for a trophic model, as seabirds tend to have few direct predators and their biomass is very low compared to other sources of carcasses. For all species we first assumed that the populations are in approximately steady state, i.e. that the populations are neither increasing nor decreasing between years on average. We calculated M_a, the annual mortality rate of adults and juveniles, based on species lifespan as follows. Lifespan of birds is positively correlated with maximum adult weight (W_{inf}, g) (Speakman 2005; Prinzinger 1993). “Lifespan” here is the maximum age at death of a (relatively small) sample of measured birds. Speakman (2005) notes that the sample size from which lifespan has been estimated is not known for most species of birds, and may be of the order of 100 birds (assumed here), but could be more if non-remarkable lifespans are discarded. Here, we use an average of the regressions of Speakman (2005) and Prinzinger (1993) (which differ by about 11–30%) to estimate lifespan from asymptotic adult weights, giving lifespans of 9–21 years for the species considered here. Age at fledging is estimated to be 23–64 days for the species considered here (average of Carrier & Auriemma 1992; Weathers 1992; Westmoreland et al. 1986).

Then, we estimated production of species that breed in the area and species that do not breed in the area separately as follows.

For species that breed in the area, the net import of live birds is likely to be close to zero. For species with a seasonally-varying population (i.e. ones that undergo migrations into and out of the study area at different times of the year), this is equivalent to assuming that the same weight of live birds enters the study area as leaves it. In this case, production is equal to mortality. We estimated production as the sum of two factors: (1) death of adult and juvenile (post-fledging) birds of near adult weight; (2) death of eggs and chicks. The number of eggs laid per pair varies by species, being commonly 1 (petrels, terns, shearwaters, penguins), 2 (oyster catchers, gulls) or 3 (shags, herons). For breeding populations, the chick mortality is estimated as the difference between the number of eggs (calculated as number of breeding pairs multiplied by the average number of eggs per pair), and the number of fledglings needed to replace adult mortality each year. The number of chicks dying in a year is converted to a weight assuming the average weight at death is approximately one third adult weight. This approach leads to estimates of annual production ratios (P/B) for breeding Hauraki Gulf seabirds of 0.27–0.66 y^{-1}.

For species that do not breed in the study area, we calculated the number of birds arriving and departing based on average numbers present (from census and observer data as explained above) and the number of birds dying in the study region (from M_a). Birds are assumed to come to the study region to feed, and we assume that the birds leave the region 10% heavier on average than when they arrive. Hence, we can estimate the growth of seasonal visitors in the study area, giving P/B between 0.06–0.11 y^{-1}. These are lower productivities than for breeding populations as expected.

The proportion of mortality that is due to direct predation is estimated to be between 0–1%. The majority is assumed to be bird death due to starvation, disease etc. A proportion of this will be exported as dead birds (i.e. carcasses over the land), and some will enter the marine part of the study area as bird carcasses, to be consumed by scavengers or degraded by bacterial action. Net export of bird biomass is calculated from the net export of live birds plus the export of bird carcasses. The group average values are P/B=0.25 y^{-1}. This is higher than production rates for seabirds estimated by some previous studies. For example, Wolff (1994) used 0.07 y^{-1} for northern Chile seabirds, and Brando et al. (2004) used 0.04 y^{-1} for Italian cormorants, but less that that suggested by Bradford-Grieve et al. (2003) of 0.30 y^{-1} for seabirds south of the Chatham Rise. Net export of biomass is estimated to be equivalent to 32% of production and transfer of material to carcasses in the marine study area is estimated to be equivalent to 67% of production. We estimate that 1% of production is directly predated, i.e. an ecotrophic efficiency of 1%.

4 Consumption

Food consumption requirements for each species were estimated by two methods. Nagy (1987) estimated daily dry weight food consumption for seabirds according to body weight. This was converted to carbon using a ratio of 0.4 gC/g wet-weight (Vinogradov 1953). In the second method, average daily energy requirement of seabirds was taken as 2.8 times the standard metabolic rate (SMR: Lasiewski & Dawson 1967; Schneider & Hunt 1982). An assimilation efficiency of 0.75 and energy/carbon ratio of 10 kcal/gC was used to give carbon requirements (Croxall 1987; Lasiewski & Dawson 1967; Schneider & Hunt 1982). These methods differed by about 9% for all bird species. Annual average consumption/biomass, Q/B, varied in the range 76–265 y^{-1}. Finally, seasonal visitors are likely to be feeding at greater than the annual average rate while in the study area, and we increase their feeding (and production) rate by a nominal 5% to account for this. The overall consumption rate of birds as a whole is estimated to be 119 y^{-1}.

For comparison, van Franeker (1992), estimated food required per bird per day from equations given by Furness & Monaghan (1987) to range from 21% of wet weight body mass for large birds to 83% of body weight for small birds, approximately equivalent to Q/B 77–303 y^{-1}. Gross food intake (g AFDW d^{-1}) was estimated as 33.06, 17.93, and 11.17, respectively, for average body masses (kg) of 0.583, 0.250, and 0.130, respectively, for South Island pied oystercatchers, bar-tailed godwit and lesser knot (Cummings et al. 1997; Lundquist et al. 2004). Carbon content of prey was calculated using 1 gAFDW = approximately 0.50 gC (Brey 2005) assuming prey consists of primarily benthic macrofauna. Assuming that these estimates are representative of New Zealand shorebirds of three varying body weights, we estimate average Q/B of birds in the marine reserve as 104, 132 and 158 y^{-1} for these three species (Lundquist & Pinkerton 2008; Pinkerton et al. 2008). So, our estimates of Q/B are within the range of those estimated previously.

Since a proportion of the consumption of some species of birds (e.g. gulls) comes not from the marine environment but from terrestrial sources, the consumption rates of birds are reduced. The proportion of food from non-marine sources is estimated to range from 0 (purely marine feeders, such as shearwaters), 0.1–0.35 (little/pied/black shags), 0.2 (oystercatcher), 0.5 (heron), and 0.35–0.6 (gulls). The overall rate of consumption of food from the marine environment is estimated as 116 y^{-1}.

5 Diet (prey)

We first correct the consumption rate to allow for prey taken from the non-marine area (see above). Following this, the proportions of marine food in six coarse categories were estimated from the literature: fish, cephalopods, crustaceans, intertidal bivalves and gastropods, intertidal soft-sediment prey (mainly polychaetes), and carcasses (including seabird carcasses). The consumptions of each of these prey categories were weighted for the consumption rate of the bird and summed. Although the proportions of different species of prey are not well known, the modes of feeding provide some information about the likely types of prey. For example, although there are some exceptions (e.g. sooty shearwater diving to 70 m), most seabirds take their prey from shallow or surface waters (less than 20 m), so small pelagic and shallow-water fish dominate the piscine part of seabird diets.

The expert opinion of David Thompson on sea bird diet was used to translate the broad categories of prey type into trophic groups used in the model. Three species of bird are estimated to take 89% of “crustaceans” consumed by birds in the study area: Buller's shearwater, 55.9%; common diving petrel, 27.4%; and fluttering shearwater, 6.0%. Crustaceans taken by Buller's shearwater are likely to be mainly pelagic euphausiids e.g. *Nyctiphanes australis* (macrozooplankton group). Crustaceans taken by the common diving petrel are likely to be euphausiids and also copepods (macrozooplankton and mesozooplankton groups respectively). Fluttering shearwaters are likely to take similar crustaceans to Buller's shearwater, i.e. pelagic euphausiids (macrozooplankton group). We hence estimate a crustacean component of the diet of “birds” of 30% macrozooplankton and 5.5% mesozooplankton (Table 33).

Three species of bird are estimated to take 78.6% of fish eaten by birds in the study area: Buller's shearwater, 39.4%; Australasian gannet 22.3%; and fluttering shearwater, 16.9%. Because of constraints imposed by bill size, Buller's shearwater are likely to take fish smaller than 10 cm (mainly in the “'juvenile fish” group), combined with some smaller fish in the water column. The Australasian gannet is likely to predate mainly pilchard, anchovy, saury, and jack mackerel (Robertson, 1992). Fish consumed by fluttering shearwaters is also likely to be a combination of “juvenile fish” and small sprat and pilchard type fish, similar to Buller's shearwater.

6 Other information: P/Q, EE, U, accumulation, imports, exports, transfers

The values for production and consumption given by the methods explained above lead to gross transfer efficiencies (P/Q) of 0.04–0.6% (overall 0.2%). This range is of a similar magnitude to that used in other models (e.g. Pinkerton et al. 2010, P/Q for flying birds of 0.48%).

Ecotrophic efficiency measures the proportion of the annual production that is available for predation as well as lost to direct predation (including as fishery landings, migration, spawning output, growth) or accumulated. The remainder of the production (a fraction of 1-E) is transferred to a detrital group. Generally, few birds are actively killed by other marine consumers (say, corresponding to 1% of total avian production). A larger proportion of bird production will be birds dying over land and lost to the terrestrial system (these are exports from the system). It is likely that most avian production will end up within the marine system as dead birds (carcasses). The ultimate fate of these carcasses is to be scavenged by other marine biota.

Jackson (1986) measured mean assimilation efficiencies (AE) of five white-chinned petrel (*Procellaria aequinoctialis*) fledglings fed on light-fish (*Maurolicus muelleri*), squid (*Loligo reynaudi*) and Antarctic krill (*Euphausia superba*). AE were found for these prey items to be (respectively) 67.5–77.9%. Here, we use 0.3 as the proportion of unassimilated food (U=1-AE) for all bird groups, in line with Pinkerton et al. (2010) but up from U=0.2 for birds used by Pinkerton et al. (2008)

Export and import of material can occur from a number of sources: (1) export from the system due to birds on average having a different weight when leaving the study area than when entering; (2) mortality of birds occurring over terrestrial habitat or over marine habitat outside of the study area; (3) different number of birds entering the study area than leaving it over a year, corrected for differences in their weight. Export by changes in weights of birds was assumed to be close to zero for those species that breed in the study region. We estimated the proportion of mortality likely to occur over land, as between 1–50% depending on species. We estimated the proportion of mortality that occurred outside the study region to be between 0–90% depending on species. Summing these three sources of export across all species gave an export to production ratio, X/P of 32%.

Table 32: Summary information for seabirds of the Hauraki Gulf region for the present day trophic model.

Species	**Scientific name**	**Breeding** N pairs	**N** N birds	**W** Mass (gWW)	**S** Proportion in area	**M** Month present	**B** tonnes WW	**P/B** y^{-1}	**Q/B** y^{-1}
Breeding species									
Sooty shearwater	*Puffinus griseus*	1 000	2 721	800	0.1	8	0.1	0.31	103
Flesh-footed shearwater	*Puffinus carneipes*	25 000	64 315	600	0.3	8	7.7	0.32	112
Fluttering shearwater	*Puffinus gavia*	50 000	112 377	300	0.8	12	27.0	0.36	137
Little shearwater	*Puffinus assimilis*	7 500	15 869	220	0.2	10	0.6	0.38	150
Common diving petrel	*Pelecanoides urinatrix*	100 000	200 000	130	0.8	10	17.3	0.42	174
Black petrel	*Procellaria parkinsoni*	2 000	5 302	700	0.25	9	0.7	0.31	107
Cook's petrel	*Pterodroma cookii*	286 000	594 022	200	0.1	9	8.9	0.39	154
Pycroft's petrel	*Pterodroma pycrofti*	3 000	6 000	160	0.1	7	0.1	0.40	164
Grey-faced petrel	*Pterodroma macroptera*	175 000	442 627	550	0.15	10	30.4	0.32	115
White-faced storm petrel	*Pelagodroma marina*	50 000	100 000	45	0.3	8	0.9	0.51	236
Blue penguin	*Eudyptula minor*	7 500	21 317	1 000	1	12	21.3	0.30	97
Australasian gannet	*Morus serrator*	15 000	45 000	2 300	1	8	69.0	0.27	76
Black shag	*Phalacrocorax carbo*	1 000	3 000	2 200	0.65	12	6.6	0.49	77
Pied shag	*Phalacrocorax varius*	1 000	3 000	2 000	0.9	12	6.0	0.50	80
Little black shag	*Phalacrocorax sulcirostris*	500	1 500	800	0.65	12	1.2	0.53	103
Little shag	*Phalacrocorax melanoleucos*	500	1 500	700	0.75	12	1.1	0.65	107
Spotted shag	*Phalacrocorax punctatus*	350	1 050	1 200	1	12	1.3	0.51	92
King shag	*Leucocarbo carunculatus*	0	0	2 500	1	12	0	0.49	55
White-faced heron	*Ardea novaehollandiae*	1 000	3 000	550	0.5	12	1.7	0.54	115
Reef heron	*Egretta sacra*	500	1 500	400	0.9	12	0.6	0.56	126
Variable oystercatcher	*Haematopus unicolor*	167	500	725	0.8	12	0.4	0.42	106
Banded dotterel	*Charadrius bicinctus*	167	500	60	0.75	12	0.03	0.66	217
New Zealand dotterel	*Charadrius obscurus*	33	100	145	0.85	12	0.01	0.61	169
Black-backed gull	*Larus dominicanus*	3 333	10 000	950	0.4	12	9.5	0.41	98
Red-billed gull	*Larus novaehollandiae*	6 667	20 000	280	0.65	12	5.6	0.46	140
Caspian tern	*Sterna caspia*	133	400	700	0.95	12	0.3	0.42	107
White-fronted tern	*Sterna striata*	2 500	5 000	160	1	12	0.8	0.43	164

Species	Scientific name	Breeding	N	W	S	M	B	P/B	Q/B
Non-breeders in region									
Buller's shearwater	*Puffinus bulleri*	0	2 000 000	425	0.25	8	141.7	0.11	149
Fairy prion	*Pachyptila turtur*	0	30 000	125	0.25	7	0.5	0.11	211
Royal spoonbill	*Platalea regia*	0	15	1 700	0.8	12	0.03	0.11	100
South Island oystercatcher	*Haematopus finschi*	0	8 750	550	0.8	12	4.8	0.07	138
Pied stilt	*Himantopus himantopus*	0	2 500	190	0.8	12	0.5	0.06	187
Pacific golden plover	*Pluvialis fulva*	0	25	130	1	12	0.00	0.11	209
Lesser knot	*Calidris canutus*	0	4 400	120	1	12	0.5	0.09	214
Wrybill	*Anarhynchus frontalis*	0	1 050	60	1	12	0.1	0.09	261
Turnstone	*Arenaria interpres*	0	85	120	1	12	0.01	0.08	214
Red-necked stint	*Calidris ruficollis*	0	5	30	1	12	0.00	0.11	318
Bar-tailed godwit	*Limosa lapponica*	0	8 650	325	1	12	2.8	0.08	161
Small albatrosses	E.g. *Diomedea antipodensis* *Diomedea gibsoni*	0	40 000	6 500	1	1	22	0.11	58
Northern giant petrel	*Macronectes halli*	0	500	4 000	1	2	0.33	0.11	67

Table 33: Diet summary information for seabirds of the Hauraki region for the present day model. Values are the proportions of prey items in the diet.

Species	Scientific name	Non-marine food	Fish	Squid	Crusta-ceans	Intertidal bivalves and gastropods	Soft sediment inverts	Carcasses
Breeding species								
Sooty shearwater	*Puffinus griseus*	0	0.9	0.05	0.05			
Flesh-footed shearwater	*Puffinus carneipes*	0	0.5	0.5				
Fluttering shearwater	*Puffinus gavia*	0	0.8		0.2			
Little shearwater	*Puffinus assimilis*	0	0.33	0.33	0.34			
Common diving petrel	*Pelecanoides urinatrix*	0			1			
Black petrel	*Procellaria parkinsoni*	0	0.15	0.75	0.1			
Cook's petrel	*Pterodroma cookii*	0	0.2	0.6	0.2			
Pycroft's petrel	*Pterodroma pycrofti*	0	0.1	0.8	0.1			
Grey-faced petrel	*Pterodroma macroptera*	0	0.3	0.6	0.1			
White-faced storm petrel	*Pelagodroma marina*	0	0.3		0.7			
Blue penguin	*Eudyptula minor*	0	0.5	0.5				
Australasian gannet	*Morus serrator*	0	0.99	0.01				
Black shag	*Phalacrocorax carbo*	0.35	1					
Pied shag	*Phalacrocorax varius*	0.10	1					
Little black shag	*Phalacrocorax sulcirostris*	0.35	1					
Little shag	*Phalacrocorax melanoleucos*	0.25	1					
Spotted shag	*Phalacrocorax punctatus*	0.00	0.9	0.1				
King shag	*Leucocarbo carunculatus*	0.25	0.9	0.1				
White-faced heron	*Ardea novaehollandiae*	0.50	1					
Reef heron	*Egretta sacra*	0.10	0.8		0.1	0.1		
Variable oystercatcher	*Haematopus unicolor*	0.20			0.1	0.8	0.1	
Banded dotterel	*Charadrius bicinctus*	0.25			0.2	0.5	0.3	
New Zealand dotterel	*Charadrius obscurus*	0.15			0.4	0.4	0.2	
Black-backed gull	*Larus dominicanus*	0.60	0.45	0.15		0.2		0.2
Red-billed gull	*Larus novaehollandiae*	0.35	0.2		0.8			
Caspian tern	*Sterna caspia*	0.05	1					
White-fronted tern	*Sterna striata*	0	1					

Species	**Scientific name**	**Non-marine food**	**Fish**	**Squid**	**Crusta-ceans**	**Intertidal bivalves and gastropods**	**Soft sediment inverts**	**Carcasses**
Non-breeders in region								
Buller's shearwater	*Puffinus bulleri*	0	0.5		0.5			
Fairy prion	*Pachyptila turtur*	0	0.04		0.96			
Royal spoonbill	*Platalea regia*	0	0.33		0.33	0.34		
South Island oystercatcher	*Haematopus finschi*	0.00			0.1	0.8	0.1	
Pied stilt	*Himantopus himantopus*	0.20			0.2	0.4	0.4	
Pacific golden plover	*Pluvialis fulva*	0.20			0.35	0.35	0.3	
Lesser knot	*Calidris canutus*	0.20			0.15	0.85		
Wrybill	*Anarhynchus frontalis*	0			0.8	0.1	0.1	
Turnstone	*Arenaria interpres*	0			0.75	0.25		
Red-necked stint	*Calidris ruficollis*	0			0.35	0.65		
Bar-tailed godwit	*Limosa lapponica*	0			0.2	0.4	0.4	
Small albatrosses	E.g. *Diomedea antipodensis* *Diomedea gibsoni*	0.00	0.5		0.5			
Northern giant petrel	*Macronectes halli*	0.00	0.5		0.5			

7 Historical parameters

7.1 Models required

Trophic models are required for four historical periods:

- 1950 – just prior to onset of industrial-scale fishing
- 1790 – before European whaling and sealing
- 1500 – early Maori settlement phase
- 1000 – before human settlement in New Zealand

7.2 Biomass

Before human contact, small burrowing seabirds (especially petrels) probably covered the fringes of the study area. These would have been quickly depleted by the coming of the Polynesian (Pacific, or brown) rat (*Rattus exulans*), which probably arrived with the first Māori settlers. The European settlers brought, amongst other predators, the black rat (*Rattus rattus*) to mainland New Zealand which would have exacerbated the decline of the shore-nesting seabirds. In addition, Māori and European settlers caught seabirds for food and other uses. We take our estimates of historical human removals of seabirds from Smith (2011). The magnitudes of the declines in seabird numbers are not well known. For example, Lalas (2007) notes: "I disagree with the paradigm that New Zealand was a seabird paradise 1000 y BP [before present]. Large predators were present and I suggest that their impact then was similar to that of mammalian predators now." Lalas (2007) estimated numbers of five species of shag between the present day and 1000 y BP, and suggested that some species were probably tenfold more abundant before human contact (black shag, *Phalocrocorax carbo*) whereas others may be more abundant now than in the past (king shag, *Phalacrocorax carunculatus*).

We estimated numbers of seabirds for each period in history (Table 34). We note that numbers in 1000 for the petrels are probably conservative as numbers of these burrow breeding species could have been two to three times higher than the numbers indicated pre human settlement because of the large breeding areas available on the mainland before Pacific rats and dogs arrived. The net effects of these changes in individual species on the biomass of the "birds" component of the trophic model are shown inTable 35. Avian biomass as a proportion of the present day biomass is estimated to be 0.67 (1950), 1.76 (1790), 2.37 (1500) and 3.62 (1000).

Table 34: Numbers of birds by species estimated for each historical model.

Species	Total number (includes breeders, non-breeders, juveniles)				
	Present	1950	1790	1500	1000
Breeding species					
Sooty shearwater	2 721	2 721	6 000	6 000	10 000
Flesh-footed shearwater	64 315	64 315	150 000	150 000	300 000
Fluttering shearwater	112 377	112 377	250 000	250 000	500 000
Little shearwater	15 869	15 869	35 000	35 000	100 000
Common diving petrel	200 000	200 000	500 000	500 000	1 000 000
Black petrel	5 302	5 302	10 000	10 000	100 000
Cook's petrel	594 022	594 022	1 200 000	1 200 000	2 000 000
Pycroft's petrel	6 000	6 000	12 000	12 000	600 000
Grey-faced petrel	442 627	442 627	500 000	550 000	600 000
White-faced storm petrel	100 000	100 000	200 000	200 000	300 000
Blue penguin	21 317	21 317	250 000	300 000	350 000
Australasian gannet	45 000	35 000	15 000	50 000	90 000
Black shag	3 000	2 500	100	10 000	15 000
Pied shag	3 000	2 500	100	10 000	15 000
Little black shag	1 500	1 250	50	0	0
Little shag	1 500	1 250	50	5 000	7 500
Spotted shag	1 050	1 050	2 000	3 000	4 000
King shag	0	0	0	10 000	15 000
White-faced heron	3 000	3 000	3 000	3 000	3 000
Reef heron	1 500	1 500	1 500	1 500	1 500
Variable oystercatcher	500	500	125	125	5 000
Banded dotterel	500	500	125	125	5 000
New Zealand dotterel	100	100	25	25	1 000
Black-backed gull	10 000	10 000	80 000	80 000	80 000
Red-billed gull	20 000	20 000	30 000	30 000	30 000
Caspian tern	400	400	1 000	1 000	1 000
White-fronted tern	5 000	5 000	40 000	40 000	40 000
Non-breeders in region					
Buller's shearwater	2 000 000	500 000	100 000	500 000	2 500 000
Fairy prion	30 000	20 000	20 000	25 000	40 000
Royal spoonbill	15	15	0	0	0
South Island oystercatcher	8 750	8 750	8 750	8 750	8 750
Pied stilt	2 500	2 500	2 500	2 500	2 500
Pacific golden plover	25	25	25	25	25
Lesser knot	4 400	4 400	4 400	4 400	4 400
Wrybill	1 050	1 050	8 000	8 000	10 000
Turnstone	85	85	85	85	85
Red-necked stint	5	5	5	5	5
Bar-tailed godwit	8 650	8 650	8 650	8 650	8 650
Small albatrosses	40 000	40 000	40 000	40 000	40 000
Northern Giant petrel	500	500	600	800	1 000

7.3 Productivity and other energetic parameters

Biomass, energetics, and other key parameters for the collected trophic group of “birds” in the historical models were calculated assuming that the present day values for these parameters for a given species have not changed. It is possible that these parameters have varied from the present day situation due to factors including climate (see Lorrey et al. 2013 for details of climate variability over the model periods), run-off (including sedimentation), predation (both by marine biota and humans), and food availability, but we think that these changes will be relatively low compared to the effects of historical climate variability on other biota. Changes in the parameters shown in Table 30 hence reflect the fact that the "birds" group is made up of many species that have different energetic parameters. Because the relative abundances of birds with different parameters change through history, these estimates of the parameters for the overall "birds" group also varies with historical period.

7.4 Fishery removals

Smith (2011) estimated the magnitude of pre-European Maori marine harvest of fish, seabirds, invertebrates and mammals based on data preserved from middens, for years (actually, periods about nominal years) 1400, 1550 and 1750. The last is taken to be representative of that in 1790. Linear interpolation is used to estimate catch in 1500. Catches of birds are estimated to be 25 tWW (1500) and 56 tWW (1790). Although there will have been some mortality of seabirds by fishing in 1950 and the present day, these are assumed to be small and are not included in the model.

7.5 Diet

Diets for the collected trophic group of "birds" in the historical models were estimated by assuming that the present day diets for each of the species of bird found in the study area were the same historically as in the present day. Because the relative abundances of birds with different diets changes through history, these estimates of the diet composition of the birds group will vary with historical period. These initial estimates of bird diet are shown in**Table 36**. Note that diets of all groups in the trophic model, including birds, can vary during model balancing to take into account changes in competition for prey between predators and changes in the biomass of prey items with time.

8 Summary of parameters for models

Table 35: Summary of parameters for birds in the trophic model.

Model	B	P/B	Q/B	P/Q	U	EE	Export X/P	Fishery
	gC m^{-2}	y^{-1}	y^{-1}	%				gC m^{-2} y^{-1}
Present	0.0025	0.26	117	0.22	0.30	0.33	0.33	0
1950	0.0017	0.29	103	0.28	0.30	0.34	0.33	0
1790	0.0036	0.33	100	0.32	0.30	0.29	0.28	3.47E-04
1500	0.0049	0.33	96	0.34	0.30	0.23	0.22	1.56E-04
1000	0.0077	0.31	103	0.30	0.30	0.25	0.24	0

Table 36: Summary of diets for birds in the trophic model.

Prey	Proportions in diet				
	Present	1950	1790	1500	1000
Fish	0.50	0.51	0.46	0.52	0.51
Squid	0.12	0.16	0.30	0.27	0.21
Crustaceans	0.36	0.29	0.21	0.19	0.26
Intertidal bivalves & gastropods	0.016	0.027	0.021	0.016	0.012
Soft sediment inverts	0.005	0.008	0.004	0.003	0.002
Carcasses	0.002	0.003	0.010	0.008	0.005
Total	1	1	1	1	1

9 Acknowledgements

This research was funded by Ministry of Fisheries project ZBD200505 (“Long-term change in New Zealand coastal ecosystems”) and by the New Zealand Ministry of Science and Innovation project C01X0501 (Coasts & Oceans OBI). We acknowledge Dr Mary Livingston and Dr Martin Cryer (Ministry for Primary Industries) for supporting this project. Dr Chris Lalas provided useful comments on a draft of this work.

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Appendix 3: Trophic modelling of Hauraki Gulf: Cetaceans

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1 General information

1.1 Species

We worked at the species level to determine or estimate model parameters and then combined then them where necessary to form larger groupings. Cetacean species considered to occur frequently enough in the study area to be included in the model were humpback whale, southern right whale, killer whale (orca), Bryde's whale, short fin pilot whale, long finned pilot whale, common dolphin, and bottlenose dolphin. Historically southern right whale cows and calves occurred seasonally (autumn and winter) in the Hauraki Gulf but in the modern period are effectively locally extinct. Transient species such as blue whale, fin whale and minke whale have sometimes been sighted in the study area but so rarely that these species were not included in the model estimates.

The main local information on cetaceans used in the current model are: (1) the number of individuals in the study area; (2) the time they are in the area for over the year. As there are few local measurements for many of the other required model parameters for cetaceans in the study area, we generally take these values from the scientific literature, sometimes derived from allometric relationships: (a) production rates (intrinsic growth rate of population, net of respiration; based on adult mortality rates); (b) consumption rates (amount of prey consumed); (c) diet (i.e. what they are feeding on); (d) ecotrophic efficiencies (proportion of total mortality due to direct predation rather than other sources of mortality such as disease, “old-age” and starvation).

1.2 Biomass carbon conversion

We assume that the carbon content of toothed and baleen whales in the Hauraki Gulf is 10% of wet weight (0.1 gC/gWW)(Vinogradov 1953), following previous trophic modelling work (e.g., Bradford-Grieve et al. 2003, Pinkerton et al. 2010) and consistent with Jelmert & Oppen-Berntsen (1996) and Pershing et al. (2010).

2 Information by species; biomass

2.1 Introduction

The number of individuals of a given species of cetacean in the study areas is likely to vary with season. In order to estimate an annual average number we used either an indication of the number in the area seasonally (e.g. an abundance estimate for the summer, autumn, winter, spring), or a number for a period of time (e.g. “100 animals for 3 months over the summer”). Energetic parameters (including production, consumption) were adjusted pro rata over this time taking into account what was known about what the animals were doing when in the study area. For example, if the animals are known to come into the area specifically to feed, consumption rates while in the study area are likely to be higher than the annual average. If birth occurs in the study area, production is likely to be higher in the study area than suggested by a proportion of the annual average production.

2.2 Humpback whale

The humpback whale (*Megaptera novaengliae*) is found in all the major ocean basins and migrates long distances; in the summer, humpbacks migrate poleward to exploit the high productivity of the cold waters and in winter travel to warm tropical waters. Globally, there may be about 22 000–40 000 humpback whales (Young 2000; SeaMap 2005) but more recent work suggests that this may be an underestimate. In the Southern Ocean, the population of humpback whales was thought to number a few thousand (Northridge 1984). Laws (1977) gives figures of 100 000 and 3000 for total southern stock sizes before and after exploitation. Tamura (2003) gives a population size for ocean south of 30°S as 10 000 (International Whaling Commission 2000). The International Whaling Commission website gives figures of humpback population (with 95% confidence levels) of 42 000 (34 000–52 000) for the Southern Hemisphere in 1997/98. Austral summer estimates of abundance in the Southern Ocean from three circumpolar surveys completed in the period 1978–79 to 2003–04 indicated that all breeding stocks are increasing and the rate of increase is more than 5% (Branch 2006). Zenkovich (1970) estimated that Southern Ocean populations of humpback whales spent 120 d y^{-1} in the Antarctic region.

Humpback whales are not included in the New Zealand National Aquatic Biodiversity Information System (NABIS). There were 397 reported sightings of humpback whales in the New Zealand region between 1981 and 2007 from the DoC incidental sightings database and a database of cetacean sightings around New Zealand assembled by Martin Cawthorn[1] (L. Torres, NIWA, pers. comm.). Most incidental sightings of humpback whales in the New Zealand region are along the north-east coast of the North Island with another concentration in the Cook Strait region. We note that the same whales may be sighted more than once in any year. In the study area, sightings of humpback whales are occasionally reported; 52 sightings comprising 107 animals over 26 years. Most sightings (62%) were of two of more individuals, with one group of fifty animals observed off Kawau Island in September 1986 and another group of thirty animals observed off Tiri Island in August 1985. Humpbacks were sighted in all months but only 7.7% of sightings were in autumn and these were either single individuals or pairs which accounted for only 6.5% of whales. Thirty-five percent of sightings occurred in spring, often in large groups, and accounted for 84% of individuals sighted. Presumably these were animals migrating from the tropical calving and mating areas to the summer feeding grounds in the vicinity of the Ross Sea.

It is not known what proportion of humpback whales in the study area are likely to be sighted, or how many of these sightings would be reported to DoC. Humpback whales are generally quite visible, and the number of people using the Hauraki Gulf is quite substantial, so it is likely that the occasional sightings of humpback whales in the study region is indicative of a modest number of humpback whales actually being present there. Based on these data, we assume 35 humpback whales in the larger region including the study area for 3 months of the year, and that these spend 25% of their time in the study region.

Humpback whales measure 11–17 m as adults and attain a weight of at least 35 t (SeaMap 2005). Mackintosh (1965) gives 33.2 t as a typical adult weight. Here, we use 30.4 t as the average weight within a population of humpback whales (Trites & Pauly 1998). Longevity is reported as 75 y (Trites & Pauly 1998).

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[1] The Cawthorn cetacean sighting database is based on sightings recorded by trained observers aboard transiting ships between New Zealand and overseas ports collated between 1979 and 1999.

Chittleborough (1965) states that *Euphausia superba* is the main food item, but that the krill *Thysanoessa macrura* is also eaten (Northridge 1984). Humpback whales are generalists, eating krill, copepods, fish, and cephalopods. Humpback whales exhibit a wide range of feeding habits intended to concentrate prey, which may be employed individually or in groups, including lunging, bubble-netting and lob-tail feeding (SeaMap 2005). Bottom feeding has also been documented. We assume a diet of humpback whales in the study region of: 50% crustacean macrozooplankton; 30% mesozooplankton; 20% gelatinous zooplankton.

2.3 Southern right whale

Southern right whales (*Eubalaena australis*) were once widely distributed throughout the waters of New Zealand. New Zealand right whales were the target of pelagic and shore whaling from the beginning of the nineteenth century and, as in all other areas where right whales were encountered, hunting was so intense that this species had virtually disappeared from these regions by the twentieth century (Dawbin 1986). Only 6 of the 78 sightings (7.6%) of right whales around the New Zealand mainland in the modern period (1981–2007) were in the Hauraki Gulf region so we assume that, on average, 6/27=0.2 (6 sightings over 27 years) southern right whales occur in the study area for the modern day model. Historically, right whale cows calved in bays along the east coast of mainland New Zealand and around the sub-Antarctic islands during the austral winter, moving offshore during the summer months (McNab 1913; Dawbin 1986). For the present day model, we assume that no calving occurs in the study area and that, when present, the whale is moving through the study area and likely to remain in the study area for only 1 month per year.

Southern right whale adults reach up to 17 m in length (females grow larger than males) and can reach weights of 80 t (SeaMap 2005). Here, we use 65 t as the mean weight in the population. Newborn animals are 4–5 m long (SeaMap 2005), and may weigh about 3 t.

Southern right whales are baleen whales and use surface and subsurface skim feeding, with the main prey being copepods and krill, apparently sometimes feeding near the bottom in shallow habitats (SeaMap 2005; Cummings 1985). We assume a diet of southern right whales in the study region of: 50% crustacean macrozooplankton; 30% mesozooplankton; 20% gelatinous zooplankton.

2.4 Bryde's whale

Globally, there are two species of Bryde’s whales, as confirmed by molecular evidence (Wada et al. 2003): *Balaenoptera brydei* and *Balaenoptera edeni*. Bryde’s whales in New Zealand waters are considered to be *Balaenoptera brydei* (N. Wiseman, Auckland University, pers. comm.). Globally, Bryde’s whales are distributed between 40° N and 40° S, predominantly in waters of 15–20 °C (O’Callaghan & Baker 2002). There are no reliable global estimates of the population size of Bryde’s whales, although there is a 1998–2002 population estimate for the Western North Pacific of 20 500 (www.iwcoffice.org). There are no robust data with which to estimate the number of this species of whale in the study area.

The extent of the distribution of Bryde’s whales in New Zealand waters includes waters north of East Cape, and as far north as Raoul Island (N. Wiseman, pers. comm.), with animals generally being sighted within about 10 n. mile of the coast (Martin Cawthorn, unpublished data). All sightings of live Bryde’s whales reported to DoC were between Whitianga and northeast of Doubtless Bay suggesting that Bryde’s whales may make seasonal migrations along the north and eastern coasts of New Zealand (Baker 1999). It is likely that the Hauraki Gulf is a favoured location as most sightings of Bryde’s whales are in the Hauraki Gulf in summer and most strandings of Bryde's whales in New Zealand were from Hauraki Gulf waters, though one of the five stranded animals was found on a lower North Island west coast beach (Foxton Beach). Within the Hauraki Gulf, Bryde's whales are distributed in relatively shallow waters. During summer (October 2000–February 2001), Bryde's whales in the Hauraki Gulf were sighted generally in waters about 40 m deep with sea surface temperatures of 19–20°C, with most sightings in early February (O'Callaghan & Baker 2002). These whales were generally alone or in loose groups (at least 1 n. mile apart) in the middle of the inner Hauraki Gulf, though Bryde's whales have been sighted near Little Barrier Island and Great Barrier Island. They are often associated with seabirds such as Australasian gannets (*Morus serrator*) and common dolphins (*Delphinus delphis*) (O'Callaghan & Baker 2002). The New Zealand population of Bryde's whales is classed by the Department of Conservation as Nationally Critical (Hitchmough et al. 2007). The numbers of animals in the Hauraki Gulf is estimated to be 18±9 (SE) (estimated from Baker & Madon 2007) and 46 (CV 0.08) by Wiseman (2008). Here, we take the number in the vicinity of the study region to be an average of these, i.e. 32 individuals.

It is not known if these Bryde's whales are resident in the Hauraki Gulf (O'Callaghan & Baker 2002). Bryde's whales, unlike other species of Balaenoptera, are not known to make long-distance migrations between summer and winter areas (Kato 2002). Instead, limited shifts in distribution toward and away from the equator in winter and summer respectively have been observed (Wiseman 2008). The Hauraki Gulf population of Bryde's whales were considered to be non-migratory in the broad geographic sense, making only local seasonal movements (Wiseman 2008 and references therein). This is consistent with sightings of Bryde's whales having been made in every month of the year except August. However, current work in the Hauraki Gulf (http://www.adopt-a-dolphin.com/nicky_wiseman.htm) suggests that some Bryde's whales are not resident there all year. Here we assume Bryde's whales are present in the study area for 11 months of the year, but that only 25% of the population is in the study area at any time.

Males are usually slightly smaller than females. Lengths are 12–17 m, with typical animal adult lengths given as 11.2 m (male) and 11.7 m (female) (Rice 1998), with typical maximum weights of 14 t (male) and 16 t (females), Gaskin (1968), based on Great Barrier Island whaling station records (quoted unseen from IWC fact sheet). Here, we use 12 t as a mean weight for the population.

Lifespan of Bryde's whales has been estimated to be 69 from ear plugs, but may possibly be as high as 91 years (Wiseman 2008). A natural mortality rate of 0.078 y^{-1} was given by Hakamada et al. (2007) giving a 1% survival at age 59 years, and 0.1% survival at 89 years. Orca are natural predators of Bryde's whales, but they are only partially consumed, with the orca taking mainly the tongue, and lower jaw and perhaps the skin and either ventral or dorsal surface (Wiseman 2008 and references therein).

Bryde's whales are baleen whales and reported as opportunistically feeding on plankton (e.g., krill and copepods), and crustaceans (e.g. pelagic red crabs, shrimp) as well as schooling fish (e.g., anchovies, herring, mackerel, pilchards, and sardines) (NOAA Fisheries Service 2009). Bryde's whales regularly dive for about 5–15 minutes (maximum of 20 minutes) after 4–7 blows at the surface, and are capable of reaching depths up to 300 m during dives. Bryde's whales use several feeding methods, including skimming the surface, lunging, and bubble nets. The diet of Bryde's whales includes: (1) fish (probably small pelagic fishes such as pilchards *Sardinops sagax*), 100% occurrence in scats; (2) amphipods (presumably Hyperids), 70% occurrence in scats; (3) euphausids, occurrence 70% in scats; (4) copepods, occurrence 30% in scats. For the purposes of the model we take the diet based on this information to be: (1) 50% small pelagic fish (including a proportion of juvenile fishes); (2) 35% crustacean macrozooplankton (euphausiids, pelagic amphipods); (3) 15% crustacean mesozooplankton (mainly copepods).

2.5 Orca/killer whale

Orca or killer whales (*Orcinus orca*) are probably the most cosmopolitan of all cetaceans, being found from ice edges to the equator, in both hemispheres, and most usually being found to feed within 800 km of the coast (Klinowska, 1991). Orca have generally been considered to constitute a single species throughout the world (Rice 1998) even though since the 1970s several groups of researchers independently concluded that, based on differences in morphology, ecology and acoustic repertoire, there were three recognisably different forms of orca in the Antarctic (Pitman & Ensor 2003, and references therein): type A, type B and type C. Recent work suggests that all three different types of orca may occur in the Ross Sea (Pitman et al. 2001; Pitman & Ensor 2003). It has been suggested that type-B and type-C orca are separate species from *Orcinus orca* (Pitman & Ensor 2003), although this is still a subject of scientific debate. Type A is the typical and largest form of *O. orca*, being black and white in colour, without a visible dorsal cape. Type-B and type-C orca have dorsal capes, and are a lighter grey colour rather than black. The white colour is often tinged yellow, probably due to a diatom film. The eyepatch size and shapes differ between the three types (Pitman & Ensor 2003). Type-B and type-C are shorter than type-A orca by about 1 m in total length. The groups are also distinguished by their diet and feeding strategies. In the Southern Ocean, Pitman & Ensor (2003) suggest that type A predominantly predate on whales but may take fish, type B seem to predominantly predate on seals, and type C seem to be exclusively fish eaters. These feeding habits may change in different areas. The migratory status of type-B and type-C orca are unknown, and these may not make such extensive migrations as type-A (Pitman & Ensor 2003 and references therein). Types B and C are likely to remain at higher latitudes, whilst type A is thought to be the most migratory. Here, we assume killer whales found in the study region are likely to be type-A.

Type-A male orca in the Antarctic grow to 6.7–8.2 m (maximum 9.5 m) and females to 5.2–7.3 m (Fad, 1996). Mikhalev et al. (1981) report maximum lengths of 9.0 m and 7.7 m for male and female (respectively) Adult male type-A orca are reported as weighing up to approximately 8000 kg, and females as weighing up to 4000 kg (Baird 2000), much higher than average weights of type B and C orca. Based on data from the live-capture fishery for *Orcinus orca* in British Columbia and Washington in the 1960s and 1970s, Bigg & Wolman (1975) calculated the relationship between body length and weight in both sexes of orca as $W=29.65L^{2.577}$ where W is the weight (kg) and L is length (m). This relationship lies within the 95% confidence intervals for the length-weight relationship given by Clark et al. (2000) for captive orca even though captive orca tend to be heavier for a given length than wild animals. Here, we assume an average length of 7.0 m and an average weight of 4400 kg in the population.

The Antarctic population of orca was reported as 160 000 (Hammond 1983; Northridge 1984), although this may have been an overestimate as the population around Antarctica (south of 60°S) has more recently been estimated at 70 000 animals (Klinowska, 1991). The New Zealand National Aquatic Biodiversity Information System (NABIS) shows orca occurring around the coast of both North and South Island, and over the Chatham Rise, and was used to develop this summary. The NABIS killer whale distribution map was based on the cetacean strandings database maintained by the Museum of New Zealand Te Papa Tongarewa, Wellington, and the cetacean sightings database held by DoC. The latter contained 208 records of sightings of killer whales reported mainly by DoC staff and dolphin-watching tour operators between 1990 and 2009.

No robust estimates of killer whale numbers in New Zealand waters exist, but a reasonable attempt at assessing population numbers was made by Visser (2000). Baker (1999) describes killer whales as common in New Zealand waters and at least 117 individuals have been photo-identified (Visser 2000). Resighting rates were high, with 75% (n=88) of the animals seen on more than two occasions. Visser (2000) concludes that "*orca in New Zealand have a population between 65 and 167 with the results from the Total Enumeration and Jolly Seber calculations suggesting that the Total Enumeration in 1997 (i.e., 115 orca) is a reliable but conservative estimate.*" Visser (2000) notes that this number is well below the population size of 500 suggested by Soulé (1987) as a viable population.

The New Zealand orca population appears to be made up of at least three sub-populations: (1) North Island only; (2) South Island only; and (3) North and South Island subpopulation. Preliminary mtDNA analysis supports the hypothesis that some New Zealand orca do not mix (Visser 2000). All sub-populations are likely to be breeding (Visser 2000). Killer whales have been sighted in New Zealand waters in all months, though sightings in the summer are commonest perhaps due to increased observer effort. Animals move north as the temperatures cool; animals sighted in the winter months in the Hauraki Gulf and Bay of Islands were in Kaikoura and Cook Strait waters in summer months (Visser 2000). Stranded animals have been reported from the east coast of the North Island, north of Hauraki Gulf (stranding database, Visser & Fertl 2000) and multiple strandings were reported at Paraparaumu Beach (17 animals) and Chatham Islands (11 animals) (Baker 1999). All sightings reported to DoC were between 32° (North Cape) and 47° S (near Stewart Island).

The Hauraki study region is located in "Region One" of Visser (2000) which covers the area east of North Island between North Cape and Waihi. This region contains the highest number of sightings of any of the six regions of that study. Visser (2000) notes that "the possibility remains that the high number of sightings reported in Region One may also be due to a high usage of this area by orca, or may reflect a large sub-population of orca in this area." Based on the relative number of sightings in each area, normalised by the average of the number of people and the amount of research effort in each region (all Visser 2000), we suggest a crude estimate of the proportion of the orca population in Region One of 22%. This corresponds to 15–37 whales (best estimate of 26) being present on average at any time in Region One. Orca tend to be transient visitors and move through the region so that this number is likely to be made up of a much larger number of individual animals. The study area makes up approximately half of Region One, suggesting an average population of about 13 orca.

Visser (2000) summarises the feeding of New Zealand orca as follows: "The prey consists of four types; rays (the most common food type), sharks, fin-fish and cetaceans (pinnipeds have not been identified as a prey source). Foraging strategies were different for each prey type, with benthic foraging for rays in shallow waters the most diverse strategy used in New Zealand. .... One of the three proposed New Zealand subpopulations appears to be generalist or opportunistic foragers, feeding on all four prey types, another sub-population slightly less so, feeding on three prey types, and the third sub-population appears to be a more specialist forager, only recorded taking one prey type (cetaceans)." Here, we take the diet of orca in the study area to be (Visser 2000): 63% rays (short tailed stingray, *Dasyatis brevicaudatus*; long tailed stingray, *Dasyatis thetidis*; eagle ray, *Myliobatis tenuicaudatus*; torpedo ray, *Torpedo fairchildi*); 12% sharks (blue shark, *Prionace glauca*; basking shark, *Cetorhinus maximus*; mako shark, *Isurus oxyrinchus*; school shark, *Galeorhinus galeus*); 16% large demersal fish (inter alia: yellow fin tuna, *Thunnus albacares*; sunfish, *Mola molabluenose*; bluenose, *Hyperoglyphe antarchia*; kahawai, *Arripis trutta*:); 9% cetaceans (mainly dolphins, including common dolphin and bottlenose dolphin).

2.6 Long-finned pilot whale

This summary of the biology and feeding of the long-finned pilot whale (*Globicephala melas*) is largely taken from Culik (2010a). We note that although long- and short-finned pilot whales (*G. melas* and *G. macrorhynchus* respectively) differ in flipper length, skull shape and number of teeth, they can be difficult to distinguish at sea so sighting information at sea is generally unreliable.

Two subspecies of long-finned pilot whales are recognized in some classifications (Rice 1998): (1) northern hemisphere subspecies, *G. m. melas*, which ranges in the North Atlantic from Greenland to the western Mediterranean; (2) southern hemisphere subspecies, *G. m. edwardii*, which is circumglobal in the Southern Hemisphere, ranging north to Brazil, South Africa, Iles Crozet, Heard Island, the southern coast of Australia, and north of New Zealand, encompassing the study area. Southward it extends at least as far as the Antarctic Convergence 47°S to 62°S and has been recorded near Scott Island (67°S, 179°W) and in the central Pacific sector at 68°S, 120°W (Rice 1998). There is little information on stocks within the species, and there is no information on global trends in abundance (Taylor et al. 2008). Population estimates for the southern hemisphere subspecies is in the order of 200 000 long-finned pilot whales (Bernard & Reilly 1999). The typical temperature range for the species is 0–25°C (Martin 1994) and is mainly found in offshore waters (Reyes 1991). Calving and breeding can apparently occur at any time of the year, but peaks occur in summer in both hemispheres (Jefferson et al. 1993).

Numbers of long-finned pilot whales in the study region are not known, but these whales are sighted in the region (Martin Cawthorn, unpublished data). This species is generally found in pods of 110, but some groups contain up to 1200 individuals (Zachariassen 1993; Bloch 1998). Movement rates or patterns in the southern hemisphere are not known. Long-finned pilot whales are one of the species most often involved in mass strandings, and regularly strand on the beaches of northern New Zealand, so it is assumed that a number of individuals regularly come into this region for some reason. Strandings of long-finned pilot whales in northern New Zealand occur year-round although more commonly in spring and summer (O'Callaghan et al. 2001). For the purposes of the model until better information is available, we will assume that 110 long-finned pilot whales (1 average-sized pod) lives are in the vicinity of the study area (i.e. off the northeast coast of New Zealand) year round, but that they spend only a portion of their time (nominally 10%) in the study region.

Adult long-finned pilot whales reach a body length of approximately 6.5 m, males being about 1 m larger than adult females (Bloch et al. 1993; Olson, 2009). Body mass reaches up to 1300 kg in females and up to 2300 kg in males (Jefferson et al. 2008). These values are lower than given by Shirihai (2008) of 2600 kg. For this study, we take the average adult weights of long- and short-finned pilot whales to be 1800 kg (mean of data from Jefferson et al. 2008).

The diet of long-finned pilot whales in the study area is not known and must be inferred from elsewhere. Pilot whales are primarily squid eaters, but will also take small medium-sized fish (Desportes & Mouritsen 1993; Jefferson et al. 1993). They feed mostly at night, when dives may last for 18 minutes or more and reach 828 m depth (Carwardine 1995; Heide-Jørgensen et al. 2002). In the northern hemisphere, the main prey was found to be squid (*Illex illecebrosus*, *Loligo pealei*, *Todarodes sagittatus*, species of the genus *Gonatus*), although cod (*Gadus morhua*), Greenland turbot (*Rheinhardtius hippoglossoides*), Atlantic mackerel (*Scomber scombrus*), turbot (*Scomber scombris*), herring (*Clupea harengus*), hake (*Merluccios bilinearis*; *Urophysis* spec.) and dogfish (*Squalus acanthias*) were also eaten (Abend & Smith 1997; Olson 2009; Mintzer et al. 2008). In the southern hemisphere, although squids are the predominant prey around the Faroe Islands, some fish, such as *Argentina silus* and *Micromesistius poutassou*, are taken too. The whales in this region do not appear to select cod, herring or mackerel, although they are periodically abundant (Reyes 1991; Desportes & Mouritsen 1993; Bernard & Reilly 1999). Off the South Island of New Zealand, long-finned pilot whales feed exclusively on cephalopods, mainly arrow squid, Nototodarus spp., and common octopus, *Pinnoctopus cordiformis* (Beatson & O'Shea 2009). In the trophic model, the diet of long-finned pilot whales is set to be 90% squid, 10% medium-large sized demersal fish, with consumption of species weighted by their estimated relative biomass in the study area.

2.7 Short-finned pilot whale

This summary of the biology and feeding of the short-finned pilot whale (*Globicephala macrorhynchus*) is based on Culik (2010b). Short-finned pilot whales are found in deep offshore areas and usually do not range north of 50°N or south of 40°S (Jefferson et al. 1993), so that the Hauraki Gulf study area is towards the southern limit of the range of this species. The number of short-finned pilot whales in the western Pacific is poorly known but may be of the order of 100 000 individuals (Culik 2010b). Numbers, movement patterns, and habitat usage of short-finned pilot whales in the study region are not known. The species prefers deep water and occurs mainly at the edge of the continental shelf and over deep submarine canyons (Carwardine, 1995). Davis et al. (1998) found that *G. macrorhynchus* in the Gulf of Mexico preferred water depths between 600 and 1000 m.

This preference for deep water habitat is also supported by diet studies. Mintzer et al. (2008) examined the stomach contents of short-finned pilot whales from the North Carolina coast and found that they predominantly consumed squid (*Brachioteuthis riisei*, *Taonius pavo*, *Histioteuthis reversa*), and also fish (*Scopelogadus beanii*). The results indicated that the whales fed primarily off the continental shelf prior to stranding. Stomach content composition differed from those of short-finned pilot whales from the Pacific coast in which neritic species dominate the diet. These findings also suggest that there is a considerable difference between the diet of short- and long-finned pilot whales (*Globicephala melas*), at least in the western North Atlantic. The latter feed predominantly on the long-finned squid (*Loligo pealei*), whereas the former feed on deep-water species.

On the basis of their preference for waters deeper than 600 m off the continental shelf, it seems likely that there are few if any short-finned pilot whales in the Hauraki Gulf study region. Also, although short-finned pilot whales are highly susceptible to stranding events (Mazzuca et al. 1999), short-finned pilot whales do not strand in New Zealand. Hence, for the trophic modelling, we assume that short-fined pilot whales do not occur in the study area.

Adult females of short-finned pilot whales reach a body length of approximately 5.5 m and males 7.2 m, with a body weight of up to 3200 kg (Jefferson et al. 2008).

2.8 Common dolphin

Common dolphins of the genus *Delphinus* are found in New Zealand coastal waters (Martin Cawthorn, unpublished data), especially off the east coast of the North Island (Webb 1973). These are often assumed to be the short-beaked common dolphin (*D. delphis*). However, extensive morphological variation (Stockin & Visser 2005) and the absence of any molecular studies prevent the taxonomic clarification of *Delphinus* in New Zealand waters, and more recently, New Zealand common dolphin have been referred to as *Delphinus* sp. (Stockin et al. 2007; Stockin et al. 2008a, b).

Generally, the conservation status of common dolphin is considered of “least concern” by the IUCN, owing to the global abundance of this species (IUCN 2007). In New Zealand waters, this species is abundant but precise population estimates are not known. Based on the New Zealand threat classification system (Hitchmough 2002), common dolphin are considered “not threatened”, but this classification is ambiguous given that no population estimates exist for this species within New Zealand waters (Meynier et al. 2008). Between February 2002 and January 2005 Stockin et al. (2008b) recorded 719 independent encounters with common dolphins in the

Hauraki Gulf, involving between 1 and more than 300 animals. Calves were observed throughout the year but were most prevalent in the austral summer months of December and January. Hence, there must be at least 300 common dolphins present in the Hauraki Gulf for at least part of the year. As calves are sighted in the study area, it is possible or likely that breeding occur in the Hauraki Gulf. Until better information becomes available, we propose to assume that 300 common dolphins are present in the study area year round. Because some of the stranded individuals examined from the Hauraki Gulf region by Meynier et al. (2008) had a selection of oceanic prey species evident within their diet, we suggest that at least some proportion of common dolphin occurring in Hauraki Gulf waters undertake foraging trips offshore. In the model, we assume 75% of the diet of common dolphins in the study area is from the study region.

Common dolphins can reach lengths of 2.3–2.6 m and weigh up to 135 kg, though 70–110 kg is typical. We take the average weight of common dolphin in the study region to be 90 kg.

Stomach contents of 42 stranded and 11 by-caught common dolphin from the North Island of New Zealand between 1997 and 2006 was analysed by Meynier et al. (2008). Their diet comprised a diverse range of fish and cephalopod species, with prevalent prey of arrow squid (*Nototodarus* spp.), pelagic fishes (jack mackerel *Trachurus* spp.; anchovy *Engraulis australis*; redbait *Emmelichthys nitidus*; yellow-eyed mullet, *Aldrichetta forsteri*) and demersal fish (grey mullet, *Mugil cephalus*; scarpee *Helicolenus percoides*; dwarf cod *Austrophycis marginata*; cardinal fish, *Epigonus* sp.) (Meynier et al. 2008). Approximately 80% of the total prey individuals were less than 10 cm long. Although cardinal fish and grey mullet dominated in terms of weight of Hauraki Gulf individuals, these species were present in only a third of the stomachs and were not considered representative by Meynier et al. (2008). The diet of common dolphin stranded within Hauraki Gulf did not represent the community present in this region, but suggested a possible selectivity for arrow squid rather than pelagic shoaling fishes (Meynier et al. 2008). The data from the Hauraki Gulf is consistent with previous investigations on the diet of common dolphin which showed a high diversity of prey, with primary prey being small pelagic shoaling fish and cephalopods (e.g. Meynier et al. 2008 and references therein). In New Zealand, underwater video footage from the Bay of islands identified kahawai (*Arripis trutta*), jack mackerel, yellow-eyed mullet, flying fish (*Cypselurus cineatus*), parore (*Girella tricuspidata*), and garfish (*Hyporamphus ihi*) as potential prey items for common dolphins in New Zealand coastal waters (Neumann & Orams 2003). We used the data from Meynier et al. (2008) of stranded animals from the Hauraki Gulf and account for the few samples by adjusting percentage weights by percentage occurrences and normalising to a total of 1, akin to the Index of Relative Importance (IRI, Cortes 1997). This gives the diet of common dolphins in the study area as: 22.7% squid (21.9 arrow squid, 0.8% broad squid, *Sepioteuthis bilineata*), and 77.3% fishes (32.2% grey mullet, 14.6% cardinal fish, 13.9% jack mackerels, 10.1% pilchard, 6.0% garfish, and all else less than 1% and neglected).

Within New Zealand waters, mortality from fishery interactions occurs for a number of marine mammal species including common dolphins (Du Fresne et al. 2007). Mid-water trawling is likely to represent the largest potential threat for common dolphin (Du Fresne et al. 2007; Rowe 2007). This method is primarily used in the jack mackerel *Trachurus* spp. fishery off the west coast of the North Island, where common dolphin have been frequently by-caught (Du Fresne et al. 2007). Although the extent of this by-catch remains unclear, earlier extrapolations by Slooten & Dawson (1995) suggest that 80 to 300 common dolphin per annum were by-caught within this fishery (Meynier et al. 2008). Probably, none of these were caught in the study area.

2.9 Bottlenose dolphin

Bottlenose dolphins (*Tursiops truncatus*) are distributed worldwide in tropical and warm-temperate waters. There are thought to be three main areas of distribution of bottlenose dolphins in New Zealand waters (which are probably separate populations): (1) northeast coast of the North Island; (2) Marlborough Sounds; and (3) Fiordland (pers. comm., Rochelle Constantine, University of Auckland). Probably the most northern sighting of bottlenose dolphins in New Zealand waters was of a large pod near McCauley Island in the Kermadec Islands group (Dawson 1985). The southernmost limit of sightings in New Zealand waters is 47°S. In New Zealand waters they are classed as 'Range Restricted' under the DoC Threat Classification system (Hitchmough et al. 2007) and as Nationally Endangered (Baker et al. 2010).

Most reported sightings and strandings of bottlenose dolphins are from the northeast North Island (Martin Cawthorn, unpublished data), though strandings have been reported from Cloudy Bay and Waitarere Beach (Warneke 2001). Bottlenose dolphins around New Zealand are predominantly sighted in coastal waters and estuaries, but oceanic populations are seen off the east coast of Northland in late summer and early autumn, often associated with pilot whales (*Globicephala* spp.) and false killer whales (*Pseudorca crassidens*) (R. Constantine pers. comm.). The mean water depth preferred by the northeast population of bottlenose dolphins was 23 m. Dolphins were generally in deeper water (mean of 31 m) outside the inner islands of the Bay of Islands in summer when water temperatures were higher and shallow water (mean 15 m) in winter (Constantine & Baker 1997).

The northeastern population concentrated in the Bay of Islands resides year round along the east coast of Northland and in the Hauraki Gulf and from an ecological and conservation point of view is isolated from other populations (Constantine et al. 2003) although recent genetic analysis suggests weak but widespread genetic connection between bottlenose populations worldwide (Tezanos-Pinto et al. 2009). Photo-identification work in this area provided a closed population estimate of 446 (95% CI = 418–487) adult dolphins, with a potential home range from at least 400 km to the south (Tauranga) to about 80 km north (Doubtless Bay) (Constantine et al. 2003) but recently some individuals were found to range as far away as Manukau Harbour (R. Constantine pers. comm.). For the purposes of this study, we assume that 50% of this population feeds in the study area.

In general, adult bottlenose dolphins are 2.0 to 3.9 m in length, with an average weight reported as 100–200 kg, though Hutchinson & Slooten (pers. comm.) suggest that an average weight of bottlenose dolphins of about 90 kg is more appropriate. For the purposes of the model, we use an average weight of 120 kg.

The diet of bottlenose dolphins is reported as small fish, crustaceans, and squid (Wells & Scott 2002; Shirihai & Jarrett 2006). The diet of bottlenose dolphins in the study region is not known, but is likely to be similar to that of the (better studied) common dolphin. Here, we assume the diet to be: 25% arrow squid, and 75% small or medium-sized fishes, namely 30% grey mullet, 15% cardinal fish, 15 jack mackerels, 10% pilchard, 5% garfish.

3 Production

Annual production of whales was estimated in two ways for all species of cetaceans:

Method 1. If the weight and number of whale populations is assumed not to change significantly from year to year, then the annual production (the biomass that is available for transfer out of the trophic compartment) may be estimated to be made up of two parts: (1) calves surviving to adulthood that replace loss due to adult mortality; (2) calves dying before reaching adulthood. The average weight of a calf dying before reaching adult size is taken as the geometric average of the birth weight and adult weight. This implicitly assumes a constant mortality rate with age and a linear growth rate. A declining mortality rate with age, and a decreasing growth rate with age, will tend to act to cancel each other out, so that this assumption is reasonable as a first approximation. Typical per capita birth rates for baleen whale species are taken from Hill et al. (2007) as half the maximum per capita recruitment rates (i.e. at low population levels where all animals breed) from their table 13. These range from 0.045–0.20 y^{-1} (Mori & Butterworth 2004; Pinkerton & Bradford-Grieve 2010), being higher for smaller cetaceans such as southern bottlenose whale and Arnoux's beaked whale, and larger for baleen whales like blue and fin whales. We estimated a per capita birth rate of 0.05 y^{-1} for orca, 0.055 y^{-1} for humpback whale, 0.05 y^{-1} for southern right whale, 0.045 y^{-1} for Bryde's whale (as the similarly sized sei whale), 0.1 y^{-1} for long-finned pilot whale and 0.2 y^{-1} for common and bottlenose dolphins. The proportion of calves surviving to adulthood is poorly known but we assume here that it has a value of about 30–60%, similar to orca (Olesiuk et al. 1990), being lower for smaller whales. Here, we assume values of the proportion of calves surviving to adulthood as: 60% orca; 40% humpback whale and southern right whale; 50% for Bryde's whale; 40% for long-finned pilot whale; and 30% for common and bottlenose dolphins. This leads to estimates of P/B between 0.028 y^{-1} (Bryde's whale) and 0.091 y^{-1} (common and bottlenose dolphins).

Method 2. Banse & Mosher (1980) relate production to animal biomass as: $P/B=12.9 \cdot M_s^{-0.33}$ where M_s is the animal weight expressed as an energy equivalent (kcal), and P/B is the annual value (y^{-1}). Fish are reported as having an energy density of about 1 kcal/gWW (Schindler et al. 1993). Mammals are likely to have a higher energy content as a result of their fat-rich blubber. Although the biochemical analysis of blubber of whales varies, 60% lipid is likely (Lavigne et al. 1986 and references therein; Koopman 2007) implying an energy content of about 9 kcal/g. Assuming that such high-lipid tissues make up about 40% of the whale's body weight, we estimate a total energy density for whales of 4.2 kcal/g. This leads to estimates of P/B between 0.021 y^{-1} (southern right whale) and 0.19 y^{-1} (common dolphin). Method 2 gives P/B values that are an average of 36% different from values by Method 1, and usually higher.

In the absence of a way to distinguish between these, we take an average of methods 1 and 2. This gives P/B for whales of between 0.023 y^{-1} (southern right whale) and 0.14 y^{-1} (common dolphin) which seem reasonable as Trites (2003) gave a range of P/B=0.02–0.06 y^{-1} for larger baleen and toothed whales. For comparison, our methods give P/B for orca of 0.04 y^{-1}, which is higher than the average orca adult mortality estimate from Bigg (1982), Olesiuk et al. (1990), and Ford et al. (1994) of approximately 2% per year (Visser 2000) as the P/B value includes the effect of elevated juvenile mortality. Bradford-Grieve et al. (2003) give P/B for whales and dolphins off New Zealand as 0.04–0.29 y^{-1}, with the highest value for the hourglass dolphin. Jarre-Teichmann et al. (1998) estimated that a trophic compartment of whales and dolphins had a P/B ratio of 0.60 y^{-1} although this seems high. Trites (2003) gave a range of P/B=0.02–0.06 y^{-1} for whales (with no distinction by size).

4 Consumption

We used up to four methods to estimate the annual average food requirements of cetaceans in the Hauraki Gulf.

Method 1 is based on Innes et al. (1986) working of data from Sergeant (1969) and has been used by a number of other studies (e.g. Reilly et al. 2004). Daily prey consumption Q_{WW} (kgWW d^{-1}) is estimated as $Q_{WW}=0.42W_{kg}^{0.67}$ where W_{kg} is the average body wet-weight (kg). The estimate is based on feeding rates of captive small cetaceans and hence estimates annual average consumption.

Method 2. A number of methods estimate consumption of mammals based on the amount of food required to supply sufficient energy to satisfy their metabolic, growth and reproductive needs. Sigurjónsson & Víkingsson (1997) give relationships for annual average daily ration of baleen and toothed whales based on both feeding rates of captive cetaceans (based on Innes et al. 1986) and energy budgets. Their results were intended to be applicable to balaenopterids in the North Atlantic near Iceland. The relationships are Q_{WW}=206.25$W^{0.783}$/1110.3 (baleen) and Q_{WW}=206.25$W^{0.783}$/1300 (toothed whales).

Method 3. To estimate consumption of cetaceans in this method, we used the relation between animal weight and daily consumption developed by Innes et al. (1987). For toothed whales: $Q=0.258\cdot W^{0.69}$, where Q is daily consumption kg/d or WW prey, and W is the animal wet weight in kg. For "other marine mammals", which we apply to seals and baleen whales, $Q=0.123\cdot W^{0.80}$ (symbols as above). These relationships give mean consumption rates and were based on a compilation of published data for captive and wild marine mammals. The relationships of Innes et al. (1987) give values similar to consumption rates for terrestrial mammals of the same size.

Method 4. Here, we use an estimate of standard (or basal) metabolic rate from Lockyer (1981): SMR=$70.5\cdot W^{0.7325}$. This results in basal metabolic rates 11–19% lower than those given by SMR=$70\cdot W^{0.75}$ (Kleiber 1975; Lavigne et al. 1986) but is considered more reliable. SMR is the resting or basal rate of animals; the average daily energy expenditure of animals will be higher than the SMR, especially if the animals are undergoing exertion such as extended swimming or foraging (Lockyer 1981). Lockyer (1981) estimated that the daily energy expenditure of large baleen whales, averaged over a year, is only 1.3 times the SMR. The active metabolism is estimated to be about 2–5 times SMR (Kenney et al. 1997 and references therein) and we use a factor of 2.8 for all cetaceans. Lockyer (1981) gives assimilation efficiencies for Antarctic baleen whales of 79–83%, and we use 80% for all cetaceans.

Conversion factors between energy, carbon, dry- and wet-weights vary between studies and with species. For fish, 0.95–1.3 kcal/gWW is reported (Steimle & Terranova 1985; Croxall et al. 1985; van Franeker et al. 1997). For crustaceans, 0.93–1.1 kcal/gWW is reported (Lockyer 1981; Croxall et al. 1985). We used weight conversion factors of 0.108 gC/gWW (fish: Schneider & Hunt 1982) and 0.030–0.055 gC/gWW (zooplankton: Weibe 1988; Ikeda & Kirkwood 1989). We use these to estimate 10.2 kcal/gC (fish) and 18.3 kcal/gC (crustaceans). These were combined according to the estimated diets of the individual cetacean species.

The four individual methods differ from the average estimate by 24% (0.1–58%). Differences between the methods are greatest for the common and bottlenose dolphins. Our estimates of annual average Q/B for Hauraki Gulf cetaceans ranged from 3.3 y^{-1} (southern right whale) to 24 y^{-1} (common dolphin). Note that these are annual average consumption rates i.e. the feeding rates which would occur if feeding were evenly spread over the whole year. There is no clear indication that cetaceans are feeding more intensely when in the Hauraki Gulf than at other times of the year when they are absent from the Hauraki Gulf, so we assume that these annual feeding rates apply when the animals are in the study area.

These estimated feeding rates for cetaceans agree reasonably well with estimates from previous studies which have attempted to estimate consumption rates for particular cetaceans. Trites (2003) quotes estimates for Q/B for marine mammals of between 11–18 y^{-1}. Recently, Hill et al. (2007) estimated consumption rates for Antarctic baleen whales based on Reilly et al. (2004) who used a revised form of the model from Innes et al. (1986). The values range from 6.9–13 y^{-1} for large whales. Bradford-Grieve et al. (2003) estimated Q/B for beaked whales and dolphins in the New Zealand subantarctic to be 11–15 y^{-1}.

5 Other information: P/Q, EE, U, accumulation, imports, exports, transfers

5.1 Long-term biomass trends

In the work presented, we assume that long-term changes in biomass per year are small for all species of cetacean.

5.2 Export

We assume here that there are no substantial differences between the average rates of feeding and mortality in the study area to outside the study area and that net import or export of material from the study area is small. However, we note that it is possible that some species of whale have higher rates of mortality in the Hauraki Gulf than elsewhere; collisions with shipping may be a significant cause of mortality to whales and shipping is likely to be more intensive in the study area than outside. For example, "Scoop Regional News" on Wednesday 1 February 2012 reported a Press Release from the Department of Conservation: "In the last 16 years there have been 41 confirmed deaths of Bryde's whales in the Hauraki Gulf. Eighteen of these dead whales were examined and 15 are most likely to have died as the result of being struck by a vessel."

Unassimilated consumption

In the present study, we use U=0.2 as the proportion of unassimilated food for all cetacean groups (Bradford-Grieve et al. 2003). Unassimilated consumption is channelled to water column detritus in the model.

5.3 Ecotrophic efficiency

Ecotrophic efficiency (E) gives the proportion of mortality that is due to predation compared to other sources of mortality such as starvation or disease. This ratio is not known for cetaceans in the study area. Direct predation on large cetaceans in the study area (humpback whale, Bryde's whale, orca, long-fined pilot whale) are likely to be minimal, so ecotrophic efficiency will be close to or actually zero. This implies that all production of these species in the study area is in the form of whale carcasses. These will sink to the sea bed and be consumed by benthic scavengers.

There will probably be some direct predation on common and bottlenose dolphins and on calves of baleen whales in the study region from orca. Based on the biomass and energetic values estimated above, there is only enough production by dolphins to provide a very small amount of the consumption of orca in the study region (0.7% from common dolphins, 0.9% from bottlenose dolphins). Hence, we set the ecotrophic efficiency of these dolphin species to near unity (0.95). We allow for 5% of the mortality of these species to be due to non-orca predation.

6 Summary of parameters

Parameters for cetaceans in the present day Hauraki Gulf trophic model are provided in Table 37 and**Table 38**. In terms of biomass: 24% humpback whale, 0.4% southern right whale, 32% Bryde's whale, 21% orca, 7% long-finned pilot whale, 7% common dolphin, and 10% bottlenose dolphin. In terms of consumption of prey: 11% humpback whale, 0.2% southern right whale, 20% Bryde's whale, 19% orca, 8% long-finned pilot whale, 19% common dolphin, and 23% bottlenose dolphin. Small cetaceans are relatively more important in terms of consumption (and production) compared to biomass because their energetic parameters (P/B and Q/B) are higher.

Table 37: Summary of data for model parameters for cetaceans in the present day model.

Name	Latin name	Individual weight	Max number in region	Proportion of time in region	Biomass	Biomass density	P/B	Q/B	U
		kg WW			t WW	gC m^{-2}	y^{-1}	y^{-1}	
Humpback whale	*Megaptera novaengliae*	30 408	35	0.06	66.5	4.11E-04	0.028	4.3	0.2
Southern right whale	*Orcinus orca*	65 311	0.2	0.08	1.2	7.47E-06	0.024	3.3	0.2
Bryde's whale	*Balaenoptera brydei*	12 000	32	0.23	88.0	5.43E-04	0.032	5.7	0.2
Killer whale (orca)	*Globicephala melas*	4 424	26	0.50	57.5	3.55E-04	0.043	8.4	0.2
Long fin pilot whale	*Delphinus sp.*	1 800	110	0.10	19.8	1.22E-04	0.061	10.6	0.2
Common dolphin	*Tursiops truncatus*	90	300	0.75	20.3	1.25E-04	0.139	23.7	0.2
Bottlenose dolphin	*Globicephala macrorhynchus*	120	446	0.50	26.8	1.65E-04	0.130	21.9	0.2

Table 38: Summary of diet estimates for cetaceans in the study area.

	Predators						
Prey	Humpback whale	Southern right whale	Bryde's whale	Killer whale (orca)	Long finned pilot whale	Common dolphin	Bottlenose dolphin
Pelagic fish			0.45				
Juvenile fish			0.05				
Large demersal fish				0.16	0.10	0.25	0.25
Small demersal fish						0.52	0.50
Reef fish	0.20	0.20					
Rays				0.63			
Sharks				0.12			
Cephalopods					0.90	0.23	0.25
Macrozooplankton	0.50	0.50	0.35				
Mesozooplankton	0.30	0.30	0.15				
Dolphins				0.09			
TOTAL	1	1	1	1	1	1	1

7 Historical parameters

7.1 Models required

Trophic models are required for cetaceans in four historical periods: 1950, 1790, 1500, and 1000.

7.2 Biomass

Biomass of cetaceans in the study area in the historical periods are generally not well known. Four factors may have affected biomass and other parameters for cetaceans in the historical trophic models. First, whales in the Hauraki Gulf were hunted for subsistence by early Maori settlers of New Zealand (Smith, 2011). Second, there was substantial whaling around New Zealand in the nineteenth century, which is likely to have reduced numbers of large cetaceans in the study area (Carroll et al. 2011; Jackson et al. 2011). Third, changes to the climate of the study area have occurred over the last 1000 years (Lorrey et al. 2013). Lorrey et al. (2013) interpreted the collection of palaeoclimate precipitation and temperature data and concluded that the "propagation of downstream changes to coastal environments via sedimentary and geomorphic processes would have undoubtedly affected nearshore aquatic ecosystems". Fourth, there are potential indirect effects of ecosystem change in the study area on cetaceans. For example, changes in fish biomass in the region may have affected cetacean biomass because fish are preyed on by cetaceans. It is likely however that the direct effects of whaling on cetacean populations are greater than changes due to climate or environmental effects.

Southern right whales: Historically, right whale cows calved in bays along the east coast of mainland New Zealand and around the sub-Antarctic islands during the austral winter, moving offshore during the summer months (McNab 1913; Dawbin 1986). New Zealand right whales were the target of pelagic and shore whaling from the beginning of the nineteenth century. As in all other areas where right whales were encountered, hunting was so intense that this species had virtually disappeared from these regions by the twentieth century (Dawbin 1986). Recent population reconstructions by Jackson et al. (2011) suggest that right whales in New Zealand waters prior to nineteenth century whaling numbered 27 000 ± 5000 (95% confidence interval), although uncertainties in the spatial distribution of catches of right whales in the southwest Pacific are such that the pre-whaling abundance could have been as high as 40 000.

In the aftermath of hunting, no southern right whales were seen in New Zealand mainland waters for over 35 years from 1928–1963 (Gaskin 1964). Since this time, only a small number of whales have been sighted around the mainland each year (Patenaude 2003), suggesting that recovery of right whales in this region has been very slow. Sightings of southern right whales around the New Zealand mainland between 1981 and 2007 from the DoC incidental sightings database and the Cawthorn sightings database total 78, with many of these occurring close to shore along coasts where shore based whaling took place in the nineteenth century. Only 6 of the 78 sightings (7.6%) of right whales around the New Zealand mainland in the modern period (1981–2007) were in the Hauraki Gulf region. We assume number of southern right whales in 1950 was the same as today (see section above for details of the present day estimate). The numbers present in the Hauraki Gulf study area in the 1790s, prior to commercial whaling, was estimated to be around 1000 cows, assuming that half of the total population of 27 000 (Jackson et al 2011) are cows that calved inshore during autumn and winter and that 7.6% (the modern proportion of sightings around mainland New Zealand) of these cows frequented the study area. This number of southern right whales is also assumed to be present in 1450 and 1000.

Humpback whale: The humpback whale was targeted by whalers in the nineteenth century and populations in the study area would have been reduced by this activity, though we do not know to what extent. Laws (1977) gives figures of 100 000 and 3000 for total southern stock sizes of humpback whales before and after exploitation. In the absence of local information on changes in whale numbers, we assume that this is indicative of reductions of the numbers of humpback whales in the study area. We assume that the reduction occurred during the period of whaling, i.e. between our periods of 1790 and 1950. We hence estimate that the number of humpback whales in the study area for some of the year before whaling is about 1170 whales. We assume the same characteristics of habitat usage historically as in the present day (namely, present for 3 months per year, 25% of time in the general region spent in the study area).

Bryde's whale: Bryde’s whale was not a main target of whalers, and so population changes around New Zealand are likely to be smaller than for the other baleen whales. We assume that present day values are 25% of values before whaling. Hence, we estimate that there were 128 Bryde’s whales in the region for the 1790, 1500 and 1000 models. We assume the same characteristics of habitat usage historically as in the present day (namely, present for 11 months per year, 25% of time in the general region spent in the study area).

Small cetaceans: Four of the cetacean species found in the study area also use the Otago-Catlins coastline, namely bottlenose dolphins (*Tursiops truncatus*), common dolphins (*Delphinus* sp.), orca (*Orcinus orca*) and pilot whales (*Globicephala* sp.). For these small cetaceans found in the study area, we estimate cetacean populations in the historical models by reference to similar work carried out by Hutchison & Slooten (2008) for the Otago-Catlins region of New Zealand. We note the conclusion of Hutchison & Slooten (2008) that: “*there is currently very little known about small cetaceans in the Otago-Catlins region except for Hector's dolphin….Systematic population surveys … would help to fill these data gaps.*” This conclusion holds for the present research on estimating parameters for cetaceans in the Hauraki Gulf region. Despite these caveats, Hutchison & Slooten (2008) tentatively estimate that populations of small cetaceans were higher historically than today, in some cases, substantially higher. The ratio of populations before human contact with New Zealand to the present day were estimated to be 19 (Bottlenose dolphin), 7.3 (Common dolphin), 2.7 (orca) and 2 (pilot whale); Hutchison & Slooten (2008). We use these ratios, and those for the other historical periods considered to estimate abundance of these cetacean species in the historical trophic models. We assume the same characteristics of habitat usage at large scales historically as in the present day. At fine scales, habitat usage will have been affected by changes in predator and prey distributions.

7.3 Productivity and other energetic parameters

Biomass, energetics, and other key parameters for the collected trophic group of “cetaceans” in the historical models were calculated assuming that the present day values for these parameters for a given species have not changed. It is possible that these parameters have varied from the present day situation due to factors including climate (see Lorrey et al. 2013 for details of climate variability over the model periods), run-off (including sedimentation), predation (both by marine biota and humans), and food availability, but we think that these changes will be relatively low compared to the effects of historical climate variability on other biota. Changes in the parameters shown in **Table 39**hence reflect the fact that the “cetaceans” group is made up of many species that have different energetic parameters. Because the relative abundances of cetaceans with different parameters change through history, these estimates of the parameters for the overall group also varies with historical period.

7.4 Removals from the study area by humans

Smith (2011) estimated the magnitude of pre-European Maori marine harvest of fish, seabirds, invertebrates and mammals based on data preserved from middens, for years (actually, periods about nominal years) 1550 and 1750. The latter is taken to be representative of that in 1750. Catches of cetaceans are estimated to be 61 tWW (1400), 1.8 tWW (1550), and 2.1 t (1790). Catches in 1400 are estimated to be 57 t pilot whales (*Globicephala* sp.) and 4.0 t dolphins. All catches in 1550 and 1790 were found to be dolphins (Smith 2011). Catch in 1500 was estimated by linear interpolation to be 22 tWW. Although there may have been some mortality of cetaceans by fishing in 1950 and the present day, these are assumed to be small and are not included in the model. There are no fishery catches of cetaceans in the 1000 model. Note that whaling catches are not shown in these figures as the 1790 period predates the main period of whaling and whaling has ceased by 1950.

7.5 Diet

Diets for the collected trophic group of "cetaceans" in the historical models were estimated assuming that the present day diets for each of the species of cetacean found in the study area were the same historically as in the present day. Because the relative abundances of species with different diets changes through history, these estimates of the diet composition of the composite cetaceans group will vary with historical period. These diet values are shown in **Table 40**. Note that diets of all groups in the trophic model can vary during model balancing to take into account changes in competition for prey between predators and changes in the biomass of prey items with time.

7.6 Summary of parameters

Parameters for cetaceans in the present day and historic Hauraki Gulf trophic models are provided in 3 and 4.

Table 39. Summary of parameters for cetaceans in the trophic model.

Model	EE	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	P/Q %	U	Export X/P	Fishery gC m^{-2} y^{-1}
Present	0.1	0.0017	0.053	9	0.58	0.2	0	0
1950	0.1	0.0035	0.083	14	0.58	0.2	0	0
1790	0.1	0.054	0.017	5.0	0.35	0.2	0	1.3E-05
1500	0.1	0.055	0.019	5.2	0.37	0.2	0	1.3E-04
1000	0.1	0.055	0.019	5.2	0.37	0.2	0	0

Table 40: Summary of diets for cetaceans in the trophic model.

Prey	Proportions in diet				
	Present	1950	1790	1500	1000
Cetaceans	0	0	0	0.053	0.053
Snapper	0.001	0.001	0.001	0.001	0.001
Jack_mackerels	0.086	0.123	0.046	0.050	0.050
Blue_mackerel	0.086	0.123	0.046	0.050	0.050
Rig	0.078	0.111	0.042	0.045	0.045
Flatfish	0.009	0.006	0.002	0.001	0.001
Trevally	0.009	0.012	0.005	0.005	0.005
Barracouta	0.009	0.012	0.005	0.005	0.005
Skipjack	0.006	0.002	0.002	0.001	0.001
Demersal_fish	0.005	0.002	0.001	0.001	0.001
Sharks	0.173	0.247	0.093	0.101	0.101
Pelagic_fish_large	0.130	0.084	0.023	0.020	0.020
Pelagic_fish_small	0.012	0.004	0.003	0.003	0.003
Squid	0.062	0.020	0.016	0.014	0.014
Gelatinous	0.151	0.193	0.072	0.078	0.078
Macrozoo	0.020	0.006	0.124	0.110	0.110
Mesozoo	0.109	0.035	0.326	0.289	0.289
Cetaceans	0.055	0.018	0.193	0.171	0.171
Total	1	1	1	1	1

8 Acknowledgements

This research was funded by Ministry of Fisheries project ZBD200505 ("Long-term change in New Zealand coastal ecosystems") and by the New Zealand Ministry of Science and Innovation project C01X0501 (Coasts & Oceans OBI). We acknowledge Mary Livingston and Martin Cryer (Ministry for Primary Industries) for supporting this project, and to the Taking Stock cetacean team for input. Sightings data used courtesy of Department of Conservation (New Zealand) and Martin Cawthorn. We acknowledge Leigh Torres (NIWA) for access to cetacean sightings data and useful comments on a draft of the work.

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Appendix 4: Trophic modelling of Hauraki Gulf: Benthic invertebrates

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1 Introduction

1.1 Trophic groups

There is a vast array of benthic invertebrates in the study area. It was necessary to combine species into trophic groups in order to have a manageable number of groups in the trophic model. There are a number of alternative ways to group invertebrates in mass-balance models, including by individual size, location, taxonomy, diet, predators, life-history or functional characteristics (e.g., feeding method). Here, we follow approaches developed by Lundquist & Pinkerton (2008) and use the following 12 benthic invertebrate groups. Information and detailed definitions of biota included in each group is given at the start of each section in this document.

1. Lobster (crayfish)
2. Crabs
3. Seastars and brittlestars
4. Kina and other echinoids
5. Carnivorous gastropods & sea slugs
6. Grazing gastropods & chiton
7. Sea cucumbers
8. Bivalves
9. Sponges
10. Encrusting invertebrates
11. Macrobenthos (benthic macrofauna)
12. Meiobenthos (benthic meiofauna)

We recognise that no method of grouping invertebrates into trophic groups for the purposes of trophic modelling is completely objective or ideal. Generally, biota were put into separate groups where information was available to do so and where biota were considered to be reasonably abundant and/or trophically important in their own right. Taxa were combined where information was scarce, where groups were of lower biomass or importance, or where ecological characteristics were similar. Note that the “encrusting invertebrate” group excludes sponges as these have a separate group of their own. Cephalopods (squid and octopus) and zooplankton are included in separate Appendices.

1.2 Organisation of this report

This appendix is organised as follows:

- Habitat definition and study area
- Datasets used in the modelling, including general information used for biomass and other estimates
- Catch histories for commercially harvested benthic invertebrates
- Detailed information on groups 1–12 of benthic invertebrates
- Summary of parameters for the present day model

- Parameter estimation for historical ecosystem models

2 Study area, habitats and approach

2.1 General approach to estimating biomass

Neither surveys of benthic invertebrate abundance at the scale of the study area (16 192 km^2) nor "stock-model" estimates of benthic invertebrates (such as are used for fish stock modelling) are feasible. Instead, we estimated the biomass of benthic invertebrates in the study region using an approach based on the density of organisms in a given habitat (Lundquist & Pinkerton 2008). In this approach, the study area is divided into a relatively small number of discrete habitat types. The area of these habitats is obtained from detailed mapping of the region within a GIS framework. The density of benthic organisms of a given type within a habitat is obtained from small-scale surveys, usually diver surveys, benthic cores or grab samples, which are detailed below (Section 3). "Type" of benthic organism is usually species but sometimes only a coarser taxonomic resolution is possible. "Density" is typically the number of individuals per square metre , but could be weight of organisms of that type per square metre. Where necessary, the numbers of organisms are converted to weight using a typical size of organism of that type in that habitat. It is noted that the typical size of a given species can vary greatly, by up to an order of magnitude, between habitats in the study area and this must be taken into account when estimating total biomass in the study region.

2.2 Habitats in the study area

The Hauraki Gulf study region was separated into regions that could be classified according to typical abundances of macroalgae, invertebrates and vertebrates (**Table 41**). Both depth (Figure 22) and exposure (Figure 23) were determined to be key factors influencing faunal and floral communities. Three exposures were defined (Coastal Exposed, Coastal Sheltered, and Estuarine), and four depths were defined for each exposure (0–9 m, 10–29 m, 30–99 m, 100–249 m). The "coastal exposed 30-99 m" habitat was subsequently split into two: "coastal exposed 30–49 m" and "coastal exposed 50–99 m" to reflect the fact that most sampling in this category occurred at shallow depths (generally less than 40 m).

Soft sediment intertidal habitats were further defined into six subcategories based on dominant fauna/flora (mangrove, seagrass, mudflat, cockle *Austrovenus* bed, *Macomona* habitat, tubeworm). To determine the amount of habitat in intertidal versus shallow subtidal categories of estuarine sediments (0 – 9 m), we used the Estuary Environments Classification (EEC) database (Hume et al. 2003, 2007), which estimates a total of 1856.97 km^2 of estuarine area in the Hauraki Gulf region. Based on estimates of the percent intertidal area of each estuary in the database, 403.03 km^2 of intertidal habitat is present (average percent intertidal of all estuaries: 43.8%; average percent intertidal of all habitat, biased by larger harbours: 21.7%). Note that this figure differs from the categories as estimated from GIS due to some estuaries (e.g., Waitemata Harbour, Whangarei Harbour, Firth of Thames) being included in full in this EEC calculation, whereas channel and deeper habitats of these harbours are included in deeper (e.g., 10–29 m) categories for this report. As mangroves are increasing at rates of approximately 4% per year (A. Swales, NIWA, pers. comm.), we use the EEC estimate (65.06 km^2 of estuarine habitat) to calculate total mangrove rather than the 49.8 km^2 derived from the GIS maps based on aerial photographs of varying ages. We used the relative percent of intertidal mud and sand habitats across the entire Hauraki Gulf estuarine environment from the EEC to estimate the total of each generic sediment characteristic habitat in the estuary intertidal. Salt marsh was estimated as all swamp habitat from the EEC (0.91 km^2). Mud was determined to include mangrove, seagrass and mudflat habitats, using GIS derived estimate of seagrass coverage plus mangrove estimates from EEC, and subtracting both values from mudflat habitat to calculate the remaining unvegetated intertidal mudflat habitat. Sand habitats were estimated to include equal proportions of each of three types of intertidal estuarine community: cockle *Austrovenus* bed, *Macomona* habitat, and tubeworm habitat.

Shallow rocky reef habitats were also further separated into depth categories according to observed macroalgal zonation patterns, as 0–2 m, 3–9 m, 10–19 m, and 20–29 m, to better reflect macroalgal biomass.

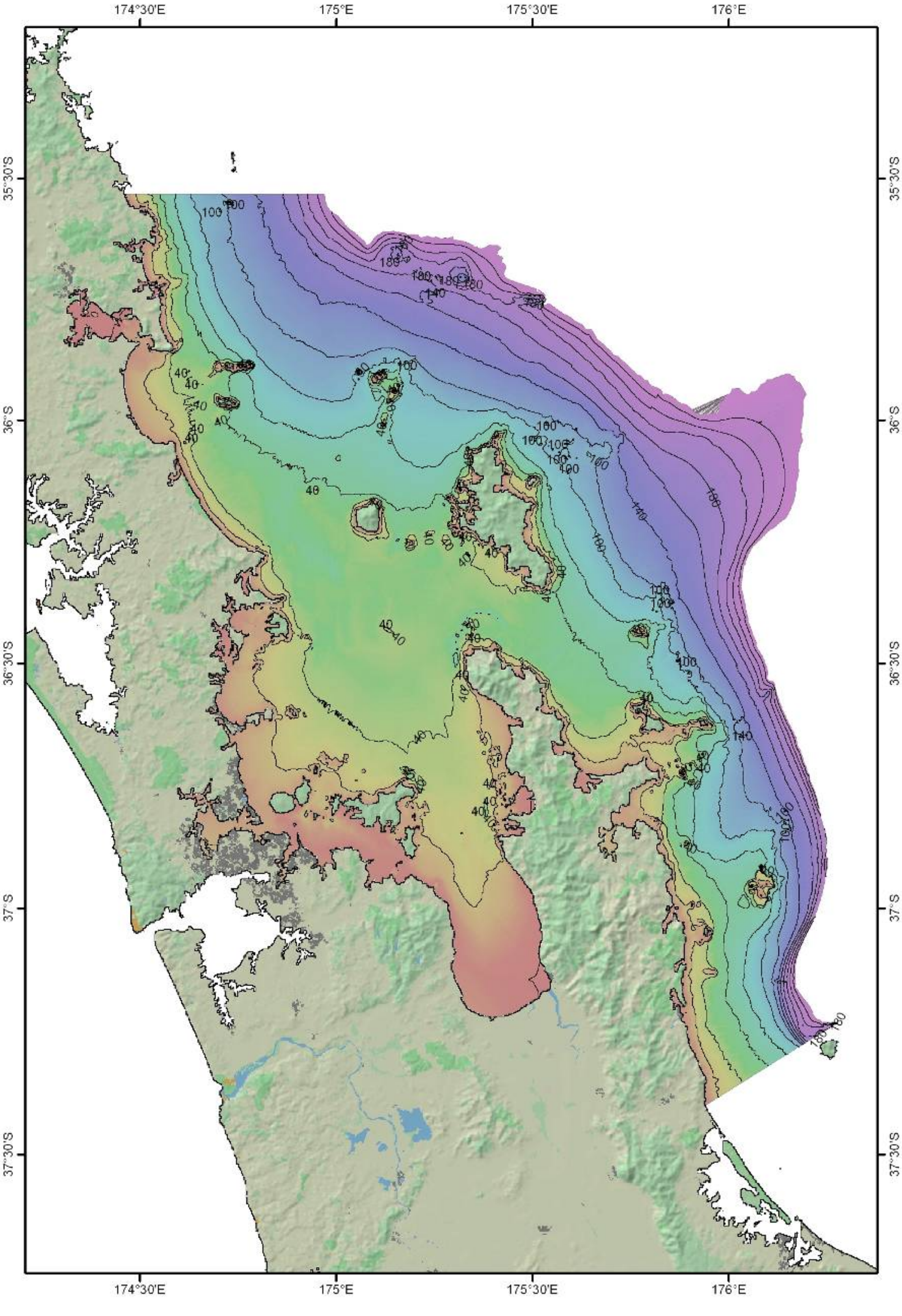

Figure 22: The Hauraki Gulf study area. Contours representing bathymetry are drawn at 20 m intervals, with red/orange indicating shallow water (less than 40 m) and purple representing deep water (more than 200 m). The study area is constrained by the 250 m depth contour.

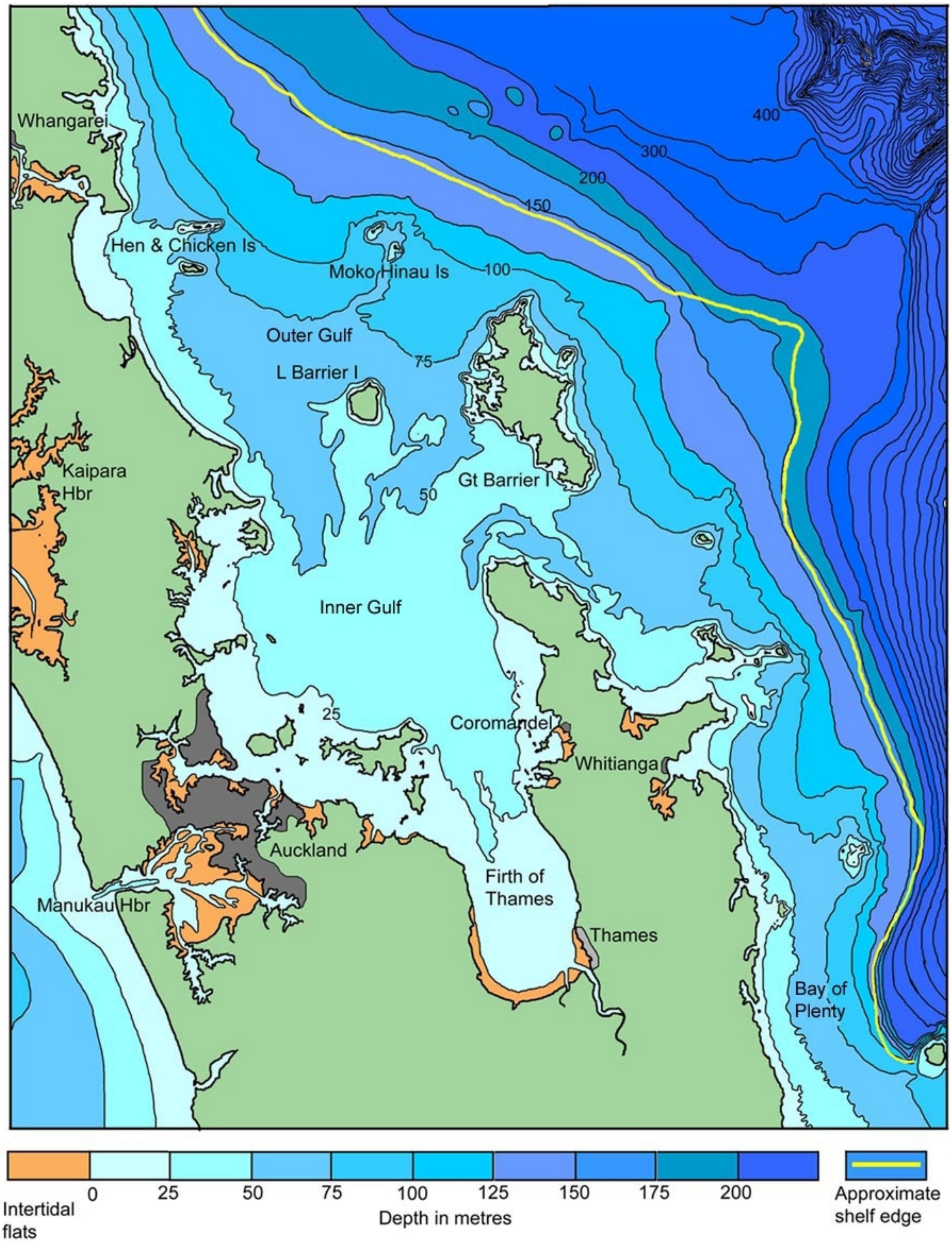

Figure 23: The Hauraki Gulf study area (courtesy of Larry Paul), showing inner gulf (coastal sheltered) and outer gulf (coastal exposed) demarcations.

Table 41: Area in each exposure/depth category for each habitat type in the trophic model.

Habitat types	Area (km^2)			
All habitat types	Coastal Exposed	Coastal Sheltered	Estuarine	Total
0–9 m	466.39	413.17	532.41	1 411.97
10–29 m	1 332.82	397.74	13.50	1 744.05
30–99 m	7 136.21	0.00	0.00	7 136.21
100–249 m	5 955.35	0.00	0.00	5 955.35
Total	14 890.76	810.91	545.90	16 247.57
Unvegetated soft sediments				
0–9 m	268.70	377.62	469.26	1 115.58
10–29 m	1 184.59	392.35	12.67	1 589.61
30–99 m	7 036.08	0.00	0.00	7 036.08
100–249 m	5 935.00	0.00	0.00	5 935.00
Total	14 424.36	769.97	481.93	15 676.27
Mangrove (0–9 m)	2.49	1.08	49.78	53.35
Seagrass (0 – 9 m)	1.49	0.59	3.31	5.40
Estuary area (Hume et al. 2003, 2007)	…	…	1 856.97	1 856.97
Intertidal estuary (EEC)	…	…	403.03	403.03
Intertidal sand (assume 1/3 each Macomona, cockle, tubeworm habitat)	…	…	152.65	152.65
Intertidal mudflat (minus seagrass from GIS)	…	…	182.04	182.04
Salt marsh	…	…	0.91	0.91
Mangrove (from EEC)	…	…	65.06	65.06
Intertidal Rocky Reef	23.75	6.90	1.24	31.89
Subtidal Rocky Reef				
0–9 m	189.91	32.29	10.04	232.24
10–29 m	148.14	5.37	0.83	154.34
30–99 m	100.11	0.00	0.00	100.11
100–249 m	20.35	0.00	0.00	20.35
Total	458.50	37.66	10.87	507.03

2.3 Length to weight conversions of shellfish and other invertebrates

Occasionally sizes (i.e., linear dimensions) of individual benthic organisms were measured and reported in benthic surveys. These were converted to individual weights using length-weight relationships for common New Zealand species (**Table 42**), mainly based on Taylor (1998a). Alternatively, length-weight relationships derived from literature reviews were used. If no conversion was available for a particular species, length-weight relationships for congeners or confamilials were used. If no data were available, a mean length-weight relationship was calculated based on averaging across all available data for a particular taxonomic group.

Table 42: Length-weight relationships for mobile invertebrates, $W=aL^b$, where W = AFDW (g) and L = linear body dimension (mm) (based on Taylor 1998a).

Taxon	Description	Body dimension	a	b	Length range (mm)
Buccinulum spp.	Predatory gastropod	Aperture length	3.964×10^{-5}	2.9096	11–23
Cantharidus purpureus	Grazing gastropod	Height	1.774×10^{-5}	2.7903	7–25
Cellana spp. (data for *C. stellifera*)	Grazing limpet	Length	2.149×10^{-6}	3.3899	13–40
Cookia sulcata	Pupu (grazing gastropod)	Length	2.153×10^{-5}	2.9192	18–85
Dicathais orbita	Predatory gastropod	Aperture length	8.596×10^{-6}	3.2809	16–50
Evechinus chloroticus	Kina	Test diameter	6.550×10^{-4}	2.1835	13–95
Jasus edwardsii	Lobster	Carapace length	7.551×10^{-4}	2.5291	50–188
Paguroidea	Hermit crab	Shell length	7.208×10^{-5}	2.2261	13–45
Plagusia chabrus	Predatory crab	Carapace width	1.162×10^{-4}	2.9224	8–58
Trochus viridis	Grazing gastropod	Width	9.473×10^{-8}	4.8496	14–23
Lunella (Turbo) smaragdus	Pupu (grazer)	Width	1.747×10^{-5}	3.0695	7–31

As an order-of-magnitude check, weights of individual shellfish were calculated using a mean density and estimated volumes as Equation 1. Note than an indicative volume was calculated assuming an approximately conical shape but the validity of this assumption is not critical.

$$M = \frac{\pi}{12} xyz \cdot \frac{\rho}{1000} \qquad [1]$$

Here, M is the approximate wet weight of a shellfish (gWW), where the shell has dimensions x, y, z (all mm), and ρ is an average shellfish density (g cm^{-3}). Mean density was estimated from an average of length-weight data given for the following species: tuatua (D. Allen (MFish), unpublished data, quoted in Ministry of Fisheries 2009); paua (McShane et al. 1994); cockles (Bradbury et al. 2005); deepwater clams (Haddon et al. 1996); Pacific oyster (Sumner, 1980). Based on these data, ρ is estimated to be between 1.6–2.6 gWW cm^{-3}, with a mean of 2.1 gWW cm^{-3}. There was no significant relationship between shellfish size and density in the range of lengths considered (10–150 mm). Comparison between individual animal weight estimated using equation (1) and from length-weight or empirical (field) observations were encouraging (Figure 24). For gastropods, the linear correlation was positive (R^2=0.91, N=37), and a median ratio of weights by the two methods of 1.1 (equation 1 divided by empirical weights). For bivalves, the correlation was again reasonable (R^2=0.46, N=29) with a median ratio of 0.6. We used empirical weights throughout this study as these are considered more reliable.

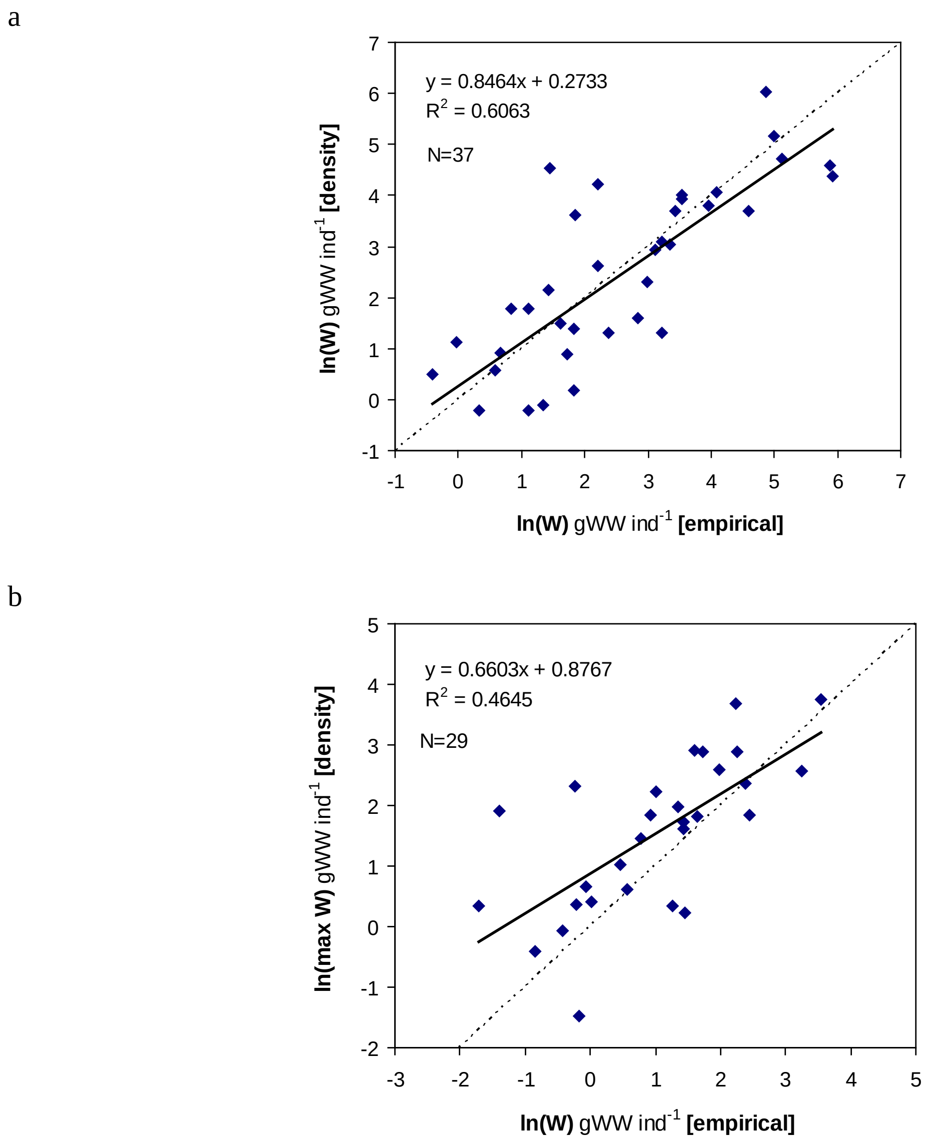

Figure 24: Comparison between density-based (equation 1) and empirical or length-weight relationships for estimating individual weight of shellfish. a: gastropods (weights include shells); b: bivalves (shell-free).

2.4 Conversion factors

We converted all wet weights to ash-free dry weight (AFDW) because the relationship between carbon and AFDW is relatively consistent between different benthic invertebrates; Brey (2005) gives 0.375 gC gAFDW^{-1}, Lundquist & Pinkerton (2008) use 0.498 gC gAFDW^{-1}, and Salonen et al. (1976) gives 0.518 gC gAFDW^{-1} with a standard deviation of 0.04 gC gAFDW^{-1}. We use a middle value of 0.473 gC gAFDW^{-1} for all benthic invertebrates.

In contrast to this consistency, the ratio of AFDW to WW varies considerably between benthic organisms (Ricciardi & Bourget 1998). We use data from the review by Ricciardi & Bourget (1998) given in Table 43, which range from 0.024–0.217 gC gAFDW^{-1} with a mean of 0.118 gC gAFDW^{-1}. For comparison, the values given in Brey (2005) imply a mean value of 0.114 gC gAFDW^{-1} for benthic invertebrates.

Table 43: Conversion factors between wet weight and ash-free dry weight for benthic invertebrates in the study area. All values were taken from Ricciardi & Bourget (1998), except for lobsters and crabs which were taken from E. Jones (NIWA, pers. comm.). No conversion values were needed for gastropods or chiton as the biomass of these taxa were estimated using size-AFDW regressions.

Group	AFDW:WW
Lobster, crabs	0.16
Gastropods (Protobranchi)	0.079
Chiton	0.272
Octopus	0.217
Brittlestars	0.065
Seastars	0.097
Sea slugs	0.175
Anemones & corals	0.133
Urchins	0.027
Sea cucumbers	0.082
Primitive worms	0.110
Shrimps	0.165
Sponges	0.105
Bivalves	0.167
Ascidians	0.024
Barnacles	0.039
Brachiopods	0.063
Bryzoans and hydrozoa	0.073
Amphipods	0.165
Isopods	0.142
Polychaetes, worms	0.156

Wet weight values quoted in this document for bivalves are shell free, i.e., after physical removal of the shell; wet weights of other organisms (including decapods, gastropods, urchins) include the exoskeleton or other calcareous support where present. Note that organisms are blotted before measuring wet weight.

2.5 Shells and exoskeletons

Shells and exoskeletons of marine invertebrates consist of minerals (e.g., calcites, aragonite) with an organic matrix made up principally of chitin (Boßelmann et al. 2007; Ruppert et al. 2004; Porter, 2007). Lobster exoskeletons consist of of crystalline magnesium carbonate, calcite, amorphous calcium phosphate, and α-chitin (Boßelmann et al. 2007). Shells of marine molluscs consist of calcium carbonate, mainly in the form of aragonite, with less than 5% chitin and conchiolin (Ruppert et al. 2004; Porter, 2007; Heinemann et al. 2011). The shell consists of three layers: the outer layer made of organic matter, a middle layer made of columnar calcite and an inner layer consisting of laminated calcite (Hayward, 1996). We assume that the proportion of chitin in shells of gastropods and bivalves and in crab/lobster exoskeletons is 2.5% by weight. Carbon in carbonate minerals is considered "inorganic" as it is not available to fuel metabolism of organisms, including bacteria. Inorganic carbon makes up approximately 12% by weight of aragonite and calcite ($CaCO_3$). Carbon in chitin in shells and exoskeletons of marine invertebrates is considered "organic" because it is available to consumers within the food web. The chemical composition of chitin $(C_8H_{13}O_5N)_n$ implies that carbon is about 47% of chitin by weight. Only and all (i.e., whether in the shell, exoskeleton or soft tissue) the organic carbon in marine organisms is included as "biomass" in the trophic model.

Organic carbon consumed by marine invertebrates has one of the following fates:

- Unassimilated: carbon excreted by the organism as urine or faeces, which is channelled to benthic detritus in the model.
- Respiration: Carbon emitted as carbon dioxide, which accounts for the difference between consumption and production in the model.
- Production – somatic growth (organic): organic carbon laid down to increase the weight of the organism (i.e., growth of individuals)
- Production – somatic growth (inorganic): organic carbon used to build inorganic-carbon in the shell or exoskeleton of organisms. The inorganic carbon may be shed periodically (e.g., moulted exoskeleton of decapods), or accumulated while the organism is alive (e.g., shells get larger as the organism grows). Either way, this increase in the mass of inorganic carbon over time due to metabolic processes of the animal represents an export of organic carbon from the system.
- Production – spawning: the release of eggs and sperm into the water column. This represents a transfer of organic carbon to a different trophic group (assumed to be mesozooplankton).

Each of these factors is estimated for groups in the trophic model as explained in the sections below.

3 Datasets used

For each depth/exposure category, the best available information was compiled to estimate the average abundance and biomass of all vegetation, and all invertebrate and vertebrate taxa. Some datasets include only subsets of the full taxa known to be present in a habitat, such that for some habitats, multiple datasets were used to calculate the full range of taxonomic groups present.

3.1 Intertidal estuarine soft sediments

For intertidal estuarine soft sediments, a review of soft sediment habitats commissioned by the Department of Conservation (DOC) determined similarities in faunal diversity for each of six habitat types (seagrass meadows and patches (*Zostera muelleri*), tubeworm bed (most frequently the spionid polychaete *Boccardia syrtis*, but also the maldanid polychaetes *Macroclymenella stewartensis* and *Asychis* spp.), adult cockle beds (*Austrovenus stutchburyi* over 20 mm longest shell dimension), adult wedge shell beds (*Macomona liliana* over 20 mm longest shell dimension), unvegetated mudflats (over 20% mud content) and unvegetated fine-sand (over 80% fine-medium sand) flats that did not contain sufficient densities of cockles, *Macomona* or tubeworms to be allotted to one of these habitats) (Hewitt et al. 2009). Eight estuaries in the Hauraki Gulf were used in the analysis (Central Waitemata Harbour, Upper Waitemata Harbour, Whitford Estuary, Okura Estuary, Kawau Bay, Weiti Estuary, Tamaki Estuary, Mahurangi Estuary).

Sampling at these sites was carried out between 1999 and 2008 by Auckland Regional Council (ARC, Ford et al. 2004) and NIWA, with the number of replicates ranging from 3–12 at each site, and the number of replicates of each habitat at each site ranging from 3–9 in each estuary. Three replicates from each site were randomly selected for analyses. All samples were collected using a 13 cm diameter, 15 cm deep core, and data normalised to compare samples sieved on 500 μm and 1 mm mesh.

Additional data were available from intertidal estuarine habitats from the Auckland Regional Council estuary monitoring programmes for Hauraki Gulf estuaries including Upper Waitemata, Central Waitemata (Figure 25), and Mahurangi (data held by NIWA) and Puhoi, Waiwera, Orewa, Okura, Mangemangeroa, Turanga and Waikopua (data held by Auckland University). Species data were similar to the DOC intertidal site, and overlapped some of the same datasets, but lacked differentiation by intertidal habitat. As such, the DOC intertidal dataset was used to enumerate biomass of benthic invertebrates in estuarine soft sediments. Additional information was used from the ARC datasets, including categorical size information for three bivalve species (*Austrovenus stutchburyi*, *Macomona liliana* and *Paphies australis*). For the Auckland University sites, length frequencies were dominated by smaller size category, under 4 mm – 83% for *Paphies*, 37% for

Austrovenus and 52% for *Macomona*, based on size frequencies across all estuarine habitats. For cockle bed habitat, we used estimates of mean size from dominant size classes at sites in the Upper Waitemata and Central Waitemata Harbours (**Figure 25**) with abundant bivalve populations to estimate mean size of cockles (15 mm) and pipis (20 mm) for intertidal estuarine habitats based on midpoints of the median size category. These sizes were significantly smaller than estimates of mean size from Ministry of Fishery surveys of commercial shellfish beds for *Paphies* (39.6 mm) and *Austrovenus* (35 mm) (Hartill & Cryer 2000).

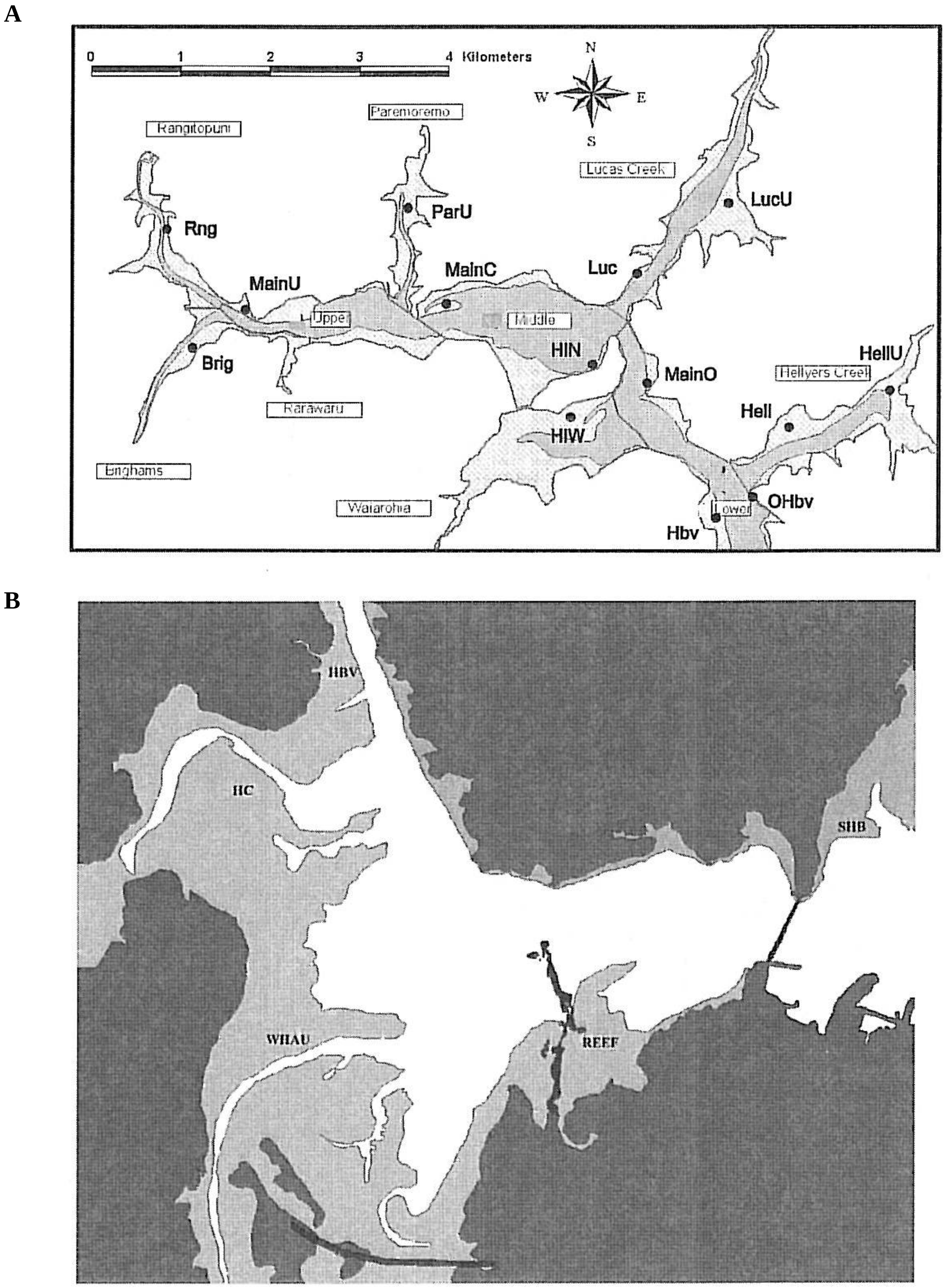

Figure 25: Map of Waitemata Harbour. A: Waitemata upper harbour, showing sampling stations; B: Waitemata main harbour showing the five long-term soft-sediment monitoring sites at Hobsonville (HBV), Henderson Creek (HC), Whau River (Whau), Te Tokaroa Reef (Reef) and Shoal Bay (ShB).

3.2 Subtidal estuarine soft sediments (0–9 and 10–29 m)

For subtidal estuarine soft sediments, we estimated invertebrate abundance based on benthic faunal surveys in Waitemata Harbour (Hayward et al. 1997, 1999) (Figure 26). Data were available for primarily hard-shelled organisms from: Broken Islands (1–59 m depth, 34 stations); Cuvier Island, east of Coromandel (4 stations); and Lady Alice Island (15 stations). Additional site surveys included Cheltenham Beach and Bean Rock stations (Hayward et al. 1999). Data from Hayward et al. (1997) were qualitatively compared to benthic faunal patterns reported in a Powell (1979) survey. Depth and position information were used to divide the stations into depth categories of estuarine subtidal habitats, with a few stations from these surveys categorised as Coastal Sheltered habitats (e.g., samples taken from Rangitoto Channel). Mean counts of each taxon were estimated by summing across all the stations (winter and summer counted as independent stations). Sampling gear was a 10 litre dredge; we assumed that the area sampled was 0.17 m^2 to calculate mean densities per area.

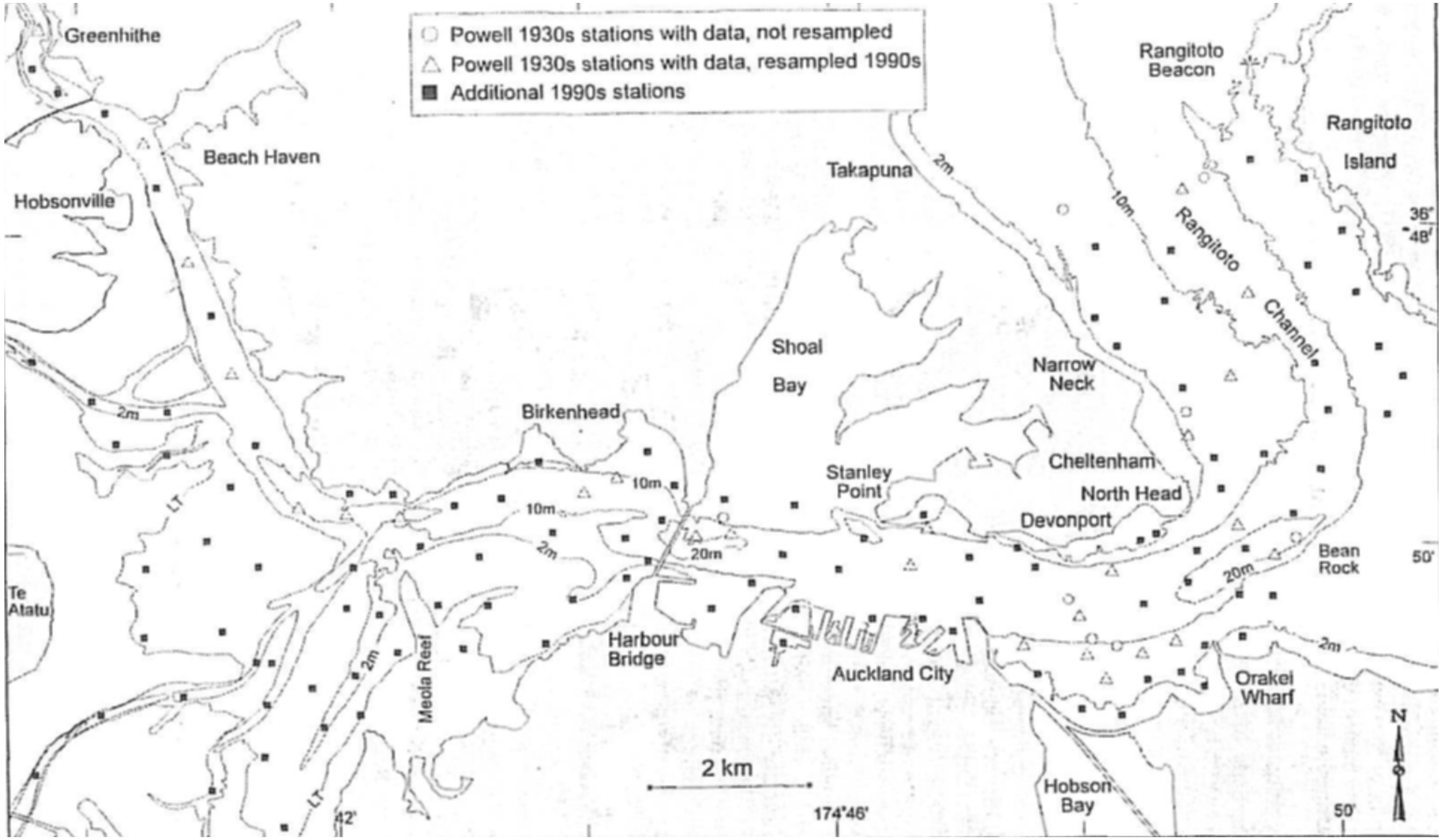

Figure 26: Location of the Waitemata Harbour study area, Auckland, New Zealand, showing the 1930s sampling stations of Powell (1979) and the 1990s stations of Hayward et al. (1997).

3.3 Coastal soft sediments

An amalgamation of a number of different studies provided information on the density of soft sediment taxa in the following areas (**Figure 27**):

1. a broad-scale survey of the Hauraki Gulf (spanning from the Coromandel Peninsula, surrounding Whangaporoa Peninsula and Waiheke Island)
2. the entrance to Te Matuku Bay
3. the greater Firth of Thames
4. outer Great Barrier Island, surrounding Arid Island
5. focused work around Tititiri Island, near the Whangaparoa Peninsula

These studies measured abundances of individuals using a 0.11 m^2 Smith-McIntyre grab sieved over a 1 mm mesh (except for Tiritiri Matangi and Great Barrier Island which used a "larger" mesh size and did not have replication). Using the revised position and depth data provided by Franz Smith who carried out many of these surveys, stations were allocated to strata by James Sturman (NIWA). Level of identification of taxa varied between the different surveys, and final categories recommended by Franz Smith were used. These were a mixture of identification to species or a coarser taxonomic level. Taxa were allocated to appropriate trophic groups and mean density values calculated.

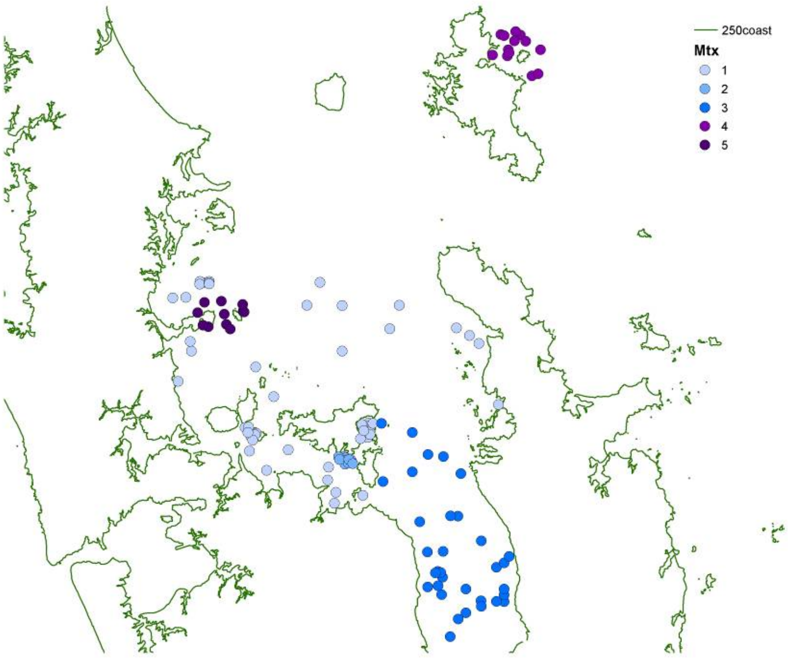

Figure 27: Areas sampled for benthic taxa in the study region by Franz Smith. Regions surveyed (Mtx in legend) were: (1) a broad-scale survey of the Hauraki Gulf; (2) entrance to Te Matuku Bay; (3) greater Firth of Thames; (4) outer Great Barrier Island, surrounding Arid Island; (5) focused work around Tititiri Island, near the Whangaparoa Peninsula.

3.4 Coastal exposed soft sediments

For coastal exposed soft sediments, we used data from benthic surveys by NIWA and Department of Conservation (DOC) from Omaha Bay (Taylor & Morrison 2008) (Figure 28). The survey primarily covered coastal exposed soft sediments with depths 0–9, 10–29 and 30–99 m although the deepest stations were about 40 m. Sampling was carried out using a diver-operated 0.25 m^2 suction sampler sampling to 0.4 m, and a 0.1 m^2 Smith-MacIntyre grab that sampled less deeply into the sediments. Samples were sieved through a 4 mm mesh. Data provided by Richard Taylor (University of Auckland) gave count data which were converted to density. The dataset also included separate estimates for some of the larger macrofauna using a dredge. Where a species was absent from the core, but was recorded in the dredge, the latter value was used. Where both techniques recorded the species, we used core samples to produce biomass estimates.

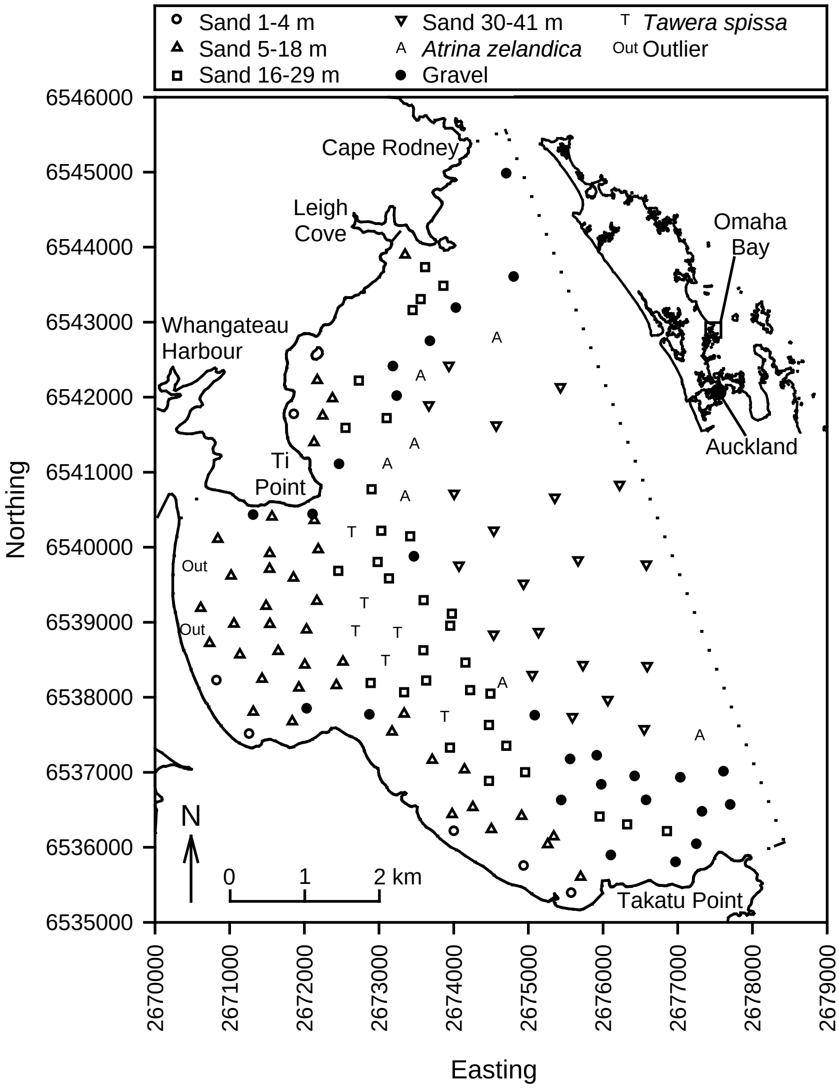

Figure 28: Ohama Bay sample sites (Taylor & Morrison 2008). Data courtesy of Richard Taylor (University of Auckland).

3.5 Coastal exposed soft sediments (30 – 99 m, 100 – 249 m)

While the majority of the model region includes these habitat categories, these are the poorest known and sampled habitats in the Hauraki Gulf region. Information on benthic invertebrates in deep strata was taken from data published in McKnight (1969). In addition, information on infaunal benthic communities of New Zealand continental shelf were extracted from Ocean Biogeographic Information System (OBIS) by searching for the specific station numbers known to be in the Hauraki Gulf area and greater than 30 m depth. Data extracted includes a species list, specimen numbers, and the information that samples were collected by GLO (Large Orange peel grab, sampling 0.25 m^2 according to Estcourt, 1967) and also sometimes an Agassiz trawl (bag 2" mesh, 6 ft width by 2 ft height). We assume that numbers represent total counts, that all taxa collected are included in OBIS (though this may not be the case), and that gastropod and polychaete groups appear under-represented in the dataset. As trawl dimensions are known, but tow time was not recorded, we excluded sites with trawl data from our calculations of mean density. We estimated mean abundance of all observed taxa by depth categories of 30–99 m and 100–249 m.

3.6 Rocky reefs

3.6.1 NIWA rocky reef project

The NIWA rocky reef project (ZBD200509) sampled rocky reef off mainland New Zealand North Island and offshore islands. Approximately ten replicate quadrats measuring 1 × 1 m^2 were sampled in each habitat type at each site. Counts of species were divided by the number of quadrats to give mean density of fauna. Sites sampled were:

- Mainland rocky reef, depths 0–9 m: Kawau Island, Leigh Reserve, Long Bay, Tawharanui, Tiritiri Matangi and Long Bay. A total of 113 quadrats were measured which covered three habitat categories: barrens, shallow mixed algae and kelp.
- Mainland rocky reef, depths of 10–29 m: Kawau Island, Leigh Reserve, Long Bay, Tawharanui, Tiritiri Matangi and Long Bay. A total of 40 quadrats were measured and all sites were dominated by kelp.
- Offshore Islands rocky reef, depths of 0–9 m: Great Barrier Island, east and west, Mokohinau islands and Poor Knights. A total of 78 quadrats were measured, covering two habitat categories, barrens and shallow mixed algae.
- Offshore islands rocky reefs, depths 10–29 m: Great Barrier Island, east and west, Mokohinau islands and Poor Knights. A total of 43 quadrats were measured, all of which were dominated by kelp.

3.6.2 Shear's rocky reef survey

As NIWA rocky reef surveys did not enumerate either macroalgae or encrusting fauna, and poorly enumerated many mobile taxonomic groups (e.g., ophiuroids, holothuroids, asteroids), we used an alternative dataset to fill these gaps. Five sites in the model region (Long Bay, Leigh, Mokohinau Islands, Hahei, Tawharanui) were surveyed as part of a Department of Conservation survey of rocky reefs (Shears & Babcock 2004b). At each site five randomly placed 1 m^2 quadrats were sampled in each of four depth ranges (less than 2, 4–6, 7–9 and 10–12 m) to provide information on the abundance and size structure of macroalgae and macro-invertebrates.

Within each quadrat all macroalgae and macro-invertebrates were measured and counted. Measurements were made using a 5 mm-interval ruler for macro-invertebrates and using a 5 cm-interval 100 cm tape measure for macroalgae. Individual fronds were measured for macroalgae as it is often difficult to determine individual plants for many species. The total frond lengths of macroalgae were measured, with additional measures of stipe length and lamina length being made for *Ecklonia radiata* and *Lessonia variegata*. For *Lessonia* the stipe length and total length of the whole plant was measured and the number of thalli counted. For *Carpophyllum* spp. stipes were counted and assigned to 25 cm length classes. For most small foliose algal species, percent cover of these species was estimated. The primary (substratum) percent cover of turfing algae, encrusting algal species, encrusting invertebrates and sediment were also recorded in each quadrat (1 m^2).

The test diameter of all sea urchins (over 5 mm) was measured as well as whether each urchin was cryptic or exposed. Largest shell dimension (width or length) of gastropods was measured, the actual measurement varied depending on species shell morphology (i.e., shell height for *Cantharidus purpureus*, shell width for *Turbo smaragdus*, *Trochus viridis* and *Cookia sulcata*). The total length of *Haliotis* species, limpets (*Cellana stellifera*) and chitons were also measured.

3.7 Combining multiple data sources

Both biodiversity and biomass of benthic invertebrates close to offshore islands (shallower than about 30 m depth) are often higher than in similar habitats in areas not near offshore islands (Lundquist, unpublished data). Consequently, measurements of biomass of benthic invertebrates from the Rangitoto Island survey were not used to derive representative estimates of biomass density in the Hauraki Gulf for the Coastal Sheltered habitats with depths of 0 – 29 m. Where the biomass of an organism (or group of organisms) in a given habitat was sampled on more than one survey and both surveys used a methodology that would detect that organism if present, if biomass was reported as zero, this was assumed to be genuine, and an arithmetic mean taken of the measurements (including the zero value). Otherwise, where we had multiple (usually two), non-zero measurements of abundance and/or biomass for an organism (or group of organisms) for a given habitat, we used the geometric mean of the values as our best estimate. A geometric mean was used to give equal significance to the measurements.

3.8 Habitats with no data

Data were not available for two habitats: “Coastal Exposed 50–99 m” and “Coastal exposed 100–249 m”. To estimate biomass of groups in these habitats we used the estimated biomass of biota in the three shallower habitats (“Coastal Exposed 0–9 m”, “Coastal Exposed 10–29 m” and “Coastal Exposed 30–49 m”) to infer the change of abundance in that group of organisms with depth. We assumed that the logarithmm of biomass changes linearly with depth. This change in biomass with depth was then used to estimate biomass in the deeper habitat categories. Biomass of crabs, gastropods, bivalves, chiton, echinoids, holothurians, detrivorous and carnivorous shrimps tended to decrease with depth, with a mean ratio of biomass in the 50–99 m category to that in the 30–49 m category of 0.33. For these groups, the mean ratio of biomass in the 100–249 m category to that in the 30–49 m category was 0.10. We found that the biomass of four benthic invertebrate groups increased with depth, namely sessile worms, amphipods, carnivorous polychaetes and detrivorous polychaetes. The mean increase in biomass for these groups from “Coastal Exposed 30–49 m” to “Coastal Exposed 50–99 m” was 1.6. For these four groups, we assumed that the increase in biomass from “Coastal Exposed 30–49 m” to “Coastal Exposed 100–249 m” was a factor of 2 as this was well estimated by this method.

No data exists to estimate this change in biomass with depth for some groups, namely: red rock lobster, octopus, some gastropods, some bivalves, some echinoids, brachiopods, bryzoans and hydrozoa. In this case, we used these mean ratios of 0.33 and 0.10 (i.e. we assumed a decrease in biomass with depth). Where data were not available for biota, we assumed that biomass in the "coastal exposed 50–99 m" habitat was half that in the "coastal exposed 30–49 m" habitat, and that biomass in the "coastal exposed 100–249 m" habitat was one third of that in the "coastal exposed 50–99 m" habitat.

4 Catch histories

4.1 Species with catch history

Several species of benthic invertebrates have been commercially harvested in the study area, and others have been taken for human consumption by non-commercial (recreational, customary) fisheries. Table 44 shows species and species-groups for which catch histories have been developed for the recent period (approximately 2001–2006). Although harvesting of other benthic invertebrates in the study area is likely to have occurred to some extent, the species given here are likely to encompass the vast majority of human removals. Details of the method used to estimate catch histories for the main commercially-harvested species of benthic invertebrate in the Hauraki Gulf is given by Francis & Paul (2008).

Table 44: Major benthic invertebrates taken from the study area for human use.

Code(s)	Name	Scientific name	Reference
SCA	Scallop	*Pecten novaezelandiae*	Francis & Paul 2008
CRA	Rock lobster	*Jasus edwardsii*	Francis & Paul 2008
COC	Cockle	*Austrovenus stutchburyi*	Francis & Paul 2008
PPI	Pipi	*Paphies australis*	Francis & Paul 2008
SUR	Kina	*Evechinus chloroticus*	Francis & Paul 2008
P	Paddle crab	*Ovalipes catharus*	Francis & Paul 2008
MUS, GLM	Green-lipped mussel	*Perna canaliculus*	Francis & Paul 2008
PHC	Packhorse rock lobster	*Sagmariasus verreauxi*	Francis & Paul 2008
SLO	Spanish lobster	*Arctides sp.*	Francis & Paul 2008
KWH, WHE	Knobbed whelk[1]	*Austrofusus glans*	MFish (2009)
PRK	Prawn (killer)	*Ibacus alticrenatus*	MFish (2009)
POY	Oysters (Pacific)	*Crassostrea gigas*	Boyd & Reilly (2002)
PAU	Paua[2]	*Haliotis iris; H. australis*	MFish (2009)
TUA	Tuatua	*Pahies subtriangulata*	Boyd & Reilly (2002)
HOR	Horse mussel	*Atrina zelandica*	MFish (2009)

[1] May include small proportion of ostrich foot shell (*Struthiolaria papulosa*)

[2] Includes *Haliotis iris* (blackfoot paua) and *Haliotis australis* (yellowfoot, queen, silver paua).

4.2 Data sources

Commercial landings data were derived from five main sources as follows:

- 1931–73: Annual Reports on Fisheries, compiled by the Marine Department to 1971 and the Ministry of Agriculture and Fisheries to 1973 as a component of their Annual Reports to Parliament published as Appendices to the Journal of the House of Representatives (AJHR). From 1931 to 1943 inclusive, data were tabulated by April–March years, but we have equated them with the main calendar year (e.g., 1931–32 landings are reported here as being from 1931). From 1944 onwards, data were tabulated by calendar year.

- 1974–82: Ministry of Agriculture and Fisheries, Fisheries Statistics Unit (FSU) calendar year records published by King (1985).
- 1983–87: Ministry for Primary Industries extract from FSU database, by calendar year.
- 1988–89: Landings were very poorly reported because of a transition between official reporting systems, so we estimated them from adjacent years (see *Adjustment of commercial landings* below).
- 1990–2006: Ministry for Primary Industries extracts from all relevant catch-effort databases, by calendar year.

4.3 Landings by port and area

Before 1983, all fisheries statistics were recorded by *port of landing* (King 1985). (They were also reported by statistical area, but this information was not published and is not readily available.) From 1983 onwards, landings were recorded by *statistical area* (King 1986).

1931–82

Ports where material from the Hauraki Gulf could have been landed include Whangarei, Auckland, Thames, Coromandel, Mercury Bay, Whangamata, and Waihi.

1983–2006

Since 1983, most fish and shellfish catches have been reported using what are now Ministry for Primary Industries General Statistical Areas. For the Hauraki Gulf, statistical area boundaries do not always match the study region boundaries so catches from the northernmost and southernmost statistical areas were apportioned based on the approximate length of coastline that occurred within the study region. Statistical areas were mapped to our regions as follows: areas 003 (33% of catches), 004–008, 009 (33% of catches).

Some shellfish species are reported using species specific statistical areas. Catches from rock lobster, paua and scallop statistical areas were mapped on to our regions as follows: rock lobster 904 (25% of catches), 905, 906; paua P111–P117; scallop 1P–1S, 2E–2Y.

Time series (1945–2001) of recreational, illegal, and traditional catch estimates have been developed for the stock assessment of rock lobster in the northern North Island FMAs CRA 1 and CRA 2 (Starr et al. 2003) and are described in detail in Section 5.

4.4 Adjustment of commercial landings

The following assumptions or adjustments were made when estimating commercial landings:

- Before 1974, oyster and mussel landings were reported as number of sacks. We assumed that mussel sacks weighed 68 kg each (150 pounds), after Greenway (1969). Oyster sacks were frequently reported to be three bushels in the Annual Reports. A bushel is a volume measurement rather than a weight, and we have assumed they also weighed 68 kg.
- From 1987 onwards, landed green weights are available for shellfish from Licensed Fish Receiver Returns (LFRR) (Ministry of Fisheries 2007). These values are several times greater than the landings we estimated from commercial fishing reports. The discrepancy is probably a result of meat weight being recorded in the latter rather than green weight. The species affected are scallop, cockle and pipi. We have used the LFRR values from 1987 onwards for

cockle and pipi (see below for treatment of scallop). We do not know if fishing reports prior to 1987 suffer from the same problem, and no corrections have been made.

- Landings of tuatua from the Hauraki Gulf region (TUA 1) have been reported on CELR forms, but these are apparently erroneous records based on landings from Kaipara Harbour (TUA 9) (Ministry of Fisheries 2007).
- Hauraki Gulf scallop landings were estimated as the sum of:
  1. The estimated green (whole) weights for Whangarei (scallop statistical areas 1O–1S) in the Northland scallop fishery (Ministry of Fisheries 2007, p. 776, table 1). Area 1O is north of the Hauraki Gulf region, but landings from that area are negligible (J. Williams, NIWA, pers. comm.).
  2. The estimated green (whole) weights for statistical areas 2E–2Y in the Coromandel scallop fishery. Data for 1991–2006 were provided by Ian Tuck (NIWA, pers. comm.). The annual totals averaged 87% of the total Coromandel landings for the same years (Ministry of Fisheries 2007). Area 2E–2Y landings for 1983–1990 were estimated as 87% of the Coromandel totals in Ministry of Fisheries (2007, p. 783, table 1).

4.5 Estimation of recreational, customary and illegal catches

Estimates of recreational, customary and illegal catches for New Zealand shellfish are few, imprecise and probably inaccurate. Estimates of annual non-commercial harvest of shellfish in New Zealand, 1999–2000, and the most common harvesting methods were given by Turner et al. (2005) based on Annala et al. (2004) and Boyd & Reilly (2002), though it is noted that the some surveys of recreational catch of shellfish are deemed unreliable (Ministry of Fisheries 2009a). The National marine recreational fishing survey data from Boyd & Reilly (2002) have hence only been used where other data are not available, and specifically, for Pacific oyster removals and tuatua.

4.6 Unreported landings and discards

Fishers may discard and/or not report catch for a number of reasons, including there being limited or no market demand, a desire to conceal the size of catches and therefore income, or damage to catches by sealice, predators, or decay. Discarding and non-reporting rates vary with many factors, including time, species, catch size, and fisher. These rates have probably declined overall since the introduction of the New Zealand Quota Management System (QMS, http://fs.fish.govt.nz/Page.aspx?pk=81) in October 1986, suggesting that at least the early landings estimated here have a negative bias. The Ministry of Fisheries Plenary (Ministry of Fisheries 2009a) reports suggestions from working groups where discarding is expected to be significant e.g., horse mussel (*Atrina zelandica*): “It is likely that there is a reasonably high level of unreported discarded horse mussel catch.” Where such suggestion exists (paddle crab, knobbed whelk, prawn killer , horse mussel), we have estimated discard rates. For paddle crab, knobbed whelk, and horse mussel we have assumed 0.5 survival rates for discarded individuals. It is not possible to assert the accuracies of these estimates.

5 Lobster (crayfish)

5.1 General information

Two species of rock lobster (crayfish) are important species in New Zealand coastal marine ecosystems: the red rock lobster *Jasus edwardsii* and the green packhorse crayfish (*Sagmariasus verreauxi*).

5.2 Catch information

Time series (1945–2001) of recreational, illegal, and traditional catch estimates have been developed for the stock assessment of rock lobster in the northern North Island FMAs CRA 1 and CRA 2 (Starr et al. 2003). Most of the study area is within CRA 2, with some in CRA 1, in particular Statistical Area 904 from CRA 1 is partially within the study area. Hence commercial catches for the study area were estimated as 25% of that from area 904 and 100% of that from areas 905 and 906 (Francis & Paul 2008). Non-commercial catch (recreational, illegal, and customary) for the study area was estimated as the sum of 50% of the non-commercial catch for CRA 1 and 75% of CRA 2 (Francis & Paul 2008). The Hauraki Gulf region makes up less than 50% of the coastline of CRA 1 and less than 75% of the coastline of CRA 2, but it contains a high proportion of both the human population and the reef habitat suitable for rock lobsters, and therefore it is assumed to account for a higher proportion of the catch than would have been suggested by coastline length alone. It should be noted that the estimate of non-commercial catch is very uncertain. Landings for 1931–1944 were set equal to the 1945 level and landings after 2001 were set equal to the 2001 level.

5.3 Biomass

Rock lobsters are included in the New Zealand QMS fisheries management system, with species codes CRA (red rock lobster *Jasus edwardsii)*, and PHC (green packhorse crayfish *Sagmariasus verreauxi*). The biomass of CRA was estimated as described in McKenzie (2010) as a "Tier 1" species i.e., one which has an associated quantitative stock assessment. However, because the area of the trophic model does not correspond to the fishery assessment areas, the assessments could not be used directly. Instead, to obtain the total biomass for the study area it was necessary to scale the total biomass contributions from CRA 1 and CRA 2 stocks separately, and then add them. Biomasses by area were estimated based on commercial catch rates by area, using information in Starr & Bentley (2005), and adding in estimated non-commercial catch rates. The CRA 1 and CRA 2 stocks were assessed in 2002 with a length-based model (Starr et al. 2003), covering the period 1945 to 2001. Catch in CRA1 was taken from figure 1 in Starr et al. (2003). The catch history components for CRA 2 were obtained in electronic form broken up by season and seven components for commercial and non-commercial catch (Starr et al. 2003, table B.2). These were summed appropriately to obtain a total catch by fishing year and hence estimate biomass in the study area. The method is described in detail in McKenzie (2010).

Assessment model output was not available for estimated proportions-at-age (as the model was length based) or length-frequencies. Instead, observed tail length frequency data are used as a proxy for this. For CRA 1 some historical data in graphical form were available from 1974 to 1978. However, for both CRA 1 and CRA 2 the biomass in 1974 is about 20% of that in 1930, increasing after then, so the historical data from CRA 1 is not useful for obtaining some estimate of the what length frequency may be like for the virgin population. Observed tail lengths were available in CRA 2 from 1990 to 2001, split by spring-summer and autumn-winter seasons, into male/immature female/mature female, and by market sampling data/catch sampling data/log book sampling data. For CRA 2 the observed length frequency data are limited to Great Barrier Island and the Bay of Plenty (Paul Starr pers. comm.).

To obtain an estimate for the 2006 length-frequency the observed catch sampling data from 2001 are used, the assumption being made that the catch sampling length frequencies are representative of the population. Within a season the data are split by male/immature female/mature female. Based on the total biomass for each in 2001 these are weighted in the proportions 3:3:1 respectively. The mean was then taken over the spring-summer and autumn winter seasons to give a tail length frequency for 2001. The tail lengths for the bins were then converted to total length (tail plus carapace) using linear regression equations taking the mean of slope and intersect for male and female (Starr et al. 2003, table 4).

It is difficult to obtain an estimate for the 1946 length-frequency as there are no observational data available. As a default the 2006 length-frequencies could be used, with the caveat that there are very likely to be more longer lobsters. However, one notable trend in the total biomass is that in 1946 much more of the biomass was made up of males than in 2006. The total biomasses in 1946 for male/immature female/mature female are in the ratio 41:15:2 respectively. Using this ratio, the same calculations were done as for 2006, to get a length-frequency estimate for 1946 (and the virgin population). The same caveat still applies that there are very likely to be more longer lobsters than in this estimate.

Meat yield ("recovery rate") of *Jasus edwardsii* is given as approximately 35% by online fishing resources (e.g., www.australianseafood.com.au). We assume that lobster exoskeletons are about 65% of total wet weight. Water is approximately 13% of exoskeleton weight, chitin about 26%, and inorganic minerals make up the remaining approximately 61% (Boßelmann et al. 2007). Based on these figures and data in Yomar-Hattori et al. (2006), and including the exoskeleton and soft tissue, we estimate that carbon makes up approximately 14% of the wet weight of lobster. About 80% of the carbon is in the form of organic carbon (soft tissue 24%; chitin 55%), and 20% is in the form of inorganic carbon (calcite and magnesium carbonate in the exoskeleton). Organic carbon is hence estimated to be 12% wet weight.

5.4 Production

Production in lobster has three parts: (i) somatic growth (i.e., individuals become larger over time); (ii) gonadal (spawning) output, including production and release into the water of eggs and sperm; (iii) shedding of exoskeleton during moulting. Here, we estimate these three components of production separately and sum to obtain an estimate of total production for this group.

(i) Production rates are based on growth and mortality parameters for the red rock lobster *Jasus edwardsii* as described below. Sizes of rock lobster are commonly measured in at least two ways: tail width and carapace length. Growth rates are poorly known because it is not possible to age rock lobster in sufficient numbers with sufficient accuracy to obtain a size-age relationship (Ministry of Fisheries 2009b). Tag-recapture experiments are generally needed to estimate growth rates of lobsters (e.g., Saila et al. 1979; McKoy & Esterman, 1981; Ministry of Fisheries 2009b). In addition, maximum sizes and growth rates of rock lobsters in New Zealand waters seem to be highly variable (MacDiarmid & Booth 2005). Here, we use the K and t_0 growth parameters (von Bertalanffy relationship for carapace length) for New Zealand North Island rock lobster from McKoy & Esterman (1981, table 4) from the Gisborne region, namely K=0.25 y^{-1} and t_0=-0.38 y. This was based on males only but we also apply these parameters to females. The maximum carapace length of males in the study region is taken to be 200 mm for males (MacDiarmid & Booth 2005) and 125 mm for females (same male:female maximum carapace length ratio as Saila et al. 1979). This growth relationship suggests that females have a harvestable tail width (over 60 mm) aged about 7 years, and males (TW over 54 mm) at 4–5 y, which is reasonable (MacDiarmid & Booth 2005).

Carapace length (CL, mm) was converted to tail width (TW, mm) using relationships given in Breen & Kendrick (1995) applicable to CRA 2, namely: TW=-4.24+0.6755CL (females) and TW=5.72+0.4706CL (males). Weight was calculated from tail width using the relationships in Ministry of Fisheries (2009b) for CRA 2, namely W = 4.16E-6 $TW^{2.9354}$ (males) and W = 1.30E-5

$TW^{2.5452}$ (females), based on (Breen & Kendrick 1995, 1998; MPI unpublished data). TW is tail width in millimetres and W is individual wet weight in kilograms.

The mean size of lobster off the east coast North Island as calculated from size-frequency data from tagging programmes, was 57 mm tail width and the average weight of lobsters captured in potlifts from 2003 to 2005 was 0.6 kg (Lundquist & Pinkerton 2008). This suggests an average individual weight of about 1 kg. Average age of males at harvesting is generally accepted to be 5–10 years. The parameters described above suggest that the age of a 1 kg male is about 6 years old, so this is consistent.

Natural mortality for rock lobsters is given as 0.12 y^{-1} for both sexes (Ministry of Fisheries 2009). A gender imbalance in favour of number of females to the number of males (perhaps 70:30) has been reported in some parts of North Island (Lundquist & Pinkerton 2008) but this may just relate to captures rather than to the population. We assume no gender imbalance in mortality or settlement in the study area. Natural mortality may increase with age, and so we assume that very few lobsters are older than 18 y. This gives a mean age in the population at sizes large enough to be harvested of 10 y. The growth rates, length-weight parameters and natural mortality given above imply an annual somatic production in terms of wet weight of P/B=0.15 y^{-1}. We convert this wet weight production ratio to a carbon based production ratio noting that the biomass of lobster is given as grams of organic carbon in the model, and production should be measured in terms of all carbon i.e., organic and inorganic forms. Organic carbon is estimated to be approximately 80% of the total carbon in lobster (based on figures in Boßelmann et al. 2007), giving an adjusted somatic P/B=0.19 y^{-1}.

(ii) Fecundity of individual mature females as a function of length (mm CL) was described by Annala & Bycroft (1987) as fecundity = $1.0CL^{2.61}$ (data from Whitianga). Fecundity is the number of eggs per female, with a range of 95 000–278 000 reported by Annala & Bycroft (1987) for this region. Egg weight is taken from MacDiaramid et al. (2000) who found a positive relationship between maternal size (CL, mm) and egg weight (EW, mg) described by: EG=0.178+0.0012CL. From the demographic parameters given above this suggests an annual egg production of P/B=0.027 y^{-1}. Measurements of clutch weight on adult females in Te Tapuwae o Rongokako marine reserve (near Gisborne, North Island, New Zealand) indicate that egg production may be the equivalent of P/B between 0.063–0.095 y^{-1} (D. Freeman, Department of Conservation, unpublished data.). Here, we take egg production as a middle value of P/B=0.052 y^{-1}. Sperm production will also require energy but the output is likely to be less than egg production, here assumed to be a third of that required for egg production. Hence, we estimate production associated with spawning as P/B=0.07 y^{-1}.

(iii) Lobster shed their exoskeletons as they grow. Assuming one moult per year (MacDiarmid, 1989), and carbon figures given above (based on Boßelmann et al. 2007; Yomar-Hattori et al. 2006), we estimate that carbon in moulted exoskeletons is equivalent to an annual P/B=0.95 y^{-1}.

Total production of lobster in the study area is hence estimated from the sum of somatic, gonadal and exoskeleton production, and is estimated to be P/B=1.2 y^{-1}. We estimate that somatic growth accounts for 16% of this production, spawning output accounts for 6% of annual production and 78% of the (carbon) production is in the form of moulted exoskeleton.

For comparison, at Leigh, Taylor (1998a) estimated that spiny lobsters had somatic only P/B = 0.07 y^{-1} (based on wet-weight). In a Chilean temperate reef ecosystem model, lobsters had a P/B = 0.45 y^{-1} (Okey et al. 2004). Production of the spiny lobster *Panulirus homarus* in South Africa has been estimated at P/B=0.42 y^{-1} (Berry & Smale 1980). We note that these estimates may be for somatic growth only (probably based on wet weight rather than carbon), and hence may not include production associated with moulting or spawning.

5.5 Consumption and growth efficiency

We estimate consumption rate for rock lobster in the study area based on a growth efficiency of P/Q=0.18. This gives an estimate of consumption rate of Q/B=6.8 y^{-1}. This is between the estimate of lobster consumption used in a Chilean temperate reef ecosystem model (Q/B=7.4 y^{-1}; Okey et al. 2004), and that suggested by Lundquist & Pinkerton (2008) of Q/B = 4.4 y^{-1}.

5.6 Diet (prey)

Diet of rock lobster in the study area is taken from a study of the stomach contents of 326 individuals from north-east New Zealand (Shane Kelly unpublished data). The diet composition of lobsters has been found to be remarkably similar between sites that are separated by about 550 km: Leigh and Wellington (Lundquist & Pinkerton 2008). Although there have been marked changes in the community composition of reefs over a period of 20–25 years (due to protection as marine reserve), these do not appear to have had a significant influence on *J. edwardsii* diet (S. Kelly, Auckland Regional Council, unpubl. data). Diet composition studies have shown that lobsters are a mix of opportunistic and selective predators, with a diet that includes 35–45% molluscs, 15–30% crustaceans (decapods, amphipods, ostracods and barnacles), 5–15% polychaetes, 0–10% algae (phaeophyta, chlorophyta, rhodophyta and *Corallina* sp.), 8–13% echinoids (*Evechinus chloroticus* and ophiuroids), 0–5% encrusting benthos, and 0–3% fish. Mollusc species in guts were represented by 46 gastropod, 22 bivalve and 8 chiton species; trochid gastropods (e.g., *Cantharidus purpureus*, *Trochus viridus*) were most common, while the family Turbinidae (e.g., *Cookia sulcata*) was extremely rare in guts despite being abundant in lobster habitats. Lobsters very rarely eat sponges (Kelly, unpublished data).

5.7 Other information: EE, U, accumulation, imports, exports, transfers

It is known that lobsters can move considerable distances including seasonal migrations of lobsters from reef to soft-sediment offshore habitats (Kelly et al. 2002). Based on tagging research in the North Island, it is estimated that fewer than 5% of lobsters move greater than 5 km (Annala 1981; Booth 1997, 2003; Kendrick & Bentley 2003). Tagging studies in Te Tapuwae o Rongokako Marine Reserve suggest that most lobsters do not move off the reef, and only the large males move away from the reef seasonally to forage on soft sediments (Lundquist & Pinkerton 2008). For this initial trophic model, we assumed that lobsters remain within the model region so that net import is zero.

It is not known if lobster populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

A proportion of the annual production will be exported to the mesozooplankton component of the trophic model as eggs and sperm. This fraction is estimated to be 5.7% based on information in the production section (P/B of eggs and sperm divided by total P/B).

Inorganic carbon in moulted and live lobster exoskeletons represents an export of organic carbon from the system as this inorganic carbon is not available to any other organisms in the system, including bacteria. Based on figures in Boßelmann et al. (2007), one moult per year (MacDiarmid, 1989) and other figures given in the section on production above, we estimate that this export of carbon to an inorganic form is equivalent to about 24% of annual production (22% in moulted exoskeletons, and 3% in living), and we set X/P=0.24.

Ecotrophic efficiency measures the proportion of the annual production that is available for predation ("passed up the food chain") as well as exported or accumulated. The remainder of the production (a fraction of 1-E) is transferred to a detrital group. In the case of lobster, two pathways for transfer of organic carbon to detritus occur:

(i) Lobsters can die from causes other than direct predation, including starvation. The proportion of lobsters dying from causes other than direct predation is not known, but it is likely that the vast majority of mortality is likely to be due to direct predation rather than other causes. Here, we assume that the proportion of annual production leading to carcasses due to causes other than direct predation and fishing is 5%.

(ii) Moulted exoskeletons contain a proportion of organic carbon that can be utilized by organisms such as bacteria. Organic material (mainly chitin) makes up about 26% of lobster exoskeleton mass (Boßelmann et al. 2007). The chemical composition of chitin $(C_8H_{13}O_5N)_n$ implies that carbon is about 47% of chitin by weight. Based on one moult per lobster per year (MacDiarmid, 1989), and figures given in the section on production above, the transfer of chitin in shed exoskeleton to organic particulate (benthic) detritus is estimated to be about 57% of total annual production of lobster.

We hence estimate an ecotrophic efficiency of lobster of E=0.38. There is no discard of whole or part lobster in the model.

The weight of settling larval rock lobster (puerulus) is likely to be much smaller than the intrinsic growth of adult lobsters per year and is set to zero in the trophic model.

Unassimilated consumption for lobster is not well known and is assumed to be U=0.3 following previous trophic models (e.g., Christensen & Pauly 1992; Bradford-Grieve et al. 2003).

Bait input from the rock lobster fishery was included in the model. CPUE, in terms of kilograms of crayfish per pot lift, is given in Ministry of Fisheries (2009) as 0.6–0.7 for the *Jasus edwardsii* NSN stock in 2006–2007. For a commercial catch of 110 t y^{-1} rock lobster (Francis & Paul 2008) this would imply 170 000 pot-lifts per year. If each pot is stocked with about 2 kg of baitfish, about 340 t bait would be required annually. The proportion of this bait that enters the marine ecosystem is not known but may not be negligible as much of the bait not consumed by landed lobsters is likely to be discarded. Other bait input to the system could be from other animals moving into the pot, consuming the bait, and then leaving again. Here, we assume bait input is one quarter of the amount used (84 tWW y^{-1}).

6 Crabs

6.1 General information

Various species of crab occur in the study area including:

- Paguroidea, including many New Zealand hermit crabs
- Rock crabs including *Plagusia chabrus* (red rock crab)
- Spider crabs (Majidae) including *Notomithrax ursus* (hairy seaweed crab)
- Swimming crabs (Portunidae) including *Ovalipes catharus* (paddle crab)
- Mud crabs (various families including Grapsidae (*Helice crassa*), Varunidae (*Austrohelice crassa*) and Macrophthalmidae (*Hemiplax hirtipes*)

The paddle crab *Ovalipes catharus* is commercially fished and included in the New Zealand Quota Management System, with a catch in the study area estimated by Francis & Paul (2008).

6.2 Individual sizes

Mean length for hermit crabs (including shell) on rocky reefs in the Hauraki Gulf is 20 mm (range 13–45 mm) (Taylor 1998a). Other estimates are mean shield length for hermit crabs of 5.97 mm based on surveys from Forest & McLay (2001), Schembri & McLay (1983) and NIWA seagrass surveys (unpublished data), estimating mean size as 70% of maximum size (Forest & McLay 2001). Shield length and shell conversions result in similar estimates of individual biomass of non-shell material, based on shell length to wet weight conversions presented in Taylor 1998a. As most of our datasets had shield length estimates rather than shell length, we use instead shield length conversions available from the North Sea (MAFCONS, 2011) here to determine individual biomass shield length-wet weight conversions ($WW=aL^b$, where $a=0.0019$ and $b = 2.89$) result in average individual biomass of 0.34 gWW for hermit crabs.

Mean body mass of paddle crabs (*Ovalipes catharus*) was estimated to be 22 gWW ind^{-1} (based on data in Section 6.4 below). Note that this is the average individual size by weight in the population; maximum size and commonly taken size will be much greater. For example, we estimate the weight of *O. catharus*, with a typical carapace width of 120 mm, to be of the order of 330 gWW (Davidson & Marsden 1987).

For *Plagusia chabrus*, we used a mean size of 35 mm from Taylor (1998a), and length-weight conversions ($WW=aL^b$, where $a=0.0014$ and $b=2.718$), resulting in mean individual weight of *Plagusia chabrus* of 22 gWW. We use this for estimating biomass of brachyran crabs on rocky reefs. In intertidal soft sediments, crabs are primarily small brachyuran crabs (*Halicarcinus, Austrohelice, Hemiplax, Hemigrapsus*) and hermit crabs, with maximum sizes usually under 40 mm carapace width. Based on typical sizes and length-weight characteristics for other brachyuran crabs we estimate a typical individual weight of 2.1–12.5 gWW, with a mean of 6.6 gWW in intertidal soft sediments.

Including the exoskeleton and soft tissue, we estimate that carbon makes up approximately 12% of the wet weight of crabs. About 61% of the carbon is in the form of organic carbon (soft tissue 22%; chitin 39%), and 39% is in the form of inorganic carbon (calcite and magnesium carbonate in the exoskeleton) (based on data in Boßelmann et al. 2007; Yomar-Hattori et al. 2006).

6.3 Biomass

Soft sediment crab abundance was estimated from all soft sediment surveys using data described in Section 3. In subtidal soft sediments small brachyuran crabs are abundant, in addition to hermit crabs and portunid crabs (especially *Ovalipes catharus*). Intertidal rocky shores have abundant grapsids and porcellanids and pagurids while common crab species in subtidal rocky shore include Plagusia, spider crabs and hermit crabs.

Density in intertidal estuarine soft sediments range from 81.6 to 335 m^{-2} for brachyuran crabs, with highest densities in intertidal seagrass and mudflat habitats (NIWA, unpublished data). Lower densities were observed for brachyuran crabs in subtidal estuarine, coastal exposed, and coastal sheltered soft sediment habitats, with high variability between habitats ranging from 0.42 to 272 m^{-2}. Hermit crab densities are also variable, though generally less than 20 m^{-2}, but offshore island estimates can be more than 600 m^{-2}. A trophic model of the Gisborne marine region suggested a crab density of 0.3 m^{-2} for subtidal soft sediments, composed exclusively of hermit crabs (Pinkerton et al., 2008; Lundquist& Pinkerton, 2008).

Rocky reef crabs were estimated using NIWA rocky reef surveys. Only *Plagusia chabrus* was observed in these surveys, and no data were collected for hermit crabs. *Plagusia* spp. are likely to be present throughout reef areas in the study area but weres only observed in shallow reefs (0–9 m) because of a lack of appropriate sampling elsewhere. We estimate 0.016 m^{-2} for brachyuran crabs for the subtidal reef portion of the study area, assuming similar figures for both offshore islands and coastal rocky reefs. For hermit crabs, we estimate 0.7 m^{-2} based on Hauraki Gulf surveys (Smith 2003). Estimates from Shears & Babcock (2004a, b) for Hauraki Gulf rocky reefs were lower, with few *Plagusia* sp. observed, and estimates of 0, 0.0046, and 0.0038 m^{-2} for 0–2 m, 3–9 m and 10–12 m. These density estimates are similar to other New Zealand surveys. Shears & Babcock (2004a, b) estimated crab density of sub-tidal reefs in Gisborne at 0.32 m^{-2} for all crabs. Densities of hermit crabs of 0.6–0.8 m^{-2} have been reported from subtidal reef surveys of offshore Hauraki Gulf islands (Smith 2003). Langlois studies around reef edges of Leigh, Tawharanui and Hahei found biomass of *P. novizelandiae* to range from less than 0.5–2.4 gDW 0.5 m^{-2}. Note that *Charybdis japonica* was discovered in the Waitemata Harbour in September 2000 (Smith, 2003) but did not show up in the surveys of Hayward et al. (1997, 1999).

Biomass of paddle crabs (*Ovalipes catharus*) in the study region is not well known. Here, we estimate biomass assuming that fishing removes a nominal 10% of the annual production of this species per year. Based on production rates (see below) and the fishery catch (Section 4 of this appendix) from the study area, we hence estimate a biomass of *O. catharus* in the study region of 704 tWW. Total biomass for this group is given in Section 17.

6.4 Production

Production in crabs has three parts: (i) somatic growth (i.e., individual crabs become larger over time); (ii) gonadal (spawning) output, including production and release into the water of eggs and sperm; (iii) shedding of exoskeleton during moulting. Here, we estimate these three components of production separately and sum to obtain an estimate of total crab production.

(i) Information on the biology and growth of the paddle crab (*O. catharus*) is given in Ministry of Fisheries (2009). This includes a length-weight relationship from Davidson & Marsden (1987) (albeit measured on *O. catharus* from Canterbury). Ministry of Fisheries (2009) also gives typical carapace widths (CW, mm) and estimates of natural mortality at difference sizes of crab from Osborne (1987). These parameters were used to construct a basic demographic model of *O. catharus* with which to estimate somatic production (production due to growth) of P/B=1.3 WW/WW/y. We convert this wet weight production ratio to a carbon based production ratio noting that biomass of crabs is given as grams of organic carbon, and production should be measured in terms of all carbon i.e., organic and inorganic forms. Organic carbon is estimated to be approximately 61% of the total carbon in crabs (based on figures in Boßelmann et al. 2007), giving an adjusted somatic P/B=2.2 y^{-1}.

(ii) Gonadal growth of *O. catharus* in the study area was estimated based on fecundity values of this species in Wellington waters, given in Ministry of Fisheries (2009). Mean egg size of *O. catharus* is estimated to be 0.1 mgWW, estimated by scaling eggs of the red rock lobster *Jasus edwardsii* according to adult size. Female reproductive output is estimated to be P/B=0.16 y^{-1}. Sperm production will also require energy but the output is likely to be less than egg production, and is here assumed to be a third of that required for egg production. Hence, we estimate production associated with spawning as P/B=0.21 y^{-1}.

(iii) Crabs shed their exoskeletons as they grow. Yomar-Hattori et al. (2006) summarised meat yields from seven species of crab and seven international studies, and showed that exoskeletons are 61–80% (mean 74%) of total crab weight. Crab exoskeletons consist of crystalline magnesium carbonate, calcite, amorphous calcium phosphate, and α-chitin (Boßelmann et al. 2007). Water is approximately 10% of exoskeleton weight, chitin about 20%, and inorganic minerals make up the remaining approximately 70% (Boßelmann et al. 2007). Based on figures in Boßelmann et al. (2007), we estimate that carbon, in organic or inorganic form, makes up about 13% of exoskeleton wet weight, half of which is inorganic (calcite and magnesium carbonate) and half of which is organic (chitin). The number of times a crab moults per year varies with species and size between approximately 1 and 4 times per year. Assuming 1.5 moults per year, we estimate that carbon (organic plus inorganic) in moulted exoskeletons is equivalent to an annual P/B=1.9 y^{-1}.

Total production of *O. catharus* in the study area is hence estimated from the sum of somatic, gonadal and exoskeleton production, and is estimated to be P/B=4.4 y^{-1}. We estimate that somatic growth accounts for 51% of the total production, spawning output makes up 4.8% of this production and 44% of the (carbon) production is in the form of moulted exoskeleton.

We used this production estimate to estimate production of rock crabs and hermit crabs in the study area assuming that the production rate in crabs scales as the mean body mass to the power -0.25 (Hildrew et al. 2007). Within similar organisms in an ecosystem, production is reported to scale approximately with the negative quarter-power of body size (Hildrew et al. 2007). This allometric scaling from P/B estimated for paddle crabs gives P/B=5.9 y^{-1} (rock crabs) and 12 y^{-1} (hermit crabs). For comparison purposes with other studies, somatic growth in terms of wet weight is estimated to be P/B=1.8 y^{-1} (rock crabs) and P/B=3.9 y^{-1} (hermit crabs).

These estimates of crab production are broadly consistent with production rates of crabs in temperate coastal ecosystems elsewhere in the literature, given that most production values quoted in the literature are actually only somatic growth production. At Leigh (North Island New Zealand), Taylor (1998a) estimated P/B=0.95 y^{-1} for brachyuran crabs (mean individual size 0.46 gWW ind^{-1}) and P/B=1.6 y^{-1} for hermit crabs (mean individual size 0.14 gWW ind^{-1}). Elsewhere, average P/B from a variety of crab species has been calculated as 3.6 y^{-1} (Edgar 1990). This study included two congeners of New Zealand species, *Halicarcinus australis* and *Macrophthalmus (Hemiplax) latifrons*, which had individual mean biomasses of 0.46 and 0.14 gWW ind^{-1}, and P/B of 4.7 and 5.2 y^{-1}, respectively (Edgar 1990). In Chile, ecosystem parameters for temperate crab species ranged from P/B = 0.5–18 y^{-1} (Wolff 1994; Ortiz & Wolff 2002).

6.5 Consumption and growth efficiency

Information from the literature suggests highly variable crab feeding rates. Zhou et al. (1998) report feeding rates for the red king crab (*Paralithodes camtscaticus*) equivalent to Q/B of 18 y^{-1}. Yamada et al. (2010) report feeding of *Carcinus maenas* and *Cancer magister,* both of weight about 160 g as equivalent to Q/B=10–13 y^{-1}. Wallace (1973) gives a length-consumption regression for the shore crab (*Carcinus maenas*), which suggests consumption rates for crabs of weight 160 g in water of temperature 15°C as Q/B=7.0 y^{-1}. Lundquist & Pinkerton (2008) suggested P/Q=0.20 for rock crabs and 0.25 for hermit crabs. Here, we estimate consumption rates for the trophic model of Q/B=29, 50 and 22 y^{-1} for rock crabs, hermit crabs and paddle crabs respectively.

6.6 Diet (prey)

Typical diets for crabs were taken from Wear & Haddon (1987) and McLay (1988). Crab diet varies with species, with herbivorous, detrivorous and carnivorous species occurring in New Zealand. McLay (1988) stated that *Plagusia chabrus* (red rock crab) is an opportunistic feeder on limpets, chitons, gastropods, mussels, barnacles, brown algae and coralline turf, and is also cannibalistic and will eat carcasses (including seabirds). *Ovalipes catharus* (paddle crab), which is found mostly on soft sediments, is an opportunistic predator, whose diet in a Hawke's Bay survey included 65% bivalves, 12% polychaetes, 12% crustaceans and 9% other crabs (Wear & Haddon 1987), which are qualitatively similar to the results of McLay (1988). The Ministry of Fisheries (2009) summarises the diet of paddle crabs (*O. catharus*) thus: "Paddle crabs are versatile and opportunistic predators. They feed mainly on either molluscs or crustaceans, but also on polychaetes, several fish species, cumaceans, and occasionally on algae. A high proportion of the molluscs eaten are *Paphies* species. These include: tuatua (*P. subtriangulata*); pipi (*P. australis*); and toheroa (*P. ventricosa*). The burrowing ghost shrimp *Callianassa filholi*, isopods and amphipods are important crustacean prey items. Cannibalism is common, particularly on small crabs and during the winter moulting season." In contrast, *Notomitrax ursus* (hairy seaweed crab) is an herbivorous crab that eats primarily calcareous algae (*Corallina officinalis*), though it will ingest other algal species (Woods 1993). Extrapolating across these studies, we suggest a diverse omnivorous diet composition for crabs of 2% crabs, 2% octopus, 15% grazing gastropods, 10% predatory gastropods, 17% bivalves, 10% macrobenthos, 5% encrusting invertebrates, 10% phytal invertebrates, 3% macroalgae, 1% mangrove and 10% various carcasses.

6.7 Fishery

Commercial fishery catch of paddle crabs was determined as described in Section 4 of this appendix (see also Francis & Paul 2008). Total Allowable Catch of paddle crabs in region P 1 (which includes the study area, the Bay of Plenty, and the east coast of Northland to Cape Reinga) is 250 tWW (Ministry of Fisheries 2009), but most of the catch is taken from the Bay of Plenty. The mean annual greenweight landings of *O. catharus* averaged over the period of fishing years 2002–2006 was estimated to be 85.6 tWW y^{-1} by Francis & Paul (2008), or 39% of the commercial catch in P 1. This is consistent with Stevens (1999) who notes that most catch is taken from the Bay of Plenty region rather than the study area. Ministry of Fisheries (2009) states that: "Paddle crabs are known to be discarded from inshore trawl operations targeting species such as flatfish, and this may have resulted in under reporting of catches." There is no information on numbers of paddle crabs discarded from such operations, or whether discarded paddle crabs are alive or dead. Here, we assume a discard fraction of 10% of the commercially reported landings and hence estimate a discard of 9.5 tWW y^{-1} from commercial fishing operations, 0.5 of which are assumed to survive discarding.

The recreational allowance in P 1 is 20 tWW and the customary catch allowance is 10 tWW in the same area. Boyd & Reilly (2002) estimated that 14 000 paddle crabs were taken by recreational fishing in area P 1 per year, although the methods used in this survey are considered unreliable by some (e.g., Ministry of Fisheries 2009). Assuming that half of these were from the study area, this amounts to approximately 0.7 tWW y^{-1}. This is consistent with Stevens (1999) who suggested minimal recreational and customary catch of paddle crabs.

Catch of other crab species in the study area is likely to be low in the recent period (Boyd & Reilly, 2002) and is set to zero in the model.

6.8 Other information: EE, U, accumulation, imports, exports, transfers

It is known that some crabs can move considerable distances including seasonal migrations, but for this initial trophic model, we assumed that all crabs remain within the model region so that net import is zero.

It is not known if crab populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

A proportion of the annual production will be exported to the mesozooplankton component of the trophic model as eggs and sperm. For rock crabs and hermit crabs, this fraction is estimated to be 4.8%, the same as for paddle crabs (estimated as P/B associated with production of eggs and sperm divided by total P/B).

Inorganic carbon in moulted and live crab exoskeletons represents an export of organic carbon from the system as this inorganic carbon is not available to any other organisms in the system, including bacteria. Based on figures in Boßelmann et al. (2007), an average of 1.5 moults per year and other figures given in the section on crab production above, we estimate that this export of carbon to an inorganic form is equivalent to about 42% of annual production (22% in moulted exoskeletons, and 20% in living), and we set X/P=0.42.

Ecotrophic efficiency (*EE*) measures the proportion of the annual production that is available for predation ("passed up the food chain") as well as exported or accumulated. The remainder of the production (a fraction of 1-EE) is transferred to a detrital group. In the case of crabs, two pathways for transfer of organic carbon to detritus occur: (i) crabs can die from causes other than direct predation, including starvation; (ii) moulted exoskeletons contain a proportion of organic carbon (in chitin) that can be utilized by organisms such as bacteria.

(i) The proportion of crabs dying from causes other than direct predation is not known, but the vast majority of crab mortality is likely to be due to direct predation rather than other causes. The proportion of annual production leading to carcasses due to causes other than direct predation is assumed to be 5%.

(ii) Organic material (mainly chitin) makes up about 20% of crab exoskeleton mass (Boßelmann et al. 2007). The chemical composition of chitin $(C_8H_{13}O_5N)_n$ implies that carbon is about 47% of chitin by weight. Based on 1.5 moults per crab per year on average and figures given in the section on crab production above, the transfer of chitin in shed exoskeleton to organic particulate (benthic) detritus is estimated to be about 22% of total annual production of crabs.

We hence estimate an ecotrophic efficiency of crabs of EE=0.73.

The weight of settling larval crabs is likely to be much smaller than the intrinsic growth of adult crabs per year and is set to zero in the trophic model.

Unassimilated consumption for crabs is not well known and is assumed to be U=0.3 following previous trophic models (e.g., Christensen & Pauly 1992; Bradford-Grieve et al. 2003).

7 Seastars and brittlestars

7.1 General information

This group includes all asteroids and ophiuroids over 2 mm in diameter. Common species include the asteroids *Astrostole scaber*, *Coscinasterias muricata*, *Stegnaster inflatis*, *Stichaster australis*, and *Patiriella regularis*, and the ophiuroids, *Ophiopsammus maculata*,, *Amphiura* spp. and *Ophiothrix* spp. Diet and energetic parameters were based on the literature (Town 1979, 1980, 1981). We note that seastars and brittlestars are likely to have different trophic niches (seastars are fully predatory while brittlestars are more detrivorous) but are grouped together here.

7.2 Individual sizes

Mean biomass is available for some species and for some ophiuroid and asteroid species, although this is often based on overseas estimates of mean size and length-weight relationships (e.g., Sköld et al. 1994; Jones & Smaldon 1989; Duineveld et al. 1987; MAFCONS 2011). Using these estimates resulted in similar biomass estimates to using Lundquist & Pinkerton (2008)'s strategy of using mean wet weight of 30 gWW for asteroids in general. Where we had species specific individual biomasses, we used these here.

Using these length-weight relationships with all size information available for New Zealand species resulted in low individual wet weight estimates of 0.10 gWW. We used this estimate for intertidal ophiuroids, as measured sizes were primarily available for shallow subtidal soft sediments with smaller species such as *Amphiura* spp. We used mean sizes of 1.67 gWW for subtidal ophiuroids (based on estimated mean size for ophiuroids of 12.1 mm for North Sea ophiuroids, Duineveld et al. 1987). For rocky reef estimates of mean size, literature values compared well with measurements from the Hauraki Gulf of 156 mm for *Coscinasterias*, 42 mm for *Stegnaster*, and 90 mm for *Stichaster* Shears & Babcock (2004a, b). A mean individual weight of *Astrostole scaber* of 35 gWW ind^{-1} is estimated below (Section 7.4).

7.3 Biomass

Asteroid and ophiuroid abundance was estimated from all soft sediment surveys using data described in Section 3. Mean densities ranged from 0 to 4.27 m^{-2} for seastars and 0 to 203.43 m^{-2} for brittlestars in soft sediment habitats, with densities generally increasing with depth. Mean densities ranged from 0 to 0.40 m^{-2} for seastars and 0.01 to 0.03 m^{-2} for brittlestars in rocky reef habitats. Subtidal rocky reef surveys in the Hauraki Gulf estimated higher numbers for seastars of 0.02, 0.16, and 0.25 m^{-2} for 0–2 m, 3–9 m, and 10–12m, respectively (Shears & Babcock 2004a, b). We note that both the data of Shears and NIWA rocky reef surveys are likely to underestimate numbers of brittlestars as these animals are generally nocturnal and cryptic (typically found in crevices). Biomass for this group is given in Section 17 of this appendix.

7.4 Size, growth, production, consumption, growth efficiency

A study of the size, weight, and basic demography of *Astrostole scaber* in the intertidal and subtidal regions is given by Town (1979). In the intertidal zone at Kaikoura (where most of the data were collected), the modal radius (R) of *A. scaber* was 75 mm and was much larger (190 mm) in the subtidal zone (Town 1979). The relationship between (eviscerated) wet weight (W, g) and seastar radius (x, mm) was given by Town (1979) as: $\ln(W+1)=2.418\ln(R+1)-7.149$ ($r^2=0.99$, $n=72$), applicable for R between about 30 and 350 mm (W between 1.5 g and 1.1 kgWW). Town (1979) concluded that *A. scabra* lives for about three years (from the age of about 1 year, R= about 25 mm) in the intertidal zone where it grows up to R=110 mm before migrating to deeper waters and attaining sexual maturity. Town (1979) gives mean weights of ages of *A. scabra* from 1+ to 5+ (his table 2.3) from which we can derive a von Bertalanffy growth curve where R_{inf}=500 mm, K=0.135 y-1, and t_0=1.22 y. Estimates of longevity in seastars vary greatly, and the estimated longevity of *A. scabra* is within the range determined for other species. These estimates range from 2 years in *Asterias rubens,* to 100+ years in *Odontaster validus*, but many are about 5–7 y. From frequencies at age we can estimate a tentative natural mortality of M=0.6 y^{-1}. The age at 95% natural mortality is hence 5.4 y. These parameters lead to an estimate of somatic (growth) production of *A. scaber* aged greater than 3 mm size equivalent to P/B=0.74 y^{-1}, and a mean individual weight within the population of 35 gWW ind^{-1}. For comparison, off northeast coast New Zealand, seastars were estimated as having an average biomass of 30 gWW ind^{-1} (Lundquist & Pinkerton 2008) which is similar.

A. scabra probably becomes sexually mature during its fourth year. This compares with estimates of between one and six years for other species (see Town 1979 for details). The predominant reproductive mode in asteroids is the liberation of gametes into the water and these typically small eggs develop into planktotrophic larvae (Town 1979). Weights of gonads of male and female *A. scabra* are significantly related to adult weight (see Town 1979 for details and regressions, his figures 3.5 and 3.6). Based on data from Town (1979) and assuming that gonadal material has a density close to 1 g ml^{-1}, (neutral buoyancy) we can estimate an annual spawning production for *A. scabra* equivalent to P/B=0.64 y^{-1}.

Hence, we estimate a total (somatic plus spawning) production for *A. scabra* in northeastern New Zealand of P/B=1.4 y^{-1}, and that spawning output is 46% total annual output. The spawning output is assumed to enter the mesopelagic zooplankton component of the trophic model. For comparison, Pinkerton et al. (2008) used production parameters for seastars of P/B=1.6 y^{-1} (based on Lundquist & Pinkerton 2008). For ophiuroids, in Sweden, disc growth and gonad production accounted for 68.9% of total annual production, which was estimated at 1.8 gAFDW m^{-2} y^{-1}. Arm regeneration was about 13.3%. Somatic P/B for ophiuroids was estimated as 0.46 y^{-1} (Sköld et al., 1994) giving a total P/B of 1.5 y^{-1}.

Consumption rate for seastars and brittlestars is estimated using a growth efficiency P/Q=0.25 following Lundquist & Pinkerton (2008). Combining production and consumption values in proportion to estimated biomass gives P/B=1.5 y^{-1} and Q/B=5.8 y^{-1} for the combined brittlestar-seastar trophic group. For comparison, Lundquist & Pinkerton (2008) suggested Q/B=6.4 y^{-1}. Gonadal output for the combined group is estimated to be 51% of total production.

7.5 Diet (prey)

Diets of carnivorous seastars and brittlestars are determined by several factors, including prey and predator size, prey availability, and prey-predator spatial overlap (Town 1981). Town (1979) briefly reviewed knowledge of the diet of *A. scabra* in several New Zealand and Australian studies which suggested that the diet may include chiefly molluscs, including paua (*Haliotis iris*), *Cantharidus purpuratus*, *Cookia sulcata*, *Turbo granosus*, and *Trochus viridis*. Indeed, *A. scabra* has been reported as the primary predator of paua (McShane & Naylor 1995). They may also predate the echinoid *Evechinus chloroticus*, the holothurian (sea cucumber) *Stichopus mollis*, and chitons (e.g. *Eudoxochiton nobilis*, *E. chloroticus*). Near Leigh (within the study area), Town (1979) suggests that *A. scabra* feeds almost exclusively on the chiton *E. chloroticus*). Diet of juvenile *A. scabra* in the intertidal zone at Kaikoura included spiral-shelled gastropods (large *Turbo smaragdus* and *Risellopsis varia*, small *Melagraphia aethiops*, and intermediate sized

Micrelenchus dilatatus) and chiton (*Ischnochiton maorianus*, *Onithochiton neglectus*, *Amaurochiton glaucus*) (Town 1981). Diet composition data are available for the seastar *Astrostole scabra* from a 1970s study of diet preferences of this generalist intertidal predator in Kaikoura (Town 1980). Diet composition of asteroids was recorded as 68% molluscs (mostly grazing gastropods) and 10.8% crustaceans (including more than 60 genera), and 15.4% unidentified.

Cushion stars feed by pushing their stomach out through their mouth and turning their stomachs inside-out over rocks and absorbing nutrients (including microphytobenthos) coating the rocks directly into the stomach lining. Cushion stars also feed by trapping pieces of food in mucous and passing them into their mouth using tentacle-like cilia on their underside. They also catch water column phytoplankton and detritus through filter feeding with their arms.

We estimate diet composition for ophiuroids as 20% planktonic and 80% benthic detritus. Asteroids dominate rocky reef biomass for this trophic group, while ophiuroids dominate soft sediment biomass of this trophic group; overall, biomass of asteroids and ophiuroids are estimated to be similar in the study area. We estimate diet over the full trophic group as 5% kina and other echinoids, 8% grazing gastropods, 8% bivalves, 5% predatory invertebrates, 2% crabs, 10% macrobenthos, 5% microphytes, 10% meiobenthos, 7% planktonic detritus, 30% benthic detritus and 5% carcasses.

7.6 Other information: EE, U, accumulation, imports, exports, transfers

Seastars are not expected to move across the boundaries of the study area to any substantial extent so we assume zero net import/export.

It is not known if seastar populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

The weight of settling seastars is likely to be much smaller than the intrinsic growth of adults and is set to zero in the trophic model.

Ecotrophic efficiency (*EE*) is not known for seastars in the study area. In the case of seastars, whole dead individuals or parts of seastars are likely to be scavenged rather than decomposed by bacterial action and so will be passed in the model to the carcass group. It is likely that that the vast majority of seastar mortality (here assumed to be 95%) is due to direct predation rather than other causes such as starvation, disease, excessive parasite loading and other factors.

Unassimilated consumption for seastars is not well known and is assumed to be U=0.3 following previous trophic models (e.g., Christensen & Pauly 1992; Bradford-Grieve et al. 2003).

8 Kina and other echinoids

8.1 General information

This group includes all echinoids over 2 mm in diameter. The common sea urchin (*Evechinus chloroticus*, kina) is most common in New Zealand waters. Kina are found primarily associated with rocky reefs, with rare observations on soft sediments usually assumed to occur during movements between reefs. Kina are found in highest abundance on intertidal rocky shores, and on shallow rocky reefs. Other echinoderms found commonly in the study area include cake urchin, sand dollar or “snapper biscuit” (*Fellaster zelandiae*, kina papa), and the heart urchin (*Echinocardium cordatum*).

8.2 Individual sizes

Density of echinoids was converted into wet weight using the length-weight conversion for regular sea urchins from the North Sea (MAFCONS, 2011) namely, $W=aL^b$, with a=0.000498 and b=2.93475 for kina, and 0.0003 and b=3.0199 for other urchins, resulting in an average size of 70.8 gWW ind^{-1} for kina and 8.67 gWW ind^{-1} for *Echinocardium cordatum*. The mean size of kina is 71 gWW if the length-weght relationship in Ministry of Fisheries (2009) is used. Mean sizes of *E. cordatum* were similar to that found in the Gulf of Carpenteria (mean size 7.05g) (Long et al. 1995). If mean size was unknown for a species, a mean individual biomass of 14.3 gWW ind^{-1} was used.

Organic carbon content of echinoderms is estimated from Ricciardi & Bourget (1998) using C:AFDW ratio from Salonen et al. (1976). Echinoderm tests are taken to be about 10% total animal wet weight (Giese, 1961). Echinoderm tests are composed of fused plates of calcium carbonate covered by a thin dermis and epidermis, that are assumed to have a similar composition to gastropod shells.

8.3 Biomass

We used estimates from NIWA rocky reef surveys to estimate abundance of kina and other rocky reef invertebrates at different depth categories for rocky reefs. Density of kina in the NIWA rocky reef surveys ranged from 0.08 to 5.26 m^{-2}, and mean size was 57 mm. Similar ranges of density of 0.72, 2.20, and 1.62 m^{-2} on average for 0–2 m, 3–9 m, and 10–12 m depths, respectively, and mean size of 67 mm was estimated by Shears & Babcock (2004a, b) in surveys of five Hauraki Gulf rocky reef sites. Other rocky reef echinoids (primarily *Holopneustes* sp. and *Centrostephanus rodgersii*) ranged in density from 0.04–0.43 m^{-2} in the NIWA rocky reef surveys. We estimated density of soft sediment echinoids (primarily *Fellaster zelandiae*, *Echinocardium cordata*) using data from soft sediment surveys as described in Section 3. Densities of soft sediment echinoids ranged from less than 1 to 53.26 m^{-2} in Hauraki Gulf soft sediment surveys. No kina were recorded on soft sediments.

8.4 Production

The biology and ecology of kina have been extensively studied (e.g., Barker 2001; Lamare & Mladenov 2000; Lamare et al. 2002). Lamare & Mladenov (2000) estimate that kina grow 8–10 mm in their first year of life. Growth rates vary considerably depending on local conditions, but kina may take 8–9 years to reach 100 mm TD (Lamare & Mladenov 2000), with *K* (von Bertalanffy) between 0.28–0.39 y^{-1}. The annual average growth rate for the population depends on the natural mortality (and hence age-frequency structure) of the population, which is likely to vary with region and is generally poorly known. It has been suggested that kina live longer than 50 years of age (Andrew 2003). If mortality corresponds to 0.1% of the population being older than this age, an instantaneous and non-age dependent mortality of 0.14 y^{-1} is implied. A natural mortality of about 0.2 y^{-1} implies that the average age in the population would be about 5 y. This model leads to a somatic annual growth of P/B=0.20 y^{-1}.

Gonad index (GI) is defined as gonad wet weight divided by total wet weight (James 2006), and this has been measured at 3–26% (Lamare et al. 2002; James 2006). Lamare et al. (2002) shows that kina can lose 13% GI over the course of a year, which is assumed to be gonadal output. This is equivalent to a gonadal P/B=0.10 y^{-1}. We assume these P/B estimates apply to other echinoids.

These values for production must be adjusted to be based only on organic carbon biomass. Based on the carbon proportions given above, we estimate total (i.e. soft tissue, shell and spawning production) production, P/B=0.83 y^{-1}. We estimate that 54% of annual production is spawning output, 22% is export (i.e. conversion of consumed organic carbon to inorganic carbon in the shell), and 2.2% is transferred to detritus as organic matter in the shell when the organism dies.

8.5 Consumption

Gross growth efficiency is denoted P/Q and equals annual production, P (gC m^{-2} y^{-1}) divided by annual consumption, Q (gC m^{-2} y^{-1}). Here, we assume a P/Q ratio for kina of 0.15, implying Q/B=5.5 y^{-1}. For comparison, consumption rates of algae by adult kina were reported as 0.69–0.88 gWW per individual per day (Barker 2001), suggesting Q/B=2.9 y^{-1} (2.6–3.3 y^{-1}). Lundquist & Pinkerton (2008) suggested that consumption rates of echinoids are likely to be of the order of 5–10 y^{-1}, and used Q/B=7.5 y^{-1} for northeastern New Zealand. Other ecosystem models in shallow temperate systems report P/B=1.4 y^{-1} and Q/B = 2.8–9.7 y^{-1} for echinoid species (Okey et al. 2004). Consumption rates of manufactured feeds in cultured kina are perhaps 1–2% body weight per day, implying Q/B between 3.7–7.3 y^{-1} (Barker 2001).

8.6 Diet (prey)

Kina are grazing herbivores, preferentially consuming drift algae from large canopy species (*Ecklonia radiata* and *Carpophyllum* spp.), though also consuming live adult and juvenile plants (Barker 2001; Schiel 1982). They have also been observed eating crustose coralline algae and encrusting sponges (Ayling 1978). We suggest a diet composition of 55% large brown canopy algae, 15% foliose algae, 15% crustose algae, 5% sponges, 5% other encrusting invertebrates and 5% microphytobenthos for kina. The main echinoid in soft sediments is *Echinocardium cordatum*, a benthic deposit feeder.

8.7 Fishery

Biomass estimates for the commercial, recreational and customary fishery are not quantified separately for the Hauraki Gulf in region SUR 1, which covers the North Island east and west coasts. SUR 1 total recorded catch from 1994 to 2003 ranged from 134.8 to 297.4 tWW y^{-1}. Francis & Paul (2008) estimated that commercial fishery removals of kina from the study area were 148 tWW y^{-1} (greenweight) for the period 2002–2006 (Section 4).

Recreational catch of kina was estimated for SUR 1 as 1 793 000 kina in 2000 (Boyd & Reilly 2002), or 764 tWW y^{-1} assuming a mean size of 71 gWW ind^{-1}. We note that some people have expressed lack of confidence in estimates of recreational catch by Boyd & Reilly (2002) (Boyd pers. comm.) but we believe that these estimates of the recreational catch of kina represent the best available data at the time of the modelling exercise. Hence, assuming that 68% of the recreational catch is from the study area (the same proportion as commercial catch), we estimate that 523 tWW kina is removed per year by recreational fishing. Total removals are hence estimated to be 671 tWW. We assume that there is no discarding of kina, and kina are removed whole.

8.8 Other information: EE, U, accumulation, imports, exports, transfers

Echinoderms are unlikely to move considerable distances and we assumed that all echinoids remain within the model region so that net import due to movement is zero.

It is not known if echinoderm populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

The weight of settling larval echinoderms is likely to be much smaller than the intrinsic growth of adult echinoids per year and is set to zero in the trophic model.

Ecotrophic efficiency (*EE*) is not known for echinoderms in the study area. In the case of echinoids, whole dead individuals or parts of individuals are likely to be scavenged rather than decomposed by bacterial action and so will be passed in the model to the carcass group. Echinoderms can die from causes other than direct predation, but it is likely that that the vast majority of mortality is due to direct predation. The proportion of annual production leading to carcasses due to causes other than direct predation and fishing is not known but is assumed to be 5%.

Unassimilated consumption for echinoderms is not well known and is assumed to be U=0.3 following previous trophic models (e.g., Lundquist & Pinkerton 2008).

9 Carnivorous gastropods and sea slugs

9.1 General information

This category includes primarily predatory and scavenging gastropods, including whelks (Buccinidae), violet snails (Janthinidae), trumpet shells (Ranellidae), murex shells (Muricidae), and volute shells (Volutidae), The group is generally referred to in this study as "carnivorous gastropods" for brevity but also includes other less common predatory invertebrates such as nudibranchs (sea slugs) and tusk shells:

- Whelks (Buccinidae): e.g., *Penion sulcatus*, *Austrofusus glans.*
- Violet snails (Janthinidae): e.g., *Janthina janthina.*
- Trumpet shells (Ranellidae): e.g., *Cabestana spengleri.*
- Murex shells (Muricidae): e.g., *Poirieria zelandica*, *Dicathais orbita* (white rock shell), *Lepsiella scobina* (oyster borer), *Neothais scalaris.*
- Volute shells (Volutidae): e.g., *Alcithoe arabica* (Arabic volute).
- Olive shells (Olividae): e.g., *Amalda australis*.
- Pagoda shells (Turbinellidae): e.g., *Coluzea wormaldi*.
- Tower shells (Conoidea): e.g., *Phenatoma rosea*.
- Wentletraps (Epitoniidae): e.g., *Cirsotrema zelebori.*
- Helmet shells (Cassidae): e.g., *Semicassis pyrum.*
- Cask shells (Tonnidae): e.g., *Tonna cerevisina*.
- Necklace shells (Naticidae): e.g., *Tanea zelandica*.
- Tusk shells (Scaphopoda).
- Nudibranchs (sea slugs)

9.2 Individual size

Taylor (1998a) gives mean size and AFDW relationships with linear body dimensions for many common gastropods, and other length-weight relationships and mean sizes were obtained from Morley (2004), online resources (Wikipedia), and Powell (1979). Average size from literature estimates was similar to mean size estimates from Shears & Babcock (2004b) mean size across five

Hauraki Gulf rocky reef surveys of *Buccinulum* spp. (29.0 mm), *Cominella virgata* (28.4 mm), *Haustrum haustorium* (34.5 mm), and *Dicathais orbita* (29.4 mm). Mean individual weight was 8.4 gWW ind^{-1}. As a check, weights of 20 common species of predatory gastropods were also estimated using the method of Section 2.3, giving a similar log-mean weight of 12.1 gWW ind^{-1}. Log-mean was used to account for the fact that smaller species tend to be more numerous. The range of individual weights was 0.89–550 gWW ind^{-1}. Species considered were *Penion sulcatus, Austrofusus glans, Janthina janthina, J. globosa, J. exigua, Cabestana spengleri, Poirieria zelandica, Murexsul octogonus, Xymene anbiguus, Dicathais orbita, Haustrum haustorium, Lepsiella scobina. Alcithoe arabica. Amalda australis, Coluzea wormaldi, Phenatoma rosea, Cirsotrema zelebori, Semicassis pyrum, Tonna cerevisina, Tanea zelandica*.

9.3 Biomass

Abundance of organisms in this group were estimated from all soft sediment surveys using data described in Section 3. Mean densities ranged from 0 to 93.6 m^{-2} for predatory gastropods, with one extraordinarily high value of 2428.72 m^{-2} recorded at a deep offshore island site (Hayward et al. 1997) which was excluded. Nudibranch abundance ranged from 0–1.88 m^{-2}, with a similarly improbable value at the same offshore island site of 120.2 m^{-2} which was excluded. Abundances of carnivorous gastropods and sea slugs were estimated for rocky reefs using the NIWA rocky reef surveys. Mean densities ranged from 0.29 to 0.43 m^{-2} for predatory gastropods and 0.03 to 0.09 m^{-2} for nudibranchs in rocky reef habitats. Subtidal rocky reef surveys in the Hauraki Gulf estimated higher numbers for seastars of 1.03, 1.35, and 1.31 m^{-2} asteroids at depths of 0–2 m, 3–9 m, and 10–12 m, respectively (Shears & Babcock 2004b), with primary species observed being *Buccinulum* spp., *Cominella virgata*, *Haustrum haustorium* and *Dicathais orbita*. Choat & Schiel (1982) indicate densities of all gastropod species of 5–38 m^{-2} in an early review of New Zealand reef habitats. Overall, predatory gastropods constituted 98% of this group, with sea-slugs making up less than 3% of the biomass.

The proportion of shell weight out of total dry weight varied among and within different morphological and taxonomic groups of shell-bearing molluscs, with a range of 59–76% (Tokeshi et al. 2000). For whelks (taken as indicative of this group), the typical weight of shell is about 70% total dry weight. Taking tissue dry weight as about 20% of tissue wet weight (Brey 2005; Gambi & Bussotti 1999) implies that whelk shells are about 32% total wet weight. Carbon makes up 3.7% tissue wet weight of this group (Ricciardi & Bourget 1998; Salonen et al. 1976; Table 43). Using values given in Section 2.5 for the chemical composition of shells, we hence estimate that organic carbon is 4.3% shell-free WW and inorganic carbon is 5.4% shell-free WW. Final estimated biomass for this group is given in Section 17 of this appendix.

9.4 Production, consumption, P/Q

Little information on trophic parameters is available for this group in the study area and values were obtained based on information in the literature. Taylor (1998a) calculated P = 0.01 g AFDW m^{-2} y^{-1} and B less than 0.01 g AFDW m^{-2} for suspension-feeding gastropods, and P = 0.47 g AFDW m^{-2} y^{-1} and B = 0.21 g AFDW m^{-2} for neogastropods. These values imply P/B = 2.24 y^{-1} which is taken as total production. We assume a spawning production equivalent to P/B=0.17 y^{-1} as for grazing gastropods. These values must be adjusted to be based only on organic carbon biomass. We hence estimate total (i.e. soft tissue, shell and spawning) production of P/B=4.9 y^{-1}. We estimate that 4.4% of annual production is spawning output, 53% is export (i.e. conversion of consumed organic carbon to inorganic carbon in the shell), and 5.4% is transferred to detritus as organic matter in the shell when the organism dies. Using this value of P/B and assuming a ratio of 0.25 for P/Q, we calculated Q/B = 20 y^{-1}.

9.5 Diet (prey)

There are numerous studies on the diet composition of carnivorous gastropods, particularly in the intertidal region in New Zealand. Predation studies show that the gastropods *Neothais scalaris* and *Lepsiella scobina* feed on intertidal barnacles (Luckens 1975). Predatory whelks in soft-sediment areas consume intertidal bivalves, particularly cockles (*Austrovenus stutchburyi*) (Stewart & Creese 2004). We initialise the diet of this group as 15% encrusting invertebrates, 30% grazing gastropods/chiton, 10% other carnivorous gastropods and sea slugs, 3% carcasses, 2% seastars/brittlestars, 30% bivalves, 5% macrobenthos and 5% phytal invertebrates.

9.6 Fishery

The commercial fishery for predatory gastropods in the study area is small. The knobbed whelk (*Austrofusus glans*) is included in the New Zealand Quota Management System, with a total allowable commercial catch limit of stock KWH 1 (which covers the study area) of 1 t y^{-1}. Francis & Paul (2008) estimate a commercial catch of this species from the study area of 0.18 tWW y^{-1}. Ministry of Fisheries (2009) states that there is likely to be a high level of unreported discarded catch with unknown survival. Using a discard fraction of 0.6 and a survival of 0.5 of discarded individuals gives a discarded weight of 0.12 tWW y^{-1}. A small quantity of Murex shells (Muricidae), such as *Poirieria zelandica* may be taken by recreational and/or customary fishing (Pupu), but this is likely to be very small at the scale of the model. Boyd & Reilly (2002) do not give any recreational catch of shellfish in this trophic group and Ministry of Fisheries (2009) suggests that recreational catch of species in this group is small.

9.7 Other information: EE, U, accumulation, imports, exports, transfers

Predatory invertebrates are unlikely to move considerable distances and we assumed that the whole biomass remains within the model region so that net import due to movement is zero.

It is not known if this group within the study area is undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

The weight of settling larvae is likely to be much smaller than the intrinsic growth of adults per year and is set to zero in the trophic model.

Ecotrophic efficiency (*EE*): In the case of carnivorous gastropods and sea slugs, whole dead individuals or parts of individuals are likely to be scavenged rather than decomposed by bacterial action and so will be passed in the model to the carcass group. Individuals can die from causes other than direct predation, but it is likely that that the vast majority of mortality is due to direct predation. The proportion of annual production leading to carcasses due to causes other than direct predation and fishing is not known but is assumed to be 5%.

Unassimilated consumption for carnivorous gastropods and sea slugs is not well known and is assumed to be U=0.3 following previous trophic models (e.g., Lundquist & Pinkerton 2008).

10 Grazing gastropods & chiton

10.1 General information

This group will be referred to as "grazing gastropods" for brevity but includes all mobile herbivorous and detrivorous molluscs in the region including paua/abalone (*Haliotis australis*, *H. iris*), chitons, limpets, top shells (Trochidae), turban shells (Turbidae), periwinkles (Littorinidae), *Cookia sulcata*, *Trochus viridis*, and *Turbo smaragdus*. Detritivorous gastropods in this group include Amphibola, Zeacumantus, Zegalerus, Maoricolpus, Strutholaria, and Sigapatella. This group also includes numerous chiton species, including both common species (e.g., *Sypharochiton pelliserpentis*, snakeskin chiton), and the rare noble chiton (*Eudoxochiton nobilis*). A list of species/groups included here is given below. Sea cucumbers (Holothurians) are excluded from this group.

- Paua (Haliotidae): e.g., *Haliotis australis, H. iris, H. virginea.*
- True limpets (Patelloidea): e.g., *Cellana radians, C. ornata.*
- Slit limpets (Fissurellidae): e.g., *Scutus antipodes.*
- Siphon limpets (Siphonariidae): e.g., *Siphonaria australis.*
- Top shells (Trochidae): e.g., *Trochus viridis, Melagraphia aethiops, Cantharidus opalus, C. purpureus.*
- Turban shells (Turbidae): e.g., *Cookia sulcata, Turbo smaragdus, Modelia granosa* (cat's eye, pupu).
- Periwinkles (Littorinidae): e.g., *Nodilittorina antipodum.*
- Ostrich foot shells (Struthiolariidae): e.g., *Struthiolaria papulosa.*
- Turret shells (Turritellidae): e.g., *Maricolpus roseus.*
- Horn shells (Batillariidae): e.g., *Zeacumantus lutulentus.*
- Corkscrew shells (Siliquariidae): e.g., *Tenagodus weldii.*
- Slipper shells (Calyptraeidae): e.g., *Crepidula costata.*
- Carrier shell (Xenophoridae): e.g., *Xenophora neozelanica neozelanica.*
- Cowries (Cypraeidae): e.g., *Cypraea vitellus.*
- Bean cowries (Triviidae): e.g., *Trivia merces.*
- Nerites (Neritidae): e.g., *Nerita altramentosa.*
- Bubble shells (Opisthbranchia): e.g., *Bulla quoyii.*
- Mud snails (Amphibolidae): e.g., *Amphibola crenata.*
- Ear shells (Ellobiidae): e.g., *Ophiicardelus costellaris.*
- Chiton, e.g., *Sypharochiton pelliserpentis*, (snakeskin chiton), noble chiton (*Eudoxochiton nobilis*).

Abundances, diets and energetic parameters were obtained from the literature: Ayling 1978; Schiel 1982; Raffaelli 1985; Creese 1988; Schiel & Breen 1991; McShane & Naylor 1995; Marsden & Williams 1996; Freeman 1998; Taylor 1998a; Brey 2005.

10.2 Individual size

Taylor (1998a) gives mean size and AFDW relationships with linear body dimensions for many common rocky reef invertebrates, and other length-weight relationships and mean sizes were obtained from: Morley (2004); Wikipedia; Beckett (1969); Grange (1974); Hartley (1980); Keestra, (1987); West (1991); Gregor (1995); Walker (2005); Briggs (1972), Hooker & Creese (1995), Powell (1979). Average size from literature estimates was similar to mean size estimates from

Shears & Babcock (2004a) across five Hauraki Gulf rocky reef surveys of *Maoricolpus roseus, Cellana stellifera, Cryptoconchus porosus, Eudoxochiton nobilis, Cantharidus opalas, Cantharidus purpureus, Cookia sulcata, Haliotis australis, H. iris, H. virginea, Micrelenchus sanguineus, Modelia granosa, Calliostoma punctulatum, Calliostoma tigris, Trochus viridis, Turbo smaragdus*. This gives a mean weight of mobile benthic grazing and detrivorous gastropods and chitons of 2.1 gWW ind^{-1} for use in the present study For comparison, this mean weight is similar to the log-mean weight of grazing and detrivorous gastropods and chitons calculated based on 46 common New Zealand species of 3.8 gWW ind^{-1} with a range of 0.027–410 gWW ind^{-1} (NIWA unpublished data) Log-mean was used to account for the fact that smaller species tend to be more numerous. Species considered were *Haliotis australis, H. Iris, H. Virginea, Cellana radians, C. ornata, C. flava, Patelloida cortica, Notoacmea pileopsis, Atalacmea fragilis, Scutus antipodes, Tugali elegans, Siphonaria australis, Cantharidus opalus, C. purpureus, Trochus viridis, Melagraphia aethiops, Diloma subrostrata, Diloma bicanaliculata, Micrelenchus sp., Zethalia zelandica, Calliostoma tigris, Calliostoma punctulatum, Callistoma selectum, Cookia sulcata, Modelia granosa, Turbo smaragdus, Astraea heliotropium, Nodilittorina antipodum, N. cincta, Struthiolaria papulosa, S. vermis, Maricolpus roseus, Zeacumantus lutulentus, Tenagodus weldii, Crepidula costata, C. monoxyla, Zegelerus tenuis, Sigapatella novaezealandiae. Xenophora neozelanica neozelanica, Cypraea vitellus, Trivia merces, Nerita altramentosa, Bulla quoyii, Haminoea zelandiae, Amphibola crenata,* and *Ophiicardelus costellaris.*

10.3 Biomass

Grazing gastropod and chiton abundances were estimated from soft sediment surveys using data described in Section 3 of this appendix. Mean densities across soft sediment habitat types ranged from 0 to 603.10 (mean 62.23) m^{-2} for grazing gastropods. Chiton abundance ranged from 0–76.02 (mean 10.42) m^{-2}. Detrivorous gastropod abundance ranged from 0–136.06 (mean 20.49) m^{-2}.

Mobile grazing mollusc abundance was estimated for rocky reefs using the NIWA rocky reef surveys. Mean densities ranged from 1.16 to13.95 m^{-2} for grazing gastropods. Chiton abundance ranged from 0.02–0.14 m^{-2}. Paua (*H. iris* and *H. australis*) abundance ranged from 0–0.53 m^{-2}. Detrivorous gastropod abundance ranged from 0–0.53 m^{-2}. Subtidal rocky reef surveys in the Hauraki Gulf estimated densities on the high end of this range, with combined densities of grazing and detrivorous gastropods, limpets and chitons of 14.42, 10.84, and 10.13 m^{-2} at depths of 0–2 m, 3–9 m, and 10–12m, respectively (Shears & Babcock 2004a, b), with species observed including *Maoricolpus roseus, Cellana stellifera, Cryptoconchus porosus, Eudoxochiton nobilis, Cantharidus opalas, Cantharidus purpureus, Cookia sulcata, Haliotis australis, Haliotis iris, Micrelenchus sanguineus, Modelia granosa, Calliostoma punctulatum, Calliostoma tigris, Trochus viridis,* and *Turbo smaragdus.*

Other New Zealand surveys of grazing and detrivorous gastropods and chitons appear similar or higher. One estimate of all mobile epifauna in the Hauraki Gulf was 14.1 m^{-2}, including grazing and predatory gastropods, crabs, sea cucumbers, pupu, limpets, paua and kina (Smith 2003). Species-specific grazer densities were 1.6 m^{-2} for *Trochus viridis,* 0.15 m^{-2} for *Cookia sulcata*, and 0.01 m^{-2} for the chiton *Cryptoconchus proposus* (Smith 2003). Choat & Schiel (1982) indicate a wider range of densities of all gastropod species of 5–38 m^{-2} in an early review of New Zealand reef habitats. A Leigh study of rocky reef productivity indicates density of 30.28 grazing gastropods m^{-2} on the seafloor and an additional 12.49 m^{-2} on seaweeds, with total biomass of 8.27 gAFDW m^{-2}, and estimated productivity (combined) of 5.31 g AFDW m^{-2} y^{-1} (Taylor 1998a).

The proportion of shell weight out of total dry weight varied among and within different morphological and taxonomic groups of shell-bearing molluscs, with a range of 59–76% (Tokeshi et al. 2000). "Snails" in Tokeshi et al. (2000) are taken as indicative of this trophic group, giving a typical weight of shell of about 72% total dry weight. Taking tissue dry weight as about 20% of tissue wet weight (Brey 2005; Gambi & Bussotti 1999) implies that shells are about 34% total wet weight. Carbon makes up 3.7% tissue wet weight of this group (Ricciardi & Bourget 1998; Salonen et al. 1976). Using values given in Section 2.5 for the chemical composition of shells, we hence estimate that organic carbon is 4.3% shell-free WW and inorganic carbon is 6.0% shell-free WW. These figures are used to estimate biomass of this group as given in Section 17 of this appendix..

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10.4 Production

To estimate growth rates for various sizes of paua, Lundquist & Pinkerton (2008) used von Bertalanffy growth characteristics of this species from McShane & Naylor (1995) in conjunction with the length-weight relationship of Schiel & Breen (1991). Lundquist & Pinkerton (2008) estimated an average production due to growth of P/B=0.76 y^{-1} by averaging growth rates of paua aged between 2 and 5 years. This may give too high a value, as paua may live more than 30 y. It is known that small paua grow faster than large paua, so to calculate an appropriate value for the population as a whole, the population was modelled. Natural mortality for paua is given as 0.02–0.25 (Sainsbury 1982; Ministry of Fisheries 2009), with a natural mortality rate for paua of 0.1 used by Schiel & Breen (1991). Modelling of paua in area PAU 5A (Fiordland area) gave natural mortality of about M=0.16 (Fu & McKenzie 2010) which we use here. This means that longevity (age that 0.1% of the population is older than) is 43 years. Hence, we obtain a somatic (growth) production for each paua in a population, and a population production of P/B=0.16 y^{-1}. Here, we used length-fecundity relationships for paua available from Poore (1973), Sainsbury (1982), and Schiel & Breen (1991), to estimate fecundity (egg production). Egg diameter of paua is about 0.2 mm (Andrew & Naylor 2003). Assuming an egg density of 1 g cm^{-3} (near neutral buoyancy) and that eggs are approximately spherical, leads to a gonadal annual production of P/B=0.051 y^{-1}. These figures imply that production due to reproductive output is 24% of total (somatic plus gonadal) annual production. We note that Lundquist & Pinkerton (2008) assumed a value of 50%.

Production rates will be higher for smaller species. We used the production estimate of paua to estimate production of other grazing and detrivorous gastropods and chitons in the study area assuming that production rate in molluscs scales as the mean body mass to the power -0.25 (Hildrew et al. 2007). Within similar organisms in an ecosystem, such negative quarter-power scaling of production with body size is reasonable (Hildrew et al. 2007). This allometric scaling gives P/B from 0.22–2.4 y^{-1} for grazing invertebrates found in the study area, with a log-mean of P/B=0.70 y^{-1}. Log-mean was used to account for the fact that smaller species tend to be more numerous. The proportion of annual production due to spawning is assumed to be the same for the group as a whole as for paua.

These values for production must be adjusted to be based only on organic carbon biomass. Based on the carbon proportions given above, we hence estimate total (i.e. soft tissue, shell and spawning production) production, P/B=1.5 y^{-1}. We estimate that 14% of annual production is spawning output, 50% is export (i.e. conversion of consumed organic carbon to inorganic carbon in the shell), and 5.0% is transferred to detritus as organic matter in the shell when the organism dies.

This value is similar to some previous estimates for molluscs in shallow temperate systems: P/B = 1.9–2.8 y^{-1} (Wolff 1994; Okey et al. 2004); 1.5 y^{-1} (Lundquist & Pinkerton 2008); Brey & Hain

(1992) give P/B of 0.305 y^{-1} for the Antarctic benthic mollusc *Lissarca notorcadensis*, but production rates are likely to be higher for the warmer waters of the study area.

10.5 Consumption and P/B

Consumption rates of paua from laboratory studies range from 8–18.7% body weight d^{-1} for juveniles, and 2–7% body weight d^{-1} for adult paua (Marsden & Williams 1996). Using 4% body weight d^{-1} as an average value results in approximately Q/B=15 y^{-1}. Lundquist & Pinkerton (2008) state that laboratory paua studies with constant food supply are likely to over-estimate consumption rate relative to in situ consumption, and estimated Q/B=8.0 y^{-1} for paua in northeast New Zealand, with P/Q=0.18. We use this value of P/Q to estimate a consumption for the grazing and detrivorous gastropods and chitons group in the study region of Q/B=8.0 y^{-1}. For comparison, Rybarczyk & Elkaim (2003) gave Q/B=7.5 y^{-1} for "Benthic deposit feeders", and Arreguin-Sanchez et al. (2002) gave Q/B=8.8 y^{-1} for "Molluscs".

10.6 Diet (prey)

Paua are grazing gastropods that have been found to eat primarily red and brown foliose algae, and some canopy brown algae in laboratory studies (Marsden & Williams 1996). In line with work on other grazing gastropods in northern New Zealand waters (Freeman 1998), we assumed that a small amount of the diet of paua is also made up of microphytobenthos and some encrusting invertebrate material. We assumed a diet of 35% macroalgae (foliose, turfing, brown non-canopy), 35% macroalgae (crustose), 20% macroalgae (brown canopy), 5% microphytobenthos and 5% encrusting invertebrates.

Most grazing gastropods are generalist herbivores (Creese 1988). Often gut content studies are difficult to quantify as the guts contain large amount of unidentifiable material, and the contribution of microalgae is rarely quantified. A review of grazing studied on New Zealand rocky reefs indicate that *Turbo smaragdus* eats foliose red and fucoid brown algae, *Amaurochiton glaucus* eats coralline algae, *Siphonaria zelandica* (a limpet) eats *Ralfsia* a crustose brown alga, and *Zeacumantus subcarinatus* eats primarily *Ulva lactuca* (sea lettuce) (Creese 1988). A functional group analysis of intertidal grazing molluscs at Leigh and Otago sites lists chiton species and *Turbo* gut contents as articulated coralline, leathery and filamentous algae. Limpets eat crustose corallines, with additional components of filamentous and foliose algae; and other gastropods were associated with filamentous and foliose algae (Raffaelli 1985). Paua are grazing gastropods, eating primarily red and brown foliose algae, and some canopy brown algae in laboratory studies (Marsden & Williams 1996). Most gastropod guts also contained small amounts of various encrusting invertebrate species in this study. A detailed study of gut contents of *Cookia sulcata*, *Trochus viridis* and *Cantharidus purpureus* at Leigh showed the majority to consist of detritus composed of *Ecklonia* fragments, unicellular algae, diatoms, fine sediment, sponge spicules, crustacean appendages, foraminifera, bryozoans, filamentous and coralline algae (Freeman 1998), implying that these gastropods were functionally detritivores, grazing primarily on the decaying tissue on distal parts of kelp, with some contribution of epiphytes and benthic sources. The deposit feeder *Amphibola crenata* was shown to eat 10–15% bacteria, 13–35% microphytes, and the remainder detritus (Juniper 1987).

Combining these diet estimates in proportion to consumption, we suggest average diet composition of this trophic group of 27% macroalgae, 2% mangrove/seagrass/saltmarsh, 18% microphytes, 10% benthic bacteria, 41% benthic detritus, and 2% encrusting invertebrates.

10.7 Fishery

Three species of shellfish in this group are covered by the New Zealand Quota Management System: Paua (*Haliotis iris*; *H. australis*) and Tuatua (*Paphies subtriangulata*). Commercial catches of these species in the study area were estimated by Francis & Paul (2008) as 37.3 and 21.2 tWW y^{-1}. Boyd & Reilly (2002) estimate annual removals of three species included in this group by recreational fishing. These removals were converted to weight where necessary using average weights from Section 2.3. Total removals are estimated to be 399 tWW y^{-1} (Table 45).

Table 45: Catch of mobile grazing invertebrates included in this group.

Shellfish	Species	Commercial catch[1] tWW y^{-1}	Recreational catch[2] tWW y^{-1}	Total
Paua	*Haliotis iris; H. australis*	37.3	59.1	263
Tuatua	*Paphies subtriangulata*	21.3	213	85.8
Cats eye	*Turbo smaragdus*	0	1.9	50.5
ALL				399

Notes:

1 Francis & Paul (2008); mean annual landings (Greenweight) in study area for period 2002–2006

2 Boyd & Reilly (2002), using average weights from Section 2.3.

10.8 Other information: EE, U, accumulation, imports, exports, transfers

Grazing and detrivorous gastropods and chitons are unlikely to move considerable distances and we assumed that the whole biomass remains within the model region so that net import due to movement is zero.

It is not known if grazing and detrivorous gastropods and chiton populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

The weight of settling larvae is likely to be much smaller than the intrinsic growth of adults per year and is set to zero in the trophic model.

Ecotrophic efficiency (E) is not known for grazing and detrivorous gastropods and chitons in the study area. In the case of grazing invertebrates, whole dead individuals or parts of individuals are likely to be scavenged rather than decomposed by bacterial action and so will be passed in the model to the carcass group. Individuals can die from causes other than direct predation, but it is likely that that the vast majority of mortality is due to direct predation. The proportion of annual production leading to carcasses due to causes other than direct predation and fishing is not known but is assumed to be 5%.

Unassimilated consumption for grazing and detrivorous gastropods and chitons is not well known and is assumed to be U=0.3 following previous trophic models (e.g. Lundquist & Pinkerton 2008).

11 Sea cucumbers (Holothuroidea)

11.1 General information

This group contains mobile, invertebrate epifauna living on hard and soft sediment with individual animal size more than 2 mm that are exclusively or predominantly detrital feeders. This group is almost entirely made up of Holothuroidea (sea cucumbers, especially *Stichopus mollis* and *Paracaudina chilensis*) and will be referred to as "sea cucumbers" for brevity. However, note that this group also includes Sipunculans (peanut worms), and Hemichordates (acorn worms). Note that all detrivorous and detrivorous/herbivorous gastropods are not included here.

11.2 Individual size

Mean sizes for holothuroids were calculated from literature surveys (Takeda et al. 1997; Ralph & Yaldwyn 1956; Sewell 1990). Average size of the most common holothuroid *Stichopus mollis* was estimated as 166.4 mm and 107.85 gWW (Sewell 1990). *Paracaudina chilensis* has a mean weight of 22 gWW (Takeda et al, 1997). We estimate mean size of 0.1 gWW for sipunculans and hemichordates.

11.3 Biomass

Abundances for taxa in this group were estimated from all available soft sediment survey information using data described in Section 3. Mean densities across soft sediment habitat types ranged from 0 to 190.17 (mean 10.24) m^{-2} for holothuroids, and 0–87.31 (mean 4.39) m^{-2} for sipunculans and hemichordates. Mobile detritivores were rarely encountered in the quadrat surveys of the NIWA rocky reef surveys and the Shears & Babcock (2004a, b) surveys. However, prior surveys of rocky reef assemblages in the Hauraki Gulf estimate an average abundance of 0.15 m^{-2} of *Stichopus mollis*, with lower abundance in the outer Gulf of 0.05 m^{-2} (Smith 2003). We use the average of these broader scale, modeled estimates (0.10 m^{-2}) of Holothuroidea abundance for all rocky reef habitats in the model. We assume that sipunculans and hemichordates have minimal contributions to biomass in rocky reef habitats. The final estimate of biomass of this group is given in Section 17 of this appendix.

11.4 Production, consumption and P/Q

We use literature estimates of trophic parameters for holothuroids in temperate systems of P/B = 0.6 y^{-1} and Q/B = 3.4 y^{-1} (Okey et al. 2004). This leads to P/Q= 0.18.

11.5 Diet (prey)

Holothuroids are mostly deposit feeders and it is often assumed that these are taking benthic detritus and/or benthic bacteria (Moriarty 1982; Uthicke 1999; Moodley et al. 2002; Josefson et al. 2002). Recent stable isotope data (NIWA, unpublished data) however suggests that holothuroids in the study area are carnivorous, and may be consuming almost entirely meiofauna. Some species of holothuroids can also take material from the water column. We assume this trophic group to be composed of solely detritivores, and estimate mean diet as 90% benthic meiofauna and 10% benthic bacteria.

11.6 Other information: EE, U, accumulation, imports, exports, transfers

Detrivorous invertebrates are unlikely to move considerable distances and we assumed that the whole biomass remains within the model region so that net import is zero.

It is not known if detrivorous invertebrate populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

A proportion of the annual production of detrivorous invertebrates will be exported to the mesozooplankton component of the trophic model for reproduction. The fraction of production exported for spawning is assumed to be 10%.

The weight of settling larvae is likely to be much smaller than the intrinsic growth of adults per year and is set to zero in the trophic model.

There is no commercial or recreational fishery for sea cucumbers and we set fishery removals to zero.

Ecotrophic efficiency (*EE*) is not known for detrivorous invertebrates in the study area. In the case of detrivorous invertebrates, whole dead individuals or parts of individuals are likely to be decomposed by bacterial action and so will be passed in the model to the benthic detrital group. Predation on detrivorous invertebrates like sea cucumbers is low; they have few natural predators. It is likely that the majority of mortality for this group is not due to direct predation and we assume an ecotrophic efficiency of 0.01.

Unassimilated consumption for detrivorous invertebrates is not well known and is assumed to be U=0.3 following previous trophic models (e.g., Lundquist & Pinkerton 2008).

12 Bivalves

12.1 General information

This group includes all bivalve molluscs in the study region. Key groups are mussels (*Aulacomya maoriana, Mytilus galloprovincialis, Perna canaliculus*), oysters (Ostreidae), scallops (Pectinidae), pipi (*Paphies australis*), venus shells (*Dosinia* spp., *Tawera spissa*) and cockles (*Austrovenus stutchburyi*). We estimated density of soft sediment bivalves using data from soft sediment surveys as described in Section 3. NIWA rocky reef datasets did not include density of attached mussels so instead we used estimates of rocky reef bivalves (primarily *Perna canaliculus, Mytilus edulis*) using data from Shears & Babcock) surveys of the Hauraki Gulf. A list of bivalve molluscs in the study region is given in the list below:

- Horse mussels (Pinnidae) e.g., *Atrina zelandica*.
- Mussels (Mytilidae): e.g., *Perna canaliculus* (green shell mussel), *Mytilus edulis* (blue mussel). Note that whereas *Perna canaliculus* (green shell mussel) probably once had very high density in soft sediments in the Hauraki Gulf (based on peak landings in 1961, Greenway 1969), intensive dredging reduced the abundance and current biomass is primarily shallow estuarine aquaculture, with some recruitment onto shallow rocky substrates.
- True oysters (Ostreidae) include *Saccostrea glomerata* (rock oysters), *Crassostrea gigas* (Pacific oysters), *Tiostrea chilensis lutaria* (Bluff/dredge/flat/Chilean oyster).
- Jingle shells (Anomiidae): e.g., *Anomia trigonopsis* (golden oyster, poro).
- Scallops (Pectinidae), include *Pecten novaezelandiae* (tipa), *Chlamys zelandiae* (fan shell, kopakopa), and *Zygochlamys delicatula* (deep water off the Otago coast) only.

- Dog cockles (Glycymerididae): e.g., *Tucetona laticostata* (large dog cockle, kuhakuha), *Glycymeris modesta* (small dog cockle).
- False cockles (Carditidae): e.g., *Cardita auteana* (dog's foot cockle), *Venericardia purprata* (purple cockle purimu).
- Lace cockles (Lucinidae): e.g., *Divaricella huttoniana*.
- True cockles (Cardiidae): e.g., *Pratulum pulchellum* (strawberry cockle).
- File shells (Limidae): e.g., *Limutula maoria*.
- Venus shells (Veneridae): e.g *Dosinia anus* (ringed venus shell, tuangi haruru), *Ruditapes largillierti* (oblong venus shell, hahari), *Irus elegans* (elegant venus shell, kuwha), *Tawera spissa* (tawera), *Bassina yatei* (frilled venus shell, pukauri), *Protothaca crassicosta* (ribbed venus shelll, karoro), *Austrovenus stutchburyi* (littleneck clam, cockle, tuangi), *Dosinia subrosea* (fine dosinia),
- Trough shells (Mactridae): e.g., *Mactra discors* (large trough shell, whangai karoro), *Mactra murchisoni* (large trough shell), *Cyclomactra ovata* (oval tough shell, ruheruhe), *Spisula aequilatera* (triangle shell, kaikaikaroro), *Zenatia acinaces* (scimiter shell, peraro), *Resania lanceolata* (lance mactra, pipi rahi).
- Pipi shells (Mesodesmatidae): e.g., *Paphies ventricosa* (toheroa), *Paphies subtriangulata* (tuatua), *Paphies australis* (pipi), *Paphies donacina* (deep water tuatua, surf clam)
- Sunset shell (Psammobiidae): e.g., *Gari stangeri* (kuwharu), *Gari convexa* (takarepo), *Soletellina nitida* (pipipi).
- Wedge shells (Tellinidae): e.g., *Macomona liliana* (hanikura).
- Piddocks (Pholadidae): e.g., *Barnea similis* (angel wing, patiotio)
- Gaper shells (Hiatellidae): e.g., *Panopea zelandica* (honehone)
- Box shells (Myochamidae): e.g., *Myadora striata* (pukira)
- Lantern shells (Periplomatidae): e.g., *Periploma angasi.*

12.2 Individual size

Average and/or maximum sizes (linear dimensions) for most species were sourced from Morley (2004) or Powell (1979). Where only maximum size was given, average size was estimated as 70% of maximum size. Where no information on maximum size was found in the above publications, we estimated maximum size based on species in the same family or in some cases, based only on the scale information of photos of specimens given on the Te Papa website[2] or conchology web sites[3]or as last option, as a 'generic' mean size based on the average of all available size data (33 mm). Mean sizes were available for 12 species from Omaha Bay (Richard Taylor, pers. comm.). Mean sizes of common intertidal bivalves (*Paphies australis, Austrovenus stutchburyi, Macomona lilian*) were calculated from mean size from the Central Waitemata Harbour monitoring programme (Townsend et al. 2008), as observed sizes were generally smaller than reported maximum and mean sizes in the literature.

Mean sizes (linear dimensions) were converted to average weights based on an available length weight relationship. Length-weight relationships (blotted tissue wet weight) were estimated for 12 species from the Omaha Bay study and were used as the basis to calculate most biomasses (Richard Taylor, pers. comm.). Note that all individual weights of bivalves quoted here, unless otherwise stated, are without shell i.e., wet (blotted) tissue weight only, which includes muscle, gonad and other organs. For other species published length-weight relationships were available: *A. stutchburyi*

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[2] http://collections.tepapa.govt.nz; Accessed June 2014

[3] http://www.conchology.be/, http://www.conchsoc.org/, http://www.aucklandshellclub.net.nz/. Accessed June 2014.

from Snake Bank (Williams et al. 2008) and Cornwallis (Hartill & Cryer, 2000), *Paphies australis* from Mair Bank (Williams et al. 2007) and Little Omaha Bay (Grant, 1994), *Ruditapes largillierti* from Whangateau harbour and Whangarei Heads (Gribben, 1998), Asian date mussels (*Musculista senhousi*) from Parkari and Orakei (Sim, 1999). For some species, length weight relationships for similar species in other geographic locations such as North Sea were used (MAFCONS, 2011). North Sea length-weight conversions included shell weight, and were converted to wet tissue weight using estimates of the proportion of total wet weight due to the shell. This factor varies with species, location, individual size, season and condition factors, so any conversion is uncertain to some degree. Some assembled estimates of shell weight as a proportion of total wet (blotted) weight were: 0.88 for scallops (Bruce Hartill, pers comm.); 0.68 for Asian date mussels; 0.75 for *Ruditapes* sp.; 0.70 for *A. stutchburyi* (James Williams, pers. comm.); green-lip mussel, shell was about 0.53 total blotted WW (Hickman & Illingworth, 1980); 0.80, based on a typical Condition Index (CI) of 0.2, (Orban et al. 2002); range of shell-bearing molluscs had ratio 0.59–0.76 (Tokeshi et al. 2000). Here, we use a middle value of 70% as a typical value of shell WW proportion for the "Bivalves" group. Carbon makes up 7.9% tissue wet weight of this group (Ricciardi & Bourget 1998; Salonen et al. 1976).

In some cases the AFDW was available for a species and this was converted to a wet tissue weight using conversion factors from Ricciardi & Bourget (1998). In absence of a species-specific length weight relationship, the length weight relationship for *T. spissa* was used as this gave a biomass closest to an "average" of the 12 species from the Omaha dataset. From the Omaha length-weight data supplied by Richard Taylor, excluding *Atrina* and *Pecten*, 195 individuals gave a mean size of 38 mm and 4.13 gWW tissue only) was estimated (Table 46). Including *Atrina* and *Pecten* gave a mean size of 82 mm and 10 gWW tissue only.

Table 46: Average and maximum sizes for bivalve species at Omaha Bay

Species	Max Size (mm)	Mean Size	% of Max size	Average blotted meat weight (gWW)
Atrina novaezealandica?	126	101	0.80	37.2
Dosinia anus	67	58.0	0.87	7.72
Dosinia maoriana	38	30.7	0.81	1.67
Dosinia subrosea	52	39.7	0.76	3.13
Gari convexa	63	55.3	0.88	4.27
Gari stangeri	52	44.4	0.85	4.25
Myadora striata	40.6	33.9	0.84	0.833
Oxyperas elongata	88	68.5	0.78	11.1
Pecten novaez.	126	87.5	0.78	11.2
Tawera spissa	23.7	20.7	0.87	0.431
Tucetona laticostata	79.6	49.1	0.62	6.73
Venericardia purpurata	36.2	25.2	0.70	0.980

As a check, weights of 49 common species of bivalves were estimated using the mean length-weight relationship, giving a log-mean weight of 22.2 gWW ind^{-1} (median 27.9 gWW ind^{-1}). Log-mean was used to account for the fact that smaller species tend to be more numerous. The range of individual weights was 0.89–295 gWW ind^{-1}. Species considered were *Solemya parkinsoni*, *Barbatia novaezealandiae*, *Altrina zelandica*, *Aulacomya maoriana*, *Perna canaliculus*,*Mytilus edulis*, *Modiolarca impacta*, *Zelithophaga truncata*, *Xenostrobus pulex*, *Modiolus areolatus*, *Saccostrea glomerata*, *Crassostrea gigas*, *Tiostrea chilensis lutaria*, *Anomia trigonopsis*, *Pecten novaezelandiae*, *Chlamys zelandiae*, *Zygochlamys delicatula*, *Limutula maoria*, *Tucetona laticostata*, *Glycymeris modesta*, *Cardita auteana*, *Venericardia purprata*, *Divaricella huttoniana*, *Pratulum pulchellum*, *Dosinia anus*, *Ruditapes largillierti*, *Irus elegans*, *Tawera spissa*, *Bassina yatei*, *Protothaca crassicosta*, *Austrovenus stutchburyi*, *Mactra discors*, *Cyclomactra ovata*, *Spisula aequilatera*, *Zenatia acinaces*, *Resania lanceolata*, *Paphies ventricosa*, *Paphies subtriangulata*, *Paphies australis*, *Paphies donacina*, *Gari stangeri*, *Gari convexa*, *Soletellina nitida*, *Macomona liliana*, *Pseudarcopagia disculus*, *Barnea similis*, *Panopea zelandica*, *Myadora striata*, and *Periploma angasi*.

12.3 Biomass

To account for separation of fishery and aquaculture species, biomass and energetic parameters were separated into the following groups in the bivalve trophic compartment. Biomass of cultured bivalves is relatively well known, but probably accounts for only a small proportion of total bivalve biomass in the study area. The annual production of green-lip mussels in aquaculture farms in the study area in 2008 was about 25 000 tWW y^{-1}, about 20% of the New Zealand annual production (Dunbar-Smith 2011). This includes shell weight according to the Ministry for Primary Industries website: "'Greenweight' is the weight of any fish, aquatic life or seaweed before any processing commences…In New Zealand, under the Fisheries Act 1996, all references to the weight of fish must be in greenweight"[4]. Greenweight was converted to tissue weight using a blotted wet tissue weight to total weight ratio of about 37% (Hickman & Illingworth 1980). The grow-out period of green-lip mussels in New Zealand is 12–24 months (Lloyd 2003) suggesting a (tissue) biomass of about 6940 tWW. In addition, about 19% of the annual production of 3300–4000 tWW y^{-1} farmed Pacific oyster is also from the study region (about 690 tWW y^{-1}, including shell). Market size of New Zealand oysters is attained in 18 to 30 months, giving an estimate of biomass cultured oysters in the study area of 208 tWW (tissue only).

Biomass of wild (uncultured) bivalves in the study area is poorly known. The available survey information does not include enough sites to adequately characterise the distribution or abundance of the major bivalve species in the region. Consequently, estimates of bivalve biomass used in the model should be considered to have large uncertainty. Horse mussels (*Atrina zelandica*) are particularly poorly covered by available survey information, so where no reasonable information was available, we assume horse mussel biomass density in a given habitat type was similar to that of other mussels. Using values given in Section 2.5 for the chemical composition of shells, we hence estimate that organic carbon is 11% shell-free WW and inorganic carbon is 27% shell-free WW. These figures are used to estimate biomass of this group as given in Section 17 of this appendix

12.4 Production, consumption, P/Q

There is reasonable information on growth rates of mussels because of their importance in aquaculture in New Zealand (Hickman & Illingworth 1980; Jeffs et al. 1999; Hawkins et al. 1999). Most of the literature concerning commercial mussel species relate to aquaculture, e.g. green lip mussels *Perna canaliculus*, although see Jeffs et al. (1999) for a review and bibliography for this species. Growth rates are available for some New Zealand surf clams, including *Spisula equilatera*, *Mactra murchisoni*, *M. discors*, *Dosinia anus*, and *Paphies donacina* (Cranfield & Michael 2001), but little information is available for most of the dominant infaunal bivalve taxa found in New Zealand soft sediments.

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[4] http://www.fish.govt.nz/en-nz/Publications/The+State+of+our+Fisheries+2008/Commercial+Fisheries/Greenweight+conversion.htm; Accessed June 2014

Many studies have examined filtration rates of mussels at different levels of nutrients and suspended sediment concentrations (James et al. 2001). Respiration rates of cultured mussels have been estimated as: for each 1 g dry weight, 0.367 mL O_2 mussel^{-1} hr^{-1} = 4.72 mg C mussel^{-1} day^{-1} = 1.2% body C day^{-1} and ingestion rates at 8.61 mg C mussel^{-1} day^{-1}. Thus the ratio of respiration to ingestion is 54.8% (James et al. 2001). Assuming weights of mussel between 9–53 gWW, with unassimilated consumption of 0.2 (Lundquist & Pinkerton 2008), these values imply a mean somatic (growth) P/B=1.0 y^{-1}, with an estimate of P/B=0.31 y^{-1} for green-lip mussels (*Perna canaliculus*).

Two basic age-growth models of green-lip mussels (*Perna canaliculus*) were developed to estimate production. Model 1 was based on age-size rates given in Ministry of Fisheries (2009) which were fitted to a von Bertalanffy growth curve giving L_{inf}=208 mm, K=0.786 y^{-1}, and t_0=-0.024 y. We used size-weight relationships for mussels from Hickman (1979). Instantaneous natural mortality for wild (non-aquaculture) mussels is not well known. Cheung (1993) estimated an annual mortality of the green-lipped mussel *Perna viridisis* as 0.98, implying M=3.9 y^{-1}. If the maximum age of mussels (1% population older than this) is 4 years, we estimate natural mortality of M=1.2 y^{-1}, and hence estimate a growth production using the population model of P/B=1.2 y^{-1} with a mean weight of 81 gWW ind^{-1}. Model 2 was based on a constant growth rate of 45 mm y^{-1} up to a shell length of 90 mm (based on Hickman 1979). Model 1 suggests that 86% of the population production is due to mussels smaller than 90 mm, so this second model captures most of the production. The estimate of P/B from the second model, with the same natural mortality as before, is P/B=1.4 y^{-1}, with a mean individual weight of 14 gWW. If market size of New Zealand oysters is attained in 18 to 30 months, this suggests a P/B of about 1 y^{-1}. Growth rates are reported to be lower by about half for shore-based compared to rope-based mussels grown in aquaculture (Hickman 1979). The vast majority of bivalves in the study area are not in aquaculture (98%) so we reduce somatic production rates of wild bivalves by a factor of 2.

We take our best estimate of production for wild green-lip mussel as an average of 0.31, 1.2/2 and 1.4/2, 1/2 i.e. P/B=0.52 y^{-1}. This may imply P/B=1.0 y^{-1} for mussels in aquaculture. For comparison, one New Zealand study has analysed trophic impacts of mussel farms in Tasman Bay, and used values of P/B=1.8 y^{-1} (Jiang & Gibbs 2005).

We then used allometric scaling by body size to scale estimates of P/B as given above to give a value of P/B for the whole bivalve group. Within similar organisms in an ecosystem, production is reported to scale approximately with the negative quarter-power of body size (Hildrew et al. 2007). We assumed that growth (somatic) production of bivalves in the study area scales according to body weight with exponent -0.25. Based on estimated biomass we estimate a somatic production for the “bivalve” group in the trophic model of P/B=1.1 y^{-1}. The somatic growth production estimated here (i.e. P/B=1.1 y^{-1}) agrees reasonably well with other values in the literature. Elsewhere, P/B by taxa range from 1.4–2.2 y^{-1} for infaunal bivalves (Edgar 1990). This range is similar to, but slightly lower than, previous estimates for production of molluscs in shallow temperate systems, where P/B = 1.9–2.8 y^{-1} (Wolff 1994; Okey et al. 2004).

MacDonald & Bourne (1987) give age-specific estimates of reproductive output as a proportion of total production for the scallop *Patinopecten caurinus* in Canada. Gonadal output varied from P/B=0.09–0.14 y^{-1} aged 3 years, to about 0.52 y^{-1} aged 8 y and 0.90 at 14 y. Honkoop et al. (1999) show that reproductive output of the intertidal bivalve *Macoma balthica* rises from P/B=0.17 y^{-1} for body mass index of 8 to P/B=0.33 y^{-1} at BMI=14. Here, we use a typical value of gonadal production (in terms of wet weight) of P/B=0.30 y^{-1}.

These values for production must be adjusted to be based only on organic carbon biomass. Based on the carbon proportions given above, we estimate total (i.e. soft tissue, shell and spawning production) production, P/B=3.3 y^{-1}. We estimate that 5.2% of annual production is spawning output, 61% is export (i.e. conversion of consumed organic carbon to inorganic carbon in the shell), and 6.2% is transferred to detritus as organic matter in the shell when the organism dies.

12.5 Consumption, P/Q

Based on James et al. (2001) and assuming unassimilated consumption of 0.2 (Lundquist & Pinkerton 2008), we propose to use a growth efficiency of bivalves in the study area of P/Q=0.2. Using this value to estimate consumption, we estimate Q/B=17 y^{-1}. For comparison, this consumption rate is similar to, but higher than, than that given by Rybarczyk & Elkaim (2003), who gave Q/B = 7.5 y^{-1} for 'benthic deposit feeders', Arreguin-Sanchez et al. (2002), who gave Q/B = 8.8 y^{-1} for 'molluscs', and Wolff (1994), who gave Q/B=9.9 y^{-1} for 'bivalves >10 mm'. Our estimate is similar to that given by Jiang & Gibbs (2005), who suggested Q/B=20 y^{-1} for 'other shellfish' based on unpublished data.

12.6 Diet (prey)

Bivalves are primarily suspension feeders (e.g., *Atrina zelandica*, *Austrovenus stutchburyi*), but also include some deposit feeding species (e.g., *Macomona liliana*, *Nucula* spp.). Mussels are generally assumed to feed primarily on phytoplankton, though Zeldis et al. (2004) also recently demonstrated that *P. canaliculus* does consume zooplankton in small quantities. Diet of mussels was given as 0.222 small zooplankton, 0.5 phytoplankton, 0.278 detritus (Jiang & Gibbs 2005: authors' own estimates). We estimate diet of the bivalve group as 50% phytoplankton, 10% microzooplankton, 10% nanoplankton, 10% water column detritus, and 20% water column bacteria.

12.7 Fishery

Commercial catches of cockle (*Austrovenus stutchburyi*), pipi (*Paphies australis*) and green-lipped mussel (*Perna canaliculus*) in the study area were estimated by Francis & Paul (2008) in Table 47. Boyd & Reilly (2002) estimate annual removals of these and two additional species (Pacific oysters, *Crassostrea gigas*; rock oyster, *Saccostrea glomerata*) by recreational fishing. We note that these estimates of recreational catch are considered unreliable by some (Ministry of Fisheries, 2009) but are considered to be the best available estimates. All recreational removals were converted to weight where necessary using average weights from Section 2.3. In addition to these wild catches, there are considerable amounts of aquculture in the Hauraki Gulf region. The annual production of green-lip mussels in aquaculture farms in the study area in 2008 was about 25 000 tWW y^{-1} (Dunbar-Smith 2011). About 19% of the annual production of farmed Pacific oyster is also from the study region, estimated to be about 690 tWW y^{-1}. Total removals are shown in Table 47. Discard of these species is assumed to be negligible.

Table 47: Estimated commercial and recreational removals of bivalves from the study region.

Common name	Species name	Commercial removals[1] tWW y^{-1}	Recreational removals[2] Ind y^{-1}	Recreational removals tWW y^{-1}	Total removals tWW y^{-1}
Cockle	*Austrovenus stutchburyi*	229.6	2 357 000	14.7	244.3
Pipi	*Paphies australis*	212.0	6 848 000	216.3	428.3
Green-lipped mussel	*Perna canaliculus*	25 000	1 989 000	105.8	25 109.6
Oysters (Pacific)	*Crassostrea gigas*	0.4	42000	1.8	2.2
Rock oyster	*Saccostrea glomerata*	690[3]	163 000	10.8	10.8
TOTAL		26 139		349.5	26 489

Notes:

1 Francis & Paul (2008); mean annual landings (Greenweight) in study area for period 2002–2006

2 Boyd & Reilly (2002), converted to biomass using average weights from Section 2.3.

3 Cultured shellfish (aquaculture farms)

12.8 Other information: EE, U, accumulation, imports, exports, transfers

It is not known if bivalve populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

A proportion of the annual production of bivalves will be exported to the mesozooplankton component of the trophic model for reproduction, as described earlier.

The weight of settling larvae is likely to be much smaller than the intrinsic growth of adults per year and is set to zero in the trophic model.

Ecotrophic efficiency (*EE*) is not known for bivalves in the study area. In the case of bivalves, whole dead individuals or parts of individuals are likely to be scavenged rather than decomposed by bacterial action and so will be passed in the model to the carcass group. Individuals can die from causes other than direct predation, but it is likely that that the vast majority of mortality is due to direct predation. The proportion of annual production leading to carcasses due to causes other than direct predation and fishing is not known but is assumed to be 5%. For comparison, Jiang & Gibbs (2005) assumed an ecotrophic efficiency of mussels as E=0.95.

Unassimilated consumption for bivalves is not well known and is assumed to be U=0.2 following previous trophic models (e.g., Lundquist & Pinkerton 2008).

13 Sponges

13.1 General information

Characteristic species of the New Zealand inshore reef and deep reef slope include *Ancorina alata*, *Stelleta* sp., *Ircinia* sp., *Geodia* sp., *Raspailia* sp., *Callyspongia* spp. and *Cliona celata*. Sponges have highly variable morphology (encrusting, flabellate, clathrate, massive, arborescent, repent, tubular, ficiform, and massive globulose), with sizes ranging from small encrusting forms to large massive sponges (e.g., *Ancorina alata*, *Stelleta maori*, *Cliona celata*). Large massive sponges can grow to 1–3 kgWW (approximately 300 × 250 × 250 mm). In contrast, thinly encrusting sponges showed a size range from 0.03–0.37 (mean 0.14) g cm^{-2} wet weight and 0.02–0.16 (mean 0.06) gDW cm^{-2} with mean patch size range of 7.8–151.8 (mean 41.7) cm^2 (Ayling 1983).

Sponges are included as a separate trophic group because they have a high relative biomass compared with other encrusting invertebrates, and differ substantially from other encrusting invertebrates in their percentage cover–biomass relationships and trophic role.

13.2 Individual size, weight and biomass

Information on three types of sponges is combined to estimate biomass: (1) encrusting sponge (*Cliona celata*); (2) finger sponge (*Raspailia topsenti*); (3) Massive sponge (*Ancorina alata*). As it can be difficult to identify individual sponges, biomass density was estimated based on percentage of the benthos covered by sponge and information on sponge biomass corresponding to each percentage of cover. Typical biomass of sponge per unit area in soft sediment habitats was calculated using estimates of coverage of sponge by habitat from survey information (Section 3 of this appendix). For soft sediments, we use 0.176 gAFDW per individual as a mean individual biomass as limited information was available to document species in most surveys (Edgar 1990). As NIWA rocky reef surveys did not collect data on encrusting species, sponge biomass was calculated using observations of sponge percentage cover from Shears & Babcock (2004a, b). Percentage cover–biomass (AFDW) relationships for sponges were estimated using relationships available in Shears & Babcock (2004b) based on either species or sponge morphology (table 8), who obtained AFDWs by drying shell-free invertebrate samples to a constant weight at 80ºC and then incinerating at 500ºC. For sponges, carbon was assumed to comprise about 50% of AFDW (Brey 2005). Biomass of sponge estimated in this study is given in Section 17 of this appendix.

13.3 Production

A high proportion of New Zealand sponges are endemic (perhaps 95%), and the energetics of sponges at a species level have generally not been well studied. Sponge growth rates are highly variable, ranging from high rates in response to disturbance of up to 3000 times normal growth rate (Ayling 1983; Bell 1998) to negative growth rates often observed for some species (Ayling 1983; Duckworth & Battershill 2001; Handley et al. 2003; Bell 1998). Ayling (1983) listed normal growth rates for 11 thinly encrusting species of sponge as ranging from –0.01 to 0.28 mm^2 per cm border per day (mean 0.084 mm^2 per cm border per day). Normal growth rates for the globular sponge *Polymastia croceus* were calculated as a 22% increase in size over 2 months (Bell 1998). *Spongia* (*Heterofibria*) *manipulatus* exhibited average growth rates in culture of 28.5% over 9 months (Handley et al. 2003). If typical changes in sponge diameter per year are assumed to be independent of sponge size (Duckworth & Battershill 2001), an appropriate P/B value will be approximately 4/T, where T (years) is the age of the oldest individual sponge. Smith & Gordon (2005) gave ages of 10–20 years for sponges of 150–200 mm, and maximum ages of 80 years for larger sponges with a diameter of 1 m. These figures suggest a P/B of 0.05–0.4 y^{-1}. Therefore, we use P/B=0.2 y^{-1} as a best estimate for sponges.

13.4 Consumption, P/Q

Sponges are thought to have some of the highest assimilation efficiencies of New Zealand reef biota (Smith & Gordon 2005). Jarre-Teichman et al. (1997, 1998) suggested a gross efficiency (P/Q) of 0.05, but this is much less than the 0.2–0.3 efficiencies typically used for other benthic invertebrates (macrobenthic infauna and epifauna, phytal invertebrates). Assuming P/Q of 0.25 gives an estimate of Q/B for sponges of 0.8 y^{-1}.

13.5 Fishery

There is no fishery for this trophic group. The mass of sponges removed recreationally is likely to be negligible compared to the very large biomass of this group in the study area. It is possible that there are significant sponge mortalities due to bottom-trawl fisheries for other species but no estimates of trawling impacts on sponges or survival of trawled sponges are available.

13.6 Diet (prey)

Sponges are filter feeders, and diet has been estimated as primarily picoplankton and ultraplankton (less than 5 microns) for *Polymastic croceus* (Bell 1998). Reiswig (1971) suggest a diet composed of 80% bacteria and particulate organic matter (POM) for a tropical sponge community. We estimate a diet composed of 10% nanoplankton, 20% phytoplankton, and 70% water column bacteria.

13.7 Other information: EE, U, accumulation, imports, exports, transfers

Sponges do not move and so net import is zero.

It is not known if sponge populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

A proportion of the annual production of sponges will be exported to the mesozooplankton component of the trophic model for reproduction. The fraction of production exported for spawning is assumed to be 10%.

The weight of settling larvae is likely to be much smaller than the intrinsic growth of adults per year and is set to zero in the trophic model.

Ecotrophic efficiency (*EE*) is not known for sponges in the study area. In the case of sponges, whole dead individuals or parts of individuals are likely to be broken into small pieces by water movement before being decomposed by bacterial action. Hence, in the model, non-consumed sponges will be passed to the water column detritus group. Most sponges are likely to die from causes other than direct predation, but proportion is not known. The proportion of annual production directly predated is assumed to be only 1%, giving an ecotrophic efficiency of E=0.11.

Unassimilated consumption for sponges is not well known and is assumed to be U=0.3 following previous trophic models (e.g., Lundquist & Pinkerton 2008).

14 Encrusting invertebrates

14.1 General information

This group contains all filter feeding sessile benthic macrofauna over 0.5 mm in diameter, excluding sponges and encrusting shellfish (mussels, oysters etc.), but including the following:

- Ascidians
- Anenomes
- Barnacles
- Brachiopods (lamp shells)
- Bryozoans
- Corals
- Hydrozoa

14.2 Individual size, percent cover, biomass

Biomass of encrusting invertebrates was estimated from soft sediment surveys using methods in Section 2 and data in Section 3 (**Table 48** and **Table 49**). Encrusting invertebrates were not enumerated in NIWA rocky reef surveys (project ZBD200509); therefore, data from Shears & Babcock (2004b) were used. Soft sediment datasets gave data in terms of number of individuals, while rocky datasets included percent cover of different sponge morphologies. Mean individual weights were taken from various literature sources to convert number of individuals to biomass for soft sediment datasets (Pederson & Peterson 2002; Edgar 1990). For rocky reefs, relationships between percent cover and biomass (gAFDW) were taken from Shears & Babcock (2004b).

Table 48: Conversions from percent cover to biomass (g AFDW) for encrusting invertebrates (Shears & Babcock 2004b).

Taxon	Structural group	Species	Percent cover	AFDW (g)
Ascidians	Compound ascidian	*Didemnum* sp.	1%	1.6
	Solitary ascidian	*Asterocarpa* sp.	1%	6.4
	Stalked ascidian	*Pseudodistoma* sp.	1%	2.2
	Sea tulip	*Pyura pachydermatina*	1%	15.0
Barnacles	Barnacles	*Balanus* sp.	1%	1.8
Brachiopods	Brachiopod		0.25%	0.4
Bryozoans	Branched bryozoan	*Cribricellina cribraria*	1%	3.5
	-	*Bugula dentate*	1%	0.7
	Encrusting bryozoan	*Membranipora* sp.	1%	0.5
Coelenterates	Colonial anemone	*Anthoothoe albocincta*	1%	2.3
	Large solitary anemone	*Phlyctinactis* sp.	1%	4.0
	Cup coral	*Monomyces rubrum*	0.25%	0.3
	Soft coral	*Alcyonium* sp.	1%	3.1
Hydrozoans	Hydroid turf	Unknown hydroid	0.25%	0.4
	-	*Amphisbetia bispinosa*	1%	8.1
	Hydroid tree	*Solanderia ericopsis*	1%	10.0
Sponges	Encrusting sponge	*Cliona celata*	1%	11.4

Finger sponge	*Raspailia topsenti*	1%	44.9
Massive sponge	*Polymastia croceus*	1%	22.2
-	*Ancorina alata*	1%	64.7

Table 49: Biomass of encrusting invertebrates by taxa.

	Weight (gWW/ind)		Biomass (t WW)			Proportion of
Taxon	Rocky reef	Soft sediment	Rocky reef	Soft sediment	All	trophic group biomass (%)
Anemones	20	0.054	3 144	3 911	7 055	4.7
Ascidians	33	1.1	27 279	782	28 061	18.8
Barnacles	15	0.0015	760	84	845	0.6
Brachiopods	...	0.080	0	559	559	0.4
Bryozoans	6.0	0.36	890	110 460	111 350	74.8
Hydrozoa	71	...	1 047	0	1 047	0.7
TOTAL			33 121	115 796	148 917	100

Organic carbon content of all broad groups of encrusting invertebrates found in the study area is reported by Ricciardi & Bourget (1998). Carbon to AFDW ratio of benthic invertebrates was taken from Salonen et al. (1976). Many of the encrusting invertebrates found in the study area include a calcarous structure. Schopf (1967) presents data on the chemical composition of bryozoa that are used to estimate the relative proportions of organic and inorganic carbon. Organic carbon is contained in body soft tissues and chitin of invertebrates, whereas carbon in mineral carbonates of the structure of encrusting invertebrates is considered inorganic as it is not available to other biota, including bacteria. Although there is considerable variation between species, data from Schopf (1967) suggests that bryozoa in the study area may have a typical proportion of 25% organic matter in terms of dry weight.

14.3 Production

Measurements of production rates for encrusting invertebrates within the study area were not available. Other ecosystem models in temperate systems give a range for P/B of 1–4 y^{-1} for similar biota (Ortiz & Wolff 2002; Okey et al. 2004). Lundquist & Pinkerton (2008) used P/B=1.5 y^{-1} for encrusting invertebrates in northeast New Zealand which we assume applies here. A proportion of the annual production of encrusting invertebrates will be exported as eggs or sperm released into the water for reproduction. The fraction of production exported is not well known for this group, and spawning output is assumed to be 10% of total annual production.

These estimates of production must be adjusted to be based only on organic carbon biomass. Based on the proportions of organic and inorganic carbon given above and assuming that spawned output has a similar C:WW ratio as zooplankton (Brey 2005), we estimate total (i.e. soft tissue, calcarous structure and spawning) production, P/B=3.3 y^{-1}. We estimate that 7.4% of annual production is spawning output, 52% is export (i.e. conversion of consumed organic carbon to inorganic carbon in the shell), and 5.2% is transferred to detritus as organic matter in the structure when the organism dies.

14.4 Consumption, P/Q

Consumption rates of encrusting invertebrates within the study area are not well known. Other ecosystem models in temperate systems give a range for Q/B of 12–17 y^{-1} for similar biota (Ortiz

& Wolff 2002; Okey et al. 2004). Sponges are thought to have some of the highest assimilation efficiencies of New Zealand reef biota (Smith & Gordon 2005), and other encrusting invertebrates may have similarly high growth efficiencies. Jarre-Teichman et al. (1998) suggested a gross efficiency (P/Q) of 0.05 for encrusting invertebrates, but this is much less than the P/Q=0.2–0.3 efficiencies typically used for other benthic invertebrates and here we assume P/Q=0.25 for encrusting invertebrates based on literature estimates for macro-invertebrates. These values imply consumption rate of Q/B=13 y^{-1}.

14.5 Fishery

There is no fishery for this trophic group.

14.6 Diet (prey)

Limited information on diet composition is available for other sessile invertebrates. Most sessile invertebrates are filter feeders (e.g., barnacles, tunicates, bryozoans). The diet of bryozoans appears to consist entirely of phytoplankton (Bullivant 1967). We assumed that the diet of heterotrophic encrusting invertebrates in the study region consists of phytoplankton, water-column bacteria and zooplankton. While the exact composition is unknown due to taxon-specific feeding preferences and seasonality of prey availability, we estimated that diet was composed of 10% microzooplankton, 30% nanoplankton, 30% phytoplankton and 30% water column bacteria.

14.7 Other information: EE, U, accumulation, imports, exports, transfers

It is not known if encrusting invertebrate populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

The weight of settling larvae is likely to be much smaller than the intrinsic growth of adults per year and is set to zero in the trophic model.

Ecotrophic efficiency (*EE*): In the case of encrusting invertebrates, whole dead individuals or parts of individuals are likely to be broken into small pieces by water movement before being decomposed by bacterial action. Hence, in the model, non-consumed encrusting invertebrates will be passed to the benthic detritus group. The proportion of encrusting invertebrates that die from causes other than direct predation is not known, and is set to 50%.

Unassimilated consumption for encrusting invertebrates is not well known and is assumed to be U=0.3 following previous trophic models (e.g., Lundquist & Pinkerton 2008).

15 Macrobenthos (benthic macrofauna)

15.1 General information

This group contains all benthic biota more than 2 mm in diameter, except those in other named trophic groups. The group includes benthic and hyperbenthic decapod crustaceans (shrimps, prawns), benthic amphipods, benthic copepods, benthic isopods, ostracods, mysids, tanaids, and cumaceans (*Colurostylis lemurum, Cyclapsis thomsoni, C. argus, Diastylopsis*). We also include in this group all larger benthic worms: oligochaetes, platyhelminthes, polychaetes and sessile worms (sabellidae, oweniidae). This group also includes phytal invertebrates, i.e., all macro-invertebrate (over 2 mm) epifauna living in, on, or amongst macroalgae, or on hard substrates. Biomass is likely to be dominated by micro-crustaceans (amphipods, isopods, ostracods, harpacticoid copepods, tanaids, cumaceans), microsized gastropods and bivalves. Larger individuals are included in other groups (e.g., bivalves, grazing invertebrates etc.).

15.2 Individual size and biomass

We used data from Western Australia from Edgar (1990) combined with the biovolume conversion method of Donovaro et al. (2002) to estimate individual weights of organisms in this group. Other information on mean weights was taken from Bouvy (1988), Taylor (1998a), and Kroger et al. (2006). The average individual weights of macrobenthos (weighted according to biomass) are: 423 mgWW ind^{-1} (soft sediment crustacean macrofauna), 6.2 mgWW ind^{-1} (soft sediment vermiform macrofauna), and 2.3 mgWW ind^{-1} (phytal invertebrates, from Lundquist & Pinkerton 2008).

15.3 Biomass

We estimated density of soft sediment benthic macrofauna using data from soft sediment surveys as described in Section 3. Benthic macrofaunal abundance varies with habitat within the model area, with higher densities in shallow areas with close proximity to the reef areas and lower densities in exposed beaches and subtidal soft sediments. We have some information on the abundance of benthic macrofauna in the study area (or failing that, northern North Island, New Zealand) with which to estimate total biomass of this group. However, many surveys did not enumerate and/or measure biomass of smaller macrobenthos, so that information on biomass in similar habitats was used to estimate benthic macrofaunal biomass where we had no or unreliable information. Consequently, biomass of this group is considered especially uncertain. Intertidal beach fauna have been surveyed at Ohope Beach, Castlepoint, and Napier (Fincham 1977), with average densities of primarily amphipods, isopods, and cumaceans of 76, 184, and 56 m^{-2} respectively. Another study at Wainui Beach reported densities of 480 m^{-2} (Stephenson 1993). Biomass for the study area of each group (carnivorous shrimps, detrivorous shrimps, amphipods, isopods, ostracods, worms, and “other” which includes mysids, tanaids, cumaceans and insects) is given in Table 50. The biomass of polychaetes based on the available data was very low: less than 1% of the total biomass of soft sediment benthic macrofauna. Given that the biomass of benthic polychaetes is generally found to be a dominant or very significant proportion of total macrobenthic biomass, this is likely to be a sampling artefact; biomass of polychaetes is likely to not have been appropriately reported. Hence, here we assume that polychaetes make up a nominal 50% of soft sediment macrobenthic biomass, with 25% of these being carnivorous polychaetes, 71% herbivorous/detrivorous polychaetes, 3% sessile worms, 1% other worms (same ratio as in survey data).

Table 50: Biomass and effective individual weights of benthic macrofauna in the study area. Annual production/biomass (P/B) values shown here were estimated using an allometric relationship based on crab somatic growth, as described in the text.

Group	Individual weight ($mgWW\ ind^{-1}$) Effective mean	Biomass (tWW)	C:WW (ratio)	Proportion biomass (%)	P/B (y^{-1})
Carnivorous shrimps	404	8 714	0.078	16.8	3.4
Detrivorous shrimps	655	4 708	0.078	9.1	3.0
Amphipods	2	412	0.078	0.8	13.3
Isopods	12	358	0.067	0.6	8.1
Sessile worms	9	486	0.074	0.9	8.7
Carnivorous polychaetes	11	3 493	0.074	6.4	8.3
Detrivorous polychaetes	8	10 102	0.074	18.5	9.1
Other worms	2	115	0.074	0.2	12.4
Other soft sediment macrobenthos	2	35 051	0.054	46.7	10.6
Phytal invertebrates	3	5	0.073	0.0	11.3
Total		63 442		100	8.3

Several publications detail phytal invertebrate abundance and productivity in New Zealand waters, primarily at Leigh (Kingsford & Choat 1985; Taylor & Cole 1994; Williamson & Creese 1996; Taylor 1998 a,b,c). We estimated abundance of phytal invertebrates in terms of their numerical density (i.e., numbers of individuals) relative to the total biomass of each macroalgal trophic group. Averaging over many studies gives a mean subtidal abundance of phytal invertebrates per g WW of algae of 1.02 for *Carpophyllum flexuosum*, 0.66 for *Carpophyllum* spp., 0.51 for *Ecklonia radiata*, 0.82 for other large brown algae, 0.25 for red foliose algae, 0.53 for green foliose algae, 0.53 for turfing algae, and 16.3 for crustose algae, as calculated by Lundquist & Pinkerton (2008). As macroalgal data were calculated as gDW, we converted to gWW using estimate of gDW = 21% gWW based on *Laminaria* spp. (Cauffopé & Heymans 2005). These considerations gave phytal biomass of 3.3–5.1 gC m^{-2} for rocky reef habitats between 0 and 29 m deep. Phytal abundances were assumed to be much smaller below these depths as macroalgal biomass reduces. In the absence of reliable data on macroalgal biomass in the intertidal region, we assumed similar densities of phytal invertebrates in the intertidal zone as in the 0–2 m rocky reef habitat. Using information on the proportion of the study area with rocky reef habitat at these depths, we hence estimate a total phytal biomass in the study region.

Total carbon biomass of the benthic macrofaunal group in the study area is shown in Section 17 of this appendix.

15.4 Production

Little information on energetics is available for most of the dominant soft sediment macrofauna found in New Zealand. The paucity of energetic information on soft-sediment fauna is typical for most trophic models worldwide. We used two methods to estimate P/B for macrofauna, and compared these with values from the scientific literature.

Method 1: The first method was based on the allometric scaling of energetics of biota (e.g., Hildrew et al. 2007 and references therein). Production rates as a proportion of body mass are generally higher for smaller species, with the scaling exponent of P/B as a function of individual weight often close to -0.25 (Hildrew et al. 2007). If we assume that production rates of all benthic macrofauna follow a similar allometric relationship, we can use the production rates of New Zealand rock lobster and three species of crab estimated earlier in this document (Section 5 and Section 6 respectively) to estimate a production rate for all groups of macrofauna using the effective mean individual weights shown in Table 50. Forcing the exponent to -0.25 gave $P/B=2.7W^{-0.25}$ (n=4) which we use here. Hence, we estimate annual production rates for macrofauna as: $P/B=3.6\ y^{-1}$ (crustacean macrofauna), $P/B=8.9\ y^{-1}$ (vermiform macrofauna), $P/B=10.6\ y^{-1}$ (phytal invertebrates). Combining production values in proportion to (carbon) biomass of these taxa gives a group estimate of $P/B=8.3\ y^{-1}$.

Method 2: Annual production values (P/B ratio) for macrofauna can be estimated from the relationship given by Brey & Gerdes (1998) showing an increase of annual community P/B with water temperature. Bottom water temperatures in the study area are likely to be between 13°C and 16°C (Zeldis et al. 2004). Using a mean bottom temperature of 14.5°C, the regression equation of Brey & Gerdes (1998) gives $P/B=2.5\ y^{-1}$.

Here, we use an average of these two values of $P/B=5.4\ y^{-1}$. For comparison, Feller & Warwick (1988) suggest that a range of 0.7–4 y^{-1} is possible for benthic macrofauna. Probert (1986) suggests that a P/B ratio of 0.4–1 y^{-1} is reasonable for benthic macrofauna of the open ocean (depths below 300 m), with values towards the higher end of this range being more likely. Edgar (1990) and Donovaro et al. (2002) gave estimates of production for some small invertebrates, though few are for genera found within New Zealand. Some comparisons of P/B by taxa include $P/B=0.8\ y^{-1}$ for an infaunal isopod and 1.5–5.6 y^{-1} for infaunal amphipods (Edgar 1990). Edgar (1990) suggested P/B=3.5–29.7 y^{-1} for polychaetes, whereas a P/B ratio of 1.8 y^{-1} is used by Cartes & Maynou (1998) for polychaetes. Literature values for production of (less taxa-specific) heterotrophic benthos in temperate systems were $P/B=15\ y^{-1}$ (Polovina 1984). Lundquist & Pinkerton (2008) used $P/B=3.0\ y^{-1}$ for heterotrophic soft sediment macrofauna in northeast New Zealand.

15.5 Consumption, P/Q

Consumption values for benthic macrofauna in the study area are not well known, and consumption is often estimated via P/Q. Commonly-used P/Q factors for small crustacean invertebrates in the literature are: 32.5%, based on direct metabolic measurements (Warwick et al. 1979); 30–40%, based on measurements of respiration rates (Herman et al. 1984); and 10%, based on the Lindeman concept of energy flow through trophic levels (Lindeman 1942; Bouvy 1988). Here, we use a slightly higher growth efficiency for smaller individuals (Hildrew et al. 2007), namely, P/Q=0.20 (crustacean macrofauna), and $P/B=0.25\ y^{-1}$ (vermiform macrofauna and phytal invertebrates). Combining production values in proportion to (carbon) biomass of these taxa gives a group estimate of P/Q=0.24. Based on the production value estimated above, we obtain a value for the consumption rate of this group of $Q/B=22\ y^{-1}$. This estimate is between the consumption rate of $Q/B=125\ y^{-1}$ suggested by Okey et al. (2004) for micro-crustaceans from a Chilean temperate reef ecosystem model, and the value of $Q/B=12\ y^{-1}$ used by Lundquist & Pinkerton (2008). Other values of consumption of macrofauna from the literature suggest Q/B = 10–30 y^{-1} (see Lundquist & Pinkerton 2008).

15.6 Diet (prey)

Diet values for crustacean macrofauna were taken from the literature (e.g., Bouvy 1988; Edgar 1990; Taylor 1998a). Soft-sediment macrofauna take food from the water column, (zooplankton, phytoplankton, water column bacteria), and from the benthos (meiobenthos, macrobenthos, benthic bacteria, and microphytobenthos). The proportions of these items in the diet of this group are not known. Polychaetes and other benthic worms have a variety of feeding and life history strategies (reviewed in Fauchald & Jumars 1979). The majority of soft sediment worms in the study area are probably detrivorous, though carnivorous polychaetes contribute a substantial biomass (15% total). We assume that carnivorous polychaetes consume 80% benthic meiofauna, 10% benthic bacteria, and 10% other benthic worms. We assume that detrivorous polychaetes consume 75% benthic bacteria and 25% benthic detritus directly.

Limited information is available on diet composition for phytal invertebrates, which have diverse ecological strategies. The amphipods tend to be detrivorous; the polychaetes tend to exhibit a range of feeding strategies; the phytal gastropods tend to be herbivorous, and the copepods are generally omnivorous. Most of these small epifauna are grazers, consuming epiphytic algae (typically diatoms), their host algae and macrophyte-derived detritus, while others (e.g., podocerid and ischyrocerid amphipods) are filter-feeders (Taylor & Cole 1994; Taylor 1998a). The exact composition of phytal invertebrate diets is unknown. We initialise the model with 0.75 microphytes, 0.25 water column detritus.

Combining these in proportion to the annual consumption rates of the groups, we initialise this model with a diet of 1% macrobenthos, 6% meiobenthos, 15% phytoplankton, 15% macroalgae, 15% microphytes, 3% mangrove/seagrass/saltmarsh, 32% benthic bacteria, 6% water column bacteria, and 8% benthic detritus.

15.7 Other information: EE, U, accumulation, imports, exports, transfers

Benthic macrofauna are unlikely to move significant distances compared to the scale of the study area and we set net import to zero.

It is not known if populations of macrobenthos within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

A proportion of the annual production of macrobenthos will be exported to the zooplankton component of the trophic model for reproduction. This fraction of production is not well known and is here set to 10%.

The weight of settling larvae is likely to be much smaller than the intrinsic growth of adults per year and is set to zero in the trophic model.

Ecotrophic efficiency (*EE*): In the case of macrobenthos, whole dead individuals or parts of individuals are likely to be consumed rather than being decomposed by bacterial action. Hence, in the model, non-consumed individuals will be passed to the carcass group. Most macrofauna are likely to die from direct predation, but the proportion suffering other kinds of mortality is not known. The proportion of annual production not directly predated is assumed to be small (5%), giving an ecotrophic efficiency of E=0.95.

Unassimilated consumption for macrobenthos is not well known and is assumed to be U=0.3 following previous trophic models (e.g., Lundquist & Pinkerton 2008).

16 Meiobenthos (benthic meiofauna)

16.1 General information

This group contains all benthic micro-invertebrates (63 μm–2 mm) living within soft sediments (soft sediment infauna). The group is likely to be dominated by nematodes, but may also include copepods, ostracods and a diverse array of small benthic invertebrates. There is limited local information on taxonomy, biomass, energetic parameters or trophic role for organisms in this group.

16.2 Biomass

There is little information on the biomass of soft sediment meiofauna (infauna) in the study region. However, meiofaunal biomass (infauna 63 μm–0.5 mm) on the Chatham Rise at depths of between 350 and 2600 m has been measured and reported by Nodder et al. (2003). Meiofauna in this region was dominated by nematodes (more than 80% of individuals) and was measured in three seasons, the values being within the envelope reported for a variety of temperate and tropical continental margins around the world (Soltwedel 2000; Feller & Warwick, 1988). Annual average meiofaunal biomass on the Chatham Rise integrated to 5 cm depth of sediments decreased systematically but weakly with water depth as in these previous studies (Soltwedel 2000; Feller & Warwick, 1988). A depth-biomass regression was determined by least-squares in log biomass space (R^2=0.67, *n*=10). Using this regression, we estimate that density decreases from 0.096 gC m^{-2} at shallow depths to 0.115 gC m^{-2} at 250 m. Based on the depth characteristics of the study region, we estimate a mean meiofaunal biomass density in the study area as shown in Section 17. We assume that carbon makes up about 10% wet-weight of meiobenthos (Feller & Warwick 1988; Soltwedel 2000).

16.3 Production, consumption, P/Q

Annual P/B ratios of meiofauna vary considerably, between about 2.5 and 15, but values between 4 and 10 y^{-1} are often taken as typical values (Feller & Warwick, 1988; Probert 1986). Here, we assume a value of P/B=7.0 y^{-1} as Lundquist & Pinkerton (2008). Annual P/Q was assumed to be 0.31 (Pomeroy 1979; Bradford-Grieve et al. 2003), though a P/Q of between 0.1 and 0.3 y^{-1} for meiofauna in deeper water was suggested by Probert (1986). We hence estimate consumption for benthic meiofauna of Q/B=23 y^{-1}.

16.4 Diet (prey)

The prime source of food for the meiobenthos is assumed to be bacteria in the sediments, with some cannibalistic contribution from other meiobenthos. We estimate 90% benthic bacteria and 10% meiofauna.

16.5 Other information: EE, U, accumulation, imports, exports, transfers

Benthic meiofauna do not move significant distances compared to the scale of the study area and net import will be zero.

It is not known if populations of benthic meiofauna within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e., we set accumulation to zero.

A proportion of the annual production of benthic meiofauna will be exported to the zooplankton component of the trophic model as part of the reproductive life-cycle of some zooplankton species. This fraction of production is not well known but expert opinion suggests that it is small and is here set to 10%. The weight of settling larvae is likely to be much smaller than the intrinsic growth of adults per year and is set to zero in the trophic model.

Ecotrophic efficiency (*EE*) is not known for meiofauna in the study area. In the case of meiofauna, whole dead individuals or parts of individuals are likely to be decomposed by bacterial action. Hence, in the model, non-consumed individuals will be passed to the benthic detritus group. Most meiofauna are likely to die from direct predation, but the proportion suffering other kinds of mortality is not known. The proportion of annual production not directly predated is assumed to be small (5%), giving an ecotrophic efficiency of E=0.95.

Unassimilated consumption for meiofauna is not well known and is assumed to be U=0.3 following previous trophic models (e.g., Lundquist & Pinkerton 2008).

17 Summary of parameters

Parameters for benthic invertebrates in the Hauraki Gulf trophic model representing the present day are given below in Table 51 and **Table 52**. Data for individual species were combined by combining these parameters in appropriate proportions according to biomass.

Table 51: Summary of parameters in the trophic model. Note that all exports and accumulations are zero. EE=Ecotrophic efficiency; B=Biomass; P/B=annual production to biomass ratio; Q/B=annual consumption to biomass ratio; P/Q=gross growth efficiency, i.e. annual production divided by annual consumption.

Group	EE	B gC m^{-2}	P/B y^{-1}	Q/B y^{-1}	P/Q	Export X/P	Fishery gC m^{-2} y^{-1}	Unassimilated U	Spawning T/P	Spawn fate	Carcass fate
Lobster	0.95	0.0067	1.2	6.8	0.18	0.24	0.0015	0.30	0.06	mesozoo	carcass
Crabs	0.95	0.7	6.2	30	0.20	0.42	0.0004	0.30	0.05	mesozoo	carcass
Seastars & brittlestars	0.95	0.20	1.4	5.7	0.25	0.00	0	0.30	0.59	mesozoo	carcass
Urchins	0.95	0.16	0.83	5.5	0.15	0.22	0.0005	0.30	0.54	mesozoo	carcass
Gastropods_carnivorous	0.95	1.0	4.3	17	0.25	0.43	0.0000	0.30	0.14	mesozoo	carcass
Gastropods_grazing	0.95	0.5	3.3	17.7	0.18	0.42	0.0008	0.30	0.18	mesozoo	carcass
Sea cucumbers	0.11	1.2	0.60	3.4	0.18	0.00	0	0.30	0.10	mesozoo	carcass
Bivalves	0.95	1.4	4.7	24	0.20	0.73	0.032	0.20	0.03	mesozoo	carcass
Sponge	0.95	0.54	0.20	0.8	0.25	0.00	0	0.30	0.10	mesozoo	benthic_detritus
Encrusting Inverts	0.75	0.22	3.3	13	0.25	0.52	0	0.30	0.07	mesozoo	benthic_detritus
Macrobenthos	0.95	0.25	5.4	22	0.24	0.00	0	0.30	0.10	mesozoo	carcass
Meiobenthos	0.95	0.11	7.0	23	0.31	0.00	0	0.30	0.10	mesozoo	benthic_detritus

Table 52: Summary of diets for benthic invertebrate groups in the trophic model: long-term average proportions of prey items by weight (in terms of organic carbon). Prey items are shown in rows with predators in columns. Columns sum to 1.

												Benthic invertebrate predators
Prey	Lobster	Crabs	Seastars	Urchins	Carnivorous gastropods	Grazing gastropods	Sea cucumbers	Bivalves	Sponges	Encrusting	Macrobenthos	Meiobenthos
Crabs	0.20	0.02	0.02									
Seastars					0.02							
Urchins	0.10	0.05	0.05									
Carnivorous gastropods	0.05	0.10	0.05		0.10							
Grazing gastropods	0.15	0.15	0.08		0.30							
Sea_cucumbers			0.05									
Bivalves	0.17	0.17	0.08		0.30							
Sponges				0.03								
Encrusting	0.03	0.05		0.03	0.15	0.02						
Macrobenthos	0.20	0.30	0.10		0.10						0.01	
Meiobenthos			0.10				0.90				0.06	0.10
Reef_fish_small												
Reef_fish_large	0.03											
Squid												
Octopus		0.02										
Microzoo								0.15		0.10		
Nanozoo								0.05	0.10	0.30		
Phytoplankton								0.50	0.20	0.30	0.15	
Macroalgae	0.05	0.03		0.43		0.27					0.15	
Mangrove_seagrass		0.01				0.02					0.03	
Microphtyes			0.05	0.03		0.18					0.15	
Bacteria_water								0.20	0.70	0.30	0.06	
Bacteria_benthic				0.25		0.10	0.10				0.32	0.90
Carcasses	0.02	0.10	0.05		0.03							
Detritus_water			0.07					0.10				
Detritus_benthic			0.30	0.25		0.41					0.08	

18 Historical parameters

18.1 Models required

Trophic models are required for benthic invertebrates in four historical periods: 1950, 1790, 1500 and 1000.

18.2 Historical fishery removals

Commercial fisheries catches of benthic invertebrates in the study area for the present day and 1950 have been estimated by Francis & Paul (2008) using methods similar to that described in Francis & Paul (2013). Non-commercial catches (recreational and customary catches) of benthic invertebrates in the study area in 1950 were only estimated for red rock lobster by Francis & Paul (2008). Recreational removals of other species for the present day were estimated as described in the text. We assumed that non-commercial catch in 1950 is the same as that at the present time.

Commercial catches in 1931 were also estimated by Francis & Paul (2008) and we assume that commercial catches in 1790 were one tenth of these values. We assume that non-commercial, European removals of invertebrates in 1790 was half that in 1950 and in the same proportions. Smith (2011) estimated the magnitude of Maori marine harvest of shellfish based on data preserved from middens, for years (actually, periods about nominal years) 1400, 1550 and 1750. The data nominally for 1750 is taken to be representative of removals in 1790.

There were no commercial or European catches in 1500. Linear interpolation is used to estimate catch by Maori in 1500 based on information from Smith (2011) covering 1400 and 1550. Smith (2011) did not report any archaeological evidence of removal of crab, lobster or kina by Maori, but removals of these groups is likely. Maori population in 1790 is estimated to be 100 000, and to be about 67 000 in 1500 (Smith 2011). We assume Maori removals of crab, lobster or kina in 1500 to be two-thirds of non-commercial removals of these groups in 1790.

There were no fishery removals in 1000. A summary of estimated historical catches of benthic invertebrates in the study area is given in Table 53.

Table 53: Estimated historical catches of benthic invertebrates in the study area. Both commercial and non-commercial ("recreational" and customary) catches are included. Present day catches were estimated from Francis & Paul (2008) and other values were obtained as described in the text.

Group	Removals (tWW y^{-1})				
	Present	1950	1790	1500	1000
Lobster	329	197	54	36	0
Crabs	86	51	26	17	0
Seastars	0	0	0	0	0
Urchins	671	764	382	255	0
Benthic predators	0.2	0	0	5	0
Benthic grazers	331	61	49	98	0
Sea cucumbers	0	0	0	0	0
Bivalves	6573	353	1017	318	0
Sponges	0	0	0	0	0
Encrusting	0	0	0	0	0
Macrofauna	0	0	0	0	0
Meiofauna	0	0	0	0	0

18.3 Other parameters for historical models

Biomass, energetics, diet and other parameters for benthic invertebrates may have varied from the present day situation due to factors including climate, run-off (including sedimentation), predation (both by marine biota and humans), primary production and food availability. Natural drivers of environmental change in New Zealand during the last millennium were examined by Lorrey et al. (2013). The collection of palaeoclimate precipitation and temperature data were interpreted using regional climate regime classification to reconstruct circulation patterns. Lorrey et al. (2013) concluded that: "Propagation of downstream changes [due to climatic variations through the last millennium] to coastal environments via sedimentary and geomorphic processes would have undoubtedly affected nearshore aquatic ecosystems" (Lorrey et al. 2013). How these climate effects may have affected benthic invertebrates is difficult to assess. Historical reconstruction of biomass has been attempted for rock lobster (McKenzie, 2010) and for mussels as described below (see summary in **Table 54**).

Paul (2012) summarised the history of the Firth of Thames dredge fishery for green-lipped mussels (*Perna canaliculus*). This species supported a dredge fishery in the Firth of Thames and inner Hauraki Gulf from about 1910 to the mid-1960s. Before the fishery began, dense subtidal beds occurred to a depth of about 30 m. Landings were modest to 1920 (about 500 tWW y^{-1}) but increased to 1400 tWW y^{-1} by 1940. Some Coromandel beds closed in the late 1940s. In the 1950s there was a rapid rise in landings, to peak at about 2800 tW y^{-1} in 1961. Landings then crashed to 180 tWW y^{-1} in 1965, and zero in 1969 (all information: Paul, 2011). Assuming a somatic P/B=0.52 y^{-1} for wild (non-aquaculture) green-lipped mussels and that 500 tWW y^{-1} (assumed shell-free weight) is "sustainable" in that it corresponds to one quarter of the annual somatic production, we estimate a virgin biomass of mussels in the region of the historical Firth of Thames dredge fishery of 3850 tWW.

Most (88%) of the present day mussel biomass in the model is from three habitats: rocky reef, coastal sheltered 0–9 m soft sediment and coastal exposed 0–9 m soft sediment (47, 25, 17% biomass respectively). If green-lipped mussels make up about 50% of this mussel biomass, the implied biomass of this species in the study area is 13 800 tWW (shell-free).

For other groups of benthic invertebrates we do not adjust biomass for benthic invertebrates *a priori*. We do not adjust energetics, diet or other key parameters for benthic invertebrates from the present day model.

Having estimated these historical values, we allow the potential for biomass and diet parameters of benthic invertebrates to change during balancing of the historical trophic models.

Table 54: Estimated historical Biomass (B) of red rock lobster (McKenzie, 2010) and wild (non-aquaculture) greenlip mussels in the study region from 1000 to the present day (based on Paul, 2011).

Period	Lobster		Greenlip mussels	
	B (tWW)	$B/B_{present}$	B (tWW)	$B/B_{present}$
Present	1 440	1	13 805	1
1950	4 700	3.3	17 651	1.3
1790	6 300	4.4	17 651	1.3
1500	6 300	4.4	17 651	1.3
1000	6 300	4.4	17 651	1.3

19 Acknowledgements

This research was funded by Ministry for Primary Industries project ZBD200505 (“Long-term change in New Zealand coastal ecosystems”) and by the New Zealand Foundation for Research, Science and Technology project C01X0501 (Coasts & Oceans OBI). We are grateful to Dr Mary Livingston and Dr Martin Cryer (Ministry for Primary Industries) for supporting this project. We thank numerous NIWA staff for assistance with data collection and processing, including James Sturman, Mark Morrison, Anne-Laure Verdier, Reyn Naylor. We are grateful to A. McKenzie, M.P. Francis and L. Paul for information on commercial landings of lobster and biomass estimates. Additional data were kindly provided by Richard Taylor (University of Auckland), Nick Shears and Franz Smith. We acknowledge that data were collected using funding from Department of Conservation, and Auckland Regional Council. Dr David Bowden (NIWA) provided useful comments on this work.

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Appendix 5: Trophic modelling of Hauraki Gulf: Fish

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1 Background and approach

1.1 Introduction

Fish are a major part of the trophic model. More than 100 species of fish are found in the Hauraki Gulf study region. In order to include these in the trophic model, we estimated the required model parameters (biomass, energetics, diet) by species if possible, or by species-group if appropriate, and then combined these into a small number of fish groups for the modelling.

1.2 Groupings in trophic model

Two kinds of grouping have been used in the modelling. First, in a relatively small number of cases (11 out of 114), different species of fishes were combined together where it is not practically possible to separate essential basic formation such as biological parameters, landings or biomass estimates. These groups are given in **Table 55**. We never separated the individual species in these groups for the purpose of estimating model parameters and usually used the dominant species to estimate parameters for that species-group in the model.

Table 55: Species-groups used in the model.

Species-group	Species included	Parameters based on
Shark (other)	Dark ghost shark (*Hydrolagus novaezealandiae*); Northern spiny dogfish (*Squalus griffini*); blue shark (*Prionace glauca*); thresher shark (*Alopias vulpinus*); mako shark (*Isurus oxyrinchus*).	Dark ghost shark; Ministry of Fisheries (2009a)
Dory (other)	Mirror dory (*Zenopsis nebulosus*); silver dory (*Cyttus novaezelandiae*)	John dory (*Zeus faber*); Ministry of Fisheries (2009a)
Flatfish	Yellowbelly flounder (*Rhombosolea leporina*); sand flounder (*R. plebeia*)	Ministry of Fisheries (2009a)
Gobies	All Gobiidae	Paul (1986)
Hapuku/bass	Hapuku (*Polyprion oxygeneios*); bass (*P. americanus*)	Ministry of Fisheries (2009a)
Jack mackerels	*Trachurus declivis*; *T. novaezelandiae*; *T. murphyi*	Ministry of Fisheries (2009a)
Moray eels (other)	All moray eels except yellow moray (*Gymnothorax prasinus*)	Francis (2001)
Stargazer (other)	Spotted stargazer (*Genyagnus monopterygius*); brown stargazer (*Xenocephalus armatus*)	Giant stargazer ; Ministry of Fisheries (2009a)
Tuna (other)	Albacore tuna (*Thunnus alalunga*); yellowfin tuna (*Thunnus albacares*); bigeye tuna (*Thunnus obesus*); slender tuna (*Allothunnus fallai*)	Albacore tuna, Santiago & Arrizabalaga (2005),
Wrasse (other)	All wrasses except banded wrasse (*Notolabrus fucicola*), orange wrasse (*Pseudolabrus luculentus*), red pigfish (*Bodianus unimaculatus*), Sandager's wrasse (*Coris sandageri*), scarlet wrasse (*Pseudolabrus miles*) and spotty (*Notolabrus celidotus*)	Paul (1986)

Second, species and/or species-groups given in **Table 55** were combined into trophic groups (or synonymously “trophic compartments”) in the model. The aim of this grouping of fishes was to have a reasonably small number of groups where the biota in a given group had a “similar” set of energetic parameters and trophic roles, and yet where there was enough information on each group to drive the modelling. A large variety of fishes occur in the study area and information on the basic ecology and trophic role of many of these species is limited. There are a number of alternative ways to group fishes in mass-balance models (**Table 56**) and none of these methods of grouping fishes into trophic groups is completely objective or ideal.

Table 56: Methods of grouping fishes in mass-balance models.

Method	Example	Pros	Cons
Single species	• Snapper • Red cod	Information and management is usually by species	Too many species and too limited information on rarer species to be feasible for all fishes
Taxonomic groups	• Triplefins • Skates and rays	Taxonomic similarity often implies similarity of size and/or similar ecosystem role	Taxonomically-similar species can have very different sizes and ecosystem roles
Size-based	• Small fishes • Medium-sized fishes • Large fishes	Energetics and potential prey are closely linked to size	Often some degree of niche separation between fishes of similar size
Lifestyle	• Demersal • Benthopelagic • Mesopelagic	Trophic role is often linked to lifestyle	Different sizes of fish with the same lifestyle can have very different energetics
Habitat / location	• Reef fish • Estuarine fish • Open water fish	Prey and predators often related to habitat and location	Can be high degree of niche separation within given habitat / location
Predominant prey	• Piscivores • Planktivores • Invertebrate feeders • Scavengers	Aligned with model that is driven by predator-prey connections	Most fishes will have a diet that varies with season and age; diet is often poorly known.

A grouping based on a mixture of factors was used here as in other food-web models (Fulton et al. 2003). We chose to group by: (1) single species, considering species separately where these are particularly important ecologically, economically or culturally; (2) similar habitat, defined by position occupied in the water column combined with location (e.g. reef fishes versus mesopelagic open water fishes); (3) similar energetic parameters (hence a grouping based on size).

Species were considered separately if they were included in the New Zealand Quota Management System (Ministry of Fisheries 2009a), and if they had a mean annual catch in the study area in the period 1990–2006 estimated to be greater than 30 t wet-weight (WW) per year and if the biomass of the species was estimated to be more than 1% of the total (non-juvenile) fish biomass in the study area. Based on this definition, we had 12 species (or species-groups): barracouta, blue (English) mackerel, flatfish, jack mackerels, kahawai, leatherjacket, red gurnard, rig, skipjack tuna, snapper, tarakihi and trevally. Ten of these had a historical biomass estimation based on unsexed biological parameters and estimated catch histories for the Hauraki Gulf study area (Francis & Paul 2008; McKenzie & MacDiarmid 2011), but for two (leatherjacket, skipjack tuna) no estimate was available.

Habitat separations were: (1) reef fish (small): reef-associated, maximum length less than or equal to 30 cm; (2) reef fish (large): reef-associated, maximum length greater than 30 cm; (3) demersal fish: non-reef associated, mainly dwelling near bottom; (4) sharks (including dogfish); (5) pelagic/meso-pelagic fish (large, i.e. more than 30 cm maximum length); (6) pelagic/meso-pelagic fish (small, i.e. less than 30 cm maximum length), including juvenile (post-larval) predominantly fishes living away from reefs in the midwater.

2 Catch and discards

The information given here is a summary of the methods used to estimate catch histories for finfish of the Hauraki Gulf. For more information, see Francis & Paul (2008).

2.1 Species identification

Landings data are not always recorded to individual species level. This sometimes results from difficulty in distinguishing closely related species, but more often from the lack of an economic or management incentive to separate the catch by species. The groupings which affected this study are jack mackerels (three species), groper (hapuku and bass), flatfish (two soles and two flounders) and skates (two species). There was insufficient information to separate the landings of these species complexes, so we retained them here.

2.2 Estimation of commercial landings

Commercial catches of fish in the study area were estimated by Francis & Paul (2008) using methods similar to that described in Francis & Paul (2013) as summarised below.

2.2.1 Data sources

Landings data were derived from five main sources as follows:

- 1931–73: Annual Reports on Fisheries, compiled by the Marine Department to 1971 and the Ministry of Agriculture and Fisheries to 1973 as a component of their Annual Reports to Parliament published as Appendices to the Journal of the House of Representatives (AJHR). From 1931 to 1943 inclusive, data were tabulated by April–March years, but we have equated them with the main calendar year (e.g. 1931–32 landings are reported here as being from 1931). From 1944 onwards, data were tabulated by calendar year.
- 1974–82: Ministry of Agriculture and Fisheries, Fisheries Statistics Unit (FSU) calendar year records published by King (1985).
- 1983–87: Ministry for Primary Industries extract from FSU database, by calendar year.
- 1988–89: Landings were very poorly reported because of a transition between official reporting systems, so we estimated them from adjacent years (see *Adjustment of commercial landings* below).
- 1990–2006: Ministry for Primary Industries extracts from all relevant catch-effort databases, by calendar year.

2.2.2 Landings by port and area

Before 1983, all fisheries statistics were recorded by *port of landing* (King 1985) (they were also reported by statistical area, but this information was not published and is not readily available). From 1983 onwards, landings were recorded by *statistical area* (King 1986). To identify catches from the Hauraki Gulf region, we made the following assumptions and calculations:

1931–82

Ports of landing for the Hauraki Gulf were: Whangarei, Auckland, Thames, Coromandel, Mercury Bay, Whangamata, Waihi. (These are the nominal ports; landings made at intermediate localities − 'landing places' − are incorporated in the values for the closest port.)

Some fish landed into Hauraki Gulf ports would have been caught outside the region of interest, and some catches from those regions would have been landed elsewhere. We adjusted the port landings based on the known or suspected fishing grounds for each species (Table 57). There was insufficient information to adjust for temporal changes in the port landing patterns.

Table 57: Percentage of landings into Hauraki Gulf ports estimated to have been caught within the Hauraki Gulf trophic model area.

Percent	Species
60	Barracouta, gemfish
70	Jack mackerel, kahawai, school shark, rig, snapper, trevally, skate, tarakihi, hapuku
80	John dory, leatherjacket, red gurnard, kingfish, porae
90	Blue cod
100	Species not listed above

From 1931 to 1943, Auckland landings included those from Manukau Harbour on the west coast of North Island. To adjust for this, we reduced the Auckland landings of grey mullet and flatfish (the only two species to be significantly affected) by 45% and 6% respectively, based on the mean ratio of Manukau landings to Hauraki Gulf landings in 1944–48 (the first five years for which separate Manukau data were available).

1983–2006

Since 1983, most fish and shellfish catches have been reported using Ministry for Primary Industries General Statistical Areas. For the Hauraki Gulf, statistical area boundaries do not match the study region boundaries so catches from the northernmost and southernmost statistical areas were apportioned based on the approximate length of coastline that occurred within the study region. Statistical areas were mapped to our region as follows: areas 003 (33% of catches), 004–008 (100% of catches), 009 (33% of catches).

2.2.3 Data treatment 1983–2006

From 1983 onwards, a variety of fishing return forms have been used to report catches made by different fishing methods, and sometimes for different vessel sizes using the same methods. Some methods and vessels report catch using a single form per fishing trip, whereas other methods and vessels use two forms. In the latter case, one form (the catch-effort return) contains details of the fishing effort including statistical area, and the *estimated catch* of the top few species (five species) caught, whereas the other form (the landing return) contains *weighed landings* of all species to which a conversion factor has been applied to raise processed weights to greenweight. One difficulty with estimated catches is that sometimes (erroneously) fishers reported processed weight rather than whole weight.

Ideally, we would have used data from the landing form, because landed fish weights are generally accurately measured, and available for all species landed (not just the species caught in greatest quantity within a single tow). However the landed catch form contains no catch location information, making it impossible to allocate landings directly to statistical areas. A compromise solution involved linking the two forms using a unique trip identifier, and using the statistical area information from the catch-effort form to apportion the landings from the landed catch form by statistical area. Sophisticated methods for doing this have been developed in the stock assessment process (Manning et al. 2004; Starr 2007). However these methods take a long time to develop and could not be applied to the large number of species covered by the present project with the resources available. We therefore used the methods described below.

Database extracts were obtained in two steps. First, all fishing trips reporting estimated catch in at least one of the statistical areas of interest were identified. Second, all estimated catches (and their associated statistical area information) and landed catches from the same trips were extracted. Data were then analysed in three steps. First, estimated catches were summed by species and calendar year, and so were the landed catches. Second, the ratio of estimated catches to landed catches was calculated by species and year. Third, the estimated catches from the statistical areas of interest were scaled up by the inverse of the ratio to provide estimated landings for all species by statistical area.

The requirement for success when using this approach is that the estimated catches represent a significant and consistent percentage of the landed catches. Catch:landing ratios markedly less than 100% suggest one or more of: (a) the species was infrequently caught and so was not often in the top few species, (b) processed weights were often reported rather than whole weights, or (c) weight estimation by fishers was poor. Catch:landing ratios markedly greater than 100% suggest (a) poor weight estimation, or (b) discarding of unwanted fish at sea. Variable catch:landing ratios suggest inconsistency in reporting methods. In this study we aggregated catches and landings over the whole fleet for the study region for each calendar year, thus smoothing out variations among fishers. Catch:landing ratios from 1990 onwards are given by Francis & Paul (2008). Ratios generally fell in a plausible and usable range (25–125%) for the top 20 species, except for gemfish (see Section 3.4.4 for gemfish).

2.2.4 Inshore versus offshore catches

The offshore limit for this study was the 250 m depth contour, which approximately coincides with the edge of the continental shelf. We identified or estimated catches made outside 250 m, and then excluded them, as follows:

- Species for which most of the biomass, and therefore presumably catch, comes from depths greater than 250 m were deleted from the analysis. These species were identified using the depth distribution plots provided by Anderson et al. (1998).
- FSU form types 16 and 17 (specified and deepwater trawlers) and QMS Trawl Catch and Effort Processing Returns (TCEPR) record bottom depth for every trawl tow. These returns are completed by most large trawlers, and many intermediate and some small trawlers. We included records from these forms only if tows were made shallower than 250 m. Unfortunately most other fishing return forms lack a field for fishing depth, or depth is poorly reported, so this procedure could not be applied to them. However, these other form types are typically filled out by smaller inshore vessels and we assumed their catches came from depths less than 250 m. Many abundant fish species straddle the 250 m depth contour (Anderson et al. 1998), so the weights of these species will have been overestimated by this procedure, particularly between about 1978 when deepwater trawling became important and 1983 when electronic data extracts first became possible.
- Oceanic pelagic species (e.g. tunas, marlins, pelagic sharks, moonfish) are usually caught near the surface over seabed depths exceeding 250 m. We arbitrarily assumed that 10% of the landings of these species were caught shallower than 250 m, except for skipjack tuna for which we assumed 15% came from inside 250 m. The latter estimate was based on the distribution of purse-seine sets for skipjack tuna between 1975 and 1986 (West 1991).

2.2.5 Adjustment of commercial landings

The following assumptions or adjustments were made when estimating commercial landings:

- In 1973 and 1974, rig (reported as pioke) and school shark landings were combined in official statistics. We estimated the catch of each species in these years by applying the average ratio of school shark to rig (0.35) in the years 1970–72 to the combined landings. Zero landings of school shark in 1978–79 resulted from concerns about mercury levels in large sharks, and an import ban on school sharks by Australia, the principal market for New Zealand sharks.
- A general problem in the data reported by King (1985) is that only species which comprised more than 1% of a port's landings were listed separately, the others being grouped as "Minor species." Some species were therefore reported for only some years in 1974–82. In most cases the missing values are small and have been ignored, but for a few species where enough adjacent values are present to show a trend, the values have been estimated.

- Estimated landings of several pelagic species caught mainly by purse seine (jack mackerels, blue mackerel, skipjack and kingfish) fluctuated markedly during the late 1970s and early 1980s. Years of low landings in the Hauraki Gulf coincided with high landings in Tauranga, a major port just south of the southern boundary of the Hauraki Gulf region. It is not known whether there was a shift in fishing effort from the Hauraki Gulf to the Bay of Plenty, or whether vessels working in the Hauraki Gulf began landing more of their fish into Tauranga instead of into one of the Gulf ports (P. Taylor, NIWA, pers. comm.). We have assumed the former applies, and made no adjustments to the landings.
- A large increase in hoki landings was reported from the Hauraki Gulf in 1995–98, peaking at an estimated 1200 t in 1997. These landings were almost entirely reported by three vessels from Statistical Area 007. This area is in the inner Gulf and Firth of Thames where hoki do not occur. The reported landings are likely to be an error for QMA 7 on the west coast of South Island and were removed from the catch history.
- 1988 and 1989 landings were estimated as follows. We calculated the ratio of the estimated landings to the landings reported under the Quota Management System (QMS) by region, species and year (QMS landings were obtained from Ministry of Fisheries 2006, 2007). QMA 1 landings were used. Inspection of the temporal trends for the period 1984 to 1994 showed that the ratios for 1988 and 1989 were lower (often much lower) than those for the adjacent years for nearly all species. The 1988 and 1989 landings were estimated by multiplying the appropriate QMS landings by the average ratio for the two previous and two following years (i.e. 1986, 1987, 1990 and 1991).

2.2.6 Validation of estimated landings

For the period since October 1986, when many commercial species were introduced into the QMS, estimated landings for each region were compared with landings reported in the Fishery Assessment Plenary reports (Ministry of Fisheries 2006, 2007) for the Fishstock area(s) within which the region is nested[5]. The Plenary landings generally come from an independent, more accurate source (Quota Management Reports and Monthly Harvest Reports) than the estimates obtained here, but they do not have the spatial resolution required for the present study. Where the estimated landings were inconsistent with the Plenary landings for the entire Fishstock, the latter were used instead.

2.2.7 Estimation of foreign fishing vessel catches

Japanese trawlers and longliners fished off northern New Zealand between 1960 and 1977 (Ministry of Fisheries 2007, p. 841). For stock assessment purposes, a pattern of Japanese snapper catches has been estimated, peaking in 1968 (Ministry of Fisheries 2007). We assumed that half of the foreign snapper catch from the SNA 1 Fishstock (North Cape to East Cape) came from the Hauraki Gulf region.

2.3 Estimation of recreational, customary and illegal catches

Estimates of recreational, customary and illegal catches for New Zealand finfish are few, imprecise and probably inaccurate. Estimates were therefore only used for the main species in each region for which sources of fishing mortality other than commercial fisheries were considered important.

2.3.1 Snapper

An assumed time series (1931–1996) of recreational catches of snapper in SNA 1 Fishstock was provided by Gilbert (1994). Hauraki Gulf recreational catches were estimated as 75% of the SNA 1 time series over this period. An estimate of 1700 t recreational catch from Hauraki

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[5] The October–September fishing year landings tabulated by Ministry of Fisheries (2006, 2007) were compared with estimated landings for the second of each pair of years (e.g. 1986–87 fishing year was compared with 1987 calendar year).

Gulf in 2004–05 was provided by B. Hartill (NIWA, pers. comm.) based on Hartill et al. (2007). This value was applied to the 2005 calendar year. The population model for Hauraki Gulf / Bay of Plenty snapper shows a steadily increasing biomass trend from 1995 onwards (Ministry of Fisheries 2007). We assumed that recreational catches would also have increased as the stock size increased, and this is consistent with the gap between the last (1996) value from Gilbert's adjusted time series (1029 t) and the value of 1700 t estimated by Hartill. We therefore linearly interpolated between these two estimates to generate estimates for the period 1997 to 2004, and extrapolated to provide an estimate for 2006.

2.3.2 Kahawai

An estimate of 145 t recreational catch from Hauraki Gulf in 2004–05 was provided by B. Hartill (NIWA, pers. comm.) based on Hartill et al. (2007). This value was applied to the 2005 calendar year. Estimates for earlier years were made by linear interpolation to an arbitrary 1943 catch of 52 t. Before 1943, commercial landings of kahawai were effectively zero, indicating a lack of interest in this species. The recreational catches were therefore set to zero for 1931–1942.

2.3.3 Red gurnard

An estimate of 25 t recreational catch from Hauraki Gulf in 2004–05 was provided by B. Hartill (NIWA, pers. comm.). This value was applied to the 2005 calendar year. Estimates for earlier years were made by linear interpolation to an arbitrary 1931 catch of 10 t.

2.3.4 Trevally

An estimate of 45 t recreational catch from Hauraki Gulf in 2004–05 was provided by B. Hartill (NIWA, pers. comm.). This value was applied to the 2005 calendar year. Estimates for earlier years were made by linear interpolation to zero in 1955. Before the mid 1950s, trevally were widely regarded as poor eating, and when caught were largely used for bait (Francis et al. 1999).

2.4 Unreported landings

Fishers may fail to report landed fish on their fishing returns. These practices may result from mistakes, a desire to conceal the size of catches and therefore income, under-the-counter sales directly from fishing vessels, “home freight” removals of high-quality species or species taken in small quantities (e.g., kingfish), and (since 1986) insufficient quota holdings to cover catches. Non-reporting rates vary with many factors, including time, species, and fisher. These rates probably declined overall following the introduction of the QMS in October 1986 and a greater degree of administrative monitoring. In fact, reporting levels increased from the early 1980s, when fishers anticipated some form of quota system and the need to establish a recorded catch history. We believe the early landings estimated here are biased lower than later landings. However we are unable to estimate the extent of this bias, and have made no corrections for it. For simplicity, we have divided most landings at 1980 for the change in estimates of unreporting (Table 58).

2.5 Discards

Fishers may discard unwanted fish or parts of fish at sea, another reason for their reported landings not representing their catch. Discarding may result from limited or no market demand, high grading (discarding of low value fish to maximise returns from high value fish of the same species), and damage to catches by sea-lice, predators, or decay. Discard rates vary with many factors, including time, species, fish length, and fisher. Discard rates have probably declined with time, but the proportions are poorly known.

For the modelling, we assumed that all estimated commercial landings were greenweight, and that all whole-fish discards from commercial vessels were dead. Whole-fish discard rates from commercial fishers were estimated by species (Table 58). In addition to whole-fish discarding, some fish can be processed at sea and the offal/offcuts discarded overboard. However, we believe that very few Hauraki Gulf species are processed at sea; the vast majority are landed whole/green. The main exceptions are groper (hapuku and bass), school shark, and rig, where approximately 50% of the carcass is discarded at sea. These part-fish discards are noted after the whole-fish discards in Table 58. There are also likely to be discards of non-commercial catches (recreational, customary). It is fairly common for recreational fishers to gut fish at sea and discard the waste. Caught fish are also used as bait, and where bag limits exist, high-grading is practiced with smaller individuals being discarded as larger ones are taken. All of this effective discarding will be of dead fish or parts of fish (e.g. offal) and are assumed to be equivalent to a discard proportion of 10% for snapper and 20% for other species.

Table 58: Discard proportions of commercial catches used in the trophic model. Where not otherwise stated, part-fish discards are assumed to be zero (as most fish caught in the Hauraki Gulf are landed whole). Discards of non-commercial catches are assumed to be zero.

Species	Estimated amounts of discarding
Snapper	10% whole fish discarded until 1980, then 5% after that date. Improved gear allowing better escapement, and more incentive to retain catch prior to and after QMS. The QMS did encourage "high-grading" for a while (dumping smaller fish to fill quota with better market-sized fish) but this is anecdotal, hard to quantify, and may have declined after the first few years.
Jack mackerel	85% whole fish discarded until 1980 (moderate unwanted bycatch); 10% whole fish discarded after 1980.
Blue mackerel	10% whole fish discarded until 1980 (very minor bycatch), 0% discarded after 1980.
Red gurnard	20% whole fish discarded throughout period (smaller fish discarded).
Trevally	85% whole fish discarded until 1960; 5% whole fish discarded after 1960
Tarakihi	0% discarded at sea; no change with date.
Kahawai	50% whole fish discarded until 1980; 20% whole fish discarded after 1980.
Rig	50% whole fish discarded until 1980; 5% whole fish discarded after 1980; 50% of the carcass discarded.
Flatfish	5% whole fish discarded throughout period.
Barracouta	25% whole fish discarded until 1980; 10% whole fish discarded after 1980.
School shark	50% whole fish discarded until 1980; 10% whole fish discarded after 1980; 50% of the carcass discarded.
John dory	30% whole fish discarded until 1980; 5% whole fish discarded after 1980.
Gemfish	50% whole fish discarded until 1980; 5% whole fish discarded after 1980.
Hapuku/ bass	0% whole fish discarded throughout period; 50% of the carcass discarded.
Kingfish	20% whole fish discarded until 1980; 5% whole fish discarded after 1980.
Grey mullet	5% whole fish discarded throughout period.
Anchovy; Pilchard; Skipjack	0% discarded at sea; no change with date.
Others[1]	50% discarded until 1980; 25% discarded after 1980.

[1] "Others" are: leatherjacket, parore, porae, frostfish, red snapper, blue cod, spiny dogfish, albacore tuna, skate, red cod, silver warehou, koheru, yellowfin tuna, garfish, giant stargazer, Japanese gurnard, stingray, porcupine fish, mirror dory, northern bastard cod, eagle ray, bronze whaler shark, ghost shark (dark), spotted stargazer, sea perch, hammerhead shark, pink maomao, elephant fish, conger eel, broadbill swordfish, northern spiny dogfish, blue shark, thresher shark, Ray's bream, hagfish.

3 Biomass: Species in the Quota Management System

3.1 Definition of terms

For clarity, a few terms need defining:

- *total biomass*: the biomass of all fish, mature and immature.
- *proportions-at-age*: the proportions-at-age of fish in the water (i.e. not subject to selectivity as is recovered from a fishery or trawl survey).
- *catchability:* in this document two species are said to have the same *catchability* if for a year of fishing effort the same proportion of the total biomass is caught for each. The fishing effort for the two species may be by different vessels, using different gear, and differ in number of fishing events.

3.2 Approach

The main species found in the study area included in the New Zealand QMS are: snapper (*Pagrus auratus*), jack mackerel (*Trachurus novaezelandiae*), red gurnard (*Chelidonichthys kumu*), groper (hapuku: *Polyprion oxygeneios*; bass (*P. americanus*), blue (English) mackerel (*Scomber australasicus*), school shark (*Galeorhinus galeus*), gemfish (*Rexea solandri*), kahawai (*Arripis trutta*), tarakihi (*Cheilodactylus macropterus*), rig (*Mustelus lenticulatus*), trevally (*Pseudocaranx gorgianus*), John dory (*Zeus faber*), barracouta (*Thyrsites atun*), and flatfish.

For the Hauraki Gulf study areas, the following were estimated for 20 key (high biomass) species (Table 59):
(1) Unsexed biological parameters: length-at-age, weight-at-length, and natural mortality.
(2) Total biomass trajectories covering the period 1930 to 2006. The biomass in 1930 is an estimate of virgin biomass in all cases (except for snapper).
(3) Proportions-at-age for 1930, 1946, 2006.

For no species does a stock assessment exist that generates the total biomass and proportions-at-age estimates outlined for the study areas. Furthermore, for many species there have been no stock assessments. Therefore to estimate total biomass and proportions-at-age estimates a variety of modifications were made to existing stock assessments, and simplifying assumptions made for those species without assessments. For more information, see McKenzie & MacDiarmid (2011).

Total biomass and proportions-at-age estimation is based on a three tier hierarchy for 20 species. For a tier one species, a stock assessment has been conducted and with some modifications and assumptions, total biomass and proportions-at-age may be derived from it for the study area. For a tier two species, no stock assessment has been conducted, but the species is judged to be linked to a tier one species by a similarity in distribution and catchability over a given period of years, this link being used to infer the biomass for the tier two species from the tier one species. For tier three species, estimated trawl catchability, relative to a tier one species, was used to infer the biomass.

Table 59: The tier ranking for species and species groups (see table notes) in the Hauraki Gulf area.

Tier	Species
One	Snapper (SNA); red gurnard (GUR); kahawai (KAH); gemfish (SKI); trevally (TRE); jack mackerels (JMA)[1]
Two	Blue (English) mackerel (EMA); John dory (JDO); rig (SPO); barracouta (BAR)
Three-A	Red cod (RCO); rough and smooth skate (SKA); frostfish (FRO); tarakihi (TAR); flatfish (FLA)[2]; giant stargazer (STA); sea perch (SPE); kingfish (KIN)
Three-B	Hapuku and bass (HPB)[3]; school shark (SCH)

Notes

[1] Jack mackerels consist of three species; assessment included aspects of tier 1 and tier 2 approaches – see McKenzie & MacDiarmid (2011) for more information.

[2] Consists of 12 or more species including sole (*Peltorhamphus novaezeelandiae*) and sand flounder (*Rhombosolea plebeia*)

[3] Consists of two species

3.3 Biological parameters

For many species the biological parameter values are not available for the study area, they sometimes have multiple estimated values and they are different between the sexes. Various approximations, such as choosing adjacent areas and averaging across sexes and multiple estimates, are used. The main biological parameters of interest for input to the trophic model are length-at-age, weight-at-length, and natural mortality. In the trophic model there is no separation by sex for the components, so the biological parameters are for both sexes combined.

The main source for the biological parameters is the Ministry of Fisheries Plenary document (Ministry of Fisheries 2007). Frequently there were no biological parameters given for the QMA area encompassing a study area, in which case biological parameters from an adjacent QMA were used instead. Where the parameters values are by sex the mean is taken of the values to obtain a combined sex estimate. If there were multiple estimates of parameters values (by sex or combined sexes) then the mean was taken of the values. A better technique than taking the mean would be to combine the original data, then re-estimate parameter values. Alternatively, the parameter values could be used to generate point estimates (say, by sex and size) that could then be used to generate an approximate overall set of parameters. Neither of these possible approaches was practical within this study.

Although it is well known that natural mortality varies with age, for all species here it was treated as a constant with age, as there was insufficient data to estimate age varying natural mortality.

3.4 Tier One

Six species (or groups of species) (snapper, red gurnard, kahawai, gemfish, trevally, jack mackerel) had quantitative stock assessments. In the Hauraki Gulf, the snapper and kahawai assessments were most likely the best, with trevally the worst (the CPUE index is suspect, McKenzie & MacDiarmid 2011). Each assessment had some problematic aspects. Firstly, biomass estimates were almost always of spawning stock biomass not total biomass, were generally for a larger area (a QMA) than the study area, often did not cover the time period 1930–2006. Also, by their nature, stock estimates are all inaccurate and all require multiple assumptions or estimated values. Secondly, the proportions-at-age series required for the study area were not produced for any of the assessments. Lastly, some stock assessments were conducted using data and specialised software that is no longer readily available. If an assessment was implemented in the stock-assessment software CASAL (Bull et al. 2005), then far more information was available in the model output, for example including proportions-at-age for any year desired as well as total biomass.

The details of how the problematic aspects of each assessment were dealt with are given below (also see McKenzie & MacDiarmid 2011). In general, to scale total biomass estimates down from a QMA to the study area, the ratio of the catches in the study area to those in the assessment was used. Typically this ratio varied substantially over the period 1931–2006. As the most recent catches were likely to be most accurate, the median value of the catch ratio over a recent period where it appeared relatively constant was used to scale the total biomass down from the QMA. A potential complication was that this ratio may change over time; in particular it increased if the fishery contracted spatially over time.

3.4.1 Snapper (SNA)

In the 1999 snapper assessment a total biomass trajectory for four year olds and above was derived covering 1850 (about when the commercial fishery started) to 1998, assuming a natural instantaneous mortality rate of M=0.075 y^{-1} (Davies, 1999). A sensitivity test was done for this assessment in which natural mortality M=0.06 y^{-1} was assumed, a value closer to that currently thought to be correct. However, the program and data for this assessment are no longer accessible, which limits its usefulness for producing some of the model outputs required, although the biomass trajectory is useful for estimating the pre-1970 biomass trajectory (see below).

The present CASAL version of the snapper model for SNA 1 is partitioned into three separate models covering East Northland, Hauraki Gulf, and Bay of Plenty. The model partition designated as "Hauraki Gulf" does not extend as far north as the study area and excludes the study area component off the east coast of Coromandel. Hence to obtain model estimates for the study the output from both the Hauraki Gulf and Bay of Plenty models is required. The versions of the models used were 8.0 (Hauraki Gulf) and 1.1 (Bay of Plenty).

The following is common to both the Hauraki Gulf and Bay of Plenty models. Age classes in the model are from 1 to 20, with a 20+ class. Five separate fishing methods were included in the models: longline, single trawl, Danish seine, other commercial, and recreational. The models start in 1970 for which an initial non-equilibrium age distribution was estimated, and finish in 2004. However, different values of natural mortality were assumed in the models: 0.065 y^{-1} (Hauraki Gulf) and 0.060 y^{-1} (Bay of Plenty).

To obtain estimates of the total biomass for the study area, the total biomass output from the Hauraki Gulf model was added to a constant proportion of that from the Bay of Plenty model. The constant was determined by requiring that the combined recreational catch in the model, which is a substantial proportion of the total catch, be close to the value of 1700 t estimated for the study area in 2005 (Francis & Paul 2008), giving a value of 0.25 for the constant. As the models only go to 2004, total biomasses estimates for 2005 and 2006 were obtained by linear extrapolation using the change from 2003 to 2004.

To obtain virgin total biomass for the study area the estimates from the two models were combined using the same value of 0.25 to incorporate the Bay of Plenty. This gave a value of 219 400 t (197 200 + 0.25×96 800). For comparison purpose, for the entire SNA 1 area, with a natural mortality of 0.06 y^{-1}, the total biomass of four year olds and above was estimated to be 275 000 t.

In the 1999 assessment model with a natural mortality of M=0.06 y^{-1}, the 1930 biomass is about 65% of the virgin biomass. Multiplying the virgin total biomass for the study area (219 400 t) by 65% gives an estimated 142 600 t for the total biomass in 1930 in the study area. Linear interpolation was then used between the derived 1930 value and the CASAL model's 1970 value.

Proportions-at-age were estimated for the virgin population, the present, and selected points between (1930, 1946). Firstly proportions-at-age were calculated separately for the Hauraki Gulf and Bay of Plenty population models, then combined with a weighting of 4:1 (derived from the 0.25 used in the total biomass calculations). As the study area includes some area north of the Hauraki Gulf model area, this ratio should be higher by some indefinite amount, but as the proportions-at-age for Hauraki Gulf and Bay of Plenty are similar the exact ratio is unimportant. The virgin proportions-at-age were obtained from the natural mortality estimates of M=0.065 y^{-1} (Hauraki Gulf) and M=0.060 y^{-1} (Bay of Plenty). Combining these gives a very large proportion in the 20 year plus group.

There were some difficulties with estimating proportions-at-age for 1946 as it was unclear just how interpolation should be done between the virgin estimates for 1850 and those for 1970 when the CASAL models begin. A simple linear interpolation between 1850 and 1970 is crude, particularly since the biomass trajectory is curvilinear. However, the biomass trajectory is essentially flat until about 1890, when the proportions-at-age differed little from 1850. A less crude linear interpolation is between 1890 and 1970, and this was done to obtain the 1946 proportions-at-age estimates. For simplicity it was assumed that the proportions-at-age in 2006 equalled those in 2004 (the last year of the model).

3.4.2 Red gurnard (GUR)

The GUR 1 stock, which includes the Hauraki Gulf study area, covers the upper part of the North Island. The catch for this stock is mainly taken as bycatch from the inshore trawl fisheries for snapper, John dory, tarakihi, and trevally (Ministry of Fisheries 2007, p. 714). The GUR 1 stock was last assessed in 1999 when it was treated as two separate stocks and divided at North Cape into western (GUR 1W) and eastern (GUR 1E) stocks (Hanchet et al. 2000). For 1931 to 1984, the catch histories for GUR 1W and GUR 1E were derived on the basis of the port of landing. For 1985 to 1997, the ratio of catches from GUR 1W and GUR 1E was assumed to be 40:60 based on the average of the ratio in earlier years and on the ratios of estimated landings from the TCEPR and CELR forms for 1990 to 1996 (Hanchet et al. 2000).

The MIAEL assessment model for GUR 1E was age based with a partition by sex. With age data included, year class strengths from 1984 to 1997 were estimated, and virgin biomass (B_0) was estimated to be about 31 000 t declining to about 60% of this in 1999 (Hanchet et al. 2000). To derive GUR 1E model output up to 2006 the assessment from 1999 was emulated in CASAL with an extension of the catch history to 2006. As in 1985 to 1997, 60% of the total landings for GUR 1 (Ministry of Fisheries 2007, p. 715) were assumed caught from GUR 1E. Using the same biological parameters as for the 1999 assessment, and taking year class strengths to be the same as were estimated or set to, the model was driven forward from a starting biomass of 31 000 t. Note that the catch history for the model does not include recreational catch, but, as the recreational catch is less than 5% of the total catch the difference will be small.

For the emulation model, as for the 1999 assessment, spawning stock biomass declined in the early 1980s, then recovered during the 1990s. However, for the emulation model the spawning stock biomass in 1999 was 84% of the virgin, instead of the 60% for the 1999 assessment. Evidently there was some difference between the emulation model and 1999 assessment model that was not accounted for; as the differences are not substantial the emulation model was used for model output. The ratio of the catch in the Hauraki Gulf study area to that in GUR 1E shows a distinct linear decline. A robust linear regression for the ratio versus fishing year was used to scale the total biomass for GUR 1E down to the Hauraki Gulf study area.

3.4.3 Kahawai (KAH)

The KAH 1 stock, which includes the Hauraki Gulf study area, covers the upper part of the North Island. The catch for this stock is mainly taken by purse seine for the Bay of Plenty region, but dominated by set nets for the Hauraki Gulf (Ministry of Fisheries 2007, table 9, p. 400). The KAH stock was last assessed in 2007 when it was treated as a single homogeneous stock. However, there are likely to be sub-area differences in the age structure due to migration, but because there were insufficient data to estimate migration this was not incorporated into the model. To quote (Ministry of Fisheries 2007, p. 402):

“Annual sampling of recreational catches, which has taken place in all three areas since 2001 (and intermittently since 1991), suggests that there are consistent regional differences in the length and age compositions of kahawai among these regions. For example, in the Hauraki Gulf, recreational landings of kahawai are regularly dominated by three year olds, with low proportions of fish older than five years. It is improbable that these regional differences in age structure can be attributed to relative fishing pressure alone, which suggests that some form of movement between areas is highly likely. There are few tag data available that can be used to estimate these migration processes, because almost all of the kahawai that have been tagged have been released in the Bay of Plenty. This provides little information about emigration from the Hauraki Gulf and from East Northland. For this reason it was not possible to partition the model into three interconnected sub-stocks, as their connectivity is inestimable. Area specific observational data were combined into a single stock model which includes most of the currently available data."

For the 2007 assessment four factors were thought to be uncertain for the model: the steepness parameter (h), natural mortality (M), non-commercial catch, and which abundance indices to fit to (Ministry of Fisheries 2007, p. 404). Instead of a single base model, 36 model runs corresponding to different assumptions for the four factors were presented. The model was insensitive to the options chosen for steepness and abundance indices. For simplicity in biomass estimates the single most reasonable model was used, with a natural mortality of 0.18 yr^{-1}, and a non-commercial catch in total of 800 t (Bruce Hartill, pers. comm.). The ratio of the catch in the Hauraki Gulf study area to that in KAH 1 was mostly constant except for a large rise in the late 1980s. The median value of the ratio from 1975 to 2006 (0.29) was used to scale the total biomass for KAH 1 down to the Hauraki Gulf study area.

3.4.4 Gemfish (SKI)

The SKI 1 and SKI 2 stocks, which include the Hauraki Gulf study area, cover the upper part of the North Island. The catch for these stocks is mainly taken by trawlers for which a targeted fishery has developed off the eastern and northern coasts (Ministry of Fisheries 2008, p. 272). Gemfish probably undertake spawning migrations and pre-spawning runs form the basis of winter target fisheries, but exact times and locations of spawning are not well known. Spawning probably takes place about July near North Cape and late August/September on the west coast of the South Island (Ministry of Fisheries 2008, p. 274). The northern gemfish stock was assessed using the hypothesis of one stock (SKI 1 and SKI 2). The model included two fishery types, based on spawning activity, with two areas. The first is on the area SKI 2, where all age classes occur and where fishing is mainly in the pre-spawning season. The second is on the spawning migrations, in the area SKI 1, where only mature age classes occur and where fishing is in the winter months.

The model output from SKI 1 was used for estimating total biomass and length frequencies in the Hauraki Gulf study area. The ratio of the Hauraki Gulf study area catch to the SKI 1 catch is very irregular up to 1980. For scaling the total biomass from SKI 1 to the study area the median value of the ratio from 1980 to 2006 was used (0.27).

3.4.5 Trevally (TRE)

The TRE 1 quota management area is located off the northeast coast of the North Island. It is a mixed fishery with significant catch being taken as bycatch from the snapper trawl fishery, or since the 1970s from targeted purse-seining. Commercial set netting and beach seine, and recreational catch have also formed non-trivial, but variable, components of the catch (Ministry of Fisheries 2007, p.968). This stock was assessed in 2005 with a major input being a CPUE index based on aerial sightings for the purse-seine fishery (McKenzie 2007). This assessment was inconclusive because the CPUE and proportions-at-age data sets disagreed with each other regarding the steepness of the fall in biomass. Current biomass estimates range from 6–18% of virgin biomass depending on the weight given to the CPUE index in the model. However, the biomass estimates from the model represent the best available, and are sufficiently accurate as inputs for the Ecopath model. One unlikely aspect of the CPUE index, as a measure of abundance, is that it drops by 60% from the first to the second year. Hence, for the model run used here, the first year of the index was dropped. The weight given to the CPUE index is the same as in the base case (CV of 0.30).

Trevally was only targeted from the mid 1950s; before then it was often dumped and records of this are poor. Higher discard rates before the mid 1950s were included in the model estimates. The ratio of the catch in the study area to that in TRE 1 is relatively constant from 1960 onward. The median value of this ratio from 1960 onward (0.26) was used to scale the total biomass for TRE 1 to the Hauraki Gulf study area.

3.4.6 Jack mackerels (JMA)

Jack mackerels in the QMS and in the trophic model consist of three species (*Trachurus declivis*, *T. novaezealandiae*, *T. murphyi*), with the Hauraki Gulf biomass likely to be 80 to 90% JMN (*T. novaezealandiae*). No jack mackerel stock assessment been done for the study area, or for the larger QMA. However, from aerial sightings data, a standardised CPUE index has been derived for the QMA, which may be indicative of biomass trends in the study area (Taylor 2006). This index was used in an exploratory stock assessment model for the study area, using the estimated catches for the area, estimated selectivities, and known biological parameters for jack mackerel. The fit to the CPUE index is reasonable for 1990 onwards (McKenzie & MacDiarmid 2011), but the early part of the index is poorly fitted. This is most likely to be due to an inconsistency between the catches taken in the model and the index. Whatever the reason may be, the biomass trajectory of jack mackerel based on these results should be considered to be very uncertain.

3.5 Tier Two

The tier two species (Table 60) have no stock assessments. However, each of them is judged to be similar in distribution and catchability to a tier one species, over a given period of years. Under this assumption of similarity the catch history of the tier two and tier one species is used to estimate the tier two species total biomass for 1930–2006, as follows.

Table 60: Tier two species which are assumed to have similar catchabilities to a given reference species over a given period of years (defined by First year and Last year).

Species code	Species name	Reference species code	Reference species	First year	Last year
EMA	blue mackerel	JMA	jack mackerels	1985	2006
JDO	John dory	SNA	snapper	1955	1970
SPO	rig	GUR	red gurnard	1955	1970
BAR	barracouta	SKI	gemfish	1985	1995

Over the period in which the tier two and tier one species were judged to be similar, the median value of the ratio of their catches was found. Using this ratio, the total biomass for the tier one species was scaled to estimate the total biomass for the tier two species, over the period of judged similarity. This total biomass trajectory is here called the comparable total biomass trajectory.

For each tier two species, a total biomass trajectory over 1930–2006 is required. Given the catch history, biological parameters, and total biomass in 1930 for a tier two species, then a total biomass trajectory from 1930–2006 is defined. A family of total biomass trajectories was derived by starting with different total biomasses in 1930 (1000 t to 10 000 t in increments of 100 t). The single trajectory was selected from this family which most closely matched the biomass in the middle year of the comparable total biomass trajectory.

However, for some tier two species, all the trajectories from the family of total biomass trajectories were above the comparable total biomass trajectory. This also included the minimal trajectory for which the catch history for the species could only just be taken without the total biomass trajectory reaching zero in some year. In these cases it was decided to select the lowest trajectory for which the catch taken in each year cannot exceed the arbitrary chosen value of half the total biomass for the year. Often there was little difference between this trajectory and the minimal trajectory for the total biomass in 1930, but more so for 2006.

For all trajectories chosen the corresponding proportions-at-age were generated for 1930, 1946, and 2006. Detailed results by tier two species are given in McKenzie & MacDiarmid (2011).

3.6 Tier Three-A

There are eight tier three-A species (**Table 61**). Like the tier two species, the tier three species have no stock assessments. However, unlike the tier two species, there are no tier one species associated with them which have a similar distribution and catchability. Instead, an estimate was made of the trawl catchability relative to a tier one species. The same procedure was then followed as for the tier two species biomass estimates, using the ratio of catches, but with the additional scaling of the relative catchability included. From 1983 onwards statistical areas are recorded for catch landings, making them more accurate, so for the catch ratios the median value is taken over 1983 to 2006.

Table 61: Tier three-A species and their estimated trawl catchability relative to reference species.

Species code	Species name	Catchability	Relative to
RCO*	Red cod	1	Snapper
FRO*	Frostfish	1	Gemfish
SKA*	Rough and smooth skates	1	Snapper
TAR	Tarakihi	0.8	Snapper
FLA	Flatfish	0.7	Snapper
KIN	Kingfish	0.5	Kahawai
STA	Giant stargazer	0.3	Snapper
SPE	Sea perch	0.8	Snapper

3.7 Tier Three-B

There are two tier three-B species (Table 62). Like the tier two and tier three-A species, the tier three-B species have no stock assessments. As for tier three-A species, there are no tier one species associated with them which have a similar distribution and catchability. Unlike tier three-A species, it is not possible to estimate relative trawl catchabilities for these species; any reasonable confidence interval on estimated trawl catchabilities would cover a ten-fold range, translating into a ten-fold difference in biomass estimates. Because the values are not well known, and using the values supplied give what seems very high initial biomasses with very little decline, it was decided not to use estimated catchabilities. Instead, we used the lowest trajectory where the commercial catch was no more than half the biomass in any year, the default trajectory for other species when other methods are not useful. The lower bound on virgin biomass was set to a nominal 100 t.

Table 62: Tier three-B species and their estimated trawl catchability relative to snapper. Note that these catchabilities are shown for completeness and were not used in estimating biomass (see text for details).

Species code	Species name	Catchability	Relative to
HPB	Hapuku and bass	0.01	Snapper
SCH	School shark	0.02	Snapper

4 Biomass: Species-habitat models

4.1 Introduction

Biomass of reef fishes in the study area was estimated based on modelling by Smith (2008) who used boosted regression tree (BRT) models to estimate the abundance of 72 species of reef fish around New Zealand on a 1 km^2 grid. This modelling was undertaken for the Department of Conservation and permission to use these data has been granted by this institution. These represent the best available information on the abundance of reef fish in the Hauraki Gulf available to this project at the time of writing.

4.2 Method

The information given here is a summary– for more information of the method, see Smith (2008). The base dataset contained observations of the relative abundance of rocky reef fishes from diver surveys around shallow, subtidal reefs of New Zealand. These data were collected over a period of 18 years from November 1986 to December 2004. The majority of the data were collected by C.A.J. Duffy of the Department of Conservation, and a small number were collected by A.N.H. Smith. The database contains predicted abundances of fish per 47 minute fish count, which approximates to an observation of about 600 m^2 of reef (A. MacDiarmid, R. Stewart, pers. comm.). The fish abundances were recorded on an ordinal scale of abundance (Table 63) using the "Roving Diver Technique" (Schmitt et al. 2002; Schmitt & Sullivan 1996; Semmens et al. 2004) which approximately represents orders of magnitude of abundance. The original dataset contained 212 species. Many species were excluded from analysis if they were considered to be pelagic, highly cryptic, more associated with soft sediment than reefs, or because they were too rare to be effectively modelled (Smith 2008). The Hauraki Gulf was relatively well represented in the dataset used by Smith (2008).

Table 63: Ordinal scale of fish abundance used for estimating reef fish abundance.

Value, x	Name	No. fish observed per segment
0	absent	0
1	single	1
2	few	2–10
3	many	11–100
4	abundant	> 100

Independent models were used to model the abundance of each of the remaining 72 species of reef fish. All statistical analyses were undertaken in R (R Development Core Team 2007) using the GBM library (Ridgeway 2006) and code developed by Leathwick et al. (2006a, b). The models were built using the boosted regression tree (BRT) method. A stepwise, 10-fold, cross-validation procedure was employed to objectively determine the number of trees to be fitted in each model, thus reducing the risk of over-fitting. A total of 15 variables were made available to the BRT models, each falling into one of three categories: environmental, geographic and dive related.

The BRT routine fitted between 675 and 9110 trees to the models. As assessed from the cross-validation routine, the models were able to explain between 28 (*Notoclinops caerulepunctus*) and 93 (*Odax cyanoallix*) percent of the deviance in species abundances around the whole New Zealand coastline, with a median of 64 percent.

Reef areas for the Hauraki Gulf study area within each of the 1 km^2 cells used by Smith (2008) were calculated based on the habitat map of the region developed for this project. For each species, estimated fish abundances on the ordinal scale were converted to numbers of fish per segment using equation [1], where N is the predicted abundance of fish per segment (about 600 m^2 of reef) and x is the value on the ordinal scale of abundance (Table 63). This assumes that the actual number of fish is given by the geometric mean of the upper and lower bounds of the range for x=1,2,3 (R^2=0.99). The average abundance associated with x=4 is hence estimated to be 176 fish/segment.

[1] $$N = \exp(1.751x - 1.835)$$

The total number of fish of a given species in a 1 km^2 cell then equals the reef area in the cell (m^2) multiplied by the fish per segment divided by the segment area (600 m^2). The total number of fish in the study area was then estimated as the sum of the total in each 1 km^2 cell. Numbers were converted to wet weight biomass using an estimate of the average size of each species of fish. Maximum lengths were taken from Francis (2001) or FishBase (Froese & Pauly 2009), and length-weight parameters (a, b) from FishBaseFishBase (Froese & Pauly 2009). Following Lundquist & Pinkerton (2008), the average weight of a given species of reef fish was taken as 0.33 of the maximum weight of that species.

5 Biomass: Other methods

5.1 Catch-based estimates

For 13 species, biomass was estimated based on an estimate of annual landings. These species were: anchovy, blue cod, blue moki, bronze whaler, common (blue) warehou, elephant fish, grey mullet, hammerhead shark, pilchard, piper/garfish, skipjack tuna, spiny dogfish, tuna (other), and yellow-eyed mullet. Total landings, including commercial landings, estimated Illegal, Unregulated or Unreported (IUU) landings (where appropriate), recreational and customary landings, were estimated as described in Section 3 (Francis & Paul 2008). Eleven of these species are included in the QMS (the exceptions are the bronze whaler and hammerhead sharks).

For the QMS species, the 2009 Ministry of Fisheries plenary documents (Ministry of Fisheries 2009a, b) were used to estimate the status of the stock relative to the MSY (maximum sustainable yield) or unfished (virgin) biomass. Anchovy was taken to be at 0.9 of the unfished biomass. Skipjack tuna biomass was taken to be twice the MSY level. For all other species, including bronze whaler and hammerhead shark, the biomass was taken to be the deterministic MSY biomass. Biological parameters (von Bertalanffy, length-weight, natural mortality) were taken from Ministry of Fisheries (2009a, b) augmented where necessary by FishBase (Froese & Pauly 2009). The recruitment steepness parameters for these species are not well known and were estimated to be between 0.3–0.8 (**Table 64**). Fish greater than a threshold length were taken to be subject to fishing mortality.

A model was then applied which had different amounts of fishing mortality until the maximum sustainable yield was obtained. The model then estimated B_{MSY}/B_0 and Y/B, the annual yield as proportion of current biomass level (y^{-1}) from which the current biomass was estimated.

Table 64: Parameters (columns 2-5) and model output (columns 6–7) used to estimate biomass for landings-based estimates as described in the text. h=steepness parameter. Fishing mortality is applied to all fish greater than the threshold length (cm). B/B_0=current biomass level as a proportion of unfished level (B_0). B/B_{MSY}= current biomass level as a proportion of deterministic maximum sustainable yield (MSY) biomass. Model estimate of B_{MSY}/B_0. Model estimate of Y/B=annual yield as proportion of current biomass level (y^{-1}).

Species	h	Threshold (cm)	B/B_0	B/B_{MSY}	B_{MSY}/B_0	Y/B (y^{-1})
Anchovy	0.8	3	0.9		0.28	0.033
Blue cod	0.7	30		1	0.33	0.104

Blue moki	0.7	10	1	0.34	0.090
Bronze whaler	0.3	50	1	0.46	0.013
Common warehou	0.7	10	1	0.33	0.148
Elephant fish	0.5	10	1	0.38	0.128
Grey mullet	0.7	10	1	0.33	0.226
Hammerhead shark	0.3	50	1	0.47	0.011
Pilchard	0.8	3	1	0.30	0.383
Piper/garfish	0.7	10	1	0.33	0.247
Skipjack	0.7	10	2	0.31	0.098
Spiny dogfish	0.5	50	1	0.38	0.095
Yellow-eyed mullet	0.7	10	1	0.30	0.400

The yield/biomass values were then used to estimate a biomass in the study area based on the estimated landings. For silver warehou, the Y/B value was taken to be the same as common warehou. For dogfish (other), the Y/B value was taken to be the same as spiny dogfish. For tuna (other), the Y/B value was taken to be the same as skipjack tuna. For Ray’s bream, the Y/B value was taken to be the same as similarly sized fish (blue warehou, blue moki, blue cod). For Japanese gurnard, the Y/B value was taken to be the same as red gurnard. For stargazer (other), the Y/B value was taken to be the same as giant stargazer. For northern bastard cod, the Y/B value was taken to be the same as the average of red and blue cod. For dory (other), the Y/B value was taken to be the same as John dory. For hagfish (*Eptatretus cirrhatus*), moonfish (*Lampris guttatus*), and porcupinefish (*Allomycterus jaculiferus*) we assume that a nominal 10% of the annual production is taken as catch.

5.2 Trawl survey-based estimates

Trawl surveys are routinely used internationally to provide fishery-independent data on stock size and distribution. They are generally designed to provide a consistent measure of abundance over time using standardised fishing gear and the same vessel. Trawl surveys have been widely used in New Zealand fisheries research, and a number provide time series data sets suitable for analysis using fish-based ecosystem indicators. Inshore surveys have been conducted around New Zealand since the 1940s; altogether, 17 voyages took place, with data available from 1964, 1965, 1980, 1984–90, 1992–94, 1997, and 2000 (Tuck et al. 2009). A wide range of surveys have been conducted in the Hauraki Gulf area, for a variety of purposes. The most consistent of the surveys appear to be the spring/summer (October–December) series conducted from the RV *Kaharoa*, with the primary purpose of providing an index of snapper and other inshore fish species, stratification in these *Kaharoa* surveys has remained relatively consistent in depth and area, and a two-phase random stratified design was employed. All trawling used a high-opening bottom trawl, with cut-away lower wings and a nominal 40 mm codend mesh size. Paul (1992) considers data since the 1960s comparable over time but here we use only data collected by the RV *Kaharoa*.

Where biomass estimates were not available from other methods, we scaled catches from recent (1990–2000) Hauraki Gulf trawl surveys, using catchabilities scaled to that of snapper, similar to the method used for tier two and three QMS species described above (**Table 65**). Relative catchabilities of fish by trawl gear used in the Hauraki Gulf survey are not well known.

Table 65: Species for which biomass estimated from trawl survey catches and their estimated trawl catchability relative to snapper. Note that these catchabilities are uncertain.

Species code(s)	Species name	Scientific name	Catchability	Estimated biomass (tWW)
EGR	Eagle ray	*Myliobatis tenuicaudatus*	0.5	400

ERA, STR, BRA, WRA	Electric ray; stingray	*Torpedo fairchildi*; *Dasyatis* spp	0.5	130
OPA	Opalfish	*Hemerocoetes monopterygius*	0.5	5.9

5.3 Juvenile fish biomass

The maximum individual weight of a juvenile fish was estimated to be 23 gWW at a maximum length of 10 cm based on the length-weight regression for all species. The average individual weight of a juvenile fish was set at 10% of this value i.e. 2.3 gWW from a simple population model with the high mortality rates for juvenile fish.

The number of recruits entering a stock per year was estimated from an estimate of total (natural plus fishing) mortality and the average weight of fish in the stock, under the assumption that there are enough recruits to keep the stock size steady in a given year. Natural mortality was estimated based on K (y^{-1}, von Bertalanffy growth parameter), water temperature (°C, here set at 10°C) and maximum length (L_{inf}, cm) following Pauly (1994) (equation 2). This relationship was reported as having R^2=0.847 (Pauly 1994).

[2] $$M = 0.985 \cdot K^{0.654} \cdot T^{0.463} \cdot L_{\text{inf}}^{-0.279}$$

The total number of fish recruiting for all stocks together in the model area in each year was then calculated as the sum of recruits for each stock separately. This was calculated as 3900 tWW/y. Natural mortality of juvenile fishes based on Pauly (1994) was estimated as M=1.3 y^{-1}. Annual production of juvenile fishes was estimated as P/B=1.9 y^{-1} following methods described below based on Banse & Mosher (1980). Total biomass of juvenile fishes was then estimated as the annual biomass export divided by (P/B-M), giving an estimate of juvenile biomass of juvenile fish in the study area of 5800 tWW.

5.4 Other reef fish

There is little information available to estimate biomass of other small fish in the study area. Biomass of the remaining two species of triplefin (estuarine triplefin and mottled triplefin) were set equal to the median biomass of other triplefins in the study region (11 tWW). Biomass of moray eels (other) was set to half the biomass of yellow moray (*Gymnothorax prasinus*) of 120 tWW. Biomasses of trumpeter (*Latris lineata*), gobies (Gobiidae), bluefish (*Girella cyanea*), orange clingfish (*Diplocrepis puniceus*), urchin clingfish (*Dellichthys morelandi*), twister (*Bellapiscis lesleyae*, *B. medius*), and giant boarfish (*Paristiopterus labiosus*) were set nominally to the 25th percentile of biomass of other reef fish (6.2 tWW).

Pink cod, or Ahuru (*Auchenoceros punctatus*), may be quite abundant in some areas, notably the Firth of Thames as shown by small-mesh trawl surveys (Paul 1986). We assumed an abundance of 1 individual per 100 m^2. The area of the Firth of Thames is approximately 1100 km^2 (Zeldis 2008) giving a biomass estimate of 215 tWW.

Redbait or red baitfish (*Emmelichthys nitidus*) is widely distributed around New Zealand in midwater schools over the outer shelf (Paul 1986) and so the biomass in the study area (which is bounded by the shelf break) is likely to be low, and here was set to a nominal 10 tWW.

Worm eels (*Scolecenchelys* spp.), including the long-finned worm eel (*S. breviceps*), are snake eels found around New Zealand to depths of about 50 m, on sandy or muddy bottoms. No abundance estimates were available for the study area, and we assumed a density of 100 individuals per km^2 in waters shallower than 50 m, leading to a biomass estimate of 32 tWW.

5.5 Other large fish

There was little information available to estimate biomasses of other large fish in the study area: carpet shark, sevengill shark, and broadbill swordfish. Until more information is available, we assumed there were approximately the same number of carpet sharks, sevengill sharks and swordfish as bronze whalers, giving biomasses of 42, 131 and 130 tWW respectively.

6 Diet

The diet and general feeding behaviour of most New Zealand fishes found in the study area are known to some degree, at least in terms of major and minor food items in broad categories. This study used data in two reference books, Francis (2001) and Paul (1986), to provide basic information of fish diet for species and species-groups used in the trophic model. Prey categories were: organic detritus; seaweed; zooplankton; salps and jellyfish; worms; phytal invertebrates; large shrimps and amphipods; crabs (including hermit crabs); crayfish (red rock lobster); sponges; bivalves and gastropods; bryozoa, ascidians, anemones, barnacles and other encrusting inverts; seastars and brittlestars; kina; other urchins; squid; octopus; fish (reef); fish (demersal); fish (pelagic); fish (pelagic and mesopelagic). Other references used to estimate diet are given in **Table 66**.

Table 66: Sources of information for diet estimates of fish in the trophic model. Where species are not listed here, diet was based on Francis (2001).

Species	Reference for diet
Ahuru	Paul (1997)
Anchovy	Paul et al. (2001)
Barracouta	Mehl (1969); O'Driscoll & McClatchie (1998); Stevens et al. (2011)
Blue cod	Stevens et al. (2011), Francis (2001)
Blue (English) mackerel	Taylor (2002)
Common (blue) warehou	Gavrilov & Markina (1979); Stevens et al. (2011); Kailola et al. (1993)
Dark ghost shark	Horn (1997), Stevens et al. (2011)
Elephantfish	McClatchie & Lester (1994)
Frostfish	Nakamura & Parin (1993)
Gemfish	Hurst & Bagley (1998), Stevens et al. (2011)
Giant stargazer	Stevens et al. (2011), Francis (2001)
Gobies	J. McKenzie, NIWA, pers. comm.
Grey mullet	Ministry of Fisheries (2007)
Hammerhead shark	Last & Stevens (1994), Paul (1997)
Hapuku and bass	Stevens et al. (2011), Francis (2001)
Hoki	Clark (1985), Stevens et al. (2011)
Jack mackerels	Stevens et al. (2011), Francis (2001)
Kingfish	Francis (2001), Walsh et al. (2003)
Leatherjacket	Russell (1983)
Northern bastard cod	Stevens et al. (2011), Francis (2001)
Pilchard	Paul et al. (2001)
Ray's bream	Paul (1986)
Red cod	Stevens et al. (2011), Francis (2001)
Redbait	Welsford & Lyle (2003)
Rig	King & Clark (1984)
School shark	Olsen (1954), Graham (1956)
Sea perch	Stevens et al. (2011), Francis (2001)
Sevengill shark	Last & Stevens (1994), Paul (1997)
Silver warehou	Kailola et al. (1993); Stevens et al. (2011)
Rough & smooth skate	Graham (1938); Graham (1939)
Skipjack tuna	Vooren (1976), Habib et al. (1980a,b,c, 1981)
Snapper	Godfriaux (1969, 1974a, 1974b); Russell (1983)
Spiny dogfish	Hanchet (1991)
Stargazer (other)	Stevens et al. (2011), Francis (2001)
Tarakihi	Godfriaux (1974b)
Trevally	Russell (1983)
Worm eel	M. Lowe (NIWA, pers. comm.)
Yaldwyn's triplefin	Thompson (1981)
Yellow-black triplefin	Thompson (1981)

Consumption (tWW y^{-1}) of each prey item by each species of fish was estimated once biomass and consumption rate (Q/B) of each fish species had been estimated. Total consumption of each prey type by each of the model groups of fish was then calculated and the diet proportions estimated. These are shown in the summary tables at the end of this document.

7 Other parameters

7.1 Wet weight-carbon conversion factors

In order to convert between wet weight and carbon we used reported values of 1gC approximately equal to 10–12 kcal (Ikeda 1996). For fish, 0.95–1.35 kcal/gWW is reported

(Steimle & Terranova 1985; Croxall et al. 1985; van Franeker et al. 1997; Parsons et al. 1984). These imply that 1 gWW is equivalent to approximately 0.095–0.11 gC. A dry:wet weight ratio of 20–30% (e.g. Hartman & Brandt, 1995; Holmes & Donaldson, 1969) implies a range of 0.09–0.12 gC gWW^{-1}. Vinogradov (1953) gave an oft-used conversion factor of 0.1 gC gWW^{-1} for fish which we will use for all conversions here.

7.2 Maximum weight

Maximum weight of individual fishes is an important parameter because it is used to estimate production and consumption rates, and in some cases, to help estimate biomass. Where information on the maximum length and length-weight relationship for a species (or species-group) were available for the area encompassing the study region from the Ministry of Fisheries Plenary Report (Ministry of Fisheries 2009a, b), this was used to estimate maximum weights. This was possible for 20 species. For a further 41 species, we used maximum lengths and length-weight relationship from FishBase (Froese & Pauly 2009) to estimate maximum weights. If this information was not available or not considered appropriate for the study area, we took the maximum length from Francis (2001) or Paul (1986) and used a linear relationship fitted between maximum length and maximum weight based on the 61 species for which this information was available (N=61, R^2=0.89). We fitted this relationship in log-log space, i.e. we estimated: $\ln(W_{inf})=A(L_{inf})+B$, where A=2.71 and B=-10.1 (W_{inf} in kilograms and L_{inf} in centimetres).

As a final check, we took recreational catch record weights from the New Zealand Sport Fishing organisation (March 2011, http://www.nzsportfishing.co.nz/nz-records/) for regions as close to the study area as possible. This information was available for 57 species. The relationship in log-log space between the maximum weight from the catch records and our estimate of maximum weight had R^2=0.87 (Figure 29). The preponderance of positive residuals from the 1:1 line is expected as the mean maximum weight from a sample of a population will always be less than the maximum weight in the sample.

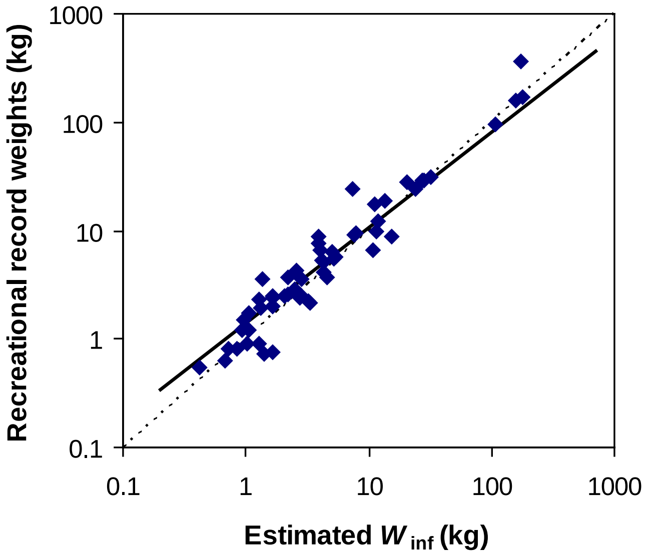

Figure 29: Relationship between maximum weight of fish species in the study area from recreational record catch weights (New Zealand Sport Fishing organisation) and estimated here using maximum lengths and length-weight relationships, as described in the text. Each point is a

different species (n=57). The solid line is the fitted relationship and the dashed line is the 1:1 relationship.

7.3 Production

Production in the model is defined as the instantaneous rate of increase in biomass of the fish species (or species-group) if there were no import, export, or mortality (including direct consumption due to predation, other sources of mortality, or fishing mortality). Alternatively, annual production (P) can be defined as equation [3] where Q is the annual consumption, U is the unassimilated fraction of consumption, and R is the respiratory output.

[3]
$$P = Q(1-U) - R$$

Two methods were used to estimate weight specific production rates (P/B) of fish populations.

Method 1: Where age-frequency information for a species is available, the production rate due to fish growth of the population is calculated as the sum of the growth rates of each year class in the population based on the time-differential of the von Bertalanffy growth curve and the length-weight relationship. This was possible for 20 species: trevally; gemfish; red gurnard; kahawai; snapper; jack mackerel; blue (English) mackerel; John dory; rig; barracouta; tarakihi; flatfish; red cod; frost fish; rough and smooth skates; kingfish; giant stargazer; sea perch; hapuku and bass; school shark.

Method 2: For all species, weight specific production rates were estimated based on the allometric equations of Banse & Mosher (1980), and Haedrich & Merrett (1992), equation [4] where P/B is the annual production rate per unit biomass (y^{-1}) and W is the weight of an individual (gWW).

[4]
$$\frac{P}{B} = 2.4W^{-0.26}$$

The allometric equations relate annual production to the average weight, not the maximum weight of an individual. For fish populations where age-frequency information is available the mean weight of an individual in the population was calculated based on the age-length information (von Bertalanffy growth curve) and the length-weight relationship. This was possible for 20 species as given above. The average ratio of mean weight to maximum weight for these species was 0.27 with a range of 0.11–0.45. Where age-frequency information was not available, the average weight of an individual is estimated to be approximately 0.33 of the maximum weight following previous modelling work (Lundquist & Pinkerton 2008).

Not all production is due to growth (for example, consumption may be used to generate spawning output rather than individual growth) so that if estimates of production by both methods given above were available, we used the higher value.

These methods led to P/B values between 0.097 and 2.3 y^{-1}, with a median value of 0.49 y^{-1}. Smaller fish had higher P/B values than larger fish as expected. Using snapper as an example, this method gives P/B=0.45 y^{-1}. The production rate for medium sized fish (median weights of 0.49 kgWW) was P/B=0.53 y^{-1}. These values are similar to but slightly higher than production values estimated for fish in Sub-Antarctic waters of New Zealand (e.g., P/B=0.3 y^{-1}: Bradford-Grieve et al. 2003). Juvenile fishes were estimated to have a mean weight of 2.3 gWW and P/B=1.9 y^{-1}. For comparison, in the trophic model of a New Zealand rocky reef ecosystem off east coast North Island, (Te Tapuwae o Rongokako), small reef fish were estimated to have

P/B=2.4 y^{-1} while larger demersal and pelagic fishes had P/B between 0.4–0.5 y^{-1} (Pinkerton et al. 2008; Lundquist & Pinkerton 2008).

7.4 Consumption

A number of allometric relationships with which to estimate fish consumption are given by Palomares & Pauly (1989, 1998) based on the fish asymptotic weight (W_{inf}), water temperature, diet type (carnivore, herbivore, omnivore), and aspect ratio of the caudal fin (= h^2/s where h is height of tail and s is surface area of tail): equations 12 of Palomares & Pauly (1989), and equations 12 and 13 of Palomares & Pauly (1998). In all three relationships, smaller fishes have higher weight-specific consumption rates (Q/B) than larger fishes. Equation 13 of Palomares & Pauly (1998) also takes into account the degree of fishing mortality relative to natural mortality because this can change the age-frequency in the population. In our study, aspect ratios of caudal fins were calculated from photographs in FishBase (Froese & Pauly 2009), Francis (2001) or Paul (1986), or taken to be similar to a species with a known caudal fin aspect ratio. Bottom water temperatures in the study area are likely to be between 13°C and 16°C (Zeldis et al. 2004), and we use a mean bottom temperature of 14.5°C.

We used the average of the consumption rate estimated from equations 12 and 13 of Palomares & Pauly (1998) as our best estimate of Q/B for each species or species-group, because this supersedes Palomares & Pauly (1989). Across all the species of fish in this study, differences between all three methods of estimating Q/B were relatively small (average difference of 15%, standard deviation 12%).

Values of Q/B estimated here for fishes in the study area were between 2.0 and 13 y^{-1}, with a median value of 5.3 y^{-1}. Snapper had a Q/B of 5.3 y^{-1} and juvenile fishes had a Q/B of 12 y^{-1}. For comparison, Bradford-Grieve et al. (2003) estimated that adult fishes of the Sub-Antarctic New Zealand (in colder water) had a Q/B of 2.6 y^{-1}. In the trophic model of a New Zealand rocky reef ecosystem off east coast North Island, small reef fish were estimated to have Q/B=16 y^{-1} while larger demersal and pelagic fishes had Q/B between 3.6–9.5 y^{-1} (Pinkerton et al. 2008; Lundquist & Pinkerton 2008), so these are similar.

7.5 Growth efficiency

Growth efficiency, P/Q is defined as the proportion of consumption that is available within the ecosystem. For the fish species considered here, P/Q values are between 3.1% and 17%, with smaller values for larger fishes. Snapper have P/Q=8.5% of and juvenile fish have P/Q=17%. The median value is 10%. Low growth efficiencies are associated with herbivorous fish (butterfish P/Q=3.9%, marblefish P/Q=3.1%, silver drummer P/Q=3.2%), and high values with small fishes (P/Q=16% twister, urchin clingfish). For comparison, in the trophic model of a New Zealand rocky reef ecosystem off east coast North Island, small reef fish were estimated to have P/Q=15% while larger demersal and pelagic fishes had P/Q between 4.2 and 12% (Pinkerton et al. 2008; Lundquist & Pinkerton 2008), so the growth efficiencies estimated here are similar.

7.6 Transfers between groups

Two types of non-trophic transfer are relevant to the fish components of the model: (1) spawning transfers, i.e. transfer of material from adult fish to zooplankton group(s) due to spawning; (2) growth transfers as fish change from eggs to larvae, to juvenile fish and thence to adults. For fish in the model that lay eggs in the midwater, we assume that eggs are likely to be in the mesozooplankton group (0.2–2 mm). For fish in the model that lay eggs on or in the seabed sediment, eggs are assumed to be in the macrobenthos group. Fish larvae are likely to span the mesozooplankton and macrozooplankton groups (2–20 mm). Apart from large reef fish, juveniles are included in the small pelagic fish group. Juveniles of large reef fish are assumed to be in the small reef fish group.

7.6.1 Spawning transfers between groups

Oviparous species (fish which lay eggs which hatch away from the mother): Spawning transfer from adult oviparous fish is to zooplankton groups and due to output of sperm and eggs during spawning. Loss of gonadal material from spawning fish can be up to 20% of adult body weight (Lagler et al. 1977). This is consistent with data for hoki from the New Zealand region. We use hoki only because aspects of its spawning are relatively well known. Hoki weight specific fecundity is estimated at 2.94E+05 eggs per kg of spawning adult fish per year (Schofield & Livingston, 1998), similar to that estimated for snapper of 9.66E+05 eggs kg^{-1} y^{-1} (Crossland 1977). Hoki eggs are approximately spherical, have a typical diameter of 1.07 mm and a density close to 1 g cm^{-3} (Schofield & Livingston, 1998). These values lead to an estimate of spawning output per female fish of 19% y^{-1}. Assuming that spawning occurs every year, that a middle value of the proportion of an adult stock spawning per year is approximately 70% (Vignaux et al. 1995; Livingston et al. 1997), and that male spawning output is much less than the female (Gould 1985), say 25%, we estimate a transfer to planktonic model groups from adult fish due to spawning of 6.6% by weight per year. This is converted to spawning output per unit of production using the P/B ratio.

Ovoviviparous species (eggs which hatch inside the mother and then they give birth to live young, including most sharks, scorpion fishes and clinid weedfishes). We assume that the transfer due to spawning of small ovoviviparous species is from adult fish to macrozooplankton (which includes small ichthyoplankton of size 2–20 mm) and to small pelagic fishes (large ovoviviparous species) of the order of 5% by weight of adult per year. This is converted to spawning output per unit of production using the P/B ratio.

Viviparous species (give birth to baby fish, with a placental link to the mother). As for ovoviviparous species, we assume that the transfer due to spawning of viviparous species is from adult fish to macrozooplankton and of the order of 5% by weight of adult per year. This is converted to spawning output per unit of production using the P/B ratio.

7.6.2 Growth transfers between groups

(1) Growth transfer – eggs (mesozooplankton) to larvae (meso- and/or macro-zooplankton): Transfers within a trophic group due to ontogenetic changes (i.e. hatching of larvae from fish eggs) do not involve a transfer between groups and so are not relevant here. It is likely that ichthyoplankton are a very small component of the meso- and macrozooplankton groups *in toto* in the study area, so here we assume that the transfer of material from the meso- to the macrozooplankton group is a negligible proportion of the annual production of the mesozooplankton group.

(2) Growth transfer – larvae (macrozooplankton) to juvenile fish: It is likely that ichthyoplankton are a very small component of the macrozooplankton group in the study area, so the export of material from the macrozooplantkon group to the juvenile fish group will be a negligible proportion of the annual production of the mesozooplankton group. Also, although there is no information on this in the study area, we assume that the intrinsic annual production of the juvenile fish group is likely to be much larger than the annual biomass of larval fish becoming juvenile fish. Hence, growth transfers into the juvenile fish group from the macrozooplankton group can be neglected.

(3) Growth transfer – juvenile to adult fish stocks: This may not be negligible and so it is necessary to estimate the transfer from juvenile to adult fish due to juveniles recruiting into the adult populations. We estimate this on a species-by-species basis. The number of fish transferring from the juvenile fish group to adult fish per species (or species-group) per year is

estimated from adult fish biomass, adult fish mean weight and adult fish annual total mortality (natural plus fishing) as described in the Juvenile Fish section. The nominal size of a recruit transferring from the juvenile to adult fish group is 10 cm and weight of 23 gWW. Hence, we estimate the transfer as a fraction of annual adult fish production to have a mean value for all fish of about 5%, but to vary widely from less than 1% (large fish) to more than 30% (small fish). Considered in terms of the export of material from the juvenile fish group, the transfer is equivalent to 35% of the annual production of juvenile fish. For comparison, this parameter was estimated using simple age and size structured population models by Pinkerton et al. (2010) to be approximately 50% which is similar.

7.7 Ecotrophic efficiency

Ecotrophic efficiencies (*EE*) are not known for fishes in the Hauraki Gulf. Ecotrophic efficiency measures the proportion of the annual production that is available for predation ("passed up the food chain") as well as exported (including as fish landings, migration, spawning output, growth transfer to another trophic group) or accumulated. The remainder of the production (a fraction of 1-EE) is transferred to a detrital group. In the case of fish, dead fish or parts of fish are likely to be scavenged rather than decomposed by bacterial action and so will be passed in the model to the carcass group. This material is from two sources: (1) fish that die from causes other than direct predation, including starvation, disease, excessive parasite loading, etc.; (2) fishery catch that is discarded at sea either as whole fish (assumed dead) or as parts of fish due to processing at sea (e.g. heads, offal). It is likely that the vast majority of fish natural mortality is likely to be due to direct predation rather than other causes (such as epizootics). The proportion of annual production leading to dead fish due to causes other than direct predation and fishing is not known but is assumed to be 1%. The amount of biomass discarded was estimated as described earlier (Table 58). This leads to estimates of ecotrophic efficiency between 0.81 and 0.99.

7.8 Unassimilated consumption

Unassimilated consumption factors are not known for fishes in the study region and were assumed to be U=0.27 for all fish groups in the model as for carnivorous fish (Brett & Groves 1979).

7.9 Export, import

There can be a net export or net import of fish biomass from the study area due to active migration and/or passive advection. The net import-export (as a proportion of annual production) of fish species in the study area is not known. For now, we assume that net export of material from the study area over the course of a year is small enough to be neglected and thus the net import/export was set to zero.

8 Summary of parameters

Parameters for fish and fish parasites in the Hauraki Gulf trophic model representing the present day are given below in Table 67,**Table 68** and **Table 69**. Data for individual species were combined using a weighted average of parameters in proportions according to biomass or the appropriate trophic flow.

Table 67: Key parameters for 114 species or species-groups used in the model.

Common name	Species	Code	Model group	W_{inf}	B	B method	P/B	Q/B	Removal	Discard/ catch	Diet
				kg	tWW		y^{-1}	y^{-1}	tWW y^{-1}		
Ahuru	*Auchenoceros punctatus*	PCO	Pelagic_fish_small	0.046	165	Spatial density	1.2	8.0	0		Planktivore
Anchovy	*Engraulis australis*	ANC	Pelagic_fish_small	0.022	91	Catch based	1.4	11.2	3.0	0	Planktivore
Banded triplefin	*Forsterygion malcolmi*	FOR_MAL	Reef_fish_small	0.055	59	Reef habitat model	1.1	7.7	0		Invert feeder
Banded wrasse	*Notolabrus fucicola*	BPF	Reef_fish_large	3.3	1 359	Reef habitat model	0.39	4.0	0		Invert feeder
Barracouta	*Thyrsites atun*	BAR	Barracouta	3.9	2 266	Tier Two	0.36	3.8	84	0.10	Planktivore
Bigeye	*Pempheris adspersa*	PEM_S	Reef_fish_small	0.11	250	Reef habitat model	0.95	8.9	0		Planktivore
Black angelfish	*Parma alboscapularis*	BKA	Reef_fish_small	0.43	19	Reef habitat model	0.66	10.1	0		Planktivore
Blue cod	*Parapercis colias*	BCO	Reef_fish_large	2.6	69	Catch based	0.44	3.8	9.6	0.25	Invert feeder
Blue (English) mackerel	*Scomber australasicus*	EMA	Blue (English) mackerel	2.5	26 538	Tier Two	0.45	4.6	2022	0	Planktivore
Blue maomao	*Scorpis violaceus*	BMA	Pelagic_fish_large	0.84	342	Reef habitat model	0.52	6.9	1.6	0.25	Planktivore
Blue moki	*Latridopsis ciliaris*	MOK	Demersal_fish	7.6	18	Catch based	0.30	4.1	2.1	0.25	Invert feeder
Blue-dot triplefin	*Notoclinops caerulepunctus*	NOT_CAE	Reef_fish_small	0.004	0.4	Reef habitat model	2.3	13.5	0		Invert feeder
Blue-eyed triplefin	*Notoclinops segmentatus*	NOT_SEG	Reef_fish_small	0.006	5.8	Reef habitat model	2.0	12.2	0		Invert feeder
Bluefish	*Girella cyanea*	BLU	Reef_fish_large	3.4	4.4	Reef median	0.39	5.8	0		Invert feeder
Bronze whaler	*Carcharhinus brachyurus*	BWH	Sharks	179	418	Catch based	0.11	2.0	7.5	0.25	Piscivore
Butterfish	*Odax pullus*	BUT	Reef_fish_large	2.1	58	Reef habitat model	0.44	11.1	1.1	0.25	Herbivore/detrivore
Butterfly perch	*Caesioperca lepidoptera*	CAE_LEP	Reef_fish_large	1.0	5 074	Reef habitat model	0.49	5.3	0		Planktivore
Carpet shark	*Cephaloscyllium isabellum*	CAR	Sharks	10.7	25	Number based	0.23	3.5	0		Invert feeder
Clown toado	*Canthigaster callisterna*	CTO	Reef_fish_small	0.14	0.01	Reef habitat model	0.88	6.6	0		Invert feeder
Common roughy	*Paratrachichthys trailli*	RHY	Reef_fish_small	0.43	1.6	Reef habitat model	0.66	5.1	0		Planktivore
Common triplefin	*Forsterygion lapillum*	FOL	Reef_fish_small	0.012	5.6	Reef habitat model	1.7	10.4	0		Invert feeder
Common (blue) warehou	*Seriolella brama*	WAR	Pelagic_fish_large	7.4	9.4	Catch based	0.32	4.4	1.9	0.25	Invert feeder
Conger eel	*Conger spp*	CON	Reef_fish_large	5	12.1	Reef habitat model	0.35	4.2	5.3	0.25	Piscivore
Crested blenny	*Parablennius laticlavius*	CBL	Reef_fish_small	0.008	1.8	Reef habitat model	1.9	11.3	0		Invert feeder
Demoiselle	*Chromis dispilus*	DEM	Pelagic_fish_small	0.15	793	Reef habitat model	0.83	7.2	0		Planktivore
Dory (other)	*Zenopsis nebulosus*	MDO	Reef_fish_large	0.97	78	Catch based	0.52	4.6	24	0.25	Invert feeder

Common name	Species	Code	Model group	W_{inf}	B	B method	P/B	Q/B	Removal	Discard/ catch	Diet
Dwarf scorpionfish	*Scorpaena papillosus*	RSC	Reef_fish_small	0.26	114	Reef habitat model	0.75	5.9	2.1	0.25	Invert feeder
Eagle ray	*Myliobatis tenuicaudatus*	EGR	Demersal_fish	23.8	802	Trawl survey	0.19	2.3	22	0.25	Invert feeder
Elephant fish	*Callorhinchus milii*	ELE	Sharks	15.4	12	Catch based	0.26	3.5	2.1	0.25	Invert feeder
Estuarine triplefin	*Grahamina nigripenne*	GNI	Reef_fish_small	0.023	5.6	Triplefin median	1.4	9.2	0		Invert feeder
Flatfish	Pleuronectidae	FLA	Flatfish	1.6	3 518	Tier Three-A	0.48	4.2	394	0.05	Invert feeder
Frostfish	*Lepidopus caudatus*	FRO	Demersal_fish	4.6	330	Tier Three-B	0.63	6.3	53	0.25	Invert feeder
Gemfish	*Rexea solandri*	SKI	Demersal_fish	11.4	646	Tier One	0.26	3.3	71	0.05	Piscivore
Giant boarfish	*Paristiopterus labiosus*	BOA	Demersal_fish	6.9	4.4	Reef median	0.32	3.7	1.3	0.25	Invert feeder
Giant stargazer	*Kathetostoma giganteum*	STA	Demersal_fish	4.6	160	Tier Three-A	0.40	3.5	9.6	0.25	Invert feeder
Goatfish	*Upeneichthys lineatus*	RMU	Demersal_fish	1.4	1 863	Reef habitat model	0.47	5.0	0		Invert feeder
Gobies	Gobiidae	GBI	Reef_fish_small	0.017	4.4	Reef median	1.5	11.8	0		Invert feeder
Golden snapper	*Centroberyx affinis*	RSN	Reef_fish_large	2.2	42	Reef habitat model	0.44	6.1	14	0.25	Piscivore
Grey mullet	*Mugil cephalus*	GMU	Demersal_fish	1.1	176	Catch based	0.50	9.7	42	0.05	Herbivore/detrivore
Hagfish	*Eptatretus cirrhatus*	HAG	Reef_fish_large	2.3	141	Catch based	0.43	3.7	8.0	0.25	Piscivore
Half-banded perch	*Hypoplectrodes sp.B*	HYP_SPB	Reef_fish_small	0.067	2.5	Reef habitat model	1.1	7.7	0		Invert feeder
Hammerhead shark	*Sphyrna zygaena*	HHS	Sharks	160	419	Catch based	0.11	2.1	6.1	0.25	Piscivore
Hapuku & bass	*Polyprion oxygeneios*	HPB	Reef_fish_large	27.5	520	Tier Three-B	0.40	4.0	101	0.50	Invert feeder
Hiwihiwi	*Chironemus marmoratus*	KEL	Reef_fish_large	0.92	413	Reef habitat model	0.52	5.4	0		Invert feeder
Jack mackerels	*Trachurus spp.*	JMA	Jack mackerels	1.3	31 390	Tier 1.5	0.54	5.3	3135	0.10	Planktivore
Japanese gurnard	*Pterygotrigla picta*	JGU	Demersal_fish	0.73	422	Catch based	0.53	4.7	12	0.25	Invert feeder
John dory	*Zeus faber*	JDO	Reef_fish_large	1.3	1 134	Tier Two	0.63	6.3	276	0.05	Piscivore
Kahawai	*Arripis trutta*	KAH	Kahawai	2.9	5 672	Tier One	0.40	5.1	707	0.16	Planktivore
Kingfish	*Seriola lalandi*	KIN	Pelagic_fish_large	31.5	1 180	Tier Three-A	0.26	4.3	18	0.05	Piscivore
Koheru	*Decapterus koheru*	KOH	Pelagic_fish_large	1.7	282	Reef habitat model	0.46	5.5	42	0.25	Planktivore
Leatherjacket	*Parika scaber*	LEA	Leatherjacket	1.3	3 232	Reef habitat model	0.44	4.4	157	0.25	Invert feeder
Long-finned boarfish	*Zanclistius elevatus*	LFB	Reef_fish_large	0.64	0.6	Reef habitat model	0.60	5.9	0		Invert feeder
Mado	*Atypichthys latus*	ATY_LAT	Reef_fish_small	0.43	0.3	Reef habitat model	0.66	6.2	0		Invert feeder
Marblefish	*Aplodactylus arctidens*	GTR	Reef_fish_large	4.2	409	Reef habitat model	0.37	11.9	0		Herbivore/detrivore
Moonfish	*Lampris guttatus*	MOO	Pelagic_fish_large	94.8	74	Catch based	0.16	2.1	1.6	0.25	Invert feeder
Moray eels (other)	*Gymnothorax sp.*	GYM_SPP	Reef_fish_large	6.1	121	Half yellow moray	0.33	3.6	0		Invert feeder
Mottled triplefin	*Grahamina capito*	GCA	Reef_fish_small	0.017	5.6	Triplefin median	1.5	9.8	0		Invert feeder

Common name	Species	Code	Model group	W_{inf}	B	B method	P/B	Q/B	Removal	Discard/ catch	Diet
Northern bastard cod	*Pseudophycis breviuscula*	BRC	Demersal_fish	0.067	51	Catch based	1.1	7.8	5.1	0.25	Invert feeder
Northern scorpionfish	*Scorpaena cardinalis*	SDL	Reef_fish_large	2.7	21	Reef habitat model	0.41	3.6	0		Piscivore
Oblique-swimming triplefin	*Obliquichthys maryannae*	OBL_MAR	Reef_fish_small	0.012	4.4	Reef habitat model	1.7	10.4	0		Invert feeder
Opalfish	*Hemerocoetes monopterygius*	OPA	Demersal_fish	0.29	24	Trawl survey	0.73	5.6	0		Invert feeder
Orange clingfish	*Diplocrepis puniceus*	DIP_PUN	Reef_fish_small	0.037	4.4	Reef median	1.3	8.4	0		Invert feeder
Orange wrasse	*Pseudolabrus luculentus*	OWR	Reef_fish_small	0.26	4.1	Reef habitat model	0.75	5.6	0		Invert feeder
Parore	*Girella tricuspidata*	PAR	Reef_fish_large	1.7	360	Reef habitat model	0.47	7.7	26	0.25	Herbivore/detrivore
Pilchard	*Sardinops neopilchardus*	PIL	Pelagic_fish_small	0.097	1 314	Catch based	0.97	7.5	503	0	Planktivore
Pink maomao	*Caprodon longimanus*	PMA	Pelagic_fish_large	2.2	178	Reef habitat model	0.44	4.6	2.9	0.25	Planktivore
Piper, garfish	*Hyporhamphus ihi*	GAR	Pelagic_fish_large	0.74	19	Catch based	0.58	9.2	6.1	0.25	Planktivore
Porae	*Nemadactylus douglasii*	POR	Demersal_fish	4.0	224	Reef habitat model	0.40	4.6	23	0.25	Invert feeder
Porcupinefish	*Allomycterus jaculiferus*	POP	Pelagic_fish_large	2.7	386	Catch based	0.41	3.7	21	0.25	Invert feeder
Ray's bream	*Brama brama*	RBM	Demersal_fish	2.7	25	Catch based	0.40	4.4	3.7	0.25	Invert feeder
Red cod	*Pseudophycis bachus*	RCO	Demersal_fish	4.2	164	Tier Three-B	0.82	8.2	9.9	0.25	Invert feeder
Red gurnard	*Chelidonichthys kumu*	GUR	Red gurnard	0.72	14 304	Tier One	0.56	5.0	384	0.19	Invert feeder
Red moki	*Cheilodactylus spectabilis*	RMO	Reef_fish_large	5.2	3 973	Reef habitat model	0.35	4.1	0		Invert feeder
Red pigfish	*Bodianus unimaculatus*	RPI	Reef_fish_large	1.7	212	Reef habitat model	0.46	4.0	0		Invert feeder
Redbait	*Emmelichthys nitidus*	RBT	Pelagic_fish_large	1.7	10	Nominal	0.46	4.7	0		Planktivore
Red-banded perch	*Hypoplectrodes huntii*	RBP	Reef_fish_small	0.12	38	Reef habitat model	0.84	7.6	2.4	0.25	Invert feeder
Rig	*Mustelus lenticulatus*	SPO	Rig	6.2	3 600	Tier Two	0.32	3.1	129	0.53	Invert feeder
Robust triplefin	*Grahamina gymnota*	GRA_GYM	Reef_fish_small	0.017	0.1	Reef habitat model	1.5	9.8	0		Invert feeder
Rock cod	*Lotella rhacinus*	ROC	Reef_fish_large	0.92	205	Reef habitat model	0.54	4.5	0		Invert feeder
Rough & smooth skate	*Raja nasuta, R. innominata*	SKA	Demersal_fish	28.6	180	Tier Three-B	0.29	2.3	33	0.25	Invert feeder
Sandager's wrasse	*Coris sandageri*	SWR	Reef_fish_large	1.7	86	Reef habitat model	0.46	3.9	0		Invert feeder
Scaly-headed triplefin	*Karalepis stewarti*	KAR_STE	Reef_fish_small	0.14	2.7	Reef habitat model	0.88	6.4	0		Invert feeder
Scarlet wrasse	*Pseudolabrus miles*	SPF	Reef_fish_large	1.06	423	Reef habitat model	0.54	5.1	0		Invert feeder
School shark	*Galeorhinus galeus*	SCH	Sharks	30.2	528	Tier Three-B	0.26	2.6	119	0.55	Invert feeder
Sea perch	*Helicolenus percoides*	SPE	Reef_fish_large	1.3	42	Tier Three-A	0.58	4.5	8	0.25	Invert feeder
Sevengill shark	*Notorynchus cepedianus*	SEV	Sharks	107	110	Number based	0.16	2.2	0		Piscivore
Sharks (other)	*Hydrolagus novaezelandiae*	GSH	Sharks	7.9	221	Catch based	0.32	3.9	28	0.25	Piscivore
Silver drummer	*Kyphosus sydneyanus*	DRU	Reef_fish_large	4.1	519	Reef habitat model	0.37	11.7	0		Herbivore/detrivore

Common name	Species	Code	Model group	W_{inf}	B	B method	P/B	Q/B	Removal	Discard/ catch	Diet
Silver warehou	*Seriolella punctata*	SWA	Demersal_fish	5.4	90	Catch based	0.34	4.7	18	0.25	Invert feeder
Skipjack tuna	*Katsuwonus pelamis*	SKJ	Skipjack	12	1 969	Catch based	0.21	6.7	193	0	Invert feeder
Slender roughy	*Optivus elongatus*	SLR	Reef_fish_small	0.030	41	Reef habitat model	1.3	11.1	0		Planktivore
Snapper	*Pagrus auratus*	SNA	Snapper	3.9	38 940	Tier One	0.45	5.3	4408	0.03	Invert feeder
Southern bastard cod	*Pseudophycis barbata*	SBR	Reef_fish_large	3.4	15	Reef habitat model	0.39	3.5	0		Invert feeder
Spectacled triplefin	*Ruanoho whero*	RUA_WHE	Reef_fish_small	0.017	22	Reef habitat model	1.5	9.8	0		Invert feeder
Spiny dogfish	*Squalus acanthias*	SPD	Sharks	7.8	124	Catch based	0.27	3.9	16	0.25	Invert feeder
Spotted black grouper	*Epinephelus daemelii*	SBG	Reef_fish_large	10.7	3.9	Reef habitat model	0.29	2.8	0		Invert feeder
Spotty	*Notolabrus celidotus*	STY	Reef_fish_small	0.43	349	Reef habitat model	0.67	5.8	0		Invert feeder
Stargazer (other)	*Genyagnus monopterygius*	SPZ	Demersal_fish	1.6	169	Catch based	0.43	5.0	10	0.25	Invert feeder
Stingray	*Dasyatis spp*	STR	Demersal_fish	13.6	841	Trawl survey	0.22	2.6	30	0.25	Invert feeder
Sweep	*Scorpis lineolatus*	SWE	Pelagic_fish_large	0.67	1 321	Reef habitat model	0.57	7.7	0		Planktivore
Swordfish	*Xiphias gladius*	SWO	Pelagic_fish_large	173	145	Number based	0.15	2.1	4.5	0.25	Invert feeder
Tarakihi	*Nemadactylus macropterus*	TAR	Tarakihi	2.2	7 960	Tier Three-A	0.43	5.3	277	0	Invert feeder
Trevally	*Pseudocaranx georgianus*	TRE	Trevally	2.2	2 734	Tier One	0.41	5.0	354	0.04	Invert feeder
Trumpeter	*Latris lineata*	TRU	Reef_fish_large	11.0	4.4	Reef median	0.28	3.8	0.53	0.25	Invert feeder
Tuna (other)	*Thunnus alalunga*	TUNA	Pelagic_fish_large	20.2	139	Catch based	0.24	6.0	18	0.25	Piscivore
Twister	*Bellapiscis lesleyae, B. medius*	BEL_LES	Reef_fish_small	0.009	5.6	Triplefin median	1.8	11.2	0		Invert feeder
Urchin clingfish	*Dellichthys morelandi*	DEL_MOR	Reef_fish_small	0.009	4.4	Reef median	1.8	11.2	0		Invert feeder
Variable triplefin	*Forsterygion varium*	FOR_VAR	Reef_fish_small	0.14	68	Reef habitat model	0.88	6.4	0		Invert feeder
Worm eel	*Scolecenchelys spp.*	SCO_SPP	Demersal_fish	0.24	33	Spatial density	0.77	5.8	0		Invert feeder
Wrasse (other)	*Notolabrus inscriptus*	WSE	Reef_fish_large	1.3	4.8	Reef habitat model	0.50	4.1	0		Invert feeder
Yaldwyn's triplefin	*Notoclinops yaldwyni*	NOT_YAL	Reef_fish_small	0.009	0.3	Reef habitat model	1.8	11.2	0		Invert feeder
Yellow moray	*Gymnothorax prasinus*	MOY	Reef_fish_large	6.1	242	Reef habitat model	0.33	4.1	0		Invert feeder
Yellow-black triplefin	*Forsterygion flavonigrum*	YBT	Reef_fish_small	0.009	15	Reef habitat model	1.8	11.2	0		Invert feeder
Yellow-eyed mullet	*Aldrichetta forsteri*	YEM	Demersal_fish	0.95	96	Catch based	0.54	8.5	2.4	0.25	Invert feeder

Table 68: Summary of parameters in the trophic model for the present day. EE=Ecotrophic efficiency; B=Biomass; P/B=annual production to biomass ratio; Q/B=annual consumption to biomass ratio; P/Q=gross growth efficiency, i.e. annual production divided by annual consumption; T/P=annual transfer as a proportion of annual production.

Group	EE	B	P/B	Q/B	P/Q	Export	Removals	Discards	Unassimilated	Spawn transfer	Growth transfer	Spawn to	Growth from
		tWW	y-1	y-1		X/P	tWW y^{-1}	tWW y^{-1}		T/P	T/P		
Snapper	0.94	38 940	0.45	5.3	0.09	0	4269	139	0.27	0.15	-0.014	Mesozoo	Pelagic_fish_small
Jack mackerels	0.93	31 390	0.54	5.3	0.10	0	2821	313	0.27	0.12	-0.038	Mesozoo	Pelagic_fish_small
Blue mackerel	0.95	26 538	0.45	4.6	0.10	0	2022	0	0.27	0.15	-0.023	Mesozoo	Pelagic_fish_small
Red gurnard	0.94	14 304	0.56	5.0	0.11	0	312	72	0.27	0.12	-0.090	Mesozoo	Pelagic_fish_small
Leatherjacket	0.92	3 232	0.44	4.4	0.10	0	118	39	0.27	0.15	-0.026	Mesozoo	Pelagic_fish_small
Tarakihi	0.95	7 960	0.43	5.3	0.08	0	277	0	0.27	0.15	-0.009	Mesozoo	Pelagic_fish_small
Kahawai	0.90	5 672	0.40	5.1	0.08	0	594	113	0.27	0.16	-0.018	Mesozoo	Pelagic_fish_small
Rig	0.89	3 600	0.32	3.1	0.10	0	61	68	0.27	0.21	-0.009	Mesozoo	Pelagic_fish_small
Flatfish	0.94	3 518	0.48	4.2	0.11	0	374	20	0.27	0.14	-0.106	Mesozoo	Pelagic_fish_small
Trevally	0.94	2 734	0.41	5.0	0.08	0	338	15	0.27	0.16	-0.014	Mesozoo	Pelagic_fish_small
Barracouta	0.94	2 266	0.36	3.8	0.10	0	76	8	0.27	0.18	-0.014	Mesozoo	Pelagic_fish_small
Skipjack	0.95	1 969	0.25	3.8	0.07	0	193	0	0.27	0.26	-0.007	Mesozoo	Pelagic_fish_small
Reef_fish_large	0.94	15 547	0.44	5.3	0.08	0	386	89	0.27	0.15	-0.050	Mesozoo	Pelagic_fish_small
Reef_fish_small	0.95	1 034	0.90	7.4	0.12	0	3	1	0.27	0.07	-0.291	Mesozoo	Pelagic_fish_small
Demersal_fish	0.93	6 318	0.40	4.4	0.09	0	284	63	0.27	0.16	-0.042	Mesozoo	Pelagic_fish_small
Sharks	0.73	1 856	0.19	2.6	0.08	0	98	80	0.27	0.26	-0.005	Macrozoo	Pelagic_fish_small
Pelagic_fish_large	0.93	4 086	0.41	5.6	0.07	0	92	26	0.27	0.16	-0.060	Mesozoo	Pelagic_fish_small
Pelagic_fish_small	0.95	11 938	1.75	10.8	0.16	0	506	0	0.27	0.01	0.000	None	None

Table 69: Summary of diets for fish groups in the trophic model: long-term average proportions of prey items by weight (in terms of organic carbon). Prey items are shown in rows with predators in columns. Columns sum to 1.

																	Predators
Prey	Snapper	Jack mackerels	Blue mackerel	Red gurnard	Leatherjacket	Tarakihi	Kahawai	Rig	Flatfish	Trevally	Barracouta	Reef_fish_large	Reef_fish_small	Demersal_fish	Sharks	Pelagic_fish_large	Pelagic_fish_small	Reef_fish_large
Phytal inverts				0.10					0.10	0.30			0.09	0.10	0.11	0.02	0.02	0.03
Sponges					0.50													
Organic detritus															0.03			0.04
Seaweed													0.08	0.01	0.02		0.04	0.07
Zooplankton		0.32	1.00				0.41			0.30	0.67	0.33	0.29	0.41	0.13	0.06	0.41	0.83
Salps, jellyfish		0.32			0.14								0.06	0.01	0.03		0.09	
Encrusting					0.36								0.02					
Worms	0.03			0.07		0.25	0.07	0.33	0.20				0.04	0.06	0.06	0.02	0.03	0.03
Bivalves, gastropods	0.20					0.25	0.07		0.20	0.10			0.02	0.10	0.10	0.13	0.02	
Squid											0.11	0.33	0.01		0.10	0.03	0.09	
Octopus	0.03															0.02		
Crabs, hermit crabs	0.20			0.43		0.25	0.07	0.33	0.20	0.20			0.20	0.09	0.11	0.13	0.05	
Large shrimps, amphipods	0.03	0.05		0.33				0.33	0.10		0.11		0.11	0.07	0.05	0.14	0.04	
Seastars, brittlestars	0.03					0.25			0.20	0.05				0.05	0.02	0.03	0.03	
Kina	0.03												0.01		0.01	0.02	0.01	
Other urchins (not kina)										0.05						0.01		
Fish (reef)	0.20			0.07									0.03	0.06	0.06	0.06	0.01	
Fish (demersal)	0.20												0.03		0.06	0.20		
Fish (pelagic)	0.03	0.32					0.39				0.11	0.33		0.04	0.09	0.14	0.16	

9 Historical parameters

9.1 Models required

Three sets of parameters were adjusted to represent conditions in four historical periods: 1950, 1790, 1500, and 1000.

9.2 Historical catch

Catch and discards of 76 species of fish in every year from the present to 1931 were estimated by Francis & Paul (2008) as explained in Section 2. These catches include customary and recreational (non-commercial) catch. These catches were used to parameterise the historical model for the present day and 1950.

Smith (2011) estimated the magnitude of pre-European Māori marine harvest of fish, seabirds, invertebrates and mammals based on data preserved from middens, for years (actually, periods about nominal years) 1400, 1550 and 1750. Catch in 1500 was estimated by linear interpolation from that in 1400 and 1550.

The population of Europeans in New Zealand in late 1700s and early 1800s was very small, perhaps a few tens or hundreds of individuals. We estimate that in New Zealand in 1790, 588 Europeans were present, most in the far south; maybe 1.2 t snapper were landed in the study area, and no other species are likely to have been taken (Alison MacDiarmid, pers. comm.). We hence estimate a total fish catch in 1790 of 2585 tWW, of which 2584 t was caught by Māori. Other catches are estimated to be 13 871 t (present day, 2006), 8300 t (1950), 1595 t (1500), and zero (1000) based on Smith (2011).

9.3 Historical productivity

Proportions of fish at age were estimated by McKenzie & MacDiarmid (2011) for 20 key species in three periods: 2006, 1946 and 1930. These proportions at age were used to estimate P/B ratios for each species in each period. The estimated values of P/B(1946) to P/B(2006) for these species were 0.33–0.99, with a median value of 0.76. All ratios are lower than 1 indicating that weight-for-weight fish populations are estimated to be less productive historically than at present because larger fish were more abundant and these grow more slowly than small fish. Ratios lower than about 0.6 are considered dubious and are set to this nominal lower limit. The median value of 0.76 was used to scale P/B values for other fished species in the 1950 model. The P/B values of unfished species were not changed from the present day model.

The estimated values of P/B(1930):P/B(2006) for 20 key species based on proportions at age were 0.32–0.92 (median 0.73). For these 20 key species, the ratios were used to scale P/B values for the present day to the 1790, 1500 and 1000 models, again, with a lower limit of 0.6. The median value was used to scale P/B values for other fished species for these historical models. The P/B values of unfished species were not changed from the present day model.

9.4 Virgin biomass

For 20 species, historical biomass trajectories were determined by McKenzie & MacDiarmid (2011), which go as far back as 1850. Biomass in 1850 is assumed to be close to virgin biomass for these species. These species were snapper, jack mackerel, blue (English) mackerel, red gurnard, trevally, tarakihi, kahawai, rig, flatfish, barracouta, school shark, John dory, gemfish, hapuku and bass, kingfish, frostfish, rough and smooth skates, giant stargazer, red cod, and sea perch. For another 12 species, virgin biomass can be estimated based on parameters given in Section 5.1. These species were: anchovy, blue cod, blue moki, bronze whaler, common (blue) warehou, elephant fish, grey mullet, hammerhead shark, pilchard, piper/garfish, spiny dogfish, tuna (other), and yellow-eyed mullet. In order to estimate virgin biomass for other fished species in the model, we assume that there is an inverse relationship between biomass as a proportion of virgin biomass and catch as a proportion of annual productivity of the stock, i.e. if a higher proportion of the annual production of a stock is taken by a fishery, the stock will be lower. An exponential form was fitted to data for the 32 species where we had data (**Figure 30**). We used data on catch and biomass from two time periods (1930 and 2006) for the 20 species where McKenzie & MacDiarmid (2011) gives historical biomass trajectories to define this relationship. The results of applying this method to species where we have data are shown in **Figure 30**b. Although the relationship shown in **Figure 30**ais quite weak (R^2=52) the method is effective because variations in catch and biomass are large (more than three orders of magnitude) compared to uncertainties in this relationship. Unfished species are assumed to be at virgin biomass at the present day.

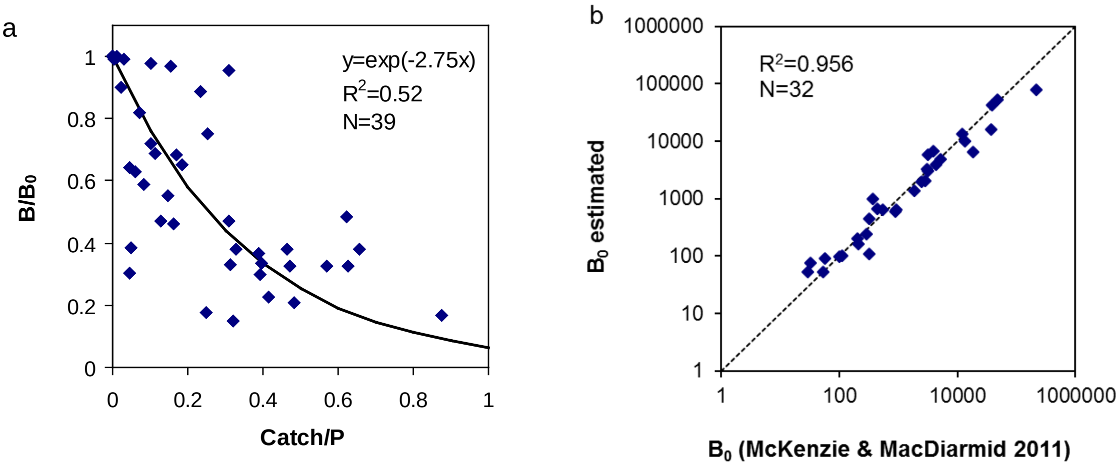

Figure 30 a: Relationship between catch as a proportion of annual productivity in the same year and biomass as a proportion of virgin biomass. b: Result of using the relationship derived from (a) to estimate virgin biomass. Virgin biomass from McKenzie & MacDiarmid (2011) is shown on the x-axis with the virgin biomass estimated here on the y-axis.

9.5 Historical biomass

A similar approach to that described above was used to estimate biomass at other historical periods when catch information had been estimated but no estimates of biomass were available (Figure 31). The difference here is that we used catch as a proportion of virgin productivity rather than as a proportion of productivity in the same year as the catch was taken. It is recognised that a variety of functional forms could be fitted to data in**Figure 31**a. However, the method used seems to work well despite the uncertainty in the relationship shown in Figure 31a because of the very high variation in the magnitudes of catches between species.

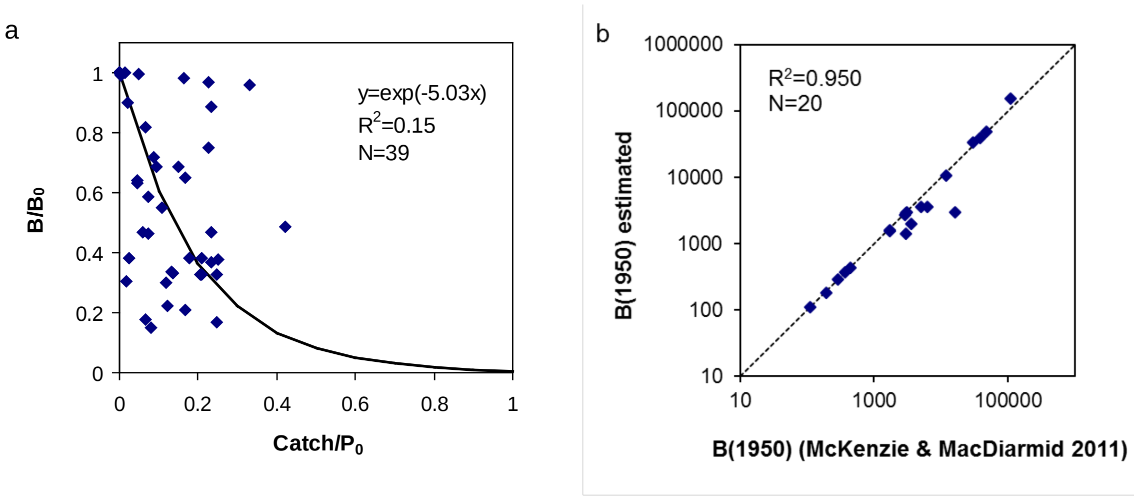

Figure 31 a: Relationship between catch as a proportion of virgin annual productivity (denoted as P_0) and biomass as a proportion of virgin biomass (B/B_0). b: Result of using the relationship derived from (a) to estimate biomass in 1950. Stock biomass in 1950 from McKenzie & MacDiarmid (2011) is shown on the x-axis with the 1950 biomass estimated using this method shown on the y-axis.

We recognise that biomasses of unfished and fished species may be different to our estimated historical values because of the effects on species of historical change in the environment and/or ecosystem. For example, more reef habitat, more food or less predation may be expected to lead to higher abundances. In this sense, the notion that a single, unvarying biomass of a fish stock existed before fishing (virgin biomass) is unlikely to be true. We have no information on how levels of recruitment of fish stocks in the Hauraki Gulf may have changed historically. Consequently, we use a starting assumption that recruitment of all fish have been largely constant since 1000, but let biomasses of fishes vary during balancing of the historical trophic models. This approach is consistent with single-species stock modelling used in fisheries assessment throughout the world where recruitment is assumed to be constant unless evidence exists to the contrary.

9.6 Diet

The diet composition for each of the fish groups in the historical models were estimated assuming that the present day diet of each species of fish was modified by changes the relative abundance of prey species. Note that the diets of all groups in the trophic model, including fishes, were also allowed to vary during model balancing to take into account changes in competition for prey between predators and changes in the biomass of prey items over time.

9.7 Other parameters

We elected to keep gross growth efficiency (P/Q) constant historically and adjusted Q/B in line with changes in P/B values. Variation in the balance between young and old fish in a population over time will change P/Q for the population as a whole but the changes are likely to be relatively small.

Unassimilated consumption for fish was not changed in the historical models.

Growth and spawning transfers will change as the balance of different fish species in the composite fish groups change, as the size of populations vary, and as productivity parameters alter. This was calculated in the same way for each historical model as in the present data model described earlier in this document.

Ecotrophic efficiency was calculated taking into account discarded fish and allowing for 1% of annual production being lost due to death of fish not associated with direct predation.

9.8 Summary parameters for historical models

Parameters for the fish groups for historical models are shown in **Table 70**(1950), **Table 71**(1790), **Table 72** (1500) and **Table 73**(1000).

Table 70: Estimates of fish parameters for the 1950 trophic model. EE=Ecotrophic efficiency; B=Biomass; P/B=annual production to biomass ratio; Q/B=annual consumption to biomass ratio; P/Q=gross growth efficiency, i.e. annual production divided by annual consumption; T/P=annual transfer as a proportion of annual production.

Group	EE	B	P/B	Q/B	P/Q	Export	Removals	Discards	Unassimilated	Spawn transfer	Growth transfer	Spawn to	Growth from
		tWW	y-1	y-1		X/P	tWW y^{-1}	tWW y^{-1}		T/P	T/P		
Snapper	0.94	108 800	0.30	3.5	0.09	0	4 312	372	0.27	0.00	-0.014	Mesozoo	Pelagic_fish_small
Jack mackerels	0.95	48 290	0.39	3.8	0.10	0	0	0	0.27	0.00	-0.035	Mesozoo	Pelagic_fish_small
Blue mackerel	0.95	38 720	0.35	3.6	0.10	0	0	0	0.27	0.00	-0.022	Mesozoo	Pelagic_fish_small
Red gurnard	0.95	30 640	0.44	3.9	0.11	0	262	62	0.27	0.00	-0.107	Mesozoo	Pelagic_fish_small
Leatherjacket	0.94	4 164	0.32	3.2	0.10	0	7	7	0.27	0.00	-0.030	Mesozoo	Pelagic_fish_small
Tarakihi	0.95	6 240	0.28	3.4	0.08	0	1 004	0	0.27	0.00	-0.020	Mesozoo	Pelagic_fish_small
Kahawai	0.95	12 100	0.25	3.2	0.08	0	73	11	0.27	0.00	-0.017	Mesozoo	Pelagic_fish_small
Rig	0.89	5 020	0.26	2.6	0.10	0	26	78	0.27	0.00	-0.010	Mesozoo	Pelagic_fish_small
Flatfish	0.94	3 570	0.42	3.7	0.11	0	218	11	0.27	0.00	-0.102	Mesozoo	Pelagic_fish_small
Trevally	0.61	16 530	0.24	3.0	0.08	0	238	1 351	0.27	0.00	-0.019	Mesozoo	Pelagic_fish_small
Barracouta	0.95	3 090	0.30	3.2	0.10	0	7	2	0.27	0.00	-0.015	Mesozoo	Pelagic_fish_small
Skipjack	0.95	5 780	0.19	2.9	0.07	0	0	0	0.27	0.00	-0.008	Mesozoo	Pelagic_fish_small
Reef_fish_large	0.94	19 978	0.39	4.6	0.09	0	57	50	0.27	0.17	-0.052	Mesozoo	Pelagic_fish_small
Reef_fish_small	0.95	1 051	0.90	7.4	0.12	0	0	0	0.27	0.07	-0.291	Mesozoo	Pelagic_fish_small
Demersal_fish	0.94	14 838	0.29	3.3	0.09	0	35	25	0.27	0.23	-0.027	Mesozoo	Pelagic_fish_small
Sharks	0.94	14 578	0.26	3.2	0.08	0	19	56	0.27	0.19	-0.005	Macrozoo	Pelagic_fish_small
Pelagic_fish_large	0.95	5 878	0.37	5.1	0.07	0	13	5	0.27	0.18	-0.051	Mesozoo	Pelagic_fish_small
Pelagic_fish_small	0.95	19 685	1.67	10.5	0.16	0	0	0	0.27	0.01	0.000	None	None

Table 71: Estimates of fish parameters for the 1790 trophic model. EE=Ecotrophic efficiency; B=Biomass; P/B=annual production to biomass ratio; Q/B=annual consumption to biomass ratio; P/Q=gross growth efficiency, i.e. annual production divided by annual consumption; T/P=annual transfer as a proportion of annual production.

Group	EE	B	P/B	Q/B	P/Q	Export	Removals	Discards	Unassimilated	Spawn transfer	Growth transfer	Spawn to	Growth from
		tWW	y-1	y-1		X/P	tWW y^{-1}	tWW y^{-1}		T/P	T/P		
Snapper	0.93	203 085	0.26	3.1	0.09	0	1	997	0.27	0.00	-0.008	Mesozoo	Pelagic_fish_small
Jack mackerels	0.95	47 805	0.37	3.6	0.10	0	0	38	0.27	0.00	-0.035	Mesozoo	Pelagic_fish_small
Blue mackerel	0.95	38 720	0.35	3.6	0.10	0	0	0	0.27	0.00	-0.022	Mesozoo	Pelagic_fish_small
Red gurnard	0.95	37 211	0.44	3.9	0.11	0	0	11	0.27	0.00	-0.111	Mesozoo	Pelagic_fish_small
Leatherjacket	0.94	4 181	0.32	3.2	0.10	0	0	13	0.27	0.00	-0.031	Mesozoo	Pelagic_fish_small
Tarakihi	0.95	13 570	0.39	4.8	0.08	0	0	0	0.27	0.00	-0.011	Mesozoo	Pelagic_fish_small
Kahawai	0.93	10 996	0.24	3.1	0.08	0	0	58	0.27	0.00	-0.017	Mesozoo	Pelagic_fish_small
Rig	0.95	5 240	0.27	2.6	0.10	0	0	0	0.27	0.00	-0.009	Mesozoo	Pelagic_fish_small
Flatfish	0.95	3 960	0.47	4.2	0.11	0	0	0	0.27	0.00	-0.107	Mesozoo	Pelagic_fish_small
Trevally	0.94	17 037	0.24	2.9	0.08	0	0	60	0.27	0.00	-0.010	Mesozoo	Pelagic_fish_small
Barracouta	0.90	2 596	0.29	3.1	0.10	0	0	37	0.27	0.00	-0.016	Mesozoo	Pelagic_fish_small
Skipjack	0.95	5 791	0.19	2.9	0.07	0	0	0	0.27	0.00	-0.008	Mesozoo	Pelagic_fish_small
Reef_fish_large	0.95	20 586	0.38	4.4	0.09	0	65	7	0.27	0.17	-0.052	Mesozoo	Pelagic_fish_small
Reef_fish_small	0.95	1 050	0.90	7.4	0.12	0	0	0	0.27	0.07	-0.291	Mesozoo	Pelagic_fish_small
Demersal_fish	0.94	10 998	0.33	3.8	0.09	0	290	32	0.27	0.20	-0.035	Mesozoo	Pelagic_fish_small
Sharks	0.87	7 056	0.19	2.3	0.08	0	899	100	0.27	0.27	-0.011	Macrozoo	Pelagic_fish_small
Pelagic_fish_large	0.95	6 050	0.36	5.0	0.07	0	0	0	0.27	0.18	-0.051	Mesozoo	Pelagic_fish_small
Pelagic_fish_small	0.95	20 435	1.68	10.5	0.16	0	0	0	0.27	0.04	0.000	None	None

Table 72: Estimates of fish parameters for the 1500 trophic model. EE=Ecotrophic efficiency; B=Biomass; P/B=annual production to biomass ratio; Q/B=annual consumption to biomass ratio; P/Q=gross growth efficiency, i.e. annual production divided by annual consumption; T/P=annual transfer as a proportion of annual production.

Group	EE	B	P/B	Q/B	P/Q	Export	Removals	Discards	Unassimilated	Spawn transfer	Growth transfer	Spawn to	Growth from
		tWW	y-1	y-1		X/P	tWW y^{-1}	tWW y^{-1}		T/P	T/P		
Snapper	0.95	208 637	0.26	3.1	0.09	0	585	65	0.27	0.00	-0.008	Mesozoo	Pelagic_fish_small
Jack mackerels	0.95	45 578	0.37	3.6	0.10	0	194	22	0.27	0.00	-0.036	Mesozoo	Pelagic_fish_small
Blue mackerel	0.95	38 428	0.34	3.5	0.10	0	18	2	0.27	0.00	-0.022	Mesozoo	Pelagic_fish_small
Red gurnard	0.95	37 319	0.44	3.9	0.11	0	2	0	0.27	0.00	-0.110	Mesozoo	Pelagic_fish_small
Leatherjacket	0.95	4 318	0.32	3.2	0.10	0	3	0	0.27	0.00	-0.031	Mesozoo	Pelagic_fish_small
Tarakihi	0.95	13 557	0.38	4.6	0.08	0	1	0	0.27	0.00	-0.011	Mesozoo	Pelagic_fish_small
Kahawai	0.94	9 303	0.24	3.1	0.08	0	142	16	0.27	0.00	-0.018	Mesozoo	Pelagic_fish_small
Rig	0.95	5 240	0.27	2.6	0.10	0	0	0	0.27	0.00	-0.009	Mesozoo	Pelagic_fish_small
Flatfish	0.95	3 864	0.46	4.0	0.11	0	7	1	0.27	0.00	-0.108	Mesozoo	Pelagic_fish_small
Trevally	0.95	17 502	0.24	2.9	0.08	0	32	4	0.27	0.00	-0.010	Mesozoo	Pelagic_fish_small
Barracouta	0.93	1 733	0.29	3.1	0.10	0	102	11	0.27	0.00	-0.019	Mesozoo	Pelagic_fish_small
Skipjack	0.95	5 791	0.19	2.9	0.07	0	0	0	0.27	0.00	-0.008	Mesozoo	Pelagic_fish_small
Reef_fish_large	0.95	20 865	0.38	4.4	0.09	0	26	3	0.27	0.17	-0.051	Mesozoo	Pelagic_fish_small
Reef_fish_small	0.95	1 050	0.90	7.4	0.12	0	0	0	0.27	0.07	-0.291	Mesozoo	Pelagic_fish_small
Demersal_fish	0.95	15 053	0.29	3.3	0.09	0	13	1	0.27	0.23	-0.029	Mesozoo	Pelagic_fish_small
Sharks	0.94	10 555	0.23	2.8	0.08	0	308	34	0.27	0.22	-0.006	Macrozoo	Pelagic_fish_small
Pelagic_fish_large	0.95	6 048	0.36	5.0	0.07	0	0	0	0.27	0.18	-0.051	Mesozoo	Pelagic_fish_small
Pelagic_fish_small	0.95	20 381	1.68	10.5	0.16	0	0	0	0.27	0.01	0.000	None	None

Table 73: Estimates of fish parameters for the 1000 trophic model. EE=Ecotrophic efficiency; B=Biomass; P/B=annual production to biomass ratio; Q/B=annual consumption to biomass ratio; P/Q=gross growth efficiency, i.e. annual production divided by annual consumption; T/P=annual transfer as a proportion of annual production.

Group	EE	B	P/B	Q/B	P/Q	Export	Removals	Discards	Unassimilated	Spawn transfer	Growth transfer	Spawn to	Growth from
		tWW	y-1	y-1		X/P	tWW y^{-1}	tWW y^{-1}		T/P	T/P		
Snapper	0.95	219 400	0.30	3.5	0.09	0	0	0	0.27	0.00	-0.008	Mesozoo	Pelagic_fish_small
Jack mackerels	0.95	48 300	0.39	3.8	0.10	0	0	0	0.27	0.00	-0.035	Mesozoo	Pelagic_fish_small
Blue mackerel	0.95	38 720	0.35	3.6	0.10	0	0	0	0.27	0.00	-0.022	Mesozoo	Pelagic_fish_small
Red gurnard	0.95	37 340	0.44	3.9	0.11	0	0	0	0.27	0.00	-0.110	Mesozoo	Pelagic_fish_small
Leatherjacket	0.95	4 376	0.32	3.2	0.10	0	0	0	0.27	0.00	-0.031	Mesozoo	Pelagic_fish_small
Tarakihi	0.95	13 570	0.28	3.4	0.08	0	0	0	0.27	0.00	-0.011	Mesozoo	Pelagic_fish_small
Kahawai	0.95	12 100	0.25	3.2	0.08	0	0	0	0.27	0.00	-0.017	Mesozoo	Pelagic_fish_small
Rig	0.95	5 240	0.26	2.6	0.10	0	0	0	0.27	0.00	-0.009	Mesozoo	Pelagic_fish_small
Flatfish	0.95	3 960	0.42	3.7	0.11	0	0	0	0.27	0.00	-0.107	Mesozoo	Pelagic_fish_small
Trevally	0.95	18 230	0.24	3.0	0.08	0	0	0	0.27	0.00	-0.010	Mesozoo	Pelagic_fish_small
Barracouta	0.95	3 150	0.30	3.2	0.10	0	0	0	0.27	0.00	-0.015	Mesozoo	Pelagic_fish_small
Skipjack	0.95	5 791	0.19	2.9	0.07	0	0	0	0.27	0.00	-0.008	Mesozoo	Pelagic_fish_small
Reef_fish_large	0.95	21 211	0.38	4.4	0.09	0	0	0	0.27	0.17	-0.051	Mesozoo	Pelagic_fish_small
Reef_fish_small	0.95	1 051	0.90	7.4	0.12	0	0	0	0.27	0.07	-0.291	Mesozoo	Pelagic_fish_small
Demersal_fish	0.95	15 229	0.29	3.4	0.09	0	0	0	0.27	0.23	-0.029	Mesozoo	Pelagic_fish_small
Sharks	0.95	14 728	0.25	3.1	0.08	0	0	0	0.27	0.20	-0.005	Macrozoo	Pelagic_fish_small
Pelagic_fish_large	0.95	6 050	0.36	5.0	0.07	0	0	0	0.27	0.18	-0.051	Mesozoo	Pelagic_fish_small
Pelagic_fish_small	0.95	20 504	1.68	10.5	0.16	0	0	0	0.27	0.01	0.000	None	None

10 Acknowledgements

This research was funded by Ministry for Primary Industries project ZBD200505 (“Long-term change in New Zealand coastal ecosystems”) and by the New Zealand Foundation for Research, Science and Technology project C01X0501 (Coasts & Oceans OBI). We acknowledge Dr Martin Cryer and Dr Mary Livingston (Ministry for Primary Industries) for project funding and stewardship. We are grateful to Adam Smith and Department of Conservation for the use of the abundance-habitat model results for reef fish (Project DOC08304). Alison MacDiarmid provided useful comments on this work.

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Appendix 6: Trophic modelling of Hauraki Gulf: Cephalopods

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1 Cephalopods

1.1 General information

Cephalopods are considered separately from fishes because they have very different energetic parameters (growth, consumption, production), and shorter lifespans. There are two cephalopod groups in the trophic model:

1. Squid. This group includes arrow squid (*Nototodarus sloani* and *N. gouldi*) broad squid (*Sepioteuthis australis*) and smaller pelagic squids. Juvenile squid are included in this group, whereas larval squid are included in the macrozooplankton group.
2. Octopus (*Octopus maorum*) and other cephalopods, including Ram's horn shell (*Spirula spirula*) and paper nautilus (*Argonauta nodosa*).

1.2 Carbon content of cephalopods

Here, we assume that carbon comprises approximately 8.4% wet weight of squid based on work by Vlieg (1988) who found arrow squid dry weight to be 22.5% of wet weight, and ash to be 6.2% of dry weight. If ash-free dry material is made of material in carbohydrate proportions ($C_6H_{12}O_6$) then carbon is about 40% dry weight or 8.4% wet weight. Vinogradov (1953) gives similar data for dry weight of Cephalopoda ranging from 13–30% of wet weight and ash of 0.9–2.4% of wet weight. We note that there may be substantial variation in carbon content of cephalopods; muscular squids (such as *Ommastrephes*) may have a carbon to wet weight ratio of 0.10 $gC\ gWW^{-1}$ whereas ammoniacal squid (such as *Histioleuthis*) may have a lower carbon content of 0.05 $gC\ gWW^{-1}$ (Clarke et al. 1996). However, the value of 8.4% used here is very similar to the carbon:wet weight ratio for squid which has been estimated to be about 8.3% (Brey 2005). Proximate biochemical composition and energy content of cephalopods was also given by Lee (1994).

2 Squid

2.1 General information

Squid are important in the marine ecosystem because they are a major food source for a wide variety of predators, including fish, marine mammals, seabirds and other squid. By far the most common squids in the New Zealand region are the arrow squids (*N. sloani* and *N. gouldi*). The species in the Hauraki Gulf study area will be mainly *N. gouldi* (Ministry of Fisheries 2009): "*Nototodarus gouldi* is found around mainland New Zealand north of the Subtropical Convergence, whereas *N. sloanii* is found in and to the south of the convergence zone." The broad squid (*S. australis*) also occurs in the Hauraki Gulf study region. Warty squids (e.g. *Moroteuthis ingens, M. robsoni*), red squids (e.g. *Ommastrephes bartrami*) live deeper in the water column (Anderson et al. 1998) and are unlikely to occur in significant quantities in the study area. Similarly, giant squid (*Architeuthis* spp.) are only typically found south and east of New Zealand (Förch, 1998).

2.2 Fishery removals

Arrow squid are included in the New Zealand Quota Management System, but only a small proportion of the approximately 50 000 tWW landings per year come from the study area. Commercial catches of arrow squid from the study area were estimated based on QMS reported catches in Ministry of Fisheries (2009), from the fishing years 2003–04 to 2007–08. It was assumed that all catches are reported. Mean annual commercial landings of arrow squid from the study area in the period 2002–2006 were estimated to be of the order of 21 tWW y^{-1} and catches of broad squid to be 6 tWW y^{-1} (Malcolm Francis, NIWA, pers. comm.).

2.3 Biomass

Biomass of squid in the QMS are not routinely estimated and indeed, biomass of squid is exceptionally difficult to estimate given that squid are difficult to catch, relatively short-lived (one or two years typically; arrow squid live for 1 year) and squid population size can change greatly from year to year. Catchabilities of squid with trawl gear are not known (Hurst et al., 2012) and likely to be considerably lower than fish but greater than zero as the Hauraki Gulf trawl survey catches both arrow and broad squid in reasonable quantities (e.g. Morrison et al. 2002). In the absence of information, we assume that catchability of large, commercially-sized squid (over 10 cm) by trawl gear is 0.2 that of snapper. Given the uncertainty in this factor, we assign high uncertainty to the biomass of squid during the balancing of the trophic model. Based on Hauraki Gulf trawl survey catches of snapper, broad squid and arrow squid, we hence estimate adult (commercially-sized) squid biomass in the study region to be 683 tWW (broad squid) and 4010 tWW (arrow squid). We need to add to this the biomass of small (sub-commercially sized but adult) squid, since we define adult squid as being over 2 cm. Based on the von Bertalanffy growth parameters (Gibson, 1995), the length-weight relationship (Mattlin et al. 1985), and adult natural mortality (see below) for arrow squid, we estimate that only 1.9% by weight of the adult (over 2 cm) squid are less than 10 cm (taken as lowest limit for commercial catches). Hence, we estimate squid biomass in the study region of 696 tWW (broad squid), 4090 tWW (arrow squid) or 4800 tWW (all squid).

South of New Zealand, Hurst & Schofield (1995, table 7) suggest that squid biomass appears to be about 1.8% of “all species biomass” in the same area. Here, our estimates of squid and demersal fish biomass suggest that total squid biomass is about 2.7% of all demersal fishes, suggesting that our estimate of Hauraki Gulf squid biomass is of the right magnitude.

2.4 Production

Cephalopods seem to be capable of exceptionally high growth rates compared to other invertebrates and fish (Boyle & Rodhouse 2005). Growth rates of squid are highly variable, and probably depend substantially on food intake (O’Dor et al. 1980; Boyle & Rodhouse 2005). Two-phase growth models are often used for cephalopods (Forsythe 1993), although two-phase growth is rarely obvious in field data (Boyle & Rodhouse 2005). In the two phase model, growth of cephalopod larvae is rapid (exponential) until adulthood. In adulthood, growth becomes slower and is often described by a power law (e.g. von Bertalanffy). Here, we assume that all cephalopods in this component of the trophic model are in the second phase of the growth. Individual growth slows and finally stops with sexual maturation, shortly followed by spawning and death (Boyle & Rodhouse 2005). Growth rates of cephalopods seems to depend substantially on food intake and may vary from near-zero somatic growth to a maximum of about 8% body weight per day ($P/B=29\ y^{-1}$) (Wells & Clarke 1996).

Von Bertalanffy growth parameters and length-weight relationships for arrow squid in the New Zealand EEZ are given in Ministry of Fisheries (2009) based on Gibson (1995) and Mattlin et al. (1985) respectively. Maximum dorsal mantle length of *N. gouldi* is 35 cm (Gibson & Jones 1993) and maximum weight is about 690 gWW. Ministry of Fisheries (2009) report: “Growth is rapid. Modal analysis of research data has shown increases of 3.0–4.5 cm per month for

Gould's arrow squid measuring between 10 and 34 cm Dorsal Mantle Length (DML).” The length-weight and von Bertalanffy growth parameters (Mattlin et al. 1985; Gibson 1995) imply DML growth rates of between 3.3–5.6 cm month^{-1} for squid of DML 10–20 cm, which are similar to those quoted by Ministry of Fisheries (2009). A much lower growth rate of 0.19 cm month^{-1} is implied by the time squid reach a DML of 34 cm. The growth rates of *N. gouldi* implied by these figures are reasonable, but towards the lower end of, somatic growth rates in the scientific literature. For arrow squid of DML 10–20 cm, values used here imply growth rates of 1.4–4.5 %WW d^{-1}. In comparison, *Illex illecebrosus* is able to grow at rates up to 5 %WW d^{-1} (depending on the food intake) (see Wells & Clarke 1996 and references therein). Pecl et al. (2004) suggests that squid growth rates of 4–9 %WW d^{-1} are likely. Boyle & Rodhouse (2005) summarise data on five species of squid which give somatic (growth) of 4.3 (0.6–11) %WW d^{-1}.

The annual-average production rate of the whole squid population depends on the natural mortality of arrow squid which is unknown. Ministry of Fisheries (2009) report: “Recent work on the banding of statoliths from *N. sloanii* suggests that the animals live for around 1 year”. This agrees with observations of statolith increments (Jackson & O’Dor 2001) which showed that squids in temperate waters are likely to have lifespans of less than 1 year. It was estimated that 946 out of every 1000 *Todarodes pacificus* (Japanese flying squid) die during the first two weeks of life (Gibson 1995), implying a daily mortality rate of 0.21 d^{-1}. Most of these will be larval squid however, and adult squid are likely to have substantially lower natural mortality. Here, based on mortalities for *Loligo pealei* off New England and *IIlex illecebrosus* in the Northwest Atlantic; Pauly 1985) we assume an age-independent natural mortality of M=0.004 d^{-1} for *N. gouldi*, with all surviving squid (22% recruiting adult squid) dying at 1 year old. This implies an average length of squid in the population of DML 20 cm, an average weight of 275 gWW, and an estimate of somatic (growth) production of the population of P/B=2.6 y^{-1}.

The energetic cost of reproduction has been analysed for squid from the winter-spawning population of *Illex argentinus* (Boyle & Rodhouse 2005): females invested 935 kJ into new tissue in the period immediately before spawning and males 250 kJ. *Illex argentinus* has a maximum mantle length of about 33 cm (Froese & Pauly 2005) with an estimated weight at maximum length of about 730 gWW, equivalent to 3100 kJ, and implying gonadal P/B of 0.30 y^{-1} (females), 0.08 y^{-1} (males), 0.19 y^{-1} (all population).

Hence, we estimate a population production (somatic plus gonadal) for arrow squid in the study area of P/B=2.8 y^{-1}, of which 7.2% is due to gonadal output. For comparison, annual P/B ratios for gonatid squid in the Bering Sea are estimated to be 6.7 (Radchenko 1992), for *Sthenoteuthis pteropus* in the tropical Atlantic to be 8.0–8.5 (Laptikhovsky 1995), and for captive *Illex illecebrosus* measured to be 2.9–9.1 at 7°C (Hirtle et al. 1981). Boyle & Rodhouse (2005) summarise growth data on five species of squid which give P/B between 2.2 and 26 y^{-1}.

These biomass, catch and production values would imply that commercial landings represent only 0.20% (broad squid) and 0.18% (arrow squid) of the annual production of the squid populations in the study area.

2.5 Consumption and growth efficiency (P/Q)

Gross growth efficiency for squid is reported as 20–40% (Boyle & Rodhouse 2005). Boyle & Rodhouse (2005) summarise data on five species of squid which give Q/B between 12 and 55 y^{-1}, and P/Q between 0.11 and 0.35 (median value of 0.25). The apparently lower food conversion efficiency of squid compared to octopus (median value P/Q=0.52) is accounted for by their greater use of energy for active movement (Boyle & Rodhouse 2005). The minimum survival consumption suggested by Wells & Clarke (1996) of 1.2–1.8 %WW d^{-1} corresponds to Q/B=4.4–6.6 y^{-1}. The highest growth rates of *Illex illecebrosus* were achieved at food intake of about 10% body weight per day or Q/B=37 y^{-1} (Wells & Clarke 1996). The daily ration of

Loligo pealei ranges from 3.2–5.8% of body weight per day (Vinogradov & Noskov, 1979) which represents a Q/B of 12–21 y^{-1}. The mean daily ration of *Illex illecebrosus* is 5.2% (Hirtle et al. 1981) or a Q/B of 19 y^{-1}. There are no measurements of squid consumption rates in the study area, so here we assume gross growth efficiency for arrow squid in the study area of P/Q=0.25, implying a Q/B=11 y^{-1}.

2.6 Diet (prey)

The diet of arrow squid has been reported to be made up of other squid (either intraspecific cannibalism or other species of squid), small pelagic and demersal fishes, and macro- and mesozooplankton, especially large copepods, mysids, euphausiids, and decapod shrimps (Mattlin & Colman 1988; Hatanaka et al. 1989; Vinogradov & Noskov, 1979; Gibson 1995). Recently, Dunn (2009) examined the diet of arrow squid *Nototodarus sloanii* on the Chatham Rise. In all, the stomach contents of 388 specimens of length 14–41 cm DML were examined. Prey items were predominantly mesopelagic fishes (IRI 72%), with some crustaceans (IRI 6%) and cephalopods (IRI 10%). The most important nekton identified for the Chatham Rise were *Maurolicus australis* (Sternoptychidae), *Lampanyctodes hectoris* (Myctophidae) and unidentified squids (Teuthoidea).

2.7 Other information: EE, U, accumulation, imports, exports, transfers

It is known that some species of squid can move considerable distances including seasonal migrations (Boyle & Rodhouse 2005; David Thompson, NIWA, pers. comm.). However, tagging experiments in New Zealand waters indicate that arrow squid move less than 5.6 km per day (Ministry of Fisheries 2009) and for this trophic model, we assumed that the majority of squid remain within the model region in the course of a year and set net import to zero.

It is not known if squid populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, i.e. we set accumulation to zero.

A proportion of the annual production will be exported to the macrozooplankton component of the trophic model as eggs and sperm. For squid, this fraction is estimated to be 4.8% as derived earlier.

The weight of recruiting squid is much smaller than the intrinsic growth of adult squid per year and is set to zero in the trophic model.

Ecotrophic efficiency (*E*) is not known for squid in the study area. Ecotrophic efficiency measures the proportion of the annual production that is available for predation ("passed up the food chain") as well as exported (including as fishery landings, migration, spawning output, growth) or accumulated. The remainder of the production (a fraction of 1-E) is transferred to a detrital group. In the case of squid, whole dead individuals or parts of squid are likely to be scavenged rather than decomposed by bacterial action and so will be passed in the model to the carcass group. This material is from two sources. First, squid can die from causes other than direct predation, including starvation, disease, excessive parasite loading, etc. However, it is likely that that the vast majority of squid mortality is due to direct predation rather than other causes. The proportion of annual production leading to carcasses due to causes other than direct predation and fishing is not known but is assumed to be 1%, giving a base estimate of ecotrophic efficiency of 0.99. Added to this is fishery catch of squid that is discarded back into the study area either as whole individuals (assumed dead) or as parts thereof. Although squid may be killed by the net but not retained, this is likely to be negligible as small squid (under 10 cm DML) make up a small proportion (less than 1%) of squid biomass and squid are landed whole.

Energy loss due to unassimilated consumption and excretion for squid is not well known, but was estimated for two species of squid (*Loligo opalscens*, *Illex illecebrosus*) based on annual energy budgets (Boyle & Rodhouse 2005). The mean of these values imply U=0.13 which we will use here. We note that this is similar to the value of unassimilated consumption assumed for octopus, (U=0.12) but somewhat lower than the value of U=0.30 used generically in other trophic models (e.g. Christensen & Pauly 1992; Bradford-Grieve et al. 2003).

3 Octopus and other cephalopods

3.1 General information

This group contains several groups of cephalopods:

- Octopus: The main octopus species in the region is likely to be *Octopus maorum* (Anderson 1999). Other large octopus species (*O. ornatus, O. dierythraeus and O. graptus*), are found in subtidal soft-sediment and rubble habitats in northeast New Zealand, *O. dierythraeus* is also found intertidally, and the two smallest species (*O. aspilosomatis* and *O. alpheus*) are found in exposed intertidal coral reef habitats (Anderson 1999).
- Ram's horn shell: *Spirula spirula* (kotakota ngu) grows to about 2.5 cm across and lives at depths of 100–1750 m.
- Paper nautilus: *Argonauta nodosa* (pupu tarakihi) is 12–15 cm across, and lives near the sea surface in deep water.

Information on many of these groups is poor, so we base the parameters for this group on *Octopus maorum.*

3.2 Fishery removals

Octopus is not included in the New Zealand Quota Management System, and landings are generally unknown but likely to be small. Mean annual commercial landings of octopus from the study area in the period 2002–2006 were estimated to be of the order of 7 tWW y^{-1} (Malcolm Francis, NIWA, pers. comm.)

3.3 Individual size

The total length of *O. maorum* estimated in northeast New Zealand (Lundquist & Pinkerton 2008) was 900–2064 mm, and weight was 1.5–9.2 kg in the outer Hauraki Gulf (Anderson 1999). Mean sizes were 1446 mm (7 kg) for males and 1167 mm (2 kg) for females (Anderson 1999). Two smaller species in New Zealand reach sizes of 5 kg (*O. tetricus*) and 60 g (*O. warringa*). The proportion of male to female octopus was about two thirds male (23 of 33 individuals captured). As no information on octopus is available in the study area, we assumed a similar sex ratio and an average individual weight of 5.3 kg, to extrapolate from individual octopus weight to total biomass.

3.4 Biomass

No estimates of octopus abundance or biomass were available for the study area. Octopus is a solitary predator and, as a cryptic species, was not observed during any of the intertidal and subtidal surveys. It is likely that octopus and other cephalopods in this group are mainly or entirely found associated with rocky reef habitats in the study area. A modeling study of a rocky reef ecosystem in northeast New Zealand (inside and outside Te Tapuwae O Rongokako marine reserve near Gisborne: Lundquist & Pinkerton 2008; Pinkerton et al. 2008) estimated octopus abundance based on by-catch rates of octopus in lobster pots using data from Tasmania and South Australia (Brock & Ward 2004; Hunter et al. 2005). On average, 4% of landings are lost to octopus predation in lobster traps in South Australia, with a range of 2–6% in Tasmania; an early report also estimated a 10% loss to octopus in Hokianga, New Zealand, in 1972 (Brock & Ward 2004; Hunter et al. 2005). A similar percentage of octopus predation in lobster pots was recorded for octopus captured in pot lifts during the lobster tagging programme in Te Tapuwae o Rongokako (D. Freeman, DOC, pers. comm.; Lundquist & Pinkerton 2008). These data allow us to estimate a density of octopus on rocky reef in New Zealand of 1 octopus per 9600 m^2. We assume this density, which is equivalent to 0.56 gWW m^{-2} occurs in all rocky reef habitats in the study area.

Anderson (1999) states that, in the Hauraki Gulf area: "*O. maorum* were frequently associated with soft-sediment substratum near scallop beds (18 of 23 individuals); and were far less common at the fringe between reef and soft-sediment habitats (three individuals), or traversing the rocky reef (two individuals) …Members of the *O. macropus* complex are found in a range of habitats and depths. Large species (*O. maorum*, *O. ornatus*, *O. dierythraeus* and *O. graptus*), are found in subtidal soft-sediment and rubble habitats (*O. dierythraeus* is also found intertidally). In contrast, the two smallest species (*O. aspilosomatis* and *O. alpheus*) are found in exposed intertidal coral reef habitats. At present published geographic distribution of the *O. macropus* complex is patchy."

The higher number of *O. maorum* found over soft-sediment substrate by Anderson (1999) is unlikely to be due to more intensive sampling of these areas as over 100 dives were conducted in each of the three habitats (soft-sediments, reefal, fringe), but sampling was more intense in and around reef habitats (450 dives). We hence assume that the density of octopus over soft sediment regions is 3.6 times greater than over reef or fringing reef habitats (=18/5) giving an octopus density in soft sediment areas of 2.0 gWW m^{-2}. We assume that this density applies to "coastal sheltered" habitats from 0–30 m.

Using areas of habitat in the study region (see Appendix 4, Section 2.2), we hence estimate a total biomass of octopus in the study area of 4080 tWW, with 94% of this biomass occurring over soft sediment and 6% occurring over rocky reefs.

We used a carbon:wet weight ratio for octopus similar to that of squid, which has been estimated to be about 8.3% (Brey 2005). This is consistent with work by Vlieg (1988) who found arrow squid dry weight to be 22.5% of wet weight, and ash to be 6.2% of dry weight; if ash-free dry material is made of material in carbohydrate proportions ($C_6H_{12}O_6$), then carbon is about 40% ash-free dry weight or about 9% wet weight. Vinogradov (1953) gave similar data for Cephalopoda, with dry weight ranging from 13 to 30% of wet weight and ash ranging from 0.9 to 2.4% of wet weight.

3.5 Production, consumption, growth efficiency

The total length of *O. maorum* ranges from 900 to 2064 mm, and its weight ranges from 1.5 to 9.2 kg in the outer Hauraki Gulf (mean = 1446 mm (7 kg) for males and 1167 mm (2 kg) for females) (Anderson 1999). Two smaller species in New Zealand reach sizes of 5 kg (*O. tetricus*) and 60 g (*O. warringa*). In this survey, the proportion of male to female octopus was about two thirds male (23 of 33 individuals captured), giving an average individual weight of 5.3 kg. Lifespan of octopus vary between about 6 months and 5 y, with lifespans between 1–3 years likely for larger species (Boyle 1983).

We are not aware of any measurements of octopus energetic parameters in the study area. However, Boyle & Rodhouse (2005) summarise data on six species of octopus (*O. cyanea*, *O. dofleini*, *O. maya*, *O. vulgaris*, *Eledone moschata*, *E. cirrhosa*) which give P/B (growth only) between 2.6 and 15 y^{-1}, and Q/B between 4.7 and 34 y^{-1}. We will use the median values from these six species (Boyle & Rodhouse 2005), i.e. P/B (growth)=4.9 y^{-1}, Q/B=12 y^{-1}. The energy invested in reproduction was estimated for female *Octopus cyanea* (see Wells & Clarke 1996), which showed that the ovary was 32% of the total body weight of a mature female with body mass about 600 gWW. We assume that the majority of this ovary weight is expelled during spawning since monthly mean values of the ovary index in *E. cirrhosa* show rapid and almost complete reductions in ovary weight corresponding to spawning (Boyle & Knobloch 1983). This allows us to estimate a reproductive output P/B=0.32 y^{-1} for females. Taking the male reproductive output as about one quarter of the female (based on *Illex argentinus*, Boyle & Rodhouse 2005), we estimate a total reproductive production of octopus of P/B=0.20 y^{-1}. Hence, total production of octopus is taken as P/B=5.1 y^{-1}, with spawning output making up 4.0% of this production.

Gross growth efficiency for octopus ranges from 0.4–0.6% compared to 0.2–0.4% for cuttlefish and squid (Boyle & Rodhouse 2005). The apparently higher food conversion efficiency of octopus compared to other cephalopods is accounted for by their lower use of energy for active movement (Boyle & Rodhouse 2005). The values used in the model (P/B=5.1 y^{-1}, Q/B=12 y^{-1}) imply a gross production efficiency P/Q=0.42. For comparison, values presented in an ecosystem model of a Chilean temperate reef were P/B=1.1 y^{-1}, Q/B=7.3 y^{-1}, P/Q=0.15 (Okey et al. 2004).

3.6 Diet (prey)

The common octopus (*O. maorum*) is a selective feeder on New Zealand reefs, consuming mainly crustaceans (especially crabs and lobsters), bivalves, fish, and other invertebrates, (Sewell 2005). Most octopus species are size-dependent cannibals, i.e., large individuals may attack and eat smaller individuals (Yarnell, 1969; Mather, 1980; Boyle et al., 1983). Anderson (1999) states that: "*O. maorum* were selective feeders, only preying on crustaceans, scallops, and any fish that could be captured. … While *O. maorum* does cannibalize smaller individuals and egg clutches, individuals will also attack and eat the co-occurring *O. tetricus*—regardless of size (small *O. maorum* will readily attack large *O. tetricus*)." In the absence of better information, we assume an initial diet composition for octopus of 50% crustaceans (20% lobster and 30% crab), 10% kina, 25% fish (15% benthic reef fish and 10% herbivorous reef fish) and 15% macrozooplankton.

3.7 Other information: EE, U, accumulation, imports, exports, transfers

Octopus home ranges are very small therefore import or export of octopus from the study area is likely to be negligible (e.g. Mather et al. 1985).

It is not known if octopus populations within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial, consistent change from year to year, i.e. we set accumulation to zero.

A proportion of the annual production will be exported to the macrozooplankton component of the trophic model as eggs and sperm. For octopus, this fraction is estimated to be 0.04 as described above.

The weight of recruiting octopus is likely to be much smaller than the intrinsic growth of adult squid per year and is set to zero in the trophic model.

Ecotrophic efficiency (*E*) is not known for octopus in the study area. Ecotrophic efficiency measures the proportion of the annual production that is available for predation ("passed up the food chain") as well as exported (including as fishery landings, migration, spawning output, growth) or accumulated. The remainder of the production (a fraction of 1-E) is transferred to a detrital group. In the case of octopus, whole dead individuals or parts of octopus are likely to be scavenged rather than decomposed by bacterial action and so will be passed in the model to the carcass group. This material is from two sources. First, octopus can die from causes other than direct predation, including starvation, disease, excessive parasite loading, etc. However, it is likely that that the vast majority of octopus mortality is due to direct predation rather than other causes. The proportion of annual production leading to carcasses due to causes other than direct predation and fishing is not known but is assumed to be 1%, giving a base estimate of ecotrophic efficiency of 0.99. Added to this is fishery catch of octopus that is discarded back into the study area either as whole individuals (assumed dead) or as parts thereof. If 8% of lobster pots contain octopus (see Section 3.4), and all these octopus are killed when the pots are removed, the fishing-related mortality is equivalent to 0.7% of annual octopus production.

The daily loss of energy in the urine of *O. vulgaris* has been shown to be between 1.5–3.1 kJ kg^{-1} d^{-1} (Wells & Wells 1990). This is equivalent to an annual loss of about 0.20 gC gC^{-1} y^{-1}. Other energy losses due to excretion include mucus losses from the body surface and in the faeces and, in the case of octopuses, shedding of sucker cuticles. Mucus production has not been quantified in cephalopods but may be significant (Boyle & Rodhouse 2005); here, we assume 0.2 g g^{-1} y^{-1}. Energy loss due to shedding of sucker cuticles is reported as about 0.34 kJ d^{-1} in *O. cyanea* with a mean body mass of 1380 g (Boyle & Rodhouse 2005) equivalent to 0.64 g g^{-1} y^{-1}. Faecal loss is generally small for cepahlopods; *O. cyanea* produced 2.7 g faeces d^{-1}, for a body weight of 1380 g, giving an annual excretion of 0.71 g g^{-1} y^{-1}. We hence estimate an annual excretion of 1.7 g g^{-1} y^{-1}. For a consumption rate of Q/B=14.9 y^{-1} (mean of six species of octopus, Boyle & Rodhouse 2005), this implies an unassimilated (plus excretory) loss of U=0.12. A default value of U=0.30 is often used for cephalopods (e.g. Lundquist & Pinkerton 2008).

4 Summary of parameters

Parameters for cephalopods in the Hauraki Gulf trophic model are given below in**Table 74**. Where appropriate, data for individual species were combined by combining these parameters in appropriate proportions according to biomass.

Table 74: Summary of parameters for cephalopods in the trophic model representing the present day. Note that spawning output is parameterised as the proportion of the annual production transferred out of the group as spawned material (eggs, sperm), written "T/P".

	EE	B	B	P/B	Q/B	P/Q	Fishery	U	Spawning
		gC m^{-2}	tWW	y^{-1}	y^{-1}		tWW y^{-1}		T/P (%)
Squid	0.99	0.025	4 780	2.8	11	0.25	26.0	0.13	7.2
Octopus	0.98	0.021	4 080	5.1	12	0.42	7.0	0.12	4.0

5 Historical parameters

Trophic models are required for cephalopods in four historical periods (1950, 1790, 1500, 1000). Natural drivers of environmental change in New Zealand during the last millennium were examined by Lorrey et al. (2013).

It seems unlikely that biomass, energetics, diet or other key parameters for either of the cephalopod groups in the trophic model would have been substantially changed by climate variations *per se*, and we do not adjust any of these parameters from the present day values in advance of balancing the historical trophic models. We recognize, of course, that cephalopod biomass and/or trophic role may be different historically than at the present time, as they may have been affected by changes to the ecosystem via indirect food-web (or non-trophic) connections. The historical trophic models attempt to investigate what changes are plausible.

6 Acknowledgements

This research was funded by Ministry for Primary Industries project ZBD200505 ("Long-term change in New Zealand coastal ecosystems") and by the New Zealand Ministry of Science and

Innovation project C01X0501 (Coasts & Oceans OBI). We acknowledge Dr Mary Livingston and Dr Martin Cryer (Ministry for Primary Industries) for supporting this project and Dr Alison MacDiarmid for her overall leadership. Dr Janet Bradford-Grieve provided useful comments on an earlier draft of this work.

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Appendix 7: Trophic modelling of Hauraki Gulf: Zooplankton

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1 General information

Zooplankton are a critical link in the food-web between phytoplankton and higher animals such as fishes and whales. Within this group are herbivores, carnivores and omnivores, including the larval stages of commercially important fish (e.g. snapper) and meroplanktonic stages of benthic invertebrates (e.g. scallops and crayfish).

In the trophic model, the zooplankton community of the Hauraki Gulf is divided into four groups based on standard size classifications for zooplankton (Harris et al. 2000; Sieburth et al. 1978), with a fifth group, the soft-bodied zooplankton, including jellyfish, salps, and chaetognaths (arrow worms). This last group is henceforth termed "gelatinous zooplankton".

1. Heterotrophic nanoplankton (2.0–20 µm): primarily heterotrophic flagellates
2. Microzooplankton (20–200 µm); primarily ciliates.
3. Mesozooplankton (0.2–20 mm); dominated by copepods.
4. Macrozooplankton (over 20 mm); primarily euphausiids, decapods and amphipods
5. Gelatinous zooplankton, including salps, jellyfish (medusa), and chaetognaths.

In the Hauraki Gulf study area, mesozooplankton are the dominant group in terms of biomass (Jillett 1971; Zeldis et al. 1995, 2005; Zeldis & Willis 2014). The mesozooplankton on the northeast shelf is temperate-subtropical in its species affiliations, having originated in the East Australian Current and Tasman Frontal Zone (Jillett 1971). In 1963–65, Jillett (1971) described the mesozooplankton communities at two stations; one inshore in the Waitemata Harbour, and the second on the inner shelf in Jellicoe Channel (Figure 32). At both these stations adult copepods (67%), calanoids (43%) and cyclopoids (21%) dominated abundance. The most common species found throughout the year were *Paracalanus indicus* (as *parvus*), *Acartia ensifera* (as *clausi*), *Temora turbinata* and *Corycaeus aucklandicus*. The zooplankton assemblages were predominantly neritic and typically dominated by seasonally abundant coastal-affiliated species, with intrusions of oceanic species observed on the inner shelf (Jillett 1971).

Zeldis et al. (2005) described mesozooplankton distributions over a detailed station grid between the two sites sampled by Jillett (1971). In this survey, the copepod *T. turbinata* and the cladoceran *Penilia avirostris* increased in summer of 1986–87 in the inner Gulf. The copepods *Euterpina acutifrons* and *C. aucklandicus* and the appendicularian *Oikopleura* spp. were most abundant in November 1987 as were bivalve larvae in November and December 1987. In contrast, the copepod *Clausocalanus* was more common in the first two seasons than in 1987–1988. Among the larger zooplankton, salps (*Thalia democratica*) were abundant in December 1985 and in November and December 1986 but were virtually absent through 1987–1988. The holoplanktonic predators *Sagitta* spp. (Chaetognatha) and hydromedusae were always more abundant in 1987–1988, as were decapods (crab and shrimp) larvae, in almost all summer months. The larvae of numerous fish species were also most abundant in 1987–1988 (snapper, jack mackerel, blue mackerel and anchovy). Zeldis et al. (2005) demonstrated the dynamics of the trophic linkages from phytoplankton to mesozooplankton to larval fish communities in the Hauraki Gulf.

The survey of the northeast continental shelf of New Zealand and the adjacent Hauraki Gulf from early spring to late summer in 1996–97 showed the influence of wind-driven upwelling events on total zooplankton abundance and species composition across the shelf and into the Gulf. The abstract in Zeldis & Willis (2014, submitted) reads: "The shelf supported low-abundance oceanic species reflecting the influence of the East Auckland Current. At transitional stations where shelf and coastal waters converge and mix, the zooplankton assemblage comprised oceanic and neritic species, supporting whale feeding activities in this area. Communities demarcated by cross-shelf movement of the front separating coastal and oceanic waters indicated the biogeographic boundary corresponding with seasonal billfish and gamefish migrations. In the Hauraki Gulf, total abundance was consistently high, and zooplankton assemblages displayed greater spatial and temporal variability in species composition [compared to shelf waters]. The seasonal succession of neritic zooplankton species in the Hauraki Gulf reflected changing trophic conditions as the ecosystem evolved from a net-autotrophic to net-heterotrophic state. Meroplanktonic larvae, cladocerans (*Podon polyphemoides* and *Evadne nordmanni*), small copepods and *Sagitta* spp. were abundant in spring when large ciliates and dinoflagellates dominated. In summer, the filter feeders *Penilia avirostris*, *Thalia democratica* and *Oikopleura* spp. were abundant when bacteria, nanoflagellates, and picophytoplankton were abundant" (Figure 32 below describes the distribution of survey stations used in this work).

Salps (Thaliacea), and other gelatinous plankton occur in the study area but their abundances, life-histories, trophic role, and energetics are poorly known. These groups of macrozooplankton can impact planktonic communities through intense grazing, and by affecting the export of material from the upper ocean (Alldredge & Madin l982; Zeldis et al. 1995). Gelatinous plankton are opportunistic colonizers, and their population sizes can rapidly increase when conditions are favourable (Zeldis et al. 1995; Paffenhofer & Lee 1987). Thaliacean blooms are common in continental slope, shelf and coastal seas (e.g. Paffenhofer & Lee 1987; Paffenhofer et al. 1995; Zeldis et al. 1995; Boysen-Ennen et al. 1991; Pakhomov et al. 2002). Salps and gelatinous zooplankton can also be important food items for seabirds (Raymond et al., 2010), mammals (e.g. Gomez-Villota, 2007) and some species of fish (notably, oreos; Dunn et al., 2009).

The microzooplankton was dominated by oligotrichs and tintinnids (protozoan ciliates) common in open shelf waters (J. Zeldis, unpublished data). This would explain the higher abundance on the shelf compared to the Gulf.

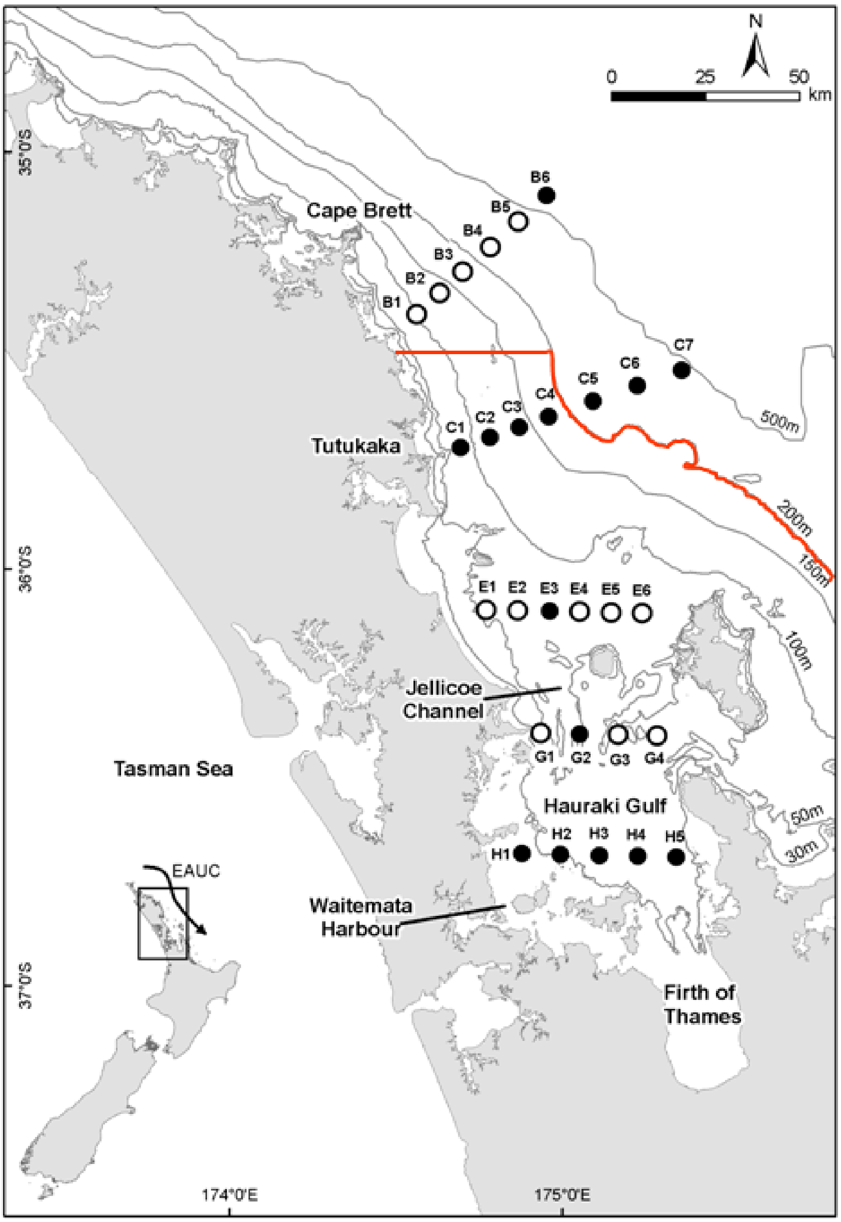

Figure 32: Location of zooplankton and hydrographic sample stations on the northeast New Zealand continental shelf and in the Hauraki Gulf in the spring and summer of 1996–97. Black circles = zooplankton and hydrographic samples; open circles = only hydrographic samples. Only zooplankton data from samples landward of the 200 m contour (red line) were used in this study.

2 Biomass

2.1 Source data

Zooplankton biomass was derived from three research programmes from which phytoplankton and bacteria biomass was estimated, (1) Snapper; (2) Bionosex; (3) CSEX.

1. The first, the ‘Snapper’ programme, described the pelagic ecosystem including zooplankton underpinning larval fish communities in the Gulf during nine, 3-week voyages spanning three snapper spawning seasons (November to January) in 1985–6, 1986–87 and 1987–88 (Zeldis et al. 2005). Zooplankton samples were taken at up to 43 grid stations at standard depths as described in Zeldis et al. (1995). Zooplankton over 100 µm between surface and near bottom were collected by a pumped water supply with an intake attached to a profiling CTD. Zooplankton samples were retained on a 100 µm mesh. Larger zooplankton (over 365 µm) were collected using double-oblique, water column integrated hauls of a plankton net (mouth diameter 80 cm, 365 µm mesh) fitted with a flowmeter. Samples were preserved in formalin, subsequently subsampled, individuals identified and enumerated in the laboratory.

2. Second, there were four Bionosex voyages in total: September 1996 (kah9614), October 1996 (tan9612), December 1996 (kah9617), and January–February 1997 (tan9702). Bionosex stations are shown in **Figure 32**. Zooplankton were captured using a 200 µm net using vertical tows to near bottom. Zooplankton biomass was measured at six Gulf stations (H1–H5, G2) and at eight Shelf stations (E3, C1–C6, B6). All the Gulf stations and five of the Shelf stations (E3, C1–C4) are in the study area.

3. Third, CSEX was a series of 13 research voyages carried out between July 2003 and March 2008. Microzooplankton carbon was measured at three CSEX stations in the study area (C1, C3, SA03). Other size fractions were not included and only Oligotrichs and Tintinnids were counted.

We note that the size fractionation of zooplankton sampled on the “Snapper” voyages do not match the standard size categories, spanning the microzooplankton and mesozooplankton size classes. The method did not sample zooplankton greater than 20 mm (macrozooplankton). Zooplankton biomass measured on the Snapper voyage was divided between micro and mesozooplankton groups which were defined according to size categories given earlier (Harris et al. 2000; Sieburth et al. 1978). Average individual dry weight of 29 groups of zooplankton taxa were measured (**Table 75**). Four groups were assigned to the “Gelatinous zooplankton” category: chaetognaths (CTG), salps (SAL), polychaetes (ZPY) and medusae (ZME). For the remaining 25 groups, we estimated an equivalent spherical diameter of individuals assuming a dry-weight to wet weight ratio of 12% (Omori 1974; Weibe 1988), and approximately neutral density (1 gWW cm^{-3}). The equivalent spherical diameter, x (µm), was reduced by a factor of 1.5 to account for the flattened shape of zooplankton in order to estimate zooplankton length and hence assign the species to the appropriate zooplankton component of the model. For x over 200 µm, all biomass is assumed to be in the mesozooplankton group. For x less than 200 µm, the proportion of biomass in the mesozooplankton group was estimated as x/100-1, with the remainder being in the microzooplankton group. This partitioned the biomass of four groups: Harpacticoid nauplii (ZCH), Calanoid nauplii (ZCN), Cyclopoid nauplii (ZCY), and Larvacean (Oikopleura sp., ZOI).

Table 75: Information on zooplankton taxa collected in the study area, Diet codes are: o=omnivorous; c=carnivorous; h=herbivorous/detrivorous. (Zeldis, unpublished data).

Code	Taxa	Species	Diet	Individual weight mgDW ind^{-1}	C/DW
BRY	Crab larvae		o	0.012	0.37
CTG	Chaetognaths		c	0.031	0.39
NAT	Natant decapod larvae		o	0.051	0.37
SAL	Salp		h	0.23	0.07
ZAC	Copepod	*Acartia spp.*	o	0.020	0.47
ZAN	Anomuran		o	0.065	0.37
ZBI	Bivalve larva		h	0.0038	0.25
ZBN	Barnacle nauplii		o	0.0020	0.47
ZCH	Harpacticoid nauplii		o	0.0008	0.47
ZCL	Copepod	*Clausocalanus spp.*	o	0.013	0.47
ZCN	Calanoid nauplii		o	0.00091	0.47
ZCO	Copepod	*Corycaeus spp.*	o	0.0029	0.47
ZCU	Copepodite		o	0.0026	0.47
ZCY	Cyclopoid nauplii		o	0.0009	0.47
ZEA	Copepod	*Euterpina acutifrons*	o	0.0020	0.47
ZEN	Cladoceran	*Evadne spp.*	h	0.0046	0.30
ZGL	Gastropod larva		o	0.0038	0.25
ZJA	*Jaxea spp.*	*Jaxea spp.*	o	4.8	0.37
ZME	Medusae		c	0.035	0.07
ZNY	Nyctiphanes		o	0.0029	0.39
ZOC	Copepod	*Oncaea spp.*	o	0.0030	0.47
ZOI	Larvacean	*Oikopleura spp.*	h	0.0010	0.07
ZON	Copepod	*Oithona nana*	o	0.0083	0.47
ZPA	Cladoceran	*Penelia avirostris*	o	0.0089	0.30
ZPI	Copepod	*Paracalanus indicus*	o	0.0062	0.47
ZPO	Cladoceran	*Podon spp.*	h	0.0046	0.30
ZPY	Polychaete		o	3.5E-05	0.35
ZSQ	Stomatopod	*Squilla spp.*	o	0.045	0.37
ZTT	Copepod	*Temora turbinata*	o	0.0092	0.47

2.2 Microzooplankton

Data are available for micro-zooplankton (Oligotrichs and Tintinnids) from the C-SEX (1998–2009) survey for most months of a year (Figure 33). A log-mean was taken to prevent occasional high values having undue influence. The annual average biomass is estimated at B=96 mgC m^{-2}. Biomass of other taxa of microzooplankton (namely harpacticoid nauplii, calanoid nauplii, cyclopoid nauplii, and larvaceans) that were not sampled on CSEX were estimated based on partitioned data from “Snapper”, at B=23 mgC m^{-2}. We hence estimate a total microzooplankton biomass for the study area of B=119 mgC m^{-2}.

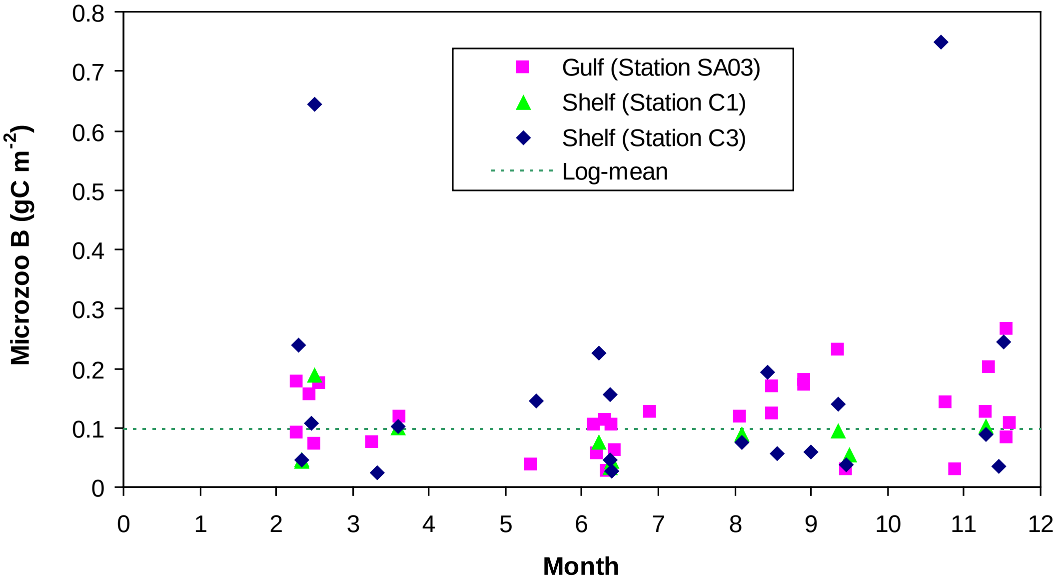

Figure 33: Water column integrated biomass of microzooplankton obtained from the CSEX series of research voyages in the study area, as explained in the text. The dashed line gives the geometric mean used in the trophic model.

2.3 Heterotrophic nanoplankton

Biomass of heterotrophic nanoplankton (individual sizes 2.0–20 μm) has not been measured in the study area. Here, we assume that the biomass of this fraction is 1.8 times the biomass of microzooplankton (Pinkerton 2011) i.e. B=220 mgC m^{-2}.

2.4 Mesozooplankton

Data on mesozooplankton biomass are available from the Snapper (1985–88) and Bionosex (1996–97) surveys which cover the spring/summer periods only. Note that biomass of four taxa in the Snapper data were partitioned between micro and mesozooplankton groups as explained above. Log-means were calculated to estimate an annual average mesozooplankton biomass of B=550 mgC m^{-2} (Gulf), 269 mgC m^{-2} (Shelf), and 409 mgC m^{-2} (all study area).

2.5 Macrozooplankton

Macrozooplankton (individuals greater than 20 mm in size (Harris et al. 2000; Sieburth et al. 1978) were not measured on these voyages, except for the occasional collection of *Jaxea* spp. and *Nyctiphanes* spp. which should probably be classified as macrozooplankton (Wear & Yaldwyn 1966; Mauchline, 1980). Given the lack of local information on this group, we estimate a biomass of macrozooplankton as 19% that of mesozooplankton (Pinkerton 2011) i.e. B=77 mgC m^{-2}.

2.6 Gelatinous zooplankton

Gelatinous zooplankton biomass is considered to include pelagic polychaetes, chaetognaths, jellyfish (medusa) and salps in Table 76. Salps typically have a carbon to dry weight ratio of

4%, much smaller than other zooplanktonic species (Pakhomov et al. 2002). Salp WW to carbon ratio has been measured at only 0.37% (Curl 1961). In 1985–88, salp biomass was high and indicative of the high productivity of the Gulf at this time. Zeldis et al. (1995) reported a gelatinous zooplankton density of 0.21 gC m^{-2} in the Hauraki Gulf. In 1996–97, total average biomass was much lower and dominated by chaetognaths. Gelatinous zooplankton abundance and biomass can vary greatly inter-annually and seasonally due to their opportunistic feeding behaviour which enables a rapid response to environmental changes by increasing feeding, growth, and reproduction in optimal conditions (Brodeur et al. 2008). It is this ability to boom or bust that has led to the suggestion that jellyfish in particular should be a key indicator species of changing climate conditions (Hay, 2006; Richardson et al., 2009). We combine these data using log-averaging and estimate a mean biomass of gelatinous zooplankton of B=22 mgC m^{-2}.

Table 76: Arithmetic mean biomass (mgC m^{-2}, with 1 standard error in brackets) for gelatinous zooplankton from the 1985–88 and 1996–97 surveys.

	GULF		SHELF
	Snapper (1985–88)	Bionosex (1996–97)	Bionosex (1996–97)
	mgC m^{-2}	mgC m^{-2}	mgC m^{-2}
Chaetognaths	18.30	28.92	11.36
Salps	218.07	0.08	0.05
Medusae	0.27	0.94	0.34
Polychaete	0	0.01	0.003

2.7 All zooplankton

As a check of our zooplankton biomass estimate, we compare phytoplankton and zooplankton biomasses. The annual average biomass of heterotrophic plankton is generally related to autotrophic biomass, though it is clear that there are significant variations by region, depth and season. The ratio of total zooplankton biomass to phytoplankton biomass has been reported as 1.7 (Southern Plateau New Zealand; Bradford-Grieve et al. 2003), 1.5 (Golden Bay, New Zealand; Jiang & Gibbs 2005), 1.1 (Ross Sea; Pinkerton et al. 2010), 0.77 (Gulf of Mexico; Arreguin-Sanchez et al. 2002), and 0.64 (Tongoy Bay, Chile; Wolff 1994). These values, across a range of systems, suggest an average heterotrophic:autotrophic plankton ratio of 1.11 which is slightly higher than the zooplankton:phytoplankton ratio from our estimates, which was 0.80.

3 Zooplankton production

There are no direct measurements of zooplankton productivity in the Hauraki Gulf. Thus we have reviewed annual productivities (P/B, y^{-1}) for zooplankton across a wide range of marine ecosystems (Table 77).

3.1 Micro-, meso- and macrozooplankton

The P/B range for microzooplankton was very wide (P/B=20–290 y^{-1}) and for this study a P/B of around 120 y^{-1} was assumed as this value is within the range of similar marine ecosystems (in terms of area, depth, latitude, primary productivity) as our study area (Link et al. 2006; Allain 2005). Mesozooplankton production within the Gulf is driven by wind-induced upwelling (Zeldis et al. 2005) producing *in situ* biomass that is greater than that on the shelf. It is thus appropriate to use P/B ratios akin to similar coastal upwelling regions such as North British Columbia (Ainsworth et al. 2002; Beattie 2001), Southern Benguela (Shannon et al. 2003), North Benguela Upwelling coast to shelf (Heymans & Baird 2000) and the New Zealand Southern Plateau (Bradford-Grieve et al. 2003) which equates to a range 20–40 y^{-1}. We have selected a P/B y^{-1} of 25. For macrozooplankton, we selected P/B=7.0 y^{-1} from the range in Table 77 of 3–25 y^{-1}.

Table 77: P/B (y^{-1}) for micro- meso- and macrozooplankton over a range of marine ecosystems from around the world.

P/B (y^{-1}) zooplankton			Location	Reference
Micro	Meso	Macro		
-	27	6.1	North British Columbia, Canada	Ainsworth et al. 2002, Beattie 2001
100	33		Central Pacific	Allain 2005
88	20	10	NZ Southern Plateau	Bradford-Grieve et al. 2003
-	8	3	Nova Scotia coast to edge of shelf 1995 to 2000	Bundy 2004
21	21	21	South Catalan Sea: coastal 50 m to 400 m: oligotrophic system	Coll et al. 2006
	90		South Brazil Bight 20–200 m inshore, wind driven upwelling	Gasalla & Rossi-Wongtschowski 2004
214	82	7.5	Baltic Sea	Harvey et al. 2003
40	40	13	North Benguela Upwelling coast to shelf	Heymans & Baird 2000
	8.4	3.4	Newfoundland	Heymans 2003
72–135	31–76		NE USA: Bering Sea, North Atlantic, Gulf of Maine	Link et al. 2006
	6.8	3.98	Gulf St Lawrence Canada	Morissette et al. 2003
20	10	12	Central Chile upwelling coast to 30 Nautical miles hake, 1992	Neira & Arancibia 2004
40	5	7	USA mid-Atlantic Bight; temperate continental shelf to 200 m	Okey 2001
	13	13	SE USA Tropical continental shelf intertidal to 500 m	Okey & Pugliese 2001
		25	Monterrey Bay California	Olivieri et al. 1993
88–290	20	10	Te Tapuwae o Rongokako, East coast New Zealand, to 50 m	Lundquist & Pinkerton 2008; Pinkerton et al. 2008
20	20	13	South Benguela Upwelling coast to shelf	Shannon et al. 2003
	6	5	East Bering Sea; temperate shelf down to 500m	Trites et al. 1999
75	25	7	Hauraki Gulf – coast to 250 m	This study

3.2 Heterotrophic nanoplankton

Mean daily P/B of heterotrophic flagellates offshore of New Zealand has been measured at P/B=0.80 d^{-1} (n=10) (P/B=292 y^{-1}) calculated from dilution grazing experiments (Julie Hall, pers. comm.). These data are from subantarctic waters in August and January-February; there was little difference in P/B between the two periods. Growth rates of heterotrophic microflagellates of more than 2 d^{-1} have been measured when conditions are not limited by iron (Chase & Price, 1997) but are less than 1 d^{-1} at the low prey Fe:C of 9 µmol mol^{-1} observed in the open subarctic Pacific (see Tortell et al. 1996). In low iron growth conditions, carbon specific growth of microflagellates was 0.7–1.6 d^{-1}. Here, we assume P/B=150 y^{-1}.

3.3 Gelatinous zooplankton

Thaliaceans are very efficient grazers, feeding by pumping water through a fine mucous net suspended in the pharyngeal cavity. They can retain and ingest virtually all cell sizes from nanoplankton to net-plankton (Alldredge & Madin l982), and so are assumed to feed on phytoplankton, organic detritus, micro-, meso- and macrozooplankton in the model. Production rates of salps can be high (Zeldis et al. 1995), and are likely to be greater than other macrozooplankton. Gross growth efficiency, P/Q, is also likely to be greater than that of other zooplankton and has been estimated to be 0.40 (Jonsson 1986; Caron & Goldman 1990).

Productivity for gelatinous zooplankton is highly variable among and within ecosystems. Growth is dependent on a combined suite of favourable biophysical variables (such as temperature, currents, coastal entrainment, stratification, food supply) for a population to boom or bust. Further there has been no consistency in the international literature on assessing biomass, or production (see Pauly et al. 2009). This has led to a wide range of P/B ratios (**Table 78**). For the purpose of this study we will assume P/B=10 y^{-1}.

Table 78: P/B (y^{-1}) for gelatinous zooplankton over a range of marine ecosystems from around the world.

P/B(y^{-1}) gelatinous zooplankton	Location	Reference
18	North British Columbia, Canada	Ainsworth et al. 2002, Beattie 2001
0.584	South Benguela, Upwelling coast to shelf	Shannon et al. 2003
14	Central Chile, upwelling coast to 30 Nautical miles hake, 1992	Neira & Arancibia 2004
0.58	Central Chile, upwelling coast to 30 Nautical miles hake, 1992	Neira & Arancibia 2004
40	NE USA: Bering Sea, North Atlantic, a Bay, Gulf of Maine 96 -2000	Link et al. 2006
0.88	East Bering Sea; temperate shelf down to 500 m 1955 -60	Trites et al. 1999
40	SE USA Tropical continental shelf intertidal to 500 m; 1995–98	Okey & Pugliese 2001
18.25	USA mid Atlantic Bight; temperate continental shelf; intertidal to 200 m	Okey 2001
26.51	South Catalan Sea 50 m to 400 m: oligotrophic system	Coll et al. 2006
10	Hauraki Gulf – coast to 250 m	This study

4 Diets

There are no data available on the diets of zooplankton from the Hauraki Gulf. Therefore we reviewed the literature and summarised published data from comparable marine ecosystems as percentage of a prey in the diet for each zooplankton group (Table 79). From this data review, we have calculated the average food proportion for each prey and scaled to a total of 100%.

The proportions in which heterotrophic nanoplankton consume their food (bacteria and phytoplankton) were as follows. Heterotrophic flagellates have been measured as consuming 4.4% of picophytoplankton biomass and 2.4% of bacterial biomass per day (Safi & Hall, 1999; Julie Hall, NIWA, unpublished data). We estimate the diet of heterotrophic nanoplankton as 10% heterotrophic flagellates, 70% phytoplankton (predominantly picophytoplankton) and 20% water column bacteria.

Microzooplankton feed predominantly on phytoplankton, detritus, bacteria and other microzooplankton. The proportions of these prey items will vary with availability (season, upwelling events, etc.). We hence assume a diet for microzooplankton of 28% phytoplankton, 32% water column detritus, 31% water column bacteria and 9% other microzooplankton. We note that consumption of separate parts of the “detritus and bacteria” assemblage by microzooplankton is poorly known and here it is assumed that microzooplankton consume these in approximately equal proportions.

Mesozooplankton diet in the study area was estimated to consist of phytoplankton, microzooplankton and other mesozooplankton. Here the diet proportions were estimated to be 42% phytoplankton, 17% water column detritus, 31% microzooplankton and 10% other mesozooplankton.

Macrozooplankton diet consists of mainly phytoplankton and mesozooplankton in proportions of 39% phytoplankton, 14% detritus, 43% mesozooplankton and 4% other macrozooplankton

Gelatinous zooplankton diet depends on the species, and in the Hauraki Gulf, gelatinous zooplankton are likely to be predominantly salps (Thaliacea). In general, Thaliacea are very efficient grazers, feeding by pumping water through a fine mucous net suspended in the pharyngeal cavity. They can retain and ingest virtually all cell sizes from nanoplankton to net-plankton (Alldredge & Madin l982), and so are assumed to feed on phytoplankton, organic detritus, micro-, meso- and macrozooplankton in the model. In the model, the diet of gelatinous zooplankton is assumed to be mesozooplankton (10%), microzooplankton (25%), heterotrophic nanoplankton (25%), phytoplankton (20%), water column bacteria (10%) and water column detritus (10%). The varied diet as shown in Table 79 may demonstrate the opportunistic feeding behaviour of this group but at present quantitative diet data are limited.

Table 79: Diet matrix (percentage of diet) for the zooplankton trophic groups over a range of marine ecosystems. "Phyto" = phytoplankton. "Detritus" refers to water column detritus, both particulate and dissolved. "Zoo"=zooplankton

							Prey
Predator	Phyto- plankton	Det- ritus	Bacteria	Micro- zoo	Meso- zoo	Macro- zoo	Gelatinous zoo
Microzoo	65[a]	5[a]	25[a]	5[a]			
	21[c]	79[c]					
		45[d]	55[d]				
	40[e]	40[e]		20[e]			
	15[f]	35[f]	40[f]	10[f]			
Mesozoo	10[a]			70[a]	10[a]		
	54[b]	33[b]		6[b]	7[b]		
	75[c]			25[c]			
	83[d]			73[d]			
	50[e]			50[e]			
	50[f]	11[f]		14[f]	20[f]		5[f]
Macrozoo	37[b]	20[b]			43[b]	5[b]	
	50[c]				50[c]		
	60[d]				40[d]		
	60[e]				40[e]		
	11f	11[f]			74f	4[f]	
Gel zoo		20[e]			64[e]	12[e]	4[e]
	9[f]	10[f]	2[f]	5[f]	69[f]		2[f]
				25[g]	25[g]		50[g]

Notes:

a. Lundquist & Pinkerton (2008); Pinkerton et al. (2008): New Zealand rocky Reef
b. Bundy (2004): eastern Scotian Shelf, Canada
c. Harvey et al. (2003): Baltic Sea
d. Heymans & Baird (2000): North Benguela
e. Shannon et al. (2003): South Benguela
f. Link et al. (2006): NE USA: Bering Sea, North Atlantic, Gulf of Maine
g. Ainsworth et al. (2002): North British Columbia, Canada

5 Other parameters: Q, P/Q, U, EE

5.1 Parameters included

This section includes a number of tables which summarise published data and other trophic parameters not yet discussed. We consider consumption rates (Q/B, y^{-1}), growth efficiency (P/Q, dimensionless), unassimilated consumption (U, dimensionless) and ecotrophic efficiency (EE, dimensionless). Ecotrophic efficiency (EE) is not known for zooplankton in the study area. Ecotrophic efficiency measures the proportion of the annual production that is available for predation ("passed up the food chain") as opposed to being transferred to a detrital group. In the case of zooplankton, dead individuals or exudants will be decomposed mainly by bacterial action or fed on directly by benthic detrivores. In marine systems, most zooplankton production is consumed, so that ecotrophic efficiencies for zooplankton are usually close to unity. We selected ecotrophic efficiency, P/Q and U parameters that we considered applicable to our trophic model based in most instances on the similarity between the Hauraki Gulf structure and function and other marine ecosystems.

5.2 Heterotrophic nanoplankton

For heterotrophic nanoplankton we assumed a growth efficiency of P/Q=0.35, giving Q/B=429 y^{-1}. Ecotrophic efficiency is likely to be high and is here set to E=0.95. Assimilation efficiency, (ingestion – excretion)/ingestion, of heterotrophic flagellates in low iron conditions is 0.84 (Chase & Price, 1997) so here, we used unassimilated consumption proportions, U=0.20.

5.3 Microzooplankton

For microzooplankton (Table 80) parameters ranged as follows:

Q/B: 20–620 y^{-1}
P/Q: 0.29–0.35; selected 0.3 which implies Q/B=250 y^{-1}
U: 0.2–0.4: selected 0.3
EE: 0.927–1.00; selected 0.99

Table 80: Summary of published trophic parameters for microzooplankton. Refer to Table 77 and Table 78 for the location of study areas.

Consumption, Q/B (y^{-1})	Growth efficiency, P/Q	Ecotrophic efficiency, EE	Unassimilated consumption, U	Respiration, R/B (y^{-1})	Reference
620			0.32		Lundquist & Pinkerton (2008); Pinkerton et al. 2008
300	0.3	0.94			Allain 2005
542		1			Harvey et al. 2003
	0.3	0.95	0.35		Shannon et al. 2003
133			0.2		Heymans & Baird 2000
20		0.99			Neira & Arancibia 2004
1928	0.29				Neira & Arancibia 2004
243–423	0.29–0.32			38–69	Link et al. 2006
125		0.985			Okey 2001
48.85			0.4		Coll et al. 2006
	0.35				Bradford-Grieve et al. 2003
250	0.30	0.95	0.30		This study

5.4 Mesozooplankton

For mesozooplankton (Table 81) parameters ranged as follows:

Q/B 50–270 y^{-1}
P/Q: 0.3–0.35; selected 0.3 which implies Q/B=83 y^{-1}
U: 0.2–0.4: selected 0.3
EE: 0.7–0.95; selected 0.95

Table 81: Summary of published trophic parameters for mesozooplankton. Refer to Table 77 and Table 78 for the location of study areas.

Consumption, Q/B (y^{-1})	Growth efficiency, P/Q	Ecotrophic efficiency, EE	Unassimilated consumption, U	Reference
52			0.32	Lundquist & Pinkerton (2008); Pinkerton et al. 2008
99	0.3			Ainsworth et al. 2002, Beattie 2001
110		0.311		Allain 2005
28	0.3	0.95		Heymans et al. 2003
270		0.402		Gasalla & Rossi-Wongtschowski 2004
25.9				Morissette et al. 2003
28	0.3	0.96		Bundy 2004
300		0.76		Harvey et al. 2003
	0.3	0.95	0.35	Shannon et al. 2003
133			0.2	Heymans & Baird 2000
20		0.99		Neira & Arancibia 2004
154	0.29			Neira & Arancibia 2004
127		0.75		Link et al. 2006
109		0.75		Link et al. 2006
43.3		0.91		Okey & Pugliese 2001
21.5		0.744		Okey 2001
48.85			0.4	Coll et al. 2006
	0.35			Bradford-Grieve et al. 2003
83	0.30	0.95	0.30	This study

5.5 Macrozooplankton

For macrozooplankton (Table 82) parameters ranged as follows:

Q/B 19–70 y^{-1}
P/Q: 0.16–0.41; selected 0.30 which implies Q/B= 23 y^{-1}
U: 0.09–0.35: selected 0.3
EE: 0.5–0.99; selected 0.95

Table 82: Summary of published trophic parameters for macrozooplankton. Refer to Table 77 and Table 78 for the location of study areas.

Consumption, Q/B (y^{-1})	Growth efficiency, P/Q	Ecotrophic efficiency, EE	Unassimilated consumption, U	Reference
52				Lundquist & Pinkerton (2008); Pinkerton et al. 2008
24.8	0.3			Ainsworth et al. 2002, Beattie 2001
19	0.18	0.95		Heymans 2003
23.84				Morissette et al. 2003
20	0.16	0.95		Bundy 2004
25		0.5		Harvey et al. 2003
	0.41	0.95	0.35	Shannon et al. 2003
32			0.09	Heymans & Baird 2000
		0.99		Neira & Arancibia 2004
32				Neira & Arancibia 2004
36–145				Link et al. 2006
22				Trites et al. 1999
43.3		0.91		Okey & Pugliese 2001
21.9		0.452		Okey 2001
50.94			0.2	Coll et al. 2006
33	0.303	0.95		Bradford-Grieve et al. 2003
70				Olivieri et al. 1993
23	0.30	0.95	0.30	This study

5.6 Gelatinous zooplankton

For gelatinous zooplankton (Table 83) parameters were as follows:

Q/B 1.4–146 y^{-1}
P/Q: 0.27–0.3; selected 0.29 which implies Q/B=34 y^{-1}
U: 0.2: selected 0.2
EE: 0.155–0.99; selected 0.95.

Table 83: Summary of published trophic parameters for gelatinous zooplankton. Refer to Table 77 and Table 78 for the location of study areas.

Consumption, Q/B (y^{-1})	Growth efficiency, P/Q	Ecotrophic efficiency, EE	Unassimilated consumption, U	Reference
			0.5	Andersen 1986
60				Ainsworth et al. 2002, Beattie 2001
	0.3		0.2	Shannon et al. 2003
		0.155		Shannon et al. 2003
14		0.99		Neira & Arancibia 2004
1.4	0.15			Neira & Arancibia 2004
146	0.28–0.27			Link et al. 2006
2		0.018		Trites et al. 1999
80		0.95		Okey & Pugliese 2001
80		0.9		Okey 2001
56.8		0.017		Coll et al. 2006
34	0.29	0.95	0.20	This study

5.7 Accumulation

It is not known if populations of zooplankton within the study area are undergoing long-term, consistent change in terms of biomass. The model will assume no substantial and consistent change from year to year, and we set accumulation to zero.

5.8 Export

Given the high rate of production and short lifespan of marine zooplankton (days to months), the proportion of the biomass being transferred across boundaries of the study area is likely to be very small. In the trophic model, we assume zero net import.

5.9 Spawning / recruitment

Spawning transfers are likely to be small compared to consumption and intrinsic production due to growth in the zooplankton groups, and are hence set to zero in the model.

6 Summary of parameters

A summary of parameters for the zooplankton components of the trophic model for the present day conditions are given inTable 84.

Table 84: Summary of zooplankton parameters used in the trophic model for the Hauraki Gulf study region.

	Size	EE	B gCm^{-2}	P/B y^{-1}	Q/B y^{-1}	P/Q	U
Heterotrophic nanoplankton	2–20 μm	0.95	0.22	150	429	0.35	0.20
Microzooplankton	20–200 μm	0.95	0.12	75	250	0.30	0.30
Mesozooplankton	0.2–20 mm	0.95	0.41	25	83	0.30	0.30
Macrozooplankton	>20 mm	0.95	0.077	7	23	0.30	0.30
Gelatinous zooplankton	All sizes	0.95	0.022	10	34	0.29	0.20

7 Historical parameters

Trophic models are required for zooplankton in four historical periods: 1950, 1790, 1500 and 1000.

Natural drivers of environmental change in New Zealand during the last millennium were examined by Lorrey et al. (2013).

It seems unlikely that biomass, energetics, diet or other key parameters for any of the zooplankton groups in the trophic model would have been substantially changed by climate variations *per se*, and we do not adjust any zooplankton parameters from the present day values in the historical trophic models. We recognize, of course, that zooplankton biomass and trophic role may be different historically than at the present time, as they may have been affected by changes to the ecosystem via indirect food-web (or non-trophic) connections.

8 Acknowledgements

This research was funded by Ministry for Primary Industries project ZBD200505 ("Long-term change in New Zealand coastal ecosystems") and by the New Zealand Ministry of Science and Innovation project C01X0501 (Coasts & Oceans OBI). We acknowledge Dr Mary Livingston and Dr Martin Cryer (Ministry for Primary Industries) for supporting this project and Dr Alison MacDiarmid for project leadership. Dr Janet Bradford-Grieve provided valuable comments on an earlier draft of this work.

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Appendix 8: Trophic modelling of Hauraki Gulf: Phytoplankton

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1 General information

Zeldis et al. (2005) found that in the summer (November–January), phytoplankton assemblages in the Hauraki Gulf were about 58% diatoms, 27% dinoflagellates and 15% nanoflagellates. Although it is known that composition of phytoplankton can affect factors such as respiration, growth (primary productivity rate), response of phytoplankton to seasonally varying oceanographic conditions (such as irradiance, nutrients), and consumption by small zooplankton, all water column phytoplankton are included in one group in the trophic model.

2 Biomass

2.1 Research voyages in the study area

Phytoplankton biomass in the water column in the study area was measured on three series of voyages: (1) Snapper; (2) Bionosex; (3) CSEX. (Table 85). Biomass calculations for zooplankton (Appendix 8) and bacteria (Appendix 10) were also derived from these surveys

The first, the 'Snapper' programme, described the pelagic ecosystem (including zooplankton) underpinning larval fish communities in the Gulf during nine, 3-week voyages spanning three snapper spawning seasons (November to January) in 1985–6, 1986–87 and 1987–88 (Zeldis et al. 2005). Water samples were taken at up to 43 grid stations at standard depths.

Table 85: Descriptions of research programmes used for the biomass estimates of lower trophic levels.

Programme	Meta variable	Spatial stratification	Temporal stratification	Integration depth	Functional Groups
Snapper 1985–88	Chl-*a*	Throughout HG inshore of Little Barrier Island	Voyages in Nov, Dec, and Jan., 1985–1988.	Near bed	Total.
	Meso- and macro zooplankton	Throughout HG inshore of Little Barrier Island	Voyages in Nov, Dec, and Jan., 1985–1988.	Near bed	By taxon, size, feeding type, total.
	Fish eggs and larvae	Throughout HG inshore of Little Barrier Island	Voyages in Nov, Dec, and Jan., 1985–1988.	Near bed	By taxon, total.
Bionosex 1996–97	Bacteria	NE shelf (Cape Brett to Little Barrier), Hauraki Gulf (outer and inner Gulf).	Voyages in Sep., Oct., Dec., and Jan.-Feb. 1996–97.	Mixed layer	Total (Hall et al. 2006)
	Chl-*a*	NE shelf (Cape Brett to Little Barrier), Hauraki Gulf (outer and inner Gulf).	Voyages in Sep., Oct., Dec., and Jan.-Feb. 1996–97.	Near bed	Total.
	Phytoplankton	NE shelf (Cape Brett to Little Barrier), Hauraki Gulf (outer and inner Gulf).	Voyages in Sep., Oct., Dec., and Jan.-Feb. 1996–97.	Mixed layer	Pico, nano to net plankton, total. (Chang et al. 2003)
	Microzooplankton	NE shelf (Cape Brett to Little Barrier), Hauraki Gulf (outer and inner Gulf).	Voyages in Sep., Oct., Dec., and Jan.-Feb. 1996–97.	Mixed layer	By taxon, total.
	Meso- and macro zooplankton	NE shelf (Cape Brett to Little Barrier), Hauraki Gulf (outer and inner Gulf).	Voyages in Sep., Oct., Dec., and Jan.-Feb. 1996–97.	Near bed or max. 70 m.	By taxon, size, feeding type, total.

Programme	Meta variable	Spatial stratification	Temporal stratification	Integration depth	Functional Groups
C-SEX 1998-2009	Bacteria	Inner to outer Shelf, outer Firth of Thames.	1998–2005, 1998–present, both seasonal	Near bed	Total.
	Chl-*a*	Inner to outer Shelf, outer Firth of Thames.	1998–2005, 1998–present, both seasonal	Near bed	Total.
	Phytoplankton	Inner to outer Shelf, outer Firth of Thames.	1998–2005, 1998–present, both seasonal	Near bed	Pico, nano to net, total.
	Microzooplankton	Inner to outer Shelf, outer Firth of Thames.	1998–2005, 1998–present, both seasonal	Near bed	By taxon, total.
	Meso- and macro zooplankton	Inner to outer Shelf, outer Firth of Thames.	1998–2005, 1998–present, both seasonal	Near bed or max 70 m.	By taxon, size, feeding type, total.

Fluorescence, chlorophyll-a concentration (chl-a), and Lugol iodine-preserved phytoplankton compositions were determined as described in Zeldis et al. (1995).

Second, there were four Bionosex voyages in total: September 1996 (kah9614), October 1996 (tan9612), December 1996 (kah9617), and January-February 1997 (tan9702). Bionosex stations are shown in Figure 34. Phytoplankton carbon was measured at three stations (H3, G2, E3) at 3–6 depths focused on the mixed layer (where primary productivity is generally highest). Chl-a at discrete depths was also measured at 17 stations (Figure 34; stations C1–C2, E1–E6, G1–G4, H1–H5), and these were integrated and converted to carbon as described below.

Third, CSEX was a series of 13 research voyages carried out between July 2003 and March 2008. There were three CSEX stations in the study area (C1, C3, SA03) where chl-a and phytoplankton carbon was measured at discrete depths (Figure 34). Again, these were integrated to give an estimate of the water column concentration of chl-a and carbon as described below. See Gall & Zeldis (2011) for details of methodology.

2.2 Water-column integration

Concentrations of chl-a at discrete depths were integrated with respect to depth to obtain an integrated water column phytoplankton carbon concentration. In order to obtain a whole water column estimate of phytoplankton biomass, the concentration of phytoplankton is assumed to decrease to zero 10 m below the deepest depth sampled. The concentration of phytoplankton is assumed to be constant between the shallowest depth sampled and the water surface. Usually the shallowest depth is 5 or 10 m.

2.3 Carbon-chlorophyll ratio

Cell carbon was measured at three selected stations (H3, G2, E3) over four seasons on the Bionosex series of voyages as reported in Chang et al. (2003) and at two stations (C3, SA03) on the CSEX series of voyages (Gall & Zeldis, 2011). Data from Bionosex indicate that the carbon to chl-a ratio (C:Chl a) of phytoplankton in the study area varies between 4.9–45, with a mean value of 18.7 (N=12).

Twenty-four measurements of the carbon-chlorophyll ratio were also made during the CSEX series of voyages, with a mean value of 25.2 (range 3.7–74, N=43). It is noted that the C:Chl ratios in table 2 of Gall & Zeldis (2011) do not include pico-phytoplankton as carbon measurements were from the microscopic analysis which do not include picoplankton. Measurement of picoplankton requires analysis by flow cytometry. Gall & Zeldis (2011) suggested including an estimate of picoplankton carbon in the microscopic analysis data as follows: "a previous study in the northeast shelf and Hauraki Gulf region (Chang et al., 2003) found mean pico-phytoplankton C to be about 5 mg m^{-3} from early spring to late summer. Inclusion of pico-phytoplankton C in the present estimates produced C:chl-a values within the literature range for phytoplankton of 10–200 (Falkowski & Raven, 1997)."

The values of carbon:chl-a measured in the Hauraki Gulf on these two sets of voyages do not show a clear variation by location or season, so we use the mean value of all data of 23.8 (N=55). We note that this carbon to chl-a ratio is lower than suggested by Zeldis et al. (2005) which assumed a carbon to chl-a ratio of 50 for the Hauraki Gulf region. For comparison, the ratio of carbon to chlorophyll-*a* in marine phytoplankton has been found to vary considerably, from 10 to over 200 gC/g Chl-*a* (Taylor et al. 1997; Lefevre et al. 2003; Falkowski & Raven, 1997). In subtropical waters near New Zealand, measurements show a seasonal variation in C:Chl-a values of approximately 50 before the spring bloom, 40 during the spring bloom, and 60 after the bloom (Boyd 2002).

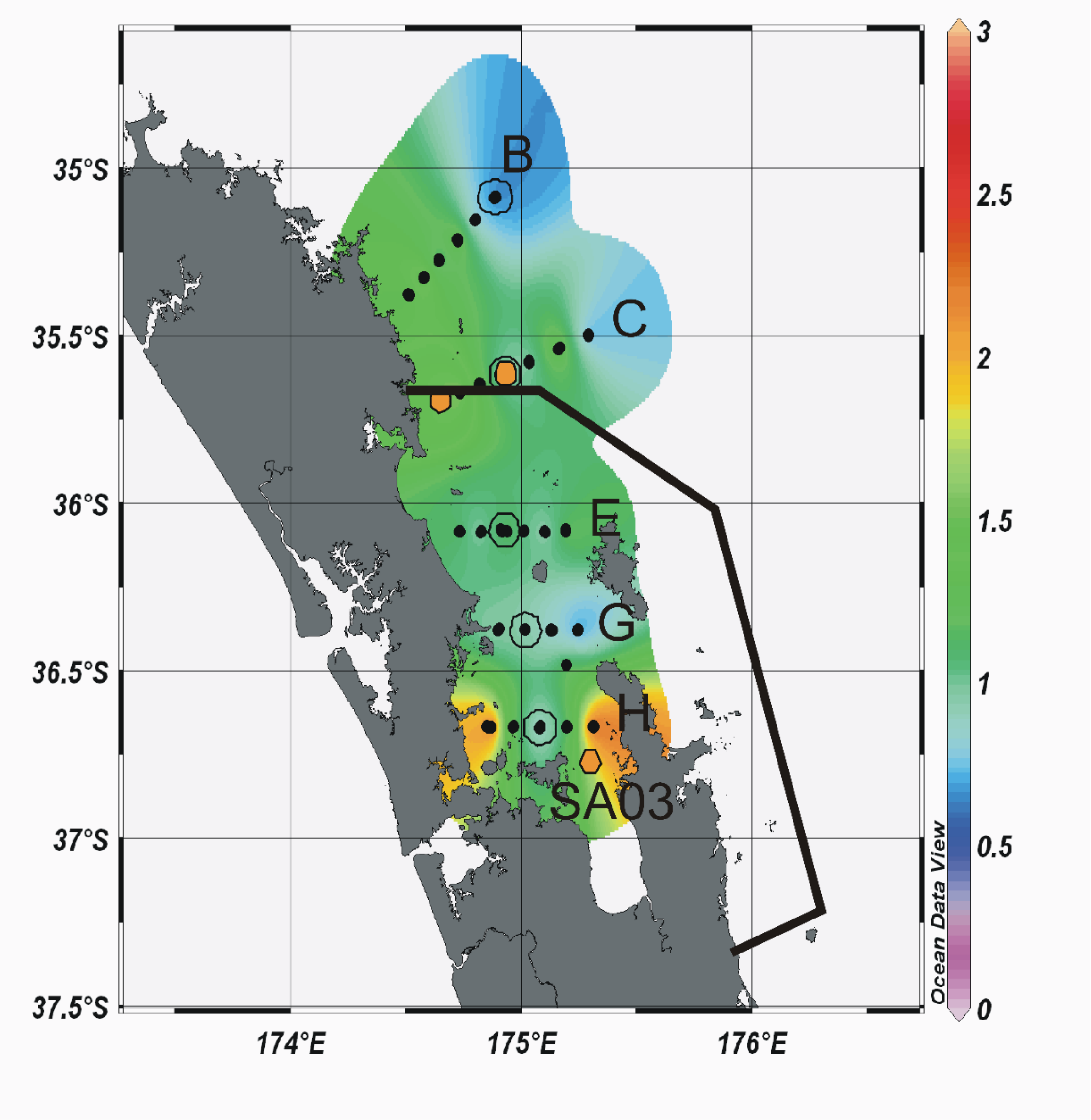

Figure 34: Sampling stations for Snapper (large circles), Bionosex (black dots) and C-SEX (orange circles) research programmes. Letters give the names of the transects, which are numbered from 1 at the western end. The heavy solid line is approximately the boundary of the study area. The background contour is near surface chl-a (mg m^{-3}).

2.4 Seasonal cycle

We used satellite measurements of ocean colour from NASA's MODIS-Aqua sensor to observe the seasonal cycle of near-surface chl-a concentration in the mixed-layer in the study region. Daily measurements of ocean colour taken by the MODIS-Aqua sensor at resolutions of 4 km were obtained from NASA via the Giovanni online data system which is developed and maintained by the NASA GES DISC (disc.sci.gsfc.nasa.gov/giovanni). These are shown in Figure 35. Preliminary validation studies in New Zealand waters indicate that the algorithm and sensor used are likely to result in estimates of chl-a that are accurate within approximately 50% of the value measured by *in situ* methods in waters off the continental shelf, but it is known that suspended sediment and/or coloured dissolved organic matter can lead to greater uncertainties in the coastal zone. Also, satellite sensors only see the surface of the ocean whereas we are interested in water-column integrated values. Consequently, we used the satellite data only to fill-in the seasonal cycle of phytoplankton abundance, and used the in-situ sampling to estimate the absolute water column integrated chl-a concentration.

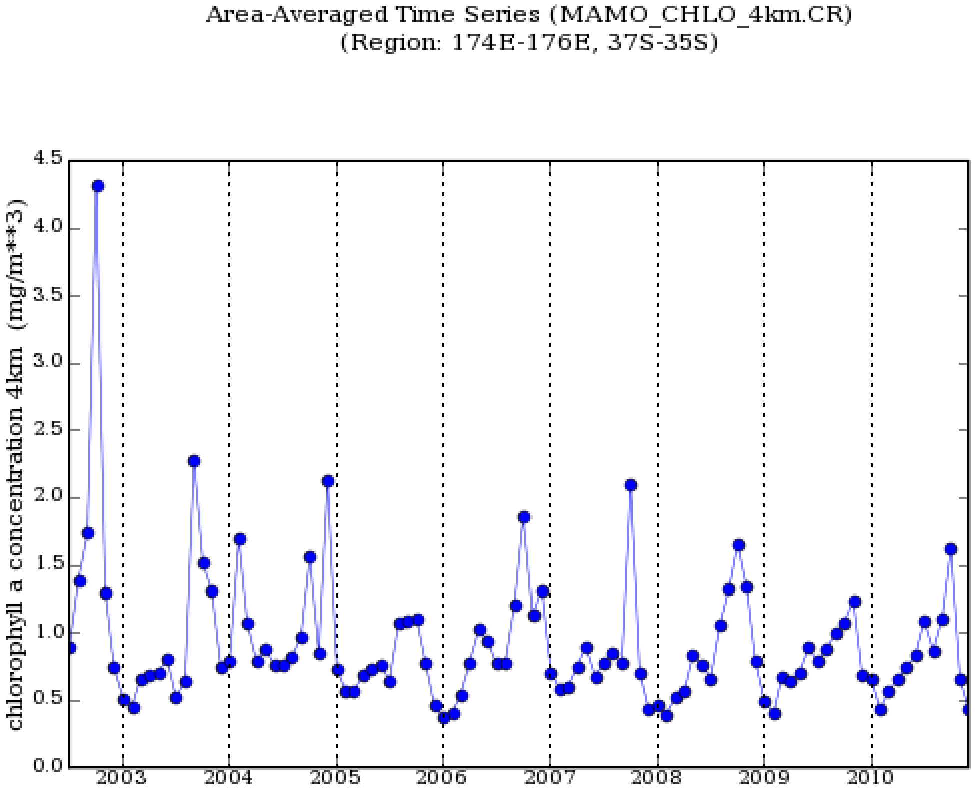

Figure 35: Surface chlorophyll-a concentration in the study region measured by the MODIS-Aqua sensor and produced with the Giovanni online data system, developed and maintained by the NASA GES DISC. The region used was Latitude(-37, -35.5), Longitude(174.5, 176) and the period of data availability is July 2002 – December 2010.

2.5 Interannual variability and trends

Zeldis et al. (2005) provided a summary of interannual variability of phytoplankton production in the Hauraki Gulf as follows. “There is evidence that the ecosystem state of the Hauraki Gulf varies interannually in response to physical forcing. Upwelling and downwelling over the adjacent continental shelf are favoured by northwesterly and southeasterly along-shelf winds, respectively (Sharples & Greig 1998; Zeldis 2004), and cause variation in nutrient supply and phytoplankton assemblages (Chang et al. 2003; Zeldis 2004). The strength of the mean wind also varies (Gordon 1985), potentially causing variation in vertical mixing regimes with consequent effects on primary productivity. Both wind direction and wind strength have an interannual signal related to El Niño – Southern Oscillation, with weaker, predominately westerly winds during summer in El Niño periods (Gordon 1985).”

It is not well known if phytoplankton biomass within the study area is undergoing long-term, consistent change. There is some evidence in the measurements of near surface chl-a concentration measured by the satellite sensor MODIS over the period July 2002–December 2010 that phytoplankton biomass may be decreasing at a rate of about 4.6% y^{-1} (Figure 36). However, the R^2 value is small (8.9%) and P=0.64 (F-test) indicating that the relationship is not significant. Hence, the trophic model will assume no substantial and consistent change from year to year and we set accumulation to zero.

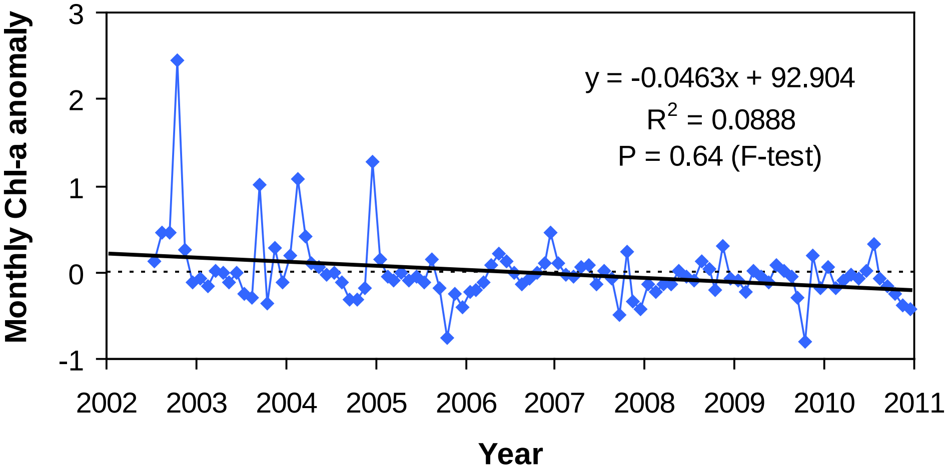

Figure 36: Monthly anomaly of surface chl-a concentration measured by the MODIS-Aqua sensor for the Hauraki Gulf. The anomaly is the chl-a value measured in a given month by MODIS-Aqua minus the mean monthly chl-a calculated over the period July 2002–December 2010. Black line: Regression line fitted by least squares, with equation and significance of F-test shown.

2.6 Phytoplankton biomass

Data from the four field campaigns and from the MODIS satellite are shown in Figure 37. We used both the estimates of phytoplankton carbon from chl-a measurements scaled by the C:chl-a ratio, and measurements of phytoplankton carbon directly. The data from the voyages was used to scale the MODIS measurements of mean monthly chl-a concentration. For illustration, the maximum and minimum scaled monthly measurements from MODIS over the period July 2002 to December 2010 are also shown. There are 8 or 9 years of data for each month. It can be seen that the *in situ* data have a similar mean annual cycle to that shown by the MODIS data, and that the spread of data measured on the research voyages is generally contained in the envelope of measurements observed remotely. The average annual phytoplankton biomass in the study region is hence estimated to be B=1.05 gC m^{-2} which is equivalent to 17.0 ktC in the study area.

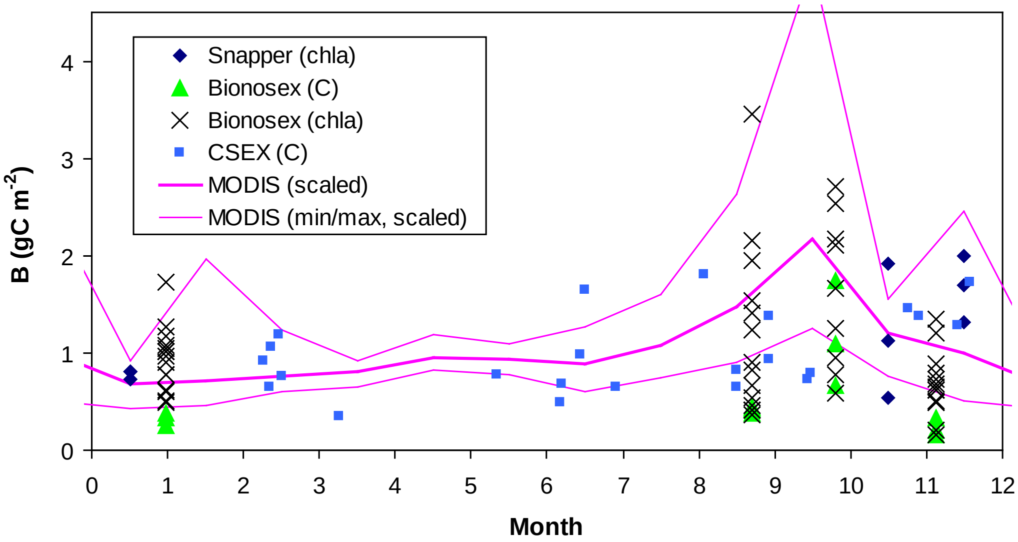

Figure 37: Various symbols: Measurements of water column integrated phytoplankton carbon concentration in the study region based on shipboard sampling of chlorophyll-a and phytoplankton carbon from Zeldis et al. (1995), Chang et al. (2003), and including data reported in Gall & Zeldis (2011). Pink line: Annual cycle fitted based on MODIS-Aqua satellite measurements of surface chl-a concentration. The thick line is based on the monthly average data from MODIS and the thin lines from the maximum and minimum measurements by MODIS over the period July 2002 – December 2010.

3 Phytoplankton production

Primary production due to phytoplankton growth was based on four sets of measurements.

First, primary production by phytoplankton in the study region was described by Zeldis et al. (2005) based on data from the 'Snapper' series of research voyages. The methodology used to estimate primary production from the 'Snapper' series of research voyages in the study region is as follows. First, measured chl-a concentrations were used to estimate a light attenuation (Riley 1956). Gross carbon uptake due to phytoplankton growth was estimated for each depth interval based on a measure of maximum photosynthetic potential (P_{max}) and incident irradiance (Parsons et al. 1984). The P_{max} was obtained from production-versus-irradiance (P-I) experiments carried out in the Hauraki Gulf in 1998–2000, namely P_{max}=3.0 gC gChl-a^{-1} d^{-1} (Zeldis et al. 2005). Zeldis et al. (2005) set surface irradiance as a constant using representative photosynthetically active radiation profile data collected in the surveys of Chang et al. (2003) in the inner Hauraki Gulf in January 1997. Net daily production was estimated taking into account length of daylight and probable reduction in irradiance either side of midday, both obtained from a simple model of cloud-free solar irradiance in the study area using solar position (Kirk 1994), Earth-sun distance (Spencer 1971), average atmospheric attenuation of visible wavelengths of light (Bird 1984; Leckner 1978), and mean extraterrestrial solar irradiance data (Wehrli 1985). The relationship between solar irradiance and primary production was taken from Parsons et al. (1984) in a similar manner to Zeldis et al. (2005). This gave annual-equivalent estimates of production between 95 and 274 gC m^{-2} y^{-1}, with a mean of 165 gC m^{-2} y^{-1}.

Second, Bury et al. (2012) used ^{13}C uptake rates measured on Bionosex voyages to estimate primary production and reports values between 120-465 gC m^{-2} y^{-1}, with an average of 229 gC m^{-2} y^{-1}.

Third, Gall & Zeldis (2011) used ^{13}C incubations on six research voyages (part of C-SEX) to measure net photosynthetic production at two stations (one Gulf, one shelf) in four seasons. Values obtained were equivalent to annual production rates of 86–508 gC m^{-2} y^{-1}, with an annual average of 204 gC m^{-2} y^{-1}.

We use an average of these three estimates of production (165, 229, 204 gC m^{-2} y^{-1}), i.e. 200 gC m^{-2} y^{-1}. For comparison, Vincent et al. (1989) modelled the upper limit to oceanic phytoplankton production as a function of latitude in the New Zealand Exclusive Economic Zone and estimated this to be 215 gC m^{-2} y^{-1} at the latitude of the study area, very close to the production rate estimated here. Our estimates of production and phytoplankton biomass imply a P/B ratio of 190 y^{-1} which is plausible; other annual phytoplankton P/B (net of phytoplankton respiration) in the literature range from 5–248 y^{-1}, with a mean of 79 y^{-1} (Table 86).

Table 86: Annual net productivity rates for phytoplankton from the scientific literature.

P/B (y^{-1})	Locality	Reference
134	Central Pacific	Allain 2005
95	Central Pacific	Allain 2005
93	Newfoundland	Heymans 2003
166	South Brazil Bight, upwelling system, 20–200 m	Gasalla & Rossi-Wongtschowski 2004
66	Gulf St Lawrence Canada	Morissette et al. 2003
52	Nova Scotia coast to edge of shelf	Bundy 2004
82	Baltic Sea	Harvey et al. 2003
20	South Benguela; Upwelling coast to shelf break	Shannon et al. 2003
40	North Benguela; Upwelling coast to shelf break	Heymans & Baird 2000
45	Central Chile upwelling coast to 30 Nautical miles hake, 1992	Neira & Arancibia 2004
31–76	NE USA: Bering Sea, Nrth Atlantic, Gulf of Maine	Link et al. 2006
6	East Bering Sea; temperate shelf down to 500 m	Trites et al. 1999
13	SE USA Tropical continental shelf intertidal to 500 m	Okey & Pugliese 2001
5	USA mid-Atlantic Bight; temperate continental shelf to 200 m	Okey 2001
20.87	South Catalan Sea 50 m to 400 m: oligotrophic system	Coll et al. 2006
248	New Zealand Southern Plateau	Bradford-Grieve et al. 2003
221	Te Tapuwae o Rongokako, East coast New Zealand, to 50 m	Pinkerton et al. 2008
190	Hauraki Gulf, New Zealand; shore to 250 m	This study

4 Other information: EE, imports, exports, transfers

Given the high rate of production and short lifespan of marine phytoplankton (few days), the proportion of the biomass being transferred across boundaries of the study area is likely to be very small. In the trophic model, we assume zero net import.

There are no transfers due to growth or other factors to be taken into account.

Ecotrophic efficiency (EE) is not known for phytoplankton in the study area. Ecotrophic efficiency measures the proportion of the annual production that is available for predation ("passed up the food chain") as opposed to being transferred to a detrital group. In the case of phytoplankton, dead individuals or exudants will be decomposed mainly by bacterial action or fed on directly by benthic detrivores. In open ocean systems, most phytoplankton production is usually directly grazed. In coastal systems, a reasonably high proportion of phytoplankton primary production may not be grazed in the water column and can be transferred to the benthos as detritus. This fraction can be 50% but is usually much less. Based on unpublished data from near-bed sediment traps in the study region in 1996 and 1997 (Scott Nodder, NIWA, pers. comm.) we estimate a particulate organic carbon flux over a typical annual cycle of about 8.6 gC m^{-2} y^{-1}, although values of 4.6–12 gC m^{-2} y^{-1} are considered possible (see Bacterial and Detritus section of model documentation). If all, or the majority, of detrital flux is from ungrazed phytoplankton, this suggests ecotrophic efficiencies for phytoplankton of 0.91 (range 0.87–0.95). We used a value of E=0.91 for phytoplankton in the study area but place relatively high uncertainty on this parameter so that the model can redefine this value based on other evidence such as the rate of formation of detritus in the water column from microzooplankton.

5 Summary of parameters

Parameters for phytoplankton in the trophic model representing the present day are given in Table 87.

Table 87: Summary of parameters in the trophic model.

	E	B	B	P/B	P	X	A
		gC m^{-2}	Mt C	y^{-1}	Mt C y^{-1}		
Phytoplankton	0.91	1.05	0.017	190	3.2	0	0

6 Historical parameters

6.1 Climate impacts on phytoplankton production

Trophic models are required for phytoplankton in four historical periods: 1950, 1790, 1500 and 1000. Natural drivers of environmental change in New Zealand during the last millennium were examined by Lorrey et al. (2013).

It seems likelythat primary productivity would (or at least may) have been affected by changes in climate in the historical models. However, the direction and magnitudes of the changes are unknown. The relationship between wetter and colder climate and primary production of phytoplankton is not clear, as this depends on various factors including incident solar irradiance (via cloud cover and atmospheric transparency), riverine run-off (which affect water turbidity and terrestrial nutrient input), vertical mixing/upwelling, and cross-shelf (onshore-offshore) mixing. On balance, it seems likely that colder temperatures will lead to lower primary productivity, but that these changes may be relatively modest. Vincent et al. (1989) modelled the upper limit to oceanic phytoplankton production as a function of latitude in the New Zealand Exclusive Economic Zone. Their modelling results suggest that a 5° increase in latitude from the latitude of the Hauraki Gulf corresponds to a decrease in primary production of 14%, whereas a 10° increase in latitude leads to a 35% decrease in annual primary production. Here, we assume that the change in climate between the present day and 1500 is equivalent to a 5° change in latitude with the corresponding decrease in primary production, which is allocated evenly between changes in phytoplankton biomass and P/B. Changes in 1790 and 1950 are estimated by linear interpolation with date. We assume that the climate is sufficiently similar in year 1000 to the present day that primary production is the same in the two periods. Estimates of historical primary productivity due to phytoplankton (net of phytoplankton respiration) are shown in Table 88.

Table 88: Assumed changes in phytoplankton biomass and productivity as a result of climate changes through recent history (see text for more details). Other parameters are assumed not to change from the present day model.

Period	B	P/B	P	Change in P from present
	gC m^{-2}	y^{-1}	gC m^{-2} y^{-1}	%
Present	1.05	190	200	0
1950	1.04	188	197	1.6
1790	1.02	184	188	5.9
1500	0.98	176	173	13.6

1000	1.05	190	200	0

6.2 Anthropogenic input of nutrients

Changes to land-use in the Hauraki region during the period of human contact are likely to have substantially changed the river catchments and hence affected the material flowing into the study area. In 1769, the English explorer Captain James Cook sailed the bark ‘Endeavour’ to Hauraki Gulf and into the Firth of Thames, and put his longboat up the Waihou River (Wilkie, 1914). His crew cut giant kahikatea trunks for ship’s spars from the luxuriant native forest they found there and Cook’s reports started a timber boom in the area. Today, the Waikato catchment is almost entirely cleared of native forest and converted to agriculture. Since the late 1900s, when land-use in the Waikato region was mainly “dryland” – sheep and beef grassland – there has been an intensification of agrarian land-use in the Waikato with dairying now the main form of farming.

Changes to land-use will have affected riverine input of dissolved nutrients to the study region, and this is likely to have affected primary production in the Hauraki Gulf region since the year 1000. Nutrients likely to affect primary production in the Hauraki Gulf include nitrate especially, but also urea and ammonia (together characterised in terms of inorganic nitrogen, DIN), and reactive phosphorus (including phosphate). To estimate changes in primary production in the study region from 1000 to the present day, we estimate changes to nutrient input and scale primary production proportionately. We consider nutrient input from three sources: (1) riverine input (Waihou, Piako, Waitoa and Kauaeranga Rivers); (2) waste from municipal wastewater treatment plants and overflows from the wastewater pipe system; (3) oceanic sources due to minxing of water across the shelf break into the Hauraki Gulf.

Nationally, there is a strong, positive correlation between increasing amounts of land used for dairy farming and increasing freshwater nitrogen loads (Parliamentary Commissioner for the Environment 2013) and recent intensification of dairying is likely to have led to increases in nutrient loadings of the Waihou and Piako Rivers compared to loadings with pastoral or bush-clad catchments. Catchments in the Coromandel Peninsula remain forested and the rivers draining them have nutrient concentrations an order of magnitude lower than in the Waihou consistent with the contrast between native-forested and agricultural catchments throughout New Zealand (Close & Davies-Colley 1990).

Changes to the nutrient loading of the Hauraki Gulf from Auckland wastewater are assumed to approximately follow changes in population size of Auckland. As these changes are more than two orders of magnitude since 1500 this approximation is reasonable. Changes to primary production occurring due to oceanographic and climate factors are assumed to follow changes described in Section 6.1 (Table 88). Variations in primary production for the study region as a whole were estimated by combining these effects in different parts of the region based on biogeochemical budgeting (Zeldis, 2004; Swaney & Giordani, 2011). The results are shown in Table 89.

Table 89: Estimated changes to primary production (PP) due to phytoplankton in the Hauraki Gulf (including Firth of Thames, FoT) study area over the period of human contact. Proportions of primary production by the areas were based on MODIS estimates of chl-a adjusted for euphotic zone depth (see Section 2 and 3, this Appendix).

	Present	1950	1790	1500	1000
Catchment type	Dairy	Dryland	Bush	Bush	Bush
Auckland population (000s)	1486	386	18	6	0

Firth of Thames 0.26 total PP (present)	Offshore nutrients	0.40	0.40	0.40	0.40	0.40
	Riverine input	0.60	0.12	0.06	0.06	0.06
	All	1.00	0.52	0.46	0.46	0.46
Hauraki Gulf 0.35 total PP (present)	Oceanic	0.80	0.80	0.80	0.80	0.80
	Auckland wastewater	0.05	0.01	0.00	0.00	0.00
	Export from FoT	0.10	0.02	0.01	0.01	0.01
	Other rivers	0.05	0.03	0.03	0.03	0.03
	All	1.00	0.86	0.84	0.84	0.84
Outer Hauraki Gulf 0.39 total PP (present)	oceanic	0.90	0.90	0.90	0.90	0.90
	rivers	0.10	0.10	0.05	0.05	0.05
	All	1.00	1.00	0.95	0.95	0.95
Model area	Relative PP due to human activities	1.00	0.82	0.78	0.78	0.78
	Relative PP due to oceanographic/climate	1.00	0.98	0.94	0.86	1.00
	Relative PP	1.00	0.81	0.74	0.67	0.78
	Total PP (gC/m^2/y)	200	162	147	135	156
	Change from present	0.0	-18.9	-26.5	-32.5	-21.9

7 Acknowledgements

This research was funded by Ministry for Primary Industries project ZBD200505 ("Long-term change in New Zealand coastal ecosystems") and by the New Zealand Ministry of Science and Innovation project C01X0501 (Coasts & Oceans OBI). We acknowledge Dr Mary Livingston and Dr Martin Cryer (Ministry for Primary Industries) for supporting the project and Dr Alison MacDiarmid for project leadership. Dr Janet Bradford-Grieve provided comments on an earlier draft of this work.

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Appendix 9: Trophic modelling of Hauraki Gulf: Mangrove, Macroalgae, Seagrass and Salt marsh

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1 Introduction

1.1 Trophic groups

There are a number of non-phytoplankton primary producers in the study area. It is necessary to combine species into trophic groups in order to have a reasonable number of groups in the trophic model. Here, we follow approaches developed by Lundquist & Pinkerton (2008) and use the following non-phytoplankton primary producer groups to estimate parameters:

- Macroalgae – canopy forming, foliose, and crustose and coralline combined
- Mangrove, saltmarsh, seagrass
- Microphytobenthos, periphyton and epiphytes

1.2 Organisation of this report

This report is organised as follows:

- Habitat definition and study area
- Detailed information on groups 1-6 of primary producers
- Summary of parameters

2 Habitat definition and study area

2.1 Habitats in the study area

The Hauraki Gulf study area was separated into regions that could be classified according to typical abundances of flora and fauna. Both depth (**Figure 38**) and exposure (**Figure 39**) were determined to be key factors influencing faunal and floral communities. Three exposures were defined (Coastal Exposed, Coastal Sheltered, and Estuarine), and four depths were defined for each exposure (0–9 m, 10–29 m, 30–99 m, 100–249 m).

Soft sediment intertidal habitats were further defined into six subcategories based on dominant fauna/flora (mangrove, seagrass, mudflat, cockle beds (*Austrovenus* and *Macomona*) and, tubeworm) (**Table 90**). To determine the amount of habitat in intertidal versus shallow subtidal categories of estuarine sediments (0–9 m), we used the definitions and data provided by the Estuary Environments Classification (EEC) database (Hume et al. 2003; 2007), which estimates a total of 1857 km^2 of estuarine area in the Hauraki Gulf region. Based on estimates of the percent intertidal of each estuary in the database, 403 km^2 of intertidal habitat is present (average percent intertidal of all estuaries: 43.8%; average percent intertidal of all habitats, biased by larger harbours: 21.7%).

Note that this figure differs from the categories as estimated from GIS due to some estuaries (e.g., Waitemata Harbour, Whangarei Harbour, Firth of Thames) being included in full in this EEC calculation, whereas channel and deeper habitats of these harbours are included in deeper (e.g. 10–29 m) categories for this report. We used the relative percent of mud and sand habitats across the entire Hauraki Gulf to estimate the total of each generic sediment characteristic habitat in the estuary intertidal. Salt marsh was estimated as all swamp habitats (0.91 km^2). Mud was determined to include mangrove, seagrass and mudflat habitats by using GIS derived estimate of seagrass coverage plus mangrove estimates from EEC, and subtracting both values from mudflat habitat to get remainder of mudflat unvegetated intertidal habitat. Sand habitats were calculated as an estimate of 1/3 each of 3 types of intertidal estuarine community: cockle *Austrovenus* and, *Macomona* habitats, tubeworm.

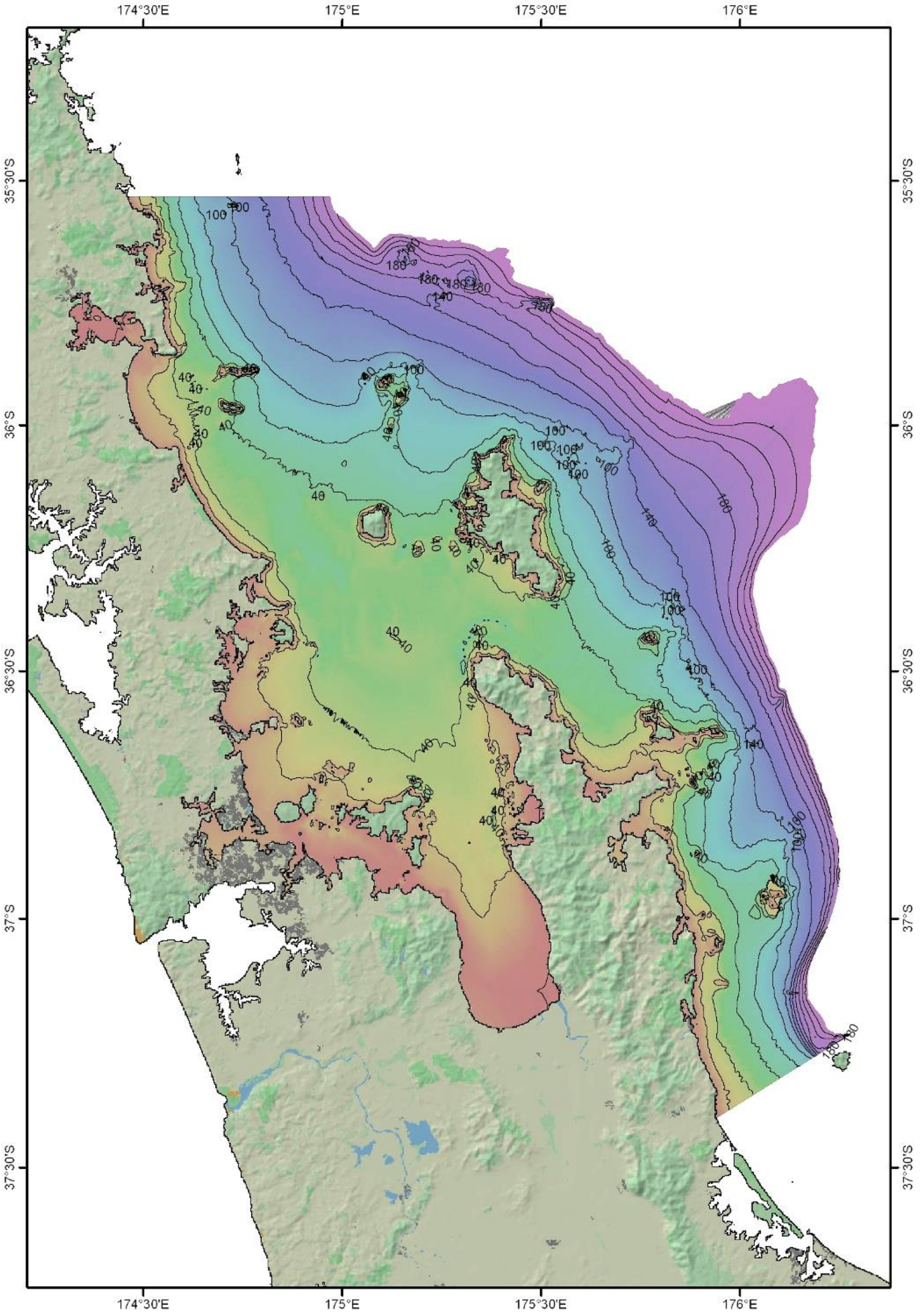

Figure 38: The Hauraki Gulf study area. Contours represent bathymetry (depth in metres).

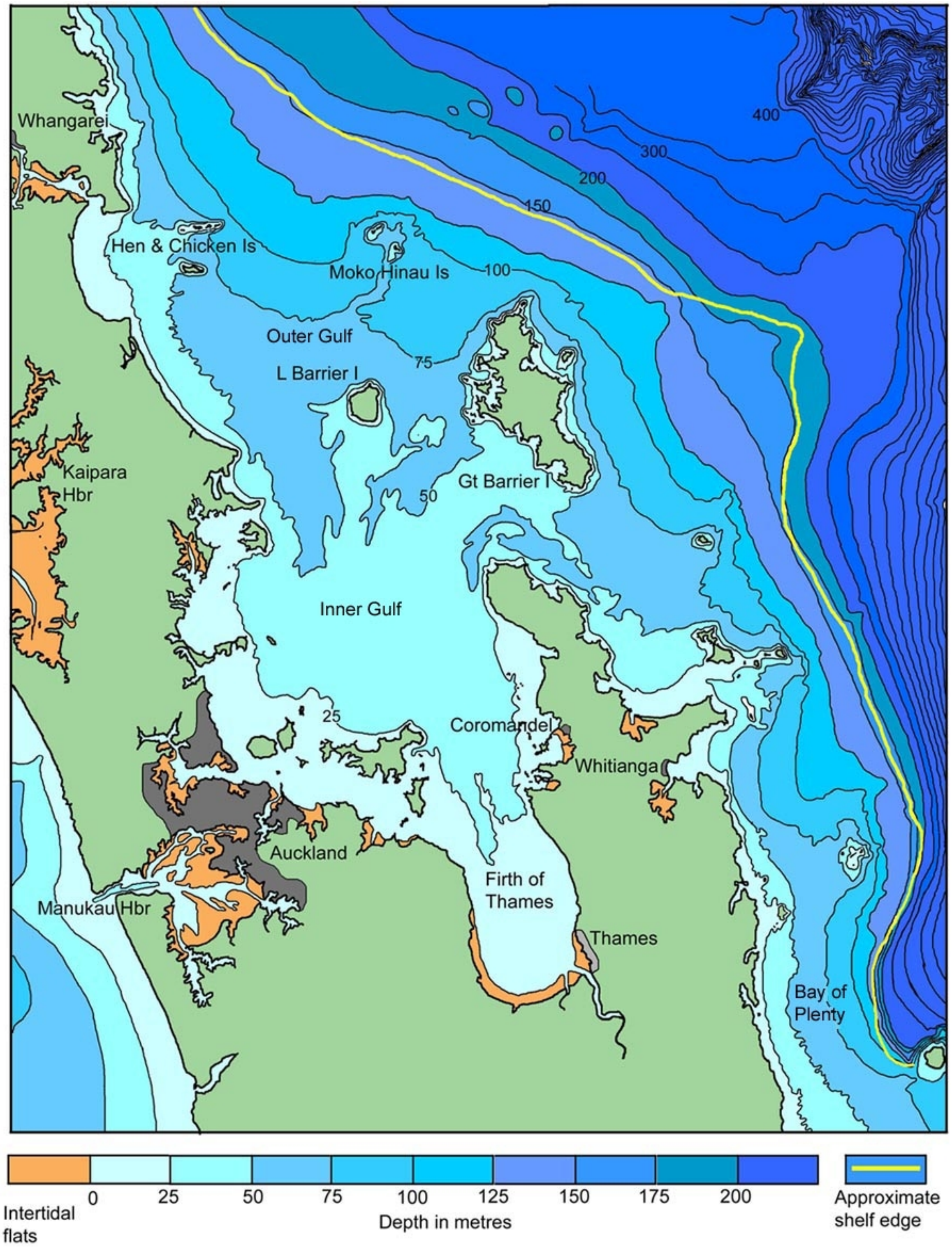

Figure 39: The Hauraki Gulf study area (courtesy of Larry Paul), showing inner Gulf (coastal sheltered) and outer gulf (coastal exposed) demarcations.

Table 90: Area in each exposure/depth category for the trophic model.

Category	Coastal Exposed	Coastal Sheltered	Estuarine	Total
All habitat types		Area (km^2)		
0 – 9 m	466.39	413.17	532.41	1 411.97
10 – 29 m	1 332.82	397.74	13.50	1 744.05
30 – 99 m	7 136.21	0.00	0.00	7 136.21
100 – 249 m	5 955.35	0.00	0.00	5 955.35
Total	14 890.76	810.91	545.90	16 247.57
Unvegetated soft sediments				
0 – 9 m	268.70	377.62	469.26	1 115.58
10 – 29 m	1 184.59	392.35	12.67	1 589.61
30 – 99 m	7 036.08	0.00	0.00	7 036.08
100 – 249 m	5 935.00	0.00	0.00	5 935.00
Total	14 424.36	769.97	481.93	15 676.27
Mangrove (0 – 9 m)	2.49	1.08	49.78	53.35
Seagrass (0 – 9 m)	1.49	0.59	3.31	5.40
Estuary area (Hume et al. 2003, 2007)	…	…	1 856.97	1 856.97
Intertidal estuary (EEC)	…	…	403.03	403.03
Intertidal sand (assume 1/3 each Macomona, cockle, tubeworm habitat)	…	…	152.65	152.65
Intertidal mudflat (minus seagrass from GIS)	…	…	182.04	182.04
Salt marsh	…	…	0.91	0.91
Mangrove (from EEC)	…	…	65.06	65.06
Intertidal Rocky Reef	23.75	6.90	1.24	31.89
Subtidal Rocky Reef				
0 – 9 m	189.91	32.29	10.04	232.24
10 – 29 m	148.14	5.37	0.83	154.34
30 – 99 m	100.11	0.00	0.00	100.11
100 – 249 m	20.35	0.00	0.00	20.35
Total	458.50	37.66	10.87	507.03

2.2 Datasets

Datasets used in this section include the rocky reef dataset detailed in Shears & Babcock (2004a, b) and the Ministry for Primary Industries data on soft sediment algae (courtesy of Kate Niell, NIWA). The latter had one study site in the Hauraki Gulf region (Whangarei) which provided spring and summer estimates of macroalgal biomass in soft sediments over nine sites, with depths ranging from 1.0 to 7.6 m. For the intertidal zone, we used macroalgal density estimates from work on the rocky reef ecosystem at Te Tapuwae o Rongokako, off the New Zealand northeast coast (Lundquist & Pinkerton 2008).

3 Macroalgae

3.1 General information

Macroalgae was divided into three trophic groups on the basis of structural attributes which are generally associated with differences in production: (1) Macroalgae (large brown, canopy); (2) Macroalgae (foliose and turfing red and green algae, brown non-canopy species); (3) Macroalgae (crustose, corallines). Canopy-forming subtidal species include *Ecklonia radiata* (kelp) and other large brown algae (*Carpophyllum flexuosum*, *C. plumosum*, *C. angustifolium*, and *C. maschalocarpum*, *Sargassum sinclairii*, *Landsburgia quercifolia*, *Lessonia variegat*a). Common foliose species observed in subtidal surveys of the region include red algae such as *Pterocladia lucida*, *Melanthalia abscissa*, *Osmundaria colensoi*, and *Plocamium* spp.; brown algae including *Hormosira banksii*, *Cystophora retroflexa*, *Zonaria turneriana*, *Halopteris* sp., *Carpomitra costata*, and *Glossophora kunthii*, *Xiphophora gladiata*; and the green algae *Caulerpa geminata*, *Codium convolutum*, *Ulva spp.*(Shears & Babcock 2004a). Turfing red and brown algae (e.g. *Distromium scottsbergii*, *Laurencia distichophylla*) and crustose coralline algae (e.g. *Corallina officinalis.*) are also common understory species.

3.2 Biomass

Subtidal abundance estimates of macroalgae in each habitat type were obtained from transect surveys across north-eastern New Zealand (Shears et al. 2004), as data on macroalgae were not collected in the NIWA rocky reef survey. Abundance of 24 algal functional groups was calculated from 870 × 1 m^2 quadrats sampled at 4 depths (0–2 m, 4–6 m, 7–9 m, and 10–12 m) at 10 sites in 5 regions in the Hauraki Gulf (Hahei, Leigh, Long Bay, Mokohinau Islands, and Tawharanui). As macroalgal species composition and abundance differs significantly with depth (Schiel 1988, 1990; Shears & Babcock 2004a, b), we estimate biomass of macroalgal categories for depths of 0–2 m, 3–9 m (average of 4–6 m and 7–9 m estimates), 10–19 m (based on 10–12 m), and 20–29 m (assuming 10% of canopy forming, 50% of foliose, and 100% of crustose abundance at depth of 10–12 m). For larger species, size was recorded for each individual algae observed; for turfing and encrusting morphologies, percent cover was recorded for each quadrat. Individual macroalgal observations were converted to gDW and then averaged across depths within the Hauraki Gulf.

For canopy algae, abundance and percent cover for each quadrat were converted to dry weights using length-weight relationships from Shears & Babcock (2004a). We calculated biomass (gDW) from observed plant lengths from size frequency measurements of *Ecklonia radiata*, *Carpophyllum maschalocarpum*, *C. flexuosum*, and other canopy forming and foliose algae from transects taken within the Hauraki Gulf (Shears & Babcock 2004a). Where multiple length-weight relationships were available, we used relationships based on data from the closest location to the study area; most often these were from north-eastern New Zealand, and more specifically the Hauraki Gulf. For non-canopy algal groups, percent cover – biomass (dry weight) relationships for algae were estimated from relationships available in Shears & Babcock (2004a) (Table 91), which were obtained by drying algal samples at 80ºC for three days and weighing final samples (Shears & Babcock 2004a).

We used information from northeast New Zealand to estimate macroalgal biomass in the intertidal zone (Lundquist & Pinkerton 2008). In this study, percent cover and presence of common species of intertidal algal species were recorded in intertidal monitoring surveys of a marine reserve. Percent composition of intertidal reef areas were dominated by turfing coralline algae, and also included the small brown algae *Hormosira banksii,* the large brown algae *Cystophora torulosa* and *C. retroflexa*. No conversions from percent cover to biomass or information on average length of the primary species (*Cystophora torulosa*, *C. retroflexa* and *Hormosira banksii*) were available to estimate subtidal biomass in this study. Thus percent cover-weight relationship for *Xiphophora gladiata* (1%=58.8 g) (Shears & Babcock 2004a) was used to convert percent cover of the three primary intertidal algal species to biomass.

Algal biomass on soft sediment was estimated from a NIWA survey of soft sediment macroalgae, with 9 sampling sites (4 intertidal, 5 subtidal with depths ranging from 1.0 to 7.2 m) in Whangarei Harbour sampled in spring and autumn (Neill et al., 2012). Mean biomass of brown macroalgae (primarily *Colpomenia sinuosa* and *Hormosira banksi* and some filamentous brown alage) was 17.0 gWW m^{-2}. Mean biomass of green algae (primarily *Codium* spp. and *Ulva* spp.) was 12.3 gWW m^{-2}. Mean biomass of red algae (primarily filamentous reds) was 36.5 gWW m^{-2}. Crustose forms were rarely observed and were not included in calculations. We assume macroalgal biomass of deeper soft sediment habitats (10–29 m) is 10% of shallow (0–9 m) habitats.

Dry weight estimates were converted to ash-free dry weight (AFDW) by multiplying the dry weight by a constant of 0.91, based on the assumption that the proportion of $CaCO_3$ and inorganic materials is relatively constant at approximately 9% of the dry weight of New Zealand algal species (R.B. Taylor, University of Auckland, unpublished data, as cited in Shears & Babcock, 2004a). Weights were converted to carbon biomass using Lamare & Wing (2001), and using unpublished data from R.B. Taylor (University of Auckland).

Table 91: Length-dry weight and/or percent cover-dry weight relationships for major algal species and groups (Shears & Babcock 2004a). Y=dry-weight (g), x=total length (cm), SL=stipe length, LL=laminae length, LB=Long Bay, CR=Cape Reinga, MKI = Mokohinau Islands. Percent cover estimates based on 1% of a 1 m^2 quadrat.

Group/Species	Equation	Collected
Large brown		
Ecklonia radiata	$\ln(y) = 2.625\ln(x) - 7.885$	CR
Stipe	$\ln(y) = 1.671\ln(SL) -3.787$	Leigh
Rest	$\ln(y) = 1.177\ln(SL\text{x}LL) - 3.879$	Leigh
Carpophyllum flexuosum	$\ln(y) = 1.890\ln(x) - 4.823$	LB
Carpophyllum maschalocarpum	$\ln(y) = 2.078\ln(x) - 5.903$	LB
Sargassum sinclairii	$y = 0.075x + 0.124$	CR
Xiphophora gladiata	1% = 58.8 g	Bligh
Small browns		
Zonaria turneriana	1% = 2.48 g	MKI
Green foliose		
Caulerpa flexilis	1% = 5.81 g	MKI
Codium convolutum	1% = 4.68 g	MKI
Ulva spp.	1% = 1.71 g	MKI
Red foliose		
Osmundaria colensoi	1% = 22.93 g	MKI
Pterocladia lucida	1% = 10 g	Leigh
Red turfing	1% = 1.74 g	MKI
Brown turfing	1% = 1.74 g	MKI
Coralline turf[a]	1% = 1.5 g	MKI
Crustose corallines[a]	1% = 0.35 g	Leigh

[a] The proportion of $CaCO_3$ in *Corallina officinalis* has been estimated as 45% of the dry-weight. The value given is the total dry-weight of samples less 45% (Shears & Babcock 2004a)

Information on the calorific content of macroalgae was used to convert biomass (AFDW) estimates to energy "currencies" for some New Zealand macroalgal species (Lamare & Wing 2001). Alternatively, we used averages for our trophic groupings based on Paine & Vadas (1969) to estimate mean calorific contents of 4.53 kcal AFDW^{-1} for Chlorophyta (green algae), 4.50 kcal AFDW^{-1} for Phaeophyta (brown algae), 4.71 kcal AFDW^{-1} Phaeophyta for foliose and turfing Rhodophyta (red algae), and 3.73 kcal AFDW^{-1} for coralline Rhodophyta. We convert kilocalories to Joules to milligrams of carbon as follows: 1 kcal = 4186.6 J; and 1 mg C = 45.7 J. On average for macroalgae, this gives 1 g (AFDW) as equivalent to 0.38 g C (±26%). Final estimates of macroalgal biomass are shown in **Table 92**.

Total macroalgal biomass is equivalent to a carbon density in the study area of 2.9 gC m^{-2}.

Table 92: Estimated biomass of macroalgae in the study region.

	Intertidal tWW	Rocky subtidal tWW	Soft subtidal tWW	All tWW	% total B
Canopy	0	430 784	0	430 784	79.9
Foliose	23 776	24 834	60040	108 649	20.1
Crustose	687	55 487	0	56 175	10.4
All	23 776	455 618	60040	539 434	100.0

3.3 Production

Primary production was estimated following Taylor et al. (1999), Chisholm (2003), Shears & Babcock (2004b), Schiel (2005), and Miller & Dunton (2007). Net production (photosynthesis minus respiration) has been estimated for many common New Zealand species (Taylor et al. 1999; Shears & Babcock 2004b) (Table 93). To estimate net production for each trophic group, we use literature values for photosynthesis and respiration to estimate a linear relationship between photosynthesis and respiration based on available species. Here respiration=0.0577 *photosynthesis + 7.0549, as estimated in Lundquist & Pinkerton (2008) with respiration and photosynthesis measured in μmol O_2 hr^{-1} g DW^{-1}. For each macroalgal species, average daily production was taken as 0.64 of the peak net production, based on the assumption that diel variation in photosynthesis will vary in the same way as incident irradiance, i.e. approximately as a half sinusoid. We assume similar production rates across depth, and between subtidal and intertidal algae, and thus make no correction for light penetration or shading based on depth or habitat type, as this information is not available for most species. We average over available species information for each algal trophic group, using a weighted average of species based on relative percent composition of total biomass of each algal group. We convert mol O_2 to mg O_2 to mg C using 1 mmol O_2 = 32.6 mg O_2; and 1 mg O_2 = 0.309 mg C (Brey 2005), assuming a photosynthetic quotient close to unity.

For crustose/coralline algae on rocky subtidal substrate we calculate an average production rate of 0.32 gC m^{-2} d^{-1} which is consistent with measurements of the productivity of reef-building crustose coralline algae on relatively flat reef in Australia of 0.17–1.3 gC m^{-2} d^{-1} (mean=0.81 gC m^{-2} d^{-1}) (Chisholm 2003). Other productivity estimates for one common species *Ecklonia radiata* are equivalent to 20.7 kgWW m^{-2} y^{-1} (Kirkman 1984), 3.1 kgDW m^{-2} y^{-1}, (Larkum 1986), and 6 kgDW m^{-2} y^{-1} at Leigh (Novaczek 1984). Fairhead & Cheshire (2004a, b) gave 5–17 mgC gDW^{-1} d^{-1} for *Ecklonia radiata*, equivalent to P/B 4.9–17 y^{-1}, whereas we estimated P/B=4.2 y^{-1}. Daily production rates with respect to biomass based on functional form averaged across the Pacific Coast of North America gave larger values for sheet and filamentous algae of: 5.16 mgC gDW^{-1} h^{-1} and 2.47 mgC gDW^{-1} h^{-1}, with lower values for coarse branching algae (1.30 mgC gDW^{-1} h^{-1}), thick leathery algae (0.76 mgC gDW^{-1} h^{-1}), jointed calcareous algae (0.45 mgC gDW^{-1} h^{-1}), and crustose algae (0.07 mgC gDW^{-1} h^{-1}) (Littler & Arnold 1982).

These considerations suggest a range of annual P/B for macroalgae listed in Table 93 of between 0.7 and 28 y^{-1}, with an average value of 8.6 y^{-1}. Annual production for *Cystophora torulosa*, a common brown foliose algae in the intertidal surveys, was estimated at P/B=3.1 y^{-1}. For comparison, a typical estimate of P/B used in trophic modeling for benthic producers is 12.5 y^{-1} (Polovina 1984). Annual production ratio P/B varies considerably between morphological groups with P/B=3.0 y^{-1} for large, canopy-forming brown algae (*Carpophyllum* spp, *E. radiata*), P/B=10 y^{-1} for foliose/turfing algae (including *Caulerpa* spp), and P/B=16 y^{-1} for crustose/coralline algae.

Estimates of macroalgal biomass and production are shown in Table 93. Combining these in proportion to estimated biomass of different groups of macroalgae in the study area gives P/B=5.2 y^{-1} for the macroalgae group. Final estimates of macroalgal biomass are shown in Table 94.

Table 93: Rates of production, and respiration for common New Zealand species (Shears & Babcock 2004b). * from Taylor et al. 1999. Note that "P/B" refers to production net of respiration and was calculated as described in the text.

Species	Type	Photosynthesis (μmol O_2 hr^{-1} g DW^{-1})	Respiration* (μmol O_2 hr^{-1} g DW^{-1})	P/B (y^{-1})
Carpophyllum maschalocarpum	Brown canopy	41.2		0.9
C. plumosum	Brown canopy	72.1		2.8
C. flexuosum	Brown canopy	68.8		2.6
C. angustifolium	Brown canopy	38.1		0.7
Ecklonia radiata	Brown canopy	95.3		4.2
Cystophora torulosa	Large brown	74.0	10.6*	3.1
Landsburgia quercifolia	Large brown	78.1		3.2
Lessonia variegata	Large brown	65.8		2.4
Sargassum sinclairii	Large brown	139.6		7.0
Xiphophora chondrophylla	Brown foliose	68.8	5.9*	3.7
Zonaria turneriana	Brown foliose	88.2	19.2*	2.1
Melanthalia abscissa	Red foliose	75.8	8.6*	3.6
Osmundaria colensoi	Red foliose	118.0	10.1*	6.4
Pterocladia capillacea	Red foliose	108.8	22.0*	3.0
Caulerpa flexilis	Green foliose	245.7		13.3
Ulva spp.	Green foliose	493.0*	39.0*	27.6
Enteromorpha spp.	Green foliose	361.0*	24.5*	21.2
Distromium scottsbergii	Brown turfing	143.0		8.2
Laurencia distichophylla	Red turfing	279.8		17.9
Hymenema variolosa	Red turfing	235.0		14.7
Crustose coralline spp.	Crustose/Coralline	307.8		19.9
Corallina officinalis	Crustose/Coralline	295.6	20.7*	19.9

Table 94: Estimated production of macroalagae in the study region.

	P/B, Intertidal	P/B, Rocky subtidal	P/B, Soft sediment, subtidal	P/B	% total P
	y^{-1}	y^{-1}	y^{-1}	y^{-1}	
Canopy	2.9	3.0	N/A	3.0	42.2
Foliose	13.0	10.1	7.0	9.1	32.9
Crustose	25.0	16.1	N/A	16.2	24.9
All	13.3	4.5	7.0	5.2	100.0

3.4 Other information: EE, accumulation, imports, exports

It is not known if macroalgae as a whole or in part is undergoing long-term, consistent change in terms of biomass within the study area. In one study, *Ecklonia radiata* biomass accumulation rate was estimated at 0.002–0.016 gDW gDW^{-1} d^{-1} (Fairhead & Cheshire 2004) but the generality of this result is not known. Until information becomes available, the model will assume no substantial and consistent change from year to year, i.e. we set accumulation to zero.

Surveys of beach cast macroalgae indicate that up to 25% of annual production is deposited on the beach, above the intertidal zone, as detritus (Zemke-White et al. 2005). We use an export value X/P=0.25 for macroalgae. The domain of this study ends at the high water mark so beach cast seaweed represents an export of material from the system. We note that beach ecosystems are interconnected; beach cast seaweed and its associated fauna will affect the intertidal and possibly subtidal ecosystem. At the scale of the current model this is likely to be a small effect and so may be neglected, but at a local beach level, such interconnectedness, including the ecological role of beachcast seaweed may be very important. Exploring this importance is beyond the scope of the present modeling study.

In contrast to beachcast seaweed, drift loss of seaweed to intertidal and subtidal reef areas (measured as losses of up to 21%, 2% and 1% to drift over 21 days for *Ecklonia radiata*, *Carpophyllum maschalocarpum* and *C. angustifolium*, respectively (Andrew 1986)) is assumed to be directly consumed by herbivorous invertebrates (and not converted to detritus prior to consumption).

In the Te Tapuwae o Rongokako rocky reef ecosystem of northeast New Zealand, the vast majority of the production of macroalgae was not directly consumed; in this rocky reef ecosystem, only about 6% of production of crustose and coralline macroalgae was estimated consumed directly, and less than 1% of the annual production of canopy and foliose macroalgae was estimated to have been directly consumed (Lundquist & Pinkerton 2008; Pinkerton et al. 2008). Instead, annual macroalgal production was broken down by mechanical action and became part of the water column and benthic detritus. In due course, this material will be consumed directly as organic detritus by detrivores or broken down by bacterial decomposition in the water column or benthos. Detrital macroalgae is suggested as an important food source in gut content analyses of phytal invertebrates (Smith et al. 1985). In modeling terms, ecotrophic efficiency of macroalgae is likely to be very low. After allowing for beach cast, we estimate a direct consumption of 1% for all macroalgae together, giving an initial estimate of ecotrophic efficiency for this group of EE=0.26.

4 Mangrove, Saltmarsh & Seagrass

4.1 General information

This group includes mangrove forests (*Avicennia marina*), saltmarsh (e.g. *Spartina maritime*) and seagrasses (*Zostera* spp.) found in the study area, excluding periphytes, epiphytes and microphytobenthos found amongst these habitats.

4.2 Mangrove

4.2.1 Mangrove: General information

Morrisey et al. (2007) reviewed the state of knowledge of mangroves in New Zealand and around the world for Auckland Regional Council. In their table 1 they summarise information on mangrove biomass density (above ground only). There were considerable variations in biomass density of mangroves, between 1.8–400 tDW ha^{-1}, with a mean of 112 tDW ha^{-1} (N=20). Morrisey et al. (2007) state that: “A review of trends in biomass and litterfall (incorporating 91 measures of litterfall [litter production] across species and locations, including New Zealand) identified trends of decreasing biomass and rates of litterfall with increasing latitude (Saenger & Snedaker 1993). From this it would be expected that values from New Zealand would fall at the lower end of the reported range, but this is not always the case." Data in Morrisey et al. (2007) included only two measurements in New Zealand, of 10 and 130 tDW ha^{-1}. Given the paucity of this information, we assume a biomass density in the study area of 70 tDW ha^{-1}.

4.2.2 Mangrove: Biomass

From the GIS mapping of habitat types developed for this study, we estimated that 53.4 km^2 (5340 ha) of mangrove habitat occurred in the study area. This is quite close (within 18%) of the 65.1 km^2 area of mangrove in the study area estimated using the Estuary Environments Classification (EEC) database (Hume et al. 2003, 2007). This accounts for 0.3–0.4% of the study area and hence, we estimate a mangrove biomass of 373 000 tDW. This large biomass occurs despite the small area of mangrove in the region because of the high biomass density of this habitat. We assume a carbon content of mangrove of 0.376 gC gDW-1 (Larkum 1981) which is close to 0.33 gC gDW^{-1} for macroalgae (Brey 2005) and 0.335 gC gDW^{-1} for seagrass (Duarte 1995). Hence, we estimate a carbon biomass of this group of 140 000 tWW.

4.2.3 Mangrove: Production

Morrisey et al. (2007) also summarise annual litterfall rates for mangroves (their table 1). Morrisey et al. (2007) state that: "Although this [litterfall] does not represent net primary production completely (since it does not include net increase in plant biomass), it represents an important component of it." Annual values of production as a proportion of biomass were 0.03–0.33 y^{-1}, with a mean of P/B=0.15 y^{-1} (N=7). Two values were available from New Zealand, P/B= 0.059 y^{-1} and P/B=0.33 y^{-1}. There is clearly considerable variability in mangrove production rates, and here we use the mean value of P/B=0.15 y^{-1}.

4.2.4 Mangrove: Other parameters

At present, mangrove forests are thought to be undergoing long-term, consistent change in terms of biomass within the study area. Mangroves are increasing at rates of approximately 4% per year (Swales et al. 2007). Assuming a biomass accumulation per year of 4% and production value given above, the accumulation rate as a proportion of annual production is A/P=0.27.

There are no imports or exports of mangrove relevant to the model.

The proportion of mangrove production directly predated in the model is likely to be very small. Most of the annual production is likely to become part of the benthic detritus and, in due course, this material will be consumed directly as organic detritus by detrivores or broken down by bacterial decomposition in the sediment. In modeling terms, ecotrophic efficiency of this group is likely to be very low, and is initially set to EE=0.01+A/P, or 0.28.

4.3 Saltmarsh

4.3.1 Saltmarsh: General information

Morrisey et al. (2007) state that: "Saltmarshes are vegetated intertidal flats dominated by low-growing halophytic shrubs, herbaceous plants and rushes. Largely confined to temperate coastlines, they occupy a similar niche to mangrove forests (Frey & Basan 1985). Throughout the upper North Island, saltmarsh and mangrove often intermingle, but the habitats differ in floristic and intertidal position. Where both are present, saltmarsh usually occupies a higher elevation and a more landward position, and as such is subject to fewer tidal inundations than the mangrove areas."

4.3.2 Saltmarsh: Biomass

Herrmann (2010) measured aboveground cordgrass (*Spartina alterniflora*) biomass from healthy, intact cordgrass stands across fourteen intertidal salt marshes on Cape Cod (US), with a mean biomass density of 3.7 tWW ha^{-1}. Wiegert & Freeman (1990) showed that total production of saltmarsh is 1.4–9.3 times the above ground production, with a median value of 2.4 times. Assuming that biomass scales in proportion to production, and that dry weight is about 20% wet weight for saltmarsh we estimate a total (above and below ground) biomass density of 180 gDW m^{-2} (1.8 tDW ha^{-1}).

Saltmarsh habitat was estimated to cover only 0.91 km^2 (91 ha) in the study area, obtained by totaling the "swamp" category in the Estuary Environments Classification for Hauraki Gulf estuaries (Hume et al. 2003; 2007). This accounts for only 0.006% of the total study area. The total biomass of saltmarsh primary producers is hence estimated at 55 164 tDW. We assume a carbon content of 0.335 gC gDW^{-1} as for seagrass (Duarte 1992), resulting in 55 tC.

4.3.3 Saltmarsh: Production

Wiegert & Freeman (1990) summarise data on biomass and productivities of saltmarshes along the southeast Atlantic Coast of US, with P/B values 2.5–7.6 y^{-1} (N=4). Total production is reported as 1.4–9.3 times the aboveground production, median of 2.4 times (N=8). We hence estimate a productivity value for saltmarsh of P/B=4.2 y^{-1}.

4.3.4 Saltmarsh: Other parameters

It is not known if saltmarshes are undergoing long-term change in terms of biomass within the study area. Until information becomes available, the model will assume no substantial and consistent change from year to year, i.e. we set accumulation to zero.

There are no imports to or exports from the saltmarsh habitats relevant to the model.

The proportion of saltmarsh production directly predated in the model is likely to be very small. Most of the annual production is likely to become part of the benthic detritus and, in due course, this material will be consumed directly as organic detritus by detrivores or broken down by bacterial decomposition in the sediment. In modeling terms, ecotrophic efficiency of this group is likely to be very low, and is initially set to EE=0.01.

4.4 Seagrass

4.4.1 Seagrass: General information

This group includes seagrass meadows, excluding periphytes and epiphytes on seagrass. In some parts of the world, seagrass represent the dominant and most highly productive coastal habitat type (Duarte & Chiscano 1999; Hemminga & Duarte 2000; Green & Short 2003). In New Zealand, the seagrass flora is represented by one species (*Zostera muelleri*), in the family Zosteraceae. New Zealand seagrass meadows are unusual in that seagrasses are primarily found intertidally and in shallow subtidal estuaries, although anecdotal evidence suggests that large subtidal meadows existed in most estuaries prior to European colonisation. The most extensive seagrass beds occur in soft substrates (sand and mud), where they may form continuous expanses of vegetation extending over several square kilometres, or mosaics of discrete patches surrounded by unvegetated sediment (Turner & Schwarz 2006).

4.4.2 Seagrass: Biomass

We estimate mean biomass of seagrass using calculations of combined above and below ground biomass in Whangapoua Harbour (Turner et al. 1996). Mean percent cover averaged from 12 replicates over 4 sampling times (autumn and spring) was 58.8%, with corresponding mean biomass of 209.3 gDW m^{-2} (2.1 tDW ha^{-1}). For comparison, Roman & Able (1988) measured production ecology of eelgrass (*Zostera marina*) in a Cape Cod salt marsh-estuarine system in Massachusetts. Live leaf-blade biomass was 199–305 gDW m^{-2}. Turner & Schwarz (2006) summarise biomass density and productivity of seagrass from 8 studies and 10 locations, 4 in Australia and 6 in New Zealand. Total biomass density was 110–1025 gDW m^{-2}, with a mean of 388 gDW m^{-2}. While seagrass biomass does vary with patch size and density, we assume that the measurement of Turner et al. (1996) in Whangapoua Harbour is broadly representative of seagrass meadows in the Hauraki Gulf.

From the GIS mapping of habitat types developed for this study, we estimated that there was 5.4 km^2 (540 ha) of seagrass habitat in the study area, with 3.3 km^2 in the interidal (estuarine) and 2.1 km^2 subtidal. We hence estimate a total weight of seagrass in the study region of 1130 tWW. The median carbon content of seagrass leaves is 33.5% of tissue dry weight (Duarte 1992). This gives a carbon biomass of 379 tC.

4.4.3 Seagrass: Production

Roman & Able (1988) measured annual leaf-blade biomass loss of 303–577 gDW m^{-2} y^{-1}. Their data imply annual aboveground productivities of saltmarsh primary producers of P/B=1.5–1.9 y^{-1}. Turner & Schwarz (2006) summarise biomass density and productivity of seagrass from 8 studies and 10 locations, 4 in Australia and 6 in New Zealand. Turner & Schwarz (2006) summarise productivity data for seagrass measured in two ways: in terms of relative leaf growth (gDW g^{-1} d^{-1}) and as total aboveground production (gDW m^{-2} d^{-1}). From both, we estimate an annual production ratio, P/B (y^{-1}). This production ratio was higher for the first method (P/B=3.7–13 y^{-1}) than the second (P/B=1.2–3.2 y^{-1}). Taking the median of estimates of P/B from Roman & Able (1988) and studies summarised in Turner & Schwarz (2006), we obtain P/B=3.2 y^{-1} and estimate an areal production of 876 gDW m^{-2} y^{-1}. Turner & Schwarz (2006) state that "Seagrasses are highly productive, with an estimated average annual production of 1012 gDW m^{-2} year^{-1} (this estimate is conservative, as root production is under-represented). Turner & Schwarz (2006) found that seagrass biomass was mainly underground (between 1.8 and 7.0 times as much biomass below ground as above, median 3.5) but root:shoot production (below:above ground) is less than unity (0.15–0.58: Hovey et al., 2011). If production underground is one quarter of that above ground, we would estimate a total production of 1100 gDW m^{-2} year^{-1}, equivalent to P/B=5.2 y^{-1}. For comparison, production rates for a congener *Z. marina* have been estimated at 1767 gDW^{-1} m^{-2} y^{-1} (Nelson & Waaland 1997).

4.4.4 Seagrass: Other parameters

It is not known if seagrass, in whole or in part, is undergoing long-term, consistent change in terms of biomass within the study area. Until information becomes available, the model will assume no substantial and consistent change from year to year, i.e. we set accumulation to zero.

There are no imports or exports of mangrove or saltmarsh primary producers relevant to the model.

Direct grazing on seagrass leaves has generally been considered to be a relatively unimportant trophic pathway in temperate seagrass beds. However, recent studies have indicated that grazing on the plants, as well as predation on reproductive structures of seagrass, may be significant, and that the importance of seagrasses to food webs has previously been greatly underestimated (Turner & Schwarz 2006). Cebrián & Duarte (1998) have reported that the extent of herbivory varies greatly both within and among seagrass species, ranging from negligible values to up to 50% of leaf production removed in some species. Here, we estimate ecotrophic efficiency for seagrass of 25%, with most carbon being transferred from seagrass to higher trophic levels via detrital pathways (Orth & van Montfrans 1984).

4.5 Summary of parameters

Information on mangrove, saltmarsh and seagrass is combined in Table 95. Overall carbon density in the study area is B=8.7 gC m^{-2}. Net export and other non-trophic transfers are set to zero.

Table 95: Summary parameters for the mangrove, saltmarsh and seagrass primary producers.

	Area ha	Density tDW ha^{-1}	B tDW	C:DW	B tC	P/B y^{-1}	P gDW m^{-2} y^{-1}	A/P	EE
Mangrove	5 335	70	373 450	0.376	140 417	0.15	1 055	0.27	0.28
Saltmarsh	91	1.8	164	0.335	55	4.2	757	0	0.01
Seagrass	540	2.1	1130	0.335	379	5.2	1 095	0	0.25
All	5 966		374 744		140 851	0.17		0.24	0.27

5 Microphytobenthos, periphyton and epiphyton

5.1 General information

This trophic group is made up of two components: microphytobenthos on soft sediment, and epiphytic macrophytes and microphytes on macroalgae, all of which have similar high rates of production and are consumed at high rates by grazers. There is little published information on any of these categories for the Hauraki Gulf region. Therefore, we use values from the literature to make estimates for each, as described below.

5.2 Microphytobenthos

Microphytobenthos was measured at 29 stations in the Firth of Thames and inner Hauraki Gulf in 2004 (John Zeldis, unpublished data). Concentrations of chlorophyll-a were 0.33–15.6 µgChl-a per gDW of sediment. The median concentration was 3.8 µgChl-a gDW^{-1}. Assuming that microphytobenthos occurs to a depth of 1 cm, and that sediment has a density of about 0.25 gDW cm^{-3} (Rios et al. 1998), these numbers imply areal biomass of 0.79–37.4 (median 9.1 mg Chl-a m^{-2}). We take the log-average values in the Firth of Thames (9.5 mg Chl-a m^{-2}) as indicative of microphytobenthos concentrations in subtidal soft sediment of depth 0–9 m as these are likely to be log-normally distributed. We take log-average values at the northern stations (2.9 mg Chl-a m^{-2}) as indicative of microphytobenthos concentrations in subtidal soft sediment of depth 10–29 m. We assume zero microphytobenthos biomass in depths greater than 30 m.

Benthic microalgal biomass (microphytobenthos) has been measured at other New Zealand locations as sediment Chl-a through both spectrophotometry and taxonomic composition via pigment analysis (Gillespie et al. 2000; Cahoon & Safi 2002). Subtidal (6–20 m) microphytobenthos biomass ranged from 20 to 200 mg Chl-a m^{-2} in sediment in Tory Channel, Marlborough Sounds (Gillespie et al. 2000). Intertidal sediment Chl-a biomass in Manukau Harbour was estimated as 11.8–340 mg Chl-a m^{-2} (weighted average 62.5 mg Chl-a m^{-2}) (Cahoon & Safi 2002). We translate average habitat specific-values (mg Chl-a m^{-2}) to our unvegetated intertidal habitats of mudflat (mud: 32.7 mg Chl-a m^{-2}), tubeworm (muddy sand: 121.2 mg Chl-a m^{-2}), Macomona (sandy mud: 61.2 mg Chl-a m^{-2}), sandflat (sand: 98.6 mg Chl-a m^{-2}), and cockle (shelly sand: 82.6 mg Chl-a m^{-2}) (Cahoon & Safi 2002).

For seagrass habitats, we use data from Whangapoua estuary seagrass habitats which showed 13.4 μg Chl-a gDW^{-1} sediment (Lundquist, NIWA, unpublished data). Chl-a concentration on mangrove sediments from June, September and November 2010 in Tauranga Harbour has been measured at 43.2 μgChl-a gDW^{-1} sediment in Te Puna estuary, 42.2 μgChl-a gDW^{-1} sediment for Waikaraka estuary, and 47.5 μgChl-a gDW^{-1} sediment for Waikareao estuary, resulting in a mean value of 44.3 μg Chl-*a* gDW^{-1} sediment for mangrove intertidal habitats (Lundquist, NIWA, unpublished data). Assuming microphytobenthos occurs to a depth of 1 cm, and that sediment has a density of about 0.25 gDW cm^{-3} (Rios et al. 1998), these numbers imply 32 mg Chl-a m^{-}2 (seagrass) and 106 mg Chl-a m^{-2} (mangrove). These values are similar to average values for shallow, temperate waters globally as summarised by Cahoon (1999) of 128±101 mg Chl-a m^{-2}. We assume microphytobenthos on sediments in salt marsh are similar to those in seagrass.

Applying these concentrations of microphytobenthos in proportion to areas of habitat in the study area estimated using a GIS-classification system, we obtain an average concentration of 2.5 mg Chl-a m^{-2}. To convert these Chl-a biomass estimates into microalgal biomass estimates (gC), we used a conversion rate of 25:1 gC:gChl-a (Parsons et al. 1984). This gives a carbon biomass of 1.4 gC m^{-2} (intertidal average), 0.24 gC m^{-2} (subtidal 0–9 m average), 0.071 gC m^{-2} (subtidal 10–29 m average), and B=0.062 gC m^{-2} (whole study area). The total wet weight biomass is estimated to be 17 600 tWW.

Primary production of subtidal soft sediment microphytobenthos was measured at 0.20 g C m^{-2} d^{-1} or 73 g C m^{-2} y^{-1} at a depth of 20 m in Tory Channel, Marlborough Sounds (Gillespie et al. 2000), implying a P/B of about 40/y. Microphytobenthos net primary production has been estimated at higher levels of 1.880, 1.035 and 0.259 gC m^{-2} d^{-1} beneath mussel farms in Tasman Bay (Christensen et al. 2003), and these higher productivities are likely to apply to regions of the Firth of Thames and elsewhere in the Hauraki Gulf under mussel and oyster aquaculture. However, as we lack maps of aquaculture, and this is a relatively small total area of the Hauraki Gulf model region, we use a value of P/B=36 y^{-1} for the microphytobenthos in the study region following Lundquist & Pinkerton (2008).

5.3 Epiphytic algae (macrophytes and microphytes)

Epiphytes on macroalgae include both larger species of erect epiphytic macrophytes, as well as microphytes (periphyton). While no information is available within the study area, international studies have shown high grazing pressure on these epiphytes relative to their host algae or seagrass (D'Antonio 1985; Smith et al. 1985; Klumpp et al. 1992). We estimate that relationships between epiphytes and macroalgae are similar to those found in seagrass (see also Section 4.4). Epiphyte biomass on seagrass has been measured at up to 67% (mean 13%) of total seagrass biomass (Nelson & Waaland 1997). Tropical seagrass communities have also shown high biomass of epiphytes, with 598–1061 mgAFDW m^{-2}, or 244–646 mgC m^{-2} bottom habitat; or 0.16–0.24 mgAFDW cm^{-2} seagrass frond (Klumpp et al. 1992). We estimate epiphytes as 6.1% of the total biomass of macroalgae summed over the three macroalgal trophic groups following Lundquist & Pinkerton (2008) who estimated this proportion for the northeast New Zealand rocky reef ecosystem.

Assuming that carbon is about 5.7% wet weight (as for macroalgae, Brey 2005) this leads to a total biomass of macrophytes and microphytes in the study area of 50 100 tWW.

Epiphyte production was estimated for a *Zostera marina* seagrass meadow in Washington, USA, during two separate years of study as 577 and 291 gC m^{-2} y^{-1}, or approximately 14% and 25%, respectively, of total productivity of the seagrass meadow (Nelson & Waaland 1997). The same study estimated a P/B ratio of approximately 14 y^{-1}. Based on this estimate, epiphytal biomass in our study area may have an average annual production of approximately 100 gC m^{-2} y^{-1} for an epiphytic algal community consisting of 5% of the total biomass of macroalgae. We assume this is a plausible estimate of productivity of macroalgal epiphytes, and estimate a P/B of about 14 y^{-1} for the epiphytes in the study region. This seems logical if our epiphytes are dominated in terms of biomass by larger foliose epiphytic algae. Epiphyte production may vary between years but we have no information on this. Better data for this group would be useful to define parameters for a trophic model, as we might expect a much higher P/B if epiphytes were dominated in terms of biomass by the smaller, highly productive periphyton. For example, Booth (1986) reports photosynthetic rates of 45–68 times greater per unit volume for epiphytic diatoms compared to their macroalgal hosts *Carpophyllum maschalocarpum* and *C. flexuosum*. This study estimated a contribution of 6–8% of the total primary productivity by epiphytic diatoms to the host-epiphyte association (Booth 1986).

5.4 Summary and other information

Combining biomass from these groups gives a total biomass of 67 700 tWW equivalent to a carbon density over the whole study area of 0.24 gC m^{-2}. To calculate average biomass for this trophic group, we sum biomass over both epiphytic algae and microphytobenthos. Calculating a weighted average of production across relative biomass of these groups gives P/B=20 y^{-1}.

It is not known if microphytes or epiphytes in whole or in part are undergoing long-term change in terms of biomass within the study area. Until information becomes available, the model will assume no substantial and consistent change from year to year, i.e. we set accumulation to zero.

There are no imports or exports of microphytes or epiphytes relevant to the model.

The proportion of production of this group directly predated in the model is not known. In the Te Tapuwae o Rongokako rocky reef ecosystem of northeast New Zealand, the vast majority of the production of epiphytes, periphytes and microphytobenthos was not directly consumed; less than 1% of the annual production of this group was estimated to have been directly consumed (Lundquist & Pinkerton 2008; Pinkerton et al. 2008). Instead, annual production was likely to have been broken down by mechanical action and became part of the water column and benthic detritus. In due course, this material will be consumed directly as organic detritus by detrivores or broken down by bacterial decomposition by bacteria in the water column or benthos. In modeling terms, ecotrophic efficiency of this group is likely to be very low, and is initially set to EE=0.01.

6 Historical parameters

6.1 Historical models required

Trophic models are required for non-phytoplankton primary producers in four historical periods: 1950, 1790, 1500, and 1000.

6.2 Biomass

The authors know of no information on the area of the study region covered by mangrove, seagrass or saltmarsh in the historical periods required. It is known that the area covered by mangroves has increased in the late modern period due to sedimentation of coastal regions following human change of terrestrial land-use. For the purposes of the trophic modelling, we assume that mangroves in the study area now cover three times the area they covered before humans arrived. Although there was significant change of coastal terrestrial habitats by Māori, here we assume that the increase in mangrove area followed increases in the total New Zealand population. Pool (1991) gave a best estimate of 100 000 for the total New Zealand population in 1769 (which we use for the 1790 model). Smith (2011) estimates a New Zealand population of 20 000 by 1400 and a population of 90 000 in 1550. Assuming a linear change, the New Zealand population in 1500 may have been about 67 000. Present day population is 4.3 m, and in 1950 was 1.9 m (World Bank statistics).

In contrast to the recent increase in mangrove habitat in the study area, seagrass and saltmarsh have probably declined substantially as human population has increased due to urban and rural reclamation of estuarine and coastal land. The decrease may be 50–80%, probably nearer the upper end of this range. Here, we assume that we currently see a 30% remnant of both seagrass and saltmarsh in the study area. As for mangrove, we assume changes in areas covered by saltmarsh and seagrass mirror changes in the New Zealand population.

We assume that biomass densities of mangrove, seagrass and saltmarsh within their habitats have not changed historically. Hence, we estimate biomasses for all non-phytoplankton groups using the present day biomass density and changes in areas of these habitats. Biomass estimates are shown in Table 96.

Table 96: Biomass of mangrove, seagrass and saltmarsh in the trophic models. Values are based on New Zealand population as explained in the text.

Date	NZ population (1,000s)	B (mangrove)	B (mangrove) factor	B (seagrass)	B (saltmarsh)	B(seagrass, saltmarsh) factor
		gC m^{-2}				
2010	4300	8.7	3.00	0.023	0.003	0.30
1950	1900	5.4	1.88	0.054	0.008	0.69
1790	100	3.0	1.05	0.077	0.011	0.98
1500	67	3.0	1.03	0.077	0.011	0.99
1000	0	2.9	1.00	0.078	0.011	1.00

6.3 Productivity and other parameters

It seems unlikely that productivity for any of the non-phytoplankton primary producers groups in the trophic model would have been substantially changed by climate variations *per se*, and we do not adjust any production parameters from the present day values in the historical trophic models.

The other key parameter for this group is ecotrophic efficiency: the proportion of the annual production that is directly grazed rather than being recycled through the detrital chain. It is not possible to estimate *a priori* whether ecotrophic efficiency for non-phytoplankton primary producers will have changed historically, but this is certainly possible (for example, there may have been more or fewer grazers historically than at present). We will, hence, allow this parameter to change in the historical models.

7 Acknowledgements

This research was funded by Ministry for Primary Industries project ZBD200505 (“Long-term change in New Zealand coastal ecosystems”) and by the New Zealand Foundation for Research, Science and Technology project C01X0501 (Coasts & Oceans OBI). We acknowledge Dr Mary Livingston and Dr Martin Cryer (Ministry for Primary Industries) for project funding and stewardship. We acknowledge assistance with data collection and processing from James Sturman, Mark Morrison, Anne-Laure Verdier (NIWA). We are grateful to Richard B. Taylor (University of Auckland) for unpublished data and assistance. Dr Jeanie Stenton-Dozey kindly reviewed a draft of this report.

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Appendix 10: Trophic modelling of Hauraki Gulf: Bacteria and Detritus

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1 Bacteria

1.1 Water column bacteria

1.1.1 Biomass

Bacteria in the water column in the study area was measured on two series of voyages: Bionosex and CSEX (Figure 40). There were three Bionosex stations (E3, G2, H3) where bacterial concentration in the water column was measured, and four Bionosex voyages in total: September 1996 (kah9614), October 1996 (tan9612), December 1996 (kah9617), and January-February 1997 (tan9702). On these voyages, bacterial biomass (mgC m^{-3}) was measured between the sea surface and the bottom of the mixed layer. “Mixed-layer depth”[6] was defined as the depth at which the potential density is 0.03 kg m^{-3} greater than the density at 5 m. In order to obtain a whole water column estimate of bacterial biomass, the concentration of bacteria below the mixed layer was assumed to be the same as that above it. Chlorophyll concentrations are known to vary spatially in the study area. The mean chl-a from all Bionosex stations in the study area (mean of stations C1–C2, E1–E6, G1–G4, H1–H5) was taken as indicative of the mean chl-a in the study area. The ratio of chl-a for the whole Hauraki Gulf to the three stations where bacteria were sampled (E3, G2, H3) varied from 0.6 to 2.5. In order to extrapolate each three point measurement of bacterial biomass to the study area, we multiplied the water column integrated bacterial biomass by the ratio of whole area chl-a to station chl-a, under the assumption that bacteria may scale spatially as chl-a. This is a reasonable assumption because chl-a concentration is indicative of the rate of primary production in the water column and this primary production forms the organic material that supports bacterial activity in the upper ocean.

There were two CSEX stations in the study area where bacterial concentration in the water column was measured (SA03 and C1). Bacterial biomass concentration (mgC m^{-3}) was measured at typically 6 depths between the sea surface and seabed on CSEX, and these were used to obtain a water column integrated bacteria biomass (mgC m^{-2}). As for the Bionosex data, we scaled the bacteria biomass values at the SA03 and C1 stations by the ratio of chl-a at that point and chl-a across the whole study area to account for spatial variation in bacterial abundance. This scaling is based on the same assumption that bacteria and chl-a covary. We used the average of Bionosex chl-a measurements as our best indicator of whole Hauraki Gulf chl-a and the average of chl-a at H4 and H5 to represent chl-a at SA03.

The annual variation is shown in Figure 41. The average obtained from the CSEX data is higher than that from the Bionosex data (0.77 gC m^{-2} compared to 0.40 gC m^{-2}). We use a log-average of all the bacterial biomass data to account for the likely log-normal distribution of biomasses in

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[6] See http://www.lodyc.jussieu.fr/~cdblod/mld.html

natural waters. This gives an estimate of annual average water column bacterial biomass for the study area of 0.61 gC m^{-2}.

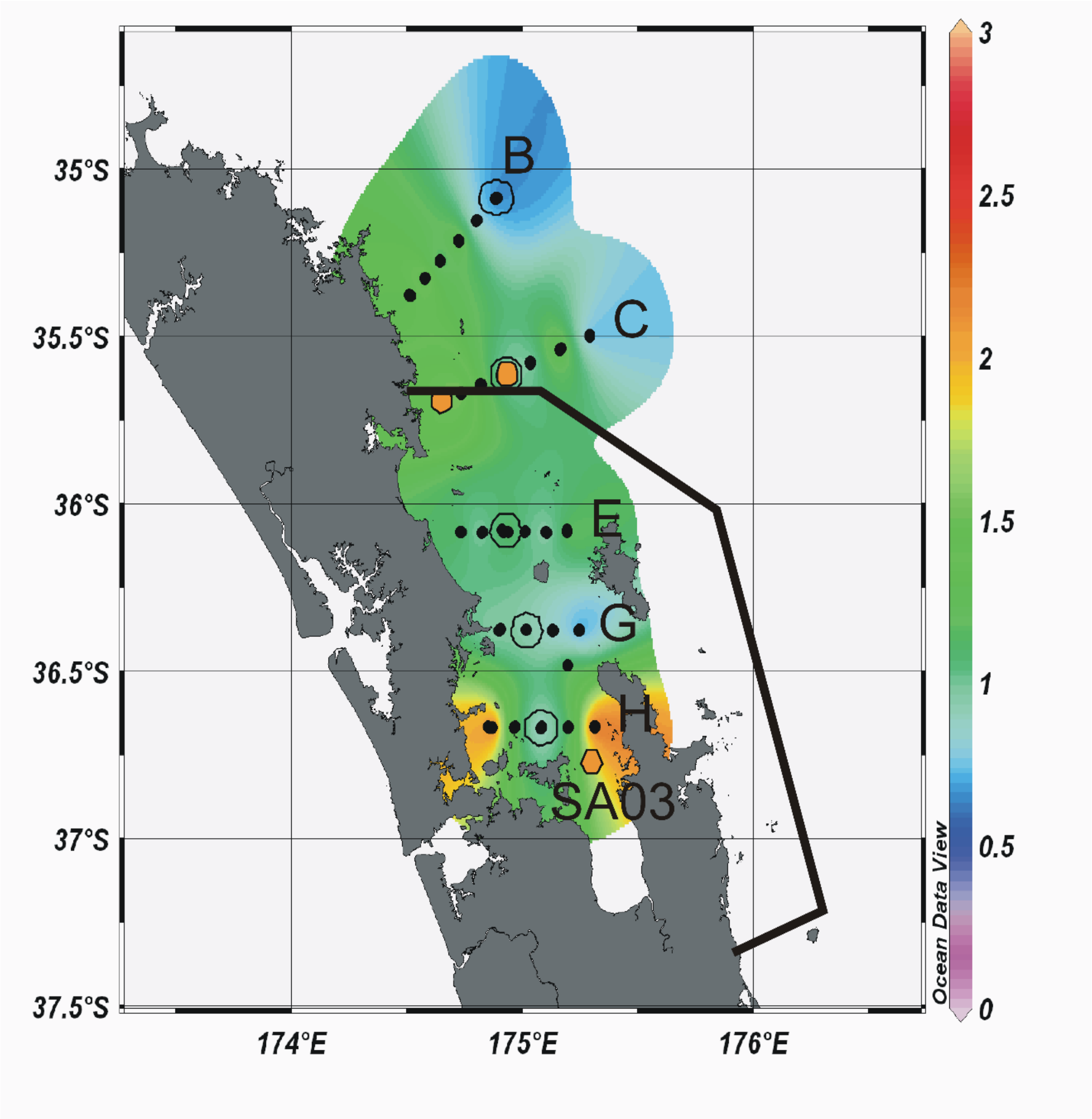

Figure 40: Sampling stations for Bionosex and C-SEX research programmes. Letters give the names of the transects, which are numbered from 1 at the western end. The heavy solid line is approximately the boundary of the study area. On Bionosex research voyages, bacterial biomass was measured at the five stations shown as large, open circles (B6, C4, E3, G2, H3). On C-SEX research voyages, bacterial biomass was measured at the three stations shown as orange circles C1, C4, SA03. The background contour is near surface chl-a (mg m^{-3}) and the other circles show sampling on these two programmes for other variables (including chl-a, zooplankton).

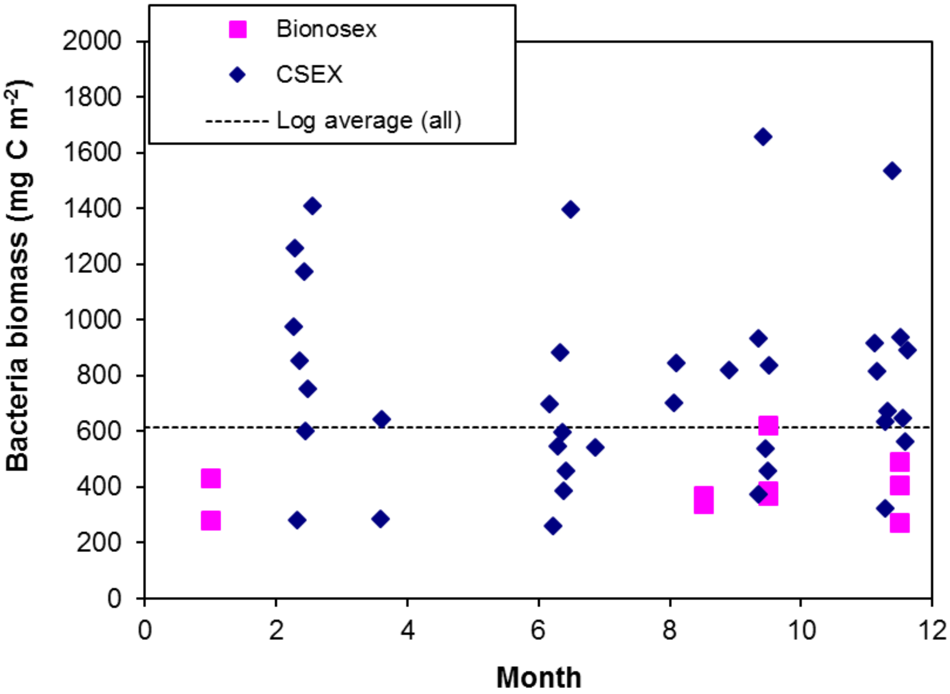

Figure 41: Water column integrated biomass of bacteria obtained from the Bionosex and CSEX series of research voyages in the study area, as explained in the text. The dashed line gives the log-average values used in the trophic model.

For comparison, bacterial biomass in Sub-Antarctic, offshore waters of the Southern Plateau, New Zealand, were estimated to be 0.6 g C m^{-2} (Bradford-Grieve et al. 2003). Bacteria biomass in New Zealand west coast shelf waters (less than 200 m deep) was 1.0 gC m^{-2} (Probert 1986). The average annual biomass of bacteria over the Chatham Rise was based on data collected in the study region (Bradford-Grieve et al., 1998; Smith & Hall, 1997; Julie Hall, NIWA, unpublished data) and is estimated to be 0.94 gC m^{-2} using the carbon conversion factor of Fukuda et al. (1998). The annual average value for bacterial biomass in the shelf and slope waters of the Ross Sea, Antarctica, is estimated to be 0.23 gC m^{-2} (Pinkerton et al. 2010).

Finally, we note that it is not known what proportion of bacterial cells in the water column of the study area are viable (i.e. actively consuming detritus and "producing") - this may be relatively low. For example, in subantarctic waters off the Kerguelen Islands, Razouls et al. (1997) found that at some times only about 10% of bacteria cells were viable, so viable biomass of bacteria may be lower than estimated here.

1.1.2 Production

There are no measurements of bacterial productivity in the water column in the study area. Bacterial production is generally assumed to be equivalent to about 25–30% of simultaneously estimated phytoplankton primary production rates across a wide range of marine and freshwater ecosystems of varying trophic status (Ducklow 2000). Here, this would imply a P/B of 43 y^{-1} (39–47 y^{-1}). For comparison, bacterial production rates in subantarctic waters of the Southern Plateau, New Zealand, were estimated to be equivalent to P/B = 87 y^{-1} (Bradford-Grieve et al. 2003). In a coastal ecosystem model for northern Chile, water column bacterial production (P/B) was estimated as 100–400 y^{-1} (Wolff 1994). Shushkina et al.(1998) estimated bacterial P/B to be 92 y^{-1} based on the analysis for low productivity waters whereas Sorokin (1981, table 2.2) gives P/B of 0.5 d^{-1} for eutrophic coastal habitats, 0.6 d^{-1} in mesotrophic temperate seas; and 1.2 d^{-1} in oligotrophic tropical seas which lead to P/B of 182–438 y^{-1}. The annual average productivity of water column bacteria in the shelf and slope waters of the Ross Sea, Antarctica, was estimated to be equivalent to P/B=35 y^{-1}. Hence, the value of P/B for water column bacteria used here is reasonable, but towards the low extreme of typical values.

1.1.3 Consumption, growth efficiency

Bacteria in the water column consume detrital and dissolved organic material in the water column. Consumption rates by bacteria are typically quantified via growth efficiency (P/Q) values. There are no measurements of consumption rates or growth efficiency of bacteria in the water column in the study area. Bradford-Grieve et al. (2003) used P/Q=0.23 for bacteria in subantarctic waters off New Zealand. Lochte et al. (1997) measured values in the Southern Ocean of P/Q=0.30 (0.28–0.31), with bacterial production/respiration, P/R=0.43 (0.38–0.44). Growth efficiencies (P/Q) for open ocean bacteria feeding on dissolved organic matter in the Southern Ocean was reported as 0.26–0.30 (Kähler et al. 1997), which was reported as being consistent with work of Lignell (1990). Here, we propose using P/Q=0.3 (Pomeroy 1979; Kirchman et al., 2001) which gives an estimate of Q/B=142 y^{-1}.

1.1.4 Other information: EE, U, accumulation, imports, exports, transfers

There is no evidence for long-term bacterial accumulation or biomass loss in the study area so this is assumed to be zero. Given the high turnover rates of bacteria, exports or imports due to water exchange are likely to be very small. Thus, unassimilated material from bacteria is assumed to be small. Ecotrophic efficiency for bacteria is not known, i.e. we do not know what proportion of bacterial cells in the water column are consumed by other organisms and what proportion die from causes other than predation and become recycled into the detrital pool. We initially and nominally set this value at EE=0.5. There will be a transfer of biomass of bacteria in the water column to bacteria in the sediments (benthic bacteria) due to settling of organic detritus from the water to sea-bed, but this is likely to be small compared to the turnover of bacteria in the water column.

1.2 Sediment/benthic bacteria

1.2.1 Biomass

There are no measurements of benthic bacterial biomass and production available for the study area. Biomass of bacteria in benthic sediments to a sediment depth of 15 cm was compiled by Deming & Yager (1992), and was shown to vary exponentially with water depths. Using data from Deming & Yager (1992) and based on the bathymetry of the study area in four broad depth categories (0–10 m, 10–30 m, 30–100 m, 100–250 m), we estimate a biomass of benthic bacteria of 2.0 gC m^{-2} for this study. This compares reasonably well with other published studies from the New Zealand region. Bacterial biomass on the Chatham Rise was estimated to be about 1.3 gC m^{-2} to a sediment depth of 15 cm (Pinkerton 2011). Probert (1986) found bacterial biomass of 1.0 gC m^{-2} for shelf waters (less than 200 m deep) off west coast New Zealand. Pinkerton et al. (2008) used a total bacteria biomass of 0.6 gC m^{-2} for a North island rocky reef ecosystem (Te Tapuwae o Rongokako).

A large fraction (about 70%) of benthic bacterial biomass may consist of dead cells (Luna et al. 2002). Among the living cells, nucleiod-containing cells represented only 4% of total bacterial counts (Luna et al. 2002) indicating that only a very limited proportion of the bacterial assemblage was actively growing. These inactive cells may be reactivated by addition of nutrients so are quiescent rather than dead (Luna et al. 2002) so we do not attempt to correct the biomass of benthic bacteria for the proportion alive or active and use the total bacterial biomass.

1.2.2 Production

There is considerable variation in measurements of annual P/B ratios of benthic bacteria in the literature. Productivity per unit biomass of bacteria depends on the proportion of bacteria that are in an active, rather than quiescent, state. Luna et al. (2002) showed in their study that when only the active fraction was considered, rates are 50–80 times higher. Here, we consider P/B in relation to a biomass that includes inactive and dead bacteria cells. Research (including Ankar 1977; Sorokin 1981; Feller & Warwick 1988; Poremba & Hoppe 1995) suggests that annual P/B ratios of benthic bacteria are likely to lie between about 10 and 150 y^{-1}. It is likely that this wide range reflects the fact that benthic bacterial productivity is affected by a large number of natural variables such as water depth, temperature, seasonal variability in the amount and type of detrital material settling on the seabed and characteristics of the sediment and its fauna. More recently, Luna et al. (2002) measured P/B values for shallow-water benthic sediments between 2.4–43 y^{-1} (referenced to all bacteria cells, not just viable cells). On the Chatham Rise, annually averaged bacteria production decreased systematically with depth (R^2=0.55, *n*=10), consistent with previous work (e.g. Alongi 1990). The bacterial biomass and production values measured by Nodder et al. (2003) suggest a mean P/B of 0.5 y^{-1} on the Chatham Rise (Pinkerton 2011). Poremba & Hoppe (1995) estimated a P/B=10.9 y^{-1} in the Celtic Sea (135–1680 m). Alongi (1990) measured specific growth rates for benthic bacteria at bathyal and abyssal stations which varied widely from P/B=0.37– 44 y^{-1}. Sorokin (1999) gives values of P/B between 7.3–15 y^{-1} off Japan. Given such a wide range of measurements and relevant factors, we propose using a value of 10 y^{-1}. Local measurements of benthic bacterial production rates are needed to obtain better estimates of this parameter.

1.2.3 Consumption, growth efficiency

A benthic bacterial growth efficiency (P/Q) of 0.3, with a possible range of 0.2–0.5, is assumed here (Kirchman, 2001; Pomeroy 1979). A P/Q value of 0.3 with a P/B=10 y^{-1} implies a Q/B of 33 y^{-1}.

1.2.4 Other information: EE, U, accumulation, imports, exports, transfers

There is no evidence for long-term accumulation of benthic bacterial biomass loss in the study area. Exports or imports of benthic bacteria are likely to be very small. Unassimilated consumption from benthic bacteria is assumed to be zero. Ecotrophic efficiency of bacteria is not known, i.e. we do not know what proportion of bacterial cells in the sediments are consumed by other organisms and what proportion die from causes other than predation and become recycled into the detrital pool. We initially and nominally set this value at EE=0.5.

2 Detritus

2.1 General information

Detritus in the trophic model is considered in three groups:

- Water column detritus, including material suspended in and sedimenting through the water-column: Water column detritus includes dissolved and particulate organic matter. The source of water column detritus includes dead phytoplankton and zooplankton cells, phytoplankton exudates, macroalgae exudates, zooplankton faecal pellets, other faecal material, and abraded algal and sessile material (e.g. abraded sponge, macroalgae).
- Benthic detritus as organic matter on the sea-floor, including material in soft sediments, particulate detritus overlying hard substrate, and detritus attached to macroalgae and other biotic structure: Detritus includes phytoplankton exudates, macroalgae exudates, zooplankton faecal pellets, other faecal material, and abraded algal and sessile material (e.g. abraded sponge, macroalgae). Dissolved organic matter in sediment pore water is also included in this category.
- Carcasses and animal remains: The model considers animal carcasses as a separate trophic group. Remains from animals smaller than and including macrozooplankton (20 mm) is not be included here, but will form part of the water column or benthic detrital groups.

We note that as detritus does not have an intrinsic production rate (P/B) or an intrinsic consumption rate (Q/B), the biomass of detritus is not used by the model. However, transfer rates involving detritus (e.g. transfer from water column to benthic detritus) and the source-consumption detrital balance are useful and valid model constraints.

2.2 Detrivores: consumption of detritus or bacteria?

It is not clear to what in what proportions benthic detrivores consume detrital organic material versus consuming benthic bacteria; the consumption of a combination of both is probably important (Plante et al. 1990). Some studies suggest that water column and benthic detritus is consumed directly only by bacteria and protozoa, and that other detrivorous organisms feed largely on bacteria (Moodley et al. 2002; Josefson et al. 2002). There is evidence, though, that copepods and microzooplankton in the water column and microprotozoa in sediments may feed directly on detritus in sediments (Kemp 1990; Fabiano et al. 2000). Here, we assume that a nominal 25% of detrivorous consumption is of detritus directly, and 75% is of bacteria.

2.3 Carcasses

The trophic group labelled “Carcasses” is made up of non-living organic matter from animals of size greater than 20 mm that have not been directly predated and have not been excreted as a waste product. It hence includes bodies of animals that have died for reasons other than predation (including disease, starvation, excess-parasite load and fishing discards), as well as large parts of animals that died due to predation but were not consumed at the time (i.e. “messy eating”). It does not include vegetation of any kind, exudants, faecal material, moulted feathers, shed scales etc. Such material is classified in the model as “detritus” (either water column or benthic). The purpose of this group in the model is to separate material that can be consumed by scavengers from material that is largely broken down by bacterial decomposition.

2.4 River inflow

A considerable quantity of particulate and dissolved detritus enters the Hauraki Gulf region from the rivers, especially Waihou and Piako. Based on river catchment modelling, it was estimated that annual input of dissolved and suspended detrital material to the study region is approximately 0.35 Mt y^{-1}, including 0.16 Mt y^{-1} from the Waihou and 0.035 Mt y^{-1} from the Piako (Hicks & Shankar 2003). The remaining input of detrital material is from smaller rivers. On a New Zealand basis, Zeldis et al. (2010) estimated that carbon comprised between 1.4 and 5.2% by weight of river-borne detrital input from the New Zealand landmass to the coastal ocean, and suggested that the best estimate was towards the lower end of this range. Taking this proportion to be 2%, we estimate a particulate carbon input from rivers to the study region of 7000 tC y^{-1}, which is equivalent to 0.43 gC m^{-2} y^{-1}. Some of the particulate detrital input of carbon may be in a refractory form rather than organic. For comparison, phytoplankton net primary production in the study region is estimated to be of the order of 1.5 MtC y^{-1}, so the detrital input may be about 0.5% phytoplankton production. Manighetti & Carter (1999) showed that this small amount of sediment input to the Hauraki Gulf from rivers is largely trapped within the inner Gulf embayments.

2.5 Detrital flux: Settling

For the site B6 in the outer Hauraki Gulf (Figure 40), suspended Particulate Organic Carbon (POC) from floating trap data varied from 86 (±19) mgC m^{-2} d^{-1} in late spring 1996 to 113 (±32) mgC m^{-2} d^{-1} in late summer 1997. For site H3, inner Hauraki Gulf, north of Waiheke Is, similar POC data gave 242 (±27) mgC m^{-2} d^{-1} in spring 1996 and 169 (±47) mgC m^{-2} d^{-1} in summer 1997. At E3, inner-mid Hauraki Gulf, there is just one robust flux number of 83 mgC m^{-2} d^{-1} in late spring 1996 (Scott Nodder, NIWA, unpublished data).

Moored near-bed sediment trap data from inner-mid Hauraki Gulf (site E3,) varied from 40–100 mgC m^{-2} d^{-1} in late September (20–21 September 1996), decreasing to values generally less than 20 mgC m^{-2} d^{-1} from late September until late October 1996 (Scott Nodder, unpublished data). From a similar mooring at B6 (outer Hauraki Gulf, off Cape Brett), POC vertical flux rates varied from 5–25 mgC m^{-2} d^{-1} from late September–late October, while values that were more typically 5–15 mgC m^{-2} d^{-1} after this until the end of the time-series in late January 2007 (Scott Nodder, unpublished data). Average values from these time-series data are as follows: E3, spring only, September–October, 18 (±20) mgC m^{-2} d^{-1}; B6, spring, September–November, 11(±5) mgC m^{-2} d^{-1}; B6, summer, December–January, 10 (±4) mgC m^{-2} d^{-1} (all: Scott Nodder, unpublished data).These data are shown in Figure 42. We suggest that flux rates may follow surface phytoplankton concentrations, as shown by data from the MODIS-Aqua ocean colour satellite sensor. Daily measurements of ocean colour taken by the MODIS-Aqua sensor at resolutions of 4 km were obtained from NASA via the Giovanni online data system which is developed and maintained by the NASA GES DISC (disc.sci.gsfc.nasa.gov/giovanni). The region used to approximate the study area was latitude (-37°, -35.5°), longitude (174.5°E, 176°E) and the period of data availability is July 2002 – December 2010. Hence, an annual cycle of flux may be obtained by scaling the MODIS chl-a data by the POC flux measurements, as shown in Figure 42.

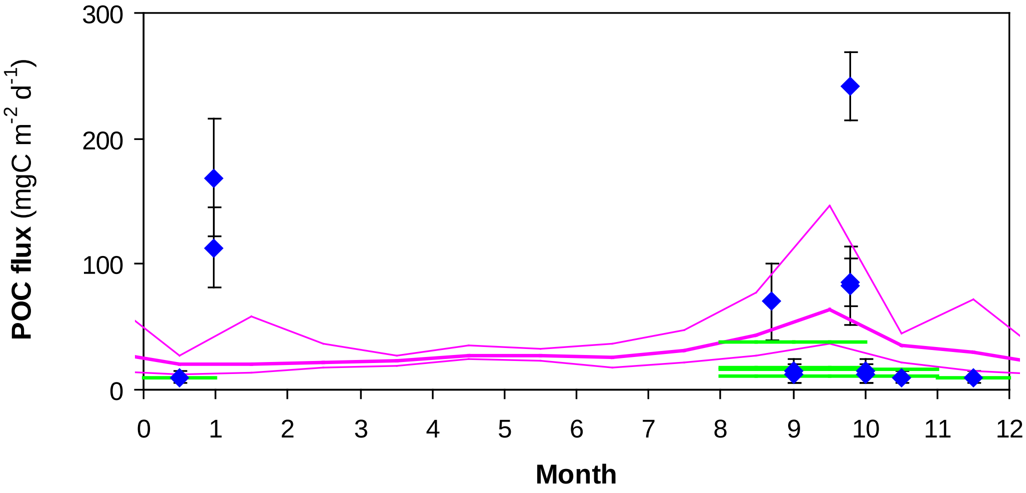

Figure 42: Particulate organic carbon (POC) vertical flux rates from trap measurements in the Hauraki Gulf region (Scott Nodder, NIWA, unpublished data). The blue dots are from floating trap data (24 hours) at B6 (outside study region), H3 and E3. The green lines are averages from moored trap data at E3 and B6. The pink lines are scaled MODIS surface chlorophyll-a concentrations for the study area (solid: long-term mean; finer: upper and lower bounds in period July 2002 – December 2010).

Annual POC flux was then estimated in four ways: (1) mean of moored trap data, giving annual flux of 4.6 gC m^{-2} y^{-1}; (2) mean of all data, weighting moored and floating trap data equally, giving annual flux of 26 gC m^{-2} y^{-1}; (3) assuming background flux of 4.6 gC m^{-2} y^{-1} with peaks of higher flux (as measured by floating traps) for about 3 months per year – this gives annual flux of 16 gC m^{-2} y^{-1}; (4) based on scaled MODIS chl-a annual cycle (as shown in Figure 42) – this gives annual flux of 11 gC m^{-2} y^{-1}. It is not known which of these is most likely to be the best estimate of vertical flux in the study area. Hence, we use the average of all four estimates, i.e. flux of 14 gC m^{-2} y^{-1} as our best estimate.

2.6 Detrital accumulation

The activity of the radiogenic isotope ^{210}Pb measured along the length of a core of deposited benthic sediment is useful in providing estimates of marine sediment accumulation rates over the dating range to about 100–150 years (e.g. Nittrouer et al., 1979; Oldfield & Appleby, 1984). Concentrations of isotopes ^{210}Pb, ^{226}Ra and ^{137}Cs were measured by the National Radiation Laboratory (Christchurch, New Zealand) on down-core sediment samples from five sites in the Hauraki Gulf region (see Sikes et al. 2009 for locations). All five sites are close to or within the study area. Sample size was limited, ^{210}Pb, ^{226}Ra and ^{137}Cs concentrations were highly variable (assessed based on counting statistics) and/or below detection limits for several of the sampling sites and depths within cores, meaning that sediment accumulation rates for the study area remain somewhat uncertain. Nevertheless, sediment accumulation rates given by Sikes et al. (2009) in the range 0.7–2.4 mm y^{-1} are consistent with previous results in the region (De Baere, 2006). There is no relationship between sediment accumulation rate and water depth (N=5, R^2=0.2), or location in the region (Sikes et al. 2009), so we use an average of the five sites of Sikes et al. (2009) to estimate sediment accumulation rates in the study area. Based on measurements of dry bulk density of sediment at these sites (0.65–0.89 g cm^{-3}) and proportions of total organic matter (TOM) in the sediment (2.2–8.3%) (both: Sikes et al. 2009) we estimate a mean organic matter (OM) accumulation rate in the study area of 5.3 mgOM cm^{-2} y^{-1}. Rios et al. (1998) give elemental composition of organic matter in marine sediments which are similar to those obtained by Eppley et al. (1977) and similar to Redfield Ratios (Redfield et al. 1963). These elemental compositions suggest that carbon is about 45% by weight of OM. Data from Sikes et al. (2009), however, show that carbon is only 15.2% (12.1–18.3%) by weight of OM, which we use here. This leads to a mean organic carbon accumulation rate in the sediments of 0.81 mgC cm^{-2} y^{-1} or 8.1 gC m^{-2} y^{-1}. We use this mean value in the model but note that it has been shown that carbon accumulates in the seabed deposits in some years and is consumed in others (Gage 2003). Total detrital flows (water column and benthic) amount to approximately 14 gC m^{-2} y^{-1} so we estimate a detrital accumulation fraction of 56%.

3 Summary of parameters

Parameters for bacteria and detritus in the Hauraki Gulf trophic model representing the present day conditions are given below in Table 97 and **Table 98**.

Table 97: Summary of parameters for bacteria in the trophic model.

	EE	B gC m^{-2}	P/B gC m^{-2} y^{-1}	Q/B gC m^{-2} y^{-1}	P/Q	U	A	X
Water column bacteria	0.5	0.61	43	142	0.3	0	0	0
Benthic bacteria	0.5	2.0	10	33	0.3	0	0	0

Table 98: Summary of parameters for detritus in the trophic model.

Parameter	Value	Units
Water column to benthos POC flux	14.4	gC m^{-2} y^{-1}
Riverine influx of detritus to water column	7000	tC y^{-1}
Riverine influx of detritus to water column	0.432	gC m^{-2} y^{-1}
Accumulation rate of carbon in sediments	8.1	gC m^{-2} y^{-1}
Accumulation/influx	56	%

4 Historical parameters

Trophic models are required for detritus and bacteria in four historical periods: 1950, 1790, 1500 and 1000. Natural drivers of environmental change in New Zealand during the last millennium were examined by Lorrey et al. (2013). It seems unlikely that biomass, energetics, or other key parameters for any of the bacteria or detrital groups in the trophic model would have been substantially changed by climate variations *per se*, and we do not adjust any of these parameters from the present day values in the historical trophic models. We recognise, of course, that biomass and trophic role of these groups may be different historically than at the present time, as they may have been affected by changes to the ecosystem via indirect food-web (or non-trophic) connections.

5 Acknowledgements

This research was funded by Ministry for Primary Industries project ZBD200505 ("Long-term change in New Zealand coastal ecosystems") and by the New Zealand Foundation for Research, Science and Technology project C01X0501 (Coasts & Oceans OBI). We acknowledge Dr Mary Livingston and Dr Martin Cryer (Ministry for Primary Industries) for project funding and Dr Alison MacDiarmid (NIWA) for overall project leadership. Dr Jeanie Stenton-Dozey (NIWA) provided useful comments on a draft of this work.

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