www.csiro.au

The trophodynamics of small pelagic fishes in the southern Australian ecosystem and the implications for ecosystem modelling of southern temperate fisheries

Marine and Atmospheric Research

C.M. Bulman, S.A. Condie, F.J. Neira,
S.D. Goldsworthy and E.A. Fulton

Final Report for FRDC Project 2008/023
March 2011

Australian Government
Fisheries Research and
Development Corporation

The trophodynamics of small pelagic fishes in the southern Australian ecosystem and the implications for ecosystem modelling of southern temperate fisheries

C.M. Bulman, S.A. Condie, F.J. Neira,
S.D. Goldsworthy and E.A. Fulton

CSIRO Marine and Atmospheric Research

Final report for FRDC project 2008/023
March 2011

The trophodynamics of small pelagic fishes in the southern Australian ecosystem and the implications for ecosystem modelling of southern temperate fisheries

C.M. Bulman, S.A. Condie, F.J. Neira, S.D. Goldsworthy and E.A. Fulton
CSIRO Marine and Atmospheric Research

Enquiries should be addressed to:

Dr Catherine M. Bulman
CSIRO Marine and Atmospheric Research
GPO Box 1538 Hobart, Tasmania 7001 Australia
+61 03 6232 5357 Cathy.Bulman@csiro.au

Copyright

Disclaimer

The results and analyses contained in this Report are based on a number of technical, circumstantial or otherwise specified assumptions and parameters. The user must make its own assessment of the suitability for its use of the information or material contained in or generated from the Report. To the extent permitted by law, CSIRO excludes all liability to any party for expenses, losses, damages and costs arising directly or indirectly from using this Report. Opinions expressed by the authors are the individual opinions of those persons and are not necessarily those of the publisher, CSIRO or the FRDC.

The Fisheries Research and Development Corporation plans, invests in and manages fisheries research and development throughout Australia. It is a statutory authority within the portfolio of the federal Minister for Agriculture, Fisheries and Forestry, jointly funded by the Australian Government and the fishing industry.

The use of this Report is subject to the terms on which it was prepared by CSIRO. In particular, the Report may only be used for the following purposes.

- this Report may be copied for distribution within the Client's organisation;
- the information in this Report may be used by the entity for which it was prepared ("the Client"), or by the Client's contractors and agents, for the Client's internal business operations (but not licensing to third parties);
- extracts of the Report distributed for these purposes must clearly note that the extract is part of a larger Report prepared by CSIRO for the Client.

The Report must not be used as a means of endorsement without the prior written consent of CSIRO. The name, trade mark or logo of CSIRO must not be used without the prior written consent of CSIRO.

National Library of Australia Cataloguing-in-Publication

Title: The trophodynamics of small pelagic fishes in the southern Australian ecosystem and the implications for ecosystem modelling of southern temperate fisheries / C.M. Bulman ... [et al.]

ISBN: 9781921826238 (pbk.)

Subjects: Pelagic fishes--Australia, Southern.Food chains (Ecology)
Marine ecology--Australia, Southern.
Marine ecosystem management--Australia, Southern

Other Authors/Contributors: Bulman, Cathy.
CSIRO. Marine and Atmospheric Research.

Dewey Number: 338.37270994

Report and cover designed by Lea Crosswell (CMAR). Printed by Print Applied Technology, Hobart.

Contents

Appendices

List of Figures

List of tables

2008/028 The trophodynamics of small pelagic fishes in the southern Australian ecosystem and the implications for ecosystem modelling of southern temperate fisheries

PRINCIPAL INVESTIGATOR: Dr C. Bulman
ADDRESS: CSIRO Marine and Atmospheric Research
GPO Box 1538
Hobart Tas 7001
ph: 03 6232 5357

OBJECTIVES:

1. To better understand the role of small pelagic fishes in the functioning of southern Australian ecosystems, particularly with respect to foodweb control, specifically in the Small Pelagic Fishery but also their effects on other fisheries.
2. To compare the performance of the most recent Atlantis and EwE ecosystem models with regard to the potential effects of a range of harvest strategies on selected small pelagic species in south-east Australia.

NON TECHNICAL SUMMARY

OUTCOMES ACHIEVED

We found that the GAB and EBS systems are largely bottom-up forced but that the more heavily fished EBS has more top-down controlling elements. We also found that different branches of the foodweb could display different forcing particularly in the EBS model. Both bottom-up and top-down controls can occur in open-shelf systems and switching between these states may indicate pressures such as climate change and fishing. None of the small pelagic species in the southeast Australia ecosystem occupy a strong wasp-waist role. However, wasp-waist species need not be the “traditional” small pelagic species and both mesopelagic fishes and krill produced the most significant results in this study, a finding which supports a study investigating the effects of depletion of these species and the small pelagic species using both an Atlantis and an EwE model.

Climate change-induced environmental changes are very likely to have major impacts particularly in top-down systems already sensitive to fishing pressure and mid-trophic levels, particularly mesopelagic and small pelagic fishes, may be at the centre of a future regime shift in waters off eastern Tasmania and Bass Strait. These groups needs to be refined and monitored to determine if Australia’s marine systems are on a trajectory that will lead to large-scale restructuring of the role of small pelagic fishes.

The small pelagic fish functional group is an important link between the primary and secondary producers and the higher predators, including the valuable wild tuna species and some other commercial species as well as marine mammals and seabirds. Large small pelagic fisheries are usually associated with the highly productive upwelling regions of eastern boundary currents such as the Benguela, Humboldt and Californian Currents. Since most of the collapses of major pelagic fisheries are caused by overfishing, understanding the dynamics of small pelagic fishes becomes especially important when they are targeted. The dramatic rise and fall of the jack mackerel fishery off east Tasmania in the 1980s might have resulted from the enormous fishing pressure at the time or, alternatively, may have been due to the sensitivity of small pelagic fishes to changes in food resources resulting from climate variability, or indeed both.

In Australia, the abundance of the small pelagic fishes is not as high as that of other regions of the world due largely to the less productive waters surrounding the continent. Regions of localised production, such as the Bonney upwelling in the Great Australian Bight (GAB) off southern Australia do, however, support valuable localised fisheries of small pelagic fishes such as sardines and anchovy. Off south-eastern Australia, where productivity is lower, small pelagic species of interest are currently redbait and jack mackerel, although blue mackerel is also important throughout the Bight and eastern Australia.

Ecosystem dynamics differ among systems depending on the type of trophic control operating in the foodweb. Understanding the type of control in a system is fundamental not only to determining sustainable levels of harvest of pelagic fishes but could also help to determine the impacts on higher predators and their fisheries. Bottom-up controlled systems are those where large predators are controlled by the lower trophic groups. Top-down systems are those where lower trophic levels are controlled by higher predators. Wasp-waisted systems are those where small pelagic species exert top-down control on lower trophic levels such as zooplankton, and a bottom-up control on top predators such as large pelagic fishes, birds, mammals and fishers.

In this study we used qualitative models and two Ecopath with Ecosim (EwE) models, one for the Eastern Bass Strait (EBS) region and one for the eastern GAB, to investigate the dynamics of foodwebs. Overall, both EwE models suggested that these systems are largely bottom-up forced but that the more heavily fished EBS has more top-down controlling elements. We also found that different branches of the foodweb could display different forcing particularly in the EBS model. Both bottom-up and top-down controls can occur in open-shelf systems and switching between these states may indicate pressures such as climate change and fishing. The heavily-fished EBS system might well be an example.

The evidence for wasp-waist control by small pelagic species was not particularly strong. Typically, wasp-waist species dominate their trophic level, channelling the energy flow through the mid-trophic level from plankton to large fish, seabirds and marine mammals. They have short but complex life histories that may result in high variability; they usually are the lowest trophic level that is mobile; and they may prey on early life stages of their predators. Although some small pelagic species in the southeast Australia ecosystem possess some of these characteristics, none exhibit a strong wasp-waist role.

However, wasp-waist species need not be the “traditional” small pelagic species that we normally associate with that term. Both mesopelagic fishes and krill produced the most significant results in this study, a finding which supports a previous study investigating the effects of depletion of these species and small pelagic species using both an Atlantis and an EwE model. The combination of a high initial biomass and heavy predation pressure on a group generally resulted in a higher likelihood of that group playing a central role in the functioning of the ecosystem e.g. as for krill in the Atlantis-SE model and for krill and mesopelagic fishes in the Ecosim-EBS model.

Future stresses, including physiological responses resulting from climate change-induced environmental changes, are very likely to have major impacts in any system, but particularly in top-down systems already sensitive to fishing pressure. Preliminary analyses (Fulton in review) suggest that mid-trophic levels, particularly mesopelagic and small pelagic fishes, may be at the centre of a future regime shift in waters off eastern Tasmania and Bass Strait. There may also be significant implications of changing upwelling strength across the southeast (which some of the downscaled climate models are currently predicting) for small pelagic fisheries. Not all of these shifts are negative and there may be some significant opportunities, but what is clear is that if these changes eventuate, they will lead to a radically different context to the fishery than exists today. Consequently, the representation of these groups in models needs to be refined to help constrain the uncertainties and identify key pieces of information for future monitoring in order to determine if Australia’s marine systems are on a trajectory that will lead to large-scale restructuring of the role of small pelagic fishes.

Acknowledgements

We thank Marcia Rollins, Ruth Sharples and Scott Cooper for database entry, migration and management.

We also thank Jeremy Lyle for sage advice and recreational fishing data. Ian Cartwright, Phil Domaschenz and members of the SPFRAG who provided helpful advice and comments.

Thanks also to Tony Smith and Penny Johnson for permission to use results for Southeast Australian Case Study from the Marine Stewardship Council Low Trophic Level study.

We are grateful to the following students for allowing us to use their data from which the GAB diet web was drawn:

- Annelise Wiebkin - Reproductive and foraging ecology of little penguins (PhD, University of Adelaide).
- Alastair Baylis - Oceanographic influences on the foraging ecology of New Zealand fur seals (PhD, University of Adelaide).
- Luke Einoder - Reproductive and foraging ecology of little penguins (PhD, University of Adelaide).
- Robin Caines - Trophic guild-structures in large pelagic fish the eastern GAB Ecosystem. (PhD, University of South Australia.
- Michelle Roberts - Diets of Arrow squid (Honours, University of Adelaide).
- Kerryn Daly - Diets and trophic guilds among SA small pelagic fisheries (Honours, University of Adelaide).
- Natalie Bool - Population and foraging ecology of little penguins, Granite Island (Honours, University of Adelaide).
- Paul Rogers - Ecology of pelagic sharks in South Australia (PhD, Flinders University).
- Lachie McLeay - Population and foraging ecology of crested terns (PhD, University of Adelaide).

In addition, Charlie Huveneers (SARDI/Flinders University) contributed to shark diets, while Brad Page (SARDI) contributed to the New Zealand fur seal diet.

1 Introduction

1.1 Background

The small pelagic fish functional group is an important link between the primary and secondary producers and the higher predators including the valuable wild tuna species and some other commercial species, as well as marine mammals and seabirds. Since most of the collapses of major pelagic fisheries was caused by fishing (Beverton, 1990), understanding dynamics associated with the small pelagic fishes becomes especially important when they are targeted. Ecosystem dynamics can be vastly different from system to system, depending on the type of control exerted by the foodweb. Bottom-up controlled systems are those where the large predators, often the valuable harvested species but including the birds and marine mammals, are controlled by the lower trophic groups. Top-down systems are those where the lower trophic levels are controlled by higher predators. Wasp-waisted systems are those where the small pelagic species exert top-down control on lower trophic levels such as zooplankton and a bottom-up control on top predators such as large pelagic fishes, birds and mammals and fishers. Understanding the type of control in a system is fundamental not only to determining sustainable levels of harvest of the pelagic fishes but could also determine the impacts on higher predators and their fisheries. This was demonstrated by Shannon *et al.* (2000) who modelled three small pelagic fish species of the Benguela upwelling system under three types of control: wasp-waist, bottom-up and top-down. They found that the small pelagic fishes collapsed under wasp-waist control and took longer to recover than bottom-up control, because in the absence of other controls their competitors had increased in biomass and retarded their recovery.

In Australia, the small pelagic fish fauna is not as abundant as that of other regions of the world, implying a tighter control and potentially greater effects of the fishery. The dramatic rise and fall of the jack mackerel fishery off east Tasmania in the 1980s might have been a result of enormous fishing pressure at the time or from the sensitivity of small pelagic fishes to changes in food resources resulting from climate variability, or indeed both. An important step towards being able to predict and evaluate the wider impacts that these small pelagic fishes might have, most significantly on the other southern fisheries, is to determine the type of foodweb control exerted by them.

Climate change is likely to have a significant influence on pelagic ecosystems through changes in:

- properties and geographical distributions of water masses;
- wind-driven upwelling and water column stability;
- primary and secondary productivity; and
- larval transport and survival.

Several reports by the AGO (Voice *et al.,* 2006) and CSIRO (Hobday *et al.*, 2008), outline potential impacts of a changing marine environment. However, Voice *et al.* (2006) state that there is little available so far that deals explicitly with predicting the impact on fish and fisheries.

Practical approaches for incorporating climate change impacts within trophic models will be scoped through:

- identification of appropriate climate change forcing for use in trophic models of temperate Australia (e.g. outputs of global climate models);
- identification of modelling approaches capable of representing the impacts of climate change on pelagic fishes and fisheries (e.g. qualitative models, climate envelope models, population models, ecosystem models); and

- identification of any new model functionality required to represent key climate change impacts within these trophic models (e.g. dependencies on water temperature, pH and changing ocean currents).

We therefore propose:

- to identify ecosystems and construct their associated foodweb or foodwebs which would best capture southern Australian ecosystems and fisheries;
- to derive scenarios influenced by climate change, recovery of seal populations, and changing fisheries, including impacts on recreational and commercial fisheries that are relevant to their management and sustainability;
- to use existing EwE models for the East Bass Strait (EBS) and Great Australian Bight (GAB), where control can be explicitly specified, to explore the implications of the types of foodweb controls; and
- to compare the results of investigations into the potential effects on the whole ecosystem and fisheries from current and theoretical harvest strategies using two current models for south-eastern Australia.

The pelagic ecosystem models we will examine as a part of this process are the EwE models developed for East Bass Strait (Bulman *et al.*, 2006), the eastern Great Australian Bight (Goldsworthy *et al.*, 2011) and the Eastern Tuna and Billfish Fishery (Young *et al.*, 2009); and the Atlantis models developed for South East Australia (Fulton *et al.*, 2004) and the NSW shelf (Savina *et al.*, 2008). These models collectively cover the area and species in the southern ecosystem, but they have each been constructed for different purposes. Further refinement and re-parameterisation will therefore be required to fully address questions related to small pelagics and climate change.

1.2 Need

There is an increasing need to develop appropriate management in the Commonwealth Small Pelagic Fishery (SPF). Past spikes in the jack mackerel fishery, more recent increases in catches of redbait in Zone A of the SPF and predicted climate change impacts pose a significant threat to the ecosystem structure and function particularly in this region but more broadly throughout the whole SPF, emphasizing our need to understand the role of small pelagics in the southern Australian ecosystem.

The SPF Management Advisory Committee identified several priorities for research such as determination of stock structure and size, the role of the species in the system, harvest strategies in response to the Ministerial Direction 2005, and interactions with TEP species and bycatch. COMFRAB called for research that would identify possible spatial management arrangements that best suit the spatial distribution of the species.

Our proposal addresses the issue of the role of small pelagics in the southern Australian ecosystem, and the potential impacts, under various types of ecosystem controls and environmental and management influences. We will also recommend an approach to developing purpose-built models to evaluate derived scenarios of management, fishery interactions and potential climate change impacts.

1.3 Project objectives

1. To better understand the role of small pelagic fishes in the functioning of southern Australian ecosystems, particularly with respect to foodweb control, specifically in the Small Pelagic Fishery but also their effects on other fisheries.

2. To compare the performance of the most recent Atlantis and EwE ecosystem models with regard to the potential effects of a range of harvest strategies on selected small pelagic species in south-east Australia.

Objective 2 has substantially changed from the original in view of recent activity in model re-developments after consultation with FRDC and AFMA (May 2010). This activity is a result of a global collaborative project funded by the Marine Stewardship Council and led by Dr Tony Smith (CSIRO) to investigate the effects of fishing lower trophic levels including small pelagic species. Consequently both the SE Atlantis and EBS EWE models have been modified appropriately in order to quantify these effects in our region and the results have been submitted as part of those from the larger global project. This has provided us with the opportunity of not only bypassing some of the steps involved in reviewing all models to determine appropriate structure—although this will be reviewed for these two models—but also the ability to compare the results of the models to a range of fishing pressures and primary production anomalies in lieu of climate change scenarios. Climate change scenarios *per se* have not been investigated as these entail more complex issues involving end-to-end coupling of several models and as such were beyond scope. However, we will still identify the most likely climate change scenarios given the current state of knowledge and identify other model functionality that might be needed in model redevelopments, and describe ongoing efforts to couple climate, biogeochemical and ecosystem modelling.

1.4 Methods

1. Collate data sets of trophic studies or literature including (but not exclusive) Blaber and Bulman (1987), Bulman and Blaber (1986), Bulman *et al*. (2001), Bulman *et al*. (2002), Coleman and Mobley (1984), Goldsworthy *et al*. (2003), Hamer and Goldsworthy (2006), McIntosh *et al.* (2006), Ward *et al*. (2001), Welsford and Lyle (2003), Young and Davis (1992); and environmental and biological data or literature including Bax and Williams (2000), Bulman *et al*. (2006), Condie and Dunn (2006), Harris *et al.* (1991), Young *et al.* (1993), Young *et al*. (1996a), Young *et al*. (1996b) relevant to the small pelagics across the southern Australian region. Additional data will also be available from the SA ecosystem study currently being developed as part of FRDC 2005/031 (Goldsworthy *et al*., 2011).

2. Derive a series of food webs focussed on the small pelagic species by defining functional groupsmost consistent with the focus on small pelagics. The underlying dietary matrices will be compared totrophic structure of existing Ecopath or Atlantis models with the intention of modifying an existingmodel/s in future model development.

3. Determine potential food-web control operating on the various systems by:

    a. altering species-specific parameters to simulate thevarious types of control in the EBS EwE model that has existing scenarios of i. seal recovery rates, ii. harvest strategies which can be modified to more closely align with current harvest strategies including targetted small pelagic iii. rudimentary approximations of climate change; and iv. targetted harvest strategies on small pelagic fishes, and the SA model. The SA models will also be especiallyimportant to answering this question becauseof potential important top-down forcing that recovering fur seals populations may be exerting on small pelagics. New Zealand fur seal population have increased 8-fold in size since the late 1980s in SA, and populations are still increasing at about 12%/year (Shaughnessy and Goldsworthy unpublished data).

    b. comparing system parameters such as food web structure, environmental and community composition data including biomass, in other small pelagic systems (e.g. the Benguela, Humboldt, & Peruvian upwellings) to discover similarities that might indicate the type of control operating.

4. Identify the most likely climate change scenarios to be operating given the current state of knowledge demonstrable through qualitative modelling techniques and identify other model functionality that might be needed in future climate model redevelopments.

5. Compare and discuss model outputs from the two existing functional models, Atlantis-SE and EwE-EBS, which have been partially modified to investigate the ecosystem effects of various levels of fishing pressure for redbait, jack mackerel and small pelagic fishes (anchovies and sardines) calcualted to deplete the biomasses, B_0, through a series from B_{75} to B_0.

2 Small pelagic fishes in Australia and beyond

2.1 Global upwelling systems: characteristics and fisheries

The most productive upwelling regions worldwide are found along the ocean's four major eastern boundary current systems, namely (1) the Benguela in the south Atlantic off southern Africa; (2) the Canary in the Atlantic off northern Africa; (3) the California in the Pacific off North America; and (4) the Humboldt in the south Pacific along South America (Figure 1). Referred to as coastal upwelling ecosystems (CUEs) by some authors, these regions are exceedingly productive due to enrichment, concentration and/or retention processes driven by a combination of local forcing and large-scale circulation, the latter being the key factor behind the properties of deep water brought to the surface by upwelling-favourable winds. The high productivity of these regions (maximum ~ 3 g C m^{-2} day^{-1}) supports large assemblages of small, plankton-feeding, broadcast-spawning pelagic fishes comprising anchovies, sardines and mackerels, and which individually and collectively support massive fisheries worldwide (Bakun and Parrish, 1982; Bakun, 1996; Roy, 1998; Cury *et al.*, 2000; Carr and Kearns, 2003; Freon *et al.*, 2005). The main embracing features of CUEs include very high primary production rates and short foodwebs, strong equatorial-ward winds that are either permanent or seasonal, and a differential vertical current structure that follows a simple Ekman model, i.e. wind-forced offshore surface flow and a compensatory onshore flow either immediately below the surface layer, along intermediate depths or adjacent to the seafloor (Bakun and Parrish, 1982; Schahinger, 1987; Cury and Roy, 1989; Pillar *et al.*, 1998; Strub *et al.*, 1998, Condie and Sherwood, 2006). In the case of the Southern Hemisphere, there is a net transport of water in the surface Ekman layer directed 90° to the left of the wind direction.

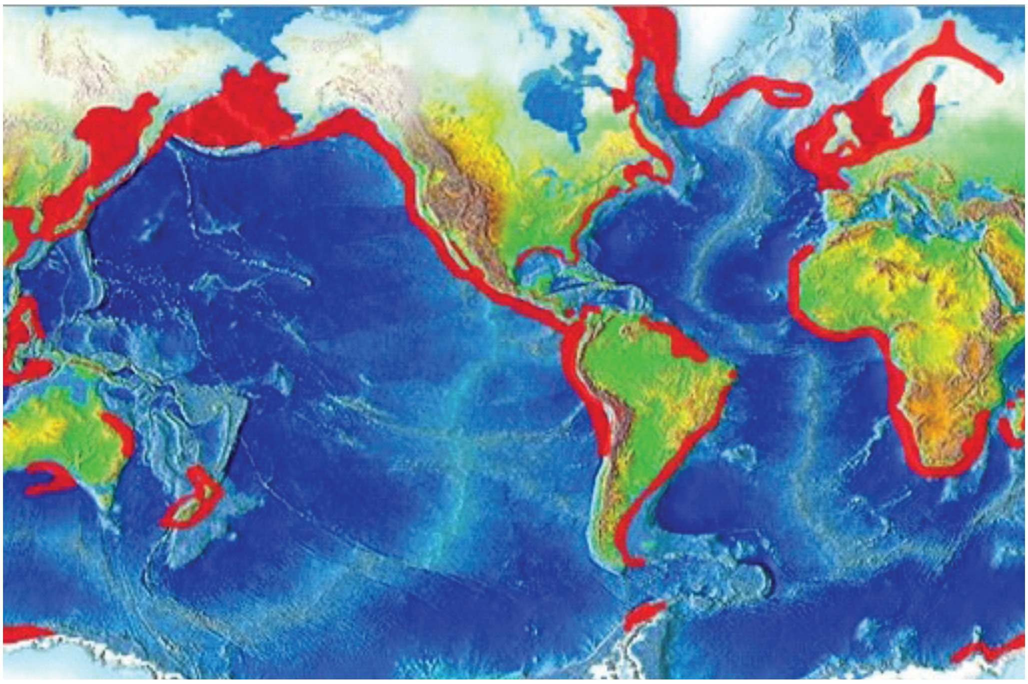


Figure 1. Location of major coastal upwelling areas worldwide (in red). Image from http://oceanservice.noaa.gov/education/kits/currents/03coastal4.html.

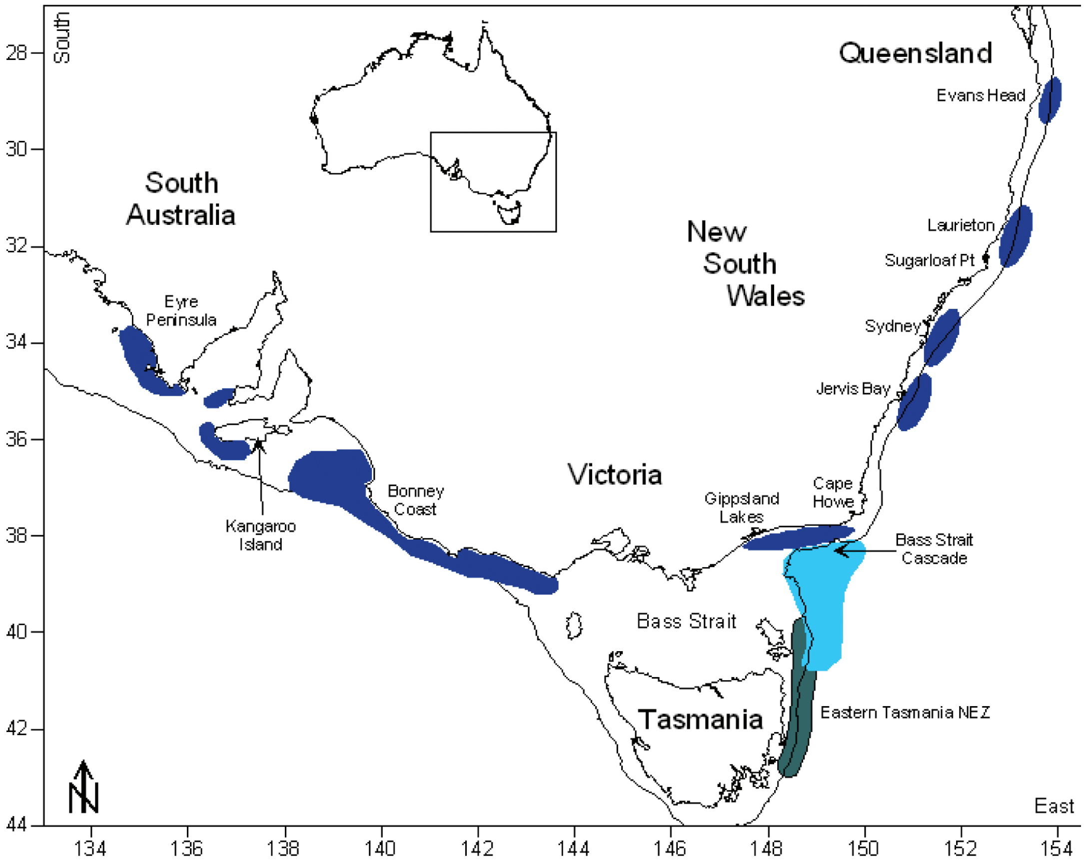


Figure 2. Location of major spring/summer coastal upwelling areas and nutrient enrichment zones (NEZs) known for south-eastern Australia; NEZ off Bass Strait cascade corresponds to a winter event. Sizes of depicted plumes are not to scale.

Figure 3. A graphical representation of the Bonney Upwelling off eastern South Australia's Bonney coast. Source: http://www.abc.net.au/nature/bigblue/diary12.htm

Table 1. Summary information on upwelling and nutrient enrichment zones (NEZs) in south-eastern Australia; * note that µmol/l = µg-at/l = mmol/m3 = µM).

Name/Locality	Main plume centre(s)	Type and induction mechanism	Dynamics	Prevailing winds	Season	Duration	Temp	Salinity	Nitrates* (NO_3-N)	Surface Oxygen	Source(s)
Bonney upwelling; Bonney Coast - Robe (eastern SA) to Portland (western Vic)	Extensive; Robe, Southend, Port McDonnell	Intermittent, wind-forcing	Onshore intrusion of cold, nutrient-rich sub-Antarctic water (from 250-300 m) following wind-driven offshore advection of inshore surface water (~ 20m thick layer)	Persistent (2-5 days) longshore south-easterlies associated to seasonal migration of subtropical high pressure system	Summer - Autumn: Nov/Dec to Mar/Apr	Few days – four months	11-14°C	35.2 ppt	6-7 µM	Lower surface values	Rochford (1977; Lewis (1981); Schahinger (1987); Butler et al.(2002); Middleton & Cirano (2002) ; Middleton and Bye (2007) ; Kämpf et al. (2004)
Eyre Peninsula, SA	Localised; west margin of Eyre Peninsula	Wind-forcing		Longshore south-easterlies	Late summer	Short-lived					Griffin et al. (1997); McClatchie et al., (2006); van Ruth et al (2010)
Kangaroo Island, SA	Localised; SW of Kangaroo Is	Wind-forcing		Longshore south-easterlies	Late summer	Short-lived					Middleton and Cirano (2002) ; Middleton and Bye (2007) ; Kämpf et al. (2004)
Eastern Victoria	Localised; Lakes Entrance to Gabo Island (~5 nm N-S by 30 nm E-W)	Combination between a strong westward flowing current, offshore anticyclonic eddies and local shelf topography	Uplifting of cold, nutrient-rich slope water from depths of around 100 m	Wind stress does not appear a contributing factor	Summer: mid to late Feb to end of Mar	Short-lived, annually intermittent	14-15°C		~3 µM		Rochford (1977)
Bass Strait Cascade NEZ	Extensive; east-ern end of Bass Strait (Banks Strait to Flinders Is.)	Not understood; possibly dynamic uplift in the cores of cyclonic eddies	Upward mixing of deep, cold, nutrient-rich sub-Antarctic water from continental slope along the shelf break front		Winter (Jun to Oct)	Relatively long-lived	12.5-13.5°C	35.2	~4-7 µM		Gibbs et al. (1986, 1991)
Eastern Tasmania NEZ	Extensive; Tas-man Is. to Flinders Is.	Episodic; wind-forcing leading to disruption in water column stability	Advection of nutrient-rich subantarctic water following strong zonal westerly wind stress driven by latitudinal changes in subtropical high pressure cells	Strong local westerlies	Spring to early summer; spring production bloom mid-Sep to end Nov	Spring bloom extends to 4 months in some years	14.5°C	34.9-35.3	~3-6 µM		Harris et al. (1987, 1988, 1991, 1992)

Name/Locality	Main plume centre(s)	Type and induction mechanism	Dynamics	Prevailing winds	Season	Duration	Temp	Salinity	Nitrates* (NO_3-N)	Surface Oxygen	Source(s)
Eden, NSW	Localised; shelf off Eden		Intrusion of cold, nutrient-rich slope water following ending of northward Bass Strait water flow		Late summer (Feb)	Short-lived	12-15°C		~2-6 µM		Rochford (1984)
Jervis Bay, NSW	Localised; shelf off Jervis Bay	EAC-associated baroclinic instability and wind-forcing	Uplifting of cold, nutrient-rich slope water forced by unstable core-cold eddy and upwelling-favourable winds	North-easterlies (10-18 m s^{-1})	Dec	Short-lived	12-14°C				Gibbs et al. (1997)
Sydney Shelf, NSW	Localised; Port Jackson to Botany Bay	Wind- and current-forcing	Combination of wind stress and intrusion of slope water onto shelf area derived from proximity of eddy of EAC meander to shelf		Aug to Apr; more prevalent during spring/ summer	Short-lived	As cool as 8°C				Tranter et al. (1986); Gibbs et al. (1998); McClean-Padman and Padman (1991); Marchesiello et al. (2000)
Laurieton upwelling, NSW	Localised; off Laurieton, ~5 nm wide by 20-30 nm in length	Possibly induced by shelf topography i.e. narrowing of shelf width ~ 10 nm; no association was found with either longshore currents or longshore/ offshore winds	Dynamic uplifting of cold, nutrient-rich water associated with strong slope southward current		Spring/summer; events more frequent in Jan-Mar than Oct-Dec	Short-lived, 12-57 days, in cycles of 9-15 days (intervals between events average 24 days)	15-17°C, from slope water at depths of 125-275 m	Decrease; 35.3-35.4	5-10 µM	Decline to below saturation values	Rochford (1975, 1984)
Evans Head, NSW	Localised; off Evans Head, ~5 nm wide by 20-30 nm in length	Possibly induced by shelf topography i.e. narrowing of shelf width to ~ 10 nm	Dynamic uplifting of cold, nutrient-rich water associated with strong slope southward current		Spring/summer	Short-lived	17-19°C, from slope water		~4 µM		Rochford (1972,1984)

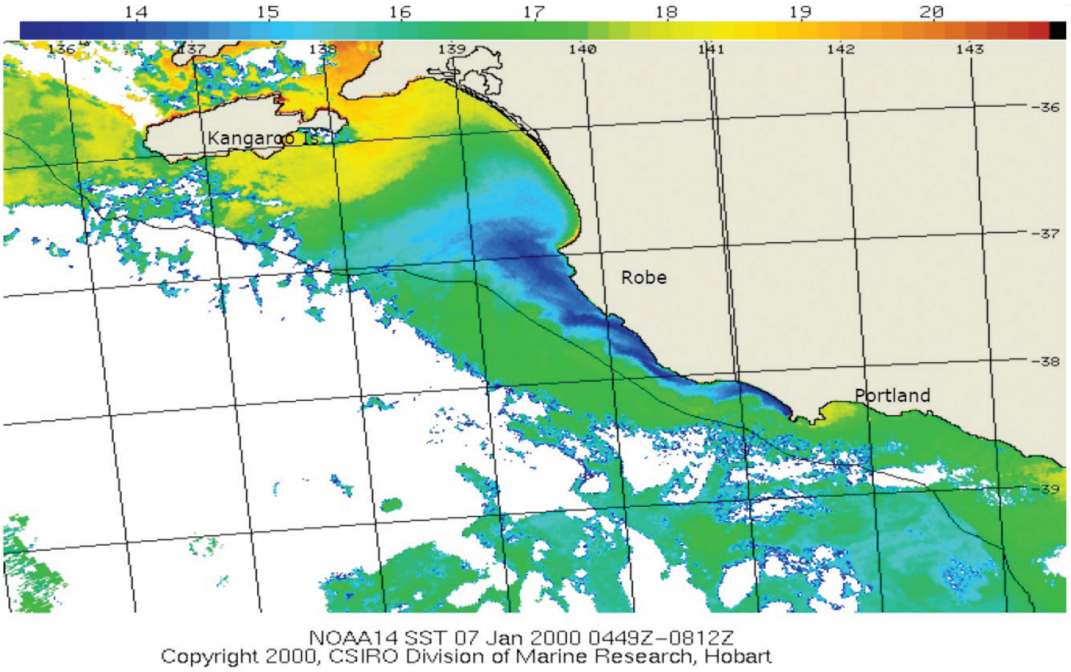


Figure 4. Satellite image showing SSTs during Bonney upwelling even along the eastern South Australia. Source: CSIRO.

The Benguela, Canary, California and Humboldt Current systems and associated CUEs sustain large populations of clupeids (sardines and alike) and engraulids (anchovies), which combined account for nearly 50% of the total landings of marine species worldwide (Freon *et al.*, 2005). So what makes CUEs so attractive to small, plankton-feeding pelagic fishes? The general consensus points to the combined effects of retention mechanisms coupled with increased food availability from upwelling intensity and strong, wind-driven turbulent mixing that enhances encounter rates between food particles and larval stages, leading to increased larval survival and subsequent juvenile recruitment (Cury and Roy, 1989; Cury *et al.*, 1998; Roy, 1998). For example, annual recruitment levels of Peruvian anchoveta (*Engraulis ringens)*, Pacific sardine (*Sardinops sagax*), West African sardines and sardinellas in regions subjected to Ekman-type upwelling fall when wind speeds reach >5–6 m s^{-1} (Cury and Roy, 1989). Such findings have led to the suggestion that an optimal environmental window exists for recruitment for these clupeoids, which is linked to wind-driven upwelling intensity and resultant turbulence mixing.

Despite the markedly enhanced productivity associated withCUEs worldwide, not all upwelling-related processes appear to favour pelagic fish populations, especially following spawning. For example, offshore advection and upwelling-associated turbulence are thought to be detrimental to spawning success as these factors contribute to the dispersion of eggs and larvae away from favourable coastal nursery habitats. Consequently, some species tend to spawn either downstream or upstream of strongly-pulsed upwelling centres that are dominated by strong offshore transport, as in the case of sardine and anchovy off California and anchovy off South Africa (Bakun and Parish, 1982; Hutchings *et al.*, 1998, 2002). In contrast, other species are able to time their spawning seasons to coincide with maximum upwelling intensity, as in the case of Peruvian anchoveta and sardinella off Senegal (Bakun and Parish, 1982; Roy, 1998; Swartzman *et al.*, 2008). Furthermore, spawning and annual recruitment success in the sardinellas are believed to be dependent on upwelling intensity (for Ekman-type CUEs) and retention processes generated by a double-cell vertical circulation structure over the shelf (Cury and Roy, 1989; Roy, 1998). Such contrasting behaviour among small pelagic fishes in different CUEs appears to be the limiting factor behind population size and hence catches, resulting in some species being significantly more abundant in some regions compared to others. In this context, both upwelling intensity and associated retention, coupled with wind-driven mixing processes, are the main physical factors thought to be responsible for the massive fish catches obtained in the Humboldt-derived Peruvian CUE (5-18^{o}S), which are up to 10 times greater than those from CUEs associated with other major currents, including the California CUE and Humboldt-derived Chilean CUE (18-30^{o}S) off central Chile (Cury *et al.*, 1998). Paradoxically, however, the Humboldt Current system is not the most productive in terms of primary production, even though upwelling is known to take place all year-round at least off Peru (Alheit and Bernal, 1993; Carr, 2002).

The structure of CUEs is controlled largely by small, plankton-feeding pelagic fishes which play a key ecological role as the link between primary/secondary producers and higher order predators such as large pelagic fishes, seabirds and marine mammals (Shannon *et al.*, 2008). As a major ecological functional group, changes in biomass of their often massive schooling populations have demonstrable effects on coastal pelagic ecosystems, including CUEs, both in terms of structure and function (refer to detailed review by Cury *et al.*, 2000). Furthermore, abundance regime shifts in pelagic fish populations, such as those between alternating anchovy and sardine stocks in the Humboldt Current ecosystem, are known to drastically restructure the entire ecosystem from phytoplankton to top predators (Alheit and Niquen, 2004). Sardines and anchovies feed in different manners and on different sized plankton, i.e. sardines prefer small zooplankton while anchovies prefer large zooplankton that are favoured by either warm or cooler periods of upwelling respectively (Cury and Shannon, 2004). Small pelagic fishes in CUEs exert control on zooplankton biomass by direct predation (“top-down” control) or limit production of their predators or top predators (“bottom-up” control). Since these pelagic fishes exert both types of control to varying degrees in all major CUEs worldwide, they are said to exert “wasp-waist” control (Cury *et al.*, 2000, 2001), a concept which has led to the view that all major upwelling ecosystems function as wasp-waist systems (Shannon *et al.*, 2008). In the context of fisheries, the concept has been applied to ecosystem-based management of forage-fish fisheries (Bakun *et al.*, 2009), based on the fact that all small pelagic fish populations comprise typically “boom or bust” species that have been responsible both for massive catches and for long-term collapses during the past century (Hutchings *et al.*, 2002; Freon *et al.*, 2005; Alheit, 2006; Schwartzlose *et al.*, 1999). While reasons for these biomass changes remain unclear, the consensus is that fishing pressure and environmental variability are likely to be contributing factors (Beverton, 1990).

2.2 Oceanographic regions in southern Australia upwelling systems and non-upwelling systems

Literature available on oceanography and upwelling systems around south-eastern Australia has increased steadily since the late 70s (Table 1). Information collated has been broadly applied regionally to aspects such as nutrient cycling and primary production (Harris *et al.*, 1987, 1991; Hallegraeff and Jeffrey, 1993; Gibbs *et al.*, 1997), spawning dynamics of key commercial fish species (Prince and Griffin, 2001; Neira and Keane, 2008; Neira *et al.*, 2009), mixed commercial fisheries such as the South East Fishery (Harris *et al.*, 1988, 1992; Prince, 2001), mass pelagic fish mortalities (Griffin *et al.*, 1997), biological oceanography involving data on early life-history stage of fishes (Dempster *et al.*, 1997; Smith and Suthers, 1999; Smith *et al.*, 1999; Gray and Kingsford, 2003; Neira, 2005; Keane and Neira, 2008, Condie *et al*., 2010), and conservation of unique upwelling areas in Commonwealth marine waters (Butler *et al.*, 2002).

Localised coastal upwelling zones (CUZs) as well as nutrient enrichment zones (NEZs) have been identified in at least 11 localities between South Australia and the Qld-NSW border in south-eastern Australia (Figure 2). Of these, the Bonney upwelling covers the greatest shelf distance

(Robe in SA to Portland in Vic (Butler *et al.*, 2002)) and falls within a region characterised by high retention (Condie *et al.*, 2010). Large NEZs have been identified along the eastern Bass Strait shelf front and off eastern Tasmania, whereas discrete upwelling hotspots occur along the western margins of the Eyre Peninsula, Kangaroo Is. and tip of the Yorke Peninsula (SA), off eastern Victoria (Lakes Entrance to Gabo Is.) and off five coastal locations along the NSW shelf. South-eastern Australian CUZs and NEZs differ in terms of season, duration and intensity, forcing mechanism and dynamics (Table 1). Most prevail during spring/summer, except the NEZ along eastern Bass Strait which flourishes during winter/spring (June to October). All events are annual and occur intermittently, and can last from as little as two weeks (Laurieton, NSW) to nearly four months (Bonney) though most are relatively short-lived.

Three main induction mechanisms of water uplift could be distinguished depending on the region where upwelling occurs: wind-forcing, current/eddy-forcing combined with local wind stress, and water mass mixing. All three result in the dynamic uplifting of cold, nutrient-rich water from the continental slope and its subsequent intrusion onto the shelf, the intensity of which depends on the local topography. Wind-induced upwelling plumes occur along the SA coast, including that along the Bonney coast, and follow the typical Ekman-type dynamics, i.e. persistent, longshore south-easterly winds, brought by moving high pressure systems, forces surface shelf water offshore which is then replaced by colder water of sub-Antarctic origin (Rochford, 1977; Lewis, 1981; Schahinger, 1987; Butler *et al.*, 2002; Middleton and Cirano, 2002; Middleton and Bye, 2007). In addition, upwelled water reaches shallow inshore coastal areas as a result of the narrowing of the shelf along that area, i.e. ~ 20 km in some sections (Figures 3 and 4).

Unlike the situation off SA, a combination between an anticyclonic eddy and local bottom topography are thought to be the likely forcing factors in the short-lived, summer upwelling off eastern Victoria (Lakes Entrance to Gabo Is), with local wind stress having little or no contributing effect (Rochford, 1977). In contrast to SA and Vic, CUZs along NSW are largely produced by a combination of mesoscale features associated with the East Australian Current (EAC) and upwelling-favourable local winds, e.g. north-easterlies (Table 1). These features comprise mostly warm-core anticlyclonic eddies that are shed from the EAC during periods when this warm, polarward current encroaches onto the slope and shelf off NSW and deflects eastwards toward the Tasman Sea. Although EAC behaviour is the common forcing feature of upwelling off NSW, local wind stress is not always a contributing factor, as in the case off Laurieton (31°39’S) where the narrowing of the shelf just to the north appears to be a significant contributor (Rochford, 1975). A lesser known upwelling mechanism constitutes the forcing of parcels of cold, nutrient-rich slope water by small, unstable cold-core eddies that surround larger, more stable warm-core eddies, as described for southern NSW to explain the significant nutrient enrichment recorded around the entrance to Jervis Bay in 1992 (Gibbs *et al.*, 1997).

In contrast to the localised upwelling hotspots off NSW, the major NEZs identified along the shelf break of eastern Bass Strait (Mallacoota to Banks Strait) and eastern Tasmania (Flinders Is. to Tasman Is.) extend over much larger regions and are caused by different oceanographic features to those responsible for upwelling off SA, western Vic and NSW (Table 1). Nutrient enrichment in the two zones is forced by different processes and occurs at different times of the year, i.e. in winter along Bass Strait and spring to early autumn off eastern Tasmania. The winter NEZ is believed to be triggered by the mixing of shallow Bass Strait water with deeper, nutrient-rich sub-Antarctic water along the eastern shelf front. This mixed, denser water drives surface productivity northwards until it cascades down the continental slope off the Vic/NSW corner under the warmer Tasman Sea, below the photic zone (Gibbs *et al.*, 1991). In contrast, the spring/summer NEZ off eastern Tasmania is produced by the onshore advection of deeply mixed, nutrient-rich sub-Antarctic water following periods of strong zonal westerlies driven by changes in the latitudinal position of subtropical high pressure systems over south-eastern Australia (Gibbs *et al.*, 1986, 1991; Harris *et al.*, 1987, 1988, 1991; Ridgway, 2007).

Comparing overall primary production between south-eastern Australian CUZ/NEZ systems and that of CUEs worldwide is complicated for various reasons, including methodology and use of different measurement units. However, some observations can be made if we employ nitrate concentrations (NO_3) as a proxy for productivity. Nitrates are brought into the euphotic zone mostly through the upwelling of cold, nutrient-rich water from deeper layers, and are removed from the upper layers by phytoplankton in quantities proportional to light availability derived from incident solar radiation. Average peak NO_3 concentrations measured in CUZs and NEZs along south-eastern Australia range between 2 and 10 µM, with median values at around 5 µM (Table 1). Such values are lower than those measured in other coastal productive regions elsewhere in the world. For example, concentrations of up to 30 µM of NO_3 have been recorded along the Benguela Current system between April and September, with most values ranging in the vicinity of 10-20 µM (Silió-Calzada *et al.*, 2008).

Comparisons based on carbon fixation rates as a measure of productivity are complicated by the different units employed across the range of studies reported in the literature. For example, integrated water-column productivity along eastern Tasmania has been measured in the range of 14-120 mg C m^{-2} h^{-1}, with the highest values obtained during the spring bloom period off Maria Is and around eastern Bass Strait islands (Jitts, 1965; Harris *et al.*, 1987, Condie *et al.*, 2010). Converted to g C m^{-2} day^{-1}, the highest value (2.9) closely matches the productivity maxima reported for CUEs associated with the four major eastern boundary currents (3 g C m^{-2} day^{-1}) (Carr and Kearns, 2003), though it would appear that such maximum values off eastern Tasmania are only short lived (Harris *et al.*, 1987).

3 Foodwebs in Southern Australia

3.1 Collation of data

The first step of our first objective was to collate data sets of trophic studies and literature relevant to small pelagic fish species across the southern Australian region. The dietary data generated by Bulman *et al. (*2001) was directly relevant to southern Australian ecosystems, including small pelagic fish communities, but was only available in un-supported database formats with limited availability. In addition, data from earlier dietary studies around Tasmania (Blaber and Bulman, 1987; Bulman and Blaber, 1986; Bulman, 2002; Bulman *et al.,*1992, 2002) were available only in hard copy or as an incomplete download from an historical database no longer in existence.

The electronic data were migrated into a database structure designed particularly for diet data and analyses by Cooper *et al.* (2009) (FRDC Project No 2004/063). Manual entry of priority species from hard copy records was completed and manual entry for lower priority species continues. This has enabled us to access and re-analyse this data and other CSIRO dietary data. Furthermore, non-CSIRO studies have also been entered into the database, including a study of small pelagic fish diets off eastern Tasmania (McLeod, 2005). The dietary study of large pelagic fishes off eastern Australia by Young *et al.* (2010) (FRDC Project No 2004/063) has now also been included in our analysis.

3.1.1 Description of database

The Pelagic Ecosystems Stomach Contents Investigation (PESCI) database was originally designed as a relational database system to store dietary data of pelagic fishes and mammals. This database also holds measurements, as well as spatial and environmental data relating to their capture. Centralising the storage allowed flexibility in data access, quality control, exploration and analyses for large pelagic fishes, and was an ideal structure into which we could upload other dietary data sets. These data sets are *projects* in the database terminology. A protocol was devised in the original project to input data. Since our data had already been collected, we had to ensure that the electronic data that was available was matched into the tables (Figure 5).

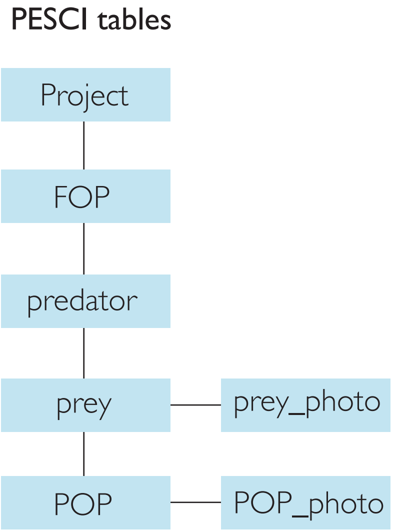


Figure 5. Table structure in PESCI database (taken from Cooper *et al*. (2009)).

The flexible, relational database design was implemented in Oracle, with a Microsoft Office Access database front-end. The front-end was modified for our data input where necessary, although electronic data sets were migrated directly where feasible. Photographs of prey were not included. To be consistent with the existing data and previous analyses, we used CAAB (Codes for Australian Aquatic Biota) codes as unique identifiers for species.

3.1.2 Data migration

Dietary data from the CSIRO multidisciplinary project on the southeastern shelf of Australia (FRDC 1994/040) comprised the largest dataset (SEFHES) migrated into PESCI. The majority of data were gathered from four FRV *Southern Surveyor* voyages (SS93/05, SS94/05, SS94/06, and SS96/06). In addition, data from several surveys on commercial vessels were added (SF9405, EJ9405, SF9602, EJ9602, and SF9701). In total, 8,655 stomachs were added, which were sampled from 120 different predator species between July 1993 and April 1997. Nearly 59.8% of the stomachs analysed (n=5,176) contained prey. Data required verification in order to consolidate data into a database with relational integrity compatible with PESCI.

Dietary data from stomachs collected on FRV *Soela* cruises during 1987-1989 on the continental slope from Kangaroo Island (SA), around Tasmania, including a directed multi-species study off the hills of southern Tasmania, and Victoria and southern NSW, were migrated from an electronic file. A total of 9794 orange roughy stomachs were sampled between April 1987 and April 1989. Data were recovered from archives, verified and re-formatted to fit the PESCI database framework.

An external dataset of four small pelagic species studied for a University of Tasmania Honours project, has also been obtained and entered into PESCI with the kind permission of David McLeod (AAD). The dataset includes data from 554 stomachs of redbait, blue mackerel, common jack mackerel and Peruvian jack mackerel collected between January 2003 and November 2004 (Appendix C). Of all stomachs sampled, 93.9% (n=520) contained prey. Spreadsheets were received and restructured into a relational database compatible with PESCI.

In addition to these datasets, a large dataset exists for a range of species including pelagic species off the east coast of Tasmania, arising from the FIRTA-funded CSIRO Southern Program in 1984-86. These data existed only as paper records with electronic summaries that were re-analysed to allow development of the foodwebs and models of the Eastern Bass Strait (Bulman *et al*., 2006). The most relevant data are now entered into the PESCI database along with other datasets for a range of demersal species from southern Tasmania and will be available in future investigations.

Data were combined and re-analysed within the PESCI framework. Examples of the output from PESCI for the whole diets of four of these small pelagic species from the South East Shelf Project are presented in Appendix D.

3.1.3 Great Australian Bight

Preliminary data from FRDC 2005/031 “Establishing ecosystem-based management for the SA pilchard fishery: developing ecological performance indicators and reference points to assess the need for ecological allocations” have been made available to this project to develop an understanding of the eastern GAB area and a preliminary foodweb. The final GAB model was derived largely from these data and will be reported separately (Goldsworthy *et al.,* 2011).

References relating to dietary studies of species of southern Australia and relevant to the SPF have also been collated into an EndNote bibliographic database (see PI). This library also contains other relevant literature such as biological parameters for species in the SPF, oceanographic studies and some management documents that will be required to develop and initialise ecosystem models. From our database and these literature sources, we have derived comprehensive foodwebs of the southern Australian regions with particular reference to small pelagic species. Bibliographic collections are ongoing.

3.2 Foodwebs

The second step was to derive a series of foodwebs focussed on small pelagic species by incorporating all sources of dietary currently available, including data from the PESCI database relevant to our area, data from SARDI-directed projects, and local literature. The first step was to derive sub-webs of direct linkages for each of the small pelagic species considered. Species initially considered were:

- *Trachurus declivis* - Jack mackerel
- *rachurus novaezelandiae* - Yellowtail scad
- *Scomber australasicus* - Blue mackerel
- *Emmelichthys nitidus* - Redbait
- *Engraulis australis* - Anchovy
- *Sardinops sagax* - Sardine
- *Arripis trutta* - Australian salmon

Species-specific foodwebs (Figures 6-12) were derived from studies from throughout the SPF and represent an overall qualitative view of linkages. All linkages are represented including those accounting for less than 1% of diet, which ordinarily would not be represented. An overall foodweb is also represented, but is not specific to any region. We combined the sub-webs into a larger representation of the whole ecosystem (Figure 13). However, the SPF encompasses the whole of southern Australia and, consequently, a range of communities and water masses. Therefore, we will need to consider the species compositions of the shelf and upper slope communities and their associations *sensu* IMCRA, water mass dynamics, existing evidence of stock structure in the small pelagic species, and dietary studies. In many cases, the evidence is sparse and it may only be possible to divide the SPF into coarse sub-regions due to its size and complexity.

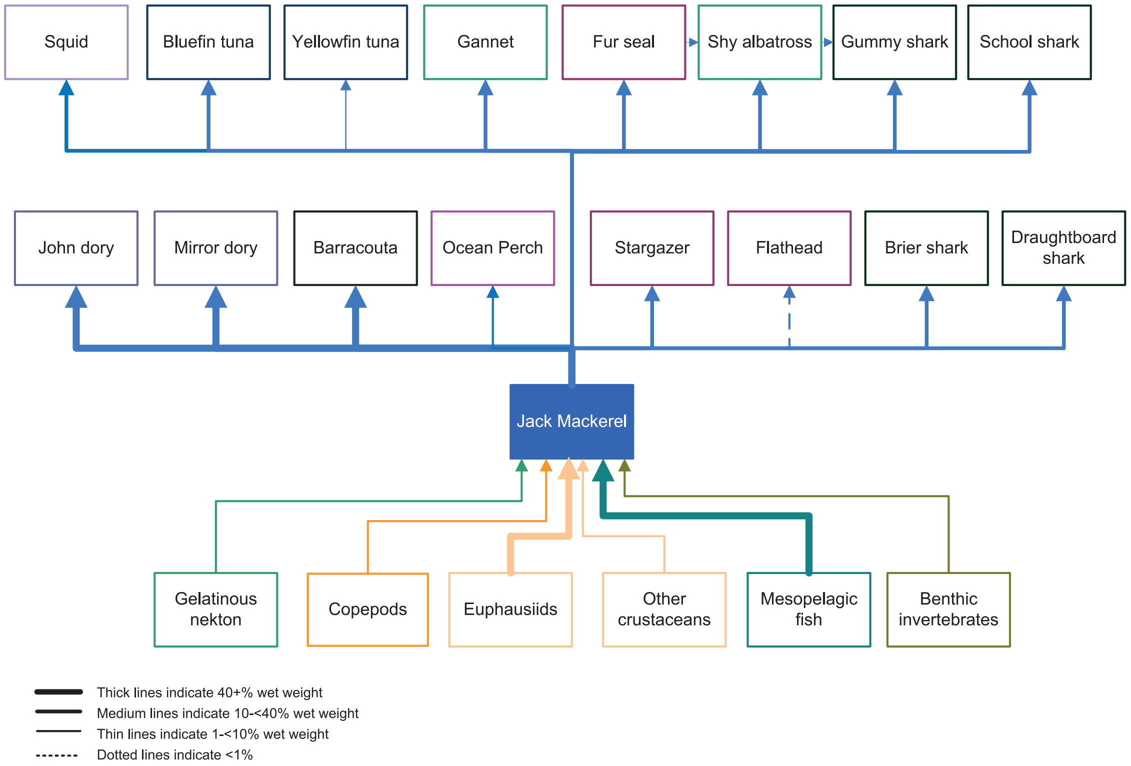


Figure 6. Foodweb of jack mackerel, *Trachurus declivis*. Data from Bulman and Blaber (1986), Bulman *et al*. (2001), McLeod (2005), Goldsworthy *et al*. (2011) and Young *et al*. (2010).

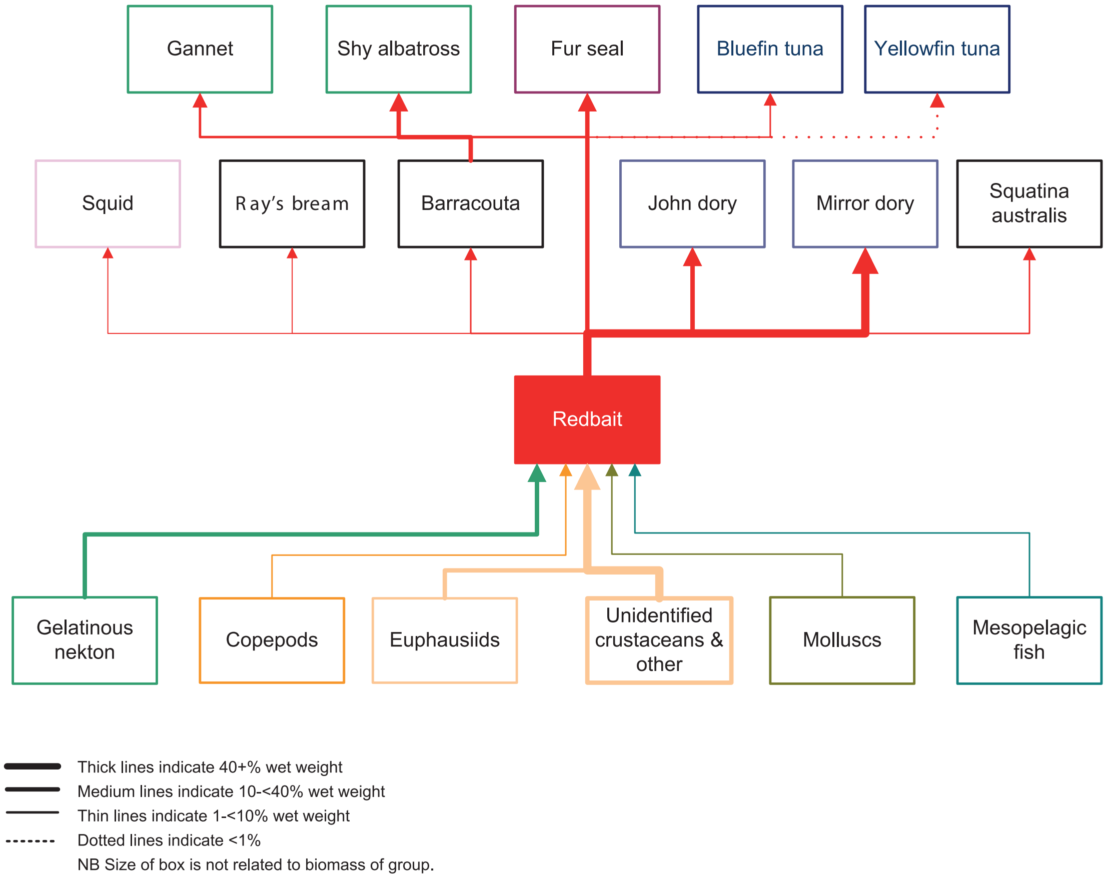


Figure 7. Foodweb of redbait *Emmelichthys nitidus*. Data from Bulman *et al*. (2001), Goldsworthy et al. (2011 data), McLeod (2005) and Young *et al*. (2010)

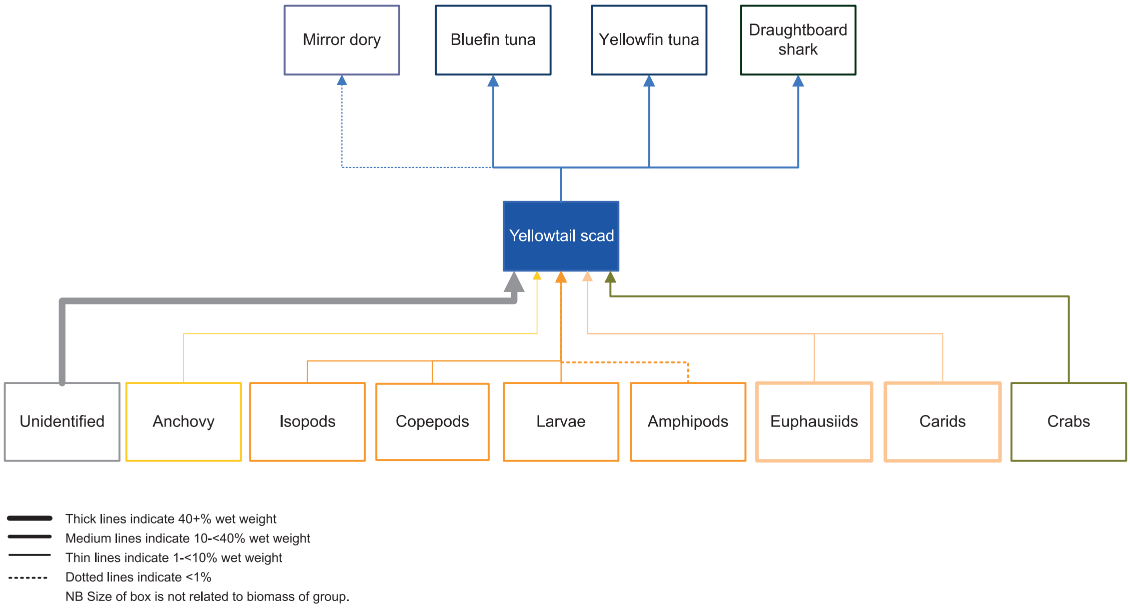


Figure 8. Foodweb of yellowtail scad *Trachurus novaezelandiae*. Data from Bulman *et al.* (2001).

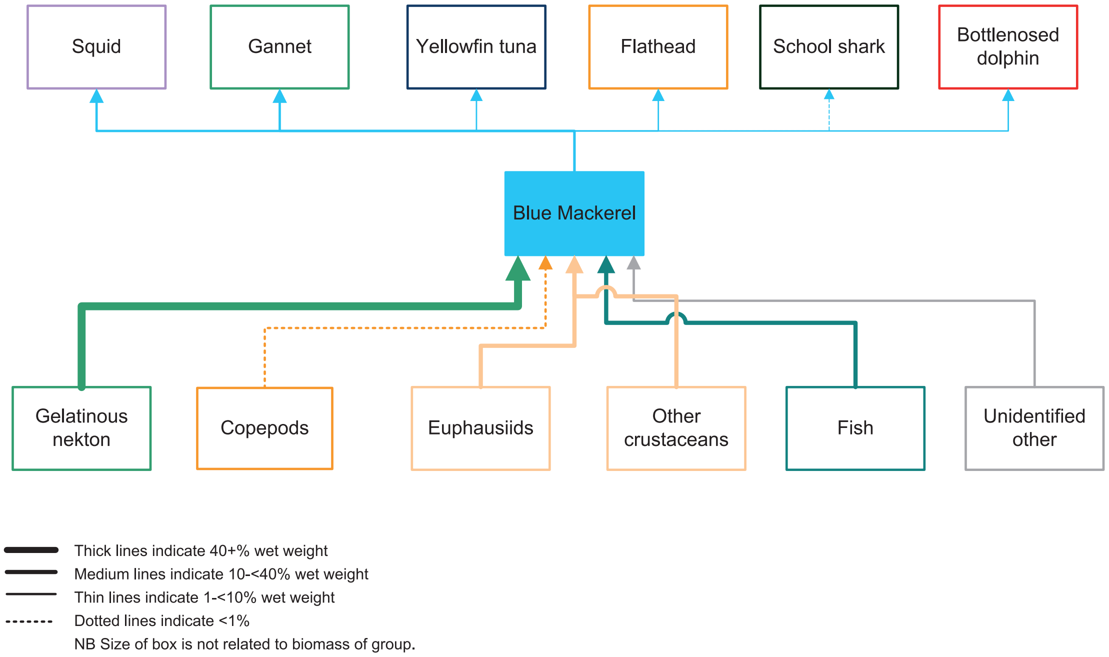


Figure 9. Foodweb of blue mackerel*Scomber australasicus*. Data from Ward *et al*. (2001), McLeod (2005) and Young *et al*. (2010).

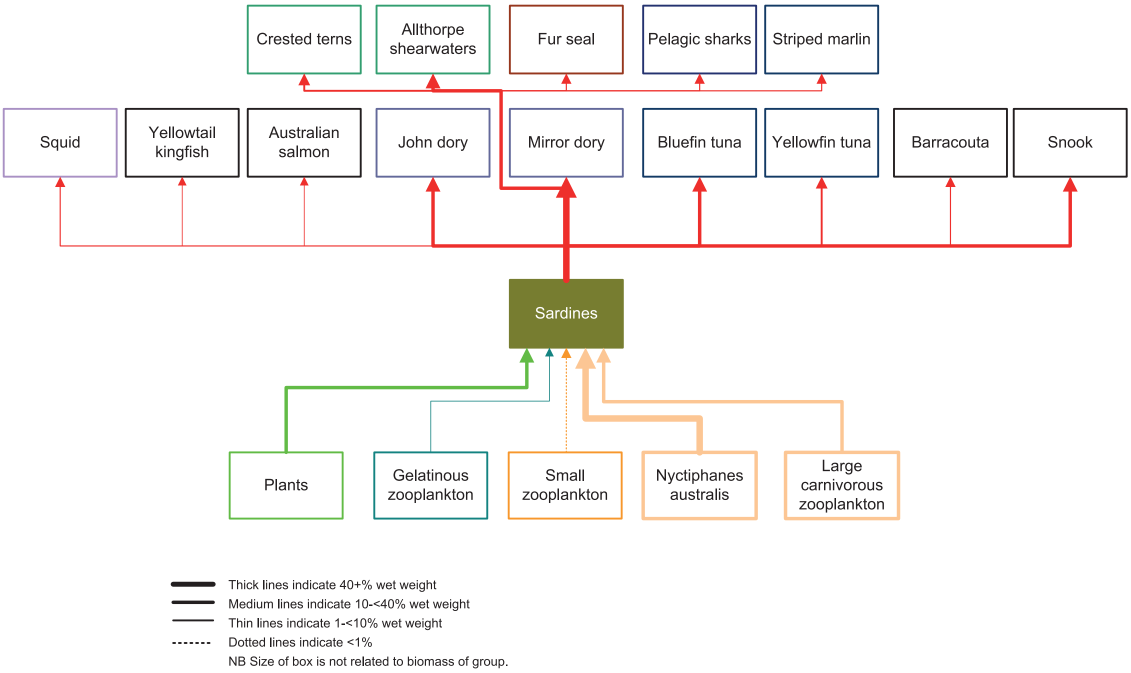


Figure 10. Foodweb of sardine *Sardinops sagax*. Data from Goldsworthy *et al*. (2011) and Young *et al*. (2010).

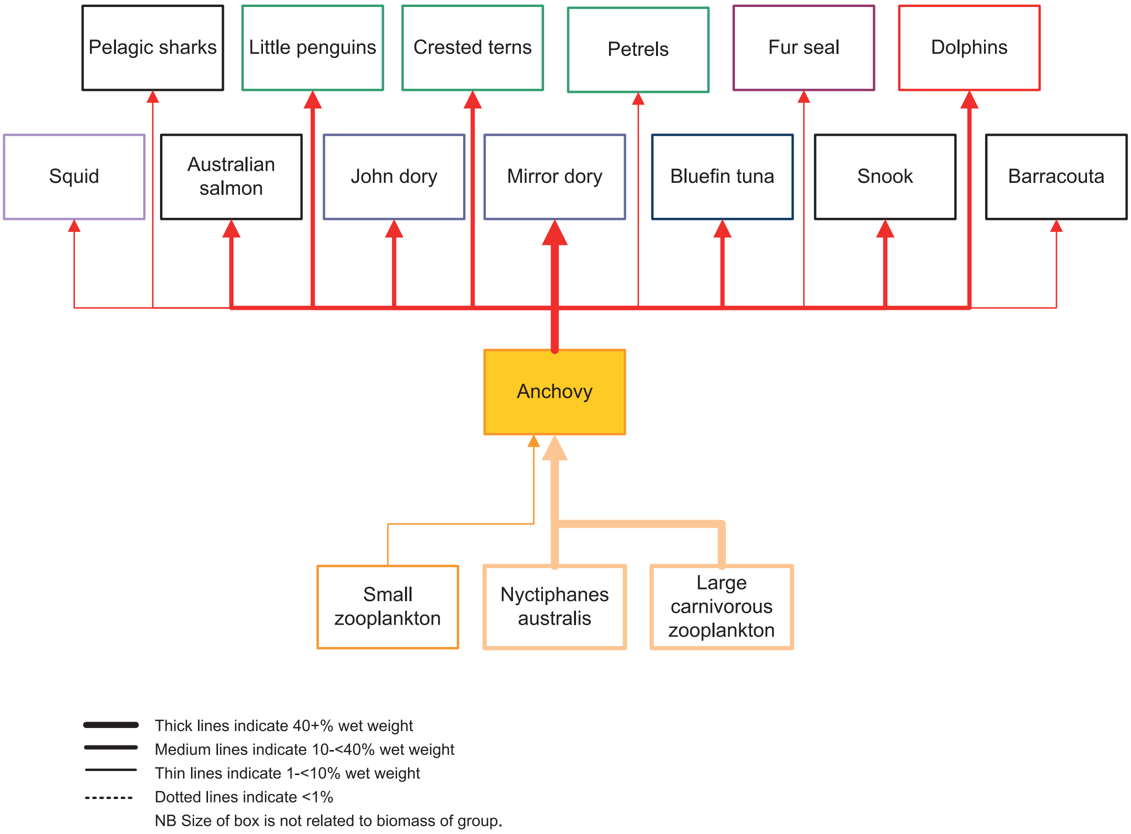


Figure 11. Foodweb of anchovy *Engraulis australis*. Data from Goldsworthy *et al*. (2011).

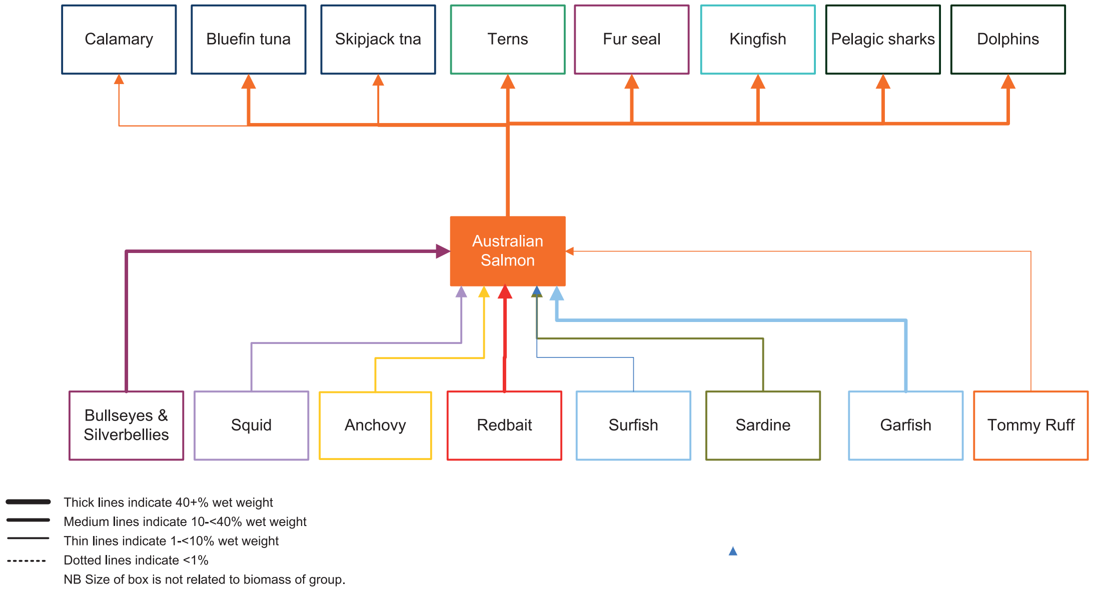


Figure 12. Foodweb of Australian salmon *Arripis trutta*. Data from Goldsworthy *et al*. (2011).

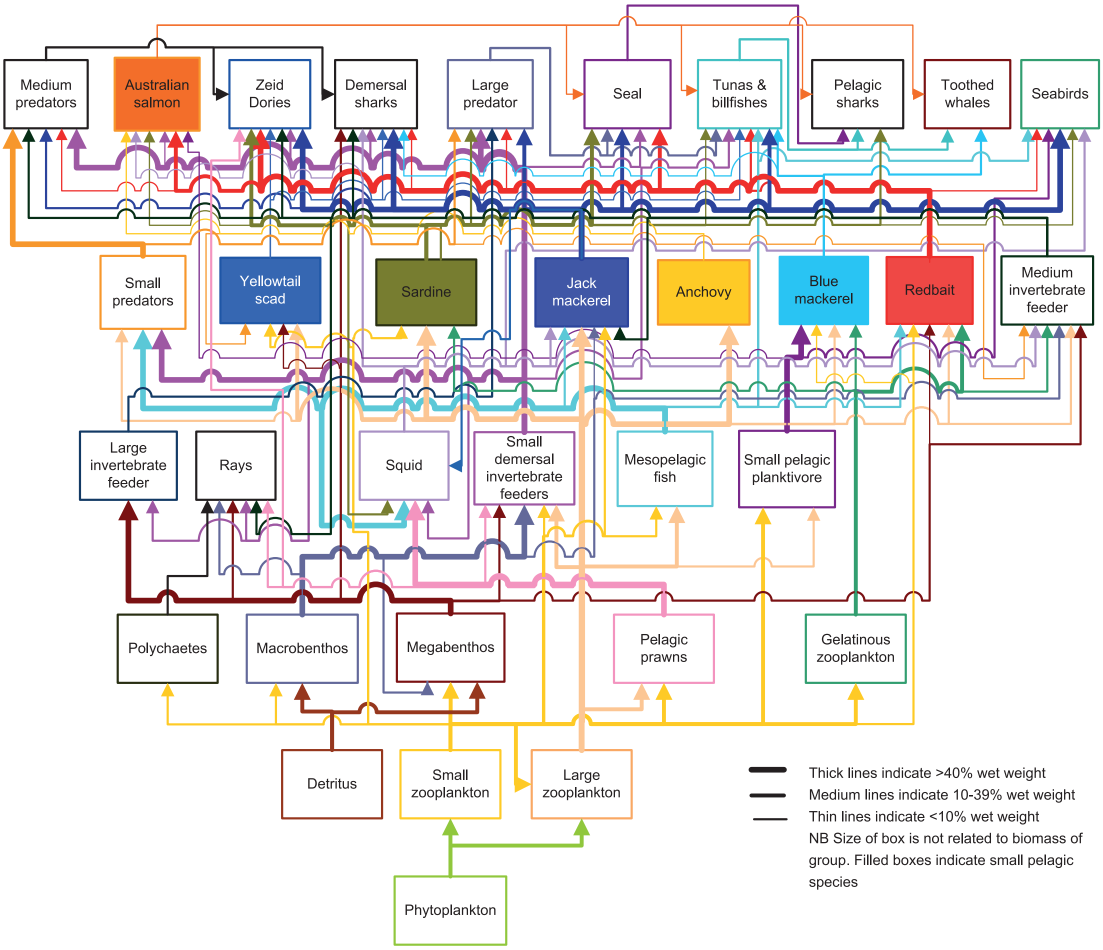


Figure 13. Generic small pelagic fish foodweb, based primarily on dietary studies in southern Australia. Pelagic species of interest to this project are depicted by coloured boxes. This representation does not explicitly differentiate between slope and shelf species.

4 Foodweb control: review

4.1 What is foodweb control?

The way in which an ecosystem will respond to a perturbation depends on the control of energy flow operating in the system. This sort of control has been quite well observed in pelagic ecosystems of upwelling systems in other parts of the world. Cury *et al. (*2000) explored control in several ecosystems dominated by small pelagic fishes (anchovies and sardines). They found top-down control of zooplankton off South Africa, Ghana, Japan and the Black Sea and bottom-up control of predatory fish and birds in the Benguela, Guinea and Humboldt currents.

The types of control usually referred to in these studies, bottom-up, top-down or wasp-waisted control, are illustrated by Freon *et al.,* 2005 (Figure 14) depicting the three types of control.

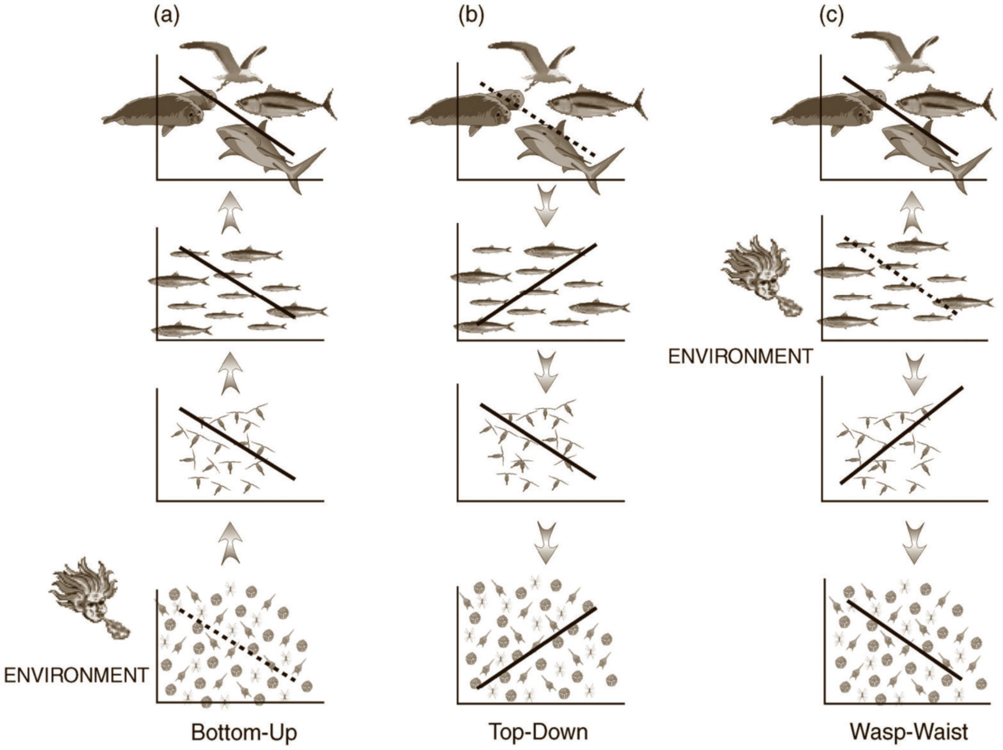


Figure 14. Types of trophic controls possible in a simple, linear pelagic ecosystem including small and large pelagic fishes. Trophic levels are represented by tuna (top level), small pelagic fishes, zooplankton and phytoplankton (lowest level). The control factor is represented by a dotted line and the responses by solid lines (figure taken from Freon *et al.* , 2005).

Conversely, top-down control means that the top predators control the abundance of their prey and therefore lower trophic levels (Figure 14b). For example, if fishing stopped or declined on tuna, then predation pressure on their prey would increase resulting in the prey populations declining. That would release predation pressure on their prey (e.g. zooplankton), allowing populations to increase and increasing grazing pressure on phytoplankton.
The reverse situation with an increased pressure on the tuna such as from fishing would result in reduced predation on prey and an increase in population. This in turn leads to increased predation on zooplankton and a reduction in grazing of phytoplankton.

In a recent review of ecosystem structure and function in the Northeast Atlantic, Mediterranean and Black Seas, Heath and Gallego (2010) concluded that high-latitude, low temperature and primary production systems were generally top-down controlled while conversely low-latitude, warmer and higher primary production systems were generally bottom-up controlled. They also found that eastern boundary current systems were more often bottom-up controlled while western boundary systems were more likely top-down controlled. While shelf systems may exhibit either control, they can also fluctuate between the two states in response to climatic or fishing pressures.

Wasp-waisted systems, however, are rather different. Rice (1995) fist denoted the term when he described a “waist” system as that where “a single taxon in a middle trophic position passes most of the food or energy from lower trophic levels to all higher predators”. In systems such as the Benguela or the Humboldt, the highly abundant sardines and anchovies play “controller”. They exert bottom-up control on their larger predators but also exert top-down control on their planktivorous prey, as in Freon’s (2005) illustration (Figure 14c). While the environment can have an effect on the recruitment of small pelagics and thus population size, it doesn’t affect primary producers. If small pelagic fishes decline, bottom-up control over their predators causes their predators to also decline but the top-down control over lower trophic levels means that prey will increase, increasing grazing pressure on phytoplankton.

4.2 Why is foodweb control important?

Bakun (1996) described the sardine-anchovy systems as wasp-waists. Using Ecosim, Shannon *et al. (*2000) showed that a wasp-waist control exerted by small pelagic fish had a greater effect on the ecosystem when fishing pressure increased on them than if just bottom-up control was assumed. Not only did the stocks of anchovy and sardine collapse more readily, allowing their competitors for zooplankton prey, chub and horse mackerel, to increase, but stocks were slower to recover. Ten years earlier, Beverton (1990) had highlighted the sensitivity of pelagic fish stocks to over-exploitations. He examined the collapses of 10 major pelagic fisheries and found that in nearly all cases fishing contributed significantly to their collapses, although fluctuating environmental conditions were also present. Nearly 20 years later, some fisheries have recovered but the Icelandic spring-spawning herring stock has apparently never been seen since (FAO 2009). However, perhaps Beverton’s (1990) most relevant insight to our present way of thinking was that the threat of fishing was not as threatening per se as might be the consequences on the wider community. During a major collapse, the structure of the community changes in such a way that recovery of the exploited fish stock may be depressed or impossible as exhibited by the Icelandic spring spawning stock, but perhaps the most observable consequences that may occur are those imposed on the higher predators of the system such as mammals and particularly birds (see Schwartzlose *et al.,* 1999).

As Beverton (1990) indicated and re-iterated by Cury *et al. (*2000) and Hunt and McKinnell (2006), marine communities are not quite as simple as depicted in Figure 14, and there may be several types of control being exhibited by different parts of the same ecosystem. In the Southern Benguela ecosystem model (Shannon *et al.,* 2008), anchovy and sardine exert bottom-up control on snoek and other large pelagic fish. Shallow hake exert top-down control on prey as do the deep hake on sardine, although small deep hake exert bottom-up control on mesopelagic and zooplankton. In the Southern Humboldt model, there is bottom-up control of sardines and anchovies on hakes and sea lions, except for a top-down control of sardine by large hake. In the northern Humboldt model, Shannon *et al. (*2008) found that hake exert a top-down control on several of their prey. Bottom-up control was found for the predator/prey interactions of sardine and mesozooplankton, mesopelagic fish and macrozooplankton and mesopelagic fish and jumbo squid. Heath and Gallego (2010) determined that the North Sea pelagic foodweb was primarily bottom-up controlled through plankton and planktivorous fish but that the benthic foodweb was top-down controlled through demersal fish predation on macrobenthos.

A potential factor in determining which control may operate on a system is the amount of redundancy of the species within the functional group i.e. the extent to which one species can be replaced by another or other species within the same functional group in the event of a natural or induced stock decline. Since the 1930s, there have been successions of dominant species being replaced by the less dominant species in small pelagic fisheries off Japan, California, South America (Peru and Chile) and Africa (Namibia and western South Africa) (Schwartzlose *et al.,* 1999). In the bottom-up controlled pelagic foodweb of the North Sea, herring replaced sprat as herrings populations recovered from a collapse in the 1970s (Heath 2005).

Field *et al.* (2006) investigated flow control in the Northern Californian Current by imposing bottom-up forcing using a range of climate indices such as upwelling indices, transport indices and the Pacific Decadal Oscillation. They also used these indices to mediate the consumption of mid-level predators by altering vulnerabilities of their prey i.e. similar to top-down control without actually forcing the top predators. Using either control improved the model fitting however simultaneous forcing did not significantly improve the fit further. They showed that generally slower-growing fishes were less susceptible to strong predator-prey interactions whereas shrimp, salmon and small flatfish were more susceptible. By exploring vulnerability parameters in ecosystem models, Shannon *et al.* (2008) found that the most sensitive interactions in controlling the Southern Benguela and both Humboldt systems were those of the anchovies and sardines accounting for over 40% of the variability in fitting the model predictions to the observed time-series of catches and abundances.

Therefore, considering the plight of pelagic fisheries in recent decades, it is important to discover which control is operating in an exploited ecosystem and how that might influence the potential outcomes on the whole community of fishing strategies and climate change hypotheses.

5 Foodweb control under climate change, fishing and recovery of top predators: qualitative models

5.1 Introduction

To generate realistic climate change scenarios, models such as EWE and Atlantis require detailed information on changes in quantities such as water temperature, pH, salinity, current patterns and primary productivity. While considerable attention is now being focused on downscaling results from climate models, reliable estimates at appropriate temporal and spatial scales are still not available, especially through time – though the period 2060-2070 has begun to be explored. There are also major uncertainties in the biological responses to these environmental changes.

As an interim measure, we can explore the potential impacts of climate change on small pelagic fish at a qualitative level using an approach referred to as "loop analysis". Loop analysis begins by defining the system structure in terms its key dynamical components and interactions between them, which can be represented pictorially in the form of a signed digraph (Figure 15). In our case the components consist of functional biological groups and human activities. The interactions are expressed qualitatively as components exerting a positive or negative influence on other components (Figure 15). This system structure can then be mathematically analysed using loop analysis to determine its stability, its predictability, and its qualitative response (increase, decrease, or neutral) to a sustained change in one or more of the system components (Levins, 1974; Dambacher *et al.,* 2003; Ramsey and Veltman, 2005; www.ent.orst.ed/loop).

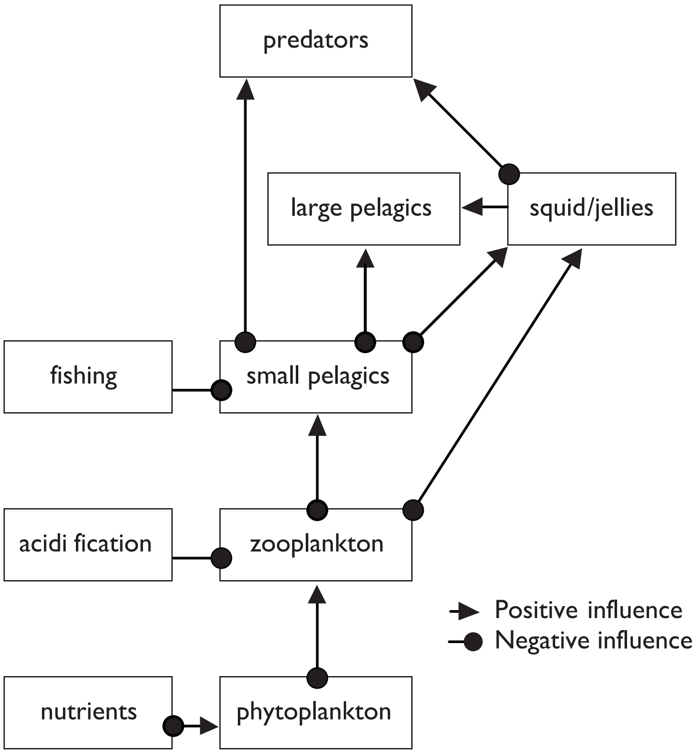


Figure 15. Digraph representing major interactions in the system influencing small pelagic fishes

The signed digraph defines a matrix of interactions (i.e. the community matrix) that can be used to predict the sign of the response of each system component to a sustained change (by calculating the adjoint of the community matrix). In many instances the sign of the predicted responses is the sum of both positive and negative feedback loops. The response sign is then ambiguous and further analysis is required to resolve it. Ambiguities can be identified by calculating an index called the weighted predictions, which is essentially the net number of feedback loops divided by the absolute number of feedback loops for each prediction (Dambacher *et al.,* 2002). If this quantity equals one, then all the feedbacks are driving the response in the same direction and the result will be same irrespective of the relative strengths of the feedbacks. Dambacher *et al.* (2003) further showed that we can have a reasonably high level of confidence in the sign of the response if the weighted prediction is greater than 0.5. However, if the weighted prediction is less than 0.5 then the prediction is likely to be unreliable. Clearly the latter is increasingly likely as the system is made more complex and the absolute number of feedback loops increases.

The qualitative modelling approach can provide important insights into dynamic behaviour of complex systems using relatively simple analyses. However, this comes with a range of limitations including:

- predicted responses are entirely qualitative and only express the direction of change;
- system is assumed to be near equilibrium
- nonlinear behaviour resulting in alternative system structures cannot be represented (although separate models can represent different behavioural regimes); and
- complex systems involving opposing feedbacks often give ambiguous responses.

While moving to quantitative models (such as EwE or Atlantis) bypasses these limitations, the associated information requirements are clearly far more onerous.

5.2 Key interactions involving small pelagic fish

The main external pressures potentially influencing small pelagic fishes are changes in environmental conditions (likely climate related) and changes in fishing pressure. Their impacts may be direct or result from trophic cascades. Figure 15 shows the key components and interactions in relation to small pelagic fish. So as to capture these elements within a generic trophic structure, the various zooplankton and other small prey identified in the previous chapter have been combined into a single group, as have large pelagic predators (e.g. tuna and sharks) and other predators (e.g. seabirds and marine mammals). Squid (and jellyfish) have been retained because they interact across a number of trophic levels. Even this relatively simple system can exhibit bottom-up control, top-down control, or wasp-waist control, depending on relative size of the components, strength of the interactions and how the system is perturbed.

The qualitative response of the system to a press perturbation would be easily predicted except for the potentially complex interactions with squid (and jellyfish). This complexity arises because these groups interact directly with small pelagic fish, as well as with their predators and their prey (Figure 15). Specifically squid prey on small pelagics (and jellyfish their juveniles), they compete with small pelagics for zooplankton, and they provide alternative prey for the predators of small pelagics. If the interactions with squid are weak, then increased nutrient levels simply propagate up through the foodweb and increase the biomass of all higher trophic levels (Figure 15). However, stronger interactions with squid introduce uncertainty into the system response due to competing feedbacks.

5.2.1 Changes in system productivity

One of the main potential marine impacts of climate change is a change in the availability of nutrients in the upper ocean. While warming of surface waters will stabilise the water column and reduce entrainment of nutrients from greater depths, changing wind patterns may increase upwelling of nutrients in some areas. Hence, under a changing climate, the trend in nutrients may vary with location. In the absence of squid (or jellyfish) the system response is bottom-up controlled, with all groups increasing with enhanced nutrient availability or decreasing with reduced nutrient availability (Figure 16a).

If squid (or jellyfish) biomasses are significant then the response to nutrient changes are much less certain (Figure 16b). The biomasses of both zooplankton and squid will likely increase if nutrients are more readily available. However, the feedbacks on small pelagic fish are predominantly negative (i.e. predation by squid and other predators, as well as competition from squid for zooplankton). This provides a mechanism by which small pelagic stocks may diminish in a more productive system (or grow in a less productive system) when squid or jellyfish are abundant.

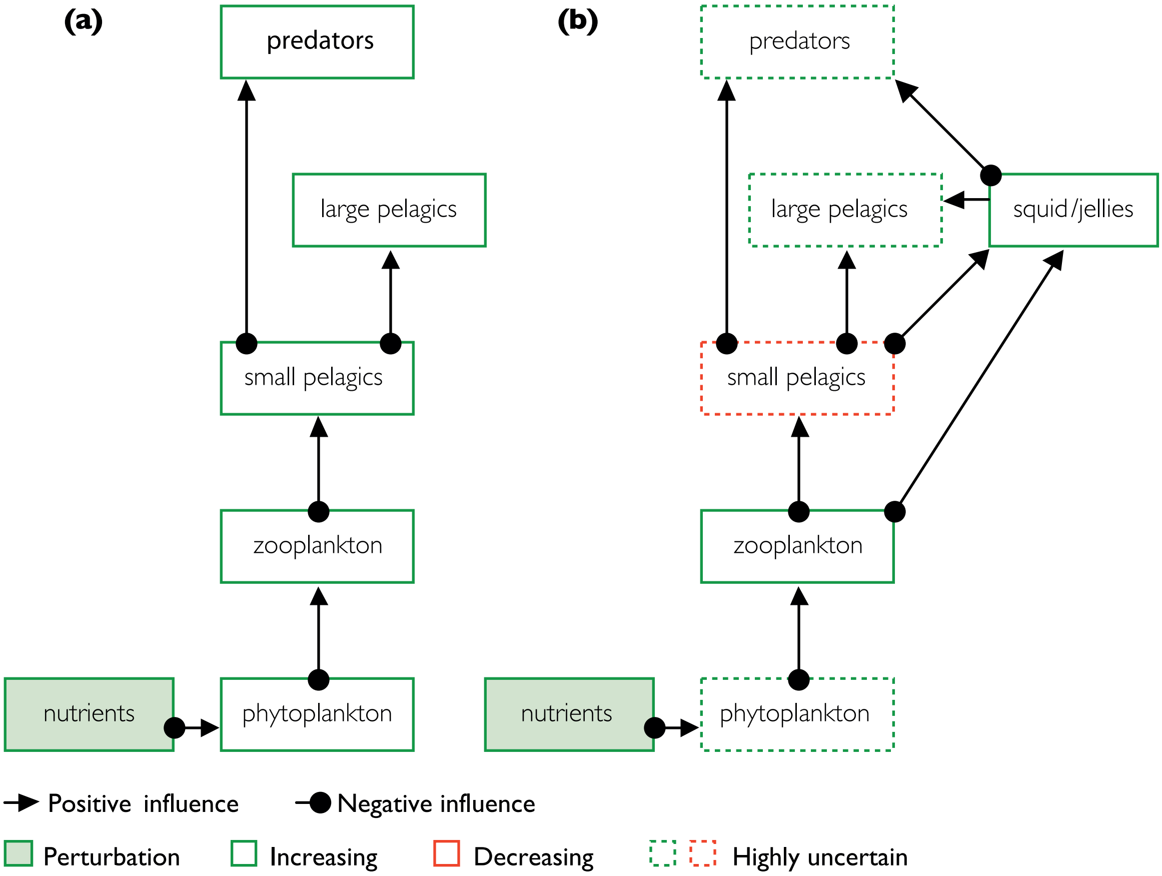


Figure 16. Digraphs representing the system response to an increase in available nutrients under scenarios in which the influence of squid and/or jellyfish is (a) small and (b) large. All responses are reversed if nutrients fall.

5.2.2 Ocean acidification

Another potential marine impact of climate change is a reduction in ocean pH. The main direct impact of higher acidity is amongst zooplankton (a large proportion of which have external calcium carbonate skeletons). A fall in zooplankton biomass will reduce grazing pressure on

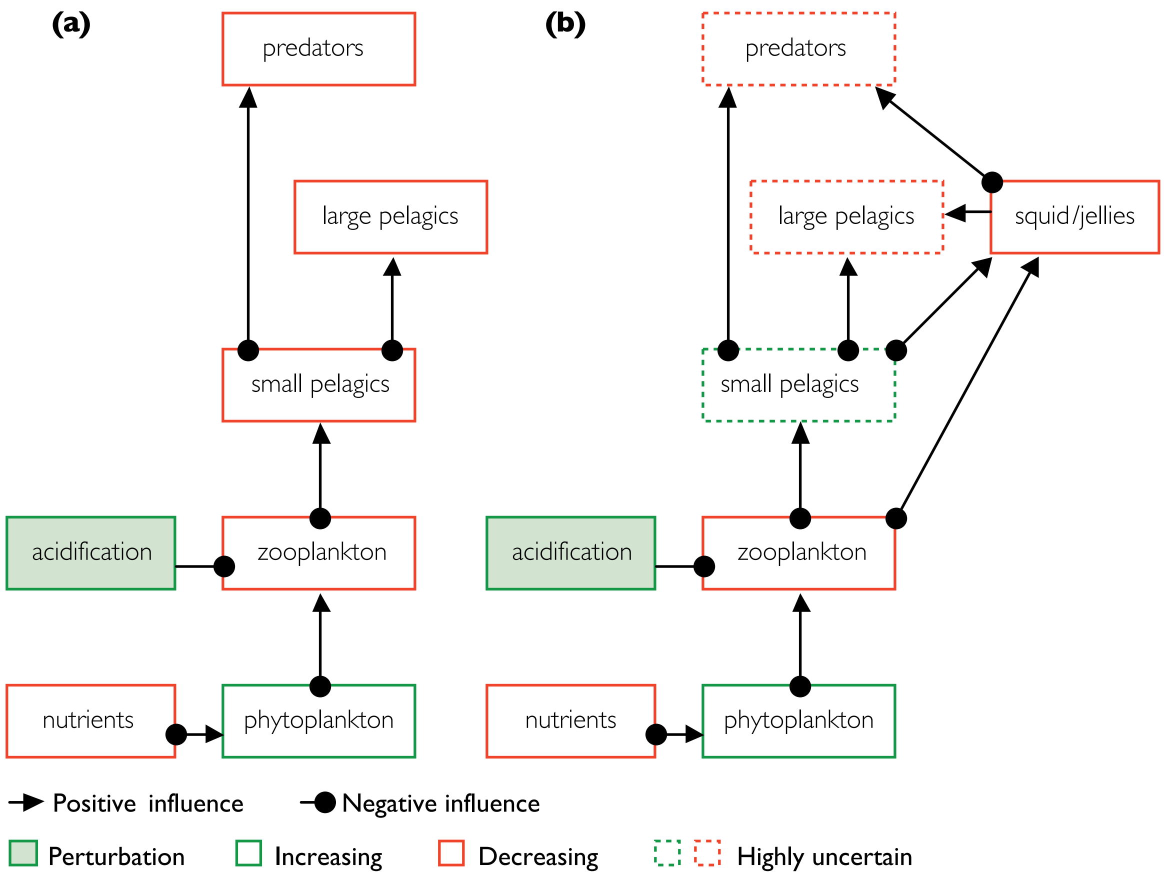


Figure 17. Digraphs representing the system response to an increase in ocean acidity under scenarios in which the influence of squid and/or jellyfish is (a) small and (b) large.

phytoplankton and might be expected to reduce the productivity of higher trophic levels (Figure 17a), thereby creating a wasp-waist system with control exerted at the zooplankton level.

While a reduction is squid is quite likely, the response of other groups is uncertain (Figure 17b). For example the lower abundance of zooplankton supporting small pelagics, may be offset by reduced predation by squid and other predators. Hence the fate of small pelagics is again determined by the relative strengths of bottom-up and top-down control and this uncertainty propagates through to the larger predators.

5.2.3 Changes in small pelagic fisheries

System responses to climate change can be confounded by changes in direct or indirect fishing pressure. Direct fishing pressure on small pelagic fish has the potential to impose wasp-waist control over the system (Figure 18a). Reductions in the biomass of small pelagics will likely result in a decline in their predators (through bottom-up control) and an increase in zooplankton (through top-down control). Despite the loss of small pelagic fish prey, squid and jellyfish may increase as their predators are diminished and alternative zooplankton prey increase (Figure 18b).

5.2.4 Natural recovery of top predators

With increased protection from hunting and fishing some major predators of small pelagic fish, such as sharks, seals and toothed whales, are recovering on timescales comparable to climate changes. This may lead to increased top-down control with a subsequent decline in small pelagics

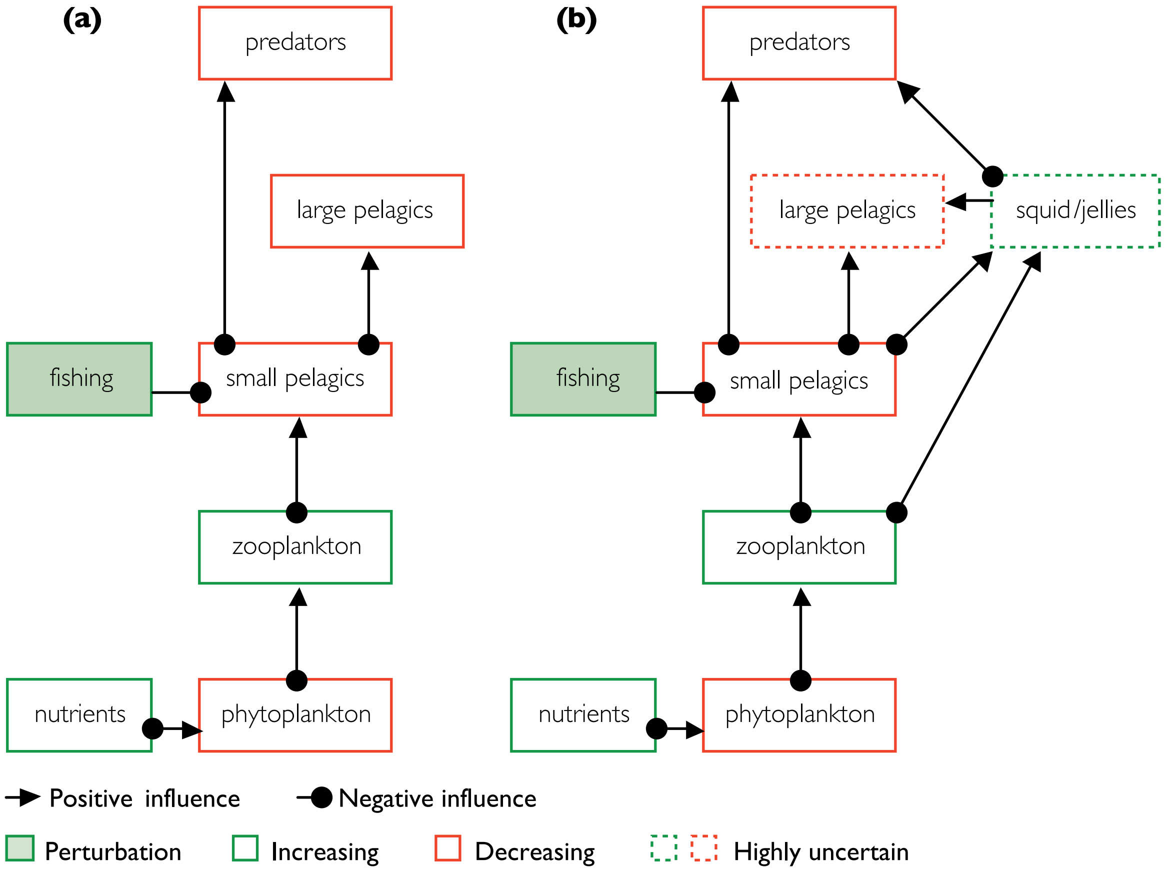


Figure 18. Digraphs representing the system response to an increase in fishing pressure on small pelagics under scenarios in which the influence of squid and/or jellyfish is (a) small and (b) large. All responses are reversed if fishing pressure decreases.

and increase in zooplankton (Figure 19a). However, squid and jellyfish may again complicate this scenario (Figure 19b). They will also experience increased predation and their decline may decrease predatory pressure on small pelagics and allow their zooplankton prey to increase.

5.3 Conclusions

The suite of qualitative models presented above demonstrates that response of small pelagic fishes to climate change is highly uncertain. Even in instances where the predominant environmental change is known, e.g. increased availability of nutrients, indirect (trophic) effects can introduce major uncertainties. The level of predation by squid (and/or jellyfish) is critical to the response of small pelagic fish to a range of likely future scenarios. In particular, their response to climate change (or recovery of top predators) may be reversed by the influence of squid (and/or jellyfish). While these groups generally increase uncertainties in responses throughout most components of the system, the coupling with small pelagics is particularly strong because they are a predator, a competitor, and provide alternative prey for other predators.

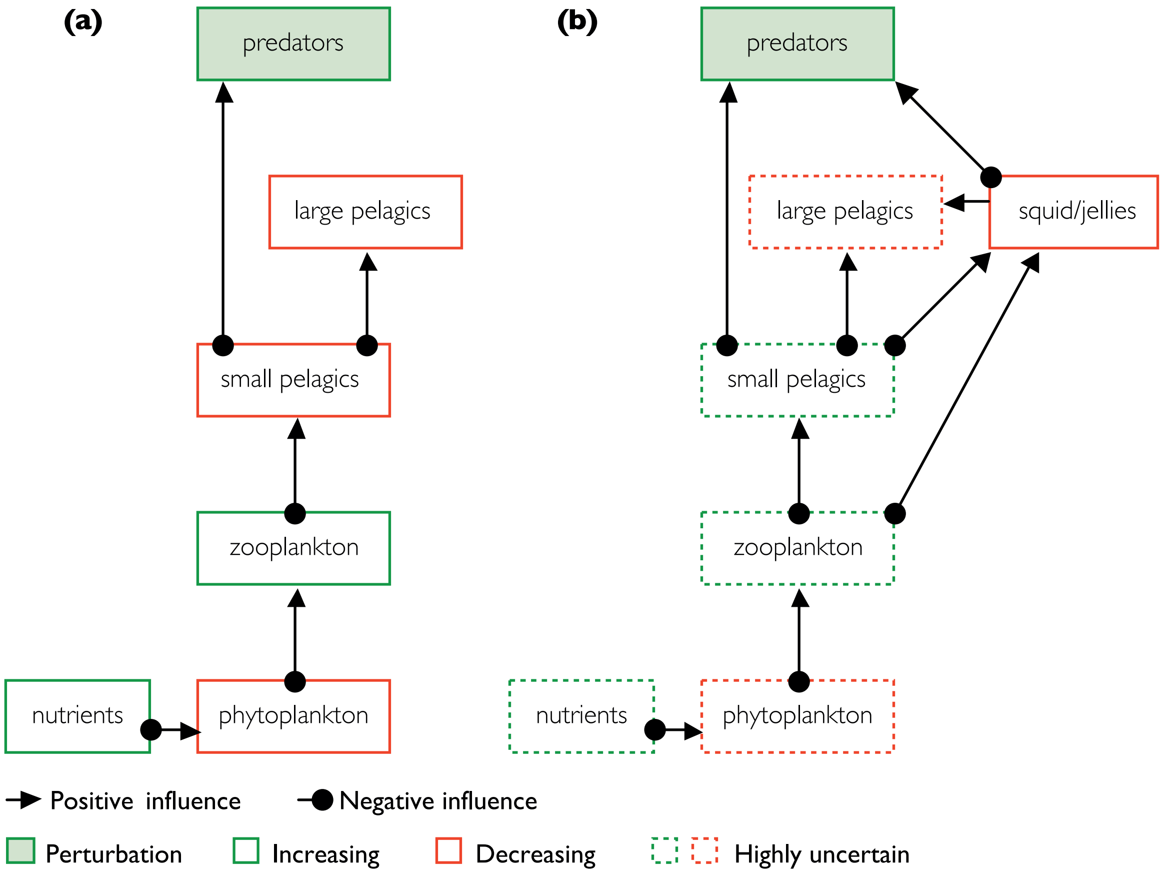


Figure 19. Digraphs representing the system response to recovery of top predators under scenarios in which the influence of squid and/or jellyfish is (a) small and (b) large. All responses are reversed if top predators decline.

6 Foodweb control: quantitative models

Part of our first objective of this project was to determine what types of controls are operating in the Small Pelagic Fishery of southern Australia and explore the wider effects of vulnerability values of predator-prey interactions on the whole ecosystem. We have used Ecopath with Ecosim (EwE) ecosystem models of eastern Bass Strait (Bulman *et al.,* 2006) and the Great Australian Bight (Goldsworthy *et al.,* 2011) to identify what types of controls are operating in the Small Pelagics Fishery of southern Australia and explore the wider effects of vulnerability values of predator-prey interactions on the ecosystem.

The model of the eastern Great Australian Bight pelagic ecosystem (Goldsworthy *et al.,* 2011) integrated data on the diets of small pelagic fishes and squid, large pelagic fish, seabirds, seals and cetaceans. Early progress in the development of that model highlighted the importance of arrow squid as predators of small pelagic fishes, and the importance of squid competitors and predators in controlling squid biomass. Important squid predators such as fur seals, whose populations are increasing rapidly, may be important in reducing predation on small pelagic fishes, and in directing greater levels of production through to higher trophic levels i.e. away from squid (S. Goldsworthy *pers. comm.).*

On the other hand, off the east coast, and particularly off Tasmania, redbait is important in the diets of many top predators including marine mammals and tunas, which suggests that impacts in the Small Pelagics Fishery will also be felt in other fisheries at best, and other functional groups of the ecosystem at worst.

In EwE, the controls of predator-prey interactions are described by terms known as vulnerabilities. The vulnerability term controls the rate of transfer between the portion of a prey biomass that is vulnerable to a predator and the non-vulnerable portion. The default vulnerability value represents a mixed flow control, but smaller values represent bottom-up control while larger numbers represent a top-down control. It is therefore possible to represent wasp-waist control by a particular trophic group on its predator or prey groups with specific predator–prey interactions.

6.1 Methods

We followed a similar method to Shannon *et al. (*2008), and ran simulations depicting the various options of flow control by altering species-specific parameters associated with foraging. The most sensitive predator-prey interactions can be found using a search-interface in EwE after which the vulnerabilities for the most sensitive can be estimated. The fit of the model-predicted biomasses compared to the CPUE observations can be changed by altering the vulnerabilities of the predator-prey interactions. However, this is an iterative process and whereas the fit for one series might improve, that of others may worsen. Ultimately, the performance of a model relies heavily on this "tuning" of these interactions using observed data and their importance should not be underestimated (Mackinson in Shannon *et al.,* 2008). However, users are advised that fitting too many individual interactions will end up in over-parameterisation with little chance of distinguishing real improvement therefore selecting a vulnerability for a predator across all its prey is preferable (EwE Users Guide 2008).

6.1.1 East Bass Strait model

The East Bass Strait model was developed based on data from an extensive multi-disciplinary study of the south-eastern corner of Australia by CSIRO in 1993-1996 and is described in detail in FRDC Report 2002/028 (Bulman *et al.,* 2006). In summary, the model covers an area of over 30,000 km^2 of the shelf and upper to midslope of the south-eastern corner of Australia. The model was constructed as at 1994, the year in which the CSIRO began the shelf surveys, specifically to focus on fisheries-related issues such as the impact of the increasing population of Australian fur seals in the region. In total, the EBS model comprised 57 groups including two detritus groups (one being discards), one primary producer group, eight invertebrate groups, three marine mammal groups, two bird groups and 41 fish groups including 19 single species groups. Jack mackerel and redbait were two species of particular interest to this model and were treated as individual species groups, while yellowtail scad and blue mackerel were considered as part of larger functional groups i.e. pelagic medium invertebrate feeders and pelagic medium predators. Peruvian jack mackerel were rarely encountered therefore were not included in the model.

Ten “fleets” were originally modelled which covered the major fishing fleets or gear types including the Commonwealth, and NSW and Victorian state fisheries. However, recreational fishing was not included in the original model, nor was a specific redbait fishery, which is restricted to Tasmanian waters outside the original study area. Efforts and catches for each of the original fleets were calculated for the period 1994-2003. For the same period, a CPUE series for commercial species was estimated to compare against model predicted biomass estimates in order to tune the model and investigate trophic flow and control. From ocean-colour observations, a time series of estimated primary productivity anomalies was derived and used as an environmental forcing function to drive primary productivity.

6.1.1.1. Changes to the EBS model

Modifications were made to this original model to either update the data or to create a hypothetical study area which included a redbait fishery based on Tasmanian data. Spawning biomass for redbait was estimated using the daily egg production method (DEPM) from surveys carried out between southern NSW and the lower west coast of Tasmania (Neira and Lyle, 2008; Neira *et al*., 2008: FRDC project 2004/039). The biomass estimated in the original EBS area was slightly greater than that predicted by the model, indicating a potential surplus in the model. However, the effect of additional redbait biomass was to lower the ecotrophic efficiency of the group in order to keep the model balanced. Redbait spawning biomass for the Tasmanian region was used in the hypothetical model. The biomass for yellowtail scad was also based on the balanced model estimate of 0.131 t km^{-2}, which is very similar to the original estimate from the CSIRO surveys of 0.129 t km^{-2} and consistent with the range of 0.125 - 2.51 t km^{-2} obtained for a spawning area further north (F.J. Neira *pers. comm.,* June 2009).

Recreational fishing effort has also been estimated for the model area and included in the fishing fleet dynamics, allowing a more complete fishing scenario. Recreational harvest estimates for the model area were based on a re-analysis of the 2000/01 national survey (FRDC 99/158) and incorporated catches taken from waters off southern NSW and eastern Victoria (excluding estuaries). While the values for species are not high, they do complete the fishing scenarios for the model. Adding this fleet, unbalanced the model by slightly increasing flathead mortality. A minor adjustment in diets brought the model back to balance. However since the mortality on flathead is still very high, the species is vulnerable to further pressure.

In the original EBS model, NSW fishery data was incorrect. A problem with dual licensing of boats in both the NSW and Commonwealth fisheries caused double-reporting of catches from 1985 through to the late 90s. This issue is documented through to 1998 and the data suggests it may have continued for a further 3 years. The double-reporting significantly influenced the outcomes of the model and we decided to try to depict the NSW fishery data more realistically. For the duration of the model simulation up to 1998, we reduced the catch of NSW fishery to a level closer to that of years following the assumed discontinuation of the double-reporting practice based on advice from Dr. K. Rowling (NSW DPI). While this is not necessarily accurate, it was considered to be a truer reflection of the level of the fishery catches.

Standardized CPUE data for commercial species from the relevant SEF zones, 20 and 30 (Haddon, 2008), replaced the original CPUE series. Once standardized against our initial condition year, 1994, the data series was quite similar to the original series used. However, standardized CPUEs were not available for all trophic groups and some rare large catches caused spikes in the CPUE series that could not realistically be fitted to model predictions. We substituted the new standardized series for the original where applicable.

All available dietary information on squid were re-examined to ensure that the most appropriate parameters were being used when investigating the suggestion that squid might significantly impact populations of small pelagics (see Appendix D). It was assumed that the squid preyed upon the juveniles of many of the small pelagic and small demersal species as suggested by data from other areas and other species. The modified diet was: 5% shallow small predators, 2.5 % each of shallow medium invert feeders and predators, 2% shallow large predators, 22% pelagic small invertebrate feeders (sardines), 20% mesopelagic fishes, 10% other squid, 15% pelagic prawns, 20% megabenthos and 10% large zooplankton.

The initial production per biomass (P/B) for squid of 2.7 was raised to 2.75 to rebalance the model. While this rate seems high in comparison to estimated annual mortality rates (0.35 for *Sepioteuthis australis* in South Australia; Smith, 1983) similar values have been used in models for the Alaska Gyre and Benguela (Christensen, 1996; Jarre-Teichmann *et al.,* 1998; Shannon *et al.,* 2008).

6.1.2 Hypothetical redbait fishery model

The EBS model was further modified to represent a hypothetical fishery for redbait similar to the Tasmanian redbait fishery. The aim was to determine whether trophic control is altered by the magnitude of the biomass of the small pelagic species. In this case, redbait was the pelagic species of relatively high biomass and therefore potentially controlling.

The biomass of redbait used in this scenario was estimated from the egg surveys conducted in 2005 off southern NSW (Neira and Lyle, 2008). The time series for this model included a redbait fleet using the data from the Tasmanian fishery, and modifying the original redbait catches. However, no attempt was made to alter species compositions or biomasses to represent the Tasmanian area specifically. The model was rebalanced by adjusting components of the diets of squid, medium-sized slope predators (such as stargazers) and mesopelagic fishes, as well as slightly increasing the P/B and biomass of shallow large predators (barracouta).

6.1.3 Eastern Great Australian Bight model

The model for the eastern Great Australian Bight (eGAB) was developed for FRDC project 2005/031 but is still in the early stages of tuning. The structure of this model is centred around higher predators in the region (i.e. Australian and New Zealand fur seals, Australian sea lions, birds, and southern blue fin tuna and large pelagic sharks) as well as anchovy, sardine and squid. Therefore, the model is structurally similar to the Eastern Bass Strait model while the specific composition of the model groups is different.

The Great Australian Bight (GAB) extends from Cape Pasley in Western Australia to Cape Catastrophe, Eyre Peninsula in South Australia. The model presented here was developed for the eastern GAB (eGAB) from the Head of the Bight to Cape Jaffa including the Investigator Strait and the lower portions of Gulf St Vincent and Spencers Gulf. The model region covers 154,000 km^2 and includes continental shelf waters to 200 m deep between 132.0° and 139.7° E longitude.

The main purpose of the model was to investigate the potential impacts of the sardine fishery on high tropic level predators, especially land-breeding seals and seabirds, which were disaggregated into single species where data on diet and population biomass permitted. The GAB is critical habitat for the southern right whale (*Eubalaena australis* – endangered under the Commonwealth EPBC Act) and the Australian sea lion (*Neophoca cinerea* – currently listed as near-threatened). About 1.5 million pairs of seabirds including 16 species also occur in the eastern Bight, mostly short-tailed shearwaters (*Puffinus tenuirostris*). Other key purposes for the model were to investigate the ecological effects of fishing on the key target species (sardines), and the functional roles and importance of mid-trophic small pelagic species, such as sardines, anchovies, jack mackerel, redbait, arrow squid and calamari (also represented as single-species functional groups where data permitted). A total of 41 functional groups were included in the eGAB ecosystem model, based on species similarity in terms of diet, habitat, foraging behaviour, size, consumption and rates of production.

Fishery data on landings, discards and effort was obtained and aggregated into eleven fleets operating within the eGAB ecosystem. Six South Australian managed fisheries: the South Australian (SA) sardine, SA Marine Scalefish line, SA Marine Scalefish net, and three prawn fisheries (Spencer Gulf; Gulf Saint Vincent; West Coast); and five fisheries managed by the Australian Government: southern bluefin tuna (SBT) purse seine, SBT pole and bait, South East trawl, GAB trawl, and the gillnet demersal shark fishery (Gillnet Hook and Trap Fishery). Annual fishery landings and effort data were obtained for all fleets between 1991-2008 (logbook data obtained from the AFMA, CSIRO, and SARDI Aquatic Sciences).

Further details on the model construction and development are presented in Goldsworthy *et al*. (2011).

6.1.4 Sensitive interactions and vulnerabilities

For all models, respective times series of catches, catch per unit effort (CPUE), and fishery efforts specific to each of models were loaded. We ran several scenarios where we altered the predator/prey vulnerability settings so that:

1. (for EBS models) the seal/redbait interaction vulnerability was 1 (to represent bottom-up control of seals by redbait)
2. (for EBS models) the seal/redbait interaction vulnerability was 10000 (to represent strong top-down control by seals on redbait);
3. (for all models) the vulnerabilities of the 25, 30 and 50 most sensitivepredator/prey interactions were found and applied;
4. and (for EBS models) a primary production forcing function was applied to primary producers group (Hoyo) (described in Bulman *et al.,* 2006) and the vulnerabilities for 25 most sensitive interactions found and applied.

After each new set of vulnerabilities was applied, the model was run over a 50 year simulation beginning in1994 for the EBS models and 1991 for the GAB model, which included the respective observation or tuning periods. The results were represented as the relative changes in biomasses of model groups compared to those of the default vulnerability scenario, rather than the comparing actual biomasses, so that we could directly compare the effects of and between the different vulnerability hypotheses.

6.2 Results of vulnerability sensitivities in EwE models

6.2.1 EBS model

The effect of changing vulnerability settings only for the seal/redbait interaction resulted in several groups being affected both in biomass and catch predictions (Figure 20, Appendix E). When the value was changed to 1, representing bottom up control on seals, both redbait biomass and catches increased by about 38%. Tuna also increased by 17% in both biomass and catch. Warehous biomass declined by nearly 15% and blue-eye trevalla declined by nearly 10%. All other changes were less than ±10%.

Setting the vulnerability to 10,000 to reflect top-down control by seals on redbait, caused a very large decline of nearly 70% in redbait biomass and catches (Figure 20, Appendix E). Tuna declined 27% while the largest positive changes were increases of 58% in warehou, 37% in blue-eye trevalla, 31% in gelatinous nekton, 27% in Chinaman leatherjacket, 23% in pelagic medium predators and shelf ocean perch, 16% in slope ocean perch, and 11% in penguins. All other groups were affected by less than ±10%. The magnitudes of the differences in biomasses were the same for catches of the corresponding species since we presumed constant exploitation rates through the projection period of the simulations.

These results are dependent on only one predator/prey interaction that we deemed to be of particular interest, and not necessarily the most sensitive of the interactions in the ecosystem. When the model was tuned to the time series of catches, CPUEs and biomasses, and the 25, 30 and 50 most vulnerable interactions were searched, it was found that the seal/redbait interaction was included in the result set. Also included were the seal/jack mackerel, tuna/redbait, tuna/jack mackerel, tuna/squid, redbait/gelatinous nekton, redbait/large zooplankton, and redbait/small zooplankton interactions (Figure 21). These interactions could lead to a typical wasp-waist control of the system if other conditions were suitable.

When 25 interactions were searched and the corresponding vulnerabilities adjusted, the vulnerabilities of the seal/redbait and the tuna/redbait interactions indicated bottom-up control by redbait. On the whole, redbait exerted top-down control on the lower trophic level groups of gelatinous nekton, large and small zooplankton (Figure 21) except for when the primary production forcing function in the 25-interaction scenario was implemented gelatinous nekton exerted bottom-up control on redbait, and in the 30-interaction scenario, small zooplankton were found to bottom-up control redbait. Overall, the control through redbait, seal/tuna-redbait-zooplankton, appeared to be both up and down, thus potentially a wasp-waist scenario.

Seal/jack mackerel interactions were always top-down controlled by seals. Other jack mackerel interactions were only found when 30 or more interactions were searched but then, as with redbait, tuna were bottom-up controlled by jack mackerel. Jack mackerel exerted a top-down control on both small and large zooplankton, and mesopelagics. This tuna-jack mackerel-zooplankton control relationship also represents an “up-and-down” control similar to the tuna-redbait-zooplankton lineage described previously.

The implementation of the primary production forcing function resulted in most of the interactions being bottom-up controlled from primary producers. The main exceptions were seal-prey and redbait-zooplankton interactions.

Other sensitive interactions of interest but not contenders for wasp-waist control were those of gemfish and flathead. In all scenarios, control on gemfish was a combination of bottom-up through cardinal fish and top-down control by seals. At 50 vulnerabilities, the mesopelagics-cardinal fish interactions became important resulting in top-down control by cardinal fish. The potential is therefore for “up-and-down” control between gemfish-cardinal fish-mesopelagics. Interactions between flathead and seals were always bottom-up.

As the interactions searched increased, flathead became increasingly influential. With the primary productivity forcing function applied and 25 most sensitive interactions searched, flathead was bottom-up controlled by the sardines and anchovies (small pelagic invertebrate feeders). However, without the forcing function, this control was reversed and cucumberfish were also top-down controlled by flathead. These species represented the greatest proportion

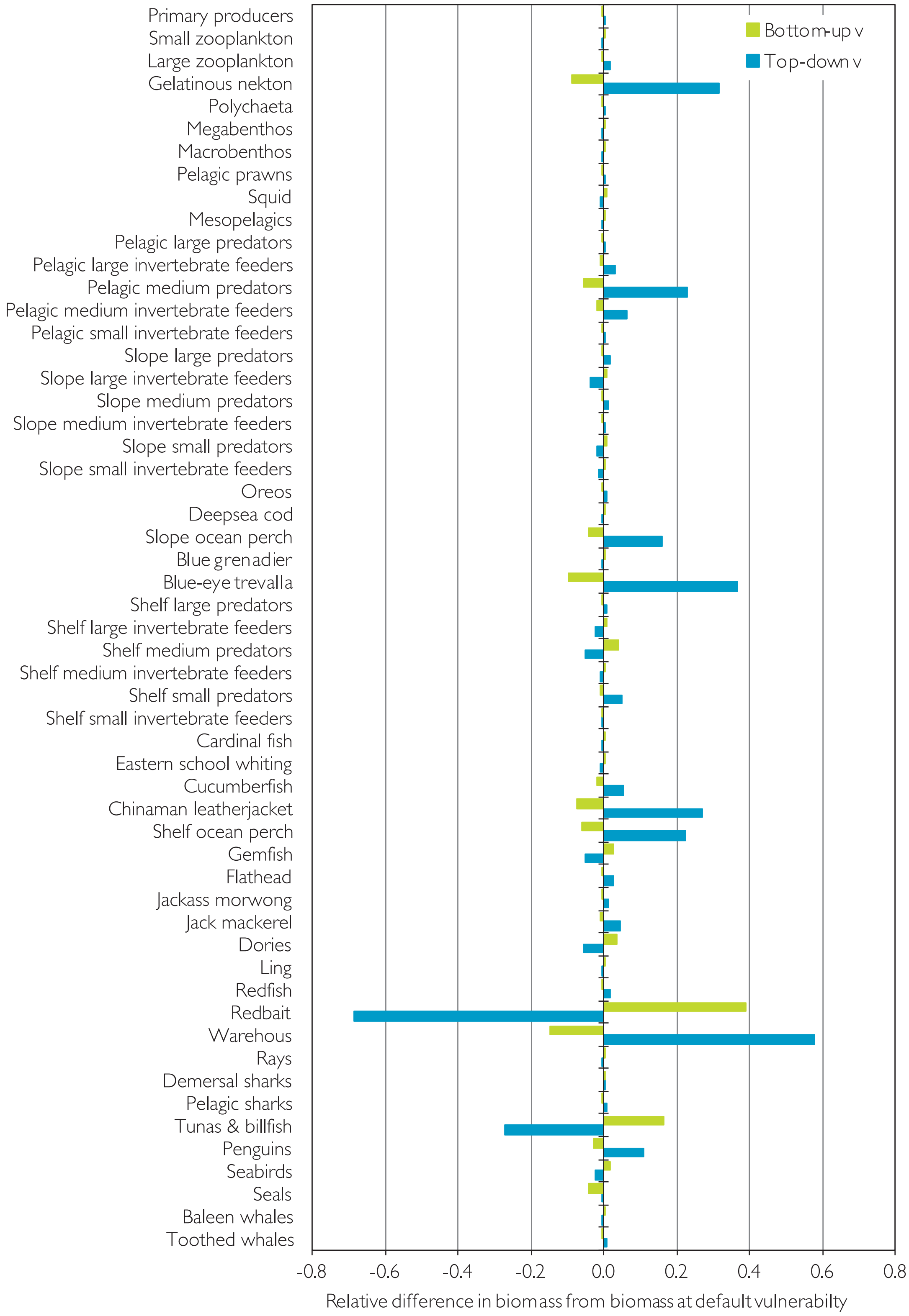
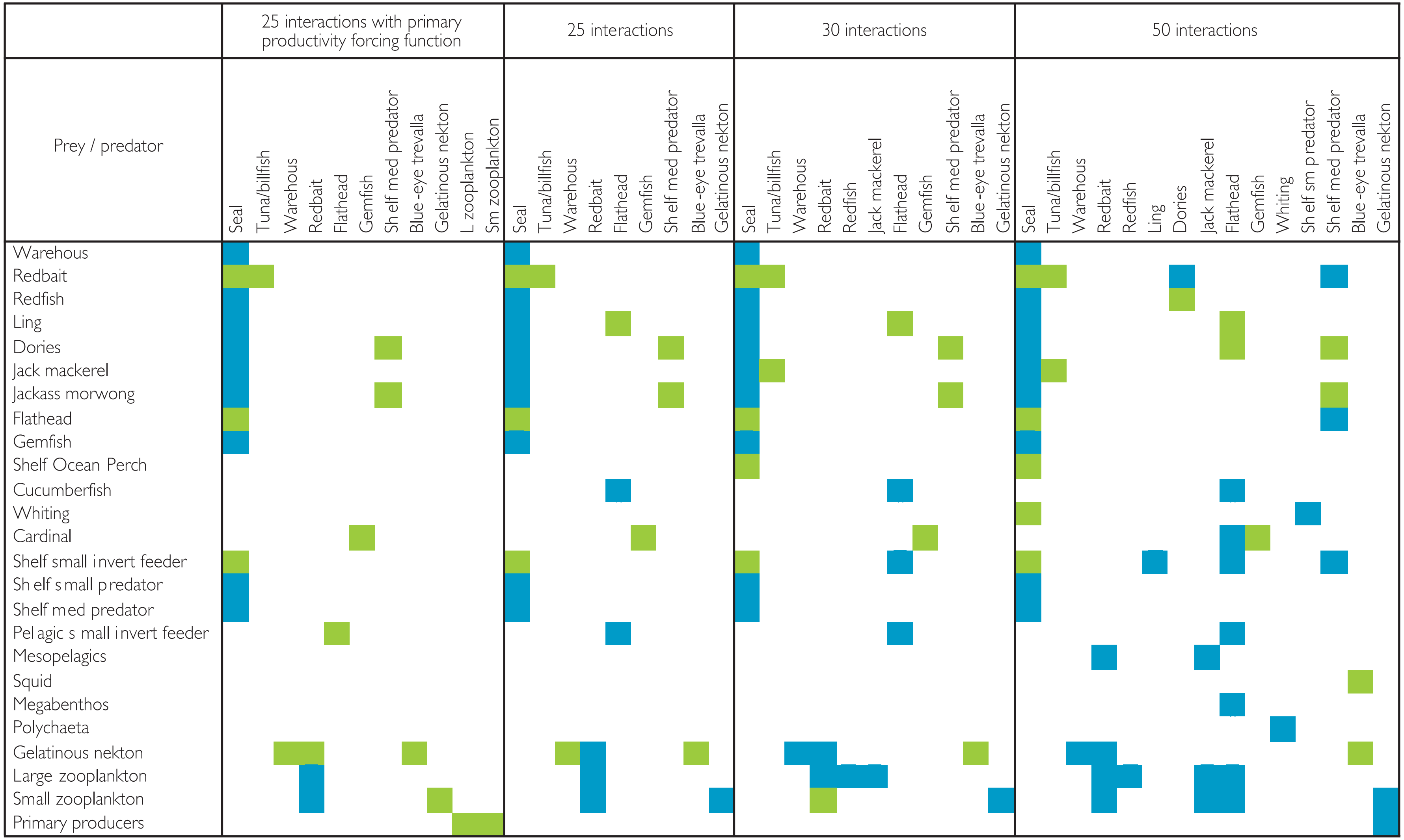


Figure 20. Relative difference in biomasses at bottom-up and top-down control vulnerability settings for seal/redbait interactions compared to biomasses at default vulnerability settings in the EBS model.

in flathead diet. Curiously, ling in the30-interaction and dories in the 50-interaction scenarios, appeared to bottom-up control flathead although neither were highly represented in the flathead diet (both ~1%). In the 50-interaction scenario, flathead were involved in a total of nine interactions mostly of top-down control and second only to the 12 of seals. The



	25 interactions with primary productivity forcing function										
Prey / predator	Seal	Tuna/billfish	Warehous	Redbait	Flathead	Gemfish	Shelf med predator	Blue-eye trevalla	Gelatinous nekton	L zooplankton	Sm zooplankton
Warehous	🟦										
Redbait	🟩	🟩									
Redfish	🟦										
Ling	🟦										
Dories	🟦						🟩				
Jack mackerel	🟦										
Jackass morwong	🟦						🟩				
Flathead	🟩										
Gemfish	🟦										
Shelf Ocean Perch											
Cucumberfish											
Whiting											
Cardinal						🟩					
Shelf small invert feeder	🟩										
Shelf small predator	🟦										
Shelf med predator	🟦										
Pelagic small invert feeder					🟩						
Mesopelagics											
Squid											
Megabenthos											
Polychaeta											
Gelatinous nekton			🟩	🟩				🟩			
Large zooplankton				🟦							
Small zooplankton				🟦					🟩		
Primary producers										🟩	🟩

	25 interactions								
Prey / predator	Seal	Tuna/billfish	Warehous	Redbait	Flathead	Gemfish	Shelf med predator	Blue-eye trevalla	Gelatinous nekton
Warehous	🟦								
Redbait	🟩	🟩							
Redfish	🟦								
Ling	🟦				🟩				
Dories	🟦						🟩		
Jack mackerel	🟦								
Jackass morwong	🟦						🟩		
Flathead	🟩								
Gemfish	🟦								
Shelf Ocean Perch									
Cucumberfish					🟦				
Whiting									
Cardinal						🟩			
Shelf small invert feeder	🟩								
Shelf small predator	🟦								
Shelf med predator	🟦								
Pelagic small invert feeder					🟦				
Mesopelagics									
Squid									
Megabenthos									
Polychaeta									
Gelatinous nekton			🟩	🟦				🟩	
Large zooplankton				🟦					
Small zooplankton				🟦					🟦
Primary producers									

	30 interactions										
Prey / predator	Seal	Tuna/billfish	Warehous	Redbait	Redfish	Jack mackerel	Flathead	Gemfish	Shelf med predator	Blue-eye trevalla	Gelatinous nekton
Warehous	🟦										
Redbait	🟩	🟩									
Redfish	🟦										
Ling	🟦						🟩				
Dories	🟦								🟩		
Jack mackerel	🟦	🟩									
Jackass morwong	🟦								🟩		
Flathead	🟩										
Gemfish	🟦										
Shelf Ocean Perch	🟩										
Cucumberfish							🟦				
Whiting											
Cardinal								🟩			
Shelf small invert feeder	🟩						🟦				
Shelf small predator	🟦										
Shelf med predator	🟦										
Pelagic small invert feeder							🟦				
Mesopelagics											
Squid											
Megabenthos											
Polychaeta											
Gelatinous nekton			🟦	🟦						🟩	
Large zooplankton				🟦	🟦	🟦					
Small zooplankton				🟩							🟦
Primary producers											

	50 interactions														
Prey / predator	Seal	Tuna/billfish	Warehous	Redbait	Redfish	Ling	Dories	Jack mackerel	Flathead	Gemfish	Whiting	Shelf sm predator	Shelf med predator	Blue-eye trevalla	Gelatinous nekton
Warehous	🟦														
Redbait	🟩	🟩					🟦						🟦		
Redfish	🟦						🟩								
Ling	🟦								🟩						
Dories	🟦								🟩				🟩		
Jack mackerel	🟦	🟩													
Jackass morwong	🟦												🟩		
Flathead	🟩												🟦		
Gemfish	🟦														
Shelf Ocean Perch	🟩														
Cucumberfish									🟦						
Whiting	🟩											🟦			
Cardinal									🟦	🟩					
Shelf small invert feeder	🟩					🟦			🟦				🟦		
Shelf small predator	🟦														
Shelf med predator	🟦														
Pelagic small invert feeder									🟦						
Mesopelagics				🟦				🟦							
Squid														🟩	
Megabenthos									🟦						
Polychaeta											🟦				
Gelatinous nekton			🟦	🟦										🟩	
Large zooplankton				🟦	🟦			🟦	🟦						
Small zooplankton				🟦				🟦	🟦						🟦
Primary producers															🟦

Figure 21. The most vulnerable predator /prey interactions for the EBS EwE model as determined by the automated search procedure . Green boxes indicate vulnerability values <2 i.e. bottom-up control and blue boxes indicate vulnerabilities values >2 i.e. top-down control. (sm=small, med=medium, l=large, invert=invertebrate).

shelf medium predators were involved in a total 5 interactions (out of 50) of which those with jackass morwong and dories were bottom-up controlled. Other fish predators, such as warehous, redfish, whiting and shelf small predators, generally exhibited top-down control. The planktonic prey also exhibited top-down control on lower trophic levels.

Overall, and apart from the dominating seal interactions, the majority of sensitive interactions involved top-down control in the fishery model (Figure 21). With 25 interactions searched, 6 of the 13 non-seal interactions were top-down controlled although only 2 with the primary productivity forcing function applied; with 30 interactions searched, 9 of 17 were top-down and with 50 interactions searched, 26 of 36 were top-down.

The effect of altering vulnerability parameters to reflect just some of the predator-prey interactions is evident on the predicted biomasses of particularly the higher trophic level groups at the end of a 50 year simulation (Figure 22). Interestingly, the effect on seal biomasses was relatively small, (-25% to 13%), even though the seal-prey interactions were the most numerous. As the number of vulnerabilities that were explored increased, the predicted biomass of seals decreased until it was less than the default vulnerability outcome. Tunas and billfishes declined from the default value by 10 to > 20% in all scenarios but even larger declines of about 40% or more were found for warehous, jack mackerel, and shelf medium predators in all scenarios. Declines greater than 20% were predicted for dories, ling, shelf small predators, jackass morwong, Chinaman leatherjacket, blue-eye trevalla, slope large predators and gelatinous nekton for most, if not all, scenarios.

On the other hand, increases over the default value of more than 40% were predicted for all redbait and flathead scenarios, and some shelf small invertebrate feeder scenarios. Lesser increases of nearly 20% were found for cucumberfish and cardinal fish scenarios. The only other groups whose biomasses were predicted to increase more than 20% were medium slope invertebrate feeders and large pelagic invertebrate feeders when 50 vulnerabilities were searched.

6.2.2 Hypothetical redbait fishery model control

The larger biomass of, and consequently larger fishery for, redbait in the hypothetical fishery model altered the predictions only slightly (Figure 23). Bottom-up control, i.e. vulnerability setting for the seal/redbait interaction value equal to 1, caused little change in any group from the results at the default vulnerability setting and none greater than ±12%. Warehou biomass declined 12% from the default biomass while redbait biomass increased by about 11%, i.e. substantially less than in the original model. The magnitudes of the differences in biomasses were the same for catches of the corresponding species since we presumed constant exploitation rates through the projection period of the simulations therefore redbait catch rates under bottom-up control also increased by about 11% over the default rates.

Altering the one interaction to top-down control caused more changes and several changes greater than 20% (Figure 23). Redbait biomass was halved under top-down control while warehous increased by nearly 70%. Blue-eye trevalla biomass increased by 50%, Chinaman leatherjacket by 37%, pelagic medium predators by 33%, and shelf ocean perch by 30%. Less significant changes were found for biomasses of seals (+13%), penguins (+16%), as well as tuna and billfish (- 15%).

Overall, the groups affected were the same when the redbait biomass was substantially higher, and with a larger fishery, than when it was at the real, but lower, level as off eastern Bass Strait. The major difference was that the top-down effect setting increased the biomasses of those affected i.e. increases were increased and decreases were lessened. The bottom-down setting caused little difference except in the case of redbait, where biomass was greatly reduced under this control.

Overall, and apart from the dominating seal interactions, the majority of sensitive interactions involved bottom-up control in the fishery model (Figure 24). With 25 interactions searched, 12 of the 13 non-seal interactions were bottom-up controlled; with 30 interactions searched,

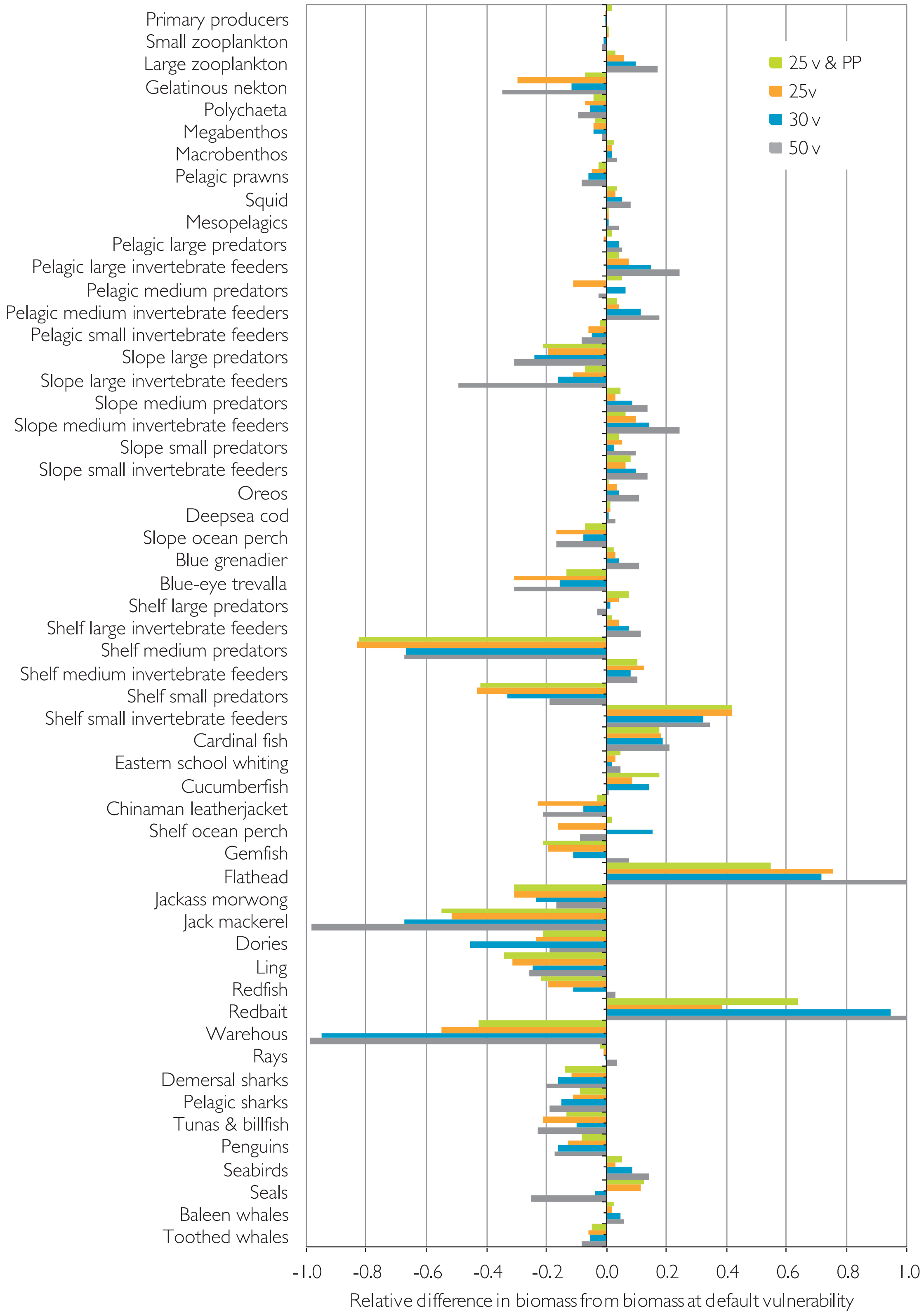


Figure 22. Relative difference in biomasses from default vulnerability biomasses for scenarios of number of fitted vulnerabilities (n= 25, 30, 50 or 25 with the primary production forcing function also fitted).

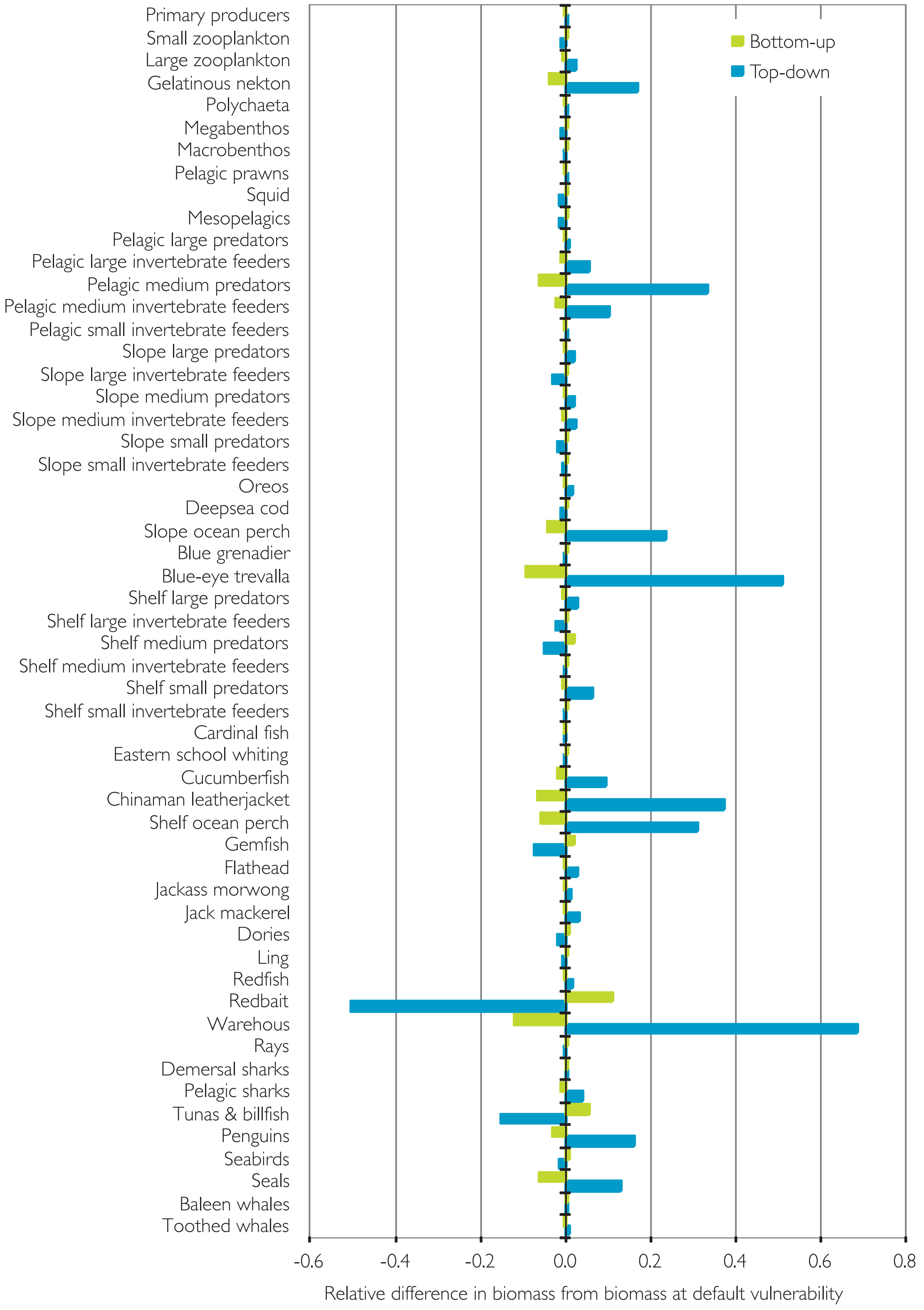


Figure 23. Relative difference from default vulnerability changes in biomass for bottom-up or top-down control vulnerability settings for seal/redbait interactions in the “redbait fishery” EBS model.

10 of 17 were bottom –up and with 50 interactions searched, 24 of 36 were bottom-up. This is a complete reversal from the EBS model where top-down control was dominant.

The seal/prey interactions were nearly all the same apart from some changes in the shelf medium predator interactions (Figure 24) which mostly changed from top-down to a bottom-up control. A sensitive interaction was found sooner between tuna and jack mackerel i.e. within the top 25 most sensitive interactions and all were consistently bottom-up. The jack mackerel/prey interactions were also the same as in those in the EBS model i.e. small and large zooplankton and mesopelagics, and also always top-down. The overall effects on the biomass of jack mackerel in this model were declines from the default value (Figure 25) but these declines were less than 10% lower than in the EBS model.

Through redbait, control was entirely bottom-up from plankton to tuna or seals, and was consistent despite the number of interactions searched (Figure 24), an almost complete reversal from the EBS model (Figure 21). The extent of the increase in redbait biomass was about 10% over the default value (Figure 25) in all scenarios. Apart from the seal and tuna interactions with redbait, other predator/redbait interactions, i.e. those with dories and shelf medium predators both of which were top-down control, no longer appeared sensitive.

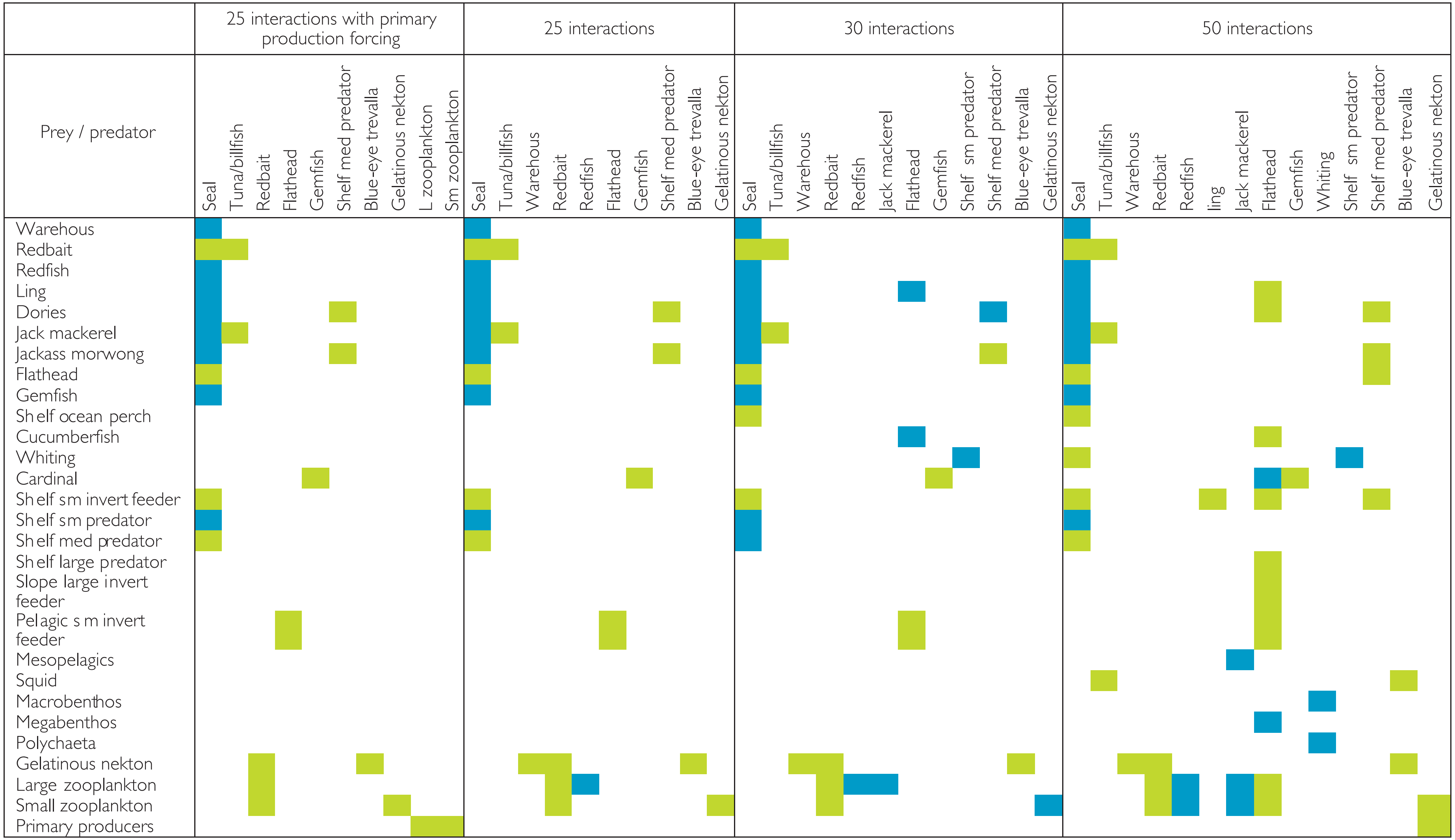
The flathead/sardine and anchovy interactions were also reversed compared to the EBS model (Figure 24). They had been top-down but were consistently bottom-up in the fishery model. By the time 50 interactions were searched, flathead were involved in 11 interactions, 7 of which were the same as those in the EBS model however all but 2 were bottom-up controlled. The top-down control by flathead in both models was on cardinal fish and megabenthos although neither were groups of great significance in terms of dietary composition (~5% each). However cardinal fish biomass increased about 20% over the default value and would have assisted in the flathead population increase (Figure 25).

Four reversals were found for the shelf medium predator/prey interactions (Figure 24), all of which were bottom–up controlled in the 50-interaction scenario compared to only 2 out 5 in the EBS model. The biomass of this group increased significantly (>30%) over the default value in most scenarios (Figure 25) compared to declines of over 60% in the EBS model. This result might be due to the reversals of the top-down interactions with flathead and small shelf invertebrate feeders, but rather odd considering that both those populations increased less in the fishery model than in the EBS. However, it is likely that the larger starting biomass of redbait may have tipped the balance in favour of the growth of the shelf medium predator group in this model, despite their interaction being non-sensitive and the vulnerability set at the default of 2 (neither bottom-up nor top-down).

Redfish remained top-down controlling small and large zooplankton as in the EBS model (Figure 24). However, biomass declined by 20% compared to that of the default vulnerability scenario (Figure 25) and about 10% more than the EBS scenarios, except where 50 or more interactions were searched. These scenarios, for both models, varied positively only a few percent from the default value.

Whiting also remained top-down controlling on polychaetes but added macrobenthos to the interactions (Figure 24). Ling reversed control from top-down to bottom-up on shelf small invertebrate feeders as did gelatinous nekton on small zooplankton and primary producers.

The effect on group biomasses was largely a dampening of the extreme effects. For example, the increase of redbait was dramatically reduced to a quarter or less compared to those in the EBS model, flathead increases were reduced to about half, and the decline in warehous was almost halved (Figure 25). These were in addition to the very large positive effect on the shelf medium predators, as discussed earlier, where 40-50% increases were found compared to



	25 interactions with primary production forcing										25 interactions										30 interactions												50 interactions													
Prey / predator	Seal	Tuna/billfish	Redbait	Flathead	Gemfish	Shelf med predator	Blue-eye trevalla	Gelatinous nekton	L zooplankton	Sm zooplankton	Seal	Tuna/billfish	Warehous	Redbait	Redfish	Flathead	Gemfish	Shelf med predator	Blue-eye trevalla	Gelatinous nekton	Seal	Tuna/billfish	Warehous	Redbait	Redfish	Jack mackerel	Flathead	Gemfish	Shelf sm predator	Shelf med predator	Blue-eye trevalla	Gelatinous nekton	Seal	Tuna/billfish	Warehous	Redbait	Redfish	ling	Jack mackerel	Flathead	Gemfish	Whiting	Shelf sm predator	Shelf med predator	Blue-eye trevalla	Gelatinous nekton
Warehous	🟦										🟦										🟦												🟦													
Redbait	🟩	🟩									🟩	🟩									🟩	🟩											🟩	🟩												
Redfish	🟦										🟦										🟦												🟦													
Ling	🟦										🟦										🟦						🟦						🟦							🟩						
Dories	🟦					🟩					🟦							🟩			🟦									🟦			🟦							🟩				🟩		
Jack mackerel	🟦	🟩									🟦	🟩									🟦	🟩											🟦	🟩												
Jackass morwong	🟦					🟩					🟦							🟩			🟦									🟩			🟦											🟩		
Flathead	🟩										🟩										🟩												🟩											🟩		
Gemfish	🟦										🟦										🟦												🟦													
Shelf ocean perch																					🟩												🟩													
Cucumberfish																											🟦													🟩						
Whiting																													🟦				🟩										🟦			
Cardinal					🟩												🟩											🟩												🟦	🟩					
Shelf sm invert feeder	🟩										🟩										🟩												🟩					🟩		🟩				🟩		
Shelf sm predator	🟦										🟦										🟦												🟦													
Shelf med predator	🟩										🟩										🟦												🟩													
Shelf large predator																																								🟩						
Slope large invert feeder																																								🟩						
Pelagic s m invert feeder				🟩												🟩											🟩													🟩						
Mesopelagics																																							🟦							
Squid																																		🟩											🟩	
Macrobenthos																																										🟦				
Megabenthos																																								🟦						
Polychaeta																																										🟦				
Gelatinous nekton			🟩				🟩						🟩	🟩					🟩				🟩	🟩							🟩				🟩	🟩									🟩	
Large zooplankton			🟩											🟩	🟦									🟩	🟦	🟦										🟩	🟦		🟦	🟩						
Small zooplankton			🟩					🟩						🟩						🟩				🟩								🟦				🟩	🟦		🟦	🟩						🟩
Primary producers									🟩	🟩																																				🟩

Figure 24. The 25, 30 or 50 most vulnerable predator /prey interactions for the hypothetical redbait fishery EwE model. Green boxes indicate values <2 i.e. bottom-up control and blue boxes indicate values >2 i.e. top-down control. (sm=small, med=medium, l=large, invert=invertebrate).

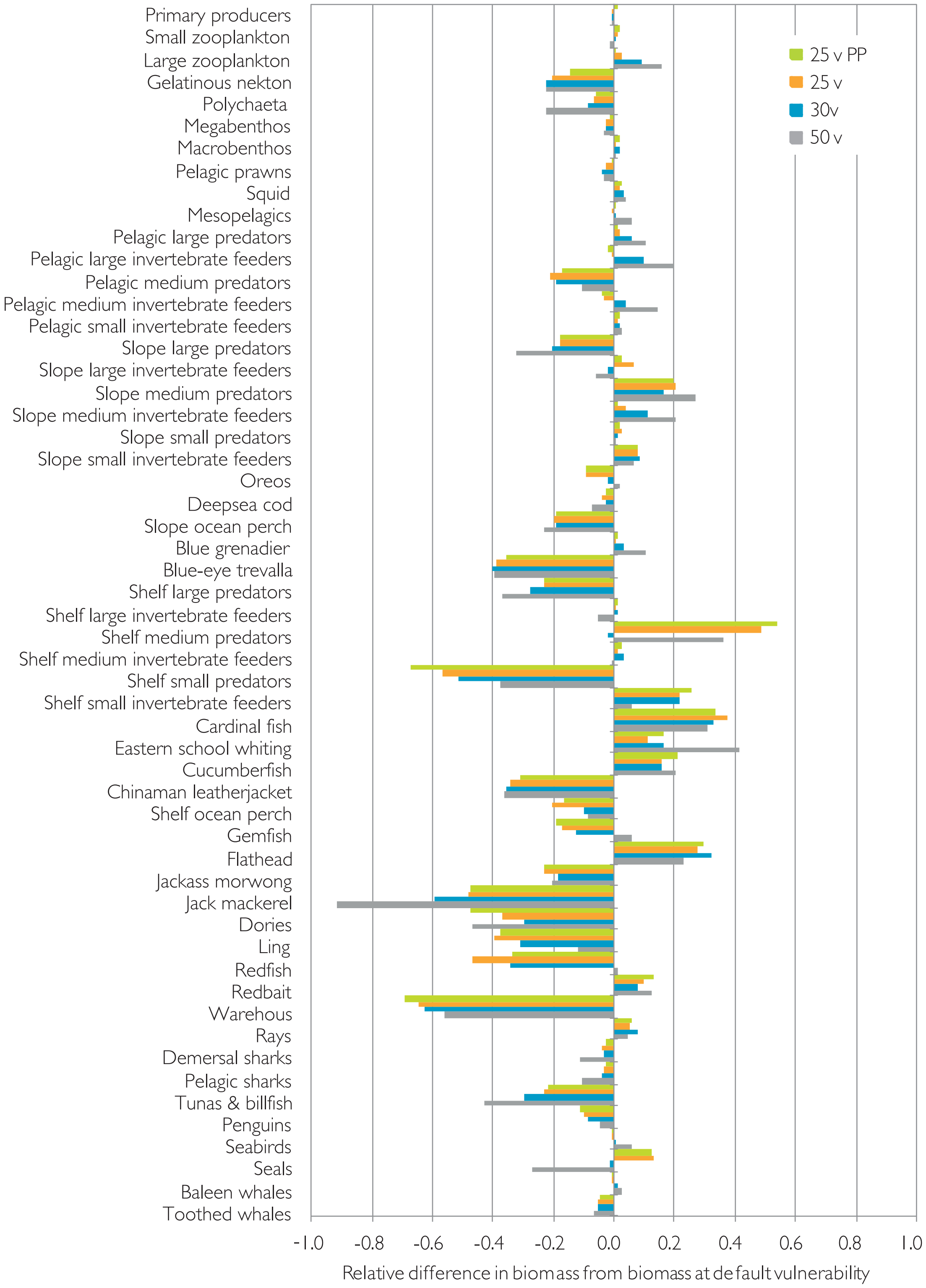


Figure 25. Relative difference in biomasses from default vulnerability biomasses for scenarios of number of fitted vulnerabilities (n= 25, 30, 50 or 25 with the primary production forcing function also fitted) for the "red-bait fishery" EBS model.

60-80% declines in the EBS model. Other less dramatic changes were seen in shelf large predator biomasses which were all more than 20% worse than the default and compared to mostly slight increases in the EBS model (-3% to 7%). Of the higher order predators, tunas were the most negatively affected by up to a 20% decrease compared to the EBS model, whereas pelagic and demersal sharks and rays were positively affected by about 10%. All other groups were affected similarly as in the EBS model with the differences generally small, but in either direction.

The groups representing yellowtail scad or blue mackerel, pelagic medium invertebrate feeders or predators, were not involved in any of the top 50 sensitive predator/prey interactions in either of the EBS models and consequently their change in biomass was little different from default.

6.2.3 Eastern Great Australian Bight

The majority of the most sensitive interactions found were bottom-up controlled. With the top 25 interactions searched, about three- quarters were bottom-up controlled, but this proportion decreased to almost half by the time 50 interactions were searched.

The dominant interactions were those of the fur seals, both New Zealand and Australian, totalling 12-16 interactions (Figure 26). Of those, only 1 or 2 were top-down controlled depending on the number of interactions searched; between NZ fur seal/medium demersal piscivore or mesopelagics or petrels. The controls through jack mackerel and redbait to both the fur seals were always bottom-up controlled. Arrow squid was also always bottom-up controlling the fur seals. Jack mackerel top-down controlled small herbivorous zooplankton in all scenarios and thus the fur seal/jack mackerel /small zooplankton represents an “up-and-down” control or a possible wasp-waist situation. Redbait, however, was bottom-up controlled by small zooplankton but only in the 50-interaction scenario representing a possible bottom-up control through the pelagic foodweb, similar, but possibly weaker connections, to that of the EBS system.

While the biomass of Australian fur seals appeared to decline dramatically (~50-60%) compared to that at default vulnerabilities (Figure 27), the absolute values were still in fact, in the order of 8- to 10-fold increases. New Zealand fur seals were not so significantly affected by applying vulnerabilities despite being the most dominant predator in the top 50 sensitive predator-prey interactions.

Gannets and petrels declined significantly in most vulnerability scenarios, however they were predicted to decline by 10-20% even at default vulnerability (Figure 27). The most significant decline (-99%) was seen in the 50-interaction scenario when New Zealand fur seals interaction were found to be top-down controlling petrels (Figure 26).

Unlike the EBS model, the tuna/redbait interaction was top-down controlled but only with 50 interactions searched (Figure 26). Instead, tuna were bottom-up controlled by anchovy at 25 interactions searched, and also blue mackerel at 30 interactions. Tuna biomass in these scenarios increased more than four times over the expected biomass at default vulnerability (Figure 27). In absolute terms this actually meant that the decline of tuna halted at around a third of its starting biomass rather than at 5%, which is a significant improvement in outcome for tuna. Anchovy did not appear to have any sensitive interactions (within the top 50) with prey groups but blue mackerel did have a top-down controlled interaction with small zooplankton, thus representing an “up-and-down” control in the tuna /blue mackerel/ small zooplankton line.

Blue mackerel biomass was significantly reduced by over 80% in the 30- and 50-interactions scenarios than at default. This in fact represented real declines in predicted biomass to 10-20 % of starting biomass compared to a 50% increase at default or with only 25 interactions searched.

In this system, pelagic sharks were the next most dominating species after fur seals. They were bottom-up controlled by tuna, sardine, arrow squid and calamary and top-down controlling over demersal sharks within the top 25 most sensitive interactions (Figure 26). Within the 30-interaction scenario, they also top-down controlled blue mackerel and the control over calamary had reversed to a top-down control. In the 50-interaction scenario, they also exhibited a top-down control over anchovy and were bottom-up controlled by octopus. The mixture of controls exhibited by this group might be a reflection of the mixture of species both inshore and offshore species contributing to a mixing of the overall diet of the group. Nevertheless, the pelagic sharks were a dominant species in this system.

Another dominant group in this system was arrow squid, which appeared to have a top-down control on large pelagic piscivores and jack mackerel, adding redbait by the time the top 50 interactions were searched (Figure 26). It seemed counter-intuitive that arrow squid would eat large pelagic piscivores, (i.e. tunas, kingfish, bonito and barracouta) let alone have a top-down control, unless juvenile stages were eaten. In fact, arrow squid ate only barracouta, presumably juveniles, but not the tuna that are nominally represented by the large pelagic piscivore grouping. Moreover, the data representing this group are only from barracouta, kingfish and bonito, therefore, we assumed that large pelagic piscivores only included barracouta, bonito and kingfish and not the tunas and similar species, and that the interaction was real. Squid also top-down controlled sardine, and, when more interactions were searched, large demersal piscivores and arrow squid thus creating a feed-back loop. This loop between arrow squid and large pelagic piscivores supports the qualitative modelling hypotheses proposed in chapter 4 regarding ambiguity of results that might arise. It also fits one of the characteristics required of a wasp-waist species (Bakun, 2006).

Through jack mackerel there was top-down control through small zooplankton. On the other hand, sardine appeared to have a bottom-up control on squid but a top-down control on small zooplankton, therefore an “up-and-down” control. They also had a bottom-up control on pelagic sharks, and thus we have another “up-and-down” control in the shark/sardine/small zooplankton chain.

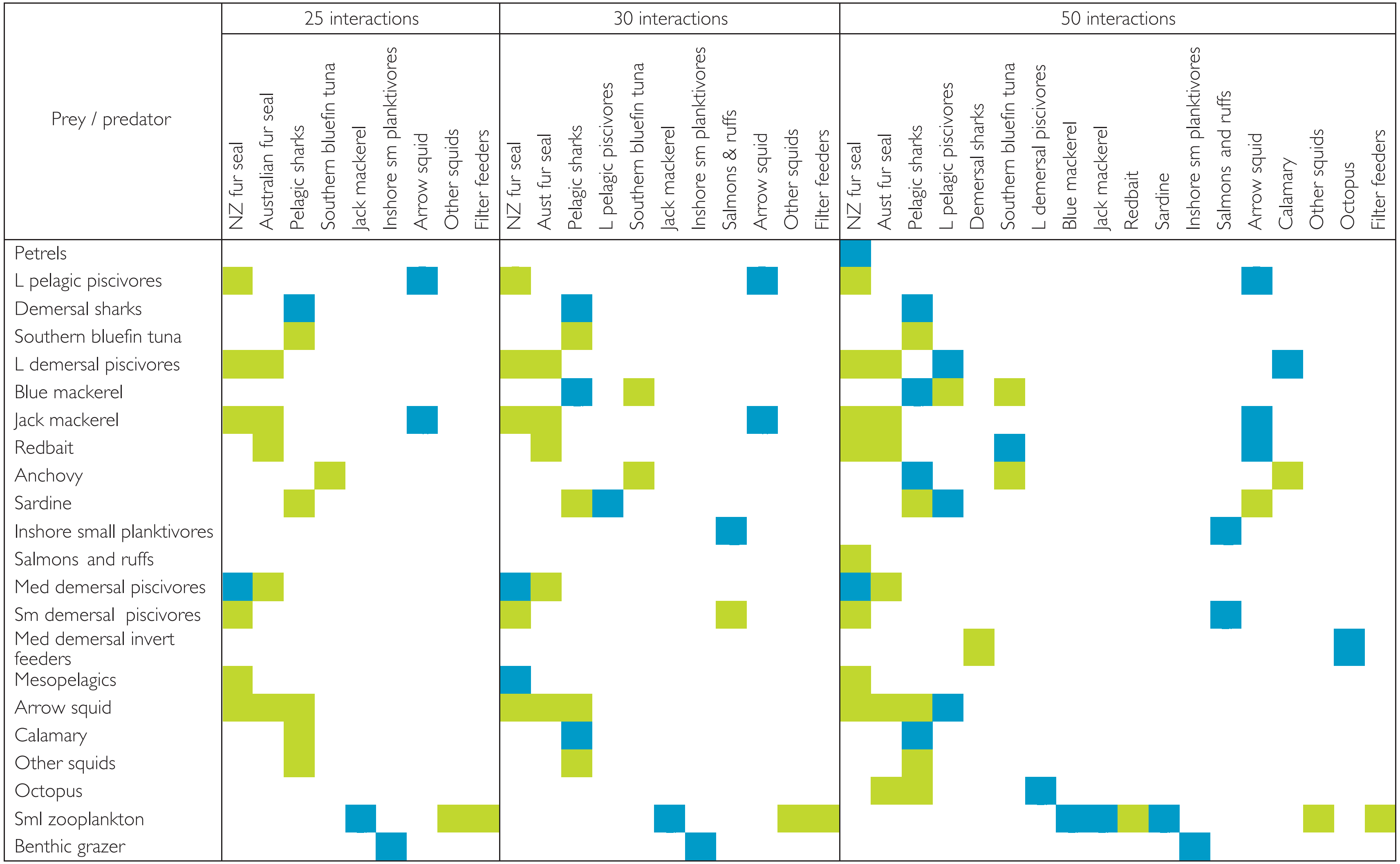
Other squids also bottom-up controlled pelagic sharks but were always bottom-up driven by small zooplankton (Figure 26). Within 50 interactions, octopus top-down controlled medium demersal invertebrate feeders (garfish) but were top-down controlled by large demersal piscivores. Calamary top-down controlled large demersal piscivores (snapper) but were bottom-up controlled by anchovy.

Generally, the cephalopod biomasses under most vulnerability scenarios (Figure 27) was better than at the default vulnerability. While for arrow squid this meant an actual increase in biomass; for the other cephalopods this was often a reduced decline in biomass.

Salmon and ruffs had a top-down control on small inshore planktivores (maray and sprat) which also top-down controlled benthic grazers (or megabenthos) (Figure 26). They had variable interactions with the small demersal piscivores (red mullet, apogonids, sweep) switching from a bottom-up control at 30-interaction scenario to a top-down control in the 50-interaction scenario.

We also found switches in the directions of control between the three scenarios for two other predator/prey interactions: the interaction between NZ fur seals and mesopelagics and between pelagic sharks and calamary. The first interaction where NZ fur seals were bottom up controlled by mesopelagics in 25- and 50-interaction scenarios but top-down in the 30-interaction scenario, the biomass of mesopelagics also flip-flopped directions (Figure 27).

Overall, the GAB system was dominated by fur seal interactions and pelagic sharks and arrow squid. The small pelagic species as prey were most often in a bottom-up controlling position



Prey / predator	25 interactions									30 interactions											50 interactions																	
	NZ fur seal	Australian fur seal	Pelagic sharks	Southern bluefin tuna	Jack mackerel	Inshore sm planktivores	Arrow squid	Other squids	Filter feeders	NZ fur seal	Aust fur seal	Pelagic sharks	L pelagic piscivores	Southern bluefin tuna	Jack mackerel	Inshore sm planktivores	Salmons & ruffs	Arrow squid	Other squids	Filter feeders	NZ fur seal	Aust fur seal	Pelagic sharks	L pelagic piscivores	Demersal sharks	Southern bluefin tuna	L demersal piscivores	Blue mackerel	Jack mackerel	Redbait	Sardine	Inshore sm planktivores	Salmons and ruffs	Arrow squid	Calamary	Other squids	Octopus	Filter feeders
Petrels																					🟦																	
L pelagic piscivores	🟩						🟦			🟩								🟦			🟩													🟦				
Demersal sharks			🟦									🟦											🟦															
Southern bluefin tuna			🟩									🟩											🟩															
L demersal piscivores	🟩	🟩								🟩	🟩										🟩	🟩		🟦											🟦			
Blue mackerel												🟦		🟩									🟦	🟩		🟩												
Jack mackerel	🟩	🟩					🟦			🟩	🟩							🟦			🟩	🟩												🟦				
Redbait		🟩									🟩										🟩	🟩				🟦								🟦				
Anchovy				🟩										🟩									🟦			🟩									🟩			
Sardine			🟩									🟩	🟦										🟩	🟦										🟩				
Inshore small planktivores																	🟦																🟦					
Salmons and ruffs																					🟩																	
Med demersal piscivores	🟦	🟩								🟦	🟩										🟦	🟩																
Sm demersal piscivores	🟩									🟩							🟩				🟩												🟦					
Med demersal invert feeders																									🟩												🟦	
Mesopelagics	🟩									🟦											🟩																	
Arrow squid	🟩	🟩	🟩							🟩	🟩	🟩									🟩	🟩	🟩	🟦														
Calamary			🟩									🟦											🟦															
Other squids			🟩									🟩											🟩															
Octopus																						🟩	🟩				🟦											
Sml zooplankton					🟦			🟩	🟩						🟦				🟩	🟩								🟦	🟦	🟩	🟦					🟩		🟩
Benthic grazer						🟦										🟦																🟦						

Figure 26. The 25, 30 or 50 most vulnerable predator /prey interactions for the eastern Great Australian Bight model. Green boxes indicate values <2 i.e. bottom-up control and blue boxes indicate values >2 i.e. top-down control. (sm=small, med=medium, l=large, invert=invertebrate).

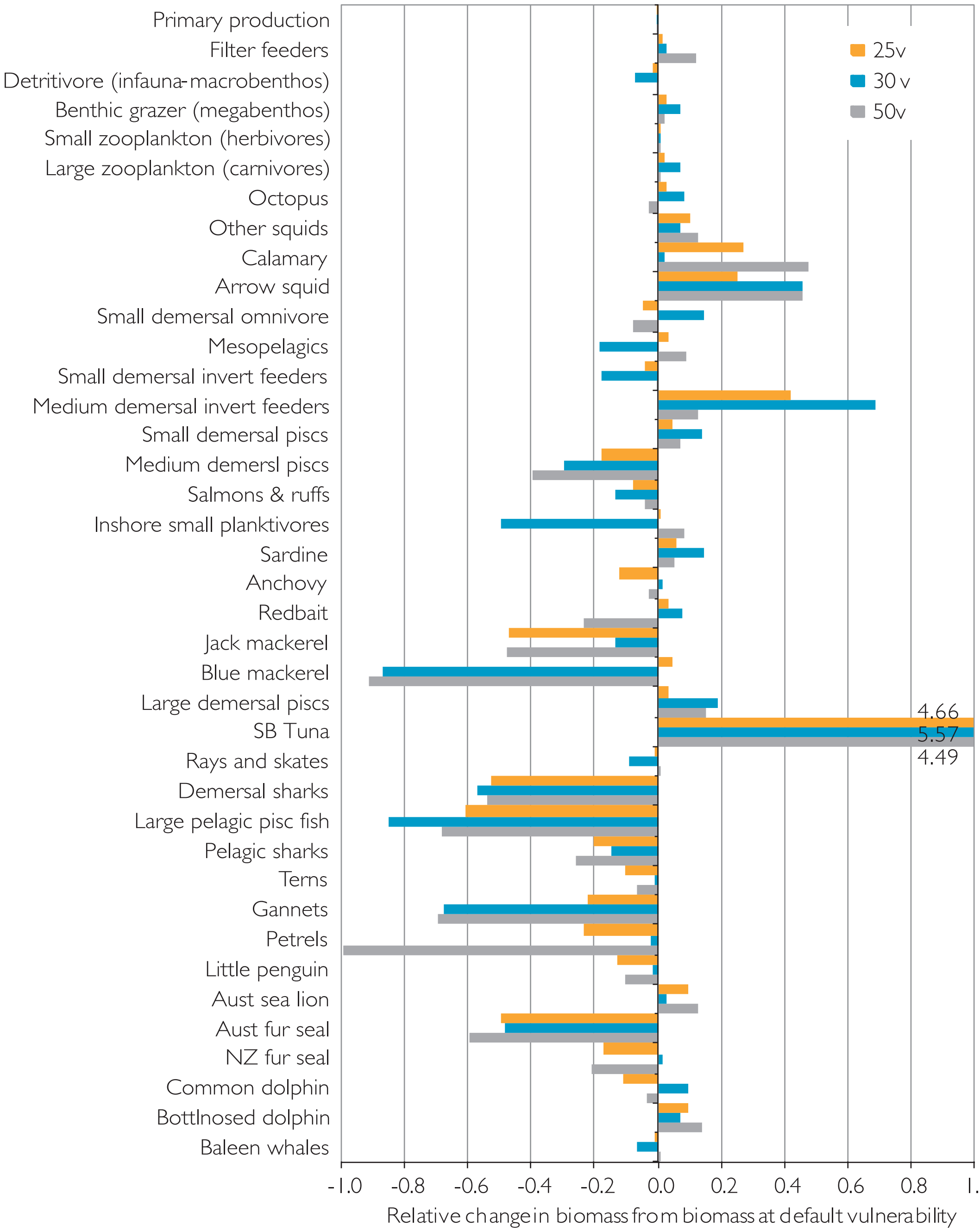


Figure 27. Relative difference in biomasses from default vulnerability biomasses for scenarios of number of fitted vulnerabilities (n= 25, 30, 50) for the eastern GAB model.

(10/11, 10/14 and 14/22 predator/prey interactions) (Figure 26). As predators, they were mostly top-down controlling with the exception of redbait which was only bottom-up controlled.

6.3 Comparison of systems and apparent control mechanisms operating in southern Australia

The EBS model results suggest that the pelagic foodweb is bottom-up dominated, particularly if the primary productivity forcing function is applied, and that benthopelagic interactions were more likely to be more top-down controlled. Although the GAB results also suggest this, in all cases there were exceptions. However, these results represent < 10% of the possible predator/prey interactions depicted in these models and are far from a complete view. While individual predator/prey interactions may be justifiable, more usually it is considered that a predator has an overall vulnerability across all its prey. Generally this was the case in these investigations even though individual interactions were being searched and so most of our conclusions would still hold true. The task of tuning a model to observations, largely through the vulnerability fitting is complex but extremely important. These investigations don't attempt to have completely captured the whole tuning process but only to highlight potentially important predator/prey interactions suggestive of the control of trophic flow in these model systems.

The dominance of the both the New Zealand and Australian fur seals in the GAB was similar to that of the Australian fur seals in the EBS model, despite the relatively low biomass (0.005% and 0.0006% in the GAB and 0.002% in the EBS, respectively, of the estimated ecosystem biomass). What was interesting was the difference between the two systems of the control exerted by the seals. In the case of the EBS, Australian fur seals were nearly always top-down controlling their predator/prey interactions whereas in the GAB, the Australian fur seals were always, and New Zealand fur seals were nearly always, bottom-up controlling their prey. Both models had biomass accumulation terms applied to the fur seals enabling the continuous growth of the populations approximately at the rate predicted by recent observations. They generally ate the same kinds of prey but not all prey interactions were deemed sensitive. Arrow squid and mesopelagics were important in the GAB fur seals though not in the EBS. Redbait was a bottom-up controlling prey in Australian fur seal diet in both models but not for NZ fur seals. On the other hand, jack mackerel was important prey for all fur seals in both models, although it was bottom-up controlling in the GAB but top-down in the EBS model. Top-down control (vulnerabilities >2), indicates that the predator will cause a similar increase in the predation mortality for its prey. High vulnerabilities imply prey has no refuge from predation and will be consumed whenever encountered by the predator. While this can lead to Lotka-Volterra dynamics, i.e. oscillating prey and predator biomasses and/or unpredictable behaviour (Walters *et al.,* 1997), this has not seen in the EBS fur seal interactions despite relatively high vulnerabilities.

Bottom-up control (vulnerability close to 1) means that an increase in predator biomass will not cause any noticeable increase in the predation mortality on its prey. Therefore, predators that were bottom-up controlled by their prey groups in the fishery model also seemed less prone to large changes. For example, in the EBS model the warehous/gelatinous nekton interaction was bottom-up controlled in both 25-interaction scenarios and the biomasses did not change very much, even between models, but when the interactions became top-down controlled (30-and 50-interactions), the changes in biomass were almost double (Figure 22). In the redbait fishery model where control was always bottom-up, the differences between all the scenarios were within about 10 or 15%. The biomass of the shelf medium predators was markedly different in the 30-interaction scenario from the others and on inspection the shelf medium predator/dory interactions “flip-flopped” from bottom–up in 25- and 50-interaction scenarios to a top-down control in the case of the 30-interaction scenario. Similarly, in the GAB, the mesopelagic biomass declined greatly when control in the NZ fur seal/mesopelagics interaction changed from bottom-up to top–down. The majority of interactions of the small pelagics as prey were bottom–up and the effects on the biomass were relatively small.

The small pelagic species, including sardine, anchovy and squids, figure in nearly half of all the sensitive interactions in the GAB whereas in the EBS system less than 20% at most involve small pelagics. The effect of the larger redbait population in the EBS was to force the system into more bottom-up control interactions within the top 50 interactions even where previously the benthopelagic elements were more top-down controlled. However, these species are the ones most likely to be the heart of the middle-out controls. In the EBS model redbait and jack mackerel were bottom-up controlling tuna and had various top-down controls on zooplankton groups, but only if the primary production forcing function was not applied. In the redbait fishery model however, the middle-out control in the redbait pathway changed to a bottom-up control pathway. There was no effect on jack mackerel interactions and the middle-out control still existed. In the GAB, middle-out control was found in the tuna/blue mackerel/small zooplankton pathway but at the same time pelagic sharks top-down controlled blue mackerel. Of anchovy and sardine, only sardine showed a middle-out control through pelagic sharks/sardine/small zooplankton and the arrow squid/sardine/small zooplankton pathways.

7 Comparison of EWE and Atlantis Models

7.1 Introduction

There is now a range of ecosystem models developed for many regions around Australia and for a variety of purposes. Within our region of interest, southern and south-eastern Australia and the Small Pelagic Fishery jurisdiction, there are basically two model types: Ecopath with Ecosim (EwE) and Atlantis. The former is off-the-shelf software freely available from ecopath.org and is widely used around the world. The concepts and equations upon which it is based are well-documented (Bulman *et al.,* 2006: p. 167-170, Christensen and Walters 2003, Walters *et al.* 1999) and will not be described again here. The EBS and GAB models (see Chapter 6) used in this investigation are of this type. The latter is modelling software developed by one of us (EAF) and is now widely used around the world. The Atlantis-SE version was originally developed to investigate alternative integrated management strategies for the SE Australian Commonwealth fisheries. This was the first whole-of-ecosystem management strategy evaluation (MSE) ever applied and found that a balance of management options were required to give the best management of the fishery. Atlantis-SE has also been used to identify robust indicators of the effects of fishing (Fulton *et al.,* 2004), and to investigate maximum sustainable yield in a multispecies context (Worm *et al.,* 2009).

As part of a global project by the Marine Stewardship Council (MSC) to investigate and evaluate the ecosystem effects of various harvest strategies on the world's lower trophic level (LTL) fish stocks, both the EBS EwE model and the Atlantis-SE model were used to investigate those effects on the relevant stocks in this region (Smith *et al.,* in press). This now provides us the opportunity to compare these two models with respect to the same questions and compare the predictions from each model and the ways in which each predicts solutions. Neither of these models was "perfect" for the investigations therefore some modifications were necessary in order to obtain meaningful results. Moreover, further modifications might be necessary in future.

Following are brief descriptions of the models that were used in the investigation, the methods and the results for a couple of relevant species in our region. The full account of the project is not available publicly at this time however we thank the MSC for permitting us to use some of our results in this report. The results presented here are from an unpublished report on the South Eastern Australian Case Study by Johnson, Bulman, Fulton and Smith.

7.2 Description of EwE and Atlantis models

The models used in these investigations are the EBS model, described in Section 6.1.1, which we will refer to as Ecosim-EBS, and the Atlantis South East model (Atlantis –SE) (Fulton *et al.,* 2007, Fulton *et al.,* in review). The Atlantis-SE model covers 3.7 million km^2 of the waters within Australia's south eastern EEZ, from (117°48'E, 46°51'S) to (160°30'E, 24°21'S) (Figure 28). In comparison, the Ecosim-EBS model constitutes a small part of the Atlantis-SE model domain, of the shelf and upper slope areas in eastern Bass Strait (see insert in Figure 28).

The Atlantis-SE model domain includes tropical, subtropical, cool temperate and subantarctic environments and from shallow thorough to abyssal depths. There is strong seasonality in the pattern of currents in this region, from both the Zeehan and East Australian currents affecting sea surface temperature, upwelling events, nutrient supplies and primary productivity. The main fishery of the region is the Southern and Eastern Scalefish and Shark Fishery (SESSF), though, there are several other fisheries in the model domain including most of the SPF. Both models comprise biological groups that are either composite functional groups or single species groups for the dominant target species in the SESSF. The Ecosim-EBS model has 55 groups and Atlantis-

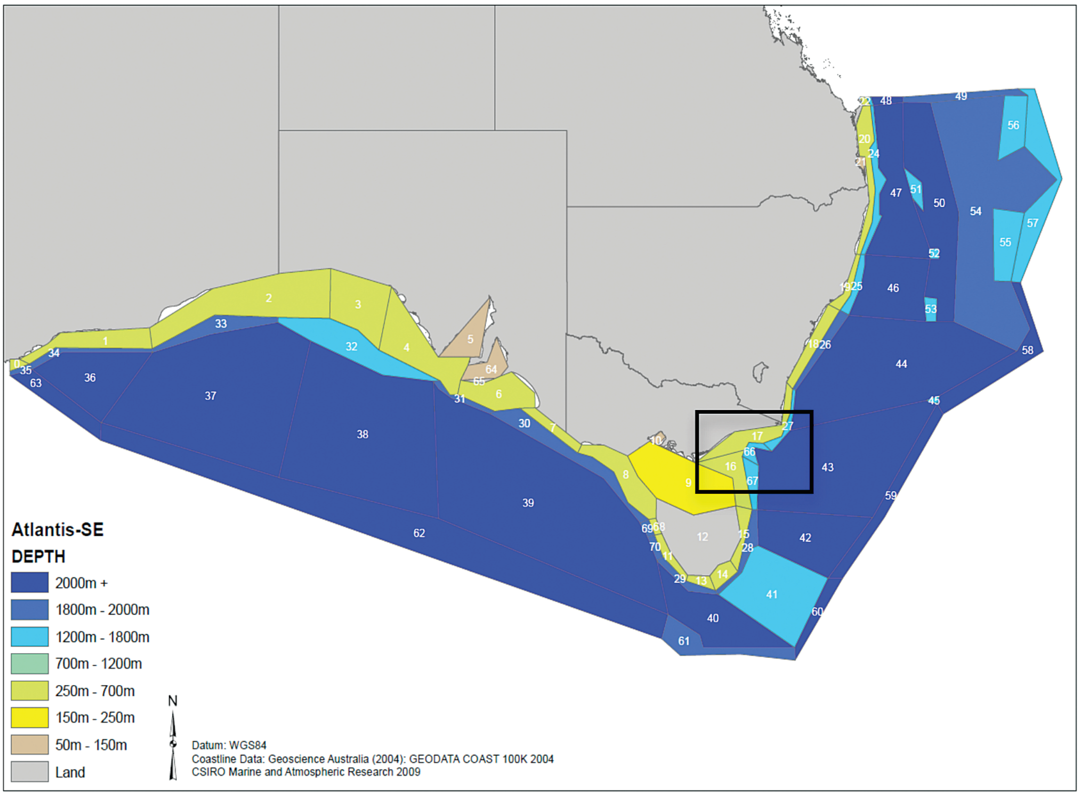


Figure 28. Atlantis-SE model domain. The box in black marks the spatial domain of the Ecosim-EBS model.

SE has 56. In addition to these living biological groups, Atlantis-SE also has pools of ammonia, nitrate, silica, carrion, and labile and refractory detritus represented dynamically whereas the EBS has two detritus groups. Diagrams of the potential dietary links for Atlantis-SE and the EBS model are in Appendix E. A significant difference between Ecosim-EBS and Atlantis-SE is that a potential diet connection in Atlantis may not be realised as it is dependent on (i) whether predator and prey are spatially coexistent, (ii) any habitat dependencies (and the state of the relevant habitats) and (iii) the relative sizes of the different groups (as gape limitation is used).

The geography of the Atlantis –SE model is represented by 71 polygonal boxes (Figure 28) based on physical and ecological properties and distributions captured in the demersal bioregionalisation. Within each box there are up to five depth layers, depending on the total depth of the box. In the open ocean boxes the maximum depth represented is 1800m. In contrast, the EBS model covers only the shelf and upper slope to about 700m and only has implicit depth structure through the functional groups. An Ecospace layer is available for the EBS model (Bulman *et al.,* 2006), which imposes a spatial structure on the model derived from depth and habitat; however, it has not been used in these analyses.

In Atlantis, environmental forcing is in the form of physical transport, salinity and temperature trends. Transports, both vertically and horizontally, were calculated from BlueLink data to create a range of environmental forcing wide enough to capture the main conditions occurring in the southeast Australia. The same BlueLink model outputs used to provide advection and diffusion for Atlantis SE were also used to provide time series of temperature and salinity in every cell of the model. For EBS model, environmental forcing was enabled through derivation of primary production anomalies calculated from ocean colour estimates in the model area over a short period of time. Environmental data was not applied to this model because the fitting of observational data to predicted data did not improve significantly and only increased the noise in the projection. Other forcing functions e.g. SST, SOI, can be applied in Ecosim if available.

Fishing pressure is represented in Atlantis and EBS as fishing mortality (F). In Atlantis, the fleets are resolved to sub-fleets defined by home-ports, crew and vessel sizes and are driven by social and economic drivers. The fishery mortality of fishes, cephalopods and crustaceans from commercial fisheries was incorporated into Atlantis-SE using average daily catch values from annual catch statistics from 1990-2004 by both federal and state fisheries and into this EBS model as annual catch values as described in section 6.1.1.

For the MSC investigations, the fleet structure of this EBS model was modified to allow the individual species of interest to be fished solely within their own fleet and to be manipulated apart from other species caught within the broader fishery. The EBS model was re-tuned using the same fitting procedure as that employed by Shannon *et al. (*2008) and as described in the investigations in section 6.1.1 where vulnerability values describing the 25 most sensitive predator/prey interactions were found so that optimal model fit was achieved. This re-fitted model, which will be referred to as Ecosim-EBS, was used in all the MSC simulations, using EwE6 Beta ver. 6.1.0.0504 and 6.1.0509 (for the MSE simulations May 2010).

7.3 The MSC LTL investigation

The original LTL groups of interest were jack mackerel (EBS) or mackerel (Atlantis), small pelagic fishes (*Engraulis australis* and *Sardinops sagax*), mesopelagic fishes (primarily *Lampanyctodes hectoris* and *Diaphus danae*), squid (various species not deep oceanic) and krill (*Nyctiphanes australis*). Redbait was also an LTL species however difficulty during Atlantis simulations did not allow a comparison with the Ecosim-EBS model.

The purpose of the investigation was to establish fishing mortality rates that would deplete the species of interest to levels of depletion commonly used in management protocols. The methods for these investigations are documented in the South East Australian Case Study (Johnson *et al.,* unpublished report) however a brief description is given here. For each model, a baseline non-fishing population level was established by removing fishing on the species. Various exploitation rates (F) were then applied to the species of interest in order to deplete the biomass to 75, 40, 20 and 0% (B_{75}, B_{40}, B_{20}, and B_0) of the unfished biomass (B_{100}). These Fs giving results within 1-2% of the target biomass were found by trial-and–error. All Fs for other groups were kept constant at status quo levels via the fishery effort. For the LTL species, biomasses and catches at the end of the simulations were plotted against each F and maximum sustainable (MSY) levels were estimated from the plots. Relative changes in biomass of all model groups due to the various depletion rates for each were plotted and compared. Here we will compare the results for two of the small pelagic species jack mackerel and small pelagics (anchovies and sardines) from both models. The results presented are taken from Johnson *et al.* (unpublished report) with permission of the authors.

7.3.1 Jack mackerel

The results of the jack mackerel depletions were quite similar from both models. In Ecosim-EBS, jack mackerel was severely depleted at F=0.1 and extirpated at F=0.25 (Figure 29). B_{75} occurred at F=0.01 and B_{40} at F =0.04 (Figure 29). F_{msy} was less than F =0.05 (Figure 30). In Atlantis-SE mackerel was extirpated at F= 0.31 (Figure 31). B_{75} occurred at F= 0.06 and B_{40} at F=0.09. The highest yield of mackerel occurred at around F= 0.06 (Figure 32) but was lower in yield.

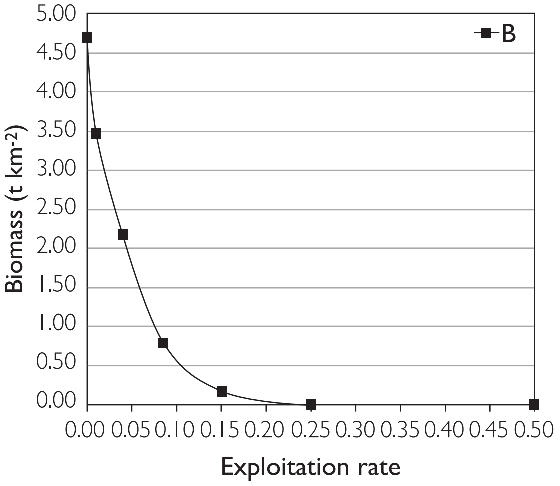


Figure 29. Biomass of jack mackerel against increasing fishing mortality. (Note that values for all trial runs are included also) From Johnson *et al.* (unpublished report).

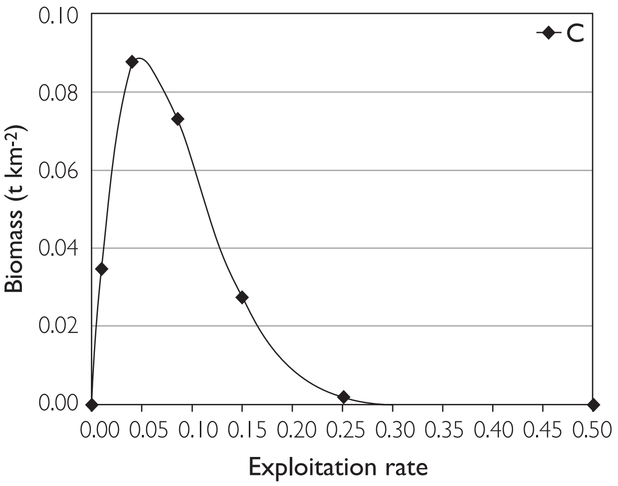


Figure 30. Yield of jack mackerel against increasing fishing mortality. From Johnson *et al.* (unpublished report

In the EBS results, there were few changes in biomass of > 20% in either direction arising from depletion of jack mackerel (Figure 33). Only tunas decreased by nearly 20% at B_{40} and more at higher exploitation rates (Figure 33). Seals declined between 10 and 20 % at B_{40} or lower. All other jack mackerel predators, such as demersal sharks, pelagic sharks and dories, declined in biomass by less than 20% irrespective of the degree to which jack mackerel was depleted. Increases were typically small (<10 %), and were largely an indirect result of the reduction in predation from seals on many fishes. Only three increased above 20%: redfish and medium pelagic piscivores increased at B_{40} or higher and medium shelf piscivores at $B_{75.}$

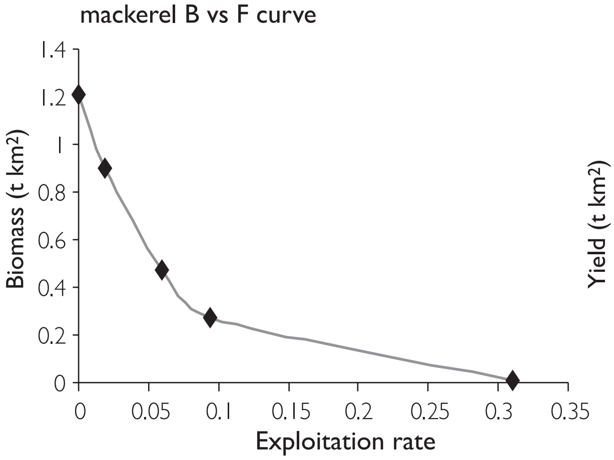


Figure 31. Decline in mackerel biomass with fishing pressure. From Johnson *et al* (unpublished report).

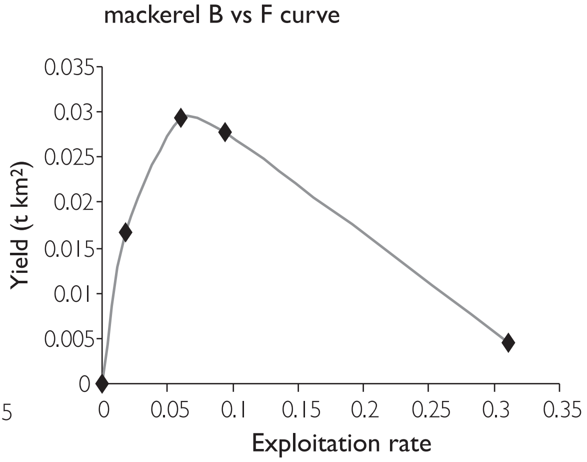


Figure 32. Yield of mackerel against increasing fishing mortality. From Johnson *et al.* (unpublished report).

In Atlantis, only two groups showed more than a 20% change in biomass as a response to the increased fishing pressure on mackerel (Figure 34). Seabirds increased nearly 25% in the B_{75} scenario, over 80% in the B_{40} scenario, but then very little at higher depletion. Baleen whales show a similar non-linear response to the depletion of mackerel. Overall, the ecosystem responses to the reduction of mackerel were similar in both models, with slight impacts on mackerel predators, no changes to prey groups, and very little change to the overall ecosystems. The main difference between the models is that Atlantis-SE showed very few changes unless the group was impacted by more than 20%, whereas Ecosim-EBS showed small increases or decreases for most

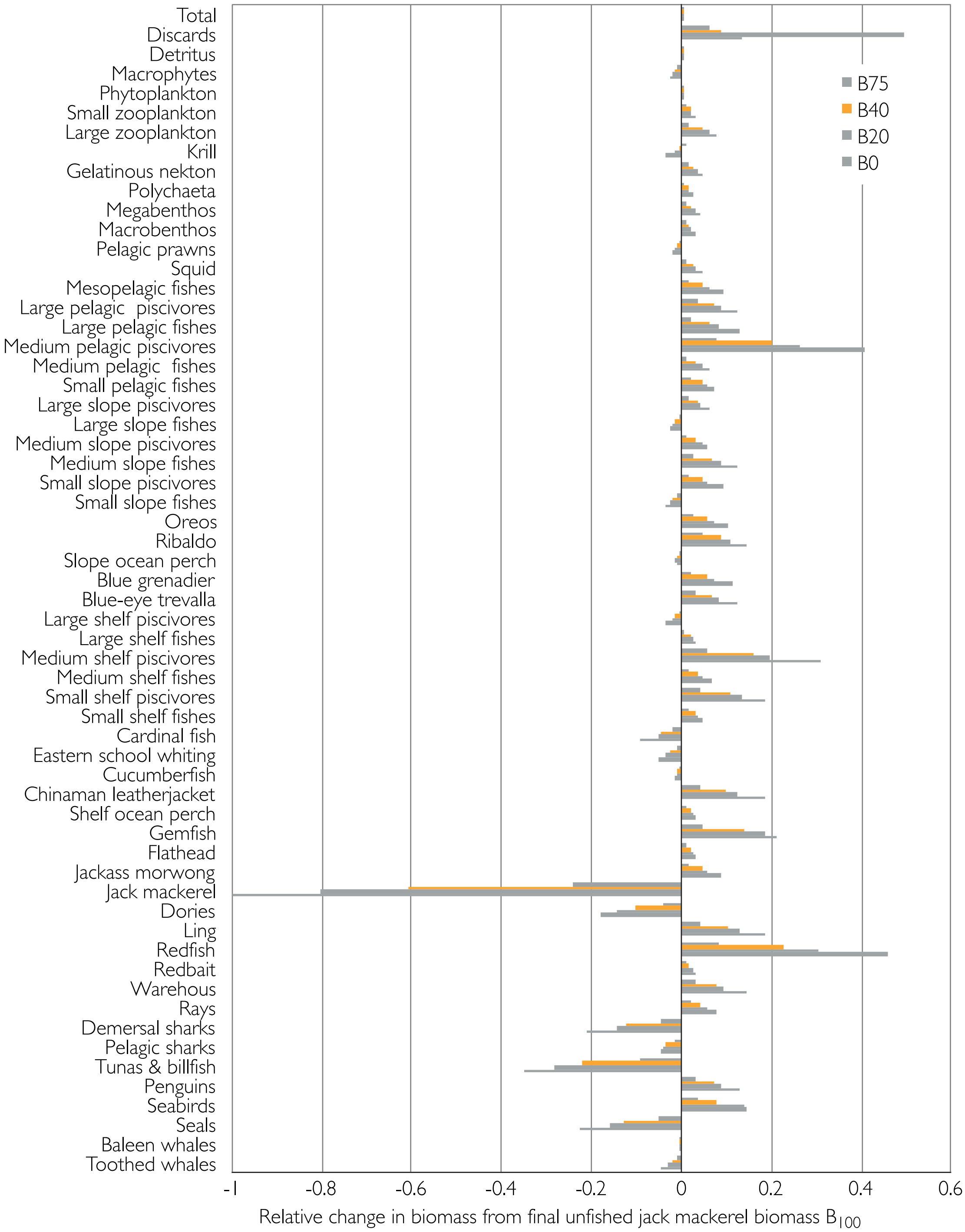


Figure 33. Relative changes in trophic groups with increasing fishing mortality on jack mackerel (Ecosim-EBS).

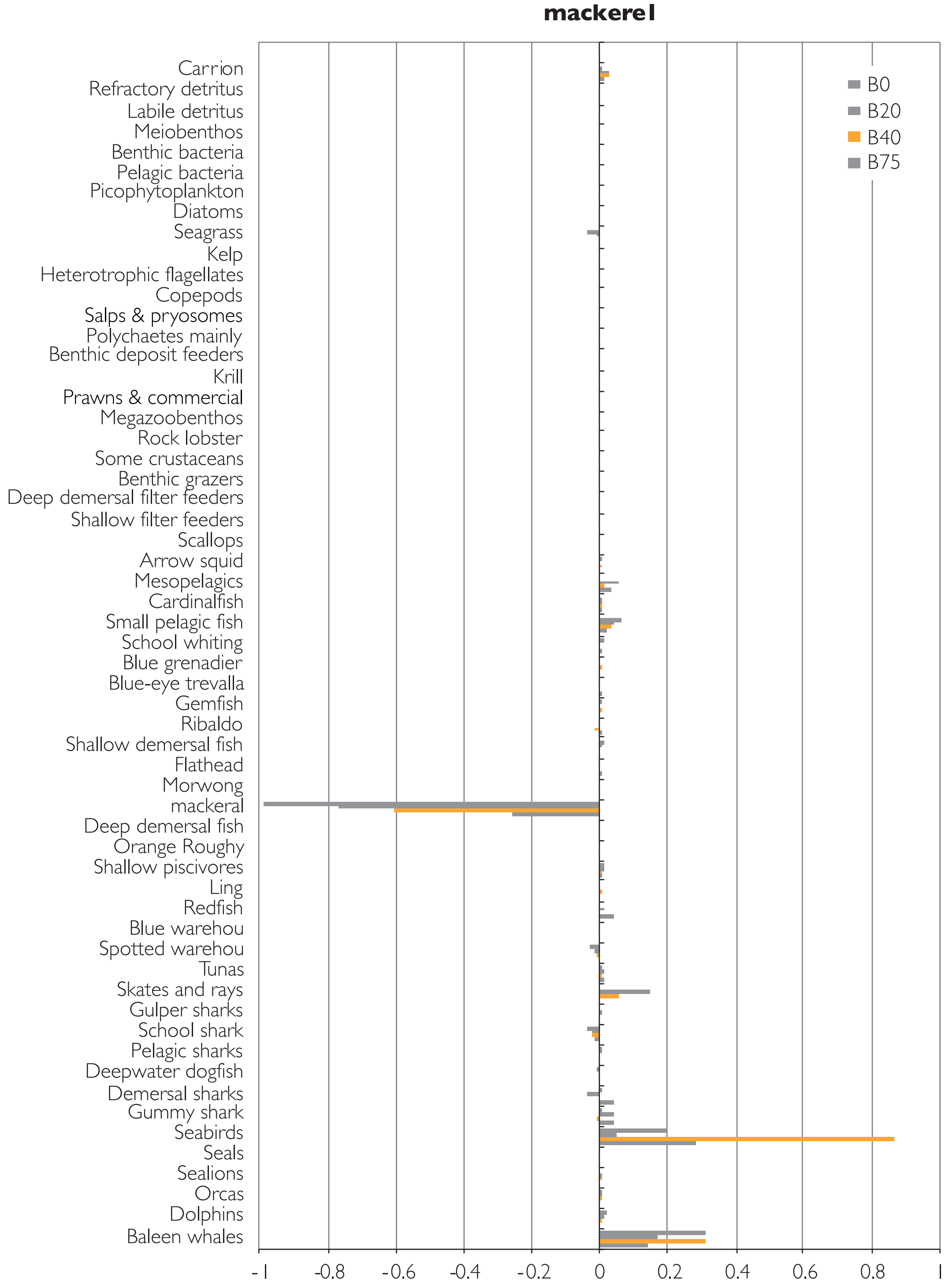


Figure 34. Ecosystem changes with increased fishing pressure on mackerel (Atlantis-SE)

groups. It was concluded that because there was comparatively little uncertainty associated with the mackerel parameterisation in either models, the results provided a degree of confidence that mackerel did not play an irreplaceable role in the function of this ecosystem. It was also noted that any modelled result should be viewed with caution.

7.3.2 Small pelagic fishes

In Ecosim–EBS, the small pelagic fishes i.e. sardines, anchovies and sprats, were quite severely depleted at an exploitation rate of 0.5 and were extirpated by 1 (Figure 35). B_{75} occurred at a rate of 0.1 and B_{40} occurred at a rate of 0.33 Maximum yield was produced at an exploitation rate of 0.25, corresponding to slightly higher than 40% of the biomass (Figure 37). In Atlantis-SE, they were depleted at an exploitation rate of 0.25 and were extirpated at 0.5 (Figure 36). B_{75} occurred at an exploitation rate of 0.05 and B_{40} occurred at around 0.15 also where the maximum yield occurred (Figure 38). The initial starting biomass/km^2 of small pelagics in Ecosim-EBS was twice that in Atlantis-SE which accounts for the higher exploitation rates necessary to deplete them and the higher yields.

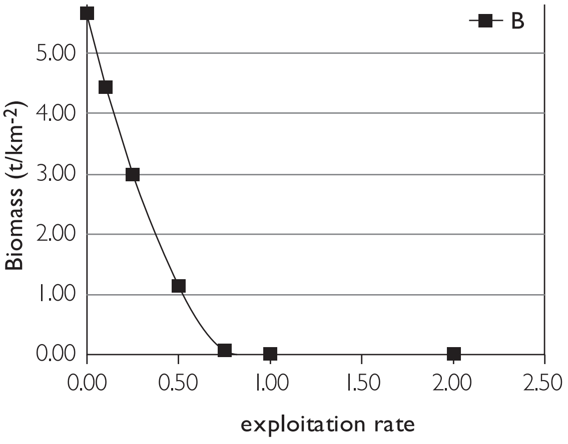


Figure 35. Ecosim-EBS biomass of small pelagic fishes with increasing fishing mortality (from Johnson *et al*., unpublished report).

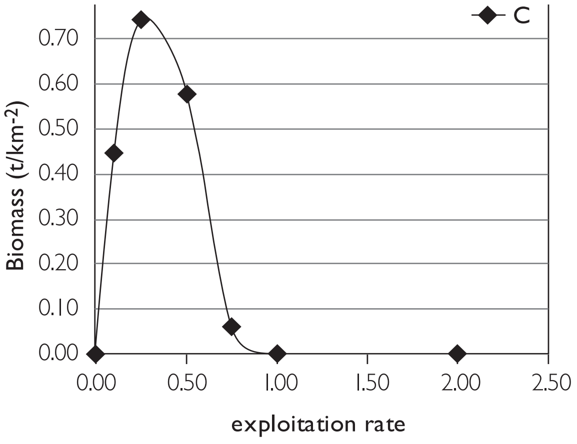


Figure 37. Ecosim-EBS yield of small pelagic fishes with increasing fishing mortality (from Johnson *et al*., unpublished report).

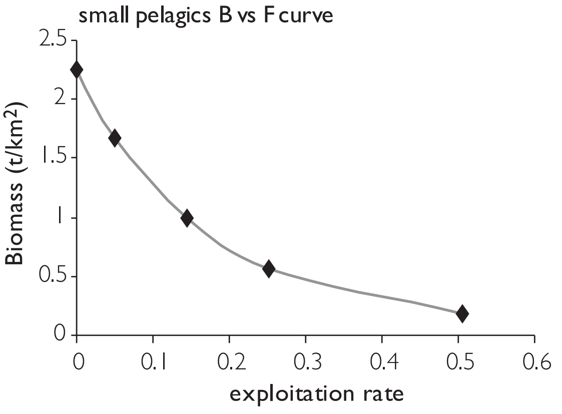


Figure 36. Atlantis-SE Biomass of small pelagic fishes with increasing fishing mortality (from Johnson *et al*., unpublished report).

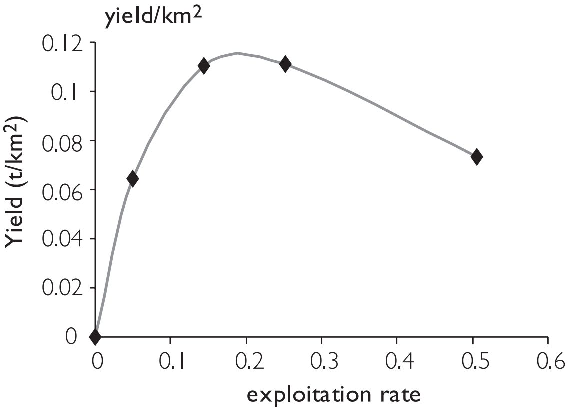


Figure 38. Atlantis-SE yield of small pelagic fishes with increased fishing mortality (from Johnson *et al*., unpublished report).

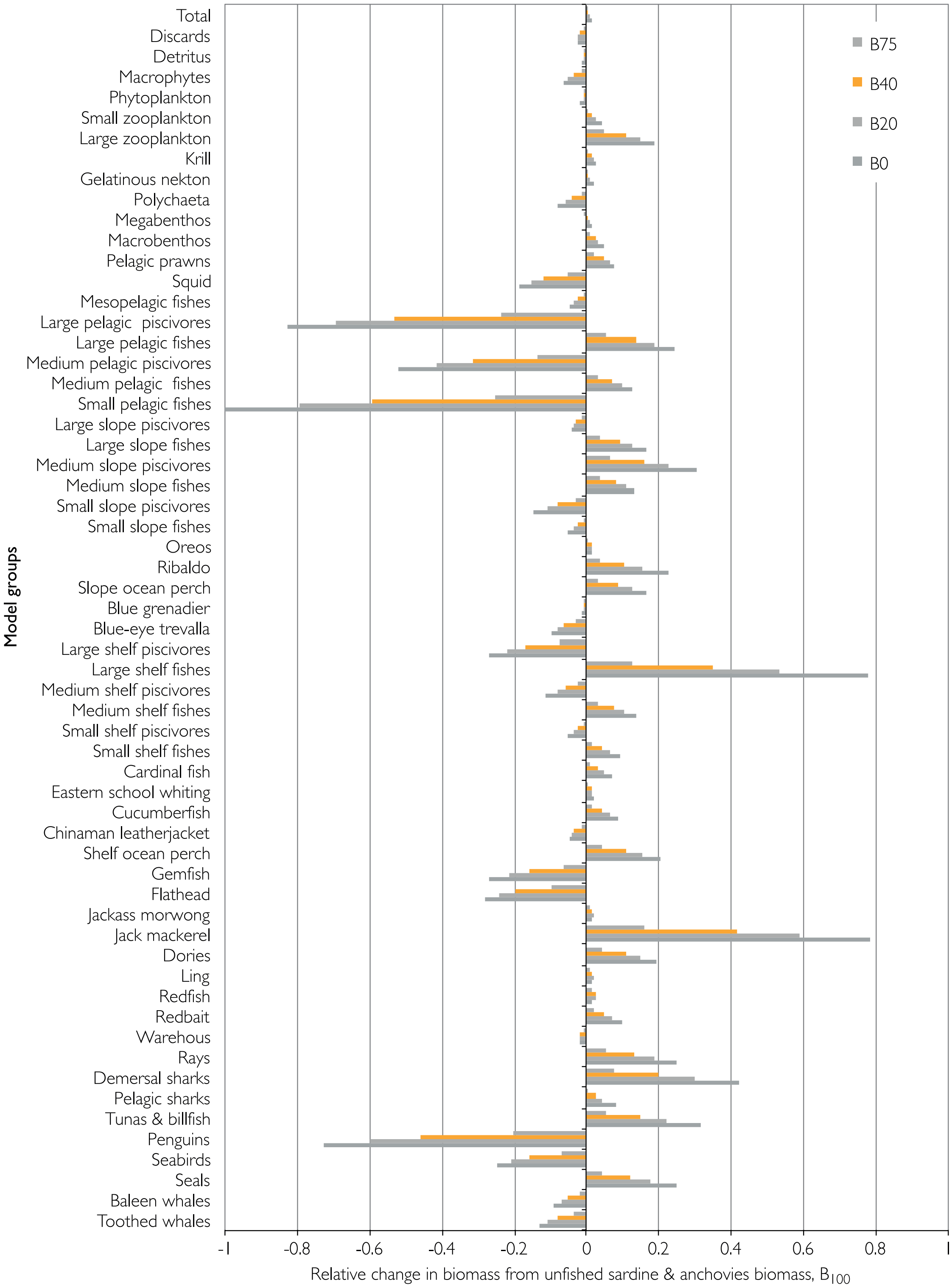


Figure 39. Relative changes in trophic groups with increasing fishing mortality on small pelagic fishes (Ecosim-EBS).

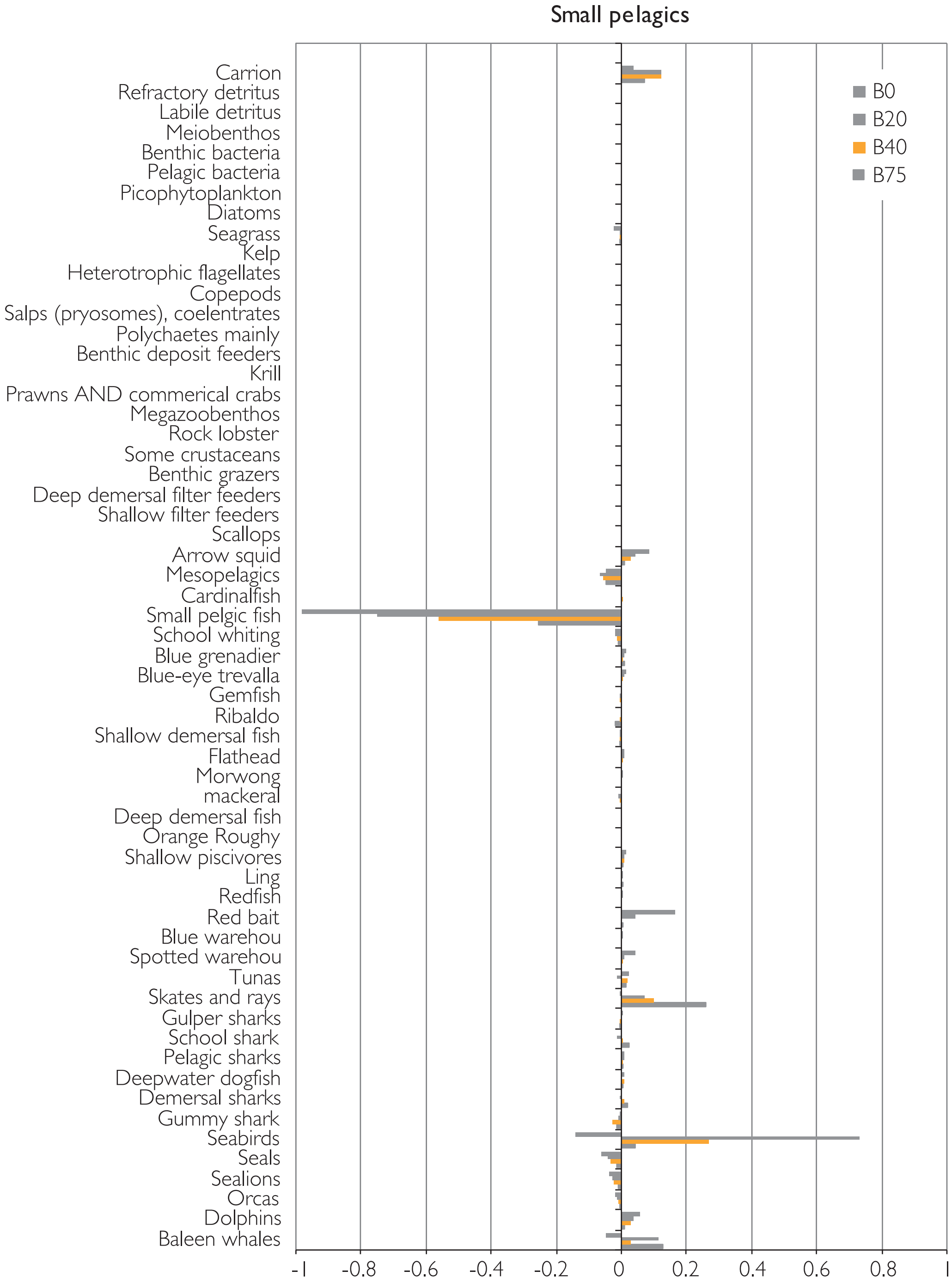


Figure 40. Relative changes in trophic groups with increasing fishing mortality on small pelagic fishes (Atlantis-SE).

The results from the Ecosim-EBS model, suggest that the only prey group of small pelagics to be affected were the large zooplankton. This group responded positively but the increases were only between 10-20% (at exploitation rates above F_{40}) (Figure 39). On the other hand, predators of sardines and anchovies (such as shelf, and particularly pelagic, medium and large piscivores, including stargazers, triglids, berycids, flatheads, barracouta, silver trevally, stripey trumpeter, hapuku, kingfish and trichiurids), declined quite significantly (> 20%) with increasing exploitation on the small pelagics. Other predators such as tuna and demersal sharks increased as a result of less predation mortality, from the declining toothed whale populations in the case of tuna and declining large piscivores in the case of demersal sharks. The large penguin declines of between 18-73% could also be attributable to declining small pelagics but also the increasing predation pressure from pelagic sharks might also be a factor.

The dramatic response of jack mackerel was an indirect consequence of the loss of small pelagics. Biomasses increased significantly even from the lowest exploitation rates by up to almost 80% at the highest exploitation rate. Less significant increases of biomass also occurred for medium and large fishes (planktivores), both demersal (gurnards, morwongs, leatherjackets, snappers, gropers, conger eels) and pelagic (blue mackerel, yellowtail scad, salmons and roughs, Peruvian mackerel also occurred. There were two probable reasons: more planktonic prey was available due to a release from predation by the small pelagic fishes, and their own predation mortality was reduced due to declining larger predator biomasses.

In contrast, the Atlantis-SE results suggest very little response to small pelagics exploitation (Figure 40). No prey groups were affected, and the only groups that showed more than a 20% change in biomass were the seabirds and rays. Seabirds, the only predator to respond, actually increased due to a small increase in biomass of some of their other prey (fishes) groups, which has a disproportionate effect on fledgling success. Fish groups that increased slightly were either (i) groups whose youngest age classes were prey of small pelagic fishes, or (ii) groups that were competitors or prey of groups whose biomass decreased. The increase in the biomass of rays, the only other major response, was an indirect effect from an increase in the size of the smallest age classes, rather than an increase in abundance. The lack of response is due in part to the small relative contribution that small pelagic fishes make to the overall biomass of the system, but also to the flexible diets used in Atlantis where diet restructuring is possible.

7.3.3 Redbait

Atlantis-SE suggested that there would be no significant ecosystem effects of fishing down redbait. However, due to model recalibration from the original state, redbait did not produce a realistic trajectory even at the status quo. Consequently, no comparison was made with the Ecosim-EBS results.

The Ecosim-EBS results for redbait suggest severe depletion at exploitation rates >5 and extirpation at 50 (Figure 41). B_{75} occurred at an exploitation rate of 0.17, B_{40} occurred at an exploitation rate of 0.5 (Figure 41), and maximum yield occurred at a rate of 0.8 (Figure 42).

Changes in the levels of redbait prey were mostly very slight increases resulting from a release from predation pressure (Figure 43), except where the extirpation of redbait resulted in an increase in gelatinous nekton of over 70% likely due to release from predation pressure by redbait. The largest decline in biomass of redbait predators was observed for tunas and billfish, with declines of more than 20% under most scenarios. Seals were the next most impacted group, but only with declines of between 10% and 20%.

As redbait were increasingly fished, some groups increased slightly due to the reduction in predation pressure from seals, e.g. shelf medium predators (triglids, stargazers, trumpeters, flatheads). Jack mackerel also benefited indirectly from increased redbait fishing as a result of reduction in predation pressure from seals. The increase in gelatinous nekton with the extirpation of redbait in turn allowed groups that were consumers of gelatinous nekton, i.e. slope ocean perch, blue-eye trevalla, Chinaman leatherjacket, shelf ocean perch and warehous, to also increase by between 40-95%.

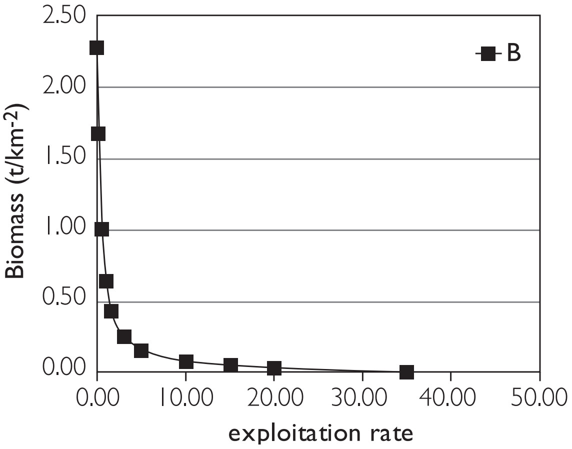


Figure 41. Ecosim-EBS biomass of redbait with increasing fishing mortality.

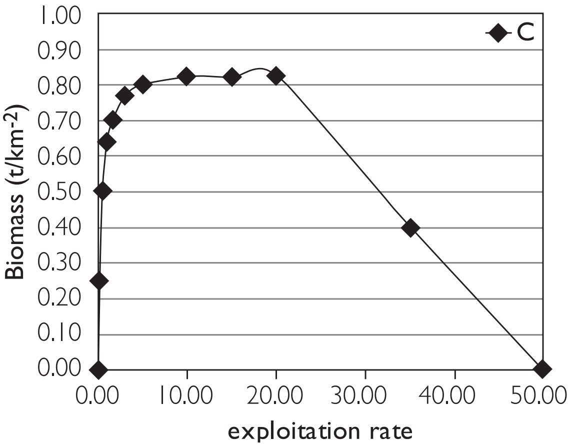


Figure 42. Ecosim-EBS yield of redbait with increasing fishing mortality.

It should be noted that the redbait fishery represented in this model is not representative of the much larger fishery off eastern Tasmania. The redbait biomass in this model area is relatively small in comparison to that estimated for eastern Tasmania and so the fishing mortality changes achievable in this model may produce less dramatic trophic impacts than might be expected in the “real” fishery.

7.4 MSE in Ecosim-EBS

A new capability in EwE, not yet publicly available, is that of a management strategy evaluation (MSE) module. One of us (CMB) and the EwE development team developed and tested it on the Ecosim-EBS model within the MSC LTL project (see previous section). The MSE was used to investigate the consequences of typical “broken-stick” harvest strategies in several of the studied ecosystems and here we present some unpublished results from the SE Australian case study with permission from the authors and the MSC.

The purpose of this part of the MSC LTL study was to investigate the effectiveness of “broken–stick” harvest strategy rules (HSR) in concert with environmental fluctuation severe enough to cause dramatic population shifts with, consequently, the high likelihood that the target population would decrease beyond the limit imposed by an HSR. A full description of the methodology is in the South Eastern Australian Case Study report (Johnson *et al.,* unpublished report) but a brief description follows.

In order to create this hypothetical situation, we derived a hypothetical oscillating forcing function that would operate on the vulnerability of the predator-prey interactions to force the target population to fluctuate about ± 50% of its biomass, in this case, the small pelagic-planktonic prey interactions. Because this changed the outcomes of the initial depletion experiments described in the previous sections, we derived new exploitation rates that would deplete the target populations to the specified levels as before. This resulted in decreasing the exploitation rates for the small pelagics (Figure 44), to levels similar to those used

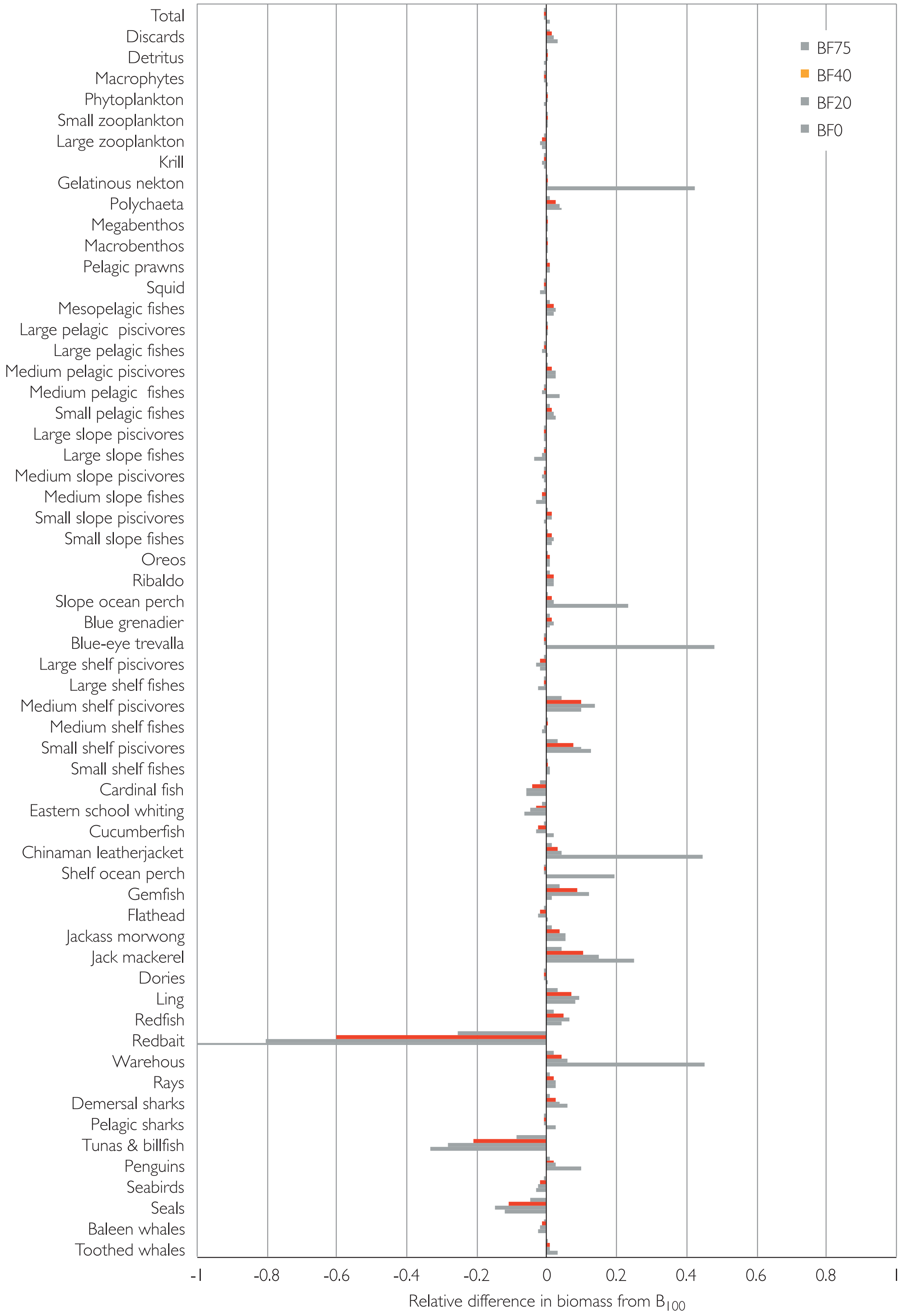


Figure 43. Relative changes in trophic groups with increasing fishing mortality on redbait (Ecosim-EBS).

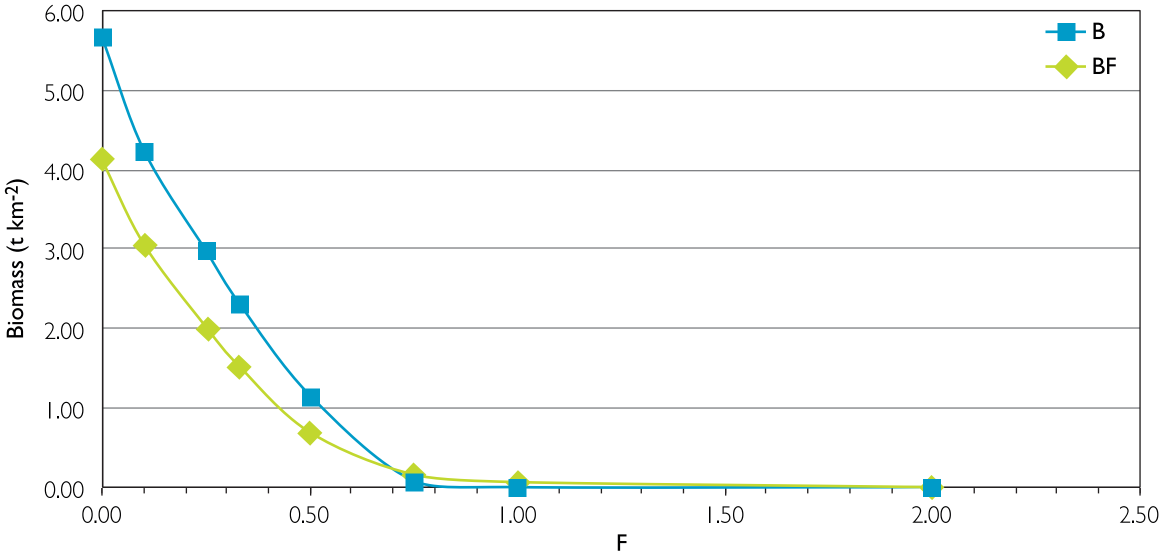


Figure 44. Biomass depletion with (blue) and without (green) environmental forcing.

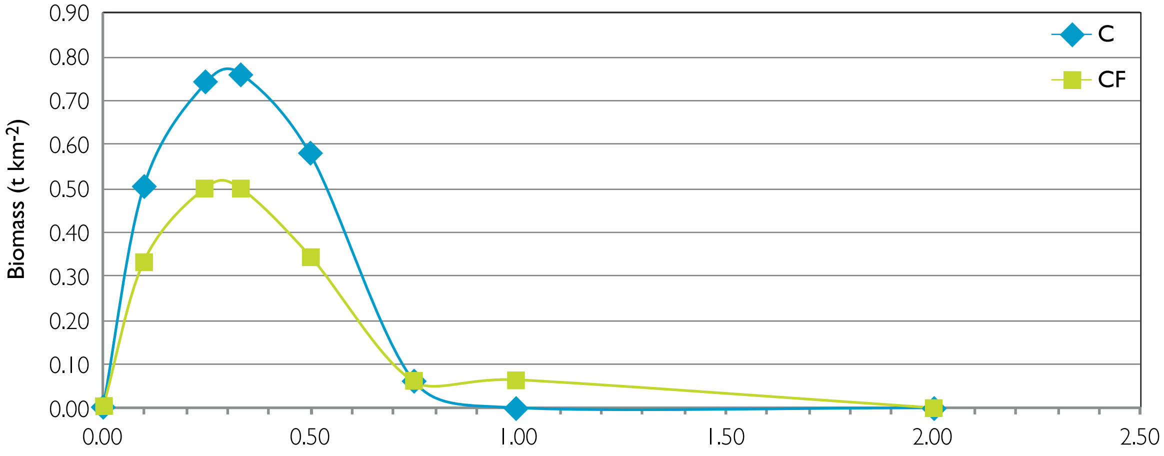


Figure 45.Catches with and without environmental forcing. Maximum catch rate is a third lower when biomass of focal group fluctuates but occurs at similar F rate.

in Atlantis-SE which had already accounted for seasonal, inter-annual and inter-decadal environmental variability. Catches were also reduced significantly as a result (Figure 45).

While outcomes of these simulations aren't relevant to this investigation as such, a brief summary of the results will be given here for completeness. The overall effect of environmental forcing over all depletion rates was negligible, i.e. the majority of all species and groups changed similarly to the unforced scenarios (see Figure 33). For the few groups for which there had been significant increases or decreases in the unforced scenarios these changes were lessened. For example, jack mackerel increases halved and jackass morwong, redfish, ling and oreos, gemfish, flathead and blue-eye did slightly better with the environmental forcing applied but these changes were not significant. Pelagic piscivores (medium and large) declined about 10% less.

The revised F rates and the forcing function were used in the MSE application. Variation was set to minimal levels to reduce noise in the results. The target fishing mortalities for the small pelagics were reset for each HSR simulation according to the appropriate biomass limit, biomass base and the F_{max}. For example, the HSR 20:40:40 parameters were set so that the

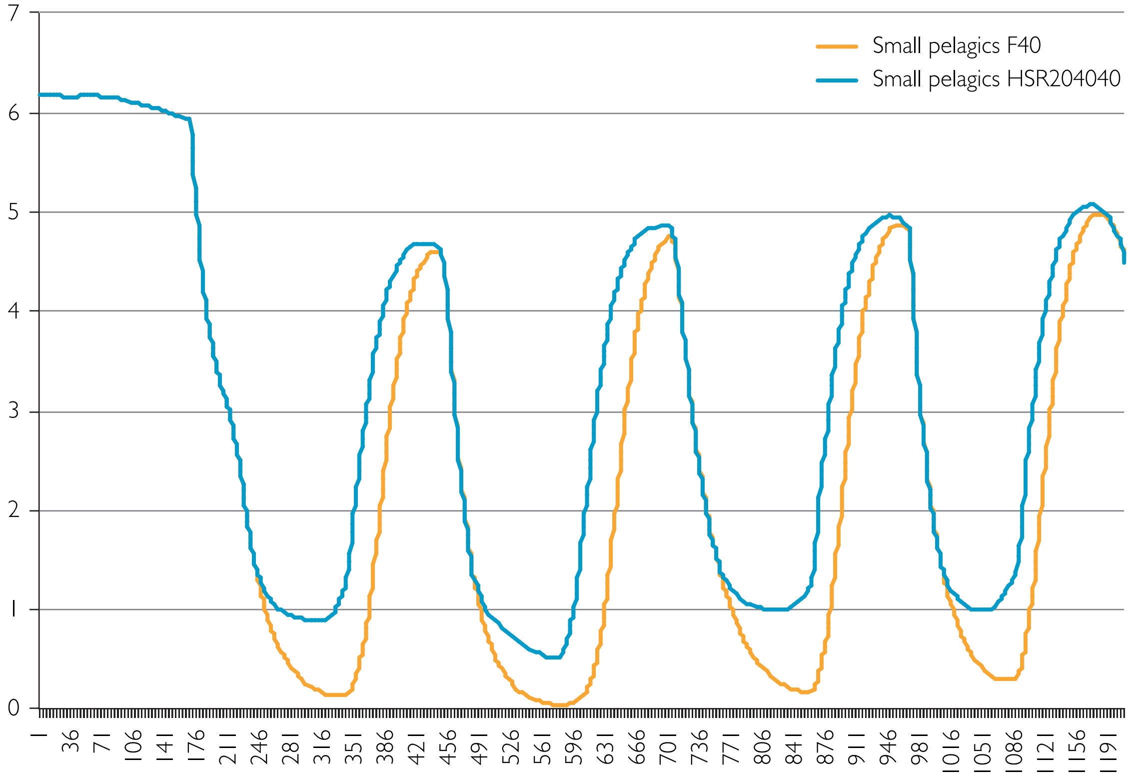


Figure 46. Biomasses of small pelagic fishes for MSE simulations of F40 and HSR20:40:40 (from Johnson et al.unpublished report).

biomass limit was 20% of the target unfished biomass, the biomass base was 40% of the target unfished biomass and the F_{max} was the fishing mortality rate that would deplete the biomass to B_{40}. Other scenarios tested were HSR 40:75:75, F_{40} and F_{75} (where no rules applied). The monthly outputs for biomasses, catches by group and by fleet, efforts by fleet and quotas by fleet were plotted and for biomasses, averaged over the whole period of fluctuation.

The biomass trajectory of the small pelagics for the HSR20:40:40 simulation was similar to that of the F_{40} but with shallower dips (Figure 46). Catches followed similar trajectories (Figure 47) but were truncated when the effort was “turned off” (Figure 48).

Similar patterns of biomass trajectory were also observed in the comparison of the HSR40:75:75 scenario to the F_{75} scenario (see Johnson *et al.* unpublished report) but the amplitude of the oscillations were generally slightly shallower and the catch and effort rates were much less than those of the previous HSR20:40:40 scenario.Overall, there were few differences in the outcomes of other groups of the ecosystem between either the HSR20:40:40 scenario compared to the F_{40} scenario (Figure 50), or the HSR40:75:75 scenario to the F_{75} scenario (see Johnson *et al.,* unpublished report) for the small pelagic fishes.

The implications of these findings are yet to be fully explored, particularly in relation to the whole of ecosystem effects. For this particular species, however, there appears to be little difference with or without the harvest strategy rule however the population does slightly better with it. The LTL investigations were preliminary, focussed only on a single species at a time, with minimal assessment uncertainty and operating in conjunction with hypothetical environmental variability. However, that configuration was applied across all scenarios and focus species, and allowed us to compare outcomes without the complication of noise due to sampling error.

The MSE module does however have the capability of parameterisation using stock assessment data and uncertainties, applying HSR on all target species, of altering recruitment parameters

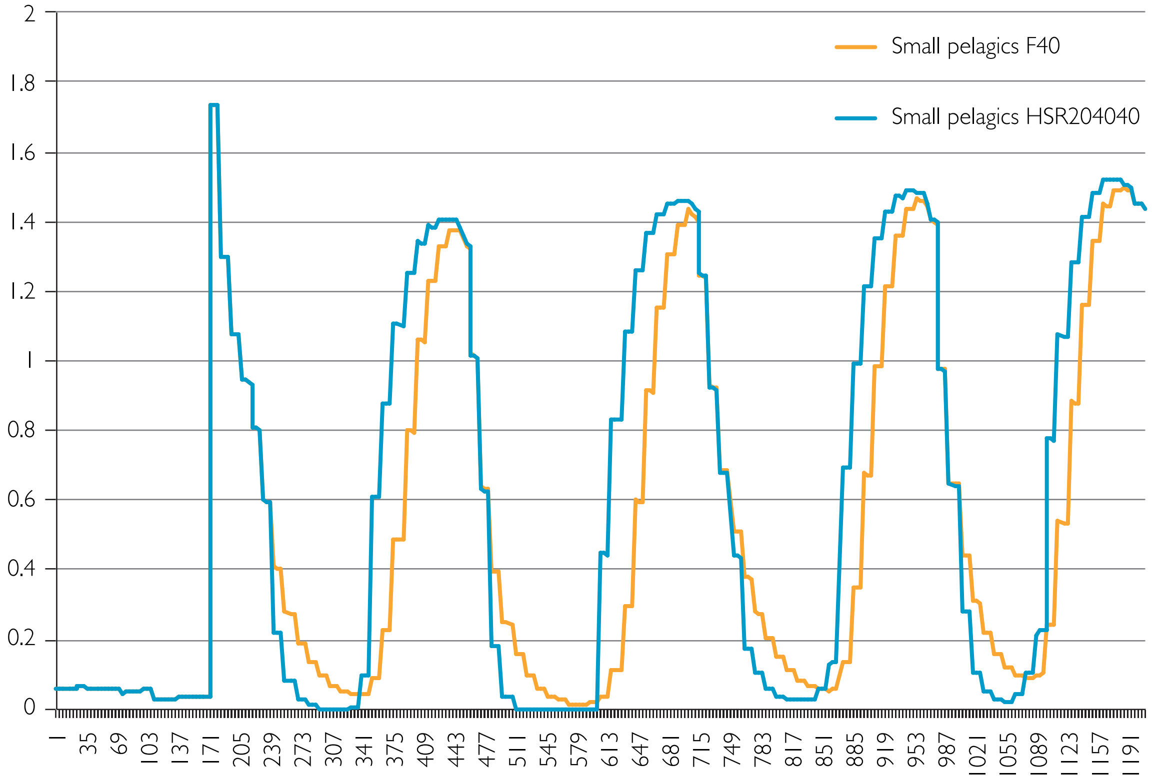


Figure 47. Catches of small pelagic fishes for MSE simulations of F40 and HSR20:40:40 (from Johnson *et al.*, unpublished report).

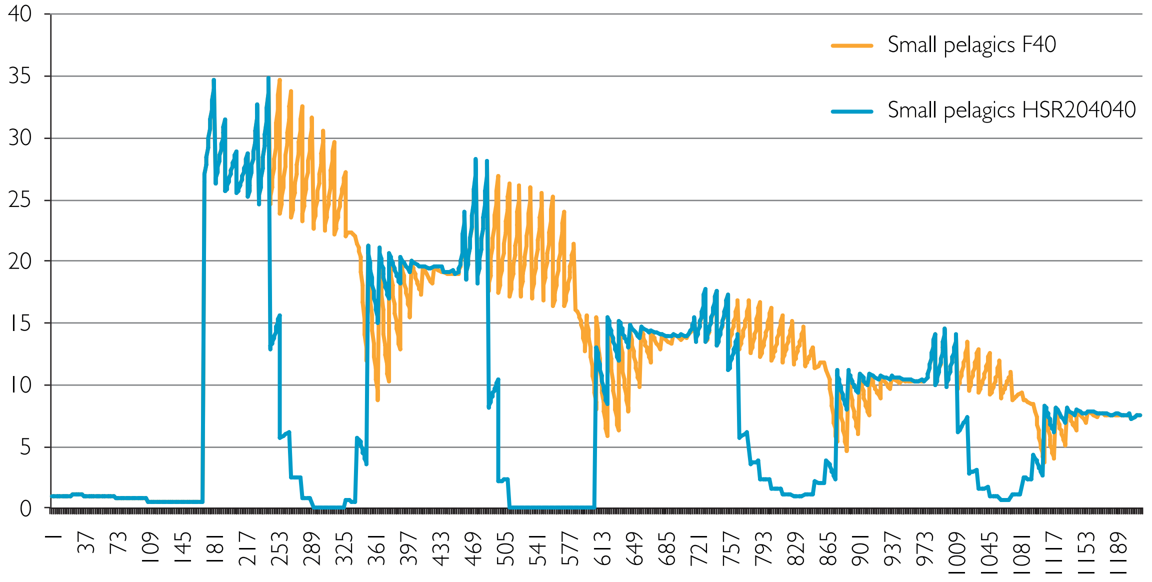


Figure 48. Fleet effort of small pelagic fishes for MSE simulations of F40 and HSR20:40:40 (from Johnson *et al.*, unpublished report).

in line with current knowledge and so on. With the results of the recent Management Strategy evaluation of the harvest strategy for the Small Pelagic Fishery (Giannini *et al.,* 2010) we should be able to run simulations that could provide some useful insights on the effects on the ecosystem. The parameters used or derived in that report could be incorporated into specific parameterisation of the small pelagic species in the EBS the model, particularly in the MSE module where stock assessment-specific data is used, thus creating a common ground and scenario.

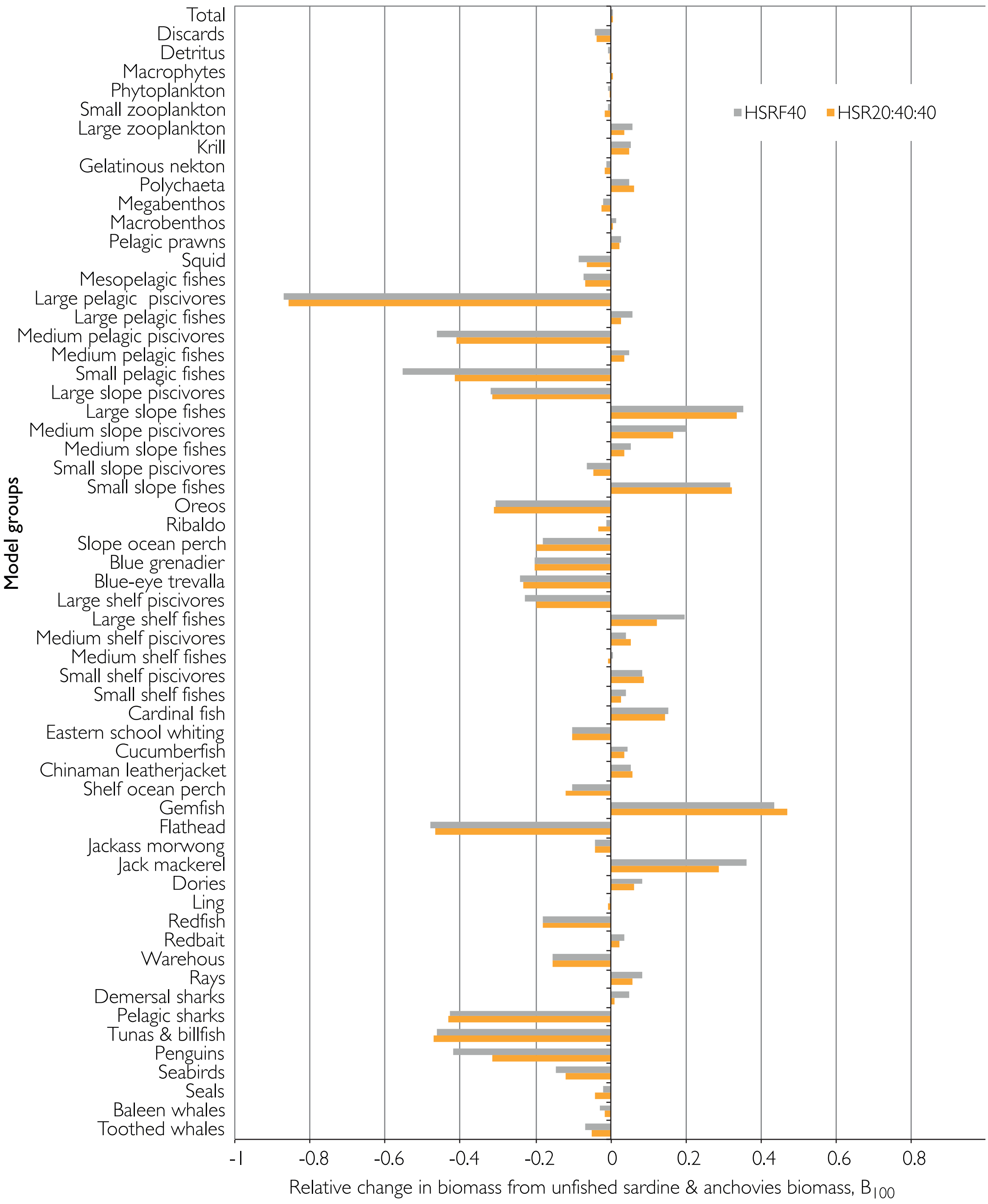


Figure 49. Comparison of relative changes between the HSR20:40:40 and F40 in the MSE simulations over 100 years. Projection period is from year 15 –year 100 with a forcing function oscillating through an approximate 20 year cycle.

As a preliminary attempt to demonstrate this functionality, we have incorporated some parameters from the MSE analyses and run an HSR20:40:40 scenario. The starting biomass was that of the unfished scenario used in the MSC investigation and we used 20%, 40% and the F_{40} obtained for the scenario without the environmental forcing function. We included a coefficient of variation of 0.3 in the assessment unlike the MSC scenarios. One difficulty of standardisation was the difference in biomass measures used between the two methods. The MSE reports in tonnes spawning biomass and the Ecosim–EBS uses t/km^2. For future comparisons we would need to ensure that parameters such as biomasses were at least consistent.

The results for 10 simulations of the HSR 20:40:40 show a steady decline to a mean of 2.1 below the biomass base point, with some simulations very close to crashing (Figure 50). Overall, the biomass was maintained above the limit point 88% of the time and above the biomass base 42% of the time.

7.5 Discussion

The ecosystem responses to the reduction of jack mackerel were similar in both models, with slight impacts on mackerel predators, no changes to prey groups, and very little change to the overall ecosystems. The main difference between the models is that Atlantis-SE showed very few changes unless the group was impacted by more than 20%, whereas Ecosim-EBS showed small increases or decreases for most groups. It was concluded that because there was comparatively little uncertainty associated with the mackerel parameterisation in either models, the results provided a degree of confidence that mackerel did not play an irreplaceable role in the function of this ecosystem (Johnson *et al.,* unpublished report).

Neither Ecosim-EBS nor Atlantis-SE produced large system changes in response to the loss of small pelagics. There were a few more Ecosim-EBS impacts and of slightly larger magnitude. They extended to prey, predators and competitors of the small pelagics but in Atlantis-SE no impacts on prey were noted. It was concluded that this was a result of only a small release that is quickly consumed by the competitors of the small pelagic fishes. The responses from the higher trophic levels were also more variable and less substantial in Atlantis-SE than Ecosim-EBS. It was concluded that these differences resulted from more flexibility in the predator diets in Atlantis-SE in than Ecosim-EBS (Johnson *et al.,*

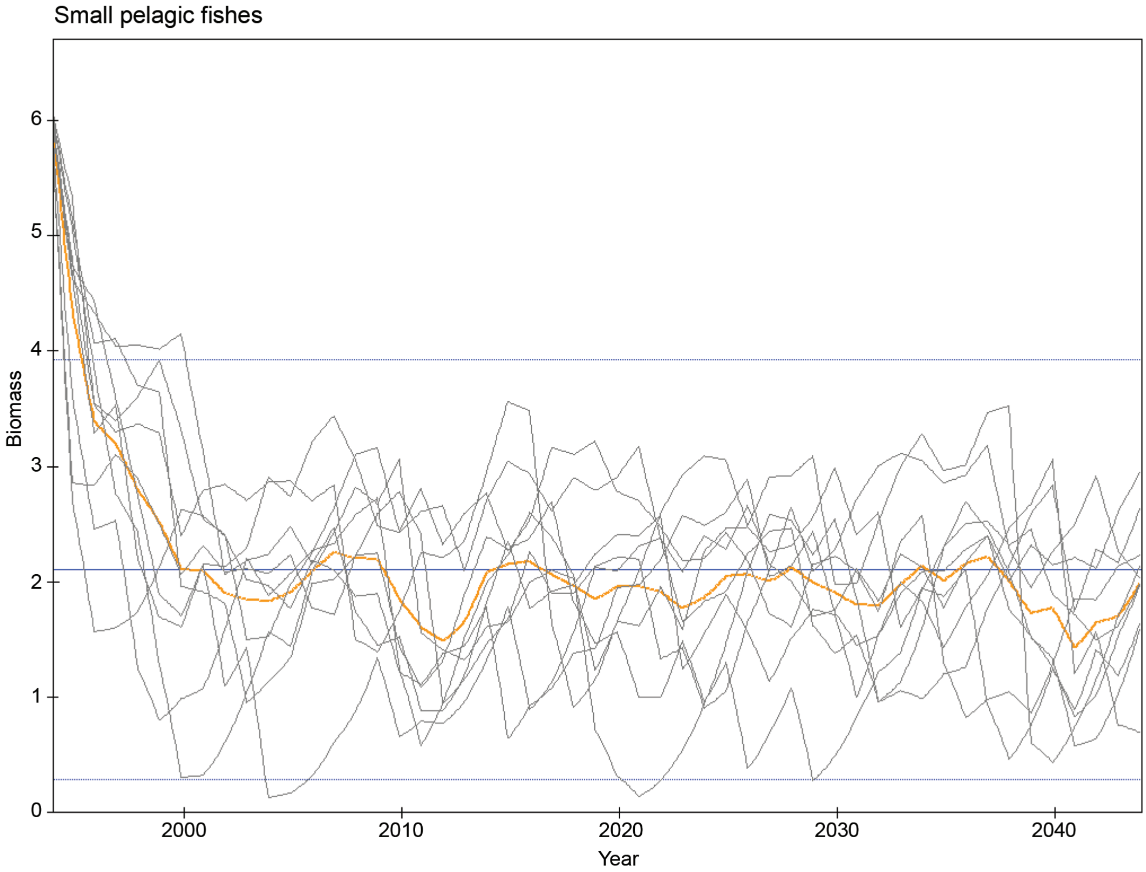


Figure 50. Simulation of MSE HSR 20:40:40 for small pelagics (mean n=10 simulation orange line).

unpublished report). Predators were not as highly dependent upon small pelagic fishes enabling alternative prey items (e.g. other forms of small fish) to replace them in their diets.

The Ecosim-EBS MSE response to the harvest strategy imposed also showed a moderate response, even when the very large environmental variability was imposed on the system initially. But the response of the model is dependent on its calibration to a reliable—and preferably long time-series. While the use of the new Ecosim-MSE is relatively quick and easy to use, Atlantis was in fact designed to investigate MSE. A recent investigation into the effect of increased fishing pressure on forage fish used four versions of Atlantis in southeastern Australia including Atlantis-SE used in the MSC study (Johnson *et al*., 2009). Each model was parameterised somewhat differently due to the original and different purposes. Results were different between model versions but, despite those differences, the trends were, not surprisingly, similar to the MSC investigation results. The loss of small pelagics caused losses of higher predators only and these losses were relatively small. Similarly, the loss of jack mackerel (and blue mackerel) had little impact on predators.

The impact of loss of redbait was only tested in Ecosim-EBS although initial simulations in Atlantis had suggested little impact. Indeed, the impacts in Ecosim-EBS were the least of all the species investigated. Compared to those caused by jack mackerel and anchovy, they were even fewer and mostly of lesser magnitude. Only two higher predators were impacted, tunas and seals, similarly to jack mackerel. The response of “jelly-feeders” to the massive increase in gelatinous nekton is likely to be a misleading result and requires further investigation.

In general, Ecosim tends to exhibit a lot of more and slightly larger responses than Atlantis particularly in the lower trophic levels. There are several causes for the differences seen between the two models due to the way in which the models are structured and linked. For example, in Ecosim-EBS model, the populations are represented as adult biomass pools only (although the option exists for multi-stanza life-stages) whereas in Atlantis all vertebrate groups have age-structure. This allows for ontogenetic dietary and habitat shifts in Atlantis. Another cause of differences between the models may be diet switching in Atlantis-SE. These factors combined allow more variability in trophic connections than possible in the present version of Ecosim-EBS model.

Habitat is also spatially explicit in Atlantis but not in this version of the EBS model. Although the EBS does have a spatial layer, its implementation still requires validation and it was not compatible with some of the dynamic functions required in these investigations. While these may have some bearing, most of the differences between the groups are likely to be due to differences in trophic links and how they are represented in the two models. The flexibility offered by Atlantis allows the compensation for the loss of a component and thus dampened effects whereas Ecosim does not.

The lack of response of groups indicates a strong bottom-up control and this is very evident in the Atlantis-SE responses. The Ecosim-EBS responses are more apparent indicating the likelihood of more top-down control. As seen in the previous section, the vulnerabilities derived from calibrating or tuning Ecosim models to time series of the major species and functional groups can be a determining factor in the responses of the model. While for the three species examined in this report the results are not particularly at odds, Johnson *et al.* (unpublished report) described the very divergent responses of the two models to depletion of krill and mesopelagic fishes. The top-down control on krill in Ecosim-EBS caused much greater and opposite fluctuations throughout the ecosystem than seen in Atlantis-SE (not top-down). The lack of baseline information on these two groups was highlighted as a major contributing factor to the difficulty in determining the most appropriate construction and is therefore a source of major uncertainty not only for these two functional groups but applicable to most species in the ecosystem to some degree.

8 Further development

To generate realistic climate change scenarios, ecosystem models such as EwE and Atlantis require detailed information on environmental trends at relevant temporal and spatial scales. These trends include:

- changes in water properties such as temperature, salinity, pH and levels of dissolved oxygen, which may be associated with movements in water masses or changes in water mass properties;
- changes in ocean transport patterns and associated spatial connectivity patterns;
- changes in vertical mixing due to changes in stratification (suppresses mixing) or upwelling and downwelling (coastal and eddy induced); and
- changes in nutrient fluxes and/or primary productivity.

While considerable attention is now being focused on downscaling results from climate models many challenges remain and reliable estimates at appropriate temporal and spatial scales are not likely to be available within the next few years. As these capabilities gradually improve, efforts need to be focused on using the improved datasets to understand key environmental trends emerging over the past two decades and their associated marine biological responses.

Major uncertainties in environmental trends are compounded by uncertainties in the biological responses to these changes. Obvious examples include:

- physiological responses to increased ocean temperatures, particularly during the larval life stages of pelagic fishes;
- physiological responses to decreasing ocean pH, particularly among calcifying phytoplankton (e.g. coccolithophores) and zooplankton (e.g. crustaceans such as krill) that are critical to pelagic foodwebs;
- changes in chemically moderated behavioural responses;
- changes in spawning behaviour and spawning success as water properties and ocean transport patterns change;
- changes in predator and prey distributions and the formation of new or novel community structures; and
- dietary shifts.

While the capability to represent these physiological and chemically moderated responses is starting to be incorporated into ecosystem models, there is very limited data available to support parameterisation at the species or functional group level. Further effort needs to be devoted to laboratory studies aimed at direct measurement of physiological responses of key species, but these studies need to be more than simple shock experiments, they need to start to try to address the adaptive capacity of species under slow change of environmental properties. Further studies also need to be directed at understanding recent variability in spawning success and recruitment of small pelagic fish as a guide to future trends. Further effort is also needed in collecting basic distributional, biological and dietary information across all functional groups to detect shifts and trends, and to develop a suitable model representing southwestern Australia.

It is clear that modelling long-term changes in pelagic ecosystems will continue to include high levels of uncertainty into the future. Here we have demonstrated that even the direction of change can be uncertain in many instances. In the short term, modelling approaches need to clearly reflect that uncertainty in their predictions. However, if we are to better constrain and validate these models, then there is also an urgent need to establish long-term observational programs of Australia's southern pelagic ecosystems that complement improvements in environmental information flow in programs such as IMOS.

9 Benefits and adoption

The main beneficiaries of this study will be the SPFRAG, industry and AFMA. However, RAGs of other fisheries in the south-east region will also profit from the understanding of the underlying trophic control processes in the various regional ecosystems. Researchers and model developers will also benefit from the adoption of this knowledge, which will enable further improvement of relevant ecosystem models. In turn, this will improve handling of model uncertainty and interpretation of predictions, particularly when comparing across-model projections.

10 Planned outcomes

1. From this investigation of the trophodynamics of the small pelagic fishes in the southern Australian and existing ecosystem models, we have a better understanding of their role in the ecosystem particularly with regard to the control they exert in the broader ecosystem. From this understanding we can better parameterise relevant models, interpret the outputs and inform managers as to potential outcomes of harvest and management strategies in not just the SPF but all fisheries.

2. We have outlined appropriate further development or models giving consideration to climate change prediction requirements. This outcome will be of benefit to not only the management of the Small Pelagic Fishery, but to that of other Commonwealth and State fisheries, including the Recreational Fishery, most of which depend on the small pelagic fishes as a food resource.

11 Conclusions

In the Northwest Atlantic, Frank *et al.* (2006) found that generally, high latitude, less species-rich and low productivity systems were mostly top-down controlled while low-latitude, more diverse and productive systems were bottom-up controlled. In addition, the eastern boundary current systems, discussed in Chapter 2, are more strongly bottom-up forced while western boundary currents, typically on continental shelves are top-down forced. The oceanography of the East Bass Strait system (Chapter 2) is more typical of a western boundary current system while that of the eastern GAB leans toward the more productive nature of an eastern boundary current. Therefore, the resultant vulnerability fields generated for the two Ecosim models, i.e. more top-down forcing in the EBS and more bottom-up forcing in the eGAB, are not unexpected. Furthermore, as Heath (2005) found in the North Sea foodweb, we found that different branches of the foodweb tended to display different characteristics particularly in the EBS model.

Both bottom-up and top-down controls can occur in open-shelf systems and switching between these states may indicate pressures such as climate change and fishing (Frank *et al.,* 2006). The heavily-fished EBS system might well be indicative of this phenomenon with more top-down control. Furthermore, top-down control means that the modelled system is much more sensitive to fishing pressure and other stressors (Christensen and Walters, 2003). In comparison, open-ocean systems tend to be bottom-up controlled but not always. Evidence of wasp-waist control was found off eastern Australia in the Eastern Tuna and Billfish Fishery, where simulated removals of mesopelagic fishes and squid, in an EwE model, had cascading consequences up and down the foodweb (Griffths *et al.,* 2010).

The typical wasp-waist species have certain characteristics (Bakun, 2006): they dominate their trophic level, channelling the energy flow through the mid-trophic level from plankton to marine mammals, seabirds and large fishes (Rice, 1995; Cury *et al.,* 2000; Freon *et al.* 2005; Bakun, 2006); they have short but complex life histories that may result in high variability; they usually are the lowest trophic level that is mobile; and they may prey on early life stages of their predators. While the small pelagic species in the ecosystem of southeast Australia certainly might fit some of these characteristics, the results presented and reviewed here do not suggest a strong wasp-waist role. Sardines and anchovies were only involved in two of the top 25 sensitive interactions in the GAB and one in the EBS compared to one-fourth to one-half of the interactions in the southern Benguela or Humboldt systems (Shannon *et al.,* 2008). However, redbait were involved in one-fifth of the 25 interactions in the EBS but only one in the GAB. By combining all the small pelagic species, we found six interactions in the GAB and seven in the EBS. Certainly, the biomasses of any of the pelagic species singly are not high. Even anchovy and sardine in the GAB are far less (spawning biomass ~171,000 tonnes: Ward *et al.,* 2009) than in the upwelling systems where they operate as wasp-waist species. Furthermore, the depletion study for the traditional small pelagics showed relatively little response from the rest of the ecosystem.

However, wasp-waist species need not be the small pelagic species that we normally associate with that term. Species such as snipe fishes off Morocco, and triggerfish off tropical west Africa (Bakun, 2006), capelin, pollock and copepods (Rice 1995) have all been described as wasp-waist species for one reason or another. As previously mentioned, the ETBF along with other pelagic Pacific ecosystems have also been found to have mesopelagic fishes, squid and small scombrids that strongly influence the dynamics of the modelled system (Olson and Watters, 2003). It has been suggested that that krill in the Southern Ocean might act as a wasp-waist species. Both the mesopelagic fishes and the krill produced the most significant results in both our studies. Are these our wasp-waist species? Particularly, in the EBS model Johnson *et al.* (unpublished report) found that the combination of a high initial biomass for a group and heavy predation pressure on that group meant a higher likelihood of that group playing a more central role in the functioning of the ecosystem e.g. as for krill in Atlantis-SE and for krill and mesopelagic fishes in Ecosim-EBS. Myctophids (= mesopelagic fishes) play an important role in the diets of many fishes including those of commercial importance such as ling and blue grenadier.

Overall, all the EwE models tend to suggest that these systems are largely bottom-up forced but that the more heavily fished EBS has more top-down controlling elements. The similarities between Atlantis and Ecosim models also support the hypothesis of bottom-up forcing but the dissimilarities between them are likely to be due to issues in model structure. Bottom-up forced systems are more resilient to overfishing and changes (Christensen and Walters, 2003, Frank *et al.,* 2006), an optimistic but very risky assumption (Christensen and Walters, 2003).

Future stresses such as climate change are very likely to have big impact in any system, particularly in top-down systems already sensitive to fishing pressure systems. Preliminary analyses (Fulton *et al.*, in review) suggest that mid-trophic levels, particularly mesopelagic and small pelagic fishes, may be at the centre of a future regime shift in the waters off eastern Tasmania and Bass Strait. There may also be significant implications of changing upwelling strength across the southeast (which some of the downscaled climate models are currently predicting) for small pelagic fisheries. Not all of these shifts are negative and there may be some significant opportunities, but what is clear is that these changes, if they eventuate, will lead to a radically different context to the fishery than exists today. Consequently, the representation of these groups in models needs to be refined to help constrain uncertainties or identify key pieces of information we should try and obtain from monitoring in order to determine if Australia's marine systems are on a trajectory that would lead to such large scale restructuring of the role of these groups.

12 References

Alheit, J. (2006). Wasp-waist populations and marine ecosystem dynamics: Navigating the “predator pit” topographies. *Progress in Oceanography* **68**, 271-288.

Alheit, J. and Bernal, P. (1993). Effects of physical and biological changes on the biomass yield of the Humboldt Current ecosystem. In: Sherman, K., Alexander, L.M. and Gold, B.D. (eds), pp 53-68, *Large Marine Ecosystems, Stress, Mitigation, and Sustainability*. Washington DC. American Association for the Advancement of Science.

Alheit, J. and Niquen, M. (2004). Regime shifts in the Humboldt Current ecosystem. *Process in Oceanography* **60**, 201-222.

Bakun , A. (1996). Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. (University of California Sea Grant, San Diego, California, USA) 323 pp.

Bakun, A. (2006) Wasp-waist populations and marine ecosystem dynamics: Navigating the ‘predator pit’ topographies. Progress in Oceanography 68, 271-288.

Bakun, A. and Parrish, R.H. (1982). Turbulence, transport, and fish in California and Peru current systems. CalCOFI Report **23**, 99-112.

Bakun, A., Babcock, E. A., and Santora, C. (2009). Regulating a complex adaptive system via its wasp-waist: grappling with ecosystem-based management of the New England herring fishery. *ICES Journal of Marine Science* **66**, 1768-1775.

Bax, N. J., and Williams, A. (2000) (eds). *Habitat and Fisheries Production in the Southeast Fishery Ecosystem*. Final Report to the FRDC Project No 94/040. (CSIRO Marine Research, Hobart, Tas.)

Beverton, R.J.H. (1990). Small marine pelagic fish and the threat of fishing; are they endangered? *Journal of Fish Biology* **37** (Supplement A), 5-16.

Blaber, S. J. M. and Bulman, C. M. (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology* **95**, 345-356.

Bulman, C., Althaus, F., He, X., Bax, N.J., and Williams, A. (2001). Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. *Marine and Freshwater Research* **52**, 537-548.

Bulman, C.M., and Blaber, S.J.M. (1986). Feeding ecology of Macruronus novaezelandiae (Hector) (Teleostei: Merlucciidae) in south-eastern Australia. *Australian Journal of Marine and Freshwater Research* **37**, 621-639.

Bulman, C.M., and Koslow, J.A. (1992). Diet and food consumption of a deep-sea fish, orange roughy Hoplostethus atlanticus (Pisces: Trachichthyidae), off southeastern Australia. *Marine Ecology Progress Series* **82**, 119-125.

Bulman, C. (2002). ‘Trophic ecology and food web modelling of mid-slope demersal fishes off southern Tasmania, Australia.’ PhD Thesis, University of Tasmania, Hobart, Tas.

Bulman, C.M., He, X., and Koslow, J.A. (2002). Trophic ecology of the mid-slope demersal fish community off southern Tasmania, Australia. *Marine and Freshwater Research* **53**, 59-72.

Bulman, C., Condie, S., Furlani, D., Cahill, M., Klaer, N., Goldsworthy, S., and Knuckey, I. (2006). ‘Trophic dynamics of the eastern shelf and slope of the South East Fishery:

impacts of and on the fishery.' Project No 2002/028. Final Report to the FRDC. (CSIRO Marine and Atmospheric Research, Hobart, Tas.)

Butler, A., Althaus, F., Furlani, D. and Ridgway, K. (2002). Assessment of the conservation values of the Bonney upwelling area: a component of the Commonwealth Marine Conservation Assessment Program 2002-2004. Report to Environment Australia. 73 pp.

Carr, M.E. (2002). Estimation of potential productivity in eastern boundary currents using remote sensing. *Deep Sea Research II* **49**, 59–80.

Carr, M-E and Kearns, E.J. (2003). Production regimes in four Eastern Boundary Current systems. *Deep Sea Research II.*

Christensen,V. (1996). Balancing the Alaska Gyre model. In: Pauly, D, and Christensen,V. (eds). Mass-Balance Models of the Northeastern Pacific Ecosystems. *Fisheries Centre Research Report* **4.** (Fisheries Centre, University of British Columbia, Vancouver.)

Christensen, V., and Walters, C.J. (2003). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**, 109-139.

Coleman, N. and M. Mobley (1984). Diets of commercially exploited fish from Bass Strait and adjacent Victorian Waters, south-eastern Australia. *Australian Journal of Marine and Freshwater Research* **35**, 549-560.

Condie, S.A., and Dunn, J.R. (2006).Seasonal characteristics of the surface mixed layer in the Australasian region: implications for primary production regimes and biogeography. *Marine and Freshwater Research* **57**, 569-590.

Condie, S.A., and Sherwood, C.R. (2006). Sediment distribution and transport across the continental shelf and slope under idealized wind forcing. *Progress in Oceanography* **70**, 255-270.

Condie, S.A, Mansbridge, J.M. and Cahill, M.L.(2010). Contrasting local retention and cross-shore transports of the East Australian Current and the Leeuwin Current and their relative influences on the life histories of small pelagic fishes. *Deep Sea Research II* doi:10.1016/j.dsr2.2010.06.003.

Cooper, S.P., Lansdell, M.J., Young, J.W. (2009). Appendix 4: PESCI database: design and capabilities. In Young, J.W., Lansdell, M.J., Hobday, A.J., Dambacher, J.M., Cooper, S.P., Kloser, R.J., Griffiths, S.P., Nichols, P.D., Revill A.T. "Determining ecosystem effects of longline fishing in the Eastern Tuna and Billfish Fishery." FRDC Final Report 2004/063. CSIRO Marine and Atmospheric Research, Hobart, Tasmania. 325 pp.

Cury, P. and Roy, C. (1989). Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 670-680.

Cury, P. and Shannon, L.(2004) Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. *Progress in Oceanography* **60**, 223–243.

Cury, P., Roy, C. and Faure, V. (1998). Environmental constraints and pelagic fisheries in upwelling areas: the Peruvian puzzle. *South African Journal of Marine Science* **19**, 159-167.

Cury, P., Shannon, L. and Shin, Y. (2001). The functioning of marine ecosystems. Reykjavik Conference on Responsible Fisheries in the Marine Ecosystem. Reykjavik, Iceland, pp. 1-4.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J. and Verheye, H.M. (2000). Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Sciences* **57**, 603-618.

Dambacher, J. M., Li, H. W. and Rossignol, P. A (2002). Relevance of community structure in assessing indeterminacy of ecological predictions. *Ecology* **83**, 1372-1385.

Dambacher, J. M., Li, H. W. and Rossignol, P. A. (2003). Qualitative predictions in model ecosystems. *Ecological Modelling* **161**, 79-93.

Dempster, T., Gibbs, M.T., Rissik, D. and Suthers, I.M. (1997). Beyond hydrography: daily ichthyoplankton variability and short term oceanographic events on the Sydney continental shelf. *Continental Shelf Research* **17**, 1461-1481.

FAO (2009). State of the World Fisheries and Aquaculture 2008. Food and Agriculture Organization of the Unite Nations, Rome, Italy.

Field, J.C., Francis, R.C., Aydin, K. (2006). Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate. *Progress in Oceanography* **68**, 238-270.

Frank, K.T., Petrie, B., Shackell, N.L., and Choi, J.S. (2006). Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecology Letters* **9**, 1096-1105.

Freon, P., Cury, P., Shannon, L., and Roy, C. (2005). Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: A review. *Bulletin of Marine Science* **76**, 385-462.

Fulton, E. A., Smith, A. D. M., and Smith, D. C. (2007). *Alternative Management Strategies for Southeast Australian Commonwealth Fisheries: Stage 2: Quantitative Management Strategy Evaluation*. (AFMA, FRDC and CSIRO Marine and Atmospheric Research, Hobart, Tasmania.)

Fulton, E.A., Fuller, M., Smith, A.D.M., and Punt, A.E.. (2004). Ecological indicators of the ecosystem effects of fishing: Final Report. Australian Fisheries Management Report R99/1546. (Australian Fisheries Management Authority, Canberra.)

Fulton, E.A, Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A.D.M., and Smith, D.C. (in review). Lessons in modelling and management of marine ecosystems: the Atlantis experience.

Giannini, F., Hobsbawn, P.I., Begg, G.A. and Chambers, M. (2010). Management strategy evaluation (MSE) of the harvest strategy for the Small Pelagic Fishery. Final Report FRDC Project 2008/064. (Bureau of Rural Sciences and FRDC, Canberra.)

Gibbs, C.F., Tomczak, Jr., M. and Longmore, A.R. (1986). The nutrient regime of Bass Strait *Australian Journal of Marine and Freshwater Research* **37**, 451-466.

Gibbs, M.T., Marchesiello, P. and Middleton, J.H. (1997). Nutrient enrichment of Jervis Bay, Australia, during the massive 1992 coccolithophorid bloom. *Marine and Freshwater Research* **48**, 473-478.

Gibbs, M.T., Middleton, J.H., and Marchesiello, P. (1998). Baroclinic response of Sydney shelf waters to local wind and deep ocean forcing. *Journal of Physical Oceanography* **28**, 178-190.

Gibbs, C.F., Arnott, G.H., Longmore, A.R. and Marchant, J.W. (1991). Nutrient and plankton distribution near a shelf break front in the region of the Bass Strait cascade. *Australian Journal of Marine and Freshwater Research* **42**, 201-217.

Gray, C.A. and Kingsford, M.J. (2003). Variability in thermocline depth and strength, and relationships with vertical distributions of fish larvae and mesozooplankton in dynamic coastal waters. *Marine Ecology Progress Series* **247**, 211-224.

Griffin, D.A., Thompson, P.A., Bax, N.J., Bradford, R.W. and Hallegraeff, G.M. (1997). The 1995 mass mortality of pilchard: no role found for physical or biological oceanographic factors in Australia. *Marine and Freshwater Research* **48**, 27-42.

Griffiths, S. P. ,Young, J. W., Lansdell, M. J., Campbell, R. A., Hampton, J., Hoyle, S. D., Langley, A., Bromhead, D., Hinton, M. G. (2010). Ecological effects of longline fishing and climate change on the pelagic ecosystem off eastern Australia. *Reviews in Fish Biology and Fisheries* **20**: 239-272.

Goldsworthy, S., Page, B., Rogers, P., Ward, T. (2011). 'Establishing ecosystem-based management for the SA pilchard fishery: developing ecological performance indicators and reference points to assess the need for ecological allocations'. Final Report to the Fisheries Research and Development Corporation. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2010/000863-1. SARDI Research Report Series No. 529. 173pp.

Goldsworthy, S. D., Bulman, C. M., He, X., Larcombe, J. W. P., Littnan, C., Gales, N. J., Hindell, M. A., & Kirkwood, R. (2003). Trophic interactions between marine mammals and Australian fisheries: an ecosystem approach. pp. 62-99. In: *Marine Mammals: Fisheries, Tourism and Management Issues* (CSIRO Publishing,Collingwood, Vic.)

Haddon, M. (2008). Catch rate standardizations 2008 (for data 1986-2007). Unpublished report to Shelf and Slope RAG. 108pp.

Hallegraeff, G.M. and Jeffrey, S.W. (1993). Annually recurrent diatom blooms in spring along the New South Wales coast of Australia. *Australian Journal of Marine and Freshwater Research* **44**, 325-334.

Hamer, D. J., & Goldsworthy, S. D. (2006). Seal-fishery operational interactions: Identifying the environmental and operational aspects of a trawl fishery that contribute to by-catch and mortality of Australian fur seals (*Arctocephalus pusillus doriferus*). *Biological Conservation* **130**, 517-529.

Harris, G.P., Griffiths, F.B., Clementson, L.A. (1992). Climate and the fisheries off Tasmania – interactions of physics, food chains and fish. *South African Journal of Marine Science* **12**, 585–597.

Harris, G.P., Davies, P., Nunez, M. and Meyers, G. (1988). Interannual variability in climate and fisheries in Tasmania. *Nature* **333**, 754-757.

Harris, G., Nilsson, C., Clementson, L., Thomas, D. (1987). The water masses of the east coast of Tasmania: seasonal and interannual variability and the influence on phytoplankton biomass and productivity. *Australian Journal of Marine and Freshwater Research* **38**, 569–590.

Harris, G.P., Griffiths, F.B., Clementson, L.A., Lyne, V. and Van der Doe, H. (1991). Seasonal and interannual variability in physical processes, nutrient cycling and the structure of the food chain in Tasmanian shelf waters. *Journal of Plankton Research* **13**, 109-131.

Heath, M.R. (2005). Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. *ICES Journal of Marine Science* **62**, 847-868.

Heath, M.R. and Gallego, A (2010). Ecosystem structure and function. In: Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Möllman, C. and Pinnegar, J.K. (Eds) 'Resolving climate impacts on fish stocks' *ICES Cooperative Research Report* **301**, May 2010.

Hobday, A.J., Poloczanska, E.S., and Matear, R.J. (2008). Implications of climate change for Australian fisheries and aquaculture: a preliminary assessment. Report to the Department of Climate Change, Canberra.

Hunt, G.L. and McKinnell, S. (2006). Interplay between top-down, bottom-up and wasp-waist control in marine ecosystems. *Progress in Oceanography* **68**, 115-124.

Hutchings, L., Barange, M., Bloomer, S.F., Boyd, A.J., Crawford, R.J.M., Huggett, J.A., Kerstan, M., Korrubel, J.L., De Oliveira, J.A.A., Painting, S.J., Richardson, A.J., Shannon, L.J., Schulein, F.H., van der Lingen, C.D. and Verheye, H.M. (1998).Multiple factors affecting South African anchovy recruitment in the spawning, transport and nursery areas. *South African Journal of Marine Science* **19**, 211-225.

Hutchings, L., Beckley, L.E., Griffiths, M.H., Roberts, M.J., Sundby, S. and van der Lingen, C. (2002). Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. *Marine and Freshwater Research* **53**, 307-318.

Jarre-Teichmann, A., and Christensen, V. (1998). Comparative modelling of trophic flows in four large upwelling ecosystems: Global versus local effects. pp 423-443. In *Global Versus Local Changes in Upwelling Systems* (ORSTOM, France.)

Johnson, P., Smith, T., and Fulton, E., (2009). Forage species management. Report AFMA Project 2008/0835. (CSIRO, Hobart and AFMA, Canberra.)

Johnson, P., Bulman, C., Fulton, B, and Smith, T. (unpublished report). MSC Low Trophic Level Project: South Eastern Australian Case Study. Final Report May 2010 report. (CSIRO Marine and Atmospheric Research, Hobart.)

Jitts, H.R. (1965). The summer characteristics if primary productivity in the Tasman and Coral seas. *Australian Journal of Marine and Freshwater Research* **16**, 151-162.

Kämpf, J., Doubell, M., Griffin, D., Matthews, R.L. and Ward, T.M. (2004). Evidence of a large seasonal coastal upwelling system along the southern shelf of Australia. *Geophysical Research Letters* **31.**

Keane, J.P. and Neira, F.J. (2008). Larval fish assemblages along the south-eastern Australian shelf: linking mesoscale non-depth-discriminate structure and water masses. *Fisheries Oceanography* **17**, 263-280.

Lewis, R.K. (1981). Seasonal upwelling along the south-eastern coastline of South Australia. *Australian Journal of Marine and Freshwater Research* **32**, 843-854.

Levins, R., (1974). The qualitative analysis of partially specified systems, *Annals of the New York Academy of Science* **231**, 123-138.

Marchesiello, P., Gibbs, M.T. and Middleton, J.H. (2000). Simulations of coastal upwelling on the Sydney Continental Shelf. *Marine and Freshwater Research* **51**, 577-588.

McClatchie,S., Middleton, J.F., Ward, T.M. (2006). Water mass analysis and alongshore variation in upwelling strength in the eastern Great Australian Bight. *Journal of Geophysical Research* **111**,1-13.

McClean-Padman, J. and Padman, L. (1991). Summer upwelling on the Sydney inner continental shelf: The relative roles of local wind forcing and mesoscale eddy encroachment. *Continental Shelf Research* **11**, 321-345.

McIntosh, R. R., Page, B., and Goldsworthy, S. D. (2006). Dietary analysis of regurgitates and stomach samples from free-living Australian sea lions. *Wildlife Research* **33**, 661-669.

McLeod, D. (2005). 'Ecological and functional equivalence in small pelagic fish off the east coast of Tasmania.' BSc Hons Thesis, University of Tasmania, Hobart, Tasmania.

Middleton, J.F. and Bye, J.A.T. (2007). A review of the shelf-slope circulation along Australia's southern shelves: Cape Leeuwin to Portland. *Progress in Oceanography* **75**,1-41.

Middleton, J.F. and Cirano, M. (2002). A boundary current along Australia's southern shelves: the Flinders Current. *Journal of Geophysical Research* **107.**

Neira, F.J. (2005). Summer and winter larval fish assemblages around offshore oil and gas platforms in south-eastern Australia. *Estuarine, Coastal and Shelf Science* **63**, 589-604.

Neira, F.J. and Keane, J.P. (2008). Ichthyoplankton-based spawning dynamics of blue mackerel (*Scomber australasicus*) in south-eastern Australia: links to the East Australian Current. *Fisheries Oceanography* **17**, 281-298.

Neira, F.J. and Lyle, J.M. (2008). 'Provisional spawning biomass estimates for redbait off southern New South Wales using the daily egg production method (DEPM).' Final Report to Australian Fisheries and Management Authority,13 pp.

Neira, F.J., Keane, J.P. and Lyle, J.M. (2009). Shelf spawning habitat of *Emmelichthys nitidus* in south-eastern Australia – implications and suitability for egg-based biomass estimation. *Estuarine, Coastal and Shelf Science* **81**, 521-532.

Neira, F.J., Lyle, J.M., Ewing, G.P., Keane, J.P., Tracey, S.R. (2008). 'Evaluation of egg production as a method of estimating spawning biomass of redbait off the East Coast of Tasmania.' FRDC project 2004/039. Marine Research Laboratories, Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Hobart, Tasmania.

Olson, R., and Watters, G. (2003). A model of the pelagic ecosystem in the eastern tropical Pacific Ocean. *Bulletin of Inter-Amercian Tropical Tuna Commission* **22**, 135-188.

Pillar, S.C., Moloney, C.L., Payne, A.I.L. and Shillington, F.A. (Eds) (1998). *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources. South African Journal of Marine Science* **19**. (Sea Fisheries Department of Environmental Affairs and Tourism. Republic of South Africa.) 512 pp.

Prince, J.D. (2001). Ecosystem of the South East Fishery (Australia), and fisher lore. *Marine and Freshwater Research* **52**, 431-449.

Prince, J.D. and Griffin, D.A. (2001). Spawning dynamics of the eastern gemfish (*Rexea solandri*) in relation to regional oceanography in south-eastern Australia. *Marine and Freshwater Research* **52**, 611-622.

Ramsey, D. and Veltman, C. (2005). Predicting the effects of perturbation on ecological communities: what can qualitative models offer? *Journal of Animal Ecology* **74**, 905-916.

Ridgway, K.R. (2007a). Seasonal circulation around Tasmania: an interface between eastern and western boundary dynamics. *Journal of Geophysical Research* **112**, C10016, doi:10.1029/ 2006JC003898.

Ridgway, K.R. (2007b). Long-term trend and decadal variability of the southward penetration of the East Australian current. L13613. *Geophysical Research Letters* **34**, doi:10.1029/2007 GL030393.

Rice, J. (1995). Food web theory, marine food webs, and what climate change may do to northern marine fish populations. In 'Climate Change and Northern Fish Populations', pp. 516–568.(Ed). R. J. Beamish. *Canadian Special Publication of Fisheries and Aquatic Sciences* **121**.

Rochford, D.J. (1972). Nutrient enrichment of east Australian coastal waters. I. Evans Head upwelling. *Division of Fisheries and Oceanography Technical Paper No*. **33**. (Commonwealth Scientific and Industrial Research Organisation, Sydney.)

Rochford, D.J. (1975). Nutrient enrichment of east Australian coastal waters. II: Laurieton upwelling. *Australian Journal of Marine and Freshwater Research* **26**, 233-243.

Rochford, D.J. (1977). The present evidence for summer upwelling off the north east coast of Victoria. Commonwealth Scientific and Industrial Research Organisation (CSIRO Australia), *Division of Fisheries and Oceanography Technical Report No*. **77**, 4 pp.

Rochford, D.J. (1984). Nitrates in eastern Australian coastal waters. *Australian Journal of Marine and Freshwater Research* **35**, 385-397.

Roy, C. (1998). An upwelling-induced retention area off Senegal: a mechanism to link upwelling an retention processes. *South African Journal of Marine Science* **19**, 89-98.

Savina, M., Fulton, E., Condie, S., Forrest, R., Scandol, J., Astles, K., and Gibbs, P. (2008). 'Ecologically sustainable development of the regional marine and estuarine resources of NSW: Modelling of the NSW continental shelf ecosystem.' CSIRO and NSW DPI Report. 71pp.

Schahinger, R.B. (1987). Structure of coastal upwelling events observed off the south-east coast of South Australia during February 1983-April 1984. *Australian Journal of Marine and Freshwater Research* **38**, 439-459.

Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., Fletcher, W. J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S. E., Maccall, A. D., Matsuura, Y., Nevarez-Martinez, M. O., Parrish, R. H., Roy, C., Serra, R., Shust, K. V., Ward, M. N., and Zuzunaga, J. Z. (1999). Worldwide Large-Scale Fluctuations of Sardine and Anchovy Populations. *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap* **21**, 289-347.

Shannon, L.J., Cury, P., and Jarre, A. (2000). Modelling effects of fishing in the Southern Benguela ecosystem. *ICES Journal of Marine Science* **57**, 720-722

Shannon, L.J., Neira, S. and Taylor, M. (2008). Comparing internal and external drivers in the southern Benguela and the southern and northern Humboldt upwelling ecosystems. *African Journal of Marine Science* **30**, 63-84.

Silió-Calzada, A., Bricaud, A. and Gentili, B. (2008). Estimates of sea surface nitrate concentrations from sea surface temperature and chlorophyll concentration in upwelling areas: A case study for the Benguela system. *Remote Sensing of Environment* **112**, 3173-3180.

Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., Mackinson, S., Marzloff, M., Shannon, L. J., Shin, Y.-J., and Tam, J. (in review). Impacts of fishing low trophic level species on marine ecosystems. Submitted to *Nature*.

Smith, H.K. (1983). Fishery and biology of Nototodarus gouldi (McCoy, 1888) in western Bass Strait. *Memoirs of the National Museum of Victoria* **44**, 285-290.

Smith, K.A., Gibbs, M.T., Middleton, J.H. and Suthers, I.M. (1999). Short term dynamics of coastal ichthyoplankton off the Sydney coast: tracers of hydrographic variability. *Marine Ecology Progress Series* **178**, 1-15.

Smith, K.A. and Suthers, I.M. (1999). Displacement of diverse ichthyoplankton assemblages by a coastal upwelling event on the Sydney shelf. *Marine Ecology Progress Series* **176**, 49-62.

Strub, P.T., Shillington, F.A., James, C. and Weeks, S.J. (1998). Satellite comparison of the seasonal circulation in the Benguela and California current systems. *South African Journal of Marine Science* **19**, 99-112.

Swartzman, G., Bertrand, A., Gutiérrez, M., Bertrand, S. and Vasquez, L. (2008). The relationship of anchovy and sardine to water masses in the Peruvian Humboldt Current System from 1983 to 2005. The Northern Humboldt Current System: Ocean Dynamics, Ecosystem Processes, and Fisheries. *Progress in Oceanography* **79**, 228-237.

Tranter, D.J., Carpenter, D.J. and Leech, G.S. (1986). The coastal enrichment effect of the East Australian Current eddy field. *Deep-Sea Research* **33**, 1705-1720.

van Ruth, P.D., Ganf, G.G. and Ward, T.M. (2010). The influence of mixing on primary productivity: a unique application of classical critical depth theory. *Progress in Oceanography* **85**, 224-235.

Voice, M., Harvey, N. and Walsh, K. (2006). (Editors) ‘Vulnerability to Climate Change of Australia’s Coastal Zone: Analysis of gaps in methods, data and system thresholds.‘ Report to the Australian Greenhouse Office, Canberra, Australia.

Welsford, D. C., & Lyle, J. M. (2003). Redbait (*Emmelichthys nitidus*): a synopsis of fishery and biological data. *Tasmanian Aquaculture and Fisheries Institute Techncial Report* **20.** (University of Tasmania, Hobart, Tasmania.)

Walters, C., Christensen, V., and Pauly, D. (1997). Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* **7**, 139-172.

Walters, C., Pauly, D., and Christensen, V. (1999). Ecospace: prediction of mesocale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* **2**, 539-554.

Ward, T.M., Ivey, A.R., McLeay, L.J., and Burch, P. (2009). ‘Spawning biomass of Sardine, *Sardinops sagax,* in waters off South Australia in 2009.’ Final Report for PIRSA Fisheries. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI publication No. F2007/000566-3.

Ward, P., Timmiss, T., and Wise, B. (2001). A review of biology and fisheries for mackerel. (Bureau of Rural Resources, Canberra, Australia.)

Worm, B., Hilborn R., Baum J., J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., and Zeller, D.(2009). Rebuilding global fisheries. *Science* **325**, 578-585.

Young, J. W., and Davis, T. L. O. (1992). Feeding ecology and interanual variations in diet of larval jack mackerel, *Trachurus declivis* (Pisces: Carangidae), from coastal waters of eastern Tasmania. *Marine Biology* **113**, 11-20.

Young, J. W., Lamb, T. D., and Bradford, R. W. (1996a). Distribution and communtiy structure of midwater fishes in relation to the subtropcial convergence off eastern Tasmania. *Marine Biology* **126**, 571-584.

Young, J. W., Bradford, R. W., Lamb, T. D., and Lyne, V. D. (1996b). Biomass of zooplankton and micronekton in the southern bluefin tuna fishing grounds off eastern Tasmania, Australia. *Marine Ecology Progress Series* **138**, 1-14.

Young, J. W., Jordan, A. R., Bobbie, C. M., Johannes, R. M., Haskard, K., & Pullen, G. (1993). Seasonal and interannual variability in krill (*Nyctiphanes australis*) stocks and their relationships to the jack mackerel (*Trachurus declivis*) fishery off eastern Tasmania. *Marine Biology* **116**, 9-18.

Young, J.W., Lansdell, M.J., Campbell, R.A., Cooper, S.P., Juanes, F., and Guest, M.A. (2010). Feeding ecology and niche segregation in oceanic top predators off eastern Australia. *Marine Biology* DOI 10.1007/s00227-010-1500-y.Young, J.W., Lansdell, M.J., Hobday, A.J., Dambacher, J.M., Cooper, S.P., Kloser, R.J., Griffiths, S.P., Nichols, P.D., and Revill, A.T. (2009). 'Determining ecosystem effects of longline fishing in the Eastern Tuna and Billfish Fishery.' FRDC Final Report 2004/063. 335 pp .

Appendix A Intellectual property

No patentable or marketable products have arisen from this work. Results will be published in scientific or non-technical literature. The raw data remains the property of the individuals from whom it originated. The intellectual property arising from this work is the property of CSIRO and FRDC and from the MSC study the property of the MSC.

Appendix B Staff

Principal Investigator: Catherine M. Bulman CMAR
Co-Investigators: Scott Condie CMAR
Francisco Neira TAFI
Simon Goldsworthy SARDI
Elizabeth A. Fulton CMAR
Jeremy Lyle TAFI
Technical support: Marcia Rollins CMAR
Ruth Sharples CMAR
Scott Cooper CMAR

Appendix C Dietary metadata

Table C1. SEFHES Data: Predator species of stomachs analysed with counts of empty and non-empty stomachs.

Scientific Name	Common Name	Non-empty Stomach Count	Empty Stomach Count
Allomycterus pilatus	Australian Burrfish	13	4
Alopias vulpinus	Thresher Shark	1	
Anoplocapros inermis	Eastern Smooth Boxfish		1
Apistidae, Neosebastidae, Pteroidae, Scorpaenidae,	Scorpionfishes		1
Apogonops anomalus	Threespine Cardinalfish	62	73
Argentina australiae	Silverside	2	
Arothron firmamentum	Starry Toadfish	11	
Asymbolus analis	Grey Spotted Catshark	2	
Asymbolus rubiginosus	Orange Spotted Catshark	9	
Atypichthys strigatus	Mado	24	7
Azygopus pinnifasciatus	Banded-fin Flounder	4	6
Bassanago bulbiceps	Swollenhead Conger		1
Beryx splendens	Alfonsino		1
Caesioperca lepidoptera	Butterfly Perch	50	15
Caesioperca rasor	Barber Perch	14	4
Callanthias australis	Splendid Perch	2	1
Callorhinchus milii	Elephantfish	2	10
Centriscops humerosus	Banded Bellowsfish	229	21
Centroberyx affinis	Redfish	355	262
Centroberyx australis	Yelloweye Redfish		3
Centroberyx gerrardi	Bight Redfish		1
Cephaloscyllium laticeps	Draughtboard Shark	89	21
Chelidonichthys kumu	Red Gurnard	20	5
Coelorinchus australis	Southern Whiptail	21	5
Coelorinchus fasciatus	Banded Whiptail	23	13
Coelorinchus gormani	Little Whiptail	8	11
Coelorinchus maurofasciatus	Falseband Whiptail	103	64
Coelorinchus mirus	Gargoyle Fish	42	16
Cyttus australis	Silver Dory	100	72
Cyttus novaezealandiae	New Zealand Dory	30	10
Dasyatis brevicaudata	Smooth Stingray	1	
Dinolestes lewini	Longfin Pike	6	4
Diodon nicthemerus	Globefish	75	5
Dipturus australis	Sydney Skate	7	
Dipturus confusus	longnose skate	56	7
Echinoidea-regular			1
Emmelichthys nitidus	Redbait	71	47
Foetorepus calauropomus	Common Stinkfish	120	68
Galeorhinus galeus	School Shark	10	2
Gastropoda Unident.1			1
Genypterus blacodes	Pink Ling	88	56
Helicolenus barathri	Bigeye Ocean Perch	46	22
Helicolenus percoides	Reef Ocean Perch	516	428

Scientific Name	Common Name	Non-empty Stomach Count	Empty Stomach Count
Heterodontus portusjacksoni	Port Jackson Shark	11	3
Hoplichthys haswelli	Deepsea Flathead	7	15
Hypoplectrodes annulatus	Blackbanded Seaperch	1	2
Idiosepiidae - undifferentiated	squids		6
Kathetostoma canaster	Speckled Stargazer	17	7
Kathetostoma laeve	Common Stargazer	14	1
Latridopsis forsteri	Bastard Trumpeter	9	7
Latris lineata	Striped Trumpeter	12	7
Lepidoperca pulchella	Eastern Orange Perch	9	16
Lepidopus caudatus	Frostfish		13
Lepidorhynchus denticulatus	Toothed Whiptail		1
Lepidotrigla modesta	Cocky Gurnard	97	49
Lepidotrigla mulhalli	Roundsnout Gurnard	115	74
Lepidotrigla vanessa	Butterfly Gurnard	18	2
Macroramphosus scolopax	Common Bellowsfish	212	45
Macrouridae and Bathygadidae	whiptails and rat-tails		38
Majidae and related families	spider crabs		4
Meuschenia freycineti	Sixspine Leatherjacket	71	1
Meuschenia scaber	Velvet Leatherjacket	66	42
Mustelus antarcticus	Gummy Shark	16	1
Myliobatis australis	Southern Eagle Ray	7	1
Narcine tasmaniensis	Tasmanian Numbfish	26	12
Nemadactylus douglasii	Grey Morwong	16	8
Nemadactylus macropterus	Jackass Morwong	301	316
Neosebastes scorpaenoides	Common Gurnard Perch	24	6
Notolabrus tetricus	Bluethroat Wrasse	9	3
Nototodarus gouldi	Gould's squid	10	23
Ophthalmolepis lineolatus	Southern Maori Wrasse	11	2
Order Octopoda	octopods	3	7
Pagrus auratus	Snapper	9	8
Paramonacanthus filicauda	Threadfin Leatherjacket	8	2
Parapercis allporti	Barred Grubfish		1
Parascyllium ferrugineum	Rusty Carpetshark	1	1
Paratrachichthys macleayi	Sandpaper Fish	2	54
Paraulopus nigripinnis	Blacktip Cucumberfish	200	53
Parequula melbournensis	Silverbelly	7	3
Parma microlepis	White-ear	4	1
Pempheris multiradiata	Bigscale Bullseye	30	6
Platycephalus aurimaculatus	Toothy Flathead	1	10
Platycephalus bassensis	Southern Sand Flathead	13	18
Platycephalus longispinis	Longspine Flathead		15
Platycephalus richardsoni	Tiger Flathead	149	212
Polyprion oxygeneios	Hapuku		1
Pseudocaranx dentex	Silver Trevally	22	65
Pseudolabrus mortonii	Rosy Wrasse	12	2
Pseudophycis bachus	Red Cod	5	6
Pseudophycis barbata	Bearded Rock Cod	3	
Pterygotrigla polyommata	Latchet	10	12

Scientific Name	Common Name	Non-empty Stomach Count	Empty Stomach Count
Rexea solandri	Gemfish	6	15
Scomber australasicus	Blue Mackerel	30	18
Scorpis lineolata	Silver Sweep	8	
Sepioteuthis australis	southern calamari		10
Seriolella brama	Blue Warehou	90	44
Seriolella punctata	Silver Warehou	100	197
Sillago flindersi	Eastern School Whiting	41	192
Squalus megalops	Spikey Dogfish	126	65
Squatina albipunctata	eastern angel shark	7	
Squatina australis	Australian Angelshark	47	
Squatina tergocellata	Ornate Angelshark	1	
Thyrsites atun	Barracouta	80	111
Todarodes filippovae	Southern arrow squid		1
Trachichthyidae	roughies	1	
Trachurus declivis	Common Jack Mackerel	314	266
Trachurus novaezelandiae	Yellowtail Scad	8	2
Trygonorrhina fasciata	Southern Fiddler Ray	8	1
Trygonorrhina sp. A	Eastern fiddler ray	5	1
Unknown/other			8
Urolophus bucculentus	Sandyback Stingaree	5	1
Urolophus cruciatus	Banded Stingaree	131	7
Urolophus kapalensis	Kapala stingaree	7	
Urolophus paucimaculatus	Sparsely-spotted Stingaree	144	12
Urolophus viridis	Greenback Stingaree	113	19
Zenopsis nebulosus	Mirror Dory	16	48
Zeus faber	John Dory	118	118
	Total	**5176**	**3587**

Table C2. Orange roughy stomachs analysed with counts of non-empty and empty stomachs.

Scientific Name	Common Name	Non-empty Stomach Count	Empty Stomach Count
Hoplostethus atlanticus	Orange Roughy	4835	4959

Table C3. McLeod Project - Predator species of stomachs analysed with counts of empty and non-empty stomachs.

Scientific Name	Common Name	Non-empty Stomach Count	Empty Stomach Count
Trachurus declivis	Common Jack Mackerel	151	3
Trachurus murphyi	Peruvian Jack Mackerel	1	0
Emmelichthys nitidus	Redbait	290	29
Scomber australasicus	Blue Mackerel	78	2
	Totals	**520**	**34**

Appendix D PESCI Diet Summaries

Table D1. Overall diet of yellowtail scad *Trachurus novaezelandiae* from the SEFHES project data.

Yellowtail Scad - *Trachurus novaezelandiae*
Number of Stomachs: 10
Number of Stomachs Containing Prey: 8
Percentage of Stomachs Containing Prey: 80%
Size range: 152-202

Major prey group	Prey Taxon	Number		Reconstituted Mass		Occurrence	
		n	%	g	%	n	%
Arthropoda		48	90.57	0.0158	10.51		
Copepoda	Candacia sp.	22	41.51	0.00150	1.00	5	62.5
	Oithona sp.	2	3.77	0.00010	0.07	1	12.5
	Oncaea sp.	3	5.66	0.00030	0.20	1	12.5
	Temora sp.	1	1.89	0.00005	0.03	1	12.5
Malacostraca	Crustacea larva	4	7.55	0.00150	1.00	2	25
	Euphausiacea larva	2	3.77	0.00180	1.20	2	25
	Gammaridea 51	1	1.89	0.00020	0.13	1	12.5
	Lanocira sp.	1	1.89	0.00170	1.13	1	12.5
	Lucifer sp.	9	16.98	0.00700	4.67	3	37.5
	Reptantia larva	3	5.66	0.00160	1.07	1	12.5
Tunicata		5	9.43	0.0002	0.11		
Ascidiacea	Ascidia larva	5	9.43	0.00016	0.11	3	37.5
Other		0	0.00	0.1340	89.39		0
	unid. remains	0	0.00	0.13400	89.39	10	125
TOTAL		53		0.15			

Table D2. Overall diet of blue mackerel *Scomber australasicus* from the SEFHES project data.

Blue Mackerel - *Scomber australasicus*
Number of Stomachs: 48
Number of Stomachs Containing Prey: 30
Percentage of Stomachs Containing Prey: 62.5
Size range: 169-373

Major prey group	Prey Taxon	Number		Reconstituted Mass		Occurrence	
		n	%	g	%	n	%
Annelida		1	0.04	0.002	0.00		
Polychaeta	Polychaeta	1	0.04	0.00011	0.00	2	6.67
	Polychaeta remains	0	0.00	0.00191	0.00	3	10.00
Arthropoda		2335	94.12	11.51	26.07		
	Cladocera	2	0.08	0.002	0.00	2	6.67
Copepoda	Copepoda remains	0	0.00	0.0001	0.00	1	3.33
	Oncaea sp.	2	0.08	0.0003	0.00	2	6.67
	Copepoda	12	0.48	0.00011	0.00	2	6.67
	Pleuromamma sp.	1	0.04	0.0005	0.00	1	3.33
	Cyclopoida	1	0.04	0.001	0.00	1	3.33
	Calanoida	70	2.82	0.0125	0.03	8	26.67
	Temora sp.	1953	78.72	0.2287	0.52	19	63.33
	Candacia sp.	1	0.04	0.0005	0.00	1	3.33
Malacostraca	Hyperiidae 3	1	0.04	0.0003	0.00	1	3.33
	Crustacea remains	0	0.00	0.7476	1.69	10	33.33

Major prey group	Prey Taxon	Number		Reconstituted Mass		Occurrence	
		n	%	g	%	n	%
	Decapoda remains	17	0.69	0.0081	0.02	1	3.33
	Crustacea larva	1	0.04	0.0004	0.00	1	3.33
	Eucarida	4	0.16	0.0023	0.01	1	3.33
	Eucarida remains	0	0.00	7.6652	17.36	5	16.67
	Crustacea	1	0.04	1.0803	2.45	2	6.67
	Euphausiacea	173	6.97	1.6954	3.84	2	6.67
	Zoea	85	3.43	0.063	0.14	8	26.67
	Hyperiidae	1	0.04	0.0008	0.00	1	3.33
	Gnathia cf. africana	1	0.04	0.0002	0.00	1	3.33
	Oxycephalidae	2	0.08	0.0003	0.00	2	6.67
	Reptantia larva	1	0.04	0.001	0.00	1	3.33
Ostracoda	Ostracoda	6	0.24	0.002	0.00	2	6.67
Chordata		2	0.08	31.76	71.92		
Osteichthyes	fish remains	0	0.00	16.1957	36.68	13	43.33
	fish	1	0.04	0.43	0.97	1	3.33
Thaliacea	Pyrosoma sp.	1	0.04	15.132	34.27	5	16.67
Cnidaria		7	0.28	0.18	0.40		
Hydrozoa	Siphonophora remains	0	0.00	0.0038	0.01	1	3.33
	Siphonophora sp.	7	0.28	0.1743	0.39	8	26.67
Hemichordata		0	0.00	0.00	0.00		
	Chaetognatha remains	0	0.00	0.0016	0.00	1	3.33
Mollusca		1	0.04	0.01	0.02		
Gastropoda	Gastropoda 12	1	0.04	0.0028	0.01	1	3.33
	Gastropoda	0	0.00	0.005	0.01	1	3.33
Tunicata		133	5.36	0.34	0.77		
Appendicularia	Oikopleura	70	2.82	0.0088	0.02	5	16.67
Ascidiacea	Ascidia 41	17	0.69	0.0021	0.00	1	3.33
	pelagic Ascidia	5	0.20	0.1107	0.25	3	10.00
	Ascidia larva	39	1.57	0.0093	0.02	9	30.00
Thaliacea	Salpa sp.	2	0.08	0.21	0.48	1	3.33
Other		2	0.08	0.36	0.81		
	unidentified	1	0.04	0.01	0.02	2	6.67
	unid. remains	0	0.00	0.3362	0.76	15	50.00
	eggs	1	0.04	0.012	0.03	1	3.33
TOTAL		2481		44.16			

Table D3. Overall diet of redbait *Emmelichthys nitidus* from the SEFHES project data.

Redbait - *Emmelichthys nitidus*
Number of Stomachs: 118

Number of Stomachs Containing Prey: 71

Percentage of Stomachs Containing Prey: 60.17%

Size range: 148-300

Major prey group	Prey Taxon	Number		Reconstituted Mass		Occurrence	
		n	%	g	%	n	%
Annelida		2	0.07	0.00	0.00		
Polychaeta	Annelida	2	0.07	0.001	0.00	1	1.41
Arthropoda		2472	81.18	7.16	32.03		
Copepoda	Acartia sp.	6	0.20	0.00135	0.01	2	2.82
	Calanoida	166	5.45	0.0956	0.43	9	12.68
	Calanus sp.	222	7.29	0.1342	0.60	14	19.72
	Candacia sp.	435	14.29	0.26864	1.20	16	22.54

Major prey group	Prey Taxon	Number		Reconstituted Mass		Occurrence	
		n	%	g	%	n	%
	Candacia sp. remains	0	0.00	0.0279	0.12	4	5.63
	Candacidae	2	0.07	0.00005	0.00	1	1.41
	Copepoda	95	3.12	0.0165	0.07	7	9.86
	Copepoda remains	0	0.00	0.10062	0.45	12	16.90
	Cyclopoida	1	0.03	0.0007	0.00	1	1.41
	Eucalanidae	1	0.03	0.0001	0.00	1	1.41
	Euchirella sp.	11	0.36	0.0105	0.05	2	2.82
	Metridia sp. cf. lucens	6	0.20	0.0005	0.00	2	2.82
	Oithona sp.	1	0.03	0.0005	0.00	1	1.41
	Oncaea sp.	195	6.40	0.00909	0.04	22	30.99
	Pleuromamma abdominalis	7	0.23	0.0108	0.05	1	1.41
	Pleuromamma gracilis	15	0.49	0.0039	0.02	1	1.41
	Pleuromamma sp.	252	8.28	0.1005	0.45	11	15.49
	Rhincalanus sp.	7	0.23	0.0058	0.03	4	5.63
	Temora sp.	835	27.42	0.09449	0.42	26	36.62
	Temora sp. remains	0	0.00	0.0201	0.09	2	2.82
Malacostraca	Anomura larva	3	0.10	0.00022	0.00	3	4.23
	Bentheuphausia amblyops	33	1.08	0.87	3.89	1	1.41
	Caprellidae	1	0.03	0.0003	0.00	1	1.41
	Crustacea	15	0.49	0.0205	0.09	7	9.86
	Crustacea larva	11	0.36	0.0038	0.02	3	4.23
	Crustacea remains	0	0.00	2.6503	11.86	24	33.80
	Cymodoce lis	2	0.07	0.0058	0.03	1	1.41
	Decapoda larva	6	0.20	0.0026	0.01	1	1.41
	Ebalia tuberculosa	1	0.03	0.0001	0.00	1	1.41
	Eucarida remains	6	0.20	0.39	1.74	2	2.82
	Euphausiacea	93	3.05	1.6154	7.23	7	9.86
	Euphausiacea larva	4	0.13	0.0047	0.02	2	2.82
	Euphuasiacea remains	0	0.00	0.44	1.97	2	2.82
	Gammaridea	1	0.03	0.0127	0.06	1	1.41
	Gammaridea 2	1	0.03	0.0038	0.02	1	1.41
	Gammaridea 3	1	0.03	0.00002	0.00	1	1.41
	Gammaridea 4	4	0.13	0.0017	0.01	3	4.23
	Hyperiidae	4	0.13	0.0024	0.01	2	2.82
	Hyperiidae 2	2	0.07	0.0001	0.00	1	1.41
	Hyperiidae 3	2	0.07	0.0003	0.00	2	2.82
	Isopoda	1	0.03	0.0007	0.00	1	1.41
	Isopoda Seriols sp.	1	0.03	0.00002	0.00	1	1.41
	Leptochela sydniensis	1	0.03	0.0023	0.01	1	1.41
	Mysidacea	1	0.03	0.0001	0.00	1	1.41
	Natantia	1	0.03	0.0022	0.01	1	1.41
	Reptantia larva	2	0.07	0.0019	0.01	2	2.82
	Thysanoessa sp.	1	0.03	0.006	0.03	1	1.41
	Thysanopoda sp.	16	0.53	0.22	0.98	1	1.41
	Zoea	1	0.03	0.001	0.00	1	1.41
Bryozoa		1	0.03	0.002	0.01		
	Brachyura	1	0.03	0.0021	0.01	1	1.41
Chordata		156	5.12	4.57	20.45		
Osteichthyes	fish remains	155	5.09	0.91142	4.08	44	61.97
Thaliacea	Pyrosoma sp.	1	0.03	3.6591	16.37	4	5.63
Cnidaria		214	7.03	1.27	5.66		
Hydrozoa	Medusa remains	0	0.00	0.0053	0.02	1	1.41
	Siphonophora sp.	214	7.03	1.2597	5.64	25	35.21
Hemichordata		14	0.46	0.02	0.07		
	Chaetognatha	14	0.46	0.0162	0.07	4	5.63
Mollusca		140	4.60	0.13	0.59		

Major prey group	Prey Taxon	Number		Reconstituted Mass		Occurrence	
		n	%	g	%	n	%
	Mollusca	1	0.03	0.0005	0.00	1	1.41
Cephalopoda	Histioteuthis sp.	6	0.20	0.0289	0.13	3	4.23
Gastropoda	Gastropoda	3	0.10	0.0112	0.05	2	2.82
	Gastropoda 15	6	0.20	0.0505	0.23	3	4.23
	Pteropoda	124	4.07	0.0407	0.18	5	7.04
Tunicata		37.00	1.22	0.95	4.27		
Appendicularia	Oikopleura	2	0.07	0.001	0.00	1	1.41
Ascidiacea	Ascidia larva	2	0.07	0.00011	0.00	2	2.82
	Ascidia (remains)	0	0.00	0.019	0.08	3	4.23
	Ascidia (pelagic)	2	0.07	0.0318	0.14	2	2.82
	pelagic Ascidia	18	0.59	0.0694	0.31	8	11.27
Thaliacea	Salpa sp.	13	0.43	0.8335	3.73	9	12.68
Other		9.00	0.30	8.25	36.91		
	unid. remains	0	0.00	8.2473	36.89	38	53.52
	eggs	9	0.30	0.00427	0.02	4	5.63
TOTAL		3045		22.35			

Table D4. Overall diet of jack mackerel *Trachurus declivis* from the SEFHES project data.

Common Jack Mackerel - *Trachurus declivis*
Number of Stomachs: 580

Number of Stomachs Containing Prey: 314

Percentage of Stomachs Containing Prey: 54.14%

Size range: 84-421

Major prey group	Prey Taxon	Number		Reconstituted Mass		Occurrence	
		n	%	g	%	n	%
Annelida		4	0.01	0.03	0.02		
Polychaeta	Annelida 4	1	0.00	0.0001	0.00	1	0.32
	Polychaeta remains	0	0.00	0.0269	0.02	1	0.32
	Polychaeta	2	0.01	0.0018	0.00	1	0.32
	Serpulidae 3	0	0.00	0.0022	0.00	1	0.32
	Serpulidae 1	1	0.00	0.0008	0.00	1	0.32
Arthropoda		28223	95.74	103.48	64.00		
	Cladocera	6	0.02	0.0001	0.00	1	0.32
Copepoda	Cyclopoida 3	4	0.01	0.0006	0.00	1	0.32
	Pleuromamma sp. remains	0	0.00	0.8076	0.50	7	2.23
	Labidocera tasmanica	1	0.00	0.0006	0.00	1	0.32
	Pleuromamma sp.	3454	11.72	0.3582	0.22	7	2.23
	Acartia sp.	13	0.04	0.0049	0.00	6	1.91
	Cyclopoida 2	19	0.06	0.0010	0.00	1	0.32
	Oncaea sp.	37	0.13	0.0017	0.00	4	1.27
	Oithona sp.	1	0.00	0.0001	0.00	1	0.32
	Eucalanidae	1	0.00	0.0001	0.00	1	0.32
	Metridia sp. cf. lucens	180	0.61	0.0397	0.02	7	2.23
	Cyclopoida	1417	4.81	0.1336	0.08	12	3.82
	Candacidae	1	0.00	0.0001	0.00	1	0.32
	Calanoida 1	253	0.86	0.0537	0.03	6	1.91
	Aetidae	230	0.78	0.3400	0.21	1	0.32
	Calanoida 2	67	0.23	0.0041	0.00	7	2.23
	Calanoida remains	0	0.00	0.0775	0.05	2	0.64
	Calanus sp.	453	1.54	0.0956	0.06	22	7.01
	Candacia sp.	7525	25.53	3.0094	1.86	66	21.02

Major prey group	Prey Taxon	Number		Reconstituted Mass		Occur-rence	
		n	%	g	%	n	%
	Candacia sp. remains	0	0.00	0.0067	0.00	2	0.64
	Temora sp.	1564	5.31	0.1913	0.12	26	8.28
	Cornucalanus sp.	3	0.01	0.0006	0.00	3	0.96
	Subencalanus longiceps	3	0.01	0.0032	0.00	1	0.32
	Copepoda remains	0	0.00	0.4500	0.28	11	3.50
	Calanoida	791	2.68	0.1536	0.10	20	6.37
	Centropages sp.	13	0.04	0.0095	0.01	1	0.32
	Centropagidae	300	1.02	0.1906	0.12	3	0.96
	Copepoda	139	0.47	0.0335	0.02	24	7.64
	Paracalanus sp.	31	0.11	0.0788	0.05	2	0.64
Malacostraca	Gammaridea 19	4	0.01	0.0037	0.00	2	0.64
	Gnathia cf. africana	1	0.00	0.0010	0.00	1	0.32
	Zoea remains	0	0.00	0.0074	0.00	1	0.32
	Euphuasiacea remains	0	0.00	1.1846	0.73	6	1.91
	Brachyura larva	7	0.02	0.0851	0.05	4	1.27
	Euphausiacea larva	16	0.05	0.0050	0.00	1	0.32
	Gammaridea	16	0.05	0.1595	0.10	10	3.18
	Euphausiacea	1904	6.46	6.7883	4.20	30	9.55
	Eucarida remains	0	0.00	20.6177	12.75	32	10.19
	Eucarida	337	1.14	4.8548	3.00	12	3.82
	Decapoda remains	0	0.00	0.5186	0.32	3	0.96
	Decapoda larva	73	0.25	0.0393	0.02	8	2.55
	Decapoda	5	0.02	0.0420	0.03	3	0.96
	Cumacea	1	0.00	0.0024	0.00	1	0.32
	Hyperiidae	7	0.02	0.0125	0.01	2	0.64
	Crustacea larva	2558	8.68	0.5062	0.31	10	3.18
	Isopoda	2	0.01	0.0079	0.00	2	0.64
	Crustacea	24	0.08	0.6523	0.40	7	2.23
	Caridea	25	0.08	0.9782	0.60	4	1.27
	Caprellidae	1	0.00	0.0002	0.00	1	0.32
	Crustacea remains	7	0.02	22.5135	13.92	119	37.90
	Reptantia	1	0.00	0.0720	0.04	1	0.32
	Hyperiidae 3	6	0.02	0.0137	0.01	3	0.96
	Nyctiphanes sp.	1144	3.88	2.7688	1.71	4	1.27
	Nematoseclis sp.	375	1.27	3.2200	1.99	1	0.32
	Bentheuphausia amblyops	49	0.17	0.2365	0.15	4	1.27
	Pontoniinae	3	0.01	0.0599	0.04	3	0.96
	Nematobrachion sp.	10	0.03	0.7610	0.47	1	0.32
	Natantia	142	0.48	0.4912	0.30	15	4.78
	Mysidacea	2	0.01	0.0006	0.00	2	0.64
	Anomura larva	194	0.66	0.0377	0.02	12	3.82
	Hyperiidae 2	2	0.01	0.0034	0.00	1	0.32
	Meganyctiphanes sp.	85	0.29	0.2800	0.17	1	0.32
	Thysanopoda sp.	3269	11.09	17.1474	10.61	19	6.05
	Ibacus sp. 2	1	0.00	0.1000	0.06	1	0.32
	Gammaridea 4	1	0.00	0.0079	0.00	1	0.32
	Zoea	48	0.16	0.0144	0.01	14	4.46
	Amphipoda	12	0.04	0.1338	0.08	6	1.91
	Lucifer sp.	3	0.01	0.0012	0.00	2	0.64
	Reptantia larva	9	0.03	0.0507	0.03	6	1.91
	Thysanoessa sp.	1307	4.43	12.9501	8.01	9	2.87
	Tessarabrachion oculatum	1	0.00	0.0261	0.02	1	0.32
	Stomatopoda	27	0.09	0.0280	0.02	2	0.64
	Scyllarus sp.	1	0.00	0.0015	0.00	1	0.32
	Lanocira sp.	14	0.05	0.0283	0.02	2	0.64
Ostracoda	Conchoecia mollis	2	0.01	0.0002	0.00	1	0.32
	Conchoecia sp	4	0.01	0.0005	0.00	2	0.64

Major prey group	Prey Taxon	Number		Reconstituted Mass		Occur-rence	
		n	%	g	%	n	%
	Ostracoda 12	1	0.00	0.0002	0.00	1	0.32
	Ostracoda 21	1	0.00	0.0001	0.00	1	0.32
	Ostracoda	6	0.02	0.0051	0.00	4	1.27
	Ostracoda 28	8	0.03	0.0106	0.01	4	1.27
	Ostracoda 11	1	0.00	0.0001	0.00	1	0.32
Bryozoa		4	0.01	0.04	0.02		
	Bryozoa 23 remains	0	0.00	0.0010	0.00	1	0.32
	Bryozoa	4	0.01	0.0351	0.02	3	0.96
Chordata		409	1.39	50.78	31.41		
Osteichthyes	Apogonops anomalus	1	0.00	0.5300	0.33	1	0.32
	Scorpaenidae	5	0.02	0.3558	0.22	1	0.32
	Fish 1	7	0.02	0.7698	0.48	5	1.59
	Fish 11	3	0.01	0.1736	0.11	2	0.64
	fish remains	285	0.97	15.6047	9.65	170	54.14
	fish	54	0.18	4.7501	2.94	50	15.92
	Maurolicus muelleri	29	0.10	19.9751	12.35	2	0.64
	Triglidae	1	0.00	0.0328	0.02	1	0.32
	Pleuronectidae	2	0.01	0.1132	0.07	2	0.64
	Lampanyctodes hectoris	17	0.06	8.4200	5.21	4	1.27
	Larval fish	5	0.02	0.0573	0.04	2	0.64
Cnidaria		112	0.38	1.86	1.15		
	Cnidaria remains	0	0.00	0.0624	0.04	2	0.64
Hydrozoa	Siphonophora sp.	111	0.38	1.6580	1.03	32	10.19
	Cnidaria	0	0.00	0.1312	0.08	2	0.64
	Coral	1	0.00	0.0046	0.00	1	0.32
Echinodermata		3	0.01	0.51	0.31		
Crinoidea	Crinoidea	3	0.01	0.4789	0.30	3	0.96
Echinoidea	Echinoidea remains	0	0.00	0.0261	0.02	3	0.96
Hemichordata		0	0.00	0.00	0.00		
	Chaetognatha	0	0.00	0.0011	0.00	1	0.32
Mollusca		591	2.00	0.61	0.38		
	Mollusca	1	0.00	0.0010	0.00	1	0.32
	Mollusca remains	1	0.00	0.0214	0.01	1	0.32
Bivalvia	Bivalvia larva	3	0.01	0.0013	0.00	1	0.32
	Bivalvia	1	0.00	0.0002	0.00	1	0.32
Gastropoda	Gastropoda 5	2	0.01	0.0073	0.00	1	0.32
	Gastropoda veliger	334	1.13	0.3881	0.24	31	9.87
	Marginellidae	8	0.03	0.0411	0.03	4	1.27
	Turbiniform shell	18	0.06	0.0272	0.02	6	1.91
	Turitellidae	4	0.01	0.0173	0.01	3	0.96
	Gastropoda	219	0.74	0.1085	0.07	48	15.29
Platyhelminthes		1	0.00	0.00	0.00		
	Platyhelminthes	1	0.00	0.0000	0.00	1	0.32
Porifera		0	0.00	0.02	0.01		
	Porifera 45	0	0.00	0.0149	0.01	1	0.32
	Porifera remains	0	0.00	0.0030	0.00	1	0.32
Tunicata		57	0.19	0.62	0.38		
Ascidiacea	Didemnidae 1	2	0.01	0.0364	0.02	2	0.64
	pelagic Ascidia or Cnidaria	3	0.01	0.4818	0.30	7	2.23
	Ascidia remains	0	0.00	0.0400	0.02	1	0.32
	Ascidia larva	52	0.18	0.0035	0.00	23	7.32
	Ascidia (pelagic) remains	0	0.00	0.0431	0.03	3	0.96
Thaliacea	Salpa sp.	0	0.00	0.0134	0.01	1	0.32
Chlorophyta		76	0.26	3.75	2.32		
	microscopic phytoplankton	34	0.12	0.0001	0.00	1	0.32
	Nematoda	2	0.01	0.0002	0.00	1	0.32
	mucus	0	0.00	0.0348	0.02	2	0.64

Major prey group	Prey Taxon	Number		Reconstituted Mass		Occur-rence	
		n	%	g	%	n	%
	unid. remains	1	0.00	2.8237	1.75	48	15.29
	unid. larva	6	0.02	0.0272	0.02	1	0.32
	sediment	3	0.01	0.8507	0.53	14	4.46
	Foraminifera	6	0.02	0.0005	0.00	4	1.27
	eggs	24	0.08	0.0097	0.01	9	2.87
TOTAL		29480		161.69			

Review of Squid diet and biology

Squid parameters and diet were re-examined to ensure that the most appropriate parameters were being used when investigating the suggestion that squid might significantly impact populations of small pelagics such as redbait particularly in Tasmanian waters. Stark (2008) reviewed several dietary studies of *N. gouldi* (Machida 1983, O'Sullivan and Cullen 1983, Smith 1983, Uozumi 1998) and found that the relative contribution of pelagic crustaceans was negatively correlated with squid size but cephalopod contribution was positively correlated. The most relevant study of squid diet was of Arrow squid *Nototodarus gouldi* from Bass Strait (O'Sullivan and Cullen 1983). The diet consisted of fish such as sardines *Sardinops sagax* and barracouta *Thrysites atun*, benthopelagic crustaceans such as the comb shrimp *Leptochela sydniensis* and an isopod *Cirolana* sp., and other squid including its own species, at % frequency of occurrence of 37:35:26 respectively. Fish contribution remained constant in the O'Sullivan and Cullen (1983) study but increased in the Uozumi 1998 study. Smith (1983) found that Arrow squid from western Bass Strait ate mostly Ommastrephid squids (57% presumably by mass) and fishes, primarily pilchards (42%). A congener in New Zealand, *N. sloani* ate euphausids, amphipods, crab zoea, myctophids, saury and squid (Saito *et al.,* 1974).

Sepioteuthis australis southern calamary is also common on the shelf and represented by the squid group is. In a study of calamary from the Tasmanian east coast, Jackson and Pecl (2003) found that 5 types of fish occurred in 87% of calamary, 3 species of octopus in 23% and crustaceans occurred in 7%, however no further resolution of species was possible. Smith (1983) investigated the fishery potential of this species in the South Australian region and determined several parameters including growth rates and an annual mortality rate of 0.35.

The species composition in the model area would also probably comprise some of the more oceanic and deepwater squids although these species would be less common in the model area being further offshore. Amongst the most common is *Todarodes filippovae* Southern Ocean squid, a large pelagic squid that can reach over 500mm mantle length and over 4 kg in weight. Pethybridge (2004) investigated their diets in southern Tasmania. It ate predominantly fish (63.4%FO) with myctophids the most commonly occurring prey (35%). Squid, largely *Histioteuthis*, occurred in 19.6% of stomachs and crustacea, natant decapods, copepods and amphipods occurred in 14.6%. Mature specimens from the Tasman Sea in the early 80s more frequently ate cephalopods (males = 71%, females 55%) than fish (36% both sexes) and crustaceans occurred rarely (5%, 7% respectively) (Dunning and Brandt 1985). The lifespan of this species was suggested to be 21-23 months (Dunning and Brandt 1985) however Jackson *et al.* (2007) found that this species appears to grow faster in cooler water and lives for only about a year. Therefore a possible P/B would be in the order of 1 to 1.75-1.91.

Ommastrephes bartrami red ocean squid is the most widely distributed ommastrephid occurring circumglobally in subtropical and temperate waters (Araya 1983, Dunning 1988). It occurs usually only off eastern Australia and is the most common pelagic squid in the Tasman Sea (Dunning 1988). In western and central North Pacific feed predominantly on myctophids and squid, and rarely on planktonic crustaceans (Watanabe *et al.*2004, 2008) but there is no data on diet in this species in Australia. Off Japan *O. bartrami* ate mostly fish (59-76%) such as myctophids, sardines, mackerel larvae and sauries, cephalopods (18-30%) and few crustaceans (2-18%) (Araya 1983). Araya (1983) estimated its life span to be about a year similar to other ommastrephids (Jackson *et al.* 2007).

Moroteuthis ingens ate predominantly fish particularly *Lampanyctodes hectoris*, *Chauliodus sloani*, *Stomias boas* and other mesopelagic fishes , and squid with cannibalism at about 24% (Jackson *et al.,* 1998).However, this species is more of a deepwater species as are the previous two, therefore none would contribute to the species composition of this group as either of the first two shelf species.

References

Araya, H. (1983). Fishery, biology and stock assessment of *Ommastrephes bartramii* inthe North Pacific Ocean. *Memoirs of the National Museum of Victoria* **44**, 269-283.

Dunning, M. C. (1988). Distribution and comparative life history studies of deepwater squid of the family ommastrephidae in Australasian waters. PhD Thesis. (University of Queensland.)

Dunning, M.C., and Brandt, S.R. (1985). Distribution and life history of deep-water squid of commercial interest from Australia. *Aust. J. Mar. Fresh. Res* **36**, 343-359

Jackson, G.D., and Pecl, G. (2003). The dynamics of the summer-spawning population of the loliginid squid (*Sepioteuthis australis*) in Tasmania, Australia - a conveyor belt of recruits. *ICES Journal of Marine Science* **60**, 290-296.

Jackson, G.D., Wotherspoon, S., and Jackson, C.H. (2007). Temporal life history plasticity of the Southern Ocean squid *Todarodes filippovae* from waters off Tasmania, Australia. *Marine Biology* **150**,575-584.

Machida, S. (1983). A Brief Review of the Squid Survey by Hoyo Maru No. 67 in Southeast Australian Waters in 1979/80. *Memoirs of the National Museum Victoria: Proceedings of the Workshop on the Biology and Resource Potential of Cephalopods, Melbourne, Australia, 9-13 March, 1981* **44**, 291-295

O'Sullivan, D. and Cullen, J.M. (1983). Food of the squid *Nototodarus gouldi* in Bass Strait. *Australian Journal of Marine and Freshwater Research* 34, 261-85.

Pethybridge, H.R. (2004). Diet of squid, *T.filippovae*: lipid and stomach analysis. BSc (Hons) Thesis, University of Tasmania.

Saito, R., Kawakami, T., Hamabe, M., and Matsushita,Y. (1974). Preliminary note on the ecology of the ommastrephid squid *Nototodarus sloani sloani* (Gray) on New Zealand waters. *Bulletin of the Tokai Regional Fisheries Laboratory* **79**, 35-68.

Smith, H.K. (1983). Fishery and biology of Nototodarus gouldi (McCoy, 1888) in western Bass Strait. *Memoirs of the National Museum of Victoria* **44**, 285-290.

Stark, K. E. (2008). 'Ecology of the Arrow Squid (*Nototodarus gouldi*) in Southeastern Australian Waters.' PhD .University of Tasmania.

Uozumi, Y. (1998). Fishery Biology of Arrow Squids, *Nototodarus gouldi* and *N. sloanii* in New Zealand Waters. *Bulletin of the National Research Institute of Far Seas Fisheries* **35**,1-111

Watanabe, H., Kubodera, T., Ichii, T., and Kawahara, S. (2004). Feeding habits of neon flying squid *Ommastrephes bartramii* in the transitional region of the central North Pacific. *Marine Ecology-Progress Series* **266**, 173-184.

Watanabe, H., Kubodera, T., Ichii, T., Sakai, M., Moku, M., and Seitou, M. (2008). Diet and sexual maturation of the neon flying squid *Ommastrephes bartramii* during autumn and spring in the Kuroshio-Oyashio transition region. *Journal of the Marine Biological Association of the United Kingdom* **88**, 381-389.

Appendix E Ecosim-EBS Results

Table E1. Ecosim-EBS biomasses and catches for various vulnerability settings for seal/redbait interactions; default =all interactions are equal, seal/redbait interaction v=1 (bottom-up control) and v=10000 (top-down control).

	Start	**Default v=2**		**Seal/redbait v=1**		**Seal/redbait v=10000**	
Group name	**Biomass**	**End Biomass**	**End Catch**	**End Biomass**	**End Catch**	**End Biomass**	**End Catch**
Toothed whales	0.0130	0.013		0.0130		0.0131	
Baleen whales	0.0060	0.006		0.0060		0.0060	
Seals	0.0431	0.072	0.0009	0.0679	0.0009	0.0704	0.0009
Seabirds	0.0030	0.003		0.0028		0.0027	
Penguins	0.0010	0.001		0.0009		0.0011	
Tunas and billfish	0.1583	0.161	0.0178	0.1162	0.0228	0.0726	0.0142
Pelagic sharks	0.0043	0.007	0.0004	0.0065	0.0004	0.0066	0.0004
Demersal sharks	1.2149	1.125	0.0171	1.1467	0.0174	1.1495	0.0174
Rays	1.2000	1.180	0.0113	1.1839	0.0113	1.1799	0.0113
Warehous	0.8990	0.812	0.0655	0.6991	0.0564	1.2966	0.1046
Redbait	2.1953	1.671	0.0000	2.0442	0.0000	0.4593	0.0000
Redfish	1.0696	1.010	0.0427	1.0029	0.0424	1.0241	0.0433
Ling	0.4398	0.400	0.0161	0.4026	0.0162	0.4018	0.0162
Dories	0.3899	0.359	0.0121	0.3700	0.0124	0.3365	0.0113
Jack mackerel	5.9940	5.051	0.0189	5.0073	0.0187	5.2851	0.0197
Jackass morwong	0.6279	0.613	0.0182	0.6079	0.0180	0.6169	0.0183
Flathead	0.3724	0.311	0.0574	0.3119	0.0575	0.3208	0.0592
Gemfish	0.1317	0.096	0.0030	0.0995	0.0031	0.0921	0.0029
Shelf ocean perch	0.1807	0.174	0.0082	0.1637	0.0078	0.2133	0.0101
Chinaman leatherjacket	0.0052	0.005	0.0006	0.0054		0.0073	
Cucumberfish	2.4901	2.763	0.0021	2.7307	0.0021	2.9361	0.0022
Eastern school whiting	1.3692	1.401	0.0159	1.4140	0.0160	1.3935	0.0158
Cardinal fish	4.6945	4.971	0.00004	4.9853	0.0000	4.9472	0.0000
Shelf small invertebrate feeders	4.4705	4.600	0.0265	4.6011	0.0265	4.6023	0.0265
Shelf small predators	0.6872	0.610	0.0008	0.5833	0.0007	0.6167	0.0008
Shelf medium invertebrate feeders	1.1610	1.236	0.0228	1.2354	0.0228	1.2202	0.0225
Shelf medium predators	0.4292	0.284	0.0037	0.2989	0.0039	0.2731	0.0036
Shelf large invertebrate feeders	0.0900	0.091	0.0002	0.0912	0.0002	0.0880	0.0002
Shelf large predators	2.5801	2.688	0.0529	2.6853	0.0529	2.7040	0.0532
Blue-eye trevalla	0.0490	0.065	0.0015	0.0566	0.0013	0.0859	0.0020
Blue grenadier	0.1508	0.149	0.0054	0.1487	0.0054	0.1480	0.0054
Slope ocean perch	0.0972	0.096	0.0048	0.0927	0.0046	0.1125	0.0056
Deepsea cod	0.0658	0.065	0.0004	0.0656	0.0004	0.0649	0.0003
Oreos	0.0117	0.011	0.0007	0.0114	0.0007	0.0115	0.0007
Slope small invertebrate feeders	0.1110	0.115	0.0002	0.1146	0.0002	0.1123	0.0002
Slope small predators	0.2715	0.272	0.0002	0.2724	0.0002	0.2646	0.0002

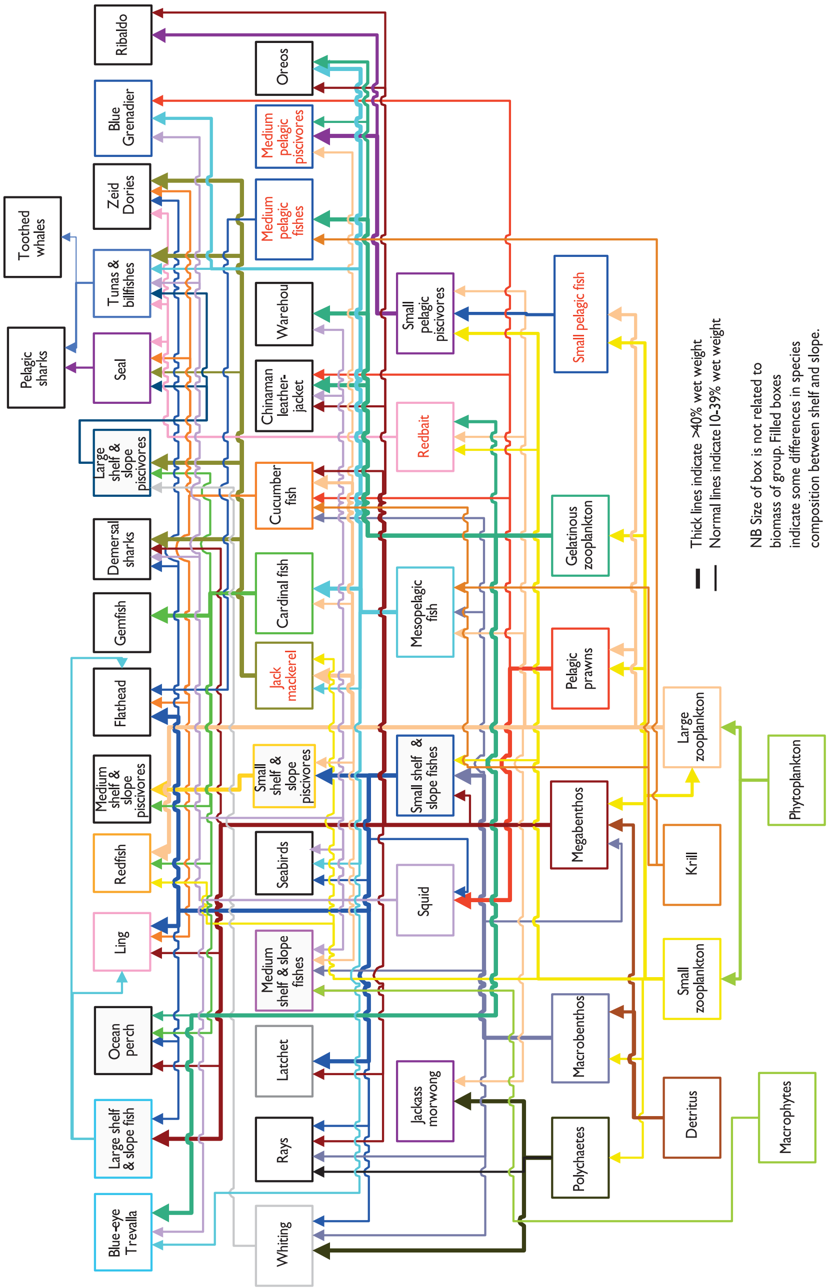
	Start	Default v=2		Seal/redbait v=1		Seal/redbait v=10000	
Group name	**Bio-mass**	**End Bio-mass**	**End Catch**	**End Bio-mass**	**End Catch**	**End Bio-mass**	**End Catch**
Slope medium invertebrate feeders	1.9800	2.032	0.0092	2.0159	0.0091	2.0277	0.0091
Slope medium predators	0.1800	0.185	0.0006	0.1808	0.0006	0.1836	0.0006
Slope large invertebrate feeders	0.7373	0.815		0.8214		0.7828	
Slope large predators	0.0720	0.065	0.0038	0.0650	0.0038	0.0664	0.0039
Pelagic small invertebrate feeders	5.9389	6.008	0.0518	6.0035	0.0518	6.0183	0.0519
Pelagic medium invertebrate feeders	0.1310	0.138	0.0004	0.1348	0.0004	0.1463	0.0004
Pelagic medium predators	0.3200	0.353	0.0217	0.3298	0.0203	0.4303	0.0265
Pelagic large invertebrate feeders	0.0393	0.039		0.0391		0.0406	
Pelagic large predators	0.0092	0.009	0.0020	0.0092	0.0020	0.0092	0.0020
Mesopelagics	38.0006	37.827	0.0000	37.8262	0.0000	37.7933	0.000001
Squid	1.6293	1.613	0.0038	1.6177	0.0039	1.5884	0.0038
Pelagic prawns	3.0585	3.062	0.0002	3.0575	0.0002	3.0784	0.0002
Macrobenthos	26.5967	26.647	0.0022	26.6451	0.0022	26.6367	0.0022
Megabenthos	7.1979	7.080	0.0146	7.0942	0.0147	7.0357	0.0145
Polychaeta	6.0748	5.989		5.9759		5.9965	
Gelatinous nekton	2.6900	3.082		2.7054		3.8947	
Large zooplankton	13.6308	13.858		13.7162		14.0524	
Small zooplankton	28.4113	28.303		28.2973		28.0006	
Primary producers	19.0000	19.006		18.9987		19.0291	
Detritus	9.9997	10.003		9.9993		10.0122	
Discards	0.1685	0.142		0.1417		0.1449	
Total	199.5440	198.747	0.5387	198.3203	0.5322	199.1047	**0.5844**

Table E2. Ecosim-EBS biomasses and catches per group for different numbers of fitted vulnerabilities to sensitive predator /prey interactions.

	Fitted 25		**Fitted 30**		**Fitted 50**		**Fitted 25 with PP forcing**	
Group name	**End Biomass**	**End Catch**	**End Biomass**	**End Catch**	**End Biomass**	**End Catch**	**End Biomass**	**End Catch**
Toothed whales	0.012		0.012		0.012		0.012	
Baleen whales	0.006		0.006		0.006		0.006	
Seals	0.080	0.0010	0.069	0.0009	0.054	0.0007	0.081	0.0010
Seabirds	0.003		0.003		0.003		0.003	
Penguins	0.001		0.001		0.001		0.001	
Tunas and billfish	0.127	0.0140	0.145	0.0160	0.124	0.0138	0.140	0.0154
Pelagic sharks	0.006	0.0004	0.006	0.0004	0.005	0.0003	0.006	0.0004
Demersal sharks	0.993	0.0151	0.942	0.0143	0.899	0.0136	0.970	0.0147
Rays	1.168	0.0112	1.173	0.0112	1.223	0.0117	1.157	0.0111
Warehous	0.365	0.0294	0.040	0.0032	0.010	0.0008	0.465	0.0375
Redbait	2.316	0.0000	3.250	0.0000	3.364	0.0000	2.738	0.0000
Redfish	0.816	0.0345	0.898	0.0380	1.039	0.0440	0.791	0.0334
Ling	0.275	0.0111	0.303	0.0122	0.298	0.0120	0.265	0.0106
Dories	0.274	0.0092	0.196	0.0066	0.291	0.0098	0.283	0.0095
Jack mackerel	2.449	0.0091	1.658	0.0062	0.080	0.0003	2.284	0.0085
Jackass morwong	0.426	0.0126	0.469	0.0139	0.510	0.0151	0.423	0.0126
Flathead	0.547	0.1008	0.533	0.0984	0.668	0.1233	0.482	0.0889
Gemfish	0.077	0.0024	0.086	0.0027	0.103	0.0032	0.076	0.0024
Shelf ocean perch	0.146	0.0069	0.200	0.0095	0.158	0.0075	0.177	0.0084
Chinaman leatherjacket	0.004	0.0005	0.005	0.0006	0.004	0.0005	0.005	0.0006
Cucumberfish	2.998	0.0023	3.160	0.0024	2.775	0.0021	3.251	0.0025
Eastern school whiting	1.443	0.0164	1.426	0.0162	1.464	0.0166	1.466	0.0166
Cardinal fish	5.876	0.0000	5.891	0.0000	6.001	0.0001	5.856	0.0000
Shelf small invertebrate feeders	6.514	0.0375	6.079	0.0350	6.180	0.0355	6.525	0.0375
Shelf small predators	0.348	0.0004	0.410	0.0005	0.493	0.0006	0.355	0.0005
Shelf medium invertebrate feeders	1.388	0.0256	1.338	0.0247	1.366	0.0252	1.365	0.0251
Shelf medium predators	0.048	0.0006	0.095	0.0012	0.093	0.0012	0.049	0.0006
Shelf large invertebrate feeders	0.095	0.0003	0.098	0.0003	0.102	0.0003	0.093	0.0003
Shelf large predators	2.793	0.0550	2.728	0.0537	2.610	0.0514	2.888	0.0568
Blue-eye trevalla	0.045	0.0010	0.055	0.0013	0.045	0.0010	0.056	0.0013
Blue grenadier	0.153	0.0056	0.155	0.0056	0.164	0.0060	0.152	0.0055
Slope ocean perch	0.080	0.0040	0.089	0.0044	0.080	0.0040	0.089	0.0045
Deepsea cod	0.066	0.0004	0.065	0.0004	0.067	0.0004	0.066	0.0004
Oreos	0.012	0.0007	0.012	0.0007	0.013	0.0008	0.011	0.0007
Slope small invertebrate feeders	0.123	0.0002	0.127	0.0002	0.131	0.0002	0.125	0.0002
Slope small predators	0.286	0.0002	0.279	0.0002	0.299	0.0003	0.283	0.0002
Slope medium invertebrate feeders	2.231	0.0101	2.317	0.0105	2.529	0.0114	2.156	0.0097
Slope medium predators	0.191	0.0006	0.201	0.0007	0.210	0.0007	0.193	0.0007
Slope large invertebrate feeders	0.723		0.683		0.414		0.758	
Slope large predators	0.052	0.0031	0.049	0.0029	0.045	0.0026	0.051	0.0030
Pelagic small invertebrate feeders	5.656	0.0488	5.723	0.0494	5.497	0.0474	5.871	0.0506
Pelagic medium invertebrate feeders	0.144	0.0004	0.154	0.0005	0.162	0.0005	0.143	0.0004

	Fitted 25		**Fitted 30**		**Fitted 50**		**Fitted 25 with PP forcing**	
Group name	**End Bio-mass**	**End Catch**	**End Bio-mass**	**End Catch**	**End Bio-mass**	**End Catch**	**End Bio-mass**	**End Catch**
Pelagic medium predators	0.314	0.0193	0.375	0.0231	0.344	0.0212	0.371	0.0228
Pelagic large invertebrate feeders	0.042		0.045		0.049		0.041	
Pelagic large predators	0.009	0.0020	0.009	0.0021	0.009	0.0021	0.009	0.0020
Mesopelagics	37.885	0.0000	37.997	0.0000	39.405	0.0000	38.050	0.0000
Squid	1.657	0.0040	1.699	0.0041	1.744	0.0042	1.674	0.0040
Pelagic prawns	2.914	0.0002	2.873	0.0002	2.801	0.0002	2.979	0.0002
Macrobenthos	27.130	0.0022	27.196	0.0022	27.561	0.0023	27.235	0.0022
Megabenthos	6.775	0.0140	6.773	0.0140	6.980	0.0144	6.815	0.0141
Polychaeta	5.576		5.654		5.419		5.721	
Gelatinous nekton	2.160		2.720		2.014		2.855	
Large zooplankton	14.650		15.239		16.215		14.274	
Small zooplankton	28.555		28.053		27.916		28.525	
Primary producers	18.925		18.980		18.961		19.360	
Detritus	9.969		9.991		9.983		10.178	
Discards	0.147		0.145		0.150		0.147	
Total	198.060	0.5130	198.877	0.4902	199.147	0.5090	200.404	**0.5177**

Appendix F Ecosim-EBS and Atlantis-SE foodwebs



NB Size of box is not related to biomass of group. Filled boxes indicate some differences in species composition between shelf and slope.

Figure F1. Foodweb of SEF 269 model.

Figure F2. Potential diet connections in Atlantis-SE. Note that for clarity the potential dietary connections of the benthic invertebrates have been omitted. Also note that this diagram is an aggregate potential diet across age classes and that the Atlantis-SE does actually include ontogenetic diet shifts.

Contact Us

Phone: 1300 363 400
+61 3 9545 2176

Email: enquiries@csiro.au

Web: www.csiro.au

Your CSIRO

Australia is founding its future on science and innovation. Its national science agency, CSIRO, is a powerhouse of ideas, technologies and skills for building prosperity, growth, health and sustainability. It serves governments, industries, business and communities across the nation.