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Estimating Secondary Production from the Epifaunal and Infaunal Macrobenthos

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MAFCONS

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1. Introduction

Traditional methods for calculating secondary production from the benthos have been applied to single animals or populations based on the change in body mass or growth over time. However, the methods used to calculate this generally involve the destruction of samples and require intensive sampling of the same population to account for changes over time. Methods include those based on cohort analysis, size class based methods and the relationship between productivity and mortality (Cushman *et al*., 1978; Wildish & Peer, 1981; Crisp, 1984; Morin *et al*., 1987). None of these methods are practical when trying to quantify secondary production at the community level. In the MAFCONS project, assessments of the secondary production from the infaunal and epifaunal benthos at between 100 and 150 stations per year over two years are being undertaken. The ultimate aim is to examine the relationship between demersal fish diversity and composition, and the distribution of secondary production and fisheries disturbance (www.mafcons.org/).

Over the last 20 years, efforts have turned towards parameterising empirical models that can be used to estimate secondary production (for review see Brey, 2002). These models describe the relationships between easily measured parameters such as biomass, individual body mass and water temperature with production (P) or the production/biomass (P/B) ratio for individual populations. Empirical relationships between these parameters are calculated using the combined published results of the traditional studies as described above. It is then possible to predict P or the P/B ratio for new sampled populations just using data for the easily measured parameters such as biomass and temperature. All of these approaches depend more or less directly on the negative exponential relationship between metabolic rate and body mass (see e.g. Peters 1983).

The earliest empirical models related the P/B ratio to one parameter. For example, the P/B ratio was related to lifespan by Robertson (1979), to adult body mass (at maturity) by Banse & Mosher (1980) and to mean individual body mass by Schwinghamer *et al*. (1986). Two-parameter models were published by Brey (1990) (P vs. biomass and mean individual body mass) and by Edgar (1990a) (P vs. mean individual body mass and bottom water temperature). Even more complex three-parameter models were published by Morin & Bourassa (1992), who related production of stream benthos to biomass, mean body mass and annual mean water temperature; Plante and Downing (1989), who related production of lake benthos to biomass, maximum body mass, and surface water temperature, and; Tumbiolo & Downing (1994), who related production of marine benthos to biomass, maximum body mass, surface water temperature and water depth. More recent models have generally all included environmental parameters (usually water temperature and sometimes depth) in recognition of the influence of these on growth rates and thus also productivity.

Brey *et al*. (1996) and Brey (1999) unified all previous habitat-specific approaches into one large model for macrofaunal benthos in general. In Brey *et al*. (1996) "Artificial Neural Networks" were trained to estimate P/B from body mass, taxon, mode of living, water temperature and water depth and it is suggested that this approach performs slightly better than the usual multiple linear models. The latest models are available on a website maintained by Brey (2002). Here the relationships are updated regularly to include any new field studies of direct measurements of population production and P/B ratios, thus increasing the number of studies that the empirical model is based on.

In all cases, models are based on data for individual species populations. Thus production is calculated for each species making up a community and all species totals are then summed to give total community production. Where species level data do not exist, the variability around mean individual weight will be likely to increase as taxonomic resolution decreases and this may affect the validity of using the empirical models that include mean individual weight as a parameter. However, Edgar's (1990a) model was parameterised using individuals that had been sorted to higher taxonomic groups but also size structured using a sieving method. Here the size structuring should reduce the variability around the mean individual weight per taxon group. When carrying out routine, large-scale surveys such as those undertaken in this project, it may not be feasible to work up the data to species level (particularly for the infaunal samples). In this report, the secondary production of size structured infaunal data has been estimated using Edgar's (1990a and b) method. This approach is also applied to the epifaunal data, which although not size structured by sieving, are available as mean individual weights per species. The validity of using this approach for the epifaunal and infaunal macrobenthos of the North Sea is explored and discussed.

2. Methods

2.1 Sampling of Infauna and Epifauna

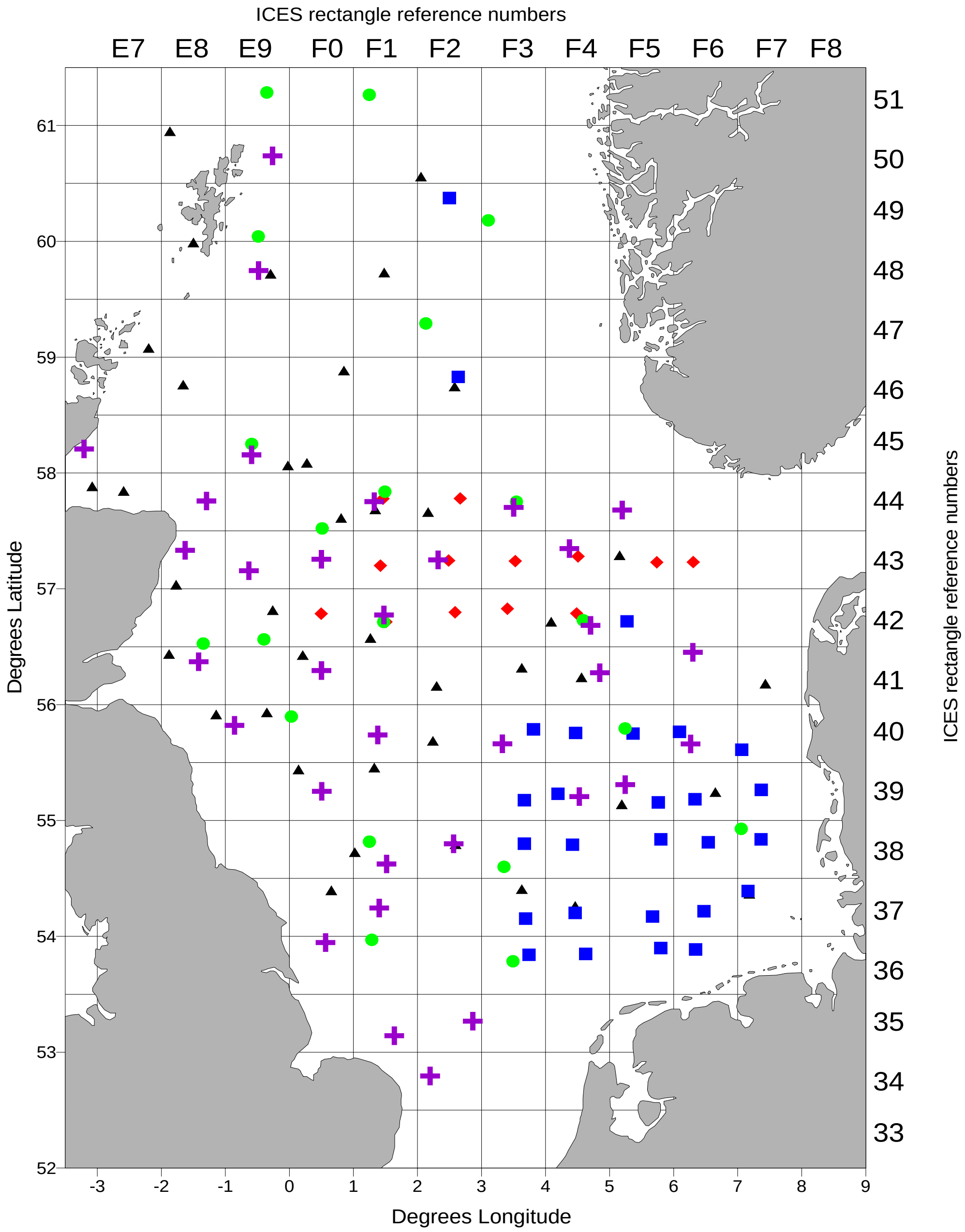
At each station, one five minute 2metre beam trawl tow was taken for epifauna and five $0.1m^2$ Van Veen grabs for infauna. Bottom water temperature data were recorded using a CTD at the time of sampling. A total of 134 Stations were sampled across the North Sea (Figure 2.1).

The following countries contributed to the 2003 MAFCONS survey:
Scotland (FRS Marine Laboratory)
England (University of Wales Swansea with CEFAS, Lowestoft;)
The Netherlands (RIVO, Ijmuiden)
Belgium (Gent University)
Germany (Senckenburg Institute and Institute for Sea Fisheries)
Norway (Institute for Marine Research).

Epibenthic samples were washed through a 5mm and 2mm sieve (internal mesh size), invertebrates and fish separated from the remains. All epifaunal animals were enumerated, weighed and measured to the highest resolved taxonomic level (species level in most cases). For the epifauna, total abundance (N) and total biomass (B) were standardised to numbers per $1000m^2$ by dividing the individual totals by the station specific swept area (m^2) and multiplying by 1000. Swept area was itself calculated by multiplying the total track fished by the width of the beam trawl (two metres).

Infaunal samples were washed through a stack of sieves (0.5mm, 1mm, 2mm and 4mm) and all material preserved before processing in the laboratory. Total abundance and total biomass of animals in the 1-4mm sieves were recorded for animals sorted to one of 71 possible taxon groups (Appendix 2; see original list in Deliverable 1, www.mafcons.org/). The criteria used to determine the taxon groups were; (1) The ease to separate out animals into these groups during the sorting process (i.e. no requirement for use of keys; obvious at first sight); (2) the likelihood of the groups within Phyla having different morphologies and different behaviours in the sieving process. A detailed description of the sample processing is given in the MAFCONS methods manual (Deliverable 1 available at www.mafcons.org/).

Figure 2.1 Stations sampled for epifauna and infauna by the participants of the EC project MAFCONS in 2003.



Institutes participating in the 2003 MAFCONS surveys:

Germany	■	The Senckenburg Institute & Sea Fisheries Institute
England	●	University of Wales Swansea & CEFAS
Norway	◆	Institute for Marine Research, Tromso
Scotland	▲	FRS Marine Laboratory, Aberdeen
The Netherlands & Belgium	✚	RIVO and Gent University

2.2 Description of Edgar's empirical model

Edgar's (1990a) empirical model is based on the relationship between production, mean individual body mass and water temperature.

$$\text{Log } P = -1.99 + 0.78 * \log B + 0.68 * \log T \qquad \text{(Epifauna)}$$

Where:
P = daily production (µg.day^{-1})
B = mean individual weight (AFDM/µg)
T = bottom water temperature (ºC)

The model was developed using a dataset of actual data for all of these parameters from studies of 41 individual species. On examining this relationship, Edgar found that models for mollusca and crustacea separated from other infauna and other epifauna. Thus all the taxa in the infaunal and epifaunal databases were assigned to any of these four groups before the empirical relationships for each one was applied (see Appendices 1 & 2). In the infaunal dataset some of the taxon groups were known to include both epifaunal and infaunal species, however, it was assumed that as these data were collected with an infaunal sampler, the infaunal species within that taxon group would be prevalent. If there were no infaunal species known within a taxon group, this was assigned as epifaunal. For the epifaunal dataset, the data were per species so it was possible to assign these to either epifauna or infauna directly based on knowledge of the living habit of the specific species. If an animal is both epifaunal and infaunal, it was assigned to the living habit for which it was known to spend over 50 % of its time.

2.3 Applying Edgar's model

For each sample (whole sample as retained on the 5mm sieve for epifauna and each sieve fraction for infauna), total biomass per taxon was converted to ash free dry mass (AFDM) using published conversion factors (Brey, 2002) (see 2.3.1. below) and the mean individual weight per species calculated using the total number of individuals and total weight (AFDM) (see 2.3.2. below). Water temperatures were taken from the environmental data recorded at each station. Daily production per taxon was then calculated and all taxa in a sample summed to give total daily production of the sampled community.

2.3.1. Converting wet mass to ash free dry mass

Using Edgar's method, all wet mass (WM) biomass values need to be converted to ash free dry mass (AFDM). Brey (2002) has a table of WM>AFDM conversion factors for invertebrates and fish at the level of taxonomic resolution for which there are sufficient data to assign a value. All conversion factors are based on calculations of the difference between wet mass and ash free dry mass for a number of examples for each group (a full reference list can be obtained from the author). Each species in the epifaunal database and taxon group in the infaunal database was assigned to a corresponding Brey group, but where no corresponding link to a Brey group was available, a number of steps were followed. If there was a known WM>AFDM conversion factor for that group from another reference source, this conversion was used and the source recorded. If no alternative source of conversion factor was available, but it was agreed that a taxon resembled a group with a Brey conversion factor, based on its behaviour in the ashing and drying procedure, this alternative group's conversion factor was used. For 'Other organic matter', where fragments of biomass were found in a sample but it was not possible to assign them to any taxonomic group, the WM>AFDM conversion was a mean of the Mollusca, Echinodermata, Annelida and Crustacea values (see Appendices 1 & 2 for assigned Brey groups).

2.3.2. Missing data

For Edgar's model both the total number of individuals and total ash free dry mass (biomass) are required to calculate the mean individual weight required by the empirical relationship. For a number of taxa in the epifaunal database there were no biomass data as the animal encountered was encrusting and thus it could not be weighed. In these cases no production could be calculated. More commonly however, for taxa from both the epifauna and the infauna, biomass data were available but abundance data were not. This occurred either because animals were colonial and thus it was not possible to count the number of individuals, or where individual animals were fragmented. In these cases it was not possible to account for production directly by applying Edgar's model. However, where biomass data were available but no abundance data were given it was still possible to assign total production using P/B ratios. A P/B ratio was assigned to the taxon group following the steps described below and then biomass multiplied by the ratio to give total production.

Four steps were followed to assign P/B ratios to taxa with missing values. Firstly, where P/B values were missing but values were available for that taxon from the same sample (and size fraction in the case of the infauna), the average P/B value for that taxon was calculated and applied. This occurred when individuals and fragments of taxa had been entered as separate records in the database, giving a record for total number and total biomass based on the whole individuals and another record for total biomass from the fragments. Secondly, where the taxon was not represented within the same station or sieve, values were applied from the "nearest neighbour" station (based on nearest geographic neighbour using a GIS-based distance matrix). Thirdly, if neither of the two methods detailed above could assign P/B values, a published P/B value for that taxon was used. Finally, where biomass was classified as 'Other Organic Matter' the average of all P/B ratios from within the same sample was assigned, based on the assumption that the unrecognisable fragments (classified as 'other organic matter') would be fragments of the taxa found within the sample.

3. Results

3.1 Secondary production from the epifauna

The distribution of epifaunal production across the North Sea in 2003, based on Edgar's (1990a and b) method, is shown in Figure 3.1.1. Total community production ranged between 0.5 and 450 milligrams per day (per m^2). Edgar (1990b) calculated total community production using the same approach as that used here, for macrofaunal communities of seagrass beds in Western Australia. Total production ranged between 4.9 and 47.2 grams per year (per m^2), which translates to 13.42 to 129.32 milligrams per day (per m^2), based on the assumption that productivity is constant across the year. This fits within the range observed in this study. Stations with over 80 milligrams production per day (per m^2) were found along the continental coast in the southern North Sea, in the central west North Sea, east of Scotland and in the northwest North Sea due northeast of Orkney.

Individual P/B ratios per species ranged between 0.02 and 0.74. Total production per species ranged between 0.904×10^{-5} to 25.45 milligrams per day (per m^2). This large difference in total production per species represents the range in number of individuals and mean individual weights recorded across the survey. At the highest epifaunal productivity station (ICES rectangle 34F2 in Figure 3.1.1.) the sample was dominated by a very large population of Ophiuroids (~115 individuals per m^2). Whilst at the second highest epifaunal production station (ICES rectangle 41E8 in Figure 3.1.1.) numbers of individuals were not as high but several of the key species had high mean individual weights. High productivity per species was found either where the mean individual weight was high and/or there was a high total number of individuals. Brey (1990) presented production values for a number of macrofaunal species using an alternative empirical relationship based on the relationship between production and mean individual weight and total biomass. Brey's values for total production per species ranged between 0.04 to 13.56 grams per year (per m^2). This would translate to 0.11 to 37.40 milligrams per day (per m^2), if it were assumed that productivity is constant across the year. These values are comparable with the upper end of the species production values found for this report.

The empirical relationship developed by Edgar (1990a) was designed to be applied to samples that have been size structured by sieving prior to analysis. The epifaunal samples analysed here contained all animals retained on a 5mm sieve with no further size classes. It is likely that the mean individual weights calculated here will have been skewed by the presence of either very high or very low body mass individuals. Jennings *et al.* (2001) estimated community production of epifauna for a number of sites in the North Sea using a size-based method. Their estimates of total community production ranged between approximately 50 and 700 grams per sample per year. If it is assumed that productivity is constant over that year and that the area sampled was on average 400m^2 (2metre-beam trawl tow for 5 minutes at 1-1.5knots), this translates to a range of 0.34 to 4.79 milligrams per day (per m^2). This range is all within the lowest productivity range of the estimated values for the MAFCONS 2003 survey as calculated here using the Edgar (1990) method without size structuring.

3.2 Secondary production from the infauna

The distribution of infaunal production across the North Sea in 2003, based on Edgar's (1990a and b) method, is shown in Figure 3.1.2. At this stage, it was only possible to analyse infaunal data from 104 stations but this will be updated to at least 110 stations when the analysis is refined and reapplied to the 2003 data (see Section 4). Total community production ranged between 50 and 7000 milligrams per day (per m^2). Only a fifth of the stations produced less than 300 milligrams per day (per m^2) from the infauna, compared to 132 out of 134 of all stations based on epifauna (see scales in Figures 3.1.1. and 3.1.2.). Given the negative exponential relationship between body size and metabolic rate these results confirm the theory that smaller animals (i.e. the infauna retained in sieves between 1-4mm) are more productive than larger animals (i.e. the epifauna retained in the 5mm sieve). The southern North Sea had the greatest aggregation of high productivity infauna stations with a number of other stations off the east coast of Scotland and one in the northern North Sea. Stations that had particularly low production based on epifauna, were not always amongst the lowest productivity stations based on infauna and *vice versa* (e.g. see ICES rectangles 38 and 39F4, 38 and 39F5 – Figures 3.1.1. and 3.1.2.).

Individual P/B ratios per infaunal taxon group ranged between 0.03 and 2.24. Total production per taxon group ranged between $1.42*10^{-3}$ to 3641.38 milligrams per day (per m^2). This is higher than was found for total production per species in the epifauna, but not really comparable because there may have been many more individuals when aggregated to a taxon group. The large difference in total production per taxon group represents the range in number of individuals and mean individual weights recorded across the survey. At the highest productivity station (ICES rectangle 38F7 in Figure 3.1.2.) all of the individual Van Veen grabs had high production from the very large sampled populations of Phoronids (between 1500-8500 individuals per sieve fraction – an area less than $0.1m^2$). Whilst at the second highest production station (ICES rectangle 37F6 in Figure 3.1.2.) numbers of individuals in any particular taxon group were not as high, but several of the key taxon groups such as Irregular Echinoids and Sedentary Polychaetes had high mean individual weights. As with the epifauna, high productivity per taxon group was found either where the mean individual weight was high and/or there was a high total number of individuals. Brey's (1990) values for total production per species, which convert to 0.11 to 37.40 milligrams per day (per m^2) are within the range of the values for the taxon groups here.

Infaunal samples were size structured by sieving through 0.5mm, 1mm, 2mm and 4mm sieves, with results presented here for the 1-4mm sieves. Individual P/B ratios per infaunal taxon group were lower in the 4mm sieves (between 0.03 to 1.65, compared to 0.05 to 2.22 for the 2mm and 0.06 to 2.24 for the 1mm sieves), confirming the theory that even within this size range metabolic rate appears to have a negative relationship with body size. Jennings *et al.* (2001) estimated community production of infauna for a number of sites in the North Sea using a size-based method where all individuals were weighed. Their estimates of total community production ranged between approximately 5 and 80 grams per sample per year. If it is assumed that productivity is constant over that year and that the area sampled was on average $0.2m^2$ ($0.2m^2$ subsample taken from an anchor dredge), this translates to a range of 68.5 to 1095.9 milligrams per day (per m^2). This is all within the range of the estimated values for the MAFCONS 2003 infauna samples as calculated here using the Edgar (1990) method with sieve size structuring. Of 104 stations analysed, 99 ranged between 50 and 2400 milligrams per day (per m2) total infaunal community production.

Figure 3.1.1. Distribution of secondary production from the epifauna (milligrams.day.m^{-2})

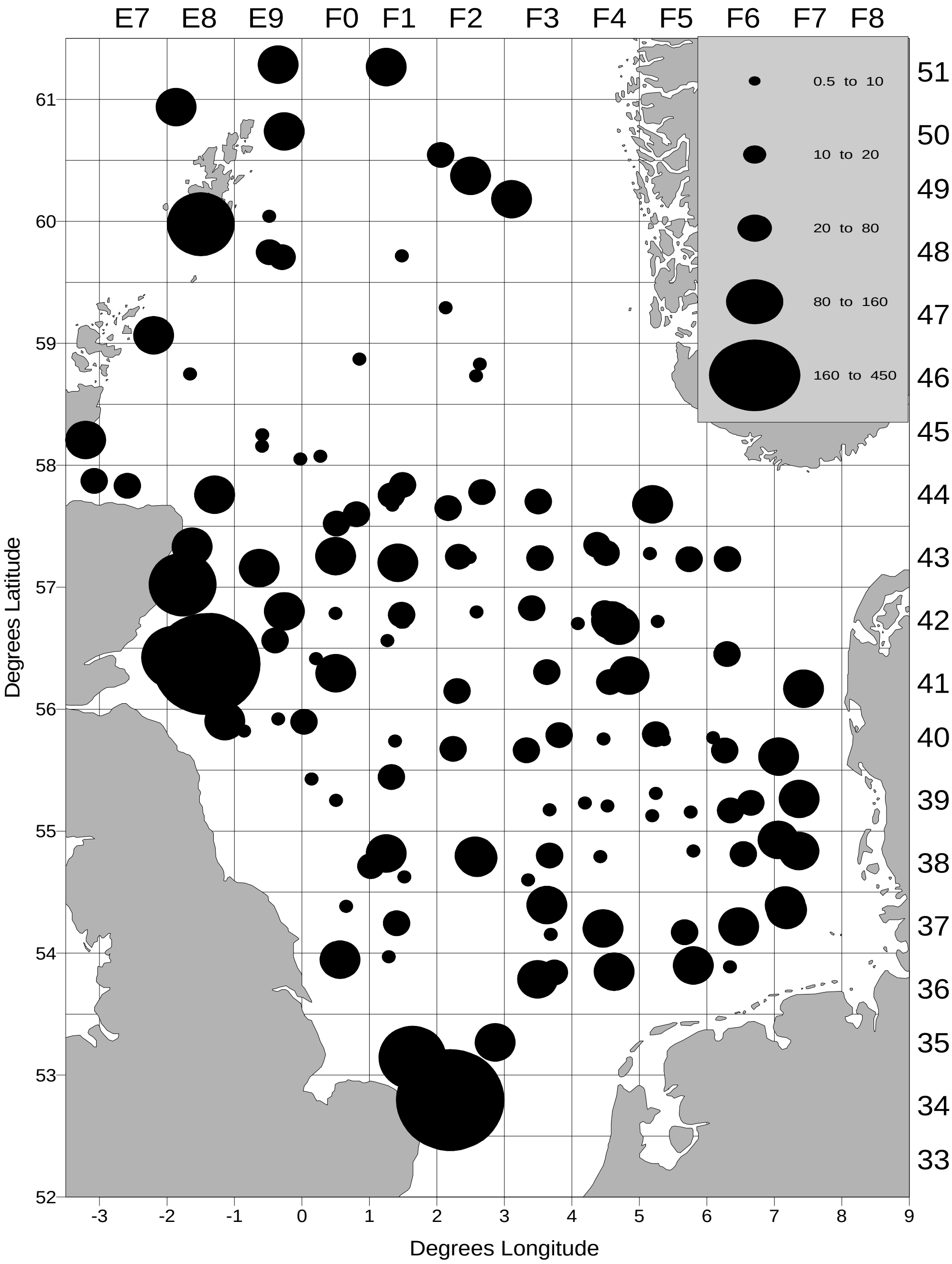
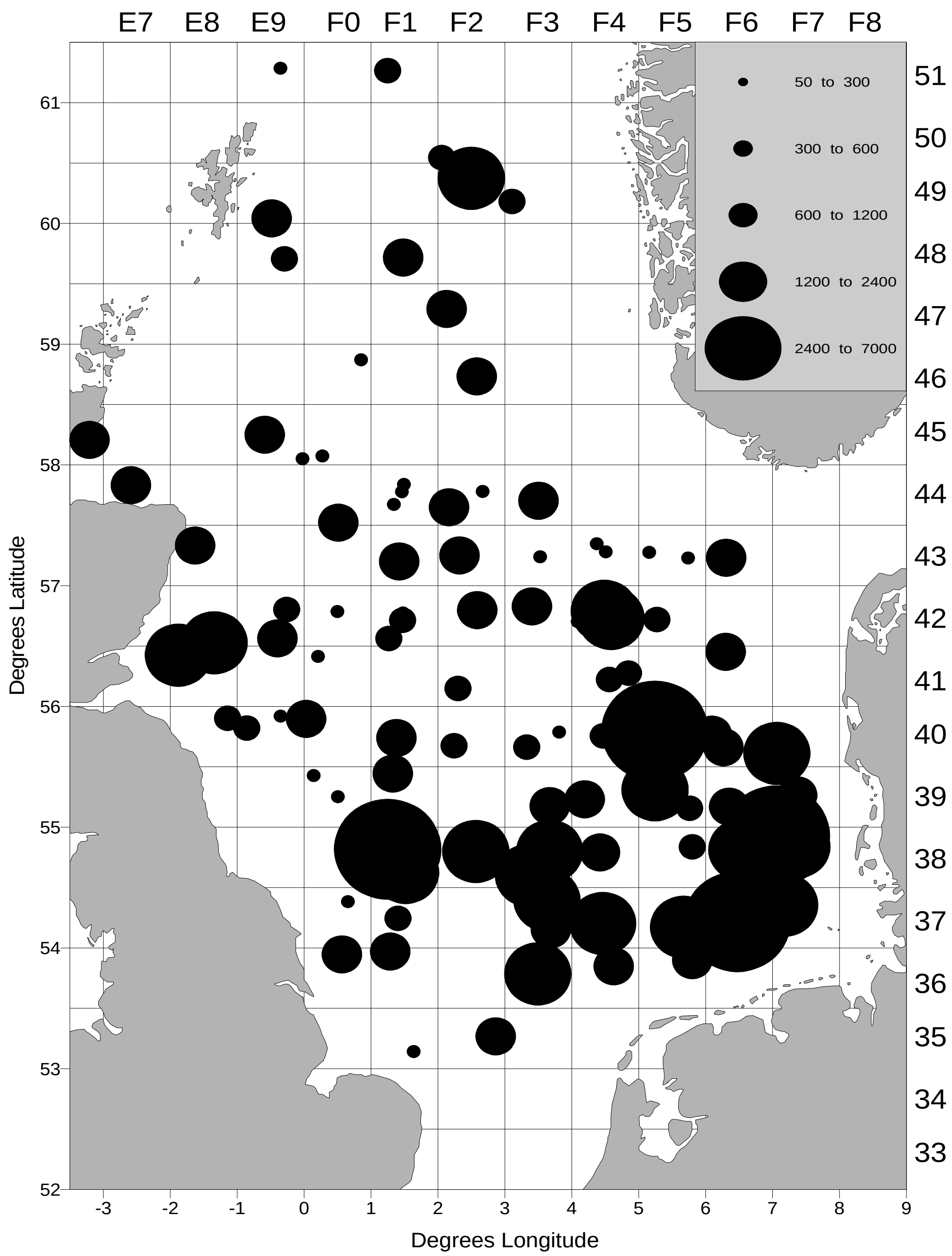


Figure 3.1.2. Distribution of secondary production from the infauna (milligrams.day.m^{-2})



4. Conclusions and Future Work

4.1 Summary of findings

Empirical models relating production of a population to easy to measure parameters such as biomass and water temperature provide a method that could be used for large-scale, routine assessments of secondary production. Edgar's (1990a & b) model provides a method that can be applied to data that are not even identified to the species level by using sieve size fractioning to decrease the error around the mean individual weights assigned per taxon group. Using Edgar's method, community level production, for both the infauna and the epifauna, was calculated for stations sampled across the North Sea as part of the EC project MAFCONS 2003 survey. Overall, secondary production was much higher per unit area from the infauna than the epifauna. However, given that the infauna as sampled, will have on average been of smaller body size than the epifauna sampled, this fits the theory that there is a negative exponential relationship between body size and metabolic rate.

Spatial distributions of total production overlapped in some areas, but were not always the same, suggesting that different factors may drive community level production for the two different benthic components. High production was particularly noticeable in the southern North Sea from the infaunal component of the benthos. For both components, the highest production stations were found to include either taxa with very high total numbers per unit area and/or taxa with very high mean individual weights. Initial comparisons with other published studies of macrofaunal production suggest the figures found here to be broadly comparable. However, the very high production stations of infauna were much higher than any of the results of the other studies found. It should be noted that all samples for this study were taken in the summer months when productivity is likely to be at a peak and future work will focus on trying to find comparable studies to further validate the results found here.

4.2 Comparison with other empirical models

Edgar's empirical relationship was based on studies of 41 species and for some of the taxa sampled here, particularly in the epifaunal samples, there are many taxa that do not have representatives within those 41 species. For example, in the Mollusca category, most of the species, for which there are measurements, are bivalves. However, in the epifaunal dataset of the MAFCONS 2003 survey, there were also Gastropods, Chitons, Nudibranchs, Caudofoveata, and even Cephalopods! The relationships for production as a function of mean individual weight and temperature for bivalves, may not be very representative for some of these other mollusc groups. In future analyses, a number of other empirical models will be tested to see how comparable the results are with Edgar's model (e.g. Tumbiolo & Downing, 1994; Brey, 1999; Jennings *et al*., 2001). The epifaunal dataset will also be size structured based on the method described in Jennings *et al* (2001) to see how this affects the estimation of overall community production.

4.3 Missing Production

Another important objective for future work will be to try to account for missed production due to catchability problems associated with the samplers used. In the case of the infauna, the Van Veen grab samples the macrofaunal component of the infauna representatively to a certain depth within the sediment, but deep dwelling animals are missed. A number of stations have also been sampled with 0.25m^2 Unsel Box Corers, which routinely penetrate down to 20-40cm in comparison with an average penetration depth of 10cm for the grab. These samples will be used to compare production for a given area based on box core samples with Van Veen grab samples and, where possible, corrections will be applied to the infaunal production estimates for missing production from deep dwelling animals. Analysis of data from the 0.5mm sieve fractions of the infaunal samples will also be undertaken to calculate how much of the infaunal production is attributable to this size fraction. The infaunal samples taken were for macrofauna and it is certain that production due to meiofauna is missing in this analysis. The contribution of meiofauna to demersal fish and macrofaunal epibenthic invertebrate diets will be assessed and a review of the literature on productivity attributable to the meiofaunal component of the benthos undertaken to try to account for the likely significance of missing this component in the assessment of secondary production.

The epifauna were sampled with a 2metre beamtrawl and it is known that this is not a fully quantitative sampler. In a study undertaken in the southern North Sea, the catchability of the 2metre beamtrawl was investigated by towing three beamtrawls directly behind eachother. Initial results from this study showed that only 34-39% of the total available productivity was sampled. When considering individual species, the lowest catch efficiency based on abundance and biomass was for the swimming crab *Liocarcinus holsatus* (only 9% of available population sampled), whilst the highest catch efficiency based on abundance and biomass was for shrimps of the genus *Processa* (72% of available abundance and 83% of available biomass) (Reiss, *pers comm.* 2005). The study by *Reiss et al*. (pers comm., 2005) did not suggest big differences in catchability between the two different habitats that were tested, suggesting that the results presented here should at least be consistent in the underestimation of numbers and biomass. However, further efforts will be made to assess whether it is possible to apply catchability correction factors to the estimation of total community production.

In this study only the 5mm-sieve fraction of the epifaunal sample was considered. Future work will examine what proportion of the total production per sample is attributable to the material retained in the 2mm sieve fraction. It is also thought that there may be missing production from the hyperbenthos, which are not representatively sampled by either the Van Veen grab or the beamtrawl. Studies undertaken in the North Sea using samplers specifically designed for the hyperbenthos will be consulted to evaluate which groups are underrepresented in the data collected for this study.

5. References

Banse, K. & Mosher, S. 1980. Adult body mass and annual production/biomass relationship of field populations. *Ecological Monographs 50*, 355-379.

Brey, T. 1990. Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. *Meeresforsch 32*, 329-343.

Brey, T. 1999. A collection of empirical relations for use in ecological modelling. *NAGA The ICLARM Quarterly 22(3)*, 24-28.

Brey, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. V.0.12 http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html Alfred Wegener Institute for Polar and Marine Research, Germany.

Brey, T., Jarre-Teichmann, A. & Borlich, O. 1996. Artificial neural network versus multiple linear regression: predicting P/B ratios from empirical data. *Marine Ecology Progress Series 140*, 251-256.

Crisp, D.J., 1984. Energy flow measurement. In: N.A. Holme & A.D. McIntyre (eds) Methods for the Study of Marine Benthos. IBP Handbook No 16, 2nd edition, Blackwell, Oxford, pp. 284-372.

Cushman, R.M., Shugart, H.H., Hildebrandt, S.G. & Elwood, J.W., 1978. The effect of growth curve and sampling regime on instantaneous-growth, removal-summation, and Hynes/Hamilton estimates of aquatic insect production: A computer simulation. *Limnology and Oceanography 23*, 184-189.

Edgar, G.J. 1990a. The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *Journal of Experimental Marine Biology and Ecology 137*, 195-214.

Edgar, G.J. 1990b. The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. *Journal of Experimental Marine Biology and Ecology 137*, 215-240.

Jennings, S., Dinmore, T. A., Duplisea, D.E., Warr, K.J. & & Lancaster, J. E. 2001. Trawling disturbance can modify benthic production processes. *Journal of Animal Ecology 70*, 459-475.

Morin, A. & Bourassa, N. 1992. Modèles empiriques de la production anuelle et du rapport P/B d´invertébrés benthiques d´eau courante. *Canadian Journal of Fisheries and Aquatic Science 49*, 532-539.

Morin, A., Mousseau, T.A., Roff, D.A., 1987. Accuracy and precision of secondary production estimates. *Limnology and Oceanography 32*, 1342-1352.

Peters, R.H. 1983. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, 329p.

Plante, C., Downing, J.A. 1989. Production of freshwater invertebrate populations in lakes. *Canadian Journal of Fisheries and Aquatic Sciences 46*, 1489-1498.

Robertson, A.I. 1979. The relationship between annual production ratio and lifespans for marine macrobenthos. *Oecologia 38*, 193-202.

Schwinghamer, P., Hargrave, B., Peer, D. & Hawkins, C.M. 1986. Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. *Marine Ecology Progress Series 31*, 131-142.

Tumbiolo, M.L. & Downing, J.A. 1994. An empirical model for the prediction of secondary production in marine benthic invertebrate populations. *Marine Ecology Progress Series 114*, 165-174.

Wildish, D.J. & Peer, D., 1981. Methods for estimating secondary production in marine Amphipoda. *Canadian Journal of Fisheries and Aquatic Sciences 38*, 1019-1026.

Appendix 1: Epifaunal species list with assigned production analysis groups

Edgar Group	Brey Group	Taxon Group	Species or Taxon
Crustacea	Amphipoda	Amphipoda	*Ampelisca brevicornis*
Crustacea	Amphipoda	Amphipoda	*Ampelisca diadema*
Crustacea	Amphipoda	Amphipoda	*Ampelisca macrocephala*
Crustacea	Amphipoda	Amphipoda	*Ampeliscidae*
Crustacea	Amphipoda	Amphipoda	*Amphipoda indet*
Crustacea	Amphipoda	Amphipoda	*Aristias neglectus*
Crustacea	Amphipoda	Amphipoda	*Caprella linearis*
Crustacea	Amphipoda	Amphipoda	*Caprellidae*
Crustacea	Amphipoda	Amphipoda	*Epimeria cornigera*
Crustacea	Amphipoda	Amphipoda	*Gammaridae*
Crustacea	Amphipoda	Amphipoda	*Gammaropsis maculata*
Crustacea	Amphipoda	Amphipoda	*Gammaropsis nitida*
Crustacea	Amphipoda	Amphipoda	*Hippomedon denticulatus*
Crustacea	Amphipoda	Amphipoda	*Iphimedia obesa*
Crustacea	Amphipoda	Amphipoda	*Lysianassidae*
Crustacea	Amphipoda	Amphipoda	*Parapleustes assimilis*
Crustacea	Amphipoda	Amphipoda	*Scopelocheirus hopei*
Crustacea	Amphipoda	Amphipoda	*Tmetonyx cicada*
Crustacea	Amphipoda	Amphipoda	*Tryphosites longipes*
Crustacea	Amphipoda	Amphipoda	*Westwoodilla caecula*
Crustacea	Cirripedia	Cirripedia	*Balanus balanus*
Crustacea	Cirripedia	Cirripedia	*Balanus crenatus*
Crustacea	Cirripedia	Cirripedia	*Lepadidae*
Crustacea	Cirripedia	Cirripedia	*Scalpellum scalpellum*
Crustacea	Cirripedia	Cirripedia	*Verruca stroemia*
Crustacea	Crustacea	Chelicerata	*Nymphon gracile*
Crustacea	Crustacea	Chelicerata	*Nymphon hirtum*
Crustacea	Crustacea	Chelicerata	*Pycnogonida*
Crustacea	Crustacea	Chelicerata	*Pycnogonum littorale*
Crustacea	Crustacea	Crustacea	*Leptomysis gracilis*
Crustacea	Crustacea	Crustacea	*Malacostraca*
Crustacea	Crustacea	Crustacea	*Mysidae*

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Edgar Group	Brey Group	Taxon Group	Species or Taxon
Crustacea	Crustacea	Crustacea	*Schistomysis kervillei*
Crustacea	Crustacea	Crustacea	*Schistomysis spiritus*
Crustacea	Cumacea	Cumacea	*Eudorella emarginata*
Crustacea	Decapoda	Decapoda	*Decapoda*
Crustacea	Decapoda	Decapoda natantia	*Calocaris macandreae*
Crustacea	Decapoda	Decapoda natantia	*Caridion gordoni*
Crustacea	Decapoda	Decapoda natantia	*Caridion steveni*
Crustacea	Decapoda	Decapoda natantia	*Crangon allmanni*
Crustacea	Decapoda	Decapoda natantia	*Crangon crangon*
Crustacea	Decapoda	Decapoda natantia	*Crangon trispinosus*
Crustacea	Decapoda	Decapoda natantia	*Crangonidae*
Crustacea	Decapoda	Decapoda natantia	*Eualus gaimardii*
Crustacea	Decapoda	Decapoda natantia	*Eualus pusiolus*
Crustacea	Decapoda	Decapoda natantia	*Hippolyte varians*
Crustacea	Decapoda	Decapoda natantia	*Natantia indet*
Crustacea	Decapoda	Decapoda natantia	*Nephrops norvegicus*
Crustacea	Decapoda	Decapoda natantia	*Pandalidae*
Crustacea	Decapoda	Decapoda natantia	*Pandalina brevirostris*
Crustacea	Decapoda	Decapoda natantia	*Pandalus borealis*
Crustacea	Decapoda	Decapoda natantia	*Pandalus montagui*
Crustacea	Decapoda	Decapoda natantia	*Pandalus sp*
Crustacea	Decapoda	Decapoda natantia	*Pandalus sp.*
Crustacea	Decapoda	Decapoda natantia	*Pasiphaea*
Crustacea	Decapoda	Decapoda natantia	*Philoceras bispinosus*
Crustacea	Decapoda	Decapoda natantia	*Philoceras echinulatus*
Crustacea	Decapoda	Decapoda natantia	*Philoceras trispinosus*
Crustacea	Decapoda	Decapoda natantia	*Philocheras echinulatus II*
Crustacea	Decapoda	Decapoda natantia	*Philocheras sculptus*
Crustacea	Decapoda	Decapoda natantia	*Pontophilus*
Crustacea	Decapoda	Decapoda natantia	*Pontophilus spinosus*
Crustacea	Decapoda	Decapoda natantia	*Processa canaliculata*
Crustacea	Decapoda	Decapoda natantia	*Processa canuliculata*
Crustacea	Decapoda	Decapoda natantia	*Processa modica modica*
Crustacea	Decapoda	Decapoda natantia	*Processa nouveli*

Edgar Group	Brey Group	Taxon Group	Species or Taxon
Crustacea	Decapoda	Decapoda natantia	*Processa nouveli holthuisi*
Crustacea	Decapoda	Decapoda natantia	*Schlerocrangon boreas*
Crustacea	Decapoda	Decapoda natantia	*Spirontocaris lilljeborgi*
Crustacea	Decapoda	Decapoda natantia	*Thoralus cranchii*
Crustacea	Decapoda	Decapoda natantia	*Upogebia deltaura*
Crustacea	Decapoda	Decapoda reptantia	*Anapagurus chiroacanthus*
Crustacea	Decapoda	Decapoda reptantia	*Anapagurus laevis*
Crustacea	Decapoda	Decapoda reptantia	*Atelecyclus rotundatus*
Crustacea	Decapoda	Decapoda reptantia	*Cancer pagurus*
Crustacea	Decapoda	Decapoda reptantia	*Corystes cassivelaunus*
Crustacea	Decapoda	Decapoda reptantia	*Ebalia cranchii*
Crustacea	Decapoda	Decapoda reptantia	*Ebalia tuberosa*
Crustacea	Decapoda	Decapoda reptantia	*Ebalia tumefacta*
Crustacea	Decapoda	Decapoda reptantia	*Eurynome aspera*
Crustacea	Decapoda	Decapoda reptantia	*Galathea*
Crustacea	Decapoda	Decapoda reptantia	*Galathea dispersa*
Crustacea	Decapoda	Decapoda reptantia	*Galathea intermedia*
Crustacea	Decapoda	Decapoda reptantia	*Galathea nexa*
Crustacea	Decapoda	Decapoda reptantia	*Galathea squamifera*
Crustacea	Decapoda	Decapoda reptantia	*Galathea strigosa*
Crustacea	Decapoda	Decapoda reptantia	*Geryon trispinosus*
Crustacea	Decapoda	Decapoda reptantia	*Goneplax rhomboides*
Crustacea	Decapoda	Decapoda reptantia	*Hyas araneus*
Crustacea	Decapoda	Decapoda reptantia	*Hyas coarctatus*
Crustacea	Decapoda	Decapoda reptantia	*Inachus dorsettensis*
Crustacea	Decapoda	Decapoda reptantia	*Inachus phalangium*
Crustacea	Decapoda	Decapoda reptantia	*Liocarcinus*
Crustacea	Decapoda	Decapoda reptantia	*Liocarcinus depurator*
Crustacea	Decapoda	Decapoda reptantia	*Liocarcinus holsatus*
Crustacea	Decapoda	Decapoda reptantia	*Liocarcinus marmoreus*
Crustacea	Decapoda	Decapoda reptantia	*Liocarcinus pusillus*
Crustacea	Decapoda	Decapoda reptantia	*Lithodes maia*
Crustacea	Decapoda	Decapoda reptantia	*Macropipus tuberculatus*
Crustacea	Decapoda	Decapoda reptantia	*Macropodia deflexa*

Edgar Group	Brey Group	Taxon Group	Species or Taxon
Crustacea	Decapoda	Decapoda reptantia	*Macropodia rostrata*
Crustacea	Decapoda	Decapoda reptantia	*Macropodia tenuirostris*
Crustacea	Decapoda	Decapoda reptantia	*Munida rugosa*
Crustacea	Decapoda	Decapoda reptantia	*Oxyrhyncha*
Crustacea	Decapoda	Decapoda reptantia	*Paguridae*
Crustacea	Decapoda	Decapoda reptantia	*Pagurus alatus*
Crustacea	Decapoda	Decapoda reptantia	*Pagurus bernhardus*
Crustacea	Decapoda	Decapoda reptantia	*Pagurus carneus*
Crustacea	Decapoda	Decapoda reptantia	*Pagurus cuanensis*
Crustacea	Decapoda	Decapoda reptantia	*Pagurus prideaux*
Crustacea	Decapoda	Decapoda reptantia	*Pagurus pubescens*
Crustacea	Decapoda	Decapoda reptantia	*Pagurus sp.*
Crustacea	Decapoda	Decapoda reptantia	*Pagurus variabilis*
Crustacea	Decapoda	Decapoda reptantia	*Porcellana platycheles*
Crustacea	Isopoda	Isopoda	*Astacilla longicornis*
Crustacea	Isopoda	Isopoda	*Astacilla sp.*
Crustacea	Isopoda	Isopoda	*Cirolana borealis*
Crustacea	Isopoda	Isopoda	*Janira maculosa*
Epifauna	Actinaria	Anthozoa	*Anthozoa*
Epifauna	Actinaria	Hexacorallia	*Actinauge richardi*
Epifauna	Actinaria	Hexacorallia	*Actinia equina*
Epifauna	Actinaria	Hexacorallia	*Actiniaria*
Epifauna	Actinaria	Hexacorallia	*Adamsia carciniopados*
Epifauna	Actinaria	Hexacorallia	*Bolocera tuediae*
Epifauna	Actinaria	Hexacorallia	*Calliactis parasitica*
Epifauna	Actinaria	Hexacorallia	*Caryophyllia smithii*
Epifauna	Actinaria	Hexacorallia	*Epizoanthus incrustatus*
Epifauna	Actinaria	Hexacorallia	*Flabellum macandrewi*
Epifauna	Actinaria	Hexacorallia	*Hexacorallia*
Epifauna	Actinaria	Hexacorallia	*Hormathia*
Epifauna	Actinaria	Hexacorallia	*Hormathia digitata*
Epifauna	Actinaria	Hexacorallia	*Hormathiidae*
Epifauna	Actinaria	Hexacorallia	*Metridium senile*
Epifauna	Actinaria	Hexacorallia	*Scleractinia*

Edgar Group	Brey Group	Taxon Group	Species or Taxon
Epifauna	Actinaria	Hexacorallia	*Stomphia coccinea*
Epifauna	Actinaria	Hexacorallia	*Urticina eques*
Epifauna	Actinaria	Hexacorallia	*Urticina sp.*
Epifauna	Actinaria	Hydrozoa	*Abietinaria abietina*
Epifauna	Actinaria	Hydrozoa	*Abietinaria filicula*
Epifauna	Actinaria	Hydrozoa	*Aglaophenia sp.*
Epifauna	Actinaria	Hydrozoa	*Bougainvillia*
Epifauna	Actinaria	Hydrozoa	*Dicoryne conferta*
Epifauna	Actinaria	Hydrozoa	*Diphasia alata*
Epifauna	Actinaria	Hydrozoa	*Diphasia sp.*
Epifauna	Actinaria	Hydrozoa	*Gonothyraea loveni*
Epifauna	Actinaria	Hydrozoa	*Grammaria abietina*
Epifauna	Actinaria	Hydrozoa	*Halecium beanii*
Epifauna	Actinaria	Hydrozoa	*Halecium halecinum*
Epifauna	Actinaria	Hydrozoa	*Halecium sessile*
Epifauna	Actinaria	Hydrozoa	*Halecium sp*
Epifauna	Actinaria	Hydrozoa	*Hydrallmania falcata*
Epifauna	Actinaria	Hydrozoa	*Hydrozoa*
Epifauna	Actinaria	Hydrozoa	*Lafoea dumosa*
Epifauna	Actinaria	Hydrozoa	*Lafoea sp*
Epifauna	Actinaria	Hydrozoa	*Lytocarpia myriophyllum*
Epifauna	Actinaria	Hydrozoa	*Nemertesia antennina*
Epifauna	Actinaria	Hydrozoa	*Nemertesia ramosa*
Epifauna	Actinaria	Hydrozoa	*Obelia longissima*
Epifauna	Actinaria	Hydrozoa	*Plumularia setacea*
Epifauna	Actinaria	Hydrozoa	*Tamarisca tamarisca*
Epifauna	Actinaria	Hydrozoa	*Thuiaria thuja*
Epifauna	Actinaria	Hydrozoa	*Tubularia*
Epifauna	Actinaria	Hydrozoa	*Tubularia indivisa*
Epifauna	Actinaria	Hydrozoa	*Tubularia larynx*
Epifauna	Actinaria	Octocorallia	*Alcyonium*
Epifauna	Actinaria	Octocorallia	*Alcyonium digitatum*
Epifauna	Actinaria	Octocorallia	*Alcyonium glomeratum*
Epifauna	Actinaria	Octocorallia	*Octocorallia*

Edgar Group	Brey Group	Taxon Group	Species or Taxon
Epifauna	Actinaria	Octocorallia	*Pennatula phosphorea*
Epifauna	Actinaria	Octocorallia	*Virgularia mirabilis*
Epifauna	Ascidiae	Ascidiae	*Ascidia sp*
Epifauna	Ascidiae	Ascidiae	*Ascidia virginea*
Epifauna	Ascidiae	Ascidiae	*Ascidiacea*
Epifauna	Ascidiae	Ascidiae	*Ascidiella aspersa*
Epifauna	Ascidiae	Ascidiae	*Ascidiella scabra*
Epifauna	Ascidiae	Ascidiae	*Ascidiella sp.*
Epifauna	Ascidiae	Ascidiae	*Ciona intestinalis*
Epifauna	Ascidiae	Ascidiae	*Corella parallelogramma*
Epifauna	Ascidiae	Ascidiae	*Eugyra arenosa*
Epifauna	Asteroidea	Asteroidea	*Asterias rubens*
Epifauna	Asteroidea	Asteroidea	*Asteroidea*
Epifauna	Asteroidea	Asteroidea	*Astropecten irregularis*
Epifauna	Asteroidea	Asteroidea	*Crossaster papposus*
Epifauna	Asteroidea	Asteroidea	*Henricia*
Epifauna	Asteroidea	Asteroidea	*Henricia oculata*
Epifauna	Asteroidea	Asteroidea	*Henricia sanguinolenta*
Epifauna	Asteroidea	Asteroidea	*Hippasteria phrygiana*
Epifauna	Asteroidea	Asteroidea	*Leptasterias muelleri*
Epifauna	Asteroidea	Asteroidea	*Luidia sarsi*
Epifauna	Asteroidea	Asteroidea	*Porania pulvillus*
Epifauna	Asteroidea	Asteroidea	*Solaster endeca*
Epifauna	Asteroidea	Asteroidea	*Stichastrella rosea*
Epifauna	Bryozoa	Bryozoa	*Alcyonidium*
Epifauna	Bryozoa	Bryozoa	*Alcyonidium diaphanum*
Epifauna	Bryozoa	Bryozoa	*Alcyonidium parasiticum*
Epifauna	Bryozoa	Bryozoa	*Bryozoa*
Epifauna	Bryozoa	Bryozoa	*Buskea dichotoma*
Epifauna	Bryozoa	Bryozoa	*Cellaria sp*
Epifauna	Bryozoa	Bryozoa	*Chartella barleei*
Epifauna	Bryozoa	Bryozoa	*Dendrobeania*
Epifauna	Bryozoa	Bryozoa	*Dendrobeania fessa*
Epifauna	Bryozoa	Bryozoa	*Dendrobeania murrayana*

Edgar Group	Brey Group	Taxon Group	Species or Taxon
Epifauna	Bryozoa	Bryozoa	*Eucratea loricata*
Epifauna	Bryozoa	Bryozoa	*Flustra*
Epifauna	Bryozoa	Bryozoa	*Flustra foliacea*
Epifauna	Bryozoa	Bryozoa	*Porella*
Epifauna	Bryozoa	Bryozoa	*Scrupocellaria*
Epifauna	Bryozoa	Bryozoa	*Securiflustra securifrons*
Epifauna	Bryozoa	Bryozoa	*Sertella (Bryozoa)*
Epifauna	Bryozoa	Bryozoa	*Sertella beaniana*
Epifauna	Bryozoa	Bryozoa	*Tubulipora*
Epifauna	Chaetognatha	Chaetognatha	*Chaetognatha*
Epifauna	Echinoidea	Echinoidea	*Echinoidea*
Epifauna	Echinoidea	Echinoidea regular	*Echinidae*
Epifauna	Echinoidea	Echinoidea regular	*Echinus*
Epifauna	Echinoidea	Echinoidea regular	*Echinus (Juveniles)*
Epifauna	Echinoidea	Echinoidea regular	*Echinus acutus*
Epifauna	Echinoidea	Echinoidea regular	*Echinus elegans*
Epifauna	Echinoidea	Echinoidea regular	*Echinus esculentus*
Epifauna	Echinoidea	Echinoidea regular	*Psammechinus miliaris*
Epifauna	Echinoidea	Echinoidea regular	*Strongylocentrotus*
Epifauna	Gastropoda	Gastropoda	*Troschelia berniciensis*
Epifauna	Holothuroidea	Holothuroidea	*Aslia lefevrei*
Epifauna	Holothuroidea	Holothuroidea	*Labidoplax digitata*
Epifauna	Holothuroidea	Holothuroidea	*Leptopentacta elongata*
Epifauna	Holothuroidea	Holothuroidea	*Paracucumaria hyndmani*
Epifauna	Holothuroidea	Holothuroidea	*Pseudothyone raphanus*
Epifauna	Holothuroidea	Holothuroidea	*Psolus phantapus*
Epifauna	Holothuroidea	Holothuroidea	*Psolus squamatus*
Epifauna	Holothuroidea	Holothuroidea	*Thyone fusus*
Epifauna	Holothuroidea	Holothuroidea	*Thyonidium hyalinum*
Epifauna	Holothuroidea	Holothuroidea	*Thyonidium sp.*
Epifauna	Ophiuroidea	Ophiuroidea	*Ophiocomina nigra*
Epifauna	Ophiuroidea	Ophiuroidea	*Ophiopholis aculeata*
Epifauna	Ophiuroidea	Ophiuroidea	*Ophiothrix fragilis*
Epifauna	Ophiuroidea	Ophiuroidea	*Ophiothrix quinquemaculata*

Edgar Group	**Brey Group**	**Taxon Group**	**Species or Taxon**
Epifauna	Ophiuroidea	Ophiuroidea	*Ophiura*
Epifauna	Ophiuroidea	Ophiuroidea	*Ophiura affinis*
Epifauna	Ophiuroidea	Ophiuroidea	*Ophiura albida*
Epifauna	Ophiuroidea	Ophiuroidea	*Ophiura ophiura*
Epifauna	Ophiuroidea	Ophiuroidea	*Ophiura sarsi*
Epifauna	Ophiuroidea	Ophiuroidea	*Ophiuroidea*
Epifauna	Other Organic Matter	Other Organic Matter	*Gubbelscheibe*
Epifauna	Other Organic Matter	Other Organic Matter	*Other organic material*
Epifauna	Polychaeta errantia	Polychaeta errantia	*Aphrodita aculeata*
Epifauna	Polychaeta errantia	Polychaeta errantia	*Aphroditidae*
Epifauna	Polychaeta errantia	Polychaeta errantia	*Hyalinoecia tubicola*
Epifauna	Polychaeta errantia	Polychaeta errantia	*Laetmonice filicornis*
Epifauna	Polychaeta errantia	Polychaeta errantia	*Lepidonotus squamatus*
Epifauna	Polychaeta sedentaria	Polychaeta sedentaria	*Filograna implexa*
Epifauna	Polychaeta sedentaria	Polychaeta sedentaria	*Hydroides*
Epifauna	Polychaeta sedentaria	Polychaeta sedentaria	*Hydroides norvegica*
Epifauna	Polychaeta sedentaria	Polychaeta sedentaria	*Pomatoceros triqueter*
Epifauna	Polychaeta sedentaria	Polychaeta sedentaria	*Serpula vermicularis*
Epifauna	Polychaeta sedentaria	Polychaeta sedentaria	*Thelepus cincinnatus*
Epifauna	Porifera	Porifera	*Axinella*
Epifauna	Porifera	Porifera	*Axinella infundibuliformis*
Epifauna	Porifera	Porifera	*Halichondria bowerbanki*
Epifauna	Porifera	Porifera	*Halichondria panicea*
Epifauna	Porifera	Porifera	*Haliclona oculata*
Epifauna	Porifera	Porifera	*Myxilla fimbriata*
Epifauna	Porifera	Porifera	*Phakellia ventilabrum*
Epifauna	Porifera	Porifera	*Porifera*
Epifauna	Porifera	Porifera	*Stelligera stuposa*
Epifauna	Porifera	Porifera	*Suberites*
Epifauna	Porifera	Porifera	*Suberites carnosus*
Epifauna	Porifera	Porifera	*Suberites ficus*
Epifauna	Porifera	Porifera	*Suberites pagurorum*
Epifauna	Porifera	Porifera	*Suberites sp*
Epifauna	Porifera	Porifera	*Ute ensata*

Edgar Group	Brey Group	Taxon Group	Species or Taxon
Infauna	Annelida	Polychaeta	*Polychaeta*
Infauna	Echinoidea	Echinoidea irregular	*Brissopsis lyrifera*
Infauna	Echinoidea	Echinoidea irregular	*Echinocardium cordatum*
Infauna	Echinoidea	Echinoidea irregular	*Echinocardium flavescens*
Infauna	Echinoidea	Echinoidea regular	*Echinocyamus pusillus*
Infauna	Echinoidea	Echinoidea regular	*Spatangus purpureus*
Infauna	Echinoidea	Echinoidea regular	*Spatangus raschi*
Infauna	Nemertea	Nemertea	*Nemertea*
Infauna	Nemertea	Platyhelminthes	*Platyhelminthes*
Infauna	Ophiuroidea	Ophiuroidea	*Amphiura brachiata*
Infauna	Ophiuroidea	Ophiuroidea	*Amphiura chiajei*
Infauna	Polychaeta errantia	Polychaeta errantia	*Alentia gelatinosa*
Infauna	Polychaeta errantia	Polychaeta errantia	*Anaitides groenlandica*
Infauna	Polychaeta errantia	Polychaeta errantia	*Eunicidae*
Infauna	Polychaeta errantia	Polychaeta errantia	*Eunoe nodosa*
Infauna	Polychaeta errantia	Polychaeta errantia	*Gattyana amondseni*
Infauna	Polychaeta errantia	Polychaeta errantia	*Gattyana cirrosa*
Infauna	Polychaeta errantia	Polychaeta errantia	*Glycera capitata*
Infauna	Polychaeta errantia	Polychaeta errantia	*Glycera rouxii*
Infauna	Polychaeta errantia	Polychaeta errantia	*Glycera sp*
Infauna	Polychaeta errantia	Polychaeta errantia	*Glycera unicornis*
Infauna	Polychaeta errantia	Polychaeta errantia	*Glyceridae*
Infauna	Polychaeta errantia	Polychaeta errantia	*Goniada maculata*
Infauna	Polychaeta errantia	Polychaeta errantia	*Harmothoe*
Infauna	Polychaeta errantia	Polychaeta errantia	*Harmothoe extenuata*
Infauna	Polychaeta errantia	Polychaeta errantia	*Harmothoe fragilis*
Infauna	Polychaeta errantia	Polychaeta errantia	*Harmothoe fraserthomsoni*
Infauna	Polychaeta errantia	Polychaeta errantia	*Harmothoe glabra*
Infauna	Polychaeta errantia	Polychaeta errantia	*Harmothoe impar*
Infauna	Polychaeta errantia	Polychaeta errantia	*Harmothoe sp.*
Infauna	Polychaeta errantia	Polychaeta errantia	*Harmothoe spinifera*
Infauna	Polychaeta errantia	Polychaeta errantia	*Hediste diversicolor*
Infauna	Polychaeta errantia	Polychaeta errantia	*Lumbrineris latreilli*
Infauna	Polychaeta errantia	Polychaeta errantia	*Marphysa bellii*

Edgar Group	Brey Group	Taxon Group	Species or Taxon
Infauna	Polychaeta errantia	Polychaeta errantia	*Neanthes fucata*
Infauna	Polychaeta errantia	Polychaeta errantia	*Neanthes virens*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nephtys assimilis*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nephtys caeca*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nephtys hombergii*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nephtys kersivalensis*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nephtys longosetosa*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nephtys paradoxa*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nephtys sp*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nereis*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nereis pelagica*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nereis zonata*
Infauna	Polychaeta errantia	Polychaeta errantia	*Nothria conchylega*
Infauna	Polychaeta errantia	Polychaeta errantia	*Notophyllum foliosum*
Infauna	Polychaeta errantia	Polychaeta errantia	*Orbinia armandi*
Infauna	Polychaeta errantia	Polychaeta errantia	*Orbinia sertulata*
Infauna	Polychaeta errantia	Polychaeta errantia	*Orbiniidae*
Infauna	Polychaeta errantia	Polychaeta errantia	*Perinereis cultrifera*
Infauna	Polychaeta errantia	Polychaeta errantia	*Phyllodoce sp*
Infauna	Polychaeta errantia	Polychaeta errantia	*Polynoidae*
Infauna	Polychaeta errantia	Polychaeta errantia	*Sthenelais boa*
Infauna	Polychaeta errantia	Polychaeta errantia	*Sthenelais limicola*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Amphictene auricoma*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Amphitrite cirrata*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Branchiomma bombyx*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Chaetopteridae*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Ditrupa arietina*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Jasmineira elegans*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Lagis koreni*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Lanice conchilega*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Notomastus latericeus*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Ophelia limacina*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Ophelina acuminata*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Owenia fusiformis*

Edgar Group	**Brey Group**	**Taxon Group**	**Species or Taxon**
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Polyphysia crassa*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Rhodine loveni*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Sabella crassicornis*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Sabellaria spinulosa*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Scalibregma inflatum*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Scolelepis squamata*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Terebellidae*
Infauna	Polychaeta sedentaria	Polychaeta sedentaria	*Terebellides stroemi*
Infauna	Sipunculida	Sipunculida	*Golfingia vulgaris*
Infauna	Sipunculida	Sipunculida	*Phascolion strombus*
Infauna	Sipunculida	Sipunculida	*Sipuncula*
Infauna	Sipunculida	Sipunculida	*Sipunculidae*
Mollusca	Bivalvia	Bivalvia	*Abra longicallus*
Mollusca	Bivalvia	Bivalvia	*Abra nitida*
Mollusca	Bivalvia	Bivalvia	*Abra prismatica*
Mollusca	Bivalvia	Bivalvia	*Acanthocardia echinata*
Mollusca	Bivalvia	Bivalvia	*Aequipecten opercularis*
Mollusca	Bivalvia	Bivalvia	*Anomia ephippium*
Mollusca	Bivalvia	Bivalvia	*Arctica islandica*
Mollusca	Bivalvia	Bivalvia	*Astarte sulcata*
Mollusca	Bivalvia	Bivalvia	*Bivalves*
Mollusca	Bivalvia	Bivalvia	*Cardiidae*
Mollusca	Bivalvia	Bivalvia	*Chamelea gallina*
Mollusca	Bivalvia	Bivalvia	*Chlamys*
Mollusca	Bivalvia	Bivalvia	*Chlamys varia*
Mollusca	Bivalvia	Bivalvia	*Circomphalus casina*
Mollusca	Bivalvia	Bivalvia	*Corbula gibba*
Mollusca	Bivalvia	Bivalvia	*Cuspidaria cuspidata*
Mollusca	Bivalvia	Bivalvia	*Donax vittatus*
Mollusca	Bivalvia	Bivalvia	*Dosinia exoleta*
Mollusca	Bivalvia	Bivalvia	*Dosinia lupinus*
Mollusca	Bivalvia	Bivalvia	*Ensis ensis*
Mollusca	Bivalvia	Bivalvia	*Gari depressa*
Mollusca	Bivalvia	Bivalvia	*Gari fervensis*

Edgar Group	Brey Group	Taxon Group	Species or Taxon
Mollusca	Bivalvia	Bivalvia	*Goodallia triangularis*
Mollusca	Bivalvia	Bivalvia	*Hiatella arctica*
Mollusca	Bivalvia	Bivalvia	*Lucinoma borealis*
Mollusca	Bivalvia	Bivalvia	*Modiolula phaseolina*
Mollusca	Bivalvia	Bivalvia	*Modiolus barbatus*
Mollusca	Bivalvia	Bivalvia	*Modiolus modiolus*
Mollusca	Bivalvia	Bivalvia	*Mysia undata*
Mollusca	Bivalvia	Bivalvia	*Nucula nitidosa*
Mollusca	Bivalvia	Bivalvia	*Nucula nucleus*
Mollusca	Bivalvia	Bivalvia	*Nucula sulcata*
Mollusca	Bivalvia	Bivalvia	*Palliolum tigerinum*
Mollusca	Bivalvia	Bivalvia	*Parvicardium exiguum*
Mollusca	Bivalvia	Bivalvia	*Parvicardium scabrum*
Mollusca	Bivalvia	Bivalvia	*Pecten maximus*
Mollusca	Bivalvia	Bivalvia	*Phaxas pellucidus*
Mollusca	Bivalvia	Bivalvia	*Pododesmus patelliformis*
Mollusca	Bivalvia	Bivalvia	*Pseudamussium*
Mollusca	Bivalvia	Bivalvia	*Pseudomussium*
Mollusca	Bivalvia	Bivalvia	*Spisula elliptica*
Mollusca	Bivalvia	Bivalvia	*Spisula solida*
Mollusca	Bivalvia	Bivalvia	*Spisula subtruncata*
Mollusca	Bivalvia	Bivalvia	*Tapes decussatus*
Mollusca	Bivalvia	Bivalvia	*Tellimya ferruginosa*
Mollusca	Bivalvia	Bivalvia	*Tellinidae*
Mollusca	Bivalvia	Bivalvia	*Timoclea ovata*
Mollusca	Bivalvia	Bivalvia	*Tridonta*
Mollusca	Bivalvia	Bivalvia	*Tridonta elliptica*
Mollusca	Bivalvia	Bivalvia	*Tridonta montagui*
Mollusca	Cephalopoda	Cephalopoda	*Alloteuthis subulata*
Mollusca	Cephalopoda	Cephalopoda	*Eledone cirrhosa*
Mollusca	Cephalopoda	Cephalopoda	*Loligo forbesii*
Mollusca	Cephalopoda	Cephalopoda	*Rossia macrosoma*
Mollusca	Cephalopoda	Cephalopoda	*Sepiola atlantica*
Mollusca	Gastropoda	Gastropoda	*Aporrhais pespelecani*

Edgar Group	**Brey Group**	**Taxon Group**	**Species or Taxon**
Mollusca	Gastropoda	Gastropoda	*Aporrhais serresianus*
Mollusca	Gastropoda	Gastropoda	*Buccinum undatum*
Mollusca	Gastropoda	Gastropoda	*Calliostoma zizyphinum*
Mollusca	Gastropoda	Gastropoda	*Capulus ungaricus*
Mollusca	Gastropoda	Gastropoda	*Colus gracilis*
Mollusca	Gastropoda	Gastropoda	*Colus islandicus*
Mollusca	Gastropoda	Gastropoda	*Colus jeffreysianus*
Mollusca	Gastropoda	Gastropoda	*Colus sp*
Mollusca	Gastropoda	Gastropoda	*Comarmondia gracilis*
Mollusca	Gastropoda	Gastropoda	*Epitonium clathrus*
Mollusca	Gastropoda	Gastropoda	*Erato voluta*
Mollusca	Gastropoda	Gastropoda	*Euspira*
Mollusca	Gastropoda	Gastropoda	*Euspira catena*
Mollusca	Gastropoda	Gastropoda	*Gibbula cineraria*
Mollusca	Gastropoda	Gastropoda	*Hinia reticulata*
Mollusca	Gastropoda	Gastropoda	*Iothia fulva*
Mollusca	Gastropoda	Gastropoda	*Liomesus ovum*
Mollusca	Gastropoda	Gastropoda	*Macandrevia cranium*
Mollusca	Gastropoda	Gastropoda	*Neptunea*
Mollusca	Gastropoda	Gastropoda	*Neptunea antiqua*
Mollusca	Gastropoda	Gastropoda	*Oenopota turricula*
Mollusca	Gastropoda	Gastropoda	*Polinices fuscus*
Mollusca	Gastropoda	Gastropoda	*Polinices montagui*
Mollusca	Gastropoda	Gastropoda	*Polinices pulchellus*
Mollusca	Gastropoda	Gastropoda	*Puncturella noachina*
Mollusca	Gastropoda	Gastropoda	*Raphitoma echinata*
Mollusca	Gastropoda	Gastropoda	*Terebratulina retusa*
Mollusca	Gastropoda	Gastropoda	*Trivia arctica*
Mollusca	Gastropoda	Gastropoda	*Trophon muricatus*
Mollusca	Gastropoda	Gastropoda	*Turritella*
Mollusca	Gastropoda	Gastropoda	*Turritella communis*
Mollusca	Gastropoda	Gastropoda	*Velutina velutina*
Mollusca	Gastropoda	Gastropoda	*Volutopsius norwegicus*
Mollusca	Gastropoda	Polyplacophora	*Hanleya hanleyi*

Edgar Group	Brey Group	Taxon Group	Species or Taxon
Mollusca	Gastropoda	Polyplacophora	*Lepidochitona cinerea*
Mollusca	Gastropoda	Polyplacophora	*Leptochiton asellus*
Mollusca	Gastropoda	Polyplacophora	*Polyplacophora*
Mollusca	Gastropoda	Scaphopoda	*Antalis*
Mollusca	Gastropoda	Scaphopoda	*Antalis entalis*
Mollusca	Gastropoda	Scaphopoda	*Antalis vulgaris*
Mollusca	Gastropoda	Scaphopoda	*Scaphopoda*
Mollusca	Nudibranchia	Nudibranchia	*Acanthodoris pilosa*
Mollusca	Nudibranchia	Nudibranchia	*Archidoris pseudoargus*
Mollusca	Nudibranchia	Nudibranchia	*Coryphella lineata*
Mollusca	Nudibranchia	Nudibranchia	*Diaphorodoris luteocincta*
Mollusca	Nudibranchia	Nudibranchia	*Tritonia*
Mollusca	Nudibranchia	Nudibranchia	*Tritonia lineata*
Mollusca	Nudibranchia	Nudibranchia	*Tritonia sp*
Mollusca	Nudibranchia	Opisthobranchia	*Acteon tornatilis*
Mollusca	Nudibranchia	Opisthobranchia	*Philine sp*
Mollusca	Nudibranchia	Opisthobranchia	*Scaphander*
Mollusca	Nudibranchia	Opisthobranchia	*Scaphander lignarius*

Appendix 2: Infauna taxon groups with assigned production analysis groups

Edgar Group	Brey Group	Taxon Group
Crustacea	Amphipoda	Amphipoda
Crustacea	Amphipoda	Caprellidae
Crustacea	Cirripedia	Cirripedia
Crustacea	Copepoda	Copepoda
Crustacea	Crustacea	Crustacea
Crustacea	Crustacea	Cumacea
Crustacea	Crustacea	Leptostraca
Crustacea	Crustacea	Mysidacea
Crustacea	Crustacea	Ostracoda
Crustacea	Crustacea	Tanaidacea
Crustacea	Cumacea	Cumacea
Crustacea	Decapoda	Decapoda
Crustacea	Decapoda	Decapoda-Natantia
Crustacea	Decapoda	Decapoda-Reptantia
Crustacea	Decapoda	Pleocyemata
Crustacea	Euphausiacea	Euphausiacea
Crustacea	Isopoda	Isopoda
Epifauna	Actinaria	Hydrozoa
Epifauna	Ascidiae	Cephalochordata
Epifauna	Bryozoa	Foraminifera
Epifauna	Bryozoa	Hydrozoa
Epifauna	Chaetognatha	Chaetognatha
Epifauna	Crustacea	Pycnogonida
Epifauna	Demersal Fish	Myxine glutinosa
Epifauna	Echinoidea	Echinoidea-regular
Epifauna	Fish	Acrania
Epifauna	Fish	Fish
Epifauna	Fish	Osteichthyes
Epifauna	Fish	Pleuronectiformes
Epifauna	Porifera	Porifera
Infauna	Actinaria	Actinaria
Infauna	Actinaria	Anthozoa

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Edgar Group	Brey Group	Taxon Group
Infauna	Actinaria	Hexacorallia
Infauna	Actinaria	Octocorallia
Infauna	Actinaria	Pennatulidae
Infauna	Annelida	Hirudineans
Infauna	Annelida	Nematoda
Infauna	Annelida	Polychaeta
Infauna	Ascidiae	Ascidia
Infauna	Ascidiae	Pleurogona
Infauna	Asteroidea	Asteroidea
Infauna	Bryozoa	Bryozoans
Infauna	Bryozoa	Entoprocta
Infauna	Echinodermata	Echinoderms
Infauna	Echinoidea	Echinoidea-irregular
Infauna	Echinoidea	Echinoids
Infauna	Holothuroidea	Holothuroidea
Infauna	Nemertea	Nemertea
Infauna	Nemertea	Platyhelminthes
Infauna	Nudibranchia	Aplacophora
Infauna	Oligochaeta	Oligochaeta
Infauna	Oligochaeta	Phoronida
Infauna	Oligochaeta	Pogonophora
Infauna	Ophiuroidea	Ophiuroidea
Infauna	Other Organic Matter	Other Organic Matter
Infauna	Polychaeta errantia	Polychaeta-errantia
Infauna	Polychaeta sedentaria	Polychaeta-sedentaria
Infauna	Priapulida	Echiura
Infauna	Priapulida	Priapulida
Infauna	Sipunculida	Sipunculida
Mollusca	Bivalvia	Bivalvia
Mollusca	Bivalvia	Caridea
Mollusca	Gastropoda	Gastropoda
Mollusca	Gastropoda	Opisthobranchia
Mollusca	Gastropoda	Scaphopoda
Mollusca	Mollusca	Mollusca

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Edgar Group	Brey Group	Taxon Group
Mollusca	Mollusca	Polyplacophora
Mollusca	Nudibranchia	Aplacophora
Mollusca	Nudibranchia	Caudofoveata
Mollusca	Nudibranchia	Nudibranchia
Mollusca	Nudibranchia	Opisthobranchia