A balanced trophic model of the Chatham Rise, New Zealand

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EXECUTIVE SUMMARY

A balanced trophic model of the Chatham Rise, New Zealand is presented. The model consolidates quantitative information on trophic links across all the major biota of the Chatham Rise and tests for data consistency. The model has 28 trophic groups and is balanced in terms of annual flows of organic carbon in an average, recent year (nominally 2000–2005). The focus of the model is on the role of demersal fish in the food web and the model has greater taxonomic resolution towards the middle-upper part of the food web, including 9 demersal fish by species (hoki, orange roughy, smooth oreo, black oreo, ling, silver warehou, hake, javelinfish, barracouta), and three ‘composite’ demersal fish groups: rattails, dogfish, ‘other demersal’. Mesopelagic fishes and juvenile fishes are separate groups in the model.

A survey of the available literature and both published and unpublished data provided an initial set of parameters describing the annual average abundance, imports, exports, energetics (growth, reproduction, consumption), and trophic linkages (diets, key predators) for each model group. We also estimated the relative level of uncertainty on these parameters. This set of parameters was not self consistent, and a method is used to adjust the initial parameter set to give a balanced model taking into account the estimates of parameter uncertainty and the large range of magnitude (>6 orders of magnitude) in trophic flows between groups. Parameters for biomass, production rate, growth efficiency, diet fractions, and other transfers of biomass between groups were adjusted simultaneously. We found that changes to the initial set of parameters needed to obtain balance were reasonably small for most groups and most parameters. The mean absolute changes for the three key parameters (biomass, B; production rate, P/B; growth efficiency, P/Q) and all groups together were 13%, 7.4% and 2.5% respectively. The average change of diet fractions to achieve balance was 1.1% (maximum change of 14.7%).

Trophic levels are reasonably close with those from other ecosystems given in the literature but trophic levels of demersal fishes in the model were higher than expected. The model suggests that macrobenthos (benthic invertebrates), macrozooplankton, and mesopelagic fishes had particularly high ecological importance in the food-web. Research towards model validation using stable isotope analyses, and further development of the model (including separating some of the composite demersal fish groups, and separation of the macrobenthos group) is ongoing. Trophic modelling of the Chatham Rise will continue under funding from the New Zealand government within the Coasts and Oceans Outcome Based Investment.

1 INTRODUCTION

Whole ecosystem modelling is being increasingly used as a tool for analysis of ecosystem structure and function (e.g. Bradford-Grieve *et al.* 2003; Pauly *et al.* 1998). Whole-ecosystem trophic models can indicate whether our knowledge of the various components of the ecosystem function is consistent with the conceptual model. Inconsistencies identified by the model can indicate priorities for future research. A coherent and consistent picture of ecosystem function, once developed, can be used to explore how the ecosystem may respond to change. Such change can be anthropogenic (e.g. different management strategies), natural (e.g. climatic variability), or mixed (long-term climate change). The model presented is based on the Ecopath approach (Christensen *et al.* 2000), where flows of a conservative tracer (here, carbon, C), through various trophic compartments of the ecosystem over a given period (here, annual) are considered. Bradford-Grieve *et al.* (2003) demonstrated that it is possible to construct an ecosystem model for the Southern Plateau, New Zealand, immediately to the south of the present study area, and much of this work from this study has been used to inform the present study. This report follows on from a preliminary version of the model (Pinkerton, 2008).

It is stressed that a trophic model much as that presented here is not, in itself, sufficient to assess the effects of fishing on the ecosystem. The development of this model should be viewed as serving a number of useful purposes:

- It forces the critical assembly of data on all components of the ecosystem in a form where they may be combined. These data will be needed for the development of future ecosystem models, including those that are seasonally resolved, spatially resolved, and capable of being run dynamically to investigate the effect on the ecosystem of fishing and environmental variability. The model tests whether our current understanding of the ecosystem structure and function is complete and consistent. In assessing completeness, the model allows us to identify critical gaps in our knowledge, data, or approach. In testing consistency, the model will help to identify priorities for future work.

- It formalises our conceptual model of ecosystem interconnectedness. The conceptual model can be used to focus discussion by researchers, managers and other stakeholders in the Chatham Rise ecosystem. For example, it may help to determine if there are bottlenecks of energy flow through the system, or key species on which the system depends. This conceptual model will be directly applicable to ecosystem modelling efforts for the Chatham Rise in the future. The model may also allow us to identify sub-systems (for example, groups of interconnected fish species) that should subsequently be modelled in more detail.

- The model gives us an overview of the type of ecosystem in the Chatham Rise, which allows system-level comparison with other ecosystems round the world. For example, how much surplus production is likely in the system? Is there likely to be high export of material from the system? In what ways does the Chatham Rise ecosystem differ from other New Zealand oceanic or international temperate ecosystems?

- The model may help to identify candidate indicators of ecosystem state, which will be useful in monitoring changes in the form and function of the Chatham Rise ecosystem over time.

1.1 Structure of report

Section 2 presents the choice of study region. This issue is critical to the success of ecosystem modelling. We also briefly summarise the chemico-physical setting of the Chatham Rise. Section 3 gives a summary of the type of model to be used here. We discuss the approach we have decided to use for the modelling, and the justification for this approach. The limitations of the modelling approach, largely constrained by data availability are explained. Ways that the modelling could be expanded in the future are given. The following sections consider each of the trophic compartments of the model in detail. The sections review the relevant parts of the literature on the various organisms, give methods for estimating biomass, energetic parameters, and trophic linkages. A summary of the model parameters determined or estimated in each of these sections is given. This leads to the start of balancing of the conceptual trophic model for the system.

The results of the current study are presented in Section 12 and discussed in Section 13 which also recommends priorities for future work on modelling ecosystem-fishing relationship for the Chatham Rise.

2 STUDY REGION

The study area for this work is the Chatham Rise, a broad submarine ridge about 800 km long and 300 km wide that extends eastwards from New Zealand landmass into the southwest Pacific Ocean. High phytoplankton abundance in this region is a conspicuous feature of ocean colour images of the Southern Ocean (e.g. Gordon *et al.* 1986; Banse & English 1997; Murphy *et al.* 2001). Elevated phytoplankton productivity is attributed to the presence of the Subtropical Front (STF) being bathymetrically locked to the Chatham Rise (Murphy *et al.* 2001; Sutton, 2001; Uddstrom & Oien, 1999). The STF above the Chatham Rise forms part of a 25,000 km-long convergence zone of northern Subtropical (ST) waters, and southern subAntarctic (SA) waters that encircles the globe. The mixing of nitrate-depleted ST water, with nitrate-rich SA water in the Chatham Rise region leads to elevated phytoplankton productivity (Boyd *et al.* 1999). Elevated oceanic productivity here is responsible for supporting the complex and valuable Chatham Rise ecosystem, including deep-water fisheries (e.g. orange roughy, oreo, hoki), an unusually rich benthic ecosystem, as well as large seabird and marine mammal populations (Francis & Fisher 1979).

For the purposes of this work, we define the study area as occupying 42°–45.5°S, 173°E–171°W, and east of the 250 m depth contour enclosing the New Zealand land mass (Figure 1). This region is approximately 1290 x 390 km, with an area of 476,000 km^2, and a mean depth of 1645 m. The top of the Chatham Rise is at a depth of 400 m, whereas the northern and southern flanks descend to more than 4000 m; the maximum depth in the study region is 5127 m. The Chatham Island group (close to 176.5°W) have an area of only 960 km^2 (<0.2% of the study region). Approximately 71% of the study area is STF water, with the remaining 29% being subAntarctic water.

The Chatham Rise substrate is a mixture of sand, silt and clay, with pronounced north-south variation. A transect at 178°30’E, Nodder *et al.* (2003) found organic-rich, low carbonate (20%) muds at greater than ~500 m on the north-side of the rise, sandy sediments dominate with moderate carbonate content (50–75%) on the upper flanks of the rise, and high carbonate (70-90%), foraminiferal ooze deeper than ~1000 m on the southern side of the rise. Many studies have also shown differences in benthic community between the northern and southern flanks of the rise, and with depth, as discussed below (Probert & McKnight, 1993; Probert *et al.* 1996; McKnight & Probert, 1997).

3 MODELLING METHODLOGY

3.1 Model structure

The trophic model developed here quantifies the transfer of organic material through a food web based on the widely used mass-balance identities of the Ecopath trophic model (Christensen & Walters 2004; Christensen et al. 2004). Biomass is presented in units of organic carbon density (gC m^{-2}) and trophic flows in units of gC m^{-2} y^{-1}. In quantifying the trophic structure of the ecosystem, the fundamental information includes the species present, abundances in terms of weight, the energetics of species (i.e. production, consumption, growth efficiency, respiration), and trophic interconnections between species through information on diets of predators. The model developed here also includes non-trophic transfers of organic carbon between groups. These transfers include: (1) unassimilated consumption (excreted material); (2) loss of material through exudants (e.g. primarily phytoplankton); (3) non-predation mortality (e.g. due to age, disease, starvation); (4) "messy eating" i.e. parts of animals that died due to predation but were not consumed at the time; (5) transfers of biota from the sea-ice habitat to the water column on melting of sea-ice in the spring; (6) growth of biota which takes them from a smaller to a larger trophic group; (7) vertical sinking flux of detritus from the water column to the benthos; (8) long-term burial of organic material in the benthic sediments. Note that (2)+(3)+(4) are often described by an ecotrophic efficiency parameter.

We make the assumptions that there are no long term (e.g. decadal) trends. It is possible that there are considerable differences between years in many parts of the Chatham Rise ecosystem. This has two implications for developing a budgetary model. First, whereas long-term changes in ecosystem state may be small, there may be significant accumulations or loss of biogenic material over any given annual period. Second, measurements made in different years are not strictly comparable. In this study we attempt to reduce the affects of interannual variability on the budget by considering an annual period that is typical of a longer period, in this case chosen to be the period between October 2002 and December 2007.

Production is defined according to Equation 1. For non-detrital groups, production represents the intrinsic rate of growth of all individuals in the population. For detrital groups, production is the total net flow of organic matter into the group, including faecal material (unassimilated consumption) from consumers, dead organisms, non-consumed predation ("messy eating"), planktonic exudants, and transfers between groups. These latter transfers include, for example, the release of organic material into the water column when ice melts, and the sinking of detrital/ungrazed material to the benthos. Carbon flow through each trophic group per year is balanced according to Equation 2 under the assumption that all parts of the ecosystem will be in balance in an average year. These balance equations provide a number of equality constraints to the system. Another set of equality constraints are provided by the fact that diet fractions of each predator sum to unity.

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

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

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

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

B_i	annual average biomass (gC m^{-2})
P_i	annual production (gC m^{-2} y^{-1}). Autotrophic production rate is net of respiration but assumed to include production of phytoplankton exudants and other detrital material.
Q_i	annual consumption (gC m^{-2} y^{-1}). Note that autotrophs and detritus have Q_i=0.
$(P/B)_i$	production/biomass ratio (y^{-1})
$(Q/P)_i$	reciprocal of the growth efficiency (dimensionless)
D_{ij}	average fraction of prey i in the diet of predator j by weight (dimensionless)
X_i	fraction of production exported over year due to advection and migration (dimensionless)
A_i	fraction of production accumulated over a year (dimensionless)
F_i	fishing removals (gC m^{-2} y^{-1}).
T_{ij}^{1-E}	detrital transfer: fraction of production transferred from group i to detrital group j as non-living material, i.e. excluding direct predation but including phytoplankton exudants, parts of organisms (e.g. due to "messy eating"), whole dead organisms and carcasses (dimensionless)
T_{ij}^{g}	growth transfer: fraction of production transferred from group i to group j due to growth, i.e. as an organism gets older and/or larger it changes from one group to another (dimensionless)
T_{ij}^{s}	seasonal transfer: fraction of production transferred from group i to group j by non-trophic, seasonal processes, e.g. due to ice melting, vertical flux of material (dimensionless)
U_{ij}	fraction of food that has been consumed by component i but which is not assimilated, instead being passed to detrital group j, (dimensionless)
n	total number of groups in the model
R_i	loss of organic carbon from the system due to respiration (gC m^{-2} y^{-1}). Respiration can be calculated as $R_i=Q_i\cdot(1-U_i)-P_i$

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

3.2 Trophic groups

We assume that living organisms in a marine ecosystem can be grouped usefully into relatively few functional groups with distinct and stable characteristics. Too few groups will not allow the model to describe the trophic structure with sufficient subtlety, whereas too many groups can lead to spurious results because of lack of information to provide good parameterisation. Here, we use 28 trophic groups. The divisions we use include taxonomy (species or groups of species), function (e.g. water column primary producers), and sampling methodology (e.g. benthic organisms by size). Ideally, groups would be chosen so that organisms combined into groups have similar characteristics such as size, energetics (growth rates, respiration rates, etc), and similar trophic links (similar prey items, predators). In reality, choice of groups is often constrained by the available information. It is assumed that the choice of groups does not affect the fundamental results of the modelling study though this has not yet been tested. The current groups are as follows.

- Apex predators (3 groups): seabirds; pinnipeds (seals and sea-lions); cetaceans
- Demersal fish (12 groups): hoki, orange roughy, smooth oreo, black oreo, rattails, ling, silver warehou, hake, javelinfish, barracouta, dogfish, other demersal;
- Mesopelagic fish (1 groups), dominated by myctophids;
- Juvenile fish (1 group);
- Cephalopods (1 group), including squid and octopus;
- Zooplankton (5 groups): Salps, macrozooplankton, mesozooplankton (mainly copepods), heterotrophic microplankton (ciliates), heterotrophic flagellates;
- Phytoplankton;
- Bacteria (1 group) including water column bacteria and benthic bacteria;
- Benthic fauna (2 groups): macrobenthos, meiobenthos;
- Detritus, including particulate and dissolved water column detritus and benthic detritus.

3.3 Ecotrophic efficiency

It is known that a substantial part of organic material (especially at lower trophic levels) is not directly consumed but enters the detrital pool where it is decomposed by bacterial action. This material is typically accounted for in ecotrophic model using a parameter for ecotrophic efficiency. Ecotrophic efficiency (E) is defined as the fraction of production that is consumed by other organisms, exported, fished or accumulated. The remainder of production in such trophic models (the fraction 1-E of production) is assumed to be remineralized by bacterial action. Whereas small organisms that die from reasons other than direct predation (e.g., disease, parasites, injury) may be decomposed by bacterial action, we suggest that larger organisms that die in the sea are more likely to be consumed by scavenging fauna than decomposed by bacterial action. Remains of these dead organisms should not therefore be included in the detrital pool, and consequently ecotrophic efficiency should be set to unity. In the model presented here, we set E=1 for all fish and larger consumer groups to represent a view of the ecosystem where bacterial decomposition plays the smallest feasible role. In the current version of the model we have not separated animals killed by direct predation from those that die from other causes – there is no “carcass” group. Instead, consumers of a species in the model include its direct predators and those which are likely to consume its carcasses or remains. For apex predators that have few direct predators, we assume that they are likely to die in the water so that their remains are likely to be consumed by benthic scavengers. There will still be a substantial flow of material to detritus in the model because of “unassimilated consumption” from each consumer. Unassimilated consumption includes faecal material and the results of “messy eating” at lower trophic levels.

It is known that a substantial part of primary organic material (i.e. phytoplankton) is not directly consumed but enters the detrital pool where it is decomposed by bacterial action. Some of the detritus will be in the form of particulate material in the water column, some as dissolved organic matter (e.g. phytoplankton exude transparent exopolymers), and some will be deposited to the sea bed in intense sedimentation events (e.g. rapid sinking of “marine snow”). Detritus has high spatial and temporal variability so that the proportion of primary organic matter entering the detrital pool rather than being consumed directly (i.e. ecotrophic efficiency) is inexactly known.

3.4 Parameter estimation

There is a huge amount of information on the physical environment of the Chatham Rise, and its flora and fauna, including physiology, life histories, energetics, and ecology. Detailed information on the estimation of the biomass, energetic parameters, and diets for each trophic group is given below. The initial estimates of all biomass, energetic, diet and transfer parameters for the trophic model are given in Table 1 and Table 2.

3.5 Balancing methodology

In this version of the Chatham Rise trophic model we used the semi-objective balancing method described in Pinkerton et al. (2010), developed for the Ross Sea. Each of the model parameters initially estimated has an associated uncertainty because the values are imperfectly and incompletely observed, and because the parameters vary between years and hence differ from our modeled average recent year. We hence adjust our preliminary estimates of all parameters to obtain a model where all the equality constraints are fulfilled. Such solutions are henceforth referred to as balance points. We allow all parameters to vary except fishing take (*F*) which is fixed at zero. Models such as this are highly under-constrained, often with >3 times more parameters to fit than constraints (Pinkerton et al. 2010), so there is a large family of possible solutions all of which are feasible according to the conceptual model. We want to find the solution that is “closest” to our initial set of estimated parameters as defined below. The problem at this stage is non-linear and we adopt an iterative approach to search for this solution by simultaneously adjusting all parameters. The system is first linearised and then Singular Value Decomposition (SVD: Press et al. 1992) is applied to find the adjustment vector which minimises the cost function, Δ (Equation 3). This balance point is the closest one to our initial parameter set taking into account relative uncertainties between parameters and ensuring even adjustment across groups in the model.

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

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

Biomass

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

Production

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

Growth efficiency^{-1}

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

Export fraction

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

Accumulation fraction

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

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

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

Transfer to detritus $$T_{ij}^{1-E\,\prime} = T_{ij}^{1-E} + K_{ij}^{1-E} \cdot \delta T_{ij}^{1-E} \quad (11)$$

Transfer by growth $$T_{ij}^{g\,\prime} = T_{ij}^{g} + K_{ij}^{g} \cdot \delta T_{ij}^{g} \quad (12)$$

Seasonal transfer $$T_{ij}^{s\,\prime} = T_{ij}^{s} + K_{ij}^{s} \cdot \delta T_{ij}^{s} \quad (13)$$

For changes to three model parameters (*B*, *P/B*, *Q/P*) the changes were applied relative to scale values, B^s, $(P/B)^s$, $(Q/P)^s$ which are initially set to the estimated starting parameter values. Using the parameter values themselves to scale the adjustments appropriately handles the large range in magnitudes of these parameters across the food web. The parameter changes were not scaled for diet and transfer fractions because these parameters are of similar magnitudes (between 0 and 1) as they are scaled by *P* to obtain the actual flows of carbon (Equation 2).

After adjustment in this way by SVD, the set of equality constraints will not be satisfied exactly because the minimisation works on a linearised version of the constraints assuming small changes. We hence iterate until the equality constraints are satisfied with an error within computational accuracy (8 iterations for within 0.0001% of true balance). On each iteration, we update the three scale parameters B^s, $(P/B)^s$, $(Q/P)^s$ by setting each to the lower of the current estimate or the initial estimate of that parameter. Updating scale values in this way means that logarithmically-equal increases and decreases of parameters over multiple iterations will lead to the same change to the cost function. For example, $K.\delta = +1$ will represent a doubling of the parameter and $K.\delta = -1$ will represent a halving of the parameter.

Parameter uncertainty

In order to use an objective balancing method, it is necessary to assign relative magnitudes to the uncertainties of all parameters in the model. The absolute magnitudes of *K* across all groups are not important, but their relative values will affect the balanced model obtained. Whereas it is possible to assign uncertainties to some parameters by using information on the variability associated with various parts of the data used in their derivations, an entirely objective approach is not possible for all parameters for all groups. As a solution to the problem of assigning uncertainties to parameters consistently, Kavanagh et al. (2004) suggested that a “data pedigree” approach was useful where parameters were assigned indices representing their relative uncertainties and these pedigree indices then mapped onto numerical uncertainty factors. We used a similar method here (see Pinkerton et al. 2010 and below for details of the method) to give values shown in Table 3. Note that the uncertainty values in this table do not imply absolute limits on plausible parameters as actual changes are determined by *K* values and the required δ values for balance.

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

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

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

Similarly, we estimated K factors for transfer fractions (K^{1-E}, K^{S}, K^{g}, K^{A}, K^{X}) using a two step methodology. First, we set base transfer parameter uncertainties for all groups in the model (K_0^{1-E}, K_0^{S}, K_0^{g}, K_0^{A}, K_0^{X}) and then adjusted these according to our estimates of the actual values of the parameters (equations 15–19).

Accumulation $$K_{i}^{A} = K_{0}^{A} \cdot \left(a \cdot A_{i}^{2} + b \cdot A_{i} + c\right) \qquad (15)$$

Export $$K_{i}^{X} = K_{0}^{X} \cdot \left(a \cdot X_{i}^{2} + b \cdot X_{i} + c\right) \qquad (16)$$

Transfer to detritus $$K_{ij}^{1-E} = K_{0}^{1-E} \cdot \left[a \cdot \left(T_{ij}^{1-E}\right)^{2} + b \cdot T_{ij}^{1-E} + c\right] \qquad (17)$$

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

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

We use constants in equations 15–19 of a = -2.8, b = 2.8, c = 0.3. This formulation gives $K_{ij}/K_{i0}=1$ for $T_{ij}=0.5$, and $K_{ij}/K_{i0}=0.3$ for $T_{ij}\rightarrow 0$ and $T_{ij}=1$. This approach prevents excessive changes occurring during balancing when initial estimates are towards an extreme of the possible range. We used base values of $K_0^{A}=0.3$, $K_0^{1-E}=0.3$, for all groups in the model where initial estimates were non-zero. We used $K_{ij}^{U}=0.1$ for all groups. We set $K_i^{F}=0$ for all groups i.e. we do not allow the balancing to adjust fishing removals. We set $K_i^{Q}=0$ for all groups so that the balancing adjusts consumption rates only via adjusting P/Q values. Note that K_0^{X}, K_0^{S}, K_0^{R} and K_0^{g} were not used in this version of the trophic model. Although still more arbitrary than ideal, this method of assigning relative uncertainties is certainly an improvement on other methods currently available, and leads to a plausible balanced model. The sensitivity of the balanced model to different K factors is an important issue and is discussed later.

3.6 Trophic levels

We calculated trophic levels (Lindeman 1942, Christensen & Pauly 1992) in the balanced model using matrix inversion based on two rules. First, primary producers, detritus and bacteria are defined as having a trophic level of 1. Second, a consumer's trophic level is the sum of the trophic levels of their prey items, weighted by diet fraction, plus one. Bacteria are defined as being at the same trophic level as primary producers. Because diets of demersal fish are not well-resolved in the current version of the model, we calculated an average demersal fish trophic level as the biomass-weighted sum of trophic levels of the individual species. Results are given in Table 7.

3.7 Ecological Importance

Based on a balanced food-web model, methods exist for calculating the average 'ecological importance' (sensu Libralato et al. 2006) of the species or model groups. Ecological importance (*EI*) is a measure of the overall effect on food-web structure of changes to the abundance of species caught by the fishery. This measure is preferred over 'keystoneness' since the meaning of the latter has become confused. Keystoneness was defined by Power et al. (1996) as the amount by which the ecological importance of a species exceeds that expected on the basis of abundance alone. Other interpretations of keystoneness essentially equate it to ecological importance (Libralato et al. 2006). In any case, ecological importance is the relevant measure in terms of assessing by how much changes in the abundances of species caught by the fishery are likely to affect the food-web, irrespective of whether those species have high or low biomass in the ecosystem.

If a balanced food-web model of the ecosystem of interest is available, the ecological importance of a given species can be calculated via the Mixed Trophic Impact (MTI) matrix, **M**. This matrix has elements m_{ij} and is often interpreted as the change in biomass of one group (the "impacted" group, *j*) due to a small change in the biomass in another group (the "impacting" group, *i*) (e.g. Libralato et al. 2006). First, a measure of the direct (one-step) trophic impact of species *i* on species *j* is written as element q_{ij} in the matrix **Q**, and defined as the difference between bottom-up (g_{ij}) and top-down effects (f_{ij}) (equation 20, Ulanowicz & Puccia 1990).

$$q_{ij} = g_{ij} - f_{ij} \qquad (20)$$

Here, g_{ij} is the proportion of prey item *i* in the diet of predator *j*, and f_{ij} is the fraction of the net production of prey item *j* that is consumed by predator *i* (Ulanowicz & Puccia 1990). "Net production" excludes respiratory output which is equal to "production" (*P*) in Ecopath and Ecosim models (Christensen & Walters, 2004; Christensen et al. 2008). The MTI matrix **M** is calculated as equation 21 to take into account indirect food-web effects, that is, impacts of one species on another via multiple steps through the food-web (Ulanowicz & Puccia 1990). Here, **I** is the identity matrix of size *n* by *n* where *n* is the number of groups in the model.

$$\mathbf{M}^t = (\mathbf{I} - \mathbf{Q}^t)^{-1} - \mathbf{I} \qquad (21)$$

Libralato et al. (2006) suggest calculating ε_i (the ecological importance of species *i*) as the root mean square value of m_{ij} calculated over all *j*. In a similar but alternative approach, here we use equation 22 which gives weak links higher and, we argue, more appropriate importance (McCann et al. 1998; Pinnegar et al. 2005).

$$EI_i = \sum_{j=1}^{n} \left| m_{ij} \right| \qquad (22)$$

3.8 Omnivory Index

Omnivory index (*OI*) is a measure of the breadth of a consumers diet and is calculated from the square of the difference in trophic level between predator and prey, as equation 23 (Christensen & Walters, 2004; Christensen et al. 2008).

$$OI_i = \sum_{j=1}^{n} (TL_j - (TL_i - 1))^2 \cdot D_{ij} \qquad (23)$$

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

4 BIRDS

4.1 Biomass

More than 70 species of birds are present in the Chatham Rise ecosystem, including species that are unique to the study region (e.g. Chatham Island taiko, *Pterodroma magentae*), and many that have declining populations to the point of being endangered species (e.g. Chatham albatross, *Thalassarche eremita*). In this work, we consider all birds in the Chatham Rise ecosystem in one trophic group. Taylor (2000a, b) give a summary of the abundance of New Zealand seabirds, divided into two groups: those that are considered threatened by the International Union for Conservation of Nature and Natural Resources (IUCN) criteria (taxa listed as Critical, Endangered or Vulnerable), and non-threatened species. The average uncertainty in the number of pairs of birds based on most recent surveys (generally since 1997) was ~20%, but occasionally >80% (Taylor 2000a, b). Non-breeding individuals were taken to comprise between 0.33 and 0.6 of the population (Taylor 2000a, b). Average bird weights were taken from Heather & Robertson (1996).

Most of the species do not live or feed exclusively within the Chatham Rise ecosystem, and to estimate bird biomass and consumption from the system it was necessary to estimate the proportion of the life of each species that can be considered to take place wholly within the study area. These estimates were based on published information on the foraging extent of the bird, and an estimate of the times spent within the study region per year. No consumption of food from the Chatham Rise ecosystem was taken to occur when the bird migrated outside the study region. We reduced the bird biomass and amount of food required from the system by 50% for those species that feed from terrestrial rather as well as marine sources (e.g. gulls, *Larus dominicanus dominicanus, L. scopulinus*). The proportions of life spent within the study region ranged from 1 for locally feeding birds resident in the Chatham Rise region (e.g. Pitt Island shag, *Stictocarbo featherstoni*), to <0.02 for widely distributed seabirds (e.g. Sooty Shearwater, *Puffinus griseus*). These were allocated a nominal uncertainty of 30%. Uncertainties in the seabird biomass estimates due to a combination of factors given above were approximately 62% of the “best” biomass estimate (average of upper and lower biomass estimates). The total biomass estimates of seabirds on the Chatham Rise were 731 t (threatened species) and 1630 t (non-threatened). Seabirds classified as “vulnerable” made up about half the species in the study region, but only 31% of the bird biomass, and 21% of the consumption requirements (see below). Seabirds classified as vulnerable include (in order of decreasing biomass): *Thalassarche steadi*, *T. platei*, *Eudyptes sclateri*, *Puffinus huttoni,* and *Thalassarche impavida* and *Procellaria aequinoctalis.* Six species of albatross each constitute more than 1% of the bird biomass of the Chatham Rise. The non-threatened seabird biomass was dominated by *Puffinus griseus, Larus dominicanus dominicanus, Pachyptila vittata,* and *Pterodroma nigripennis*. We assume that 10% of wet weight of seabirds is carbon (Vinogradov 1953).

4.2 Production

Production is considered in two parts: (1) birds entering the adult population and replacing those adult birds that die each year; (2) chick and juvenile birds dying before reaching adulthood. The former is estimated as: [(no. pairs breeding per year)x(no. eggs per pair)x(proportion of eggs that survive to adult)x(average weight of adult)]. The number of eggs per pair was taken from Heather & Robertson (1996). The proportion of eggs surviving to adult is taken to be 0.2 for a single egg laid, decreasing to 0.05 when 4 eggs per pair are laid. Numbers of breeding birds as a proportion of the total population is estimated from census numbers to lie between 31–86%, with a median value of 47%. The average weight of a chick/juvenile at death is taken to be the geometric mean of the hatching weight and the adult weight. A geometric mean is taken as mortality is assumed to be approximately constant with age. As mortality is actually likely to be higher for younger birds, this method may overestimate production. Summing these productions gives annual P/B values for individual species between 0.06–0.26 y^{-1}, this variation arising from differences in the number of eggs per breeding pair, and the proportion of the population breeding per year. The average P/B values (weighted by biomass) for all birds together is estimated to be 0.12 y^{-1}. Crawford *et al.* (1991) used P/B=0.20 y^{-1} for southwest African seabirds and Wolff (1994) used 0.07 y^{-1} for northern Chile seabirds, so our value looks reasonable.

4.3 Consumption

Food consumption requirements for each species were estimated by two methods. Nagy (1987) estimated daily dry weight food consumption for seabirds according to body weight. This was converted to carbon using a ratio of 0.4 gC gWW^{-1} (Vinogradov 1953). In the second method, average daily energy requirement of seabirds was taken as 2.8 the standard metabolic rate (SMR: Laeiewski and Dawson 1967). An assimilation efficiency of 0.75 and energy/carbon ratio of 12.5 kcal/gC were used to give carbon requirements (Croxall 1987; Lasiewski & Dawson 1967; Schneider & Hunt 1982). These methods differed by less than 15% for all bird species, and the results of the two methods were averaged. Food requirements for individual species were then summed in proportions equal to their contribution to total bird biomass. The annual Q/B values for the bird group is 104 y^{-1} respectively, comparable but larger than previous work (e.g. 62 y^{-1} for northern Chile seabirds: Wolff 1994). We assume an average factor of 0.108 gC/g wet wgt for squid, macrozooplankton, and fish (Scheider & Hunt 1982).

4.4 Diet

The diet of seabirds is taken to be composed of squid, macrozooplankton (crustacea), and fish (mainly small midwater fish) (Croxall 1987). Albatross feed on fish, squid, and macrozooplankton mainly taken from the ocean surface with some shallow plunging. Some carrion, such as small seabirds, may also be taken (Heather & Robertson 1996). Diet of petrels is reported as cephalopods, crustaceans (especially macrozooplankton), and small fish, taken principally by dipping, surface-seizing, surface-diving, and pursuit diving. Skua prey on eggs and young of breeding birds near the coast, as well as feeding on small midwater fish, and macrozooplankton by surface feeding (Mund & Miller 1995). Skua can also take seal remains and parts of other carcasses. We estimate an initial diet for the bird component of the model as 41% midwater fish (mainly myctophids), 5% juvenile fish from the midwater, 10% squid and 44% macrozooplankton.

4.5 Export

The impacts of fishing on marine birds are many, but generally not systematically observed (Tasker *et al.* 2000; Taylor 2000a, b). Birds are incidentally killed by fisheries activities, by collision with lines or other parts of the ship, entanglement in nets, and ensnarement on hooks. Birds can also become entangled in lost fishing gear, disturbed by fishing activity, or affected by pollution from fishing vessels. Discarded material (e.g. offal, discarded bycatch) from fishing vessels may positively impact some seabird species (e.g. James & Stahl 2000). As all birds killed by interactions with fisheries remain local, there is no removal of bird biomass from the ecosystem by fishing vessels and these effects do not impact the model described here.

5 CETACEANS

5.1 Biomass

There are a number of species of toothed whales and dolphins that are likely to have the Chatham Rise study region in their living range (e.g. Gaskin, 1982; Baker, 1990). These include Arnoux's beaked whale (*Berardius arnuxii*), southern bottlenose whale (*Hyperoodon planifrons*), hourglass dolphin

(*Lagenorhynchus cruciger*), Andrew's beaked whale (*Mesoplodon bowdoini*), straptoothed beaked whale (*Mesoplodon layardii*), spectacled porpoise (*Phocoena dioptrica*), goosebeak whale (*Ziphius cavirostris*), southern rightwhale dolphin (*Lissodelphus peronii*), bottlenose dolphin (*Tursiops truncatus*), harbour porpoise (*Phocoena phocoena*). The sperm whale (*Physeter macrocephalus*), orca (*Orcinus orca*), and baleen whales including *Eubalaena australis* (right whale), *Balaenoptera acutorostrata* (minke whale), *B. musculus* (blue whale), *B. physalus* (fin whale), *B. borealis* (sei whale), and *Megaptera novaeangliae* (humpback whale). Average adult weights of other cetacean species are taken from Shirihai (2008): long-finned pilot whales, 2600 kg; hourglass dolphin, 84 kg; Andrew's beaked whale, 1300 kg; Spectacled porpoise, 88 kg, Goosebeak whale, 3000 kg; Southern right whale dolphin 88 kg; Harbour porpoise, 69 kg, bottlenose dolphin 150 kg; straptoothed beaked whale, 2200 kg; minke whale, 4800 kg; fin whale 55,500 kg; humpback whale, 30,000 kg; sei whale 17,000 kg; blue whale 103,000 kg, right whale 25,000 kg; orca (type C) 3020 kg; sperm whale 18,500 kg.

Little is known of the migration patterns, global abundances, or numbers in the study region of the Chatham Rise of any of these species. Knowledge of beaked whales is particularly scarce. Baleen whale populations are assumed to migrate through the Southern Plateau region and may enter the Chatham Rise study area. All six species of baleen whale given above are thought to breed in tropical, subtropical or warm temperature waters in winter and feed in polar or cold temperate waters in summer, with spring and autumn migrations between the two regions (Brown & Lockyer, 1984). It is generally assumed that whales do not feed on their migration from the Antarctic to the tropics, or if they do feed, do so at low intensity. Lockyer (1981) suggests that baleen whales feed intensively in the Antarctic for about 120 d/y and consume at a rate approximately $^{1}/_{10}$th of this at other times of the year. In this case, the Q/B value appropriate for the model (i.e. the rate of feeding while in transit through the Chatham Rise) will be approximately 0.1 times as great as the annual average Q/B value. Sperm whales and right whales are known to migrate to the New Zealand region to feed, with the main area of feeding being the area off Kaikoura, which is within the Chatham Rise study area.

5.2 Diet

The diet of beaked whales, toothed whales and dolphins is composed mainly of fish (including demersal fish), and squid (Brown & Lockyer, 1984; Berzin, 1972). For example, Southern bottlenose whales are thought to take primarily squid (Northridge 1984), but probably also eat fish and possibly some crustaceans. Type-C orca (which probably constitute most of the individuals around New Zealand) apparently feed mainly on fish (Pitman & Ensor 2003, and references therein). Baleen whales feed almost exclusively on krill in the Southern Ocean, taking other pelagic crustaceans (copepods, amphipods) elsewhere.

5.3 Consumption

There are a number of ways to estimate the food requirements of whales. First, studies have obtained daily consumption rates for baleen whales by examining stomach fullness of dead animals, and estimating the number of feedings per day (e.g., Nemoto 1968; Macintosh 1970; Zenkovich 1970). There is a wide range of estimates of daily consumptions because of variations in the amounts in stomach, number feeds per day, and time of sampling relative to feeding. The first method applied in the current study is based on Innes et al. (1986, 1987) and has been used by various workers (e.g., Armstrong & Siegfried 1991; Tamura 2001, 2003). Daily prey consumption Q_{WW} (kgWW d^{-1}) is estimated as $Q_{WW}=0.42W_{kg}^{0.67}$ where W_{kg} is the average body wet-weight (kg). Prey and predators are taken as having approximately the same carbon:WW ratio. An alternative approach to estimating consumption is based on considerations of the energy requirements of the animals. The standard metabolic rate (SMR: Lasiewski & Dawson 1967) is the resting or basal rate of animals. Standard Metabolic Rates of mammals in the southern ocean may be greater than mammals of a corresponding size in temperate waters, by a factor estimated to be 1.5–2

(Irving 1970). The relation: SMR (kcal/d)=$71.3W^{0.892}$, where W is the animal weight in kg, was given by Irving (1970). This relationship gives values within 20% of that give by Sigurjonsson & Vikingsson (1997) of SMR=$206.25W^{0.783}$. The average daily energy expenditure of animals is often taken as being higher than the SMR if the animals are undergoing exertion such as swimming long distances. Lockyer (1981) estimated that the daily energy expenditure of large baleen whales, averaged over a year, is 1.3 times the SMR, because of the energetic requirements of migration. Lockyer (1981) gives assimilation efficiencies for Antarctic baleen whales of 79–83%, and we use 80%.

We use an average factor of 0.11 gC gWW^{-1} (wet weight) (Schneider & Hunt 1982) for fish prey items of whales. Krill have a lower carbon content, measured to be 0.048 gC gWW^{-1} (Weibe 1988). An energy/carbon ratio of 10 kcal gC^{-1} were used to give carbon requirements where a mixed or fish-based diet is used (Croxall 1987; Lasiewski & Dawson 1967; Schneider & Hunt 1982). For baleen whales, where diet is mainly crustaceans, energy density per gWW is lower (0.93 kcal/gWW: Lockyer 1987a) which is equivalent to 19.3 kcal/gC.

We assume our best estimate of food consumption by whales is given by an average of five methods (Irving 1970; Lockyer 1981; Innes et al. 1986; Armstrong & Siegfried 1991; Sigurjonsson & Vikingsson 1997). Differences between these methods are of the order of 29%. These annual average consumption rates i.e. the feeding rates which would occur is feeding were evenly spread over the whole year, and must be adjusted to take into account seasonal differences in feeding rates. Baleen whales are known to feed more intensively in the Antarctic in summer than at other times of the year. Reilly et al. (2004) and Sigurjonsson & Vikingsson (1997) use the values of Lockyer (1981) for the relative feeding rates in the summer and rest of the year where it is taken that baleen whales feed intensively in the Antarctic for about 120 d/y and consume at a rate approximately $^{1}/_{10}{}^{th}$ of this at other times of the year. In this case, the Q/B value appropriate for baleen whales in the model (i.e. the rate of feeding while in transit through the Chatham Rise) will be approximately 0.1 times as great as their annual average Q/B value.

For toothed whales, we average the results of four methods given above (Irving 1970; Innes et al. 1986; Sigurjonsson & Vikingsson 1997; Lockyer 1981). These methods give reasonably consistent estimates of consumption, differing from each other by about 23%. The values of Q/B for annual average feeding range from 8.0 y^{-1} (sperm whale) to 27.8 y^{-1} (Southern bottlenose dolphin). In the absence of other information, we assume that feeding of toothed cetaceans while over the Chatham Rise is approximately equal to their annual average feeding rate. For comparison, Bradford-Grieve et al. (2003) used a value of Q/B=14.6 y^{-1} for hourglass dolphins (4% of weight per day).

5.4 Production

Banse & Mosher (1980) relate production to animal biomass as: P/B=$12.9 \cdot M_s^{-0.33}$ where M_s is the animal weight expressed as an energy equivalent (kcal), and P/B is the annual value (y^{-1}). Fish are reported as having an energy density of about 1 kcal gWW^{-1} (Schindler et al. 1993). Mammals are likely to have a higher energy content as a result of their fat-rich blubber. Although the biochemical analysis of blubber of whales varies, 60% lipid is likely (Koopman 2007) implying an energy content of about 9 kcal/g. Assuming such high-lipid tissues make up about 40% of the whale's body weight, we estimate a total energy density for whales of 4.2 kcal/g. This gives P/B for whales of between 0.019 y^{-1} (blue whale) and 0.16 y^{-1} (bottlenose dolphin). For comparison, Bradford-Grieve et al. (2003) give P/B for whales off New Zealand as 0.038–0.060 y^{-1}. Jarre-Teichmann et al. (1998) estimated that a trophic compartment of whales and dolphins had a P/B ratio of 0.60 y^{-1} although this seems very high. Trites (2003) gave a more reasonable range of P/B=0.02–0.06 y^{-1} for whales (no distinction between baleen and toothed).

6 PINNIPEDS

Two species of pinniped occur in the study area: New Zealand fur seal (*Arctocephalus forsteri*) and Hooker's (New Zealand) sealion (*Phocarctos hookeri*). Although southern elephant seals *Mirounga leonine*) have been seen in the New Zealand region, this species is unlikely to reach as far north as the Chatham Rise on a regular basis (Shirihai 2008).

6.1 New Zealand fur seal

The New Zealand fur seal (*Arctocephalus forsteri*) is found in breeding colonies on the islands and coasts of New Zealand, with a New Zealand population of perhaps 75,000 individuals (Shirihai 2008). The population is mainly located on the east coast of South Island, with a population there estimated to be about 54,000 (Shirihai 2008). Recent estimates of the fur seal population of the Otago coast are 20,000–30,000 (Chris Lelas, ZBD200505, pers. comm.). This estimate includes stocks of about 9,600 individuals on Auckland, Campbell, Bounty and Antipodes Islands on the Southern Plateau (Wilson 1974; Crawley & Warneke, 1979). Fur seals are caught during bottom and midwater trawl operations, particularly for hoki (*Macrourus novazelandiae*), squid (*Nototodarus* spp.) and southern blue whiting (*Micromesistius australis*) around the coastline of South Island and the offshore islands in the southern waters of the New Zealand EEZ (Baird 2005). We use an estimate of population of 40,000 fur seals that may feed in the study region at some time of the year.

The proportion of time fur seals spent foraging in the Chatham Rise study region is not well known. Satellite tracking of New Zealand fur seals shows that they may forage up to 200 km beyond the continental slope, into water deeper than 1000 m. The 250 m depth contour (study area boundary) is about 100 km away from the coast. At these latitudes, the remaining 100 km is equivalent to about 1.5° longitude which is the maximum distance fur seals are likely to penetrate into the study area. The study area is 16° wide, so a maximum of 9% of the study area may be accessible to fur seals. Most fur seal breeding colonies are south of the study area and west of New Zealand, and fur seals are likely to spend more time foraging inshore than offshore. We hence estimate that of the order of only 1% of their food is likely to come from the Chatham Rise area and reduce their biomass in the study region pro rata. Adult males weigh 120–200 kg and adult females 40–70 kg (Crawley & Warneke, 1979; Shirihai 2008). New born pups weight about 3.6 kg (Shirihai 2008). Assuming a 50:50 sex ratio and using a median weight for males and females, the average annual wet biomass in the study area is 44 t.

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

Based on published but vague information without a foreseeable improvement, Chris Lalas (pers. comm.) estimates that fur seals consume mainly arrow squid (individuals to 1.5 kgWW) in summer–autumn and octopus (typically 2–5 kg) in winter–spring, but are also likely to take large teleost fishes, especially barracouta (2–3 kg), supplemented mainly by hoki and jack mackerel (c. 1 kg). We estimate while in the study region a diet of 50% fish (demersal and mesopelagic), and ca. 50% squid.

6.2 Hooker's (New Zealand) sealion

Hooker's sealion (*Phocarctos hookeri*) is New Zealand's only endemic seal. Males are reported to weigh about 350 kg and females 110 kg (Gales, 1995), a little less than that given by Shirihai (2008) of 320–450 kg (adult males) and 90–230 kg (adult females). New born pups weight about 7.5 kg (Shirihai 2008). We assume a 50:50 sex ratio and use a median weight for males and females. We take carbon as 10% wet weight as for fur seals.

The main breeding colonies (95% pups born) are on Auckland and Campbell islands, where the total population is probably about 12,500 (Gales & Fletcher, 1999), within the estimate of 11,100–14,000 (Shirihai 2008). In addition, about 200 individuals breed on the Otago coast (Chris Lalas, pers. comm.); breeding began in 1994, with numbers increasing at about 10% annually. The proportion of time sea-lions spent foraging in the Chatham Rise study region is not well known. Assuming that less than 1% (say 0.5%) of their food is from the study region, and reducing biomass pro rata gives an average annual wet biomass of 14 tonnes.

Hooker's sealion take a broad variety of prey, mainly small fish, cephalopods (especially octopus), crustaceans (including crabs, crayfish and prawns), and occasionally, penguins. Hooker's sealion can dive to depths of over 500 m (mean 123 m) and spend up to 11 minutes (mean 4–6 minutes) submerged per dive (Shirihai 2008). Fish taken on the dives may be a mixture of midwater and demersal species. The diet of Hooker's sea lions breeding on the Otago coast has been well studied on a monthly basis since 1991 by Chris Lelas of the University of Otago. Recent unpublished trends show some distinct seasonal and annual changes and also sex and age differences in diet (Chris Lelas pers. comm.). The diet is made up of octopus (typically 2–5 kg), 20-30%; teleost fishes (to 10 kg), 20–30%; cartilaginous fishes (to 5 kg), 20–30%; swimming crabs, 5%; fur seal (for large males, only), c. 10%; arrow squid, 1-5%.

6.3 Consumption

We estimated food consumption requirements for both species of pinnipeds were estimated by three methods, using an average of all three methods as our best estimate. These were then combined between species in relation to biomass. Nagy (1987) estimated daily dry weight food consumption for eutherian mammals (with placenta) according to body weight as Q_d=0.235$W^{0.822}$, where Q_d is the daily consumption in g dry weight; W is the animal weight (g). Dry weight of prey items was converted to carbon using a ratio of 0.3 gC gDW^{-1} (Vinogradov 1953). This method gave Q/B values of 28.6–32.6 y^{-1}. An estimate of oxygen consumption of a southern elephant seal by Hindell & Lea (1998) suggested that Nagy's (1994) equation may overestimate field metabolic rate.

In the second and third methods, consumption of seals was estimated based on the amount of food they require to supply sufficient energy to satisfy their standard metabolic rate (SMR). There is conflicting evidence on whether the metabolic rate of pinnipeds is significantly greater than that of terrestrial mammals of a similar size in natural (i.e. non-captive) conditions (e.g., Riedman 1990, and references therein). Some studies have shown metabolic rates for pinnipeds in cold-regions to be 1.5–3 times higher than terrestrial mammals in temperate regions (e.g., Costa et al. 1986). Other work found that metabolic rates of pinnipeds were only slightly higher (1.1–1.2 times) than those of a terrestrial mammal of similar size (see Riedman 1990). Here, we used the relation: SMR (kcal d^{-1})=$71.3 \cdot W^{0.892}$, where W is the animal weight in kg which was developed for marine mammals in polar areas (Irving 1970). The third method used SMR=$70.5 \cdot W^{0.7325}$ (Lockyer 1981). In both cases, the average daily energy requirement of seals was taken as 2.8 times the standard metabolic rate (Lasiewski & Dawson 1967). An assimilation efficiency of 0.8 and energy/carbon ratio of ~10 kcal gC^{-1} were used to give carbon requirements (Croxall 1987; Lasiewski & Dawson 1967; Schneider & Hunt 1982). The latter figure is appropriate for fish, and we recognize that squid has a somewhat lower energy density relative to carbon than fish (e.g., van Franeker et al. 1997, and references therein). An average of these SMR-based estimates gave values of Q/B between 21.0–27.2 y^{-1}.

The overall estimate for the pinniped group is Q/B=26.7 y^{-1}. For comparison, other work reports daily food intake for captive seals as 10% of body weight (Laws 1984), and 3.3% for harp seals (Nordoy et al. 1995). These imply Q/B values of between 12–37 y^{-1}, assuming seals and their prey have the same carbon to wet weight ratio. If seals have a slightly higher C:WW ratio than their prey, these Q/B values will be lower. Jarre-Tiechmann et al. (1998) estimate that Cape fur seals have a Q/B ratio of 19 y^{-1}. Pinniped energetics have been reviewed by Lavigne et al. (1982, 1986), and a summary is given by Knox (2007). Bradford-Grieve et al. (2003) used Q/B=46 y^{-1} for New Zealand fur seals based on Laws (1984).

6.4 Production

We estimated production following Banse & Mosher (1980) who related production to animal biomass as: $P/B=12.9 \cdot M_s^{-0.33}$ where M_s is the animal weight expressed as an energy equivalent (kcal), and P/B is the annual value (y^{-1}). Mammals are likely to have a higher energy content than fish (c. 1 kcal/gWW: Schindler et al. 1993) as a result of their fat-rich blubber. Although the biochemical analysis of blubber of mammals varies, 60% lipid is likely (Koopman 2007) implying an energy content of about 9 kcal/g. Assuming such high-lipid tissues make up about 20% of body weight, we estimate a total energy density of 2.6 kcal/g. This method gives P/B for bottlenose dolphin of 0.16 y^{-1} which we use for the cetacean group as a whole.

6.5 Export

In the Bounty/Campbell Plateau region Hooker's sealion are caught incidentally around the Auckland Islands in the southern squid trawl fishery and New Zealand fur seal are caught around the Bounty Islands in the southern blue whiting fishery (Baird, 1996, 1997, 1999; Baird et al., 1999; Doonan, 1999). The estimated numbers caught in each fishery have been averaged over the years that estimates have been made based on observer data. Therefore an average of 71 Hooker's sea lions were caught annually from 1988 to 1999 and 119 New Zealand fur seals were caught annually from 1993 to 1998. This export is negligible for the purposes of the trophic model.

7 FISH

New Zealand commercial fisheries are predominantly managed by a Quota Management System (QMS: see http://www.fish.govt.nz/information/quotams.html for current information). In this work, we consider fish as either adults, or juveniles. In this model, juveniles become adults when they enter/become vulnerable to the commercial fishery. Hence, "adult" fish in this study include all fish that are of a size where they may be caught by a commercial fishery. Small fish which have not recruited into the fisheries and which are not normally caught by commercial fisheries are termed "juvenile" for the purposes of this study. According to this definition, the "juvenile" fish category includes small sexually mature fish which are not commonly taken by the fisheries.

7.1 Adult fish

The main commercial fisheries of the Chatham Rise are hoki (*Macruronus novaezelandiae*, 57%), orange roughy (*Hoplostethus atlanticus*) and oreos (*Pseudocyttus maculatus*, *Allocyttus niger*, *Neocyttus rhomboidalis*). Many species of non-QMS deepwater sharks commonly occur in the study region, including dogfish and rattails (Macrouridae). Other species caught as by-catch on the Chatham Rise include javelinfish (*Lepidorhynchus denticulatus*), six species of slickhead including brown slickheads (*Alepocephalus australis, A. antipodianus*), deepsea flathead (*Hoplichthys haswell*), various chimaeras (*Chimaera sp.*; longnose chimaera, *Harriotta raleighana*), spineback (*Notocanthus sexspinis*), and basketwork eel (*Diastobranchus capensis*).

7.1.1 Biomass

Current absolute biomass of some commercially important Chatham Rise fish stocks are estimated as part of the QMS process using deterministic stock assessment analyses (Annala *et al.* 2003). We used data from stock models given in the 2009 plenary report (Ministry of Fisheries 2009) to estimate biomass of hoki, smooth oreo, black oreo, ling and hake. As no consensus of stock size for orange roughy on the Chatham Rise is available, with estimates of current stock size between about 30 and 200 t, we used a biomass of orange roughy of 100 t. Biomass of other species were estimated based recent trawl surveys of the Chatham Rise (average of strata 1–20 in period 1992–2007: Tuck et al. 2009) using an assumed catchability estimated from species where biomass estimates from stock models are available (hoki, hake, black oreo). Catchability by scientific trawl gear of rattails and javelinfish were assumed to be half the mean catchability values. Generic dogfish ("dogfish") includes 26 species identified in the scientific trawl survey data, including ghost shark (*Hydrolagus novaezealandiae*), spiny (*Squalus acanthias*), pale ghost shark (*Hydrolagus bemisi*) shovelnose spiny dogfish (*Deania calcea*). Generic rattail ("rattails") includes 22 species, including Bollons/big eye rattail (*Caelorinchus bollonsi*), Olivers rattail (*Caelorinchus oliverianus*), oblique banded rattail (*Caelorinchus aspercephalus*), and the banded rattail (*Caelorinchus fasciatus*). The generic "demersal fish" category includes 149 species identified in the trawl survey, including lookdown dory (*Cyttus traverse*), spiky oreo (*Neocyttus rhomboidalis*), alfonsino (*Beryx splendens*), sea perch (*Helicolenus* spp.), white warehou (*Seriolella caerulea*), common roughy (*Paratrachichthys trailli*), and giant stargazer (*Kathetostoma giganteum*).

Wet-weight (WW) biomass values were converted to gC m^{-2}, the unit used as "currency" in the ecosystem model using a ratio of carbon to wet weight of fish between 5.3% and 12.5% (mean 8.3%) based on values from Ikeda (1996), Parsons (1984), McLusky (1981) and Cohen & Grosslein (1987) who gave 1 g ww =0.14 g dry weight, 1 g dry weight =0.38 gC, 1 g ww =1.25 kcal, and 1 gC~10-12 kcal (respectively). Here, in keeping with other models, we assume that carbon is 10% wet weight for fish.

Where it is known that fish migrate into and out of the study area at different times of the year (e.g. hoki), biomass, production and consumption values for the fish have been reduced according to the pro rata time estimated to be spent in the study area.

7.1.2 Production

Production by fishes in the model was estimated using the allometric equations of Banse & Mosher (1980). The equations lead to annual P/B values between 0.33 y^{-1} (hoki) and 0.21 y^{-1} (ling) which is likely to be reasonable for middle-depth species though may overestimate production rates of some deep water species which have anomalously low natural mortality and production rates. We reduced the estimated production rate of Banse & Mosher (1980) by applying a factor of 0.5 for orange-roughy (P/B=0.19 y^{-1}), and 0.7 for oreo (P/B= 0.24–0.28 y^{-1}). In other work, P/B for orange roughy was estimated as a very comparable 0.15 y^{-1} (Pankhurst & Conroy 1987). For demersal fishes on the Southern Plateau, New Zealand, Bradford-Grieve *et al.* (2003) gave P/B=0.40 y^{-1} compared to our value of 0.30 y^{-1} for generic demersal fishes.

7.1.3 Consumption

The consumption of prey required for maintenance and growth of fish depends on their size, type and life strategy, as well as their physical environment. Palomares & Pauly (1998) derived an empirical multivariate relationship to predict food consumption (Q/B) of fish populations from total mortality, food type, fish morphometrics (based on tail shape), and temperature. Here, we assumed all fish to be carnivorous. Tail shape was taken from photographs of adult fish. Temperature was estimated from the average depth of fish occurrence on the Chatham Rise (Anderson *et al.* 1998), and the depth-temperature relationship for the Chatham Rise from Nodder *et al.* (2003). The bottom water temperature estimated based on the mean depth of the fish was 6.9°C on average. Maximum fish weights were taken from Annala *et al.* (2003), supplemented by data from FishBase (2000). Where data was missing, or for eel-like fish (e.g. hoki, rattails, ling) where the Palomares & Pauly (1998) relationship does not hold, we estimated Q/B from maximum fish lengths and Q/B values derived from other Chatham Rise species. We hence estimate a consumption rate (Q/B) for demersal fish on the Chatham Rise of between Q/B=2.7 y^{-1} (hoki) and Q/B=1.9 y^{-1} (ling). For comparison, Bradford-Grieve *et al.* (2003) gave Q/B=2.6 y^{-1} compared to our value of 2.5 y^{-1} for generic demersal fishes.

Consumption rates of orange roughy and oreos were reduced as for production values, giving Q/B= 1.3–1.6 y^{-1} for deep-waters species. These values imply a mean growth efficiency for all demersal fishes on the Chatham Rise of P/Q=0.13 (range 0.09–0.13), similar to Bradford-Grieve *et al.* (2003) which gave P/Q=0.115 for demersal fishes.

Consumption of juvenile fish species were estimated in the same way, except that the maximum fish lengths were taken to be equal to the length of the fish when it started to be caught in the commercial fishery (Annala *et al.* 2003). Values for juvenile fish on the Chatham Rise fish was estimated at 5.2 y^{-1}. Bulman & Koslow (1992) give values of 4.2 y^{-1} for juvenile orange roughy and Bradford-Grieve *et al.* (2003) used Q/B=3.0 y^{-1}.

7.1.4 Fishery and Export

Export of fish in the model has three components: commercial and recreational fish catch, net migration of fish from the study area, and transfer of fish from the "juvenile/young" compartment to the "adult" compartment due to growth over the year. Recreational fish catch is negligible. Commercial catches are derived from QMS reported catches in the 2009 Ministry of Fisheries plenary (Ministry of Fisheries 2009), from the fishing years 2003/2004 to 2007/2008. Values given by statistical area are used to estimate catches from the Chatham Rise study region using information on the distribution of fishing and species. We assume that all catches are reported. Quantitative estimates of net biomass export due to migration are scarce, and we make the assumption that the net annual migration of fish from Chatham Rise stocks is small. Transfer of juvenile and young fish into the adult fish compartment may be estimated using weight-growth rate-frequency data, but was assumed to be small in the current version of the model.

7.1.5 Long-term trends in biomass

Research suggests that the abundances of some fish on the Chatham Rise have shown a trend over the last 10 years (Livingston *et al.* 2003; O'Driscoll pers. com.). As accumulation rates were often variable between years, equivocal, or small (as a proportion of annual production), we assumed no trends in abundance in this model.

7.1.6 Diet

Information on diets for fish on the Chatham Rise primarily based on results of the Ministry of Fisheries project ZBD200402 (Stomach analysis of middle-depth fish species of the Chatham Rise) as given in Dunn et al. (2009), and papers resulting from this project (e.g. Dunn et al. 2010a, b; Connell et al. 2010; Stevens & Dunn 2010). In addition, information from the primary literature was used. In New Zealand, there have been over 20–30 years of research surveys and extensive examination of stomach contents of fish species (e.g. Clark 1985; Clark *et al.* 1989; Rosecchi *et al.* 1988). The data from more than 27 scientific papers on fish diets around New Zealand has recently been summarized by Stevens *et al.* (2007). Much of this work provides only limited qualitative information on diet composition, usually in terms of presence/absence on material in the fish stomachs, and there are few studies assessing how much energy intake of fish is from different sources. Also, only few of the studies have looked specifically at continental slope areas near to the study region. Clark (1985) found that hoki south of the study area were essentially plankton (water column) feeders, feeding mainly on natant decapods, amphipods and mesopelagic fish. Work by Bulman & Blaber (1986) shows that the proportion of energy obtained by hoki from mesopelagic fish can vary between 20 and 70%, depending on location and hoki size. Oreo (both black and smooth) in the study area were found to be predominantly plankton feeders, taking salps, in addition to natant decapods, and amphipods (Clark *et al.* 1989). The same study showed some species of rattails (*Macrouridae*) to feed predominantly on benthic invertebrates. Tarakihi (*Nemadactylus macropterus*) is also a predominant benthic feeder (Probert 1986 and references therein). For other species, benthic invertebrates may be an important part of their diet, for example spiny dogfish (*Squalus spp.*), and common warehou (*Serioletta brama*). Diets were weighted according to the total consumption of food by that species, based on biomass and Q/B values estimated as above. The fact that diets of fish change considerably with fish size, location, and probably with food availability means that diet figures should always be considered approximate. We note however that Dunn & Horn (2010) showed substantial similarities in diet of hoki, hake and ling on the Chatham Rise over 3 recent years.

7.1.7 Discarded Fish

Discarded fish include both target and non-target species that are returned to the sea as a result of economic, legal or personal considerations (Anderson *et al.* 2000). The percentage of catch that was retained for three key target fisheries (hoki, orange roughy, and oreos) were weighted according to the size of the fishery on the Chatham Rise (approximated by the average annual commercial catch), and averaged (Anderson *et al.* 2000; Anderson *et al.* 2001; Anderson 2004a, b). In the model, we reduced the catches by the proportion discarded. The percentage of the catch that is retained ranges from >95% for major commercial species (hoki, orange roughy, oreos, ling, silver warehou, hake, arrow squid), through 35% (rattails), 17% (dogfish), to <15% for bycatch species (slickheads, chimaera). For all species together, approximately 11% of fish-catch is discarded for the Chatham Rise as a whole. At a sinking rate of 10 cm/s, material will take less than 11 hours to reach the sea-bed of the Chatham Rise, so bacterial action on the material in the water column will be negligible. We hypothesise that only a small proportion of discarded material will reach the sea-bed, and that the majority will be consumed by carnivores as it sinks.

7.2 Mesopelagic Fish

Mesopelagic fish are a ubiquitous and often abundant component of temperate ecosystems. Mesopelagic fish over the Chatham Rise are primarily the myctophid lantern fishes *Symbolophorus boops* Richardson 1845 and *Lampanyctodes hectoris* Günther 1876, and the sternoptychid *Maurolicus australis* Hector 1875, often called pearlside (McClatchie & Dunford 2003). These species of mesopelagic fish are typically 5 cm in length and 1.3 g in weight. Work has shown that they often comprise a significant proportion of the diet of commercial fish species on the Chatham Rise and surrounding regions (e.g. Clark *et al.* 1989; Clark 1985). Mesopelagic fish biomass on the Chatham Rise was estimated from fisheries acoustic surveys in November-December 2000 using new estimates of target strength to interpret the acoustic backscatter measurements (McClatchie & Dunford 2003). This work gives an estimate of 665,000 t of mesopelagic fish in the study region, with an uncertainty estimated to be 25%. We have assumed that mesopelagic fish biomass is stable within 5% from year to year.

The energetic parameters for the New Zealand mesopelagic fish stocks are not well known. We have used data for *M. muelleri* for which P/B=1.15 y^{-1} (Ikeda 1996). Similar P/B ratios (0.87–1.38 y^{-1}) are given for mesopelagic fish off California (Childress *et al.* 1980). Consumption/biomass ratio for the mesopelagic fish assemblage was estimated as Palomares & Pauly (1998), giving a value of 16.0 y^{-1}, which is very close to previous studies (10.6 – 16.7 y^{-1}: Bradford-Grieve *et al.* 2003; Pakhomov *et al.* 1996). In the absence of information to the contrary, we assumed mesopelagic fish populations to be stable between years (within 5%). Mesopelagic fish are not caught by commercial fisheries. The diet of *M. muelleri* is described by Ikeda *et al.* (1994), and include a variety of meso- and macro-zooplankton species, especially copepods.

8 SQUID

Squid are important in the marine ecosystem because they are a major food source for a wide variety of predators, including fish, marine mammals and seabirds. By far the most common squid taken on the Chatham Rise is the arrow squid (*Nototodarus sloani*). Other squid occurring on the Chatham Rise (Livingston *et al.* 2003) include warty squid (*Moroteuthis ingens, M. robsoni*), red squid (*Ommastrephes bartrami*), and giant squid (*Architeuthis*). Warty, and red squids live deeper in the water column (Anderson *et al.* 1998), are caught in much small quantities than arrow squid. Giant squid are found in waters 300–600 m deep south and east of New Zealand (Förch, 1998).

Biomass estimates of all species of squid are not routinely estimated (Annela *et al.* 2003a, b), and their catchabilities with trawl gear are not known and likely to be considerably lower than fish. If we assume that the catchability of squid with trawl gear is half that of fast-swimming, similarly-sized demersal fish, we can perhaps obtain an order-of-magnitude estimate of squid biomass on the Chatham Rise. Doing so, leads to an estimate of adult (commercially-sized) squid biomass in the study region of 9,400 t. We now need to estimate the biomass of small (sub commercially sized squid). Work on the banding of statoliths from *N. sloani* suggests that the animals live for around 1 year, with rapid length growth of more than 3 cm per month (Gibson 1995; Annala *et al.* 2003a). Using von Bertalanffy growth parameters and length-weight relationship from Annala *et al.* (2003a) gives an estimate of typical adult weight of 350 gWW and a juvenile weight of 18 gWW. Juvenile mortality of squid on the Chatham Rise is unknown, but it is estimated that 946 out of every 1000 *Todarodes pacificus* (Japanese flying squid) die during the first 2 weeks of life (Gibson 1995), so perhaps of the order of 5% of squid survive to be of commercial catch size. Together, this implies that the biomass of sub-commercially sized squid is similar to that of commercially sized squid. Hence, we estimate a biomass for all squid on the Chatham Rise of 18,700 t. South of New Zealand, Hurst & Schofield (1995, Table 7) suggest that squid biomass appears to be about 1.8% of “all species biomass” in the same area. Here, we estimate total squid biomass is about 1.5% that of all demersal fishes, so this provides some suggestion that our estimate of squid biomass is of the right magnitude.

We estimate commercial catches of arrow squid from the study area based on QMS reported catches in the 2009 Ministry of Fisheries plenary (Ministry of Fisheries 2009), from the fishing years 2003/2004 to 2007/2008. We assume that all catches are reported, and that 25% of the catch from SQU1T and SQU1J is from the study region, giving a recent annual average catch of arrow squid of about 12,700 t, or about 6% of the annual squid production (adults and juveniles combined).

Here, we assume that carbon comprises approximately 8.4% wet weight of squid based on work by Vlieg (1988) who found arrow squid dry weight to be 22.5% of wet weight, and ash to be 6.2% of dry weight. If ash-free dry material is made of material in carbohydrate proportions ($C_6H_{12}O_6$) then carbon is ~40% dry weight or 8.4% wet weight. Vinogradov (1953) gives similar data for dry weight of Cephalopoda ranging from 13-30% of wet weight and ash is 0.9–2.4% of wet weight.

Annual P/B ratios for gonatid squid in the Bering Sea are estimated to be 6.7 (Radchenko 1992), for *Sthenoteuthis pteropus* in the tropical Atlantic to be 8.0-8.5 (Lapitkhovskij 1995), and for captive *Illex illecebrosus* measured to be 2.9–9.1 at 7^{o}C (Hirtle *et al.* 1981). O’Dor *et al.* (1980) point out that growth rates of *I. illecebrocsus* from field data are well below those for captive animals, indicating that food supply of the natural population can be an important limiting factor. The von Bertalanffy growth parameters, natural mortality of 0.99 y^{-1} and fishing mortality selected to give the commercial squid catch, lead to P/B value for arrow squid >10 cm of 3.1 y^{-1}. The von Bertalanffy growth parameters and length-weight relationship for arrow squid in Annala *et al.* (2003) suggest P/B of 26 y^{-1} for small squid (<10 cm). For the whole squid population, these can be combined to give an annual average P/B of 10.5 y^{-1}. In the absence of other data, we average this estimate with those data from the literature, to obtain our best estimate of P/B of 8.6 y^{-1}.

The daily ration of *Loligo pealei* ranges from 3.2–5.8% of body weight per day (Vinogradov & Noskov, 1979) which represents a Q/B of 12–21 y^{-1}. The mean daily ration of *Illex illecebrosus* is 5.2% (Hirtle *et al.* 1981) or a Q/B of 19 y^{-1}. An average of these values gives Q/B=17 y^{-1}. This would lead to a very high value of P/Q of more than 0.5 whereas it is unlikely that P/Q can be greater than about 0.35, suggesting a value of Q/B of 25 y^{-1} which we will use here.

The diet of squid has been reported to be made up of squid, mesopelagic fish (myctophids), macrozooplankton (especially mysids, euphausiids, and decapod shrimps), and a small proportion of adult and juvenile fish (Mattlin & Colman 1988; Hatanaka *et al.* 1989; Vinogradov & Noskov, 1979; Gibson 1995; Dunn et al. 2010). We assume no net migration of squid into or out of the study area per year. The interannual accumulation rate is assumed to be small.

9 PLANKTON

9.1 Time and Space Scales in the Plankton

Phytoplankton and zooplankton abundance in the ocean is characterised by a wide range of spatial scales (spanning $<10^{-3}$ and $>10^{7}$ m), and temporal scales (seconds to decades): Lovejoy *et al.* (2001); Abraham (1998); Yamazaki *et al.* (2002). Phytoplankton doubling times are typically of the order of 1 d, whereas larger zooplankton may have characteristic timescales closer to 7–10 d. This study uses a characteristic plankton timescale of 8 d, i.e. we assume that plankton abundances in a given parcel of water are independent of plankton abundances in the same parcel of water more than 8 d previously. The corresponding characteristic spatial length is obtained from this timescale by considering the upper ocean dynamics in the study area. Note that while very large zooplankton (e.g. krill) may modify their distributions by swimming (Trathan *et al.* 1993) it is assumed here that all zooplankton (like phytoplankton) are truly planktonic, and drift with their respective water masses. The STF over the Chatham Rise is an area of vigorous mixing and eddy activity (e.g. Heath 1976; Belkin 1988; Uddstrom & Oien 1999; Stanton 1997; Chiswell 1994; Sutton 2001).

9.2 Phytoplankton

The Chatham Rise ecosystem is profoundly influenced by the primary production of phytoplankton in the upper ocean overlying the rise. This productivity is, in turn, related to the concentrations of macro-nutrients (nitrate, phosphate, silicate), micro-nutrients (iron), light availability, and water column stability (Boyd *et al.* 1999). Phytoplankton abundance and primary production vary spatially, seasonally and inter-annually, and cannot be adequately characterised from shipboard sampling. Ocean colour satellite measurements of phytoplankton abundance is available for the study region at moderate resolution (4 km) for >10 y (Murphy *et al.* 2000). Validation studies indicate that the ocean colour measurements of chlorophyll-a concentration are accurate within approximately 30% of the true value in this region (Richardson *et al.* 2002). Data were composited into four seasonal periods each of three months lengths, starting with austral spring (September–November), that we assume to represent long-term average seasonal conditions.

To convert surface values of chlorophyll concentration to water column averages, we assumed that phytoplankton were well mixed between the surface and the seasonal thermocline. This depth was identified for each of ~4000 pixels through the study region using a threshold density difference of 0.15 kg m^{-3} based on climatological data from the CSIRO Atlas of Regional Seas (CARS2000: Dunn &

Ridgway 2002), and varied between an average of 37 (summer) and 119 m (winter). Carbon-chlorophyll ratios for marine phytoplankton have been found to vary considerably between 20 to >200 $gCg^{-1}Chl$-*a* (Taylor et *al.* 1997; Lefevre *et al.* 2003). Data from SOIREE (Boyd 2002) and other experiments in iron-limited waters suggest a seasonally-invariate value of 80-100 $gCg^{-1}Chl$-*a* for subAntarctic waters are reasonable. In Subtropical waters, work suggests a seasonal variation in C:Chl values of approximately 50 before the spring bloom, 40 during the spring bloom, and 60 after the bloom (Boyd 2002; Boyd unpublished data). Phytoplankton biomass in the study region for the four seasons (spring, summer, autumn, winter) is calculated to be 2.9, 1.0, 1.7, 1.9 gCm^{-2} respectively.

Carbon fixation by phytoplankton (net of respiration) was calculated using the model of Behrenfeld *et al.* (2002), for the 12-month period May 2000–April 2001. Chlorophyll-a concentration in the surface waters was obtained from ocean colour measurements from SeaWiFS as Murphy *et al.* (2001), and the climatological mixed-layer depth from CARS2000 was used as above (Dunn & Ridgway 2002). The model required *a priori* knowledge of the state of nutrient limitation. For Subtropical waters of the study area (nominally north of 44°S), we assumed nutrient-limited conditions in spring and summer, and nutrient-sufficient conditions at other times. For the purposes of the Behrenfeld *et al.* (2002) model, (macro-) nutrients were never assumed to be limiting in subAntarctic waters. The model as implemented may not accurately reflect production in Subtropical waters as production in these waters tends to be limited by the availability of iron, which may cause unique stoichiometric changes in the composition and productivity of photosystems that are represented in the model (Behrenfeld *et al.* 2002). Consequently, it likely that modelled values of production are towards the upper limit of possible values in subAntarctic waters.

The 10-90% range of modelled values within the study region over the year was 43–381 $gCm^{-2}y^{-1}$. This range agrees well with in situ measurements of phytoplankton production in the study region by Bradford-Grieve *et al.* (1997) who report values of between 23 $gCm^{-2}y^{-1}$ (winter, subAntarctic waters) and 360 $gCm^{-2}y^{-1}$ (spring, STF). The average value for subAntarctic waters in the study region of 102 $gCm^{-2}y^{-1}$ is higher than the 80 $gCm^{-2}y^{-1}$ figure estimated by Moore & Abbott (2000) for the subAntarctic water ring as a whole, as the study area is taken to be more productive than average subAntarctic waters.

Ocean colour measurements of phytoplankton abundance during the annual modelled period suggested that the summer was more productive than normal (by 18%), whereas the other seasons were close the average for the 1997-2003 period (within 4%). Modelled production values were adjusted to reflect the longer-term average conditions. For spring–winter seasons, average productivities for the whole study area estimated by the model are 162, 110, 67 and 79 $gCm^{-2}y^{-1}$ (respectively). This corresponds to 50 m tC fixed by phytoplankton in the study area per year, net of phytoplankton respiration, which represents the average annual upper limit of ecosystem carrying capacity.

Average P/B values for the study region as a whole ranged from 38 y^{-1} (autumn) to 106 y^{-1} (summer). These are low compared to values of 152–256 y^{-1} given by Shushkina *et al.* (1998) based on 20 ecosystem cruises around the world. We extracted a large number (>19,000) of points from the modelled biomass and production data for the larger region around New Zealand (30°-50°S, 160°W-175°E). For this region, P/B values were between 32–330 y^{-1}, and P/B and B were negatively correlated, with a correlation coefficient of -0.52. Hence, calculating an annual average P as the product of an annual average P/B and B, will overestimate the true average value of P by c. 70%. For this reason, we calculated an appropriate phytoplankton P/B value from the annual P estimate and annual average B value.

9.3 Heterotrophic microplankton

The average annual biomass of heterotrophic microzooplankton (ciliates) is calculated using data collected in a number of months (Bradford-Grieve *et al.*, 1998; Hall *et al.* 1999; Julie Hall, NIWA, unpubl. data).

Integrations are made to 100 m and the assumption is made that there are no ciliates below 100 m if there are no measurements below this depth. Ciliate carbon biomass was calculated using a factor 0.19 pg C μm^{-3} (Putt & Stoecker, 1989). The average annual ciliate biomass is 0.167 g C m^{-2}.

Mean daily P/B of ciliates is 0.24 (n=5) calculated from dilution grazing experiments (J. H., unpubl. data). These data are from subAntarctic waters in August and January-February; there was little difference in P/B between the two periods. A ciliate production rate of 0.3 d^{-1} (110 y^{-1}) is near the mean of estimates from a number of studies tabulated by Kiørboe (1998) although growth rates of up to 0.9 d^{-1} have been measured (Verity et al., 1993). Also in the subarctic Pacific ciliate production of 0.10 d^{-1} is given by Landry et al. (1993) although this may be too low if predators were not fully excluded from incubations. We therefore use an annual P/B=88 y^{-1}. We assume that production/consumption is 0.36. The proportions in which ciliates consume their food (phytoplankton and heterotrophic flagellates) can only be estimated although we know that ciliates consume 70% of the biomass of heterotrophic flagellates and autotrophic biomass per day (J.H., unpubl. data).

9.4 Heterotrophic flagellates

The average annual biomass of heterotrophic flagellates (as carbon) is calculated using data collected in a number of months (Bradford-Grieve et al., 1998; Hall et al. 1999; J.H., unpubl. data). Integrations are made to 100 m and the assumption is made that there are no heterotrophic flagellates below 100 m if there are no measurements below this depth. Heterotrophic flagellate carbon biomass was calculated using calculated cell volumes (Chang & Gall, 1998). The average annual heterotrophic flagellate biomass is 0.307 g C m^{-2}.

Mean daily P/B of heterotrophic flagellates is 0.80 (n=10) (292 y^{-1}) calculated from dilution grazing experiments (J.H., pers. comm.). These data are from subAntarctic waters in August and January-February; there was little difference in P/B between the two periods. Growth rates of heterotrophic microflagellates of > 2 d^{-1} have been measured when conditions are not limited by iron (Chase & Price, 1997) but are <1 d^{-1} at the low prey Fe:C of 9 μmol mol^{-1} observed in the open subarctic Pacific (see Tortell et al., 1996). In low iron growth conditions, carbon specific growth of microflagellates was 0.7-1.6 d^{-1}. The lower end of these growth rates is similar to the growth rates calculated for subAntarctic waters from dilution grazing experiments. We assume that P/Q=0.35.

The proportions in which heterotrophic flagellates consume their food (bacteria and phytoplankton) can only be estimated. We know that heterotrophic flagellates consume 4.4% of picophytoplankton biomass and 2.4% of bacterial biomass per day (Safi & Hall, 1999; J.H. unpubl. data). Assimilation efficiency, (ingestion – excretion)/ingestion, of heterotrophic flagellates in low iron conditions is 0.84 (Chase & Price, 1997) although we initially use 0.70.

9.5 Mesozooplankton

The average annual biomass (wet weight and as carbon) of mesozooplankton is calculated using data collected in 1993 (Bradford-Grieve et al., 1998), and historical data collated by Bradford (1980). These data have been adjusted for the average depth of the water column over the region. Mean annual carbon biomass 0-615 m from these data is 1.1 g C m^{-2}. The production/biomass ratio for mesozooplankton for low productivity water is about 12 (Shushkina et al., 1998). This may be compared with P/B of a subtropical copepod *Acrocalanus inermis* which was measured by Kimmerer (1983) and varied from 0.07-0.36 d^{-1} and 0.2 d^{-1} (Vidal, 1980). Baird & Ulanowicz (1989) estimated an average P/B ratio of 0.37 d^{-1} over an entire year in Chesapeake Bay, an enclosed coastal system. Secondary production is not continuous in subtropical/subAntarctic water because primary production is very low in winter (Bradford-

Grieve et al., 1997). Therefore P/B is estimated by assuming that secondary production occurs over only 6 months of the year and P/B=0.11 d^{-1} for 182 d/y giving P/B for mesozooplankton of 20 y^{-1}.

Food intake has been determined experimentally (see Parsons et al., 1984) and ranges from 10-20% of body weight per day for large crustaceans to 40-60% per day for small crustaceans. *Paracalanus* sp. may eat 1.5 μg N μg body N^{-1} d^{-1} (Checkley, 1980) although their specific ingestion of C was 3.6 d^{-1} when feeding on N-deficient *Thalassiosira.* For large copepods such as *Calanus finmarchicus,* Ohman & Runge (1994) showed that, in the lower estuary region of the Gulf of St Lawrence, total food was ingested (diatoms dominant) at the rate of 42–48% of body C d^{-1} and in the open gulf total food was ingested (dominated by aloricate ciliates) at a rate of up to 4% of body C d^{-1}. At all these stations the copepods were laying eggs although the authors consider the possibility that these copepods might not have been in equilibrium with the food supply. The implication appears to be that protozoa may be a much better food source that autotrophic food particles. It was assumes that P/Q is 0.35. We assume that the mesozooplankton feed on phytoplankton, microzooplankton, and mesozooplankton (Bradford-Grieve et al., 1998, Zeldis et al., 2002). Assimilation of copepods is assumed to be 0.7 for animals that are feeding on microzooplankton (Pavlovskaya & Zesenko, 1985).

9.6 Macrozooplankton

The mesopelagic fauna in the vicinity of the Subtropical Front is determined from the work of Robertson et al. (1978). Macrozooplankton are assumed to be mainly euphausiacea, although decapoda and amphipoda, are also included. The biomass of macrozooplankton is unknown over the Chatham Rise at present. SubAntarctic open water macrozooplankton biomass ranges from 0.012–4.4 g DW m^{-2} and subAntarctic around islands ranges from 0.007–2.86 g DW m^{-2} (Pakhomov et al., 1994). To calculate macroplankton biomass we assume that their ecotrophic efficiency is 0.95. Production / biomass ratios are taken from the literature. *Euphausia lucens* has P/B = 10.14-16.01 y^{-1} (Stuart & Pillar, 1988) which is high relative to that of *Nematoscelis megalops* (5–6 y^{-1}) (Lindley, 1982). Cartes & Maynou (1998) use P/B ranging from 1.24–4.75 for euphausiids and 8.05 for peracarids. Here we use P/B=10 y^{-1} because of lower food availability and colder temperatures as Bradford-Grieve et al. (2003).

Consumption to biomass ratios have been estimated to be 1.205% DW/WW (or about 9% WW/WW) for the mesopelagic shrimp *Pasiphaea multidentata* (Q/B is therefore about 33 y^{-1}) to 0.061% DW/WW for the crab *Geryon longipes*, with mean values of 0.364% DW/WW (Q/B 10.7 y^{-1}) on the middle slope and 0.524% DW/WW (Q/B 15 y^{-1}) on the lower slope (Cartes & Maynou, 1998). Stuart & Pillar (1990) show that *E. lucens* is an omnivore that ingests on a carbon specific basis 15-60% phytoplankton, the remainder being mainly small copepods. 5-14% of body C d^{-1} was ingested by adults and Q/B ranged from 17–51 y^{-1}. Q/B of 33 y^{-1} was used. The diet of macrozooplankton (euphausiids) may include phytoplankton, microzooplankton, and mesozooplankton with copepods dominating the diet (Barange et al., 1991). Therefore we assume that macrozooplankton eat, phytoplankton, microzooplankton, and mesozooplankton.

9.7 Salps and gelatinous plankton

Salps (*Thaliacea*), and other gelatinous plankton occur throughout the Chatham Rise but their abundances, life-histories, trophic role, and energetics of *Thaliacea* here are poorly known. These groups of macrozooplankton can impact planktonic communities through intense grazing, and by affecting export of material from the upper ocean (Alldredge & Madin l982; Zeldis et al. 1995). Gelatinous plankton are opportunistic colonizers, and their population sizes can rapidly increase when conditions are favourable (Zeldis et al. 1995; Paffenhofer & Lee 1988). Thaliacean blooms are common in continental slope, shelf and coastal seas (e.g. Paffenhofer & Lee 1988; Paffenhofer et al. 1995; Zeldis et al. 1995; Boysen-Ennen et al. 1991; Pakhomov et al. 2002). Salps and gelatinous zooplankton can also be important food items for seabirds and some species of fish (notably, oreos).

Salps typically have a carbon to dry weight ratio of 4%, much smaller than other zooplanktonic species (Pakhomov et al. 2002). Salp wet weight to carbon ratio has been measured at only 0.37% (Curl 1961). Atkinson et al. (2004) show salp densities in the Ross Sea (Antarctic) of 2–60 individuals m^2, equivalent to a carbon density of approximately 2–60 mgC m^{-2}. Pakhomov et al. (2002) suggests typical salp concentrations through the Southern Ocean of <0.1–30 mgC m^{-2}. Boysen-Ennen et al. (1991) measured zooplankton and macrozooplankton biomass through the Weddell Sea (Antarctica) in February–March. Salps made up 10–35% of the total macrozooplankton biomass, with individual lengths between 7.0 and 8.5 mm. Here, we propose to use a biomass of salps and gelatinous plankton of 0.05 gC m^{-2} for the Chatham Rise. This is equivalent to 16% of the biomass of other macrozooplankton. Zeldis et al. (1995) measured a median salp density of 0.21 gC m^{-2} in the Hauraki Gulf. Here, we assume a density of 0.05 gCm^{-2} for the Chatham Rise.

Thaliaceans are very efficient grazers, feeding by pumping water through a fine mucous net suspended in the pharyngeal cavity. They can retain and ingest virtually all cell sizes from nanoplankton to net-plankton (Alldredge & Madin l982), and so are assumed to feed on phytoplankton, organic detritus, micro-, meso- and macro-zooplankton in the model. Production rates of salps can be high (Zeldis et al. 1995), and are likely to be greater than other macrozooplankton, or P/B=3 y^{-1}. Gross growth efficiency, P/Q, is likely to be greater than that of other zooplankton and has been estimated to be 0.40 (Jonsson 1986; Caron & Goldman 1990). These allow us to estimate Q/B=7.5 y^{-1}. Unassimilated consumption of salps is estimated to be 0.5 (Anderson 1986)

10 BENTHIC INVERTEBRATES

10.1 Chatham Rise benthic ecosystem

Characteristics of the benthic ecosystem of the Chatham Rise region vary with depth and with location. In particular, many studies have shown differences in benthic community between the northern and southern flanks of the rise (Probert & McKnight 1993; Probert *et al.* 1996; McKnight & Probert 1997). East-west variation (along the length of the rise) seems less significant than north-south or depth variations. We define five regions for the Chatham Rise benthic model: deeper than 1500 m (north); 500 – 1500 m (north); shallower than 500 m; 500 – 1000 m (south); deeper than 1000 m (south).

The benthic ecosystem compartments and linkages used here are based widely-used energetic models of benthic communities (e.g. Smith 1987, 1989; Christiansen *et al.* 2001; Gage 2003; Piepenburg *et al.* 1995; Nodder *et al.* 2003; Bradford-Grieve *et al.* 2003). Various sources of food to the benthic ecosystem are distinguished: water-column detritus made up a complex mixture of faecal pellets, dead phytoplankton, zooplankton cells, and “marine snow” (aggregates of different types of detrital particles, bound together loosely by transparent exopolymers: Alldredge & Jackson, 1995; Turner 2002); phytoplankton and zooplankton extracted from the water column by epifaunal filter-feeders. Work reported by Gage (2003) shows that concentrated food sources, such as carcasses, quickly attract dense aggregations of a range of scavenging organisms, including fish (rattails, dogfish, and ling) and mobile scavenging megabenthos. For this reason, carcasses are not taken to be part of the water column or benthic detritus, but are assumed to be consumed by the macrobenthos and selected fish species.

10.2 Macrobenthos

This group is very diverse and includes all benthic epifauna >20 mm in size, and encompasses the megabenthos and hyperbenthic invertebrates like Decapoda and Peracarida. Decapoda on the Chatham

Rise include galatheids (squat lobsters) like *Munida gracilis*; scampi *Metanephrops challengeri*), Caridea (shrimps; Pasiphaediae shrimps like *Pasiphaea barnardi*; species including *Oplophorus novaezeelandiae, Notopandalus magnoculus*) and Dendrobranchiata (prawns, like *Sergestes arcticus*). Peracarida on the Chatham Rise include mysid shrimps, isopoda and bentho-pelagic amphipods.

Only sparse measurements of the macrobenthos and megabenthos of the Chatham Rise are currently available, but it is possible that better information will become available in due course through the Oceans 20-20 surveys. In future versions of this trophic model when improved data are available, the macrobenthos group will be subdivided. For now, point measurements made on the Chatham Rise have been extrapolated to the entire study region. Wherever possible this has been done by following the method for estimating the biomass of macrobenthos as explained below. Macrofaunal biomass (organisms 0.5–20 mm) as measured on a number of N-S transects close to longitude 180° was found to be dominated by polychaetes (50–70%), with significant contributions of amphipods, isopods and ophiuroids (Nodder *et al.* 2003; Probert *et al.*, 1996). Macrofaunal biomass tends to decrease with increasing depth (by a factor of ~6 between 500 m and 2000 m depth), and be higher on the southern side of the Chatham Rise than the northern flank by a factor of ~1.2 for the same depth (Probert & McKnight, 1993; Probert *et al.* 1996; Nodder *et al.* 2003). We estimated total macrofaunal biomass for the Chatham Rise based on data in Nodder *et al.* (2003) as follows. The study region was divided into 18,525 bathymetric pixels, each with an area of ~27 km^2 and the mean macrofaunal density of each pixel was calculated using two separate regressions of macrofaunal biomass on depth, one for each side of the Chatham Rise: R^2=0.75 (north) and 0.92 (south), *n*=32 (each side). These regressions were then modified to account for changes in macrobenthic density along the length of the rise assuming these longitudinal variations very generally follow variations in surface phytoplankton productivity (via detrital material supply from the upper-ocean to the benthos). The change is estimated to be ~1.8 between the latitudinal extremes of the study region, and this latitudinal gradient was consistent with Probert *et al.* (1996). The mean macrofaunal biomass integrated over the study area was 2.2 Mt wet weight. Carbon is assumed to comprise 4.3% wet weight of macrofauna (Rowe 1983), giving a macrofaunal density of 0.21 gC m^{-2}.

Note that this result is based on data measured only in autumn and predominantly based on non-mobile epifauna. Biomass of mobile hyperbenthic or bentho-pelagic invertberates is poorly known and is likely to have been underestimated by the present method. Values of macrofaunal biomass measured in early spring by Probert & McKnight (1993) were higher by a factor of ~7 than those of Nodder *et al.* (2003). This is attributed to a combination of methodological sampling differences between the studies, and a lack of replicate samples from a given location in the earlier study. Other indicators of benthic biomass and activity reported by Nodder *et al.* (2003) were found to vary seasonally by factors of less than ~4, with no consistent seasonal pattern. We assume that autumn macrofaunal biomass is indicative of the annual average macrofaunal biomass, with an uncertainty factor of 2, i.e. the range of possible annual average macrofaunal biomass is taken to be 0.10–0.41 gC m^{-2}.

A P/B ratio for macrofauna can be estimated from the relationship given by Brey & Gerdes (1998) showing an increase of annual community P/B with water temperature. Annual average bottom water temperature over the Chatham Rise was estimated from depth (e.g. Nodder *et al.* 2003), and the regression equation of Brey & Gerdes applied for each bathymetric pixel (as above) to give a mean P/B of 0.82 y^{-1}. A P/B ratio of 1.83 y^{-1} is used by Cartes & Maynou (1998) for polychaetes, whereas Feller & Warwick (1988) suggest that a range of 0.7–4 y^{-1} is possible. Probert (1986) suggests a P/B ratio of 0.4–1 y^{-1} is reasonable, with values towards the higher end of this range being more likely.

In order to estimate food consumption by the macrobenthos, we assume that P/Q is 0.35 (0.25–0.45) following Bradford-Grieve *et al.* (2003). The macrobenthos is taken as being comprised of (in decreasing order of importance): deposit feeders, infaunal predators, and filter feeders, dominated by polychaetes. We have assumed that the macrobenthos is fuelled largely by consumption of sediment bacteria, meiobenthos, with some macrofanual cannibalism. Although some benthic Crustacea have been shown to also eat euphausiids (Cartes and Maynou, 1998), this is not considered to be significant in view of the very small proportion of phytoplanktonic pigment reaching the benthos (<22 μg Chl m^{-2} d^{-1}: Nodder and Gall, 1998).

10.3 Meiobenthos

Meiofaunal biomass (infauna 63 μm–0.5 mm) on the Chatham Rise was dominated by nematodes (>80% of individuals) and was measured in three seasons, at depths between 350 and 2600 m by Nodder *et al.* (2003). The values were within the envelope reported for a variety of temperate and tropical continental margins around the world (Soltwedel 2000, figure 2; Feller and Warwick, 1988). Annual average meiofaunal biomass on the Chatham Rise integrated to 5 cm depth of sediments decreased systematically with water depth as in these previous studies. A depth-biomass regression was determined by least-squares in log biomass space (R^2=0.67, *n*=10). This result was modified for likely longitudinal variations as described for macrofaunal biomass above. Using the modified regression we estimate total meiofaunal biomass on the Chatham Rise was 0.24×10^6 t wet-weight, equivalent to a mean meiofaunal density of 0.050 gCm^{-2} (assuming carbon makes up ~10% wet-weight of meiobenthos: Feller and Warwick 1988; Soltwedel 2000). The range of meiofaunal biomass is taken as 0.03–0.10 gC m^{-2} (nominal uncertainty of a factor of 2).

Annual P/B ratios of meiofauna vary considerably, between about 2.5 and 15, but 10 y^{-1} is often taken as an average value (Feller & Warwick, 1988; Probert 1986). Annual P/Q was assumed to be 0.31 (Pomeroy 1979; Bradford-Grieve *et al.* 2003), though a P/Q of between 0.1 and 0.3 y^{-1} was suggested by Probert (1986). The prime source of food for the meiobenthos is assumed to be bacteria with some cannibalistic contribution from other meiobenthos.

10.4 Detrital particulate flux to the benthos

Nodder & Northcote (2001) measured vertical downward particulate carbon flux on the northern and southern flanks of the Chatham Rise in three seasons at two depths (300 and 1000 m) in water depths of c.1500 m. The flux at 1000 m depth was always greater than the flux at 300 m, by a factor of between 1.1 and 4. The elevation of particulate carbon flux with depth is well-reported phenomenon and has been attributed to a number of factors, including local resuspension of detritus from the flanks of the Chatham Rise as documented previously (Nodder 1997; Nodder & Alexander 1998). We take the flux at 300 m to be a reasonable estimator of the net input of organic detrital carbon to the benthos from the upper water column, since pulses of flux at 300 m seem to be correlated with blooms in the upper ocean observed by ocean colour satellite data (Nodder, unpublished data). We assume that there is zero net lateral (i.e. “horizontal”) advection of resuspended material into the study region, i.e. that resuspended benthic detrital material entering the study region is close to that leaving the region. There are currently no measurements to test this hypothesis, but the currents are generally low over the study region (<10 cm s^{-1}), suggesting that <6% of water in the study region crosses the boundaries of the region each day, and that local vertical effects will predominate over lateral advective processes.

The average particulate carbon flux at 300 m averaged by season is positively correlated with mean seasonal surface phytoplankton concentration derived from 6 years of remotely-sensed ocean colour measurements (R^2=0.52, *n*=7). A least-squares regression of detrital flux at 300 m against surface chlorophyll-a concentration was used to estimate of the mean annual particulate carbon flux to the benthos for the whole study region, giving a value of 3.1 gC m^{-2} y^{-1}. Mesoscale variability (scales of ~100 km) in detrital supply has been shown to be significant (Newton *et al.* 1994), and is probably related to the eddy field affecting the distribution of algal blooms in the surface waters. Interannual variations are also likely to be significant, and we assumes a nominal uncertainty in the detrital flux supply of a factor of 2, i.e. 1.5 – 6.2 $gCm^{-2}y^{-1}$.

10.5 Benthic Community Carbon Budget

Sediment Community Oxygen Consumption (SCOC) across the centre of the Chatham Rise was measured by Nodder *et al.* (2003). Carbon remineralization by the benthic community was calculated by assuming a respiration quotient of 0.85 for mixed carbohydrate and lipid components (Hargrave 1973; Smith 1987, 1989). The autumn, spring and summer seasonal measurements were used to estimate an annual average value of benthic infaunal community carbon remineralization rate, and this was observed to follow approximately a power-law decrease with depth, from >12 $gCm^{-2}y^{-1}$ at 450 m to 4 $gCm^{-2}y^{-1}$ at 2500 m (R^2=0.39, *n*=9). Values were progressively reduced by 10% per 500 m to account for the likely elevation of remineralisation rates measured by the shipboard incubations relative to in situ measurements due to pressure and temperature related effects on the translocated organisms (Jahnke *et al.* 1989; Glud *et al.* 1994; Witbaard *et al.* 2000). This relationship was used to estimate the annual mean carbon remineralization rate for the study region as a whole, giving 6.8 $gCm^{-2}y^{-1}$ as the total infaunal community respiration. The uncertainty is estimated to be a factor of 2. Studies suggest that the megabenthos may contribute 10–30% to total benthic community respiration (Smith *et al.* 1987; Piepenburg *et al.* 1995). We assume that the respiration of epifaunal macrobenthos is 0–20% of the total infaunal respiration. These considerations give an annual average, total benthic community respiration in the range 3.8–27.1 $gCm^{-2}y^{-1}$.

Assuming zero net interannual change of benthic biomass, these estimates give a required organic carbon flux to the benthos in the range 3.8–27.6 $gCm^{-2}y^{-1}$. Of this required, 97% of the carbon is remineralized, and 3% is buried. This result is consistent with Gage (2003: fig 11.17) who summarises data from the German BIOTRANS site in spring and summer, and showed that remineralization accounts for up to 94% of the required daily sedimentation to the benthos, and burial <2%. Our estimate of particulate detrital flux to the benthos of 1.5–6.2 $gCm^{-2}y^{-1}$ is towards the lower end of that required to supply the needs of the benthic community and the long term burial of carbon. Such a shortfall has been observed in other studies (e.g. Smith 1987; Christiansen *et al.* 2001; Nodder *et al.* 2003), one potential explanation being that benthic organisms (primarily the benthic bacteria) are able to use dissolved organic carbon from water permeating the sediments. Testing this hypothesis requires further fieldwork. Notwithstanding this observation, our estimates of C required and that supplied to the benthos do overlap, which lends support to our figures.

11 DETRITUS AND BACTERIA

11.1 Benthic bacteria

Measurements of benthic bacterial biomass and production are available at 10 stations across the Chatham Rise (Nodder *et al.* 2003) close to 180°E. Most measurements were made of the top 3 cm of sediment only. Data from 8 summer stations showed that bacterial production in each 1 cm layer of sediment decreased with sediment depth, so that bacterial production integrated to 9 cm depth was 1.6 times the production integrated between 0–3 cm. We assume that production below 9 cm depth is negligible, and use this factor to estimate bacteria production and viable bacterial biomass for the whole depth of sediment, from measurements between 0–3 cm. Bacterial biomass and productivity data measured by Nodder *et al.* (2003) are very variable by season and depth, perhaps because of variability in detrital supply to the benthos from the water column affected by the production in the surface waters of the STF. Bacteria production in winter was not measured and was assumed to be 60% of the average for the other seasons, following average surface chlorophyll concentrations. Seasonal variation in total bacterial biomass was taken to follow bacterial production.

Bacterial biomass showed no systematic variation with depth (R^2<0.02, *n*=10). The annual mean benthic bacterial biomass was 1.3 gC m^{-2}, with a standard deviation of 1.0 gC m^{-2}. The biomass is comparable with that estimated using the regression of Deming & Yager (1992) of about 1.5 g C m^{-2} to a sediment depth of 15 cm. Probert (1986) found bacterial biomass of 1.0 gCm^{-2} for Shelf waters (<200 m deep) off west coast New Zealand. Note that we have no measurements of the proportion of the total bacterial biomass measured by Nodder *et al.* (2003) that is viable.

Annually averaged bacteria production decreased systematically with depth (R^2=0.55, *n*=10), consistent with previous work (e.g. Alongi 1990). Bacterial production integrated over the study region based on this regression result (as described earlier) was 0.64 gC m^{-2} y^{-1}. We assume a nominal uncertainty in this estimate of production of a factor of 2 i.e. we take productivity to lie in the range 0.32–1.3 gC m^{-2} y^{-1}. These values are considerably lower than the average bacterial production of 16.9 gC m^{-2} y^{-1} reported by Kemp (1994) for slope sediments (<2000 m), and by Alongi (1990) for 600 m depth of 34.7 gC m^{-2} y^{-1}. The bacterial biomass and production values measured by Nodder *et al.* (2003) suggest mean P/B of 0.5 y^{-1} which we use here There are considerable variations in measurements of annual P/B ratios of benthic bacteria in the literature, but this value is lower than most. Poremba and Hoppe (1995) found values of 10.9 y^{-1} in the Celtic Sea (135–1680 m). Alongi (1990) measured specific growth rates for benthic bacteria at bathyal and abyssal stations which vary widely from 0.37 – 43.8 y^{-1}. Sorokin (1999) gives values of P/B between 7.3–14.6 y^{-1} off Japan. Earlier work (Ankar 1977; Gerlach 1978; Sorokin 1981; Feller & Warwick 1988) suggest that annual P/B ratios of benthic bacteria are likely to lie between about 20 and 150 y^{-1}, with 55 y^{-1} as an average value. These may be higher than estimated based on Chatham Rise data perhaps because a proportion of the benthic bacteria on the Chatham Rise are not viable, so that P/B values for the viable bacteria are higher. Testing of this awaits further data. A benthic bacterial growth efficiency (P/Q) of 0.3, with a possible range of 0.2–0.5, is assumed here (Kirchman, 2000; Pomeroy 1979). A P/Q value of 0.3 with P/B=0.5 y^{-1} implies Q/B of 1.64 y^{-1}.

11.2 Water column bacteria

We base our estimates of water column bacteria biomass and energetics on Bradford-Grieve et al. (2003). The average annual biomass of bacteria was based on data collected in the study region (Bradford-Grieve et al., 1998; Smith and Hall, 1997; J.H., unpublished data) and is estimated to be 0.94 gC m^{-2} using the carbon conversion factor of Fukuda et al. (1998). The annual P/B value for water column bacteria is estimated to be 87.4 y^{-1}. Shushkina et al.(1998) estimate bacterial P/B to be 92 y^{-1} based on the analysis of for low productivity waters whereas Sorokin (1999, Table 2.2) gives P/B of 0.5 d^{-1} for eutrophic coastal habitats, 0.6 d^{-1} in mesotrophic temperate seas; and 1.2 d^{-1} in oligotrophic tropical seas which seem too high (leading to P/B of 182–438 y^{-1}).

Bacteria in the water column consume detrital and dissolved organic material in the water column. Consumption rates by bacteria are typically quantified via growth efficiency (P/Q) values. Bradford-Grieve et al. (2003) used P/Q=0.23 for bacteria in subantarctic waters off New Zealand. Lochte et al. (1997) measured values in the Southern Ocean of P/Q=0.30 (0.28–0.31), and P/R=0.43 (0.38–0.44). Growth efficiencies (P/Q) for open ocean bacteria feeding on dissolved organic matter in the Southern Ocean was reported as 0.26–0.30 (Kaehler et al. 1997), which was reported as being consistent with work of Lignell (1990). Here, we propose using a P/Q for bacteria in the water column of 0.23 which gives an estimate of Q/B=383 y^{-1}.

Based on the values given above and in Section 11.1, even though water column bacterial biomass is only 42% of total bacterial biomass, we estimate that water column bacteria contributes 99.2% of total bacterial production and 99.4% of total bacterial consumption.

11.3 Detrital Accumulation

Long-term (i.e. >decadal) benthic biomass accumulation on the Chatham Rise at depths shallower than 1500 m was estimated as Nodder *et al.* (2003) based on data from E. Sikes (Rutgers University, USA). The measurements indicate that, at some times of the year, carbon accumulated at the rate of 2.7–12 gC m^{-2} y^{-1}, increasing with depth. However, geological measurements in the area suggest that net accumulation over long time periods (1000 years) at depths greater than about 1500 m is negligible (H. Neil and L. Carter, NIWA). In this study we assume that accumulation that occurs in some seasons is balanced by a net consumption of benthic carbon at other times of the year, so that long-term average annual benthic carbon accumulation rates are low, between 0–0.5 gC m^{-2} y^{-1} over the study area. Total detrital flows (water column and benthic) amount to approximately 75 gC m^{-2} y^{-1} so we estimate a detrital accumulation fraction of less than 0.67%, initially set to 0.5%. It has been shown that carbon accumulates in the seabed deposits in some years and is consumed in others so that although net decadal accumulation rates are low, annual accumulations may be significant (Gage 2003). We have no data to test such interannual variability and assume that measurements used here are representative of "typical" conditions. More field data is required to test this assumption.

12 RESULTS

12.1 Model balancing

The model had 289 unknown variables and 53 constraints, implying a highly under-constrained system as expected. The balancing procedure applied Singular Value Decomposition to the linearised system over 8 iterations to give a steady solution within 0.0001% of true balance for all groups. The main changes to biomass, P/B, and diets are summarized below in Table 4. The balanced model values are given in Table 5 and Table 6. Plot of the ecological importances of groups in the model is shown in Figure 2.

13 DISCUSSION & CONCLUSIONS

13.1 Flow characteristics

The transfer of organic matter from across groups of trophic levels can be useful in identifying characteristics of the system. In the pilot trophic model presented here, 91% of the net primary production is transferred to microzooplankton (heterotrophic flagellates and ciliates), with 3.8% being transferred direct to higher pelagic consumers (meso and macrozooplankton, macrobenthos), 4.8% to detritus, and 0.2% to benthic invertebrates. In the model, the ultimate fate of 46% of primary production is respiration by pelagic microzooplankton and bacteria in the water column. This compares to a value of about 72% for respiration by microzooplankton ("zoo1") in the study of the Chilean upwelling system by Neira & Arancibia (2004), and 64% for the Benguela upwelling system (Shannon & Jarre-Teichmann 1999).

13.2 Comparison with international ecosystems

Particular organisms may be expected to have broadly similar trophic levels (TL) in similar types of ecosystems where they are feeding on similar prey. Trophic levels were calculated for the final model (Table 5) and compared with other trophic models that used compatible methodologies for estimating trophic level. Comparing trophic levels in this way is a fairly crude way of comparing models, but may highlight major inconsistencies in the parameters or diets used here. Some models did not model bacteria explicitly, and instead defined detritus as having TL=1 (e.g. Jarre-Teichman et al. 1998, Arreguin-Sanchez et al. 2002, Jiang and Gibbs 2005). This will not affect trophic levels provided that detrivores in these models are assumed to consume detritus directly, and this is defined as having a trophic level of 1. In the model here, we assume detrivores consume bacteria rather than detritus itself, but this poorly known.

Trophic levels for the groups in the Chatham Rise model agree well with those from trophic models elsewhere. For example, for birds TL=5.0 compares reasonably well with 3.8 (Arreguin-Sanchez et al. 2002) and 4.5 (Jarre-Teichman et al. 1998). Birds in the Chatham Rise are likely to more closely resemble the fish-eating birds of the open ocean Benguela system modelled by Jarre-Teichman et al. (1998) rather than the coastal invertebrate feeders as in the model by Arreguin-Sanchez et al. (2002). Macrobenthos at TL=2.9 compares with values for crabs and predatory invertebrates: 3.3–3.4 (Wolff 1994) and 2.4–2.8 (Arreguin-Sanchez et al. 2002), and 2.0–2.1 (Jiang & Gibbs 2005). Microzooplankton here have TL=2.6–3.6 compared to values for “zooplankton” of 2.2–2.4 (Jarre-Teichman et al. 1998), 2.0 (Mendoza 1993, Jiang & Gibbs 2005) and 2.2 (Arreguin-Sanchez et al. 2002). Trophic levels for most demersal fish in the Chatham Rise model at 4.2–5.0 (mean 4.7) are higher than coastal ecosystem studies, for example, 3.3 (Jarre-Teichman et al. 1998), 2.7–3.5 (Wolff 1994), 3.2–3.9 (Mendoza 1993) and 3.1–3.8 (Jiang & Gibbs 2005). Trophic level values for demersal fish in the Chatham Rise model presented here are more similar to the range of for the Chilean upwelling system model of 3.4–5.1 (Neira & Arancibia 2004), and for the Benguela system of 3.5–4.7 (Shannon et al. 2001).

Note that trophic levels for fish are very sensitive to the diets of demersal fish in the balanced model. For comparison, Fishbase (Froese & Pauly 2003) gives trophic level of 4.2–4.5 for hoki (*Macruronus novaezelandiae*) based on Bulman & Blaber (1986) compared to the model estimate of 5.0. Fishbase (Froese & Pauly 2003) gives trophic level of 4.1–4.3 for orange roughy (*Hoplostethus atlanticus*) based on Bulman & Koslow (1992) which is similar to, but again lower than, our estimate of 4.6. Better consideration of diet of orange roughy in the Chatham Rise model may help to reconcile these differences in the future, and a study of stomach contents of orange roughy from this region is underway.

13.3 Trophic resolution

As the model has a strong focus on demersal fish, it will be necessary to revisit which fish species should be included as separate compartments. The current model has the following 12 demersal fish groups: hoki, orange roughy, smooth oreo, black oreo, rattails, ling, silver warehou, hake, javelinfish, barracouta, dogfish, other demersal. Three of these are “composite groups”: rattails, dogfish, other demersal. A version of the model currently under development expands the number of fish groups to 26: hoki, orange roughy, smooth-oreo, black oreo, javelinfish, dark ghost shark, big-eye rattail, silver warehou, ling, sea perch, spiny dogfish, lookdown dory, pale ghost shark, shovelnose spiny dogfish, barracouta, white warehou, giant stargazer, Ray’s bream, Baxter’s lantern dogfish, smooth skate, orange perch, Oliver’s rattail, spiky oreo, alfonsino, hake, other demersal. It is also important to revise the estimates of fish biomass, catch, productivities, and consumption parameters. It is noted that stock sizes of fish in the Chatham Rise can change rapidly, and biomass and catch data used in the model presented here may need to be periodically updated.

13.4 Validation and further developments

The model presented has not been validated, and its results should be treated with caution at this stage as there remain considerable uncertainties with regard to many model parameters. We intend to validate this model using information on the stable isotopic composition of tissues of many organisms of the Chatham Rise. The interplay of physical, biological and chemical processes in the environment produces distinct isotopic signatures in the tissues of biota. These natural abundance signatures are increasingly used as tracers in environmental studies. Carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) can track trophic connections within ecosystems and provide information on the structure of foodwebs. Carbon isotopes are a powerful tool for identifying primary sources of organic material within ecosystems and showing benthic reworking (Fry & Sherr, 1984; Peterson & Fry, 1987). In a relatively small area like the Chatham Rise, variations in $\delta^{13}C$ tend to be low compared to $\delta^{15}N$ variations and may be of limited value except for highly mobile organisms, or those with a mixture of benthic and pelagic feeding. Nitrogen isotope ratios often show distinct enrichments per successive trophic level and have strong applications in food web and dietary studies (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; van der Zanden & Rasmussen, 2001). Together, analysis of carbon and nitrogen stable isotopes have the potential to quantitatively validate food-web models such as that presented here. The results to date, although preliminary, give interesting insights on the trophic relationships between species (Nodder unpublished data). Further stable isotope and biomarker data is under analysis and results will become available for use in model validation in due course.

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16 TABLES

Table 1. Trophic group parameters for the trophic model estimated from local data and literature as described in the text. *B*=Biomass, *P/B*=Production, *Q/B*=Consumption, *P/Q*=Growth efficiency, *E*=Ecotrophic efficiency, *A/P*=Accumulation as fraction of P, F=Fishery take, *U*=Unassimilated consumption. There are no explicit seasonal, growth, spawn or carcass transfers in the model. Export is also set to zero for all groups. N/A=Not applicable

	Group	***B*** (gC m^{-2})	***P/B*** (y^{-1})	***Q/B*** (y^{-1})	***E***	***P/Q***	***A/P***	***F*** (gC m^{-2} y^{-1})	***U***
1	Birds	5.0E-04	0.12	104	1	1.2E-03	0	0	0.3
2	Cetaceans	3.2E-04	0.16	28	1	5.6E-03	0	0	0.2
3	Pinnipeds	1.2E-05	0.18	27	1	6.7E-03	0	0	0.2
4	Hoki	7.0E-02	0.33	2.7	0.99	0.12	0	6.8E-03	0.2
5	O_roughy	2.1E-02	0.19	1.5	0.99	0.13	0	2.1E-03	0.2
6	Smooth_oreo	3.1E-02	0.24	1.3	0.99	0.18	0	1.6E-03	0.2
7	Black_oreo	2.0E-02	0.28	1.6	0.99	0.18	0	3.9E-04	0.2
8	Rattails	2.2E-02	0.30	2.5	0.99	0.12	0	0	0.2
9	Ling	1.5E-02	0.21	2.0	0.99	0.11	0	9.3E-04	0.2
10	S_warehou	5.4E-03	0.32	3.7	0.99	0.09	0	1.5E-03	0.2
11	Hake	4.7E-03	0.24	1.9	0.99	0.13	0	5.5E-04	0.2
12	Javelinfish	1.9E-02	0.31	2.5	0.99	0.12	0	0	0.2
13	Barracouta	3.9E-03	0.29	2.7	0.99	0.11	0	1.0E-03	0.2
14	Dogfish	2.2E-02	0.25	2.4	0.99	0.11	0	1.2E-03	0.2
15	Demersal	3.3E-02	0.30	2.5	0.99	0.12	0	1.8E-03	0.2
16	Mesopelagic	1.2E-01	1.15	16	0.99	0.072	0	0	0.2
17	Juv_fish	4.2E-02	0.43	5.2	0.99	0.083	0	0	0.2
18	Squid	3.3E-03	8.6	25	0.99	0.35	0	2.24E-03	0.2
19	Salps	5.0E-02	3.0	7.5	0.95	0.40	0	0	0.5
20	Macrozoo	3.1E-01	2.0	6.7	0.95	0.30	0	0	0.4
21	Mesozoo	1.7E+00	20	57	0.95	0.35	0	0	0.25
22	Het_micro	2.6E-01	88	248	0.95	0.35	0	0	0.16
23	Het_flag	4.8E-01	292	830	0.95	0.35	0	0	0.3
24	Phytoplankton	1.8E+00	62	0	0.95	NA	0	0	NA
25	Macrobenthos	2.0E-01	0.82	2.3	0.95	0.35	0	0	0.2
26	Meiobenthos	5.0E-02	9.7	31	0.95	0.31	0	0	0.2
27	Bacteria	2.2E+00	37	162	1	0.23	0	0	0
28	Detritus	NA	NA	NA	NA	NA	0.005	NA	NA

Table 2. Diet parameters for the trophic model estimated from local data and literature. Values given are the proportion (by organic carbon weight) of a given prey item in the diet of predator. Entries of “0.00” imply that the diet fraction is >0% and <0.5%.

	Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	25	26	27
1	Birds																								0.00		
2	Cetaceans																								0.00		
3	Pinnipeds			0.00																					0.00		
4	Hoki		0.07	0.06						0.05		0.13			0.05	0.05			0.01								
5	O_roughy									0.01		0.00			0.02	0.03											
6	Smooth_oreo		0.02	0.02						0.02		0.01			0.04	0.05											
7	Black_oreo		0.02	0.01						0.01		0.01			0.03	0.04											
8	Rattails		0.02	0.02	0.04					0.10		0.25			0.04	0.04											
9	Ling		0.01	0.01								0.00			0.02	0.02											
10	S_warehou		0.00	0.00						0.00		0.00			0.01	0.01											
11	Hake		0.00	0.00						0.00					0.01	0.01											
12	Javelinfish		0.02	0.01						0.01		0.01			0.03	0.04											
13	Barracouta			0.04						0.00		0.00			0.01	0.01											
14	Dogfish		0.02	0.01						0.01		0.01				0.04											
15	Demersal		0.03	0.03		0.05	0.00	0.02	0.05	0.02		0.01			0.05	0.06			0.01								
16	Mesopelagic	0.41	0.44	0.27	0.48	0.15	0.05	0.30	0.15	0.18				0.04	0.20	0.05			0.20								
17	Juv_fish	0.05	0.06	0.04	0.04	0.05	0.01	0.04	0.05	0.10				0.01	0.05	0.01		0.02	0.04								
18	Squid	0.10	0.20	0.47	0.01	0.05			0.15	0.07		0.03	0.03		0.05	0.10		0.11	0.06								
19	Salps	0.06	0.02				0.86	0.35	0.05		0.91				0.10	0.05	0.05	0.10									
20	Macrozoo	0.38	0.08		0.32	0.20	0.03	0.05	0.15	0.13	0.06	0.06	0.27	0.95	0.10	0.15	0.33	0.31	0.40						0.05		
21	Mesozoo					0.05			0.10			0.05	0.45		0.05	0.05	0.62	0.31	0.28	0.10	0.45	0.15					
22	Het_micro																			0.30	0.10	0.20					
23	Het_flag																			0.30	0.15	0.55	0.60	0.10			
24	Phytoplankton																			0.20	0.30	0.10	0.40	0.70	0.54		
25	Macrobenthos				0.12	0.45	0.05	0.25	0.30	0.27	0.03	0.43	0.25		0.15	0.20		0.15							0.10		
26	Meiobenthos																								0.31	0.20	
27	Bacteria																			0.10				0.20		0.80	
28	Detritus																										1.00

Table 3. Uncertainty (*K*) parameters for the Chatham Rise trophic model.

	Group	K^B	K^P	K^{1-E}	K^{QP}	K^A	K^U	K_0^D
1	Birds	0.4	0.3	0.3	0.02	0	0.1	0.3
2	Cetaceans	0.4	0.3	0.3	0.02	0	0.1	0.3
3	Pinnipeds	0.4	0.3	0.3	0.02	0	0.1	0.3
4	Hoki	0.05	0.3	0.3	0.02	0	0.1	0.02
5	O_roughy	0.05	0.3	0.3	0.02	0	0.1	0.1
6	Smooth_oreo	0.05	0.3	0.3	0.02	0	0.1	0.1
7	Black_oreo	0.05	0.3	0.3	0.02	0	0.1	0.1
8	Rattails	0.5	0.3	0.3	0.02	0	0.1	0.2
9	Ling	0.05	0.3	0.3	0.02	0	0.1	0.1
10	S_warehou	0.1	0.3	0.3	0.02	0	0.1	0.1
11	Hake	0.05	0.3	0.3	0.02	0	0.1	0.1
12	Javelinfish	0.5	0.3	0.3	0.02	0	0.1	0.1
13	Barracouta	0.1	0.3	0.3	0.02	0	0.1	0.1
14	Dogfish	0.5	0.3	0.3	0.02	0	0.1	0.2
15	Demersal	0.5	0.3	0.3	0.02	0	0.1	0.2
16	Mesopelagic	0.5	0.3	0.3	0.05	0	0.1	0.3
17	Juv_fish	0.5	0.3	0.3	0.1	0	0.1	0.3
18	Squid	1	0.5	0.3	0.2	0	0.1	0.3
19	Salps	1	0.5	0.3	0.1	0	0.1	0.5
20	Macrozoo	1	0.5	0.3	0.1	0	0.1	0.5
21	Mesozoo	1	0.5	0.3	0.1	0	0.1	0.5
22	Het_micro	1	0.5	0.3	0.2	0	0.1	1
23	Het_flag	1	0.5	0.3	0.2	0	0.1	1
24	Phytoplankton	1	0.3	0.3	0	0	0	0
25	Macrobenthos	2	0.5	0.3	0.2	0	0.1	1
26	Meiobenthos	2	0.5	0.3	0.2	0	0.1	1
27	Bacteria	2	1	0.3	0.2	0	0.1	0
28	Detritus	0	0	0	0	0.3	0	0

Table 4. Changes to Biomass (B), Production (P/B), growth efficiencies (P/B) and diet fractions (D) during the SVD balancing process. Each line shows the parameter, the trophic group in the model, the original value of the parameter, an arrow (**->**), the final value of the parameter (in the balanced model), and the % change in square brackets. For diet fractions, the actual change in diet fraction (not the proportion) is shown. Within each type of parameter, the changes are ranked in decending magnitude. Changes of more than 10% are shown for biomass and energetic parameters (B, P/B and P/Q) and all diet fraction changes of more than 3% are shown.

```
1 B Bacteria 2.2397826 -> 0.76188207 [ -0.65984106 ]
 2 B Het_flag 0.48253673 -> 0.24022068 [ -0.50217120 ]
 3 B Mesozoo 1.6629442 -> 1.2086643 [ -0.27317809 ]
 4 B Macrozoo 0.31099999 -> 0.39559447 [ 0.27200798 ]
 5 B Rattails 0.022202680 -> 0.027955882 [ 0.25912195 ]
 6 B Het_micro 0.26248741 -> 0.19811929 [ -0.24522366 ]
 7 B Phytoplankton 1.8423948 -> 2.1977521 [ 0.19287790 ]
 8 B Squid 0.0032962470 -> 0.0039312965 [ 0.19265836 ]
 9 B Dogfish 0.022062669 -> 0.018073872 [ -0.18079393 ]
 10 B Demersal 0.033041045 -> 0.028756316 [ -0.12967899 ]
 11 B Salps 0.050000001 -> 0.056176745 [ 0.12353487 ]
```

```
1 P/B Bacteria 36.963245 -> 24.712622 [ -0.33142715 ]
 2 P/B Het_flag 292.00000 -> 220.26240 [ -0.24567670 ]
 3 P/B Hoki 0.32992285 -> 0.27088072 [ -0.17895740 ]
 4 P/B Rattails 0.29617485 -> 0.34222210 [ 0.15547318 ]
 5 P/B Mesozoo 20.000000 -> 17.217152 [ -0.13914240 ]
 6 P/B Macrozoo 2.0000000 -> 2.2720080 [ 0.13600399 ]
 7 P/B Het_micro 88.000000 -> 76.968162 [ -0.12536180 ]
 8 P/B Dogfish 0.25457790 -> 0.22681292 [ -0.10906283 ]
```

```
1 P/Q Birds 0.0011883890 -> 0.0013784364 [ 0.15992013 ]
 2 P/Q Het_flag 0.35199806 -> 0.39997967 [ 0.13631215 ]
 3 P/Q Juv_fish 0.083246440 -> 0.091744191 [ 0.10207945 ]
```

```
1 D Het_flag<-Phytoplankton 0.69999999 -> 0.84721836 [ 0.14721838 ]
```

```
2 D Mesozoo<-Het_flag 0.55000001 -> 0.41124636 [ -0.13875365 ]
3 D Mesozoo<-Mesozoo 0.15000001 -> 0.27795162 [ 0.12795162 ]
4 D Juv_fish<-Squid 0.10893670 -> 0.00000000 [ -0.10893670 ]
5 D Het_flag<-Het_flag 0.10000000 -> 0.020517140 [ -0.079482861 ]
6 D Het_flag<-Bacteria 0.20000000 -> 0.13226449 [ -0.067735508 ]
7 D Mesopelagic<-Mesozoo 0.62000000 -> 0.68130396 [ 0.061303956 ]
8 D Macrobenthos<-Phytoplankton 0.53596842 -> 0.59316375 [ 0.057195330 ]
9 D Het_micro<-Het_flag 0.60000002 -> 0.54457582 [ -0.055424203 ]
10 D Het_micro<-Phytoplankton 0.40000001 -> 0.45542418 [ 0.055424174 ]
11 D Macrobenthos<-Macrobenthos 0.10307085 -> 0.049217592 [ -0.053853255 ]
12 D Juv_fish<-Mesozoo 0.30726320 -> 0.35866400 [ 0.051400803 ]
13 D Demersal<-Demersal 0.064185828 -> 0.014902175 [ -0.049283653 ]
14 D Demersal<-Rattails 0.042924020 -> 0.00000000 [ -0.042924020 ]
15 D Juv_fish<-Macrozoo 0.30726320 -> 0.34913218 [ 0.041868981 ]
16 D Mesopelagic<-Macrozoo 0.32736841 -> 0.28675706 [ -0.040611352 ]
17 D Squid<-Juv_fish 0.039999999 -> 0.0026843578 [ -0.037315641 ]
18 D Squid<-Macrozoo 0.40000001 -> 0.43583435 [ 0.035834347 ]
19 D Demersal<-Macrobenthos 0.20000000 -> 0.23546964 [ 0.035469639 ]
20 D Dogfish<-Rattails 0.035356011 -> 0.00000000 [ -0.035356011 ]
21 D Mesozoo<-Het_micro 0.20000000 -> 0.23503676 [ 0.035036759 ]
22 D Rattails<-Demersal 0.050000001 -> 0.015921400 [ -0.034078600 ]
23 D Macrobenthos<-Macrozoo 0.051535424 -> 0.017621939 [ -0.033913485 ]
24 D Birds<-Macrozoo 0.38047469 -> 0.41308262 [ 0.032607938 ]
25 D Squid<-Mesozoo 0.28000000 -> 0.31159753 [ 0.031597528 ]
26 D Macrobenthos<-Meiobenthos 0.30921254 -> 0.33979424 [ 0.030581704 ]
```

Table 5. Trophic group parameters for the balanced trophic model. B=Biomass, P/B=Production, Q/B=Consumption, E=Ecotrophic efficiency, A/P=Accumulation as a proportion of production, F= Fishery removals, U=Unassimilated consumption, N/A=Not applicable. Total flow of organic matter to detritus is gC m^{-2} y^{-1}.

	Group	***B*** (gC m^{-2})	***P/B*** (y^{-1})	***Q/B*** (y^{-1})	***E***	***P/Q***	***A/P***	***F*** (gC m^{-2} y^{-1})	***U***
1	Birds	4.7E-04	0.12	86	1.00	1.4E-03	0	0	0.30
2	Cetaceans	3.1E-04	0.15	27	1.00	5.7E-03	0	0	0.20
3	Pinnipeds	1.2E-05	0.18	27	1.00	6.7E-03	0	0	0.20
4	Hoki	6.7E-02	0.27	2.2	0.99	0.13	0	6.8E-03	0.20
5	O_roughy	2.1E-02	0.18	1.5	0.99	0.13	0	2.1E-03	0.20
6	Smooth_oreo	3.1E-02	0.24	1.3	0.99	0.18	0	1.6E-03	0.20
7	Black_oreo	2.0E-02	0.28	1.5	0.99	0.18	0	3.9E-04	0.20
8	Rattails	2.8E-02	0.34	2.9	1.00	0.12	0	0	0.20
9	Ling	1.5E-02	0.20	1.8	0.99	0.11	0	9.3E-04	0.20
10	S_warehou	5.4E-03	0.32	3.7	0.99	0.087	0	1.5E-03	0.20
11	Hake	4.7E-03	0.23	1.9	0.99	0.13	0	5.5E-04	0.20
12	Javelinfish	1.8E-02	0.30	2.5	0.99	0.12	0	0	0.20
13	Barracouta	3.9E-03	0.29	2.7	0.99	0.11	0	1.0E-03	0.20
14	Dogfish	1.8E-02	0.23	2.1	0.99	0.11	0	1.2E-03	0.20
15	Demersal	2.9E-02	0.27	2.3	1.00	0.12	0	1.8E-03	0.20
16	Mesopelagic	1.3E-01	1.2	17	1.00	0.073	0	0	0.20
17	Juv_fish	4.3E-02	0.43	4.7	1.00	0.092	0	0	0.20
18	Squid	3.9E-03	9.4	26	1.00	0.37	0	2.2E-03	0.20
19	Salps	5.6E-02	3.2	8.0	0.95	0.40	0	0	0.50
20	Macrozoo	4.0E-01	2.3	7.6	0.96	0.30	0	0	0.40
21	Mesozoo	1.2E+00	17	49	0.94	0.35	0	0	0.25
22	Het_micro	2.0E-01	77	211	0.95	0.36	0	0	0.16
23	Het_flag	2.4E-01	220	551	0.96	0.40	0	0	0.31
24	Phytoplankton	2.2E+00	65	0	0.95	NA	0	0	NA
25	Macrobenthos	2.2E-01	0.83	2.4	0.95	0.35	0	0	0.20
26	Meiobenthos	5.0E-02	9.7	31	0.95	0.31	0	0	0.20
27	Bacteria	7.6E-01	25	100	1.00	0.25	0	0	0.00
28	Detritus	NA	NA	NA	NA	NA	2.97E-03	NA	NA

Table 6. Diet matrix for balanced trophic model of Chatham Rise showing percentages of prey in diet of each predator. Predators are shown on the x-axis and prey on the y-axis. Entries of “0.00” imply that the diet fraction is >0% and <0.5%.

	Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	25	26	27
1	Birds																								0.00		
2	Cetaceans																								0.00		
3	Pinnipeds			0.00																					0.00		
4	Hoki		0.07	0.06						0.05		0.13			0.06	0.07			0.02								
5	O_roughy									0.01		0.00			0.01	0.01											
6	Smooth_oreo		0.02	0.02						0.02		0.01			0.04	0.05											
7	Black_oreo		0.02	0.01						0.01		0.01			0.04	0.05											
8	Rattails		0.00	0.02	0.04					0.08		0.24															
9	Ling		0.01	0.01								0.00			0.02	0.02											
10	S_warehou		0.00	0.00						0.00		0.00			0.00												
11	Hake		0.00	0.00						0.00					0.00	0.00											
12	Javelinfish		0.02	0.01						0.01		0.01			0.04	0.05											
13	Barracouta			0.04						0.00		0.00			0.00												
14	Dogfish		0.02	0.01						0.01		0.01				0.04											
15	Demersal		0.02	0.02		0.05	0.00	0.02	0.02	0.02		0.01			0.03	0.01											
16	Mesopelagic	0.41	0.45	0.27	0.48	0.15	0.05	0.30	0.16	0.19				0.04	0.22	0.06			0.20								
17	Juv_fish	0.03	0.06	0.04	0.04	0.05	0.01	0.04	0.04	0.10				0.01	0.04	0.01			0.00								
18	Squid	0.08	0.20	0.47	0.01	0.05			0.14	0.08		0.03	0.03		0.05	0.10			0.04								
19	Salps	0.07	0.02				0.87	0.35	0.05		0.91				0.11	0.06	0.03	0.11									
20	Macrozoo	0.41	0.08		0.32	0.20	0.03	0.05	0.16	0.14	0.06	0.06	0.27	0.95	0.11	0.18	0.29	0.35	0.44						0.02		
21	Mesozoo					0.05			0.11			0.05	0.45		0.06	0.06	0.68	0.36	0.31	0.10	0.46	0.28					
22	Het_micro																			0.30	0.10	0.24					
23	Het_flag																			0.30	0.15	0.41	0.54	0.02			
24	Phytoplankton																			0.20	0.30	0.08	0.46	0.85	0.59		
25	Macrobenthos				0.12	0.45	0.05	0.25	0.32	0.27	0.03	0.44	0.25		0.17	0.24		0.18							0.05		
26	Meiobenthos																								0.34	0.18	
27	Bacteria																			0.10				0.13		0.82	
28	Detritus																										1.00

Table 7. Output parameters for the Chatham Rise trophic model. The table shows: trophic levels, omniovory indices, ecological importances, rank of ecological importance, respiration/biomass (R/B) values, and flow of material to dteritus. [1] = Total flow of material to detritus (gC m^{-2} y^{-1}). NA=Npt applicable

	Group	Trophi Level	Omnivory Index	Ecological importance (EI)	Rank EI	R/B (gC m^{-2} y^{-1})	Flow to detritus (gC m^{-2} y^{-1})
1	Birds	5.0	0.32	0.49	22	60	1.20E-02
2	Cetaceans	5.5	0.17	0.24	25	21	1.66E-03
3	Pinnipeds	5.7	0.03	0.02	28	21	6.59E-05
4	Hoki	5.0	0.39	2.13	10	1.5	2.93E-02
5	O_roughy	4.6	0.54	0.79	18	0.99	6.18E-03
6	Smooth_oreo	4.3	0.10	0.50	21	0.82	8.23E-03
7	Black_oreo	4.6	0.50	0.44	24	0.95	6.30E-03
8	Rattails	4.7	0.56	1.40	14	1.9	1.60E-02
9	Ling	5.0	0.62	0.77	19	1.3	5.40E-03
10	S_warehou	4.2	0.01	0.22	26	2.6	4.01E-03
11	Hake	4.8	0.82	0.54	20	1.3	1.77E-03
12	Javelinfish	4.4	0.14	0.46	23	1.7	9.22E-03
13	Barracouta	4.6	0.05	0.08	27	1.8	2.12E-03
14	Dogfish	5.0	0.55	1.43	13	1.5	7.70E-03
15	Demersal	4.9	0.62	2.73	7	1.5	1.30E-02
16	Mesopelagic	4.5	0.00	3.09	4	12	4.24E-01
17	Juv_fish	4.4	0.06	1.31	15	3.4	4.03E-02
18	Squid	4.8	0.22	1.18	16	11	2.02E-02
19	Salps	3.2	0.54	2.20	9	0.80	2.32E-01
20	Macrozoo	3.5	1.21	3.33	3	2.3	1.24E+00
21	Mesozoo	3.6	0.54	2.76	6	20	1.62E+01
22	Het_micro	2.6	0.33	1.87	11	100	7.53E+00
23	Het_flag	2.2	0.14	2.82	5	162	4.27E+01
24	Phytoplankton	1	NA	4.17	1	NA	6.87E+00
25	Macrobenthos	2.9	1.17	3.95	2	1.1	1.12E-01
26	Meiobenthos	3.2	0.23	1.11	17	15	3.40E-01
27	Bacteria	2	0	1.51	12	75	3.43E-01
28	Detritus	1	NA	2.42	8	NA	76.2[1]

17 FIGURES

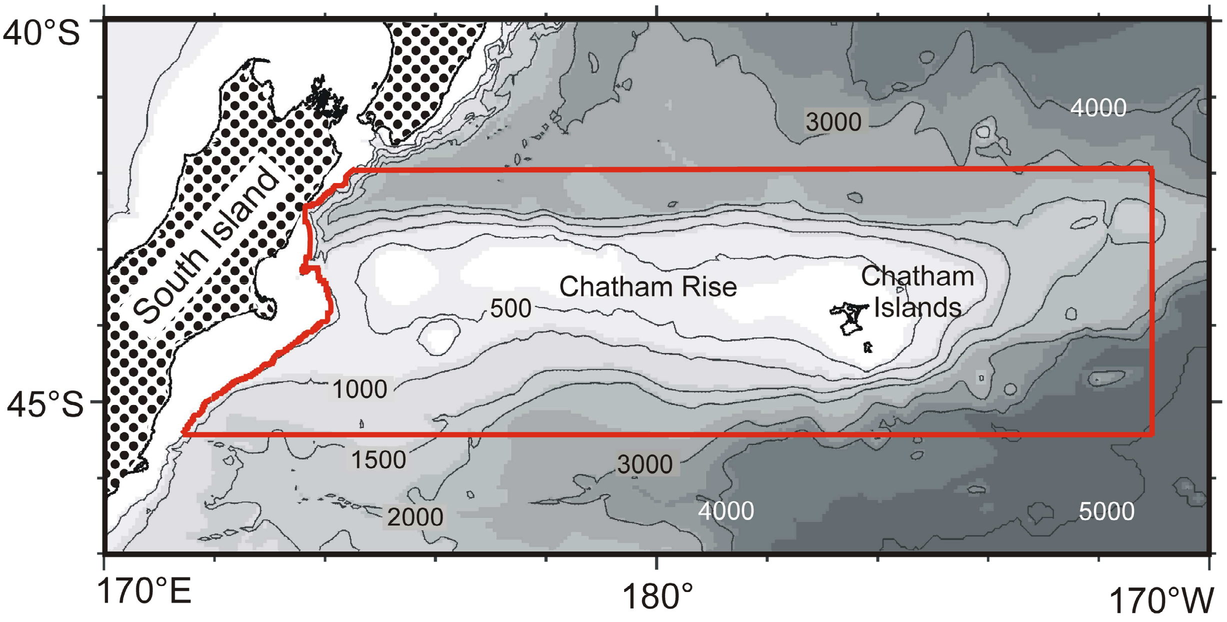

Figure 1. Chatham Rise ecosystem model study area.

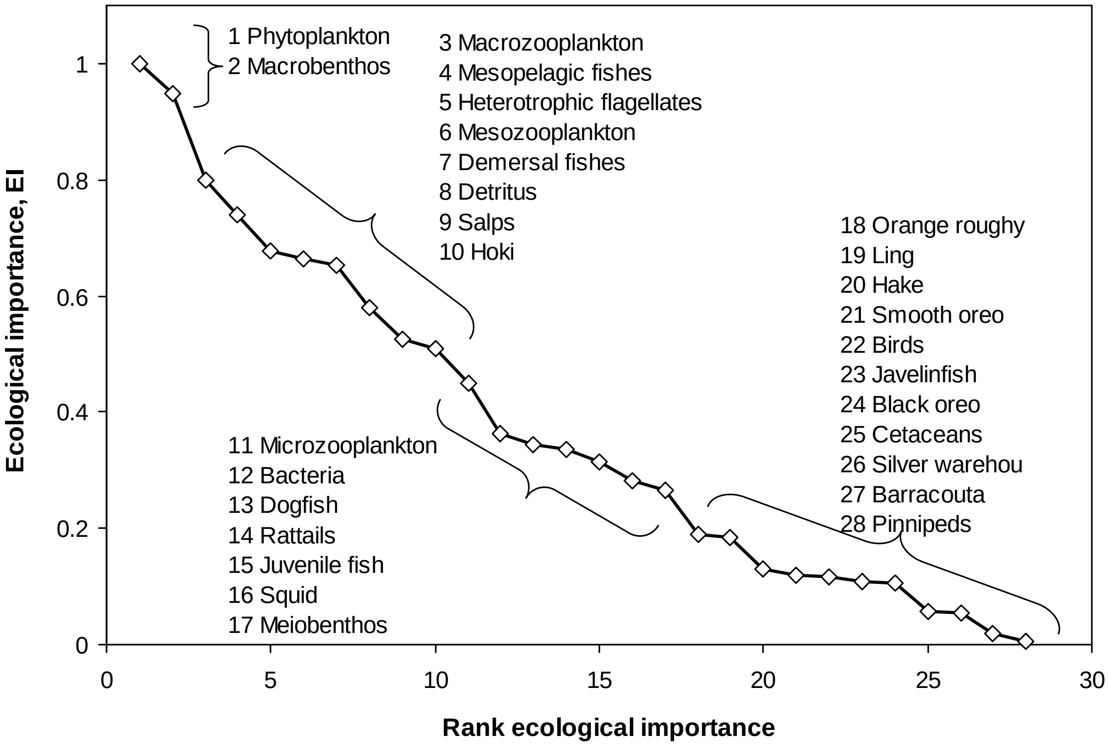

Figure 2. Ecological importance from the ecosystem model of the Chatham Rise (Pinkerton 2010) shown in descending order of importance (white diamonds). The labels are in equivalent descending order of importance, numbers being their rank importance.