Collation of data for ecosystem modelling of Te Tapuwae o Rongokako Marine Reserve

SCIENCE FOR CONSERVATION 288

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ABSTRACT

In New Zealand, our understanding of coastal marine ecosystems is surprisingly limited. Ecosystem models that link all species in a food web via energy transfer can be valuable tools for increasing our understanding of these ecosystems. We present the data required to build a balanced ecosystem model for the coastal marine region surrounding and including Te Tapuwae o Rongokako Marine Reserve, near Gisborne, New Zealand. We consolidate species into 22 groups and discuss them in detail, presenting additional information for subgroups and individual species as available. We review the literature and field data used to estimate values for each group as well as for the system as a whole. We also outline how we defined the spatial extent of many groups. For each group, we discuss the variability within estimates of four main data types (biomass, production rates, consumption rates and diet preferences) and we outline different ways to estimate diet composition to maximise the realism of such models. We are relatively confident that the data presented here accurately represent the structure and function of the ecosystem. However, there are many groups for which better information would improve model reliability. Therefore, we should aim to fill these knowledge gaps in the future, to better inform ecosystem models for coastal marine systems.

Keywords: rocky reef, temperate, ecosystem model, trophic model, New Zealand, marine reserve

1. Introduction

1.1 BACKGROUND

Our understanding of coastal marine ecosystems in New Zealand is surprisingly limited. Though we are continually adding to our knowledge of population, community and ecosystem processes, our ability to predict the impacts of acute and chronic disturbances on coastal marine communities is limited. Our ultimate goal is to predict with confidence how different management strategies (e.g. no-take reserves, customary fisheries reserves such as taiapure and mataitai, and commercial and recreational fishing regulations) and varying environmental conditions will affect coastal marine communities. Long-term monitoring at some marine reserves in northeastern New Zealand has demonstrated restored abundances of previously fished predator populations such as snapper (*Pagurus auratus*) and lobster (*Jasus edwardsii*), and subsequent changes in community structure through indirect effects and trophic cascades, where changes in abundance of species at the top of the food chain result in changes to species at lower levels of the food chain (Shears & Babcock 2003). In these reserves, the restoration of these predator populations has resulted in decreased abundance of *Evechinus chloroticus* (sea urchin or kina) and increased abundance and productivity of algal (kelp) assemblages. However, recovery times of harvested populations (and the marine community as a whole), and the time taken for other indirect trophic effects to occur, differ between reserves, depending on environmental variability and the relative importance of grazing invertebrates at each site (Kelly et al. 2000; Davidson et al. 2002; Kelly et al. 2002; Shears & Babcock 2003; Willis et al. 2003). In addition, some trophic impacts have been unexpected due to our incomplete understanding of the ecological processes that occur in subtidal rocky reef ecosystems (Langlois & Ballantine 2005).

Many new ecological tools can help us to predict disturbance impacts and long-term changes in coastal marine communities. Trophic ecosystem models, where all species in an ecosystem are connected via energy transfer, are one tool we can use to better understand the ecological processes and interactions in a typical New Zealand coastal ecosystem.

1.2 REGION OF STUDY

Te Tapuwae o Rongokako Marine Reserve near Gisborne, North Island, New Zealand, was chosen as the area of emphasis for this project. The present study aimed to characterise different species assemblages and trophic levels in the marine reserve to assess how different management regimes (taiapure, mataitai, commercial and recreation fishery regulations, and marine protected areas) contribute to meeting customary conservation objectives. This project discusses the development of an ecosystem model that synthesises the available information on the coastal marine species and habitats in the region to determine the baseline ecological interactions that define this coastal marine ecosystem.

The reserve consists of a 2452-ha no-take area that includes both hard- and soft-sediment intertidal and subtidal communities to depths of approximately 50 m. At the time of the marine reserve application in 1998, nine habitat types were identified within the reserve: sandy beaches, intertidal reef platforms, inshore reef—shallow weed zones, inshore reef—urchin barrens, inshore reef—kelp forest, inshore reef—deep reef slope, sediment flats, offshore reef—rock pinnacles, and deep mud flats (DOC & Ngati Konohi 1998). During the application process the boundary was amended, and when the reserve was gazetted in 1999, Monowai Rocks (the offshore reef habitat listed above) was excluded (DOC 2003). The area has high cultural significance as the resting place of the ancestor Paikea ('whale rider'), and the local Maori (Ngati Konohi) jointly proposed that this area be designated as a marine no-take reserve. Ngati Konohi have also proposed to manage the area to the north for traditional fishing as a mataitai customary fishery reserve (proposal in process). In the customary fishery, targeted species include many intertidal grazers (kina, paua, pupu (gastropods) and ngakihi (limpets)) and macroalgae, which are collected primarily from the extensive intertidal reef platforms in the region.

This region is particularly suitable for a study of ecological processes and interactions in a typical New Zealand coastal ecosystem because trophic cascades may be occurring as a result of the increase in the abundance of large predators that has occurred since the reserve was gazetted. For example, in Te Tapuwae o Rongokako Marine Reserve, there has been an increase in lobster (*Jasus edwardsii*) density, and lobsters have been observed migrating onto the intertidal reef platform and feeding on intertidal invertebrates at high tide. However, the impact of this increasing abundance of predators on the abundance of intertidal grazing species is unknown. A detailed understanding of the ecological dynamics of this coastal marine ecosystem can increase our understanding of this system, and potentially allow predictions to be made of long-term changes in community structure due to various management and/or environmental regimes.

1.3   ECOSYSTEM MODELLING

Trophic models can be used to analyse the effects of varying environmental conditions or the implementation of different management options (e.g. reserve status, traditional fishing (mataitai), and commercial and recreational fishing) on different trophic groups and the responses of other components of the system. More generally, a complete trophic model should inform us about how New Zealand coastal marine ecosystems function.

To better understand the effects of reserve protection within Te Tapuwae o Rongokako Marine Reserve and among the neighbouring habitats, models can be used to describe ecological processes and interactions between species and trophic groups. In this report, we describe the data collection phase, which is the first step in creating a balanced trophic model for this region to quantify transfers of organic material between different species. Our objective is to provide a review of how we have made parameter estimates for this coastal marine ecosystem, to assist with any future ecosystem models of New Zealand coastal marine ecosystems. The estimates we discuss are suitable for usage in the 'Ecopath with Ecosim' mass-balance food web model (Christensen & Walters 2004; Christensen et al. 2005), or similar trophic models based on organic matter transfer between different species such as the one we used (for model balancing, see Pinkerton et al. in press).

We first present a brief review of a typical trophic ecosystem modelling approach, and parameters required for most trophic modelling packages. We then review the protocol we used to define the spatial and temporal scale for the model dataset, and define habitats within the model region. We then discuss the parameter estimates for 22 trophic groups chosen to represent the relevant interactions within the model system. Finally, we present spreadsheets of the data to be entered into a preliminary model, following which balancing or other model manipulation would be required.

Coastal marine ecosystems in other parts of New Zealand are likely to have different parameters that are important, due to different abundances of various trophic groups and possibly also differences in diet and trophic parameters. However, the information provided in this report should enable other researchers to determine the combination of input parameters (e.g. biomass, production, consumption and diet compositions of different trophic groups) for trophic groups in their own region, which can then be used to develop a balanced trophic model using the trophic model software of their choice.

2. The model

Here we present a brief review of trophic ecosystem models to illustrate the trophic groups and parameters required to build a trophic model of a coastal New Zealand ecosystem. While we describe groups based on our analysis of the Te Tapuwae o Rongokako region, our goal is to present a review of published information for coastal trophic groups in New Zealand, and examples of methods that can be used to generate the parameters from available data.

2.1   CARBON-BUDGET MODELLING APPROACH

We present methods for data collation to generate the parameters necessary to develop a trophic ecosystem model based on the fundamental conservation of carbon approach used by 'Ecopath with EcoSim' (hereafter referred to as Ecopath) (e.g. Christensen & Walters 2004; Christensen et al. 2005). Ecopath and other trophic mass-balanced models (such as the model used in the National Institute of Water & Atmospheric Research (NIWA) analysis of the Te Tapuwae o Rongokako dataset; Pinkerton et al. in press) represent ecosystem dynamics through a set of linear equations that represent functional groups within the ecosystem. The NIWA trophic model differs from the standard Ecopath approach primarily in its balancing method and its treatment of detrital groups, as explained in sections 2.1.1–2.1.3. Otherwise, data collation and parameters for both models are the same.

Mass-balanced models represent a static (non-time evolving) snapshot of the energy flows within an ecosystem. The approach should be considered descriptive and does not employ any 'mechanistic' information about the system. Organic carbon is generally used as the model 'currency' (though other 'energy' currencies could be used). Here we develop parameters based on a time interval of 1 year.

Carbon flow through a given 'compartment' (species or trophic group) over a fixed period of time is balanced according to Equation 1:

$$\int B_i \left(\frac{P_i}{B_i} \right) EE_i - \sum_{j=1}^{n} B_j \left(\frac{Q_j}{B_j} \right) DC_{ji} - EX_i = 0 \tag{1}$$

where B_i is the biomass of compartment (species or trophic group) i, P_i/B_i is the production/biomass ratio, EE_i is the ecotrophic efficiency of i (see below), Q_j/B_j is the consumption/biomass ratio of j, DC_{ji} is the fraction of prey i in the average diet of predator j, EX_i is the export of i, and n is the total number of trophic compartments. This equation is not applied to the detrital compartments.

2.1.1   Ecotrophic efficiency

'Ecotrophic efficiency' is defined by Ecopath as the fraction of production that is used in the system, i.e. consumed by other groups in the food web or exported. Ecotrophic efficiency is typically used in carbon-budget models to establish a balance point so that all flows of organic carbon in the system are accounted for. Values of ecotrophic efficiency between 0 and 1 imply that some biomass is not available to predators or exported or accumulated in the system. This material is

typically assumed to enter the detrital pool, where it is decomposed by bacterial action. Note that material that is 'unavailable to the system' cannot be consumed by scavengers in normal ecosystem models. Ecotrophic efficiencies less than zero or greater than unity have no biologically valid interpretation and imply that the system is not realistic. Generally, ecotrophic efficiencies are calculated within Ecopath as part of the balancing process, i.e. three of the parameters B_i, P_i/B_i, Q_j/B_j or EE_i need to be inputed, and the fourth (usually EE_i) is then calculated from the other three.

We (the authors) believe that this approach may be realistic for smaller organisms (phytoplankton, micro- and mesozooplankton, and meiobenthos), but is inappropriate for larger organisms (macrozooplankton, fish, etc.). Whereas small organisms that die for reasons other than direct predation (e.g. old age, disease or injury) may be remineralised by bacterial action, we suggest that larger organisms that die in the sea are unlikely to be broken down by bacterial action but rather will be consumed by a range of scavenging or predatory fauna. These dead organisms should not, therefore, be included in the detrital pool. Instead, in most cases, we think it is reasonable to assume that a particular species is likely to be consumed by similar organisms when it is dead as to when it is alive, i.e. that predators of an organism will take it whether it is alive or dead. As a result, the NIWA trophic model handles detritus, and thus ecotrophic efficiency, in a different way from the Ecopath software. It is assumed that ecotrophic efficiency can only be zero or unity: zero is used for all trophic groups that have no predators, and one is used for all other groups.

2.1.2   Export and detritus

The net export from a compartment is the result of a combination of four components:

$$EX_i = ACC_i + EM_i - IM_i + F_i \qquad (2)$$

where ACC_i is the accumulation of biomass over timescales longer than a year; EM_i (emigration) is loss of material from the system, e.g. due to advection, swimming out of the system, or beach cast of macroalgae; IM_i (immigration) is material entering the system by similar processes; and F_i is removal of biomass by fishing over the course of a year. The input of bait to the ecosystem is included as a negative fishing export (i.e. an import).

Phytoplankton and other autotrophs are defined as having exactly zero consumption (i.e. these organisms create their own energy and do not consume other trophic groups). In Ecopath, the detrital compartment(s) (typically the nth) accumulates all 'lost' production (i.e. that which is not available to other trophic groups) from all the $(n-1)$ non-detrital groups. Ecopath users can constrain the system with respect to detritus based on how many detrital and/or detritus-consuming trophic groups are included in the model. However, the biomass of particulate and dissolved material in Te Tapuwae o Rongokako Marine Reserve is poorly known, we lack measurements of the long-term accumulation rates of benthic detritus and the input of dissolved detrital material from rivers, and the biomass and productivities of bacteria (assumed to be the main consumers of detrital material) in the study area are not known. Therefore, the NIWA trophic

model does not use detritus as a constraint on the cycling of organic matter in the ecosystem, instead choosing to make different assumptions about how detritus is incorporated into the system (described below, and in more detail in section 4.1).

Model balancing

The system of trophic groups is described by a set of n linear equations that has m unknown (or poorly known) parameters, where $m > n$. For each trophic compartment, the set of m parameters includes B, P/B, Q/B and EX, as well as the diet fractions for the system, which describe the transfer of material from one trophic group to another (Ecopath also includes EE for each trophic compartment). An additional set of constraints specifies that the diet fractions for each predator sum to unity.

This formulation of the model is an under-constrained system, so that we may expect a number of solutions to span the feasible parameter space. However, we note that the system is likely to have a single optimal solution since, for example, B always occurs with either P/B or Q/B so that these are not independent variables within the system. Standard matrix algebra that is typically used to solve ecosystem budget problems can give highly unreliable results where the transfer is singular. The Ecopath solution to this problem is to limit the number of model parameters that are allowed to vary to one per constraint, so that there is a unique solution. However, the NIWA trophic model differs from Ecopath as we do not think a unique 'balance point' is appropriate. Instead, rather than subjectively varying individual parameters to find a balanced model, the NIWA trophic model uses Singular Value Decomposition (Press et al. 1992) to explore the feasible parameter space. The balancing procedure finds a balance point such that the total magnitude of the changes to all parameters from the initial estimate is minimised. All parameters are changed simultaneously, including biomass, diet composition, production and consumption. Changes are calculated relative to estimated uncertainty factors for each parameter, allowing for the fact that some parameters are better known than others. In contrast, Ecopath obtains a balance point by allowing only one parameter per trophic compartment to vary. Diet fractions in Ecopath are fixed. It is likely that future versions of Ecopath will incorporate methods of determining a range of feasible solutions that are similar to the balancing method of the NIWA trophic model.

For each balanced snapshot of the ecosystem, carbon flow is balanced within each compartment using Equation 3:

$$\left(\frac{Q_i}{B_i}\right) = \left(\frac{P_i}{B_i}\right) + \left(\frac{R_i}{B_i}\right) + \left(\frac{Q_i}{B_i}\right)U_i \tag{3}$$

where the symbols are as in Equation 1, R_i is the respiration of component i, and U_i is the fraction of food consumed by component i that is not assimilated. Respiration must be positive for all compartments in an ecosystem for the solution to be considered reasonable, which implies that:

$$\left(\frac{P_i}{Q_i}\right) < (1 - U_i) \tag{4}$$

3. Methods

Here we describe the data and decisions required to develop an ecosystem model, and the procedures we used to extrapolate biomass estimates for each trophic group across the model region. We discuss two methods we used to extrapolate biomass estimates. First, we discuss habitat-based estimates of biomass of taxa surveyed in the subtidal monitoring of the marine reserve (lobsters and reef fish) and estimates of biomass of structure-forming species, such as macroalgae and encrusting invertebrates, based on habitat classifications for northeastern New Zealand. We then discuss the procedure we used to estimate parameters of trophic groups for which we did not have habitat-specific estimates of abundance. Estimates of trophic parameters and diet composition for each trophic compartment are discussed in section 4.

3.1 DATA AND DECISIONS REQUIRED

The first step in model development is to define the region to study. Within this region, we then determine which species and groups of species are present, and their interconnections (predator-prey relations). Next, we group the member species into trophic compartments. This leads to the development of a conceptual model of the ecosystem.

3.1.1 Defining the model region

The data described in this report have been compiled in order to develop an organic-carbon budget model for the coastal region encompassing Te Tapuwae o Rongokako Marine Reserve near Gisborne, New Zealand. Model values are presented in units of areal carbon density ($g\,C/m^2$) for biomass, and $g\,C\,m^{-2}\,y^{-1}$ for trophic flows.

We defined two study areas for this work: (1) the marine reserve itself and (2) a larger area encompassing the marine reserve and the surrounding marine area. Since the majority of the information on trophic groups in the region was for areas within the marine reserve, we parameterised our model based solely on the area within the marine reserve. However, we do present additional information from outside the reserve when available. Based on known territoriality of larger predators (reef fish and lobsters) and tagging studies within Te Tapuwae o Rongokako (D. Freeman, DOC, unpubl. data), we have assumed that there is minimal emigration from the reserve.

The area of the reserve (1) was defined by the Marine Reserve (Te Tapuwae o Rongokako) Order 1999, which stated that 'The marine reserve extends from near the Waiomoko River mouth in the north, to near the Pouawa River mouth in the south … The northern boundary is 5 km … in length. The southern boundary is 3.5 km … in length and the seaward boundary is 7.5 km … in length' (Fig. 1; DOC 2003). The four corner points of the reserve were taken to be located at 38.6117°S 178.1836°E, 38.6407°S 178.1974°E, 38.6021°S 178.2689°E and 38.5783°S 178.2200°E (Booth 2003). We defined the corners of the

Figure 1. Te Tapuwae o Rongokako Marine Reserve (TTMR), north of Gisborne, New Zealand. The location of the Cape Rodney to Okakari Point Marine Reserve, near Leigh, is also noted for later comparison. Note that panel B has been rotated anticlockwise by 45° in this image.
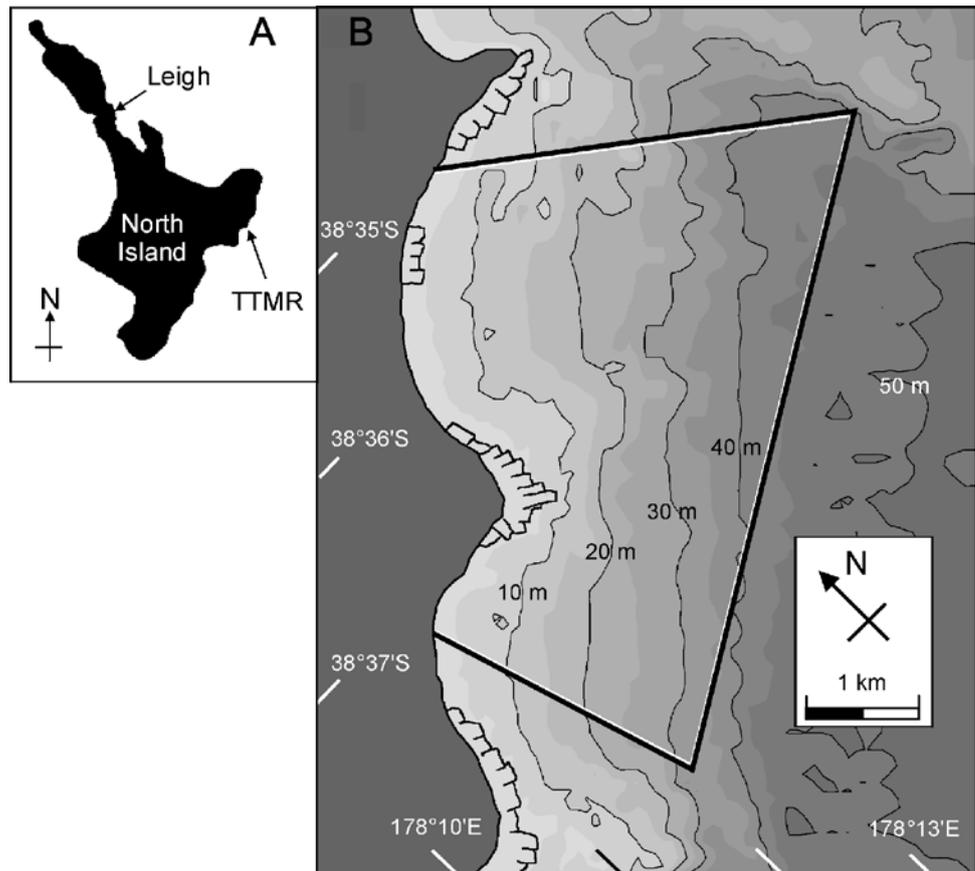
larger area (2) as 38°39.0047′S 178°7.5363′E, 38°40.5618′S 178°9.0304′E, 38°35.8076′S 178°18.3414′E and 38°32.9510′S 178°15.7146′E. This larger area was taken to be representative of similar substrates to those within the reserve and entirely contained the reserve within it.

We took the landward boundary as the high water mark that is consistent with mean high water springs. Mean high water spring tide levels for the region as taken from Port of Gisborne tide tables were 1.92 m above datum. Using the same data, mean low water spring tide levels were 0.54 m above datum. The datum for the Port of Gisborne is 4.091 m below B.M. GB 01 (LINZ code ACVP), and 1.23 m below mean sea level. The bathymetry grids were based on Stephens et al. (2004) and are relative to mean sea level.

3.1.2 Defining trophic groups

From our knowledge of the functioning of coastal marine food webs in northeastern New Zealand, we provisionally defined the food web of the reserve area as having 22 generalised functional compartments (Table 1). Other researchers might choose to lump or separate any of these groups for their particular model, based on relative importance in a particular system (e.g. kina and paua may be a focal group in a model characterising a trophic cascade and reduction in urchin barren habitat within a marine protected area). Here, we present each functional category, with details for subgroups or individual species when available.

We keep the information about separate species and subgroups intact so that trophic groupings can be re-examined subsequently. For each of the species or

trophic compartments we then determine the energetic parameters required for the model. These are as follows:

- Biomass (B)
- Production/Biomass (P/B)
- Consumption/Biomass (Q/B)
- Net emigration (emigration – immigration) (EM – IM)
- Fishery losses and bait input (F)
- Long-term accumulation (ACC)
- Unassimilated consumption (e.g. detritus and ecotrophic efficiency) (U and EE)
- Diet fractions

TABLE 1.   FUNCTIONAL TROPHIC GROUPS FOR WHICH DATA ARE PRESENTED. SEE SECTION 4 FOR SCIENTIFIC NAMES.

TROPHIC GROUP	REPRESENTATIVE TAXA
Birds	Gulls, shags, herons, oystercatchers
Lobsters	
Mobile invertebrates (herbivores)	Kina, paua, limpets, chitons, other grazing gastropods
Mobile invertebrates (carnivores)	Seastars, brittlestars, whelks, octopuses, crabs, nudibranchs
Sea cucumbers	
Phytal, macro- and micro-invertebrates	Amphipods, isopods, microcrustacea, polychaetes, infaunal bivalves
Sponges	
Sessile invertebrates	Mussels, anemones, crinoids, barnacles, hydroids, sea squirts, bryozoans, corals, ascidians, polychaetes, bivalves, scallops
Cryptic reef fishes	Triplefins, wrasses, blennies, gobies, rockfish, eels
Fishes (invertebrate feeders)	Red moki, scarlet wrasse, porae, leatherjacket, blue moki, spotty, banded wrasse, snapper, goatfish, hiwihiwi
Fishes (piscivores)	Kahawai, rock cod, blue cod, kingfish, red-banded perch, jack (horse) mackerel, john dory, opalfish, barracouta
Fishes (planktivores)	Sweep, trevally, blue maomao, butterfly perch, common warehou, anchovy, demoiselle
Fishes (herbivores)	Butterfish, marblefish, parore, drummer
Microphytes	Epiphytic diatoms, microphytobenthos, epiphytic algae
Macroalgae (brown, canopy)	
Macroalgae (foliose, turfing, brown non-canopy)	
Macroalgae (crustose and coralline)	
Meso- and macrozooplankton	
Microzooplankton	
Phytoplankton	
Bacteria	
Detritus	

3.1.3   Defining the study period

We present parameters to create a model that represents this coastal marine ecosystem following the establishment of Te Tapuwae o Rongokako Marine Reserve, based principally on data collected between 2000 and 2003. The data used to estimate parameters in the model have been spatially and seasonally resolved as far as is permitted by the relatively scarce data defining animal abundance, distributions and diet composition in the region. It is important to note that the monitoring programme for the marine reserve was not established for the purpose of generating trophic model data. Rather, its focus was to monitor species for which the reserve was expected to show potential benefits (e.g. lobsters and reef fish). Thus, we have expansive datasets for some trophic groups, while other groups (e.g. phytal invertebrates and encrusting invertebrates) were not included in the monitoring programme, even though they may be of particular importance for a trophic model. Nevertheless, the Te Tapuwae o Rongokako Marine Reserve monitoring programme has been particularly helpful in allowing habitat-specific estimations of abundance for numerous trophic groups, as explained throughout this report.

The data from the monitoring programme are also not ideal for determining seasonal changes in the abundance of various groups, as most monitoring surveys are performed in summer. For example, lobster abundance is calculated from summer transects when lobsters are present on the reef, but little is known about seasonal variations in lobster abundance on the reef and surrounding soft-sediment habitats (though additional data are being collected on movement rates of lobsters to determine these seasonal variations). Similarly, little is known about inter-annual variability in diet composition of lobsters and other mobile reef species, both in this area and throughout most of New Zealand. Therefore, future models should consider the seasonal aspect of the ecosystem, as important trophic bottlenecks may be missed by an annual-average model. We have retained and reported information on the seasonal variation in trophic parameters where possible to facilitate the development of a seasonally resolved model in the future.

The initial model is based on a period of 1 year, i.e. we consider flows averaged over a single 1-year period that is representative of conditions following protection of the reserve area. In the following sections, we estimate parameters using data from different years: even though it is known that there may be a considerable amount of inter-annual variability in the ecosystem in addition to the intra-annual (seasonal) variability mentioned previously, the limited amount of data availability did not allow us to estimate parameters for all groups for one specific time period. Combining available information from different years, we are conceptually providing data on a 'typical' recent year. If we assume that the basic functioning of the ecosystem does not fundamentally change from year to year, perturbation or scenario testing based on this 'typical' model is likely to provide useful insights into the sensitivity of the ecosystem to inter-annual environmental variability.

Most data on the abundance (number of individuals) and/or biomass (g C) of flora and fauna in the study area are from the period 2000–2003, i.e. the period following reserve establishment, as there was inadequate sampling conducted in the area prior to establishment of the reserve. For example, 85 diver transects were surveyed inside the reserve and 66 transects were surveyed outside the reserve between 2000 and 2003, and these covered most habitat types found in

the area. In contrast, in 1990, before the reserve was established, there were only 18 surveys inside the reserve and 5 surveys outside the reserve, which covered only four of the possible ten subtidal habitats (see section 3.2.1). Therefore, although comparison of fish biomass in the habitats that were surveyed before and after the reserve was established suggests that average fish abundance has increased by over 700% since the reserve was established, and many species (e.g. blue moki *Latridopsis ciliaris*, butterfly perch *Caesioperca lepidoptera* and goatfish *Upeneichthys lineatus*) that were not found at all during the 1990 surveys were abundant both inside and outside the reserve in 2000–2003, these changes may simply be the result of insufficient sampling effort during the 1990 surveys.

Due to the insufficient number of diver surveys measuring fish abundance in 1990, we are unable to generalise with confidence about the likely change in fish biomass after the reserve was established. This is also true for other trophic compartments. For example, we have no measurements of the biomass of macroalgae, phytal invertebrates, encrusting invertebrates or predatory invertebrates prior to establishment of the marine reserve. Therefore, we present species abundance data and trophic parameters to build a trophic model that represents the 'current' state of Te Tapuwae o Rongokako Marine Reserve, based on data from 2000–2003. When available, we present additional information for the larger region including areas outside the reserve.

3.2   HABITAT-BASED ESTIMATION OF BIOMASS

Abundance of different trophic groups is often closely associated with habitat type. For example, reef fish species may be closely associated with canopy-forming kelps but not found in deep reef or sandy areas. In determining total abundance of all trophic groups across the entire model region, it is valuable to know what proportion of the total area is covered by each habitat type. Similarly, we can calculate habitat-specific estimates of abundance if we know the habitat type of each biomass sample. Extrapolating habitat-specific biomass across the proportion of each habitat type found in the model region will reduce the uncertainty in estimates of total biomass. Here we discuss habitat-based estimates of biomass of taxa surveyed in the subtidal monitoring of the marine reserve (lobsters and reef fish), and estimates of biomass of structure-forming species, such as macroalgae and encrusting invertebrates, based on habitat classifications for northeastern New Zealand. We discuss two methods: Delaunay triangulation, which is appropriate for extrapolating point samples to estimate habitat types across an entire region; and estimates based on GIS maps for which the proportion of each habitat type is already known.

3.2.1   Reserve monitoring data

The primary data used to estimate biomass in the model were collected from ongoing monitoring programmes, tagging experiments, and other surveys of Te Tapuwae o Rongokako Marine Reserve and the surrounding region (Table 2) (D. Freeman, DOC, unpubl. data). Density data were collected for many taxa (reef fish species, lobster *Jasus edwardsii*, paua *Haliotis iris* and *H. australis*, and kina *Evechinus chloroticus*) in reserve and non-reserve locations. Size

frequency distributions were collected for lobster, paua and kina, and for six reef fish species (blue cod *Parapercis colias*, red moki *Cheilodactylus spectabilis*, blue moki *Latridopsis ciliaris*, butterfish *Odax pullus*, snapper *Pagrus auratus* and tarakihi *Nemadactylus macropterus*) (Freeman 2005). Intertidal reef platforms were analysed for percentage cover of algal groups and encrusting invertebrates, and abundance of mobile invertebrates (Freeman 2006). Movement and migration rates of lobsters were estimated from tagging programmes. The intertidal community assemblage was surveyed in 220 m² of non-reserve habitat (122.5 m² at site Makorori, 97.5 m² at site Turihaua) and 147.5 m² of reserve habitat (43.75 m² at site Reserve, 103.75 m² at site Reserve-Moat); surveys yielded counts or percentage cover estimates of all macroscopic organisms in five quadrats (0.25 m²) for each 20 m of transect through the intertidal zone from shore to the subtidal zone.

The subtidal marine reserve and surrounding habitats were surveyed to estimate habitat types. For each of about 300 subtidal locations, habitat information was collected via sidescan (Earth Sciences Department, University of Waikato) and/or drop camera surveys (ASR Ltd). This information was then converted to Shears et al.'s (2004) subtidal rocky reef qualitative habitat classification for northeastern North Island by Debbie Freeman (DOC), with expanded habitat categories for *Ecklonia* forest that incorporated different understorey algal species (Table 3). Point estimates of habitat type were also obtained from subtidal monitoring transects to estimate reef fish and lobster abundance (D. Freeman, DOC, unpubl. data). We generated a habitat map of the study area based on all available habitat point estimates; where habitat types were unknown for a location, they were estimated based on surrounding habitat types using Delaunay triangulation (see section 3.2.2). Habitat types for soft-sediment areas were not separated into more detailed classifications, as this information was not available.

TABLE 2.   MONITORING DATA AVAILABLE FOR TE TAPUWAE O RONGOKAKO MARINE RESERVE.

TROPHIC GROUP	YEAR	DEPTH	SIZE OF TRANSECT	COMMENTS
Lobster (counts and sizes)	2000–2003 (annually)	Subtidal (5–25 m)	50 m × 10 m	
Lobster tagging survey	2003–2005	Subtidal	N/A	
Paua/kina (counts and sizes)	2000–2003 (annually)	Intertidal channel	Channel length, varying	
Reef fish (counts, sizes of six species, habitat information)	2000–2003 (annually)	Subtidal (5–25 m)	100 m × 5 m × 3 m above substrate	Also includes habitat-specific lobster counts
Intertidal community assemblages (algae, mobile and sessile invertebrates) (counts and percentage cover)	2000, 2003	Intertidal	5 transects per site, 5 quadrats (0.25 m²) every 20 m	
Habitat: sidescan (Earth Sciences Department, University of Waikato); drop camera (ASR Ltd); transects (Department of Conservation)	Various	Subtidal	N/A	
Subtidal community assemblages (Shears & Babcock 2004b)	2002	Subtidal	40 1-m² depth-stratified quadrats at two reserve sites, 35 1-m² quadrats at two adjacent sites	Additional 28 1-m² quadrats (reserve) and 27 1-m² quadrats (adjacent sites) collected from depth transects from shallow intertidal to edge of reef

TABLE 3.   HABITAT TYPES DEFINED WITHIN THE MODEL REGION. ABBREVIATED DESCRIPTIONS FROM SHEARS ET AL.'S (2004) CLASSIFICATIONS OF SUBTIDAL ROCKY REEF ASSEMBLAGES IN NORTHEASTERN NEW ZEALAND. Kelp forest habitat types (EckCaul, EckCflex and EckFolred) have been expanded, as explained in text.

MODEL HABITAT TYPE	DESCRIPTION	SHEARS ET AL.'S (2004) HABITAT NAME	EQUIVALENT HABITAT FROM GIS MAP (FIG. 3)
1 Deep reef/ sponge garden	Sparse/no brown macroalgae. Generally coralline turf and bryozoan-covered reef, with conspicuous sponge fauna. Sometimes *Caulerpa articulata* meadows.	Sponge flats	100% sponge garden
2 EckCaul	*Ecklonia radiata* forest with conspicuous understorey of *Caulerpa*, primarily *C. articulata*, with some *C. geminata*.	50% *Ecklonia* forest, 50% *Caulerpa* mats	50% *Ecklonia* forest, 50% mixed algae
3 EckCflex	Mixed forest of *Ecklonia radiata* and *Carpophyllum flexuosum*—'stands' of tall *C. flexuosum*.	Mixed algae	50% *Carpophyllum*, 50% *Ecklonia* forest
4 EckCor	*Ecklonia radiata* forest with coralline turf/Crustose Coralline Algae (CCA) understorey. No/few conspicuous foliose algae beneath kelp canopy.	50% *Ecklonia* forest, 50% urchin barrens	100% *Ecklonia* forest
5 EckFolred	*Ecklonia radiata* forest with conspicuous understorey of foliose red algae, primarily *Plocamium* spp. and *Osmundaria colensoi*.	50% *Ecklonia* forest, 50% red foliose algae	50% *Ecklonia* forest, 50% mixed algae
6 MixedBr	Shallow (< 5 m) mixed brown macroalgae—primarily *Carpophyllum maschalocarpum* and *C. flexuosum*, with some *Ecklonia radiata*.	Shallow *Carpophyllum*	75% *Carpophyllum*, 25% mixed algae, 5% *Ecklonia* forest
7 CorCovReef	Reef covered in coralline turf or CCA—no sponges, no/sparse macroalgae. Also classified as urchin barrens. Influenced by silt deposition or sand scour.	Urchin barrens	100% coralline-covered reef
8 DeepCobbles	Gravel/cobble areas. Few epifauna—occasional sponge, bryozoan. Occasional larger boulder with sponges. Mollusc shells.	Cobbles	100% deep cobbles
9 Sand	Rippled sand, occasionally covered in fine layer of silt.	N/A	100% sand
10 Intertidal	Intertidal rocky reef and sandy beach areas as defined from bathymetry charts.	N/A	Beach: 100% sand; intertidal reef: approximately 60% coralline-covered reef; 20% mixed algae; 20% sand

3.2.2   Method 1—extrapolation of point-based habitat measurements

For many trophic groups, biomass was estimated using a novel habitat-based method on surveys of the study area. The underlying assumption was that the biomass of the trophic group was related to the area of suitable habitat. As part of this approach, it is necessary to extrapolate point measurements of habitat type across the study area. These points were not uniformly distributed in space, and a method that copes with unstructured spatial information was required. The method we used had the following steps:

1. **Determine a number of discrete habitat-type classifications for the study region (Table 3).**   One challenge we faced was choosing our habitat definitions, as multiple habitat definitions were available based on different surveys of the study area. We defined subtidal habitats using the habitat classifications defined for northeastern North Island (Table 3; Shears et al. 2004). We chose to reference these published habitat classifications to maintain consistency for further studies, and because of the availability

of habitat-specific data on biomass of many algal and invertebrate groups. When additional data were available, we expanded on these initial habitat categories, as explained below.

2. **For each trophic group, determine the biomass according to habitat type.** This biomass was based on local subtidal survey information for lobsters and reef fish, and data from the New Zealand literature for macroalgae and encrusting invertebrates (Table 4; Shears et al. 2004). We calculated habitat-based averages of abundance for lobster and individual reef fish from subtidal survey data, as habitat type was known for each survey sample. Habitat-specific abundance and percentage cover (per m^2) for macroalgae and encrusting invertebrates were based on the averages for northeastern North Island (Table 4). The available habitat data were expanded beyond the initial Shears et al. (2004) categories, with three more specific kelp forest categories that consisted of *Ecklonia* forest with three different understorey algal groups of coralline algae, foliose red algae or *Caulerpa* spp. This was possible because information at this degree of specificity was collected during Department of Conservation (DOC) subtidal monitoring surveys. To estimate algal and encrusting invertebrate biomass for these 'new' habitats, we estimated biomass based on an equal abundance of the two relevant habitat types in Shears et al.'s descriptions (EckCaul = 50:50 mix of *Ecklonia* forest and *Caulerpa* mats; EckFolred = 50:50 mix of *Ecklonia* forest and red foliose algae; and EckCor = 50:50 mix of *Ecklonia* forest and urchin barrens, e.g. coralline-covered reef).

TABLE 4.   SUBTIDAL BIOMASS OF VARIOUS SPECIES ACCORDING TO HABITAT TYPES DEFINED FOR TE TAPUWAE O RONGOKAKO MARINE RESERVE.

Habitat-specific abundance and percentage cover (per m^2) for dominant species are based on averages for northeastern North Island as reported by Shears et al. (2004). Intertidal calculations (referring to approximately 3% of the total area) are described separately.

SPECIES	HABITAT TYPE*								
	1	2[†]	3	4[†]	5[†]	6	7	8	9
Abundance (individuals/m^2)									
Ecklonia radiata	0	8.7	3.9	8.6	8.9	1.7	0	0	0
Carpophyllum spp. (*C. maschalocarpum, C. plumosum, C. angustifolium*)	0	1.2	12.6	0.25	1.75	87.7	0.1	0	0
Carpophyllum flexuosum	0	0.45	3	0.9	0.45	0.2	0.9	0	0
Other large brown algae	0.5	0.55	11.6	0.6	0.5	4.6	0.5	0	0
Percentage cover (%)									
Red foliose algae	0	2.6	1.6	0.8	20.05	7.6	0	0	0
Caulerpa spp.	0	30.4	0.3	0.4	0.4	0	0.2	0	0
Turfing algae	0	9.3	14.4	9.45	15.7	8.3	10.4	2.2	0
Encrusting algae	2.5	33.75	44.3	60.4	41.25	55.7	66.8	23	0
Sponges and other encrusting invertebrates[‡]	14.5	2.5	1.6	4.45	2.85	1.7	5	0	0
Sediment	82.5	12.95	21.9	12.15	10.3	7.5	5.9	37	100

*   See Table 3 for definitions of these habitat types.

[†]   Mixed habitat based on equal abundance of two habitat types in Shears et al.'s (2004) descriptions.

[‡]   Assumed to be composed of 75% sponges and 25% other encrusting invertebrates.

3. **Extrapolate these biomasses to the whole study area, using Delaunay triangulation (Fig. 2).**   A number of methods are available for extrapolating the biomass information on the irregular grid to a high spatial resolution regular grid. Here we used Delaunay triangulation, though methods such as kriging are also possible (though more computationally intensive). In this study, point measurements of habitat were transformed into a set of non-overlapping triangles using Delaunary triangulation, an iterative process of connecting points with their two nearest neighbours to form triangles that are as equiangular as possible. Delaunay triangulation is a proximal method such that a circle drawn through the three vertices of each triangle contains no other node. Delaunay triangulation has several advantages over other triangulation methods: triangles are as equiangular as possible, thus reducing potential numerical precision problems; any point on the surface is as close as possible to a node; and the triangulation is independent of the order the points are processed. The values at the vertices of the triangles are then used to predict the biomass value of all regular grid points within the triangle using inverse distance weighting. This spatial extrapolation was implemented using the high level programming language Interactive Data Language (IDL, Research System Inc., USA).

Figure 2.   Estimating biomass over the study regions using Delaunay triangulation. The background shading is the bathymetry as in Figure 1. The small outline denotes the reserve area for which the 'best' data are available, while the larger outline denotes the larger area for which the trophic parameters are discussed for most groups. Land is shown in black. Each triangle vertex represents a location where there is information on habitat type. The white lines indicate the Delaunay triangles used to extrapolate the data to the whole region.
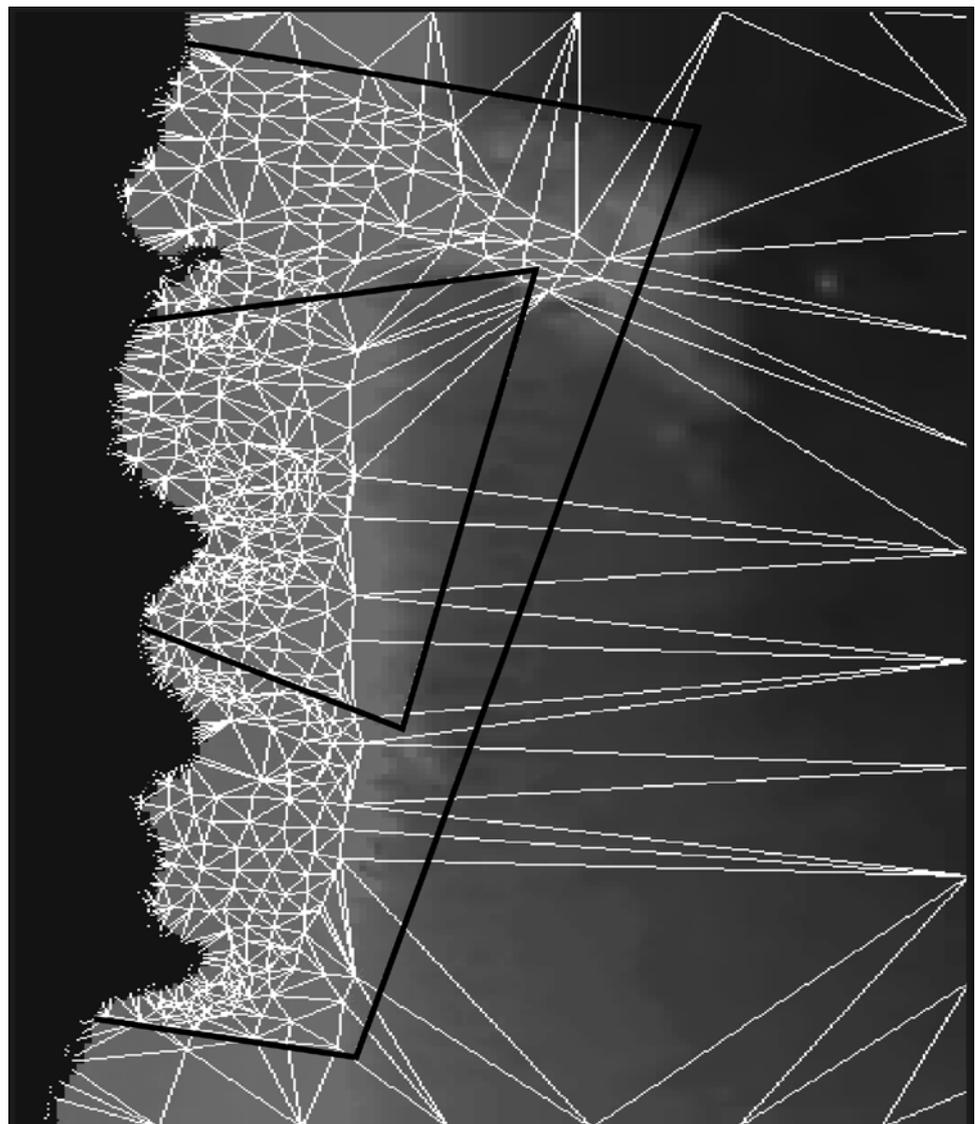
3.2.3   Method 2—GIS habitat maps

If reliable habitat maps are available for an area, the proportion of each habitat type (and habitat-specific biomass) can be estimated more directly than Method 1. We translated existing habitat maps of the region (which included the reserve and much of the larger area discussed in this report) into Geographic Information Systems (GIS), which included seven habitat types (Fig. 3). These maps were necessary to perform more detailed categorisation of intertidal habitats, which were not available from the Delaunay triangulation subtidal habitat mapping exercise outlined in Method 1.

Using topographical maps, the area of intertidal reef in the reserve was estimated to be 821 000 m^2. Although this is only approximately 3% of the total reserve area, the intertidal reef is important because it harbours high concentrations of macroalgae, including *Hormosira banksii*, *Cystophora* spp., and coralline and

Figure 3.   GIS habitat map of Te Tapuwae o Rongokako Marine Reserve and seabed habitats (from Wilson et al. 2007).
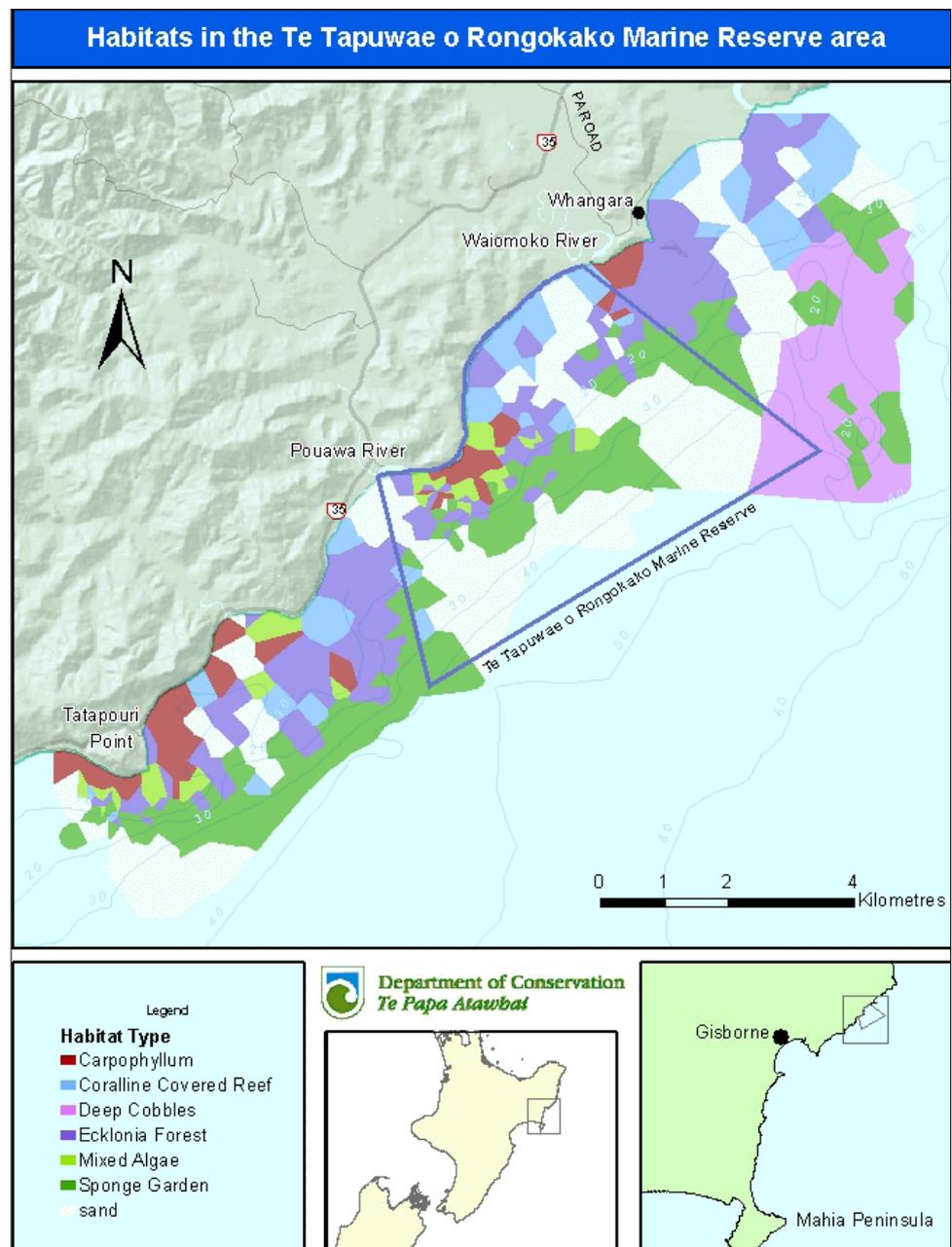
turfing algae. The proportions of various habitats on this reef were estimated from five intertidal walking transects across the reef (D. Freeman, DOC, pers. comm.) (Table 5). These data were combined using aerial photographs of the exposed reef to give an estimated coverage of habitats on the exposed intertidal reef platform. We assumed that all intertidal reef areas that were not reported as being covered by a habitat type in Shears & Babcock (2004b) were comprised of non-colonised (bare) reef and/or sand. These habitat areas were then used to calculate habitat-specific estimates of biomass for some of the trophic groups, as outlined in section 4.

Percentage cover and presence of common intertidal algal species were recorded during intertidal monitoring surveys of the marine reserve. This showed that intertidal reef areas were dominated by turfing coralline algae, and also included the small brown alga *Hormosira banksii*, and the large brown algae *Cystophora torulosa* and *C. retroflexa* (Table 6). Bare or other unvegetated categories made up about 25% of the intertidal reef on average in the reserve.

TABLE 5.   LOCATION OF 'WALKING TRANSECTS' ACROSS THE EXPOSED REEF IN TE TAPUWAE O RONGOKAKO MARINE RESERVE.

DATE	LOCATION	MAP REFERENCE OF START (EASTING, NORTHING)
11 Mar 2000	North Pariokonohi Point	2962957, 6276057
12 Mar 2000	Causeway	2962850, 6276687
19 Mar 2000	Pariokonohi Point	2962427, 6275437
04 May 2000	North of Pouawa Road end	2962150, 6275400
04 May 2000	South of Pouawa Road end	2961917, 6275340

TABLE 6.   APPROXIMATE HABITAT PROPORTIONS ON THE INTERTIDAL REEF IN THE RESERVE AREA, ESTIMATED FROM INTERTIDAL WALKING TRANSECTS.

HABITAT	PROPORTION (%)	EQUIVALENT MODEL HABITAT (TABLE 3)
Sand	19.0	Sand
Coralline	57.0	CorallineCovReef
Bare rock	5.6	None
Barnacles	1.2	None
Hormosira banksii	4.0	MixedAlgae
Cystophora spp.	14.0	MixedAlgae

3.2.4   Comparison of the two habitat mapping methods

Since we had sufficient data to calculate biomass for various trophic groups based on the four expanded *Ecklonia* kelp forest habitat types (with differing understorey species), and biomass of these understorey species has a significant impact on total biomass for the different macroalgal trophic groups, we used the most detailed information available to define habitat-based calculations of biomass using Method 1. However, to ensure that the two methods gave similar results, we compared the results of Method 1 (Delaunay triangulation) and Method 2 (GIS habitat maps) by looking at the distribution of seven GIS habitats inside

TABLE 7.   COMPARISON BETWEEN HABITAT PROPORTIONS ESTIMATED USING METHOD 1 (DELAUNAY TRIANGULATION OF SUBTIDAL HABITAT SURVEYS COMBINED WITH INTERTIDAL WALKING TRANSECTS) AND METHOD 2 (GIS MAP FROM AERIAL PHOTOGRAPHS).

	METHOD 1 (%)	METHOD 2 (%)	DIFFERENCE (%)
1. Carpophyllum	3.60	3.49	3
2. CorallineCovReef	7.00	7.36	-6
3. DeepCobbles	2.82	2.78	1
4. EckloniaForest	10.33	10.50	-2
5. MixedAlgae	3.50	3.64	-5
6. SpongeGarden	20.12	20.47	-2
7. Sand	52.63	51.77	1
Total	100.00	100.00	

the subtidal region of the reserve (Table 7). To make the data comparable, the four *Ecklonia* forest habitat types from the triangulation exercise were lumped into one *Ecklonia* category, and the triangulation data (subtidal) were combined with walking transect data (intertidal). Differences between the proportions of individual habitats estimated by the two methods were generally very small (< 7%) (Table 7), which gives us confidence that the areas of the various habitats are reasonably well known for Te Tapuwae o Rongokako Marine Reserve.

Estimation of biomass for groups lacking habitat-specific estimates

For most trophic groups, we lacked local, habitat-specific estimates of biomass, and thus used data from the scientific literature to estimate biomass. We used data for the exact species and from within the model region to estimate biomass, where such information was available. In most cases, however, 'local' information was not available; therefore, alternative information was obtained from other locations from northeastern New Zealand or from congeneric species if species-specific information was not available. For most groups, we estimated biomass separately for both hard and soft substrates.

3.3   ESTIMATION OF DIET COMPOSITION AND CONVERSION OF BIOMASS INTO CARBON

Diet composition for a given species/group refers to the fraction of each trophic group it consumes. This is usually estimated from studies of stomach contents. There was a paucity of site-specific diet composition data, as well as a lack of recent, local and detailed species-specific diet composition data for most species included in the model. Therefore, diet composition estimates were primarily based on one-off surveys from the Hauraki Gulf. Most of the available information was for fish species, with little local information available for most invertebrate taxa. In some cases, point counts of gut contents were used to estimate percentage volume in the diet. Where only presence/absence data were available (usually percentage of guts containing a particular prey item), we used educated guesses and literature descriptions of important diet components to estimate percentage volume of each diet type. Where biomass information was not available, we assumed that literature estimates of volume were equivalent to estimates of biomass of each diet type.

Unassimilated consumption (U) was taken from estimates in previous trophic models (e.g. Christensen & Pauly 1992; Bradford-Grieve et al. 2003). Unassimilated consumption was taken as 0.2 for birds, 0 for bacteria, and 0.3 for other trophic groups.

Various abundance and biomass metrics were converted to a carbon energy budget using available conversion rates from the literature, or estimates based on similar species or trophic groups when data were not available.

4. Estimation of trophic group parameters

Here we detail estimates of the trophic parameters (biomass, production, consumption and diet composition) required as input to the ecosystem model. We describe each of the 22 trophic compartments separately, discussing individual species within each compartment as appropriate.

4.1   DETRITUS

We combined three potential detrital categories into the more general trophic group of 'detritus': water column detritus, benthic detritus and dead animals/carcasses. It is important to note that we did not distinguish between 'particulate detritus' and dissolved organic carbon. Detritus includes organisms killed in ways other than direct predation (e.g. old age, disease, starvation or injury).

We assumed that for a given trophic group that has one or more predators, individuals that have been killed by means other than direct predation will still be consumed in the same proportions and by the same fauna as live individuals. For example, we assumed that the same animals that predate live lobsters will also consume dead lobsters. We believe that most organisms die by being predated upon, so this assumption is not likely to be critical to the model results. Dead organisms from a trophic group that has few or no predators within the model (e.g. bird carcasses) are assumed to have been consumed by either generalist predators or benthic bacteria.

Since bait from various fisheries is an input of material, it could be considered as its own trophic group (carcasses). We have not done this here, as the bait input from the scientific tagging programme in the marine reserve is minimal and not a significant contribution to biomass in the system. However, this separate trophic group should be included in other model systems where there are likely to be substantial inputs of bait through various commercial and recreational fisheries. Bait input could also be categorised as detritus, assuming it will be consumed by generalist scavenger organisms.

No measurements of detrital biomass were available for either the water column or benthos of the study area. By definition, detritus does not have either production or consumption rates. In Ecopath, the model is generally allowed to estimate detrital biomass; detritus can then have multiple consumers, providing a balancing constraint for the model. The trophic model used here treats detritus much more simply by only allowing bacteria to consume it. Thus, we assumed that detritivores were actually consuming bacteria (that are consuming detritus) rather than detritus directly, meaning that detritus is balanced within the model but only has one consumer. We chose to do this because there is substantial uncertainty regarding bacterial biomass, production and consumption, and choices of trophic parameters for bacteria can have large impacts on model balancing. There is also additional uncertainty surrounding potential selectivity

in consumption of either detritus or the bacteria feeding on detritus, providing additional challenges for model balancing based on largely unknown parameters. By allowing only bacteria to consume detritus we have, in effect, reduced our uncertainty surrounding bacterial and detrital parameters to one trophic group (bacteria) whilst still including detritivory in the model.

The role of kelp-derived detritus (or particulate organic material) has been studied in other systems, showing that kelp-derived carbon (organic detritus) is taken up into the coastal food web via bacteria and is consumed by benthic suspension feeders (Newell & Field 1985; Duggins et al. 1989). Other studies have shown that there are gradients in intertidal productivity and nutrient concentrations (Bustamante & Branch 1995, 1996), and measurements suggest that 65–70% of the intertidal POM is kelp-derived (Newell & Field 1985; Bustamante & Branch 1996). In the study area, there was no information available to estimate the total contribution to the food web of macroalgal-derived detritus. However, given the high production and biomass of macroalgal trophic groups, we need to gain a better understanding of the fate of kelp-derived detritus. In the future, stable isotope samples within the study area would help to elucidate the exact contribution of kelp-derived detrital material to diets of various trophic groups versus the contribution via direct consumption of macroalgae by grazers. However, at this point we could only include the role of kelp and kelp-derived detritus indirectly, by allowing direct consumption of macroalgae, as well as bacterial consumption of macroalgal detritus (drift algae) and particulate organic matter (via bacterial consumption on the detritus trophic group), which are then transferred into other trophic groups via consumption of bacteria.

4.2 BACTERIA

Many coastal trophic models do not explicitly include either benthic or water column bacteria as separate trophic groups, because bacterial biomass, production and consumption are generally poorly known (e.g. Jarre-Teichmann et al. 1997; Arreguin-Sanchez et al. 2002; Rybarczyk & Elkaim 2003; Jiang & Gibbs 2005). We discuss estimates from the literature for both water column and benthic bacteria separately. However, due to uncertainty in estimation of biomass, production and consumption of water column and benthic bacteria in the model region, we combine both categories of bacteria into one trophic group.

4.2.1 Benthic bacteria

No measurements of benthic bacterial biomass and production are available for the study area. It is likely that benthic bacterial biomass and productivity will vary with season and depth, due to variation in detrital supply to the benthos from the water column as a result of changes in the production of both pelagic primary producers (e.g. phytoplankton) and benthic producers (e.g. kelp-derived detritus, as discussed in section 4.1) in the water column. Bacterial biomass on the Chatham Rise was estimated to be about $1.5\,g\,C/m^2$ to a sediment depth of 15 cm (M. Pinkerton, NIWA, unpubl. data). These measurements did not take into account the proportion of the total bacterial biomass that is viable.

There is considerable variation in measurements of annual P/B ratios of benthic bacteria in the literature. Productivity per unit biomass of bacteria depends on whether only viable (actively producing) bacteria or all bacteria (i.e. including cells in a quiescent state) are included. Earlier work (Ankar 1977; Sorokin 1981; Feller & Warwick 1988) suggested that annual P/B ratios of benthic bacteria are likely to lie between about 20/y and 150/y, with 55/y as an average value. Net growth efficiency (P/Q) for water column and benthic bacteria is typically taken as 0.3 (e.g. Pomeroy 1979).

4.2.2   Water column bacteria

There are no local measurements of bacterial biomass in the water column. Bacterial biomass in subantarctic offshore waters of the Southern Plateau, New Zealand, were estimated to be $0.6\,g\,C/m^2$, with $P/B = 87/y$ and $Q/B = 380/y$ (Bradford-Grieve et al. 2003). Bacteria biomass in New Zealand west coast shelf waters ($< 200\,m$ deep) was $1.0\,g\,C/m^2$ (Probert 1986). In another coastal ecosystem model in northern Chile, water column bacterial production (P/B) was estimated as 100–400/y (Wolff 1994).

4.2.3   Summary—Bacteria

To represent combined benthic and water column bacteria, we used starting values of $B = 0.6\,g\,C/m^2$, $P/B = 100/y$ and $Q/B = 400/y$. Typically, Ecopath users allow the model to determine bacterial biomass during the balancing process.

4.3   PHYTOPLANKTON

Phytoplankton biomass and net primary production were estimated using satellite measurements of ocean colour to estimate near-surface chlorophyll-*a* concentration.

4.3.1   Surface chlorophyll concentration

We used satellite measurements of ocean colour to estimate near-surface chlorophyll-*a* concentration in the mixed-layer (Hooker et al. 1992). Daily measurements of ocean colour taken by the SeaWiFS satellite at Global Area Coverage (GAC) resolutions of 1 km and 4 km were processed at NIWA using SeaDAS v4.4 (Fu et al. 1998; Murphy et al. 2001). Preliminary validation studies indicated that the algorithm used (OC4v4) gave estimates of chlorophyll-*a* that were accurate within approximately 30% of the value measured by *in situ* methods in this region (Richardson et al. 2002). Since satellite data can be unreliable within 1 km of the coast, especially where there are considerable concentrations of suspended sediment in the water column that can lead satellite sensors to overestimate chlorophyll concentration, we took satellite concentrations from a large box offshore from the marine reserve where suspended sediment concentrations were likely to be low. We also used the median chlorophyll concentration rather than the mean value to reduce the influence of a few high values. The box extent was 38°36.5′S to 38°47.5′S, and 178°13′E to 178°27′E, corresponding to c. $20\,km^2$ (Fig. 4).

Figure 4. Example of 1-km-resolution surface chlorophyll-*a* concentrations from the SeaWiFS ocean colour sensor over an annual cycle. The white boxes indicate the region from which data were extracted.
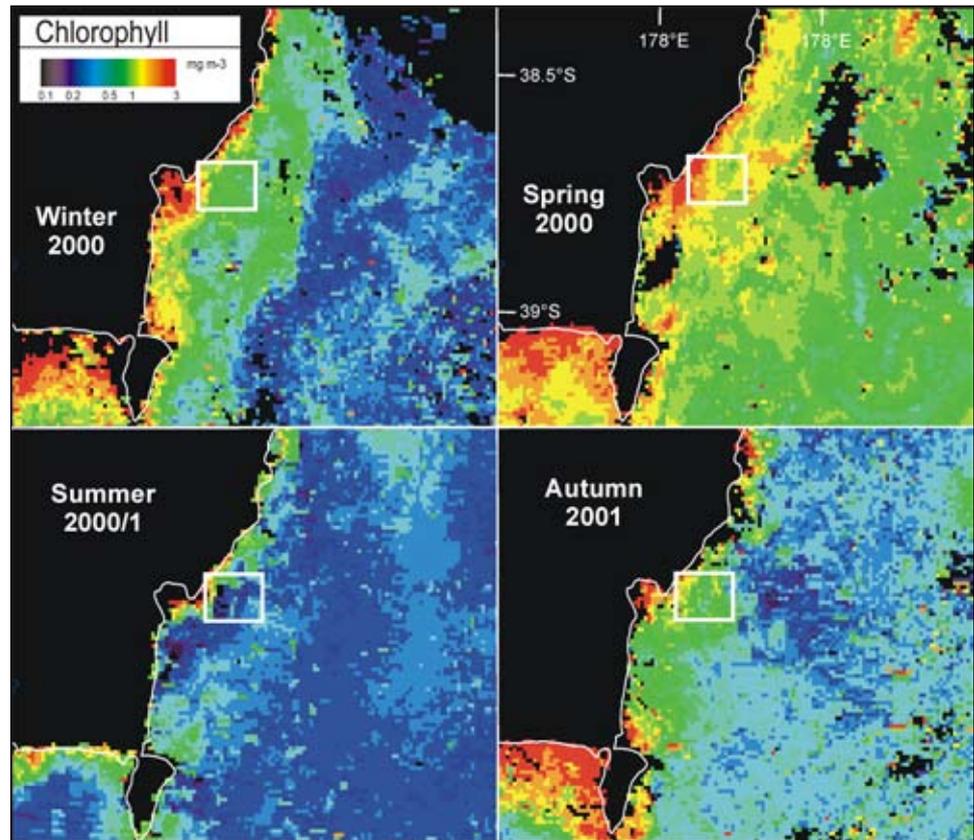
Surface chlorophyll-*a* concentrations within the box offshore from Te Tapuwae o Rongokako Marine Reserve showed a seasonal cycle (Fig. 5), with peaks of chlorophyll in the spring (1.5 mg Chl-*a*/m^3) and autumn (0.7 mg Chl-*a*/m^3). Chlorophyll-*a* concentrations in the winter and summer were typically lower (0.3–0.5 mg Chl-*a*/m^3). Since phytoplankton abundance shows a log-normal distribution in space and time, log averages (geometric means) are often used to obtain long-term typical values of chlorophyll concentration. Hence, we determined that the appropriate annual (log) average chlorophyll concentration in the water column in the offshore area near the reserve is of the order of 0.47 mg Chl-*a*/m^3.

Figure 5. Seven years of measurements of chlorophyll-*a* concentration in the box offshore from Te Tapuwae o Rongokako Marine Reserve, taken from measurements of ocean colour by the SeaWiFS satellite sensor. Median values are shown.
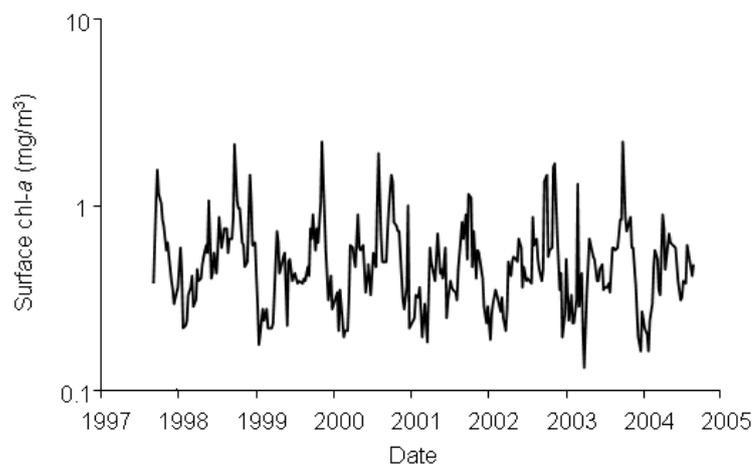
Note that it is possible that phytoplankton biomass, chlorophyll concentration and phytoplankton primary production are different nearer the shore than offshore for a number of reasons:

- Average light levels received by the phytoplankton in the water column may be higher in shallower than deeper waters, even allowing for the fact that higher suspended sediment concentrations near-shore may result in greater light attenuation than offshore. We corrected for this effect as described below in section 4.3.3.

- Nutrients recycled from the sea floor may be available to phytoplankton in the water column. We have no information on this, but the effect is likely to be relatively small.

- Macronutrient (nitrate, phosphate, silicate) input from land run-off may result in higher production than in offshore waters. However, Close & Davies-Colley (1990) characterised rivers in the vicinity of the reserve as having relatively low nutrient loads ($< 100\,\text{mg/m}^3$ nitrate).

- Grazing pressure/predation on phytoplankton may be different by region. There are no data available to compare grazing rates of phytoplankton between the reserve and offshore region, but we assume that this effect is small.

Note that there is likely to be significant mixing and exchange of water inside and outside the reserve, which will mitigate these differences. We compared ocean colour satellite data in inshore regions to the north of the reserve with values further offshore. These comparisons suggested that surface chlorophyll concentrations near the coast may be approximately 1.5–3 times higher than those corresponding to the offshore box. However, the near-shore measurements to the north of the reserve are likely biased high due to the presence of suspended sediment. In the absence of direct measurements of phytoplankton productivity or biomass in Te Tapuwae o Rongokako Marine Reserve, we propose here to assume that near-surface chlorophyll concentrations in the water column in the reserve are similar to those offshore in the adjacent area.

4.3.2 Water column phytoplankton biomass

Three factors are taken into consideration to convert surface chlorophyll concentration (mg Chl/m^3) to phytoplankton biomass (g C/m^2):

1. **Total depth of water:** The average depth in Te Tapuwae o Rongokako Marine Reserve is calculated to be 11 m.

2. **Distribution of phytoplankton vertically through the water column:** There are no vertical measurements of chlorophyll or water column structure in the study region. In shallow coastal waters with limited freshwater inflow like the study region, it is unlikely that there is persistent vertical stratification. Thus, we assumed phytoplankton was uniformly distributed over the whole depth.

3. **Carbon-to-chlorophyll ratio for phytoplankton:** The ratio of carbon to chlorophyll-*a* in marine phytoplankton has been found to vary considerably, from 20 to $> 200\,\text{g C/g Chl-}a$ (Taylor et al. 1997; Lefevre et al. 2003). In subtropical waters near New Zealand, work suggests a seasonal variation in C:Chl-*a* values of approximately 50 before the spring bloom, 40 during the spring bloom, and 60 after the bloom (Boyd 2002; P. Boyd, NIWA, unpubl. data). A linear interpolation between these latter values was used to estimate C:Chl-*a* ratios through the year.

Applying these three factors to the satellite data gave an annual average phytoplankton biomass of $0.24\,g\,C/m^2$, with an estimated range of uncertainty of about 0.12–$0.48\,g\,C/m^2$.

4.3.3 Net primary production

Carbon fixation by phytoplankton (net of respiration) will be termed net primary production (NPP). This was estimated using the model of Behrenfeld & Falkowski (1997), which has been applied to the subtropical open-ocean waters east of the North Island. As with phytoplankton biomass, the relationship between phytoplankton production close inshore (in the marine reserve) and offshore in the oceanic waters is not known. It is likely to be affected by nutrient run off from the land, suspended sediment in the water column and the shallowness of the bathymetry, as discussed above. As the impacts of these factors are unknown, we assume here that their combined effect is small, although we have no way of testing this. If, however, the modelling indicates that phytoplankton play a significant role in the trophic dynamics of the ecosystem, it would be useful to start measuring a time-series of phytoplankton biomass and primary production in the region.

In the open ocean model of Behrenfeld & Falkowski (1997), chlorophyll-*a* concentration was obtained from SeaWiFS measurements of ocean colour, as described above. Sea-surface temperature and estimates of cloud cover were obtained from AVHRR satellite data. Mixed-layer depth was estimated based on climatological data from the CSIRO 'Atlas of Regional Seas' (Dunn & Ridgway 2002; Ridgway et al. 2002). Data were composited to give daily estimates of carbon fixation at 4-km resolution. Model estimates of assimilation rates (water column integrated photosynthesis per unit surface chlorophyll concentration) were calculated and compared with *in situ* measurements of net primary production that were made at 54 stations within c. 80 km of the coast off the East Cape in January 1978 using the ^{14}C uptake method (Strickland & Parsons 1972; Bradford et al. 1982). Daily net production rates were estimated from measurements of hourly production by scaling based on modelled incident irradiance (Kirk 1994; Behrenfeld & Falkowski 1997). We assume that significant primary production only occurs over the euphotic zone; that is, where scalar irradiance in the water column is greater than 1% of the surface value (Kirk 1994). *In situ* measurements in the summer yielded a median assimilation rate of 970 $(mg\,C\,d^{-1}\,m^{-2})\,(mg\,Chl\text{-}a\,m^{-3})^{-1}$ with a wide interquartile range of 360–1400 $(mg\,C\,d^{-1}\,m^{-2})\,(mg\,Chl\text{-}a\,m^{-3})^{-1}$. Variability in assimilation numbers is expected, as primary productivity fluctuates on short time and space scales due to variation in incident light and local nutrient availability. The open-ocean production model of Behrenfeld & Falkowski (1997) gave assimilation numbers in the summer that were c. 2.8 times higher than the *in situ* values measured here. Therefore, the model values were reduced by this factor to give Fig. 6.

Two further effects were also considered when using offshore values to estimate net primary production by phytoplankton in Te Tapuwae o Rongokako Marine Reserve. First, the depth of production is much less near the shore, because the depth of water (10 m) is less than the depth of the photic zone (c. 50 m). Second, average light levels in the photic zone will tend to be greater in shallow waters than in deep waters. Bio-optical work by NIWA in many regions around
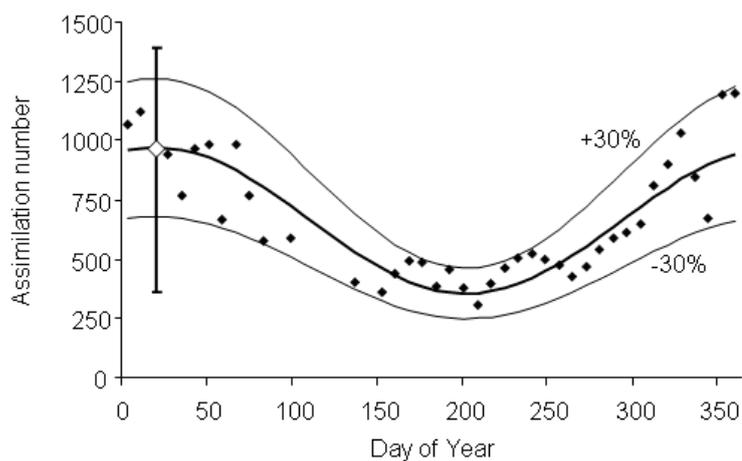
Figure 6.   Assimilation numbers (water column integrated photosynthesis per unit surface chlorophyll concentration ($mg\,C\,d^{-1}\,m^{-2}$) ($mg\,Chl\text{-}a\,m^{-3}$)$^{-1}$ for the area immediately offshore from Te Tapuwae o Rongokako Marine Reserve. The open diamond and error bars indicate the 25th–75th percentile range for assimilation numbers measured in 1976 (Bradford et al. 1982). The black diamonds show modelled net primary production during the year 2000 (Behrenfeld & Falkowski 1997), which have been scaled to reconcile them with *in situ* measurements. A sinusoid was fitted to these values, and the ±30% ranges are shown (solid lines).

New Zealand since 1999 has shown that for surface Chl-*a* concentrations of $0.2\text{–}1\,mg\,Chl/m^3$ (mean $0.47\,mg\,Chl/m^3$), the diffuse attenuation coefficient for scalar photosynthetically-active radiation (PAR) will be in the range of 0.09–0.18/m (mean 0.12/m) (M. Pinkerton, NIWA, unpubl. data). This implies that the available light in the inshore region will be c. 4.2–6.2 times greater than that at the midpoint of the offshore photic zones, the exact amount depending on phytoplankton concentration. However, if there is suspended sediment in the marine reserve, this will reduce the light available for photosynthesis. Therefore, if we assume that attenuation by sediment is approximately as great as that by phytoplankton in the reserve area, the light available for photosynthesis will be about 1.8–3.9 times higher than offshore, with the corresponding increase in production. Applying these factors to the values of net primary production estimated by the model for the offshore region, we estimated that annual (log) average net primary production in Te Tapuwae o Rongokako Marine Reserve will be c. $40\text{–}130\,g\,C\,m^{-2}\,y^{-1}$, with a best estimate of c. $78\,g\,C\,m^{-2}\,y^{-1}$ (Fig. 7).

Figure 7.   Net primary production by phytoplankton in Te Tapuwae o Rongokako Marine Reserve, based on modelled data as described in the text.
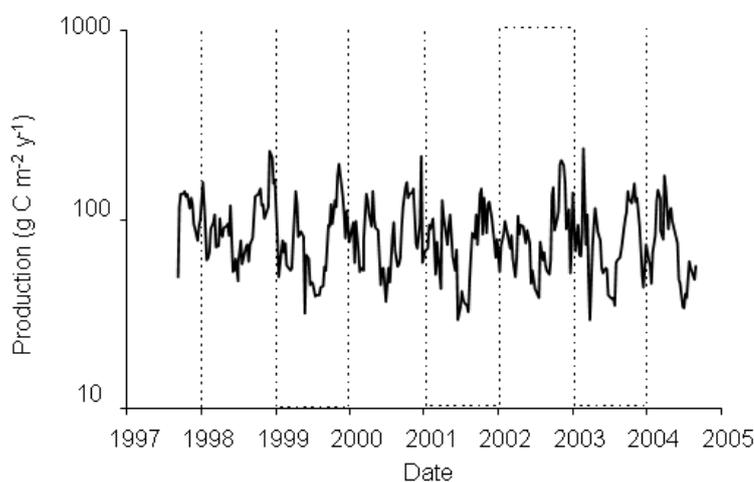
This value of net primary production by phytoplankton is somewhat less than was measured offshore by Bradford-Grieve et al. (1997), who reported values of $360\,g\,C\,m^{-2}\,y^{-1}$ during spring in the Subtropical Front. This difference is reasonable, given the range of uncertainty related to the factors explained above.

4.3.4 Production to biomass ratio

The values given above lead to an annual P/B of 320/y, which corresponds well with values for phytoplankton net primary production in the literature (e.g. 250/y; Bradford-Grieve et al. 2003).

4.3.5 Summary—Phytoplankton

In summary, based on satellite data from the period 1997–2004, we made the following estimates for marine phytoplankton in Te Tapuwae o Rongokako Marine Reserve:

- Annual average phytoplankton biomass: $0.12–0.48\,g\,C/m^2$, with a best estimate of $0.24\,g\,C/m^2$.
- Phytoplankton production (net of respiration): $40–130\,g\,C\,m^{-2}\,y^{-1}$, with a best estimate of about $80\,g\,C\,m^{-2}\,y^{-1}$.
- Production:biomass ratio (P/B): 320/y.

4.3.6 Further work

To significantly improve these estimates of biomass and phytoplankton productivity for Te Tapuwae o Rongokako Marine Reserve, a time series of *in situ* measurements is required. The first priority would be to sample chlorophyll-*a* concentration in the surface water at regular intervals for more than 1 year. Since phytoplankton abundance seems to be highly variable from week to week, at least one sample per week would be required. It is possible to re-estimate chlorophyll-*a* concentration within 2 km of the coast by reprocessing the ocean colour data using an algorithm to account for the presence of sediment. However, the accuracy of these data would be questionable without *in situ* bio-optical measurements to characterise the properties of the sediment in the region.

The primary productivity model used in this work (Behrenfeld & Falkowski 1997) was developed for deep oceanic waters, and its accuracy in shallow coastal regions has not been tested. Therefore, it would be useful to obtain monthly (or preferably weekly) measurements of phytoplankton primary production close to Te Tapuwae o Rongokako Marine Reserve using the ^{14}C method to check the values estimated by the model.

We expect that the majority of primary productivity in Te Tapuwae o Rongokako Marine Reserve will be due to macroalgae rather than phytoplankton in the water column, and that phytoplankton biomass will play a minor role as a food source in the reserve. If this is true, our estimates of phytoplankton biomass and productivity presented here will be sufficiently accurate for our purposes. Phytoplankton biomass (as per the above calculations from satellite data) was estimated to be less than 1% of the total biomass of all primary producers (see model results for macroalgae). In contrast, production rates of phytoplankton were estimated to be 1–2 orders of magnitude higher than production rates for other primary producer groups.

4.4 MICROPHYTOBENTHOS AND EPIPHYTAL ALGAE

This trophic group is made up of two components: microphytobenthos on soft sediment, and epiphytic macrophytes and microphytes on macroalgae. We combine these groups, as they have similar high rates of production and are consumed at high rates by grazers. There is little to no information on any of these categories for Te Tapuwae o Rongokako Marine Reserve. Therefore, we used values from the literature to make estimates for each, as described below.

4.4.1 Microphytobenthos

At other locations in New Zealand, benthic microalgal biomass (microphytobenthos) has been measured as sediment Chl-*a* through both spectrophotometry and taxonomic composition via pigment analysis (Gillespie et al. 2000; Cahoon & Safi 2002). In Tory Channel, Marlborough Sounds, at depths of 6–20 m, chlorophyll biomass ranged from 20 to 200 mg Chl-*a*/m^2 in sediment (Gillespie et al. 2000). In Manukau Harbour, sediment Chl-*a* biomass was estimated to be 11.8–340 mg Chl-*a*/m^2 (weighted average 62.5 mg Chl-*a*/m^2) (Cahoon & Safi 2002). Comparing different soft-sediment habitats in Manukau Harbour, average values (mg Chl-*a*/m^2) were: mud, 32.7; sandy mud, 61.2; muddy sand, 121.2; sand, 98.6; and shelly sand, 82.6 (Cahoon & Safi 2002). To convert these Chl-*a* biomass estimates into microalgal biomass estimates (g C), we used a conversion rate of 25:1 g C : g Chl-*a* (Parsons et al. 1984), which suggested a typical microphytobenthos biomass of about 2 g C/m^2 for the sandy sediments. Since soft sediment makes up c. 80% of the study region, we estimated a microphytobenthos biomass of 1.6 g C/m^2 for the soft-sediment areas within the study region.

In Tory Channel, primary production from soft-sediment microphytobenthos was measured as 0.20 g C m^{-2} d^{-1} or 73 g C m^{-2} y^{-1} at a depth of 20 m (Gillespie et al. 2000), implying a P/B of c. 40/y. Although microphytobenthos net primary production has been estimated at higher levels of 1.880, 1.035 and 0.259 g C m^{-2} d^{-1} beneath mussel farms in Tasman Bay (Christensen et al. 2003), these higher productivities are unlikely to apply to Te Tapuwae o Rongokako Marine Reserve region. Therefore, we use the estimated value of 40/y for the microphytobenthos in the study region.

4.4.2 Epiphytic algae (macrophytes and microphytes)

Epiphytes on macroalgae include both larger species of erect epiphytic macrophytes and microphytes (periphyton). International studies have shown high grazing pressure on these epiphytes relative to their host algae or seagrass; thus, epiphytes are an important primary producer group within our trophic model (D'Antonio 1985; Smith et al. 1985; Klumpp et al. 1992). Although there are no available data on epiphyte biomass on macroalgae in the study area, we estimate that relationships between epiphytes and macroalgae are of a similar order of magnitude to those found in seagrass (see also section 4.7.2). Epiphyte biomass in a temperate seagrass meadow in Washington, USA, has been measured at up to 67% (mean 13%) of total seagrass biomass (Nelson & Waaland 1997). Tropical seagrass communities in the Phillipines have also shown high biomass of epiphytes, with 598–1061 mg ash-free dry weight (AFDW)/m^2 or 244–646 mg C/m^2 bottom habitat; or 0.16–0.24 mg AFDW/cm^2 seagrass frond (Klumpp et al. 1992). Assuming epiphytic loads are smaller on macroalgae, as macroalgae have higher growth

rates, we estimated that ephiphyte biomass is conservatively c. 50% of that of measured temperate seagrass epiphytes (mean 13%), or 5% of the total biomass of macroalgae summed over the three macroalgal trophic groups.

Epiphyte production was estimated for a *Zostera marina* seagrass meadow in Washington, USA, during two separate years of study as 577 and 291 g C/m², or approximately 14% and 25%, respectively, of total productivity of the seagrass meadow; the same study estimated a P/B of approximately 14/y (Nelson & Waaland 1997). Based on this estimate, epiphytal biomass in our study area has an annual production of approximately $100 \, g \, C \, m^{-2} \, y^{-1}$ for an epiphytic algal community consisting of 5% of the total biomass of macroalgae. Since this appears to be a plausible estimate of productivity of macroalgal epiphytes, we estimated a P/B of c. 14/y for the epiphytes in the study region. This seems logical if our epiphytes are dominated in terms of biomass by larger foliose epiphytic algae.

Clearly, it would be useful to have better data for this group to define parameters for a trophic model, as we might expect a much higher P/B if epiphytes were dominated in terms of biomass by the smaller, highly productive periphyton. For example, Booth (1986) reported that the photosynthetic rates of epiphytic diatoms were 45–68 times greater per unit volume than their macroalgal hosts *Carpophyllum maschalocarpum* and *C. flexuosum*, and estimated that epiphytic diatoms contributed 6–8% of the total primary productivity to the host-epiphyte association (Booth 1986).

4.4.3 Summary—Microphytobenthos and epiphytal algae

To calculate average biomass for this trophic group, we summed biomass over both epiphytic algae and microphytobenthos. We estimated a microphytobenthos biomass of 1.6 g C/m² and P/B of 40/y, and an epiphytic algae biomass (including macrophytes and microphytes) of 5% of the total macroalgal biomass (calculated in section 4.5) and P/B of 14/y. Summing biomass of these groups gave an estimate of 8.52 g C/m². A weighted average of production across relative biomass of these groups gave a P/B of 21.0/y.

4.5 MACROALGAE

4.5.1 Biomass

Macroalgae were divided into three trophic groups on the basis of structural attributes:

1. Large brown, canopy-forming species, e.g. *Ecklonia radiata* (kelp), *Carpophyllum flexuosum* and *C. maschalocarpum*.

2. Foliose and turfing red and green algae, and brown non-canopy species. Subtidal surveys of the region have shown that common foliose species include red algae such as *Pterocladia lucida*, *Laurencia thyrsifera*, *Melanthalia abscissa*, *Osmundaria colensoi*, *Phacelocarpus labillardieri* and *Plocamium* spp.; brown algae including *Zonaria turneriana*, *Halopteris* sp., *Carpomitra costata* and *Glossophora kunthii*; and the green alga *Caulerpa geminata* (Shears & Babcock 2004b). Turfing red and brown algae are also common understorey species.

3. Crustose and coralline algae, which are common understorey species.

Transect surveys across northeastern North Island provided subtidal abundance estimates by habitat type for four algal species/groups (*Ecklonia radiata*, *Carpophyllum* spp., *Carpophyllum flexuosum* and other large brown algae) and percentage cover estimates for red foliose algae, turfing algae, crustose algae (including coralline turfs) and *Caulerpa* spp. (a green foliose alga) (Table 4) (Shears et al. 2004). We used the percentage cover estimates by habitat type to estimate subtidal biomass of other algal species. The abundance and percentage cover estimates were extrapolated over all habitat types in the model area using triangulation, as outlined in section 3.2.2 (Fig. 8A–H). Our habitat mapping extrapolation gave similar density estimates to the depth transects in the Gisborne area (N. Shears, Auckland University, unpubl. data), which gave a mean of 8.9 individual *Ecklonia*/m^2 for four sites, averaged over all depths. Recorded numbers of *Carpophyllum* spp. from depth transects were highest at shallow subtidal depths, with a maximum recorded in Gisborne depth transects of 130 individuals/m^2 *Carpophyllum maschalocarpum*.

Percentage cover and presence of common species of intertidal algal species were recorded during intertidal monitoring surveys of the marine reserve. Intertidal reef areas were dominated by turfing coralline algae, and also included the small brown alga *Hormosira banksii*, and the large brown algae *Cystophora torulosa* and *C. retroflexa* (Table 6). Bare or other unvegetated categories made up on average c. 25% of the intertidal reef in the reserve.

For canopy algae, average densities (individuals/m^2) combined over all habitats were converted into wet weights using length-weight relationships from Shears & Babcock (2004b) (Table 8). We calculated average plant lengths and ash-free dry weights (AFDW) averaged across all habitats using size-frequency measurements of *Ecklonia radiata*, *Carpophyllum maschalocarpum*, *C. flexuosum* and *Sargassum sinclairii* (other large brown algae) from transects taken within the study region (Shears & Babcock 2004b). Dry weight estimates were converted into AFDW by multiplying them by 0.91, based on the assumption that the proportion of CaCO$_3$ and inorganic materials is c. 9% of the dry weight of New Zealand algal species (R.B. Taylor, University of Auckland, unpubl. data, as cited in Shears & Babcock 2004b) (Table 8). Additional length-weight relationships for algal species not common in the study area can be found in Appendix 3 of Shears & Babcock (2004b). Where multiple relationships were available, we used relationships based on data from the closest location to the study area; most often these were from northeastern New Zealand, and more specifically the Hauraki Gulf.

For non-canopy algal groups, percentage cover-biomass (dry weight) relationships for algae were estimated from relationships available in Shears & Babcock (2004b) (Table 8), which were obtained by drying algal samples at 80°C for 3 days and weighing final samples (Shears & Babcock 2004b).

For intertidal habitats, we converted average percentage cover of intertidal algal species to AFDW using conversions described below (averaged across the foliose/turfing and crustose/coralline macroalgal groupings), and extrapolated biomass to the total intertidal reef area. For intertidal large brown algae, there was no information available on conversions from percentage cover to biomass or on average length of the primary species (*Cystophora torulosa*, *C. retroflexa* and *Hormosira banksii*) from the subtidal Gisborne surveys (Shears & Babcock
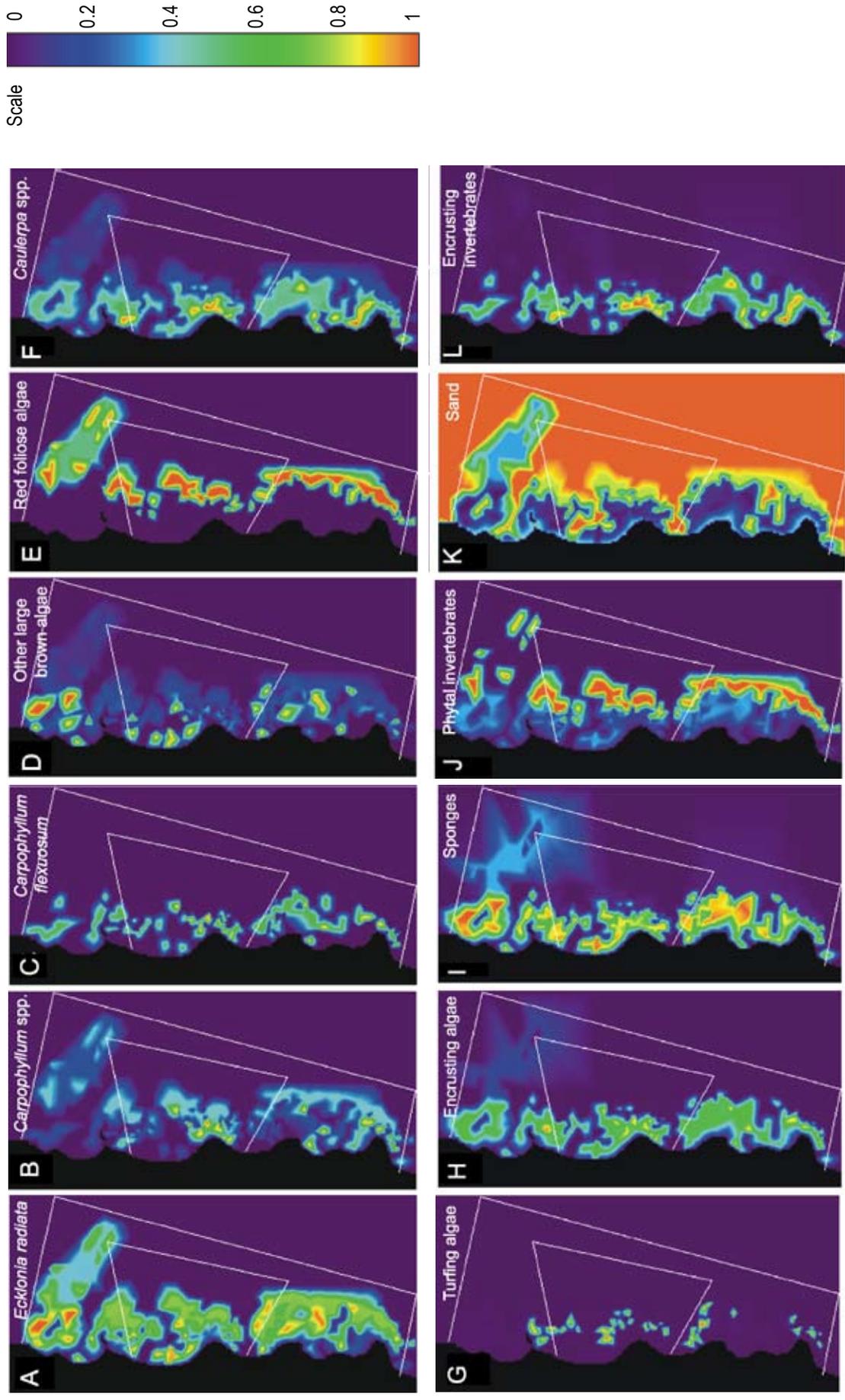
Figure 8. Spatial distribution of selected taxa over the study region obtained by triangulation of data as explained in the text. Each plot is scaled according to the colour bar shown at the right-hand side of the figure. Maximum values for each taxon correspond to red on the colour bar; blue and purple colours indicate lower estimated values. To aid interpretation of values, we plotted density of individuals for large canopy-forming macroalgae; percentage cover for foliose and encrusting macroalgae, encrusting invertebrates, and sediment; and wet weight for phytal invertebrates, as described for each taxon in the text. Maximum values are as follows: A. *Ecklonia radiata* (0–8.9/m²); B. *Carpophyllum* spp. (0–87.7/m²); C. *Carpophyllum flexuosum* (0–3.0/m²); D. other large brown algae (0–11.6/m²); E. red foliose algae (0–20.0% cover); F. *Caulerpa* spp. (0–30.4% cover); G. turfing algae (0–15.7% cover); H. encrusting algae (0–66.8% cover); I. sponges (0–14.5% cover); J. soft sediment and/or sand (0–100% cover); K. phytal invertebrates (0–35.3 g WW/m²); L. encrusting invertebrates (0–19.2% cover). The white lines indicate the reserve area and larger study region used here.

TABLE 8.   LENGTH-DRY WEIGHT AND/OR PERCENTAGE COVER-DRY WEIGHT
RELATIONSHIPS FOR MAJOR ALGAL SPECIES AND GROUPS.

All values were obtained from Shears & Babcock (2004b), except for *Xiphophora gladiata*, which
was reported in Shears & Babcock (2007). y = dry weight (g), x = total length (cm), SL = stipe length
(cm), LL = laminae length (cm). LB = Long Bay, CR = Cape Reinga, MKI = Mokohinau Islands,
Bligh = Bligh Sound. Percentage cover estimates based on 1% of a 1-m^2 quadrat.

GROUP/SPECIES	EQUATION	COLLECTION SITE
Large brown		
Ecklonia radiata	$\ln(y) = 2.625\ln(x) - 7.885$	CR
Stipe	$\ln(y) = 1.671\ln(SL) - 3.787$	Leigh
Remainder	$\ln(y) = 1.177\ln(SL*LL) - 3.879$	Leigh
Carpophyllum flexuosum	$\ln(y) = 1.890\ln(x) - 4.823$	LB
Carpophyllum maschalocarpum	$\ln(y) = 2.078\ln(x) - 5.903$	LB
Sargassum sinclairii	$y = 0.075x + 0.124$	CR
Xiphophora gladiata	1% = 58.8 g	Bligh
Small brown		
Zonaria turneriana	1% = 2.48 g	MKI
Green foliose		
Caulerpa flexilis	1% = 5.81 g	MKI
Codium convolutum	1% = 4.68 g	MKI
Ulva spp.	1% = 1.71 g	MKI
Red foliose		
Osmundaria colensoi	1% = 22.93 g	MKI
Pterocladia lucida	1% = 10 g	Leigh
Red turfing	1% = 1.74 g	MKI
Brown turfing	1% = 1.74 g	MKI
Coralline turf*	1% = 1.5 g	MKI
Crustose corallines*	1% = 0.35 g	Leigh

*   The proportion of CaCO$_3$ in *Corallina officinalis* has been estimated as 45% of the dry weight.
     Therefore, the value given is 55% of the total dry weight.

2004b). Instead, we used the percentage cover-weight relationship for a
species with similar size and morphology, *Xiphophora gladiata* (1% = 58.8 g)
(Shears & Babcock 2004b) to convert percentage cover of the three primary
intertidal algal species to biomass.

Calorific contents of common New Zealand algal species are available to convert
biomass (AFDW) estimates to energy currencies for some New Zealand macroalgal
species (Table 9) (Lamare & Wing 2001). Using average biomasses for our trophic
groupings based on Paine & Vadas (1969), we estimated mean calorific contents
of 4.53 kcal/g AFDW for Chlorophyta (green algae), 4.50 kcal/g AFDW for
Phaeophyta (brown algae), 4.71 kcal/g AFDW for foliose and turfing Rhodophyta
(red algae), and 3.73 kcal/g AFDW for coralline Rhodophyta.

To convert kcal to J to mg C, we used the following: 1 kcal = 4186.6 J; and
1 mg C = 45.7 J. On average for macroalgae, this gives 1 g (AFDW) as equivalent
to 0.38 g C (± 26%).

TABLE 9. ENERGY CONVERSIONS FOR 28 NEW ZEALAND ALGAL SPECIES (LAMARE & WING 2001).
Conversions from kcal to g carbon are explained in the text.

SPECIES	kcal/g AFDW	kcal/g WW	SPECIES	kcal/g AFDW	kcal/g WW
Chlorophyta			**Rhodophyta**		
Bryopsis sp.	4.37	0.48	*Carpomitra costata*	4.17	–
Caulerpa brownii	3.88	1.56	*Corallina officinalis*	4.97	0.58
Codium fragile	3.83	0.13	*Euptilota formosissima*	4.52	–
Enteromorpha sp.	4.14	0.91	*Gigartina decipiens*	3.03	0.59
Ulva lactuca	3.96	0.62	*Gigartina* sp.	3.88	0.39
Phaeophyta			*Lenormandia chauvinii*	3.99	0.70
Cystophora scalaris	5.18	0.59	*Pachymenia lusoria*	3.80	0.71
Cystophora tortulosa	3.76	0.36	*Plocamium* sp.	4.26	–
Durvillaea antartica	3.64	0.51	*Polysiphonia* sp.	4.54	0.29
Ecklonia radiata	4.58	0.41	*Stictosiphonia hookeri*	3.68	0.85
Halopteris funicularis	4.00	–			
Hormosira banksii	4.08	0.39			
Lessonia variegata	3.37	0.32			
Macrocystis pyrifera	3.67	0.42			
Marginariella sp.	4.66	0.42			
Scytosiphon lomentaria	4.12	0.43			
Undaria pinnatifida	4.14	0.79			
Xiphophora gladiata	3.74	0.53			
Zonaria turneriana	4.80	1.75			

4.5.2 Production

We discuss three ways to estimate macroalgal production. While we only used one of these in our parameter estimates, we present all three methods and their likely biases, as differences in available data for other researchers may allow only one of the three methods to be used.

1. Stipe elongation rates

For *Ecklonia radiata* only, we calculated growth rate based on a typical stipe elongation rate of 5–10 cm per month in northern North Island waters at depths of less than 15 m (Schiel 2005). Using raw data on stipe and total length of *E. radiata* from subtidal Gisborne surveys (Shears & Babcock 2004b), we estimated annual plant growth assuming monthly growth rates of 7.5 cm of stipe tissue per individual plant. By converting to carbon using length-weight relationships for *E. radiata* (Table 8; Shears & Babcock 2004b), we estimated an annual P/B of 1.0/y for *E. radiata*. This will be a minimum estimate for P/B, as it does not include production lost as exudates from the surface of the plant, or elongation of the laminae. Similar estimates of production based on growth of *E. radiata* have calculated annual production rates of 3.1 kg dry weight (DW) m^{-2} y^{-1} (Larkum 1986) and 20.7 kg wet weight (WW) m^{-2} y^{-1} (= approximately 1.9 kg DW m^{-2} y^{-1}) (Kirkman 1984) for Australian sites. Growth rates measured at Leigh showed production of up to 6 kg DW m^{-2} y^{-1} at 7 m depth and 0.3–0.5 kg m^{-2} y^{-1} at 15 m depth, with the expectation that at least half of this tissue and an unknown amount of exudates will be sloughed or torn off (Novaczek 1984). The similarity of our values to those of other studies gives us

confidence in the use of stipe elongation rates for measuring production rates of *Ecklonia radiata*. Disadvantages of the stipe elongation method include lack of seasonal variation in growth rates such as spring growth pulses and lower growth rates in winter, a lack of differentiation between growth rates of stipes and blades, and inability to differentiate between net growth and tissue lost as exudates.

2. *Monthly growth measurements*

A second method allows the use of seasonal or monthly values, extrapolated over a calendar year to generate an annual average production. Here we use a dataset measuring the growth rate of giant kelp (*Macrocystis pyrifera*) in Paterson Inlet (Stewart Island/Rakiura, New Zealand) to illustrate how incorporating seasonal variability in growth changes estimates of annual production (J. Holborow, DOC, unpubl. data). These data showed a strong spring pulse of growth of c. $3.7\,g\,C\,m^{-2}\,d^{-1}$, with lower growth ($<0.5\,g\,C\,m^{-2}\,d^{-1}$) during the rest of the year. We calculated total annual production by integrating monthly values over the year. By extrapolating these values to large brown canopy species (*Ecklonia radiata*, *Carpophyllum* spp.) found in our study area, this method suggested an annual average production to biomass ratio (P/B) of approximately 1.4/y. Again, this method will result in a biased low estimate as it measures only growth, not production of exudates.

3. *Net production measurements*

We believe this third method, which calculates net production (photosynthesis minus respiration), is the most accurate, though most time-consuming method, to estimate production. Unlike methods 1 and 2, it incorporates material lost as exudates, which is a potentially large input of primary productivity into the ecosystem. Net production has been estimated for many common New Zealand species (Taylor et al. 1999; Shears & Babcock 2004a) (Table 10), and can be extrapolated across other species for which direct measurements are not available. To estimate net production for each trophic group, we used literature values of photosynthesis and respiration for available algal species to calculate a regression of respiration on photosynthesis (Respiration $= 0.0577 *$ Photosynthesis $+ 7.0549$). This then allowed us to estimate respiration for many species for which we lacked data. For each macroalgal species, average daily production was taken as 0.64 of the peak net production, based on the assumption that diel variation in photosynthesis will vary in the same way as incident irradiance, i.e. approximately as a half-sinusoid. Since for most species there is no information available about variation in light penetration or shading based on depth or habitat type, we assumed similar production rates across depth, and between subtidal and intertidal algae. For each algal trophic group, we averaged available species information, using a weighted average based on each species' relative percentage composition of total biomass in the group. We converted $mol\,O_2$ to $mg\,O_2$ to $mg\,C$, as follows: $1\,mmol\,O_2 = 32.6\,mg\,O_2$; and $1\,mg\,O_2 = 0.309\,mg\,C$ (Brey 2001), assuming a photosynthetic quotient close to unity.

Values marked with an asterisk are taken from Taylor et al. (1999).

SPECIES	TYPE	PRODUCTION (μmol O$_2$ hr^{-1} g DW^{-1})	
		PHOTOSYNTHESIS	RESPIRATION*
Carpophyllum maschalocarpum	Brown canopy	41.2	
C. plumosum	Brown canopy	72.1	
C. flexuosum	Brown canopy	68.8	
C. angustifolium	Brown canopy	38.1	
Ecklonia radiata	Brown canopy	95.3	
Cystophora torulosa	Large brown	74.0	10.6*
Landsburgia quercifolia	Large brown	78.1	
Lessonia variegata	Large brown	65.8	
Sargassum sinclairii	Large brown	139.6	
Xiphophora chondrophylla	Brown foliose	68.8	5.9*
Zonaria turneriana	Brown foliose	88.2	19.2*
Melanthalia abscissa	Red foliose	75.8	8.6*
Osmundaria colensoi	Red foliose	118.0	10.1*
Pterocladia capillacea	Red foliose	108.8	22.0*
Caulerpa flexilis	Green foliose	245.7	
Ulva sp.	Green foliose	493.0*	39.0*
Enteromorpha sp.	Green foliose	361.0*	24.5*
Distromium scottsbergii	Brown turfing	143.0	
Laurencia distichophylla	Red turfing	279.8	
Hymenema variolosa	Red turfing	235.0	
Crustose coralline spp.	Crustose/coralline	307.8	
Corallina officinalis	Crustose/coralline	295.6	20.7*

Summary—Macroalgal production

These three methods suggest a range of annual P/B for macroalgae of between
1.9/y and 41/y, with an average value of 13/y. We believe that method 3 is the
most reliable method (though also requiring the most data), and used it in this
study as data were available to make reliable calculations for local species. We
suggest that methods 1 and 2 give reasonable estimates for large canopy-forming
macroalgae, though these will be slightly low biased as material lost as exudates
are not calculated. However, estimates of production for smaller macroalgae from
methods 1 and 2 are likely to be more severely underestimated. For example,
P/B for *Cystophora torulosa*, a common brown foliose alga in the intertidal
surveys, was estimated using method 3 at 5.24/y. Methods 1 and 2, which we
illustrated using large canopy macroalgal species, estimated lower P/B estimates
of 1.0/y and 1.4/y, respectively. For comparison, a typical estimate of P/B used in
trophic modelling for benthic producers is 12.5/y (Polovina 1984).

Estimates of production suggest considerable differences between groups. Using
the third method averaged over large, canopy-forming brown algae (*Carpophyllum*
spp., *E. radiata*), we estimated that P/B = 2.9/y, which, as expected, is of a
similar order of magnitude but higher than the values given using methods 1
and 2. For foliose/turfing algae (including *Caulerpa* spp), we estimated that
P/B = 13/y. For crustose/coralline algae, this method estimated that P/B = 25/y.
Although this seems high, this productivity, together with previous estimates

of biomass corresponding to high cover of coralline algae, lead to an average production rate of $0.75\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$, which is consistent with measurements of the productivity of reef-building crustose coralline algae on relatively flat reef in Australia (0.17–$1.3\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$; mean = $0.81\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$) (Chisholm 2003). Daily production rates with respect to biomass based on functional form averaged across the Pacific Coast of North America gave larger values for sheet and filamentous algae ($5.16\,\mathrm{mg\,C\,g\,DW^{-1}\,h^{-1}}$ and $2.47\,\mathrm{mg\,C\,g\,DW^{-1}\,h^{-1}}$), with lower values for coarse branching algae ($1.30\,\mathrm{mg\,C\,g\,DW^{-1}\,h^{-1}}$), thick leathery algae ($0.76\,\mathrm{mg\,C\,g\,DW^{-1}\,h^{-1}}$), jointed calcareous algae ($0.45\,\mathrm{mg\,C\,g\,DW^{-1}\,h^{-1}}$), and crustose algae ($0.07\,\mathrm{mg\,C\,g\,DW^{-1}\,h^{-1}}$) (Littler & Arnold 1982).

4.5.3 Export

Surveys of beach cast macroalgae indicate that up to 25% of annual production is deposited on the beach as detritus (Zemke-White et al. 2004). For this study, we assumed the proportion to be 20%. This material represents an export of organic material from the system, as it is not consumed by any other trophic groups in the model. In contrast, drift loss to intertidal and subtidal reef areas (measured as losses of up to 21%, 2% and 1% to drift over 21 days for *Ecklonia radiata*, *Carpophyllum maschalocarpum* and *C. angustifolium*, respectively; Andrew 1986) is assumed to be directly consumed by herbivorous invertebrates (and not converted to detritus prior to consumption); detrital macroalgae appear to be an important food source in gut content analyses of phytal invertebrates (Smith et al. 1985).

4.5.4 Summary—Macroalgae

Due to large differences in biomass and production between the three macroalgal categories, we kept these three primary producer groups separate in the model, and used method 3 (photosynthesis – respiration measurements) as the most reliable method of estimating production. We estimated a biomass of $132\,\mathrm{g\,C/m^2}$ and a P/B of 2.9/y for canopy-forming macroalgae, the dominant macroalgal producer in our model region. For foliose and turfing macroalgae, we estimated a lower biomass of $8.76\,\mathrm{g\,C/m^2}$ and a higher P/B of 13.0/y. For crustose and coralline algae, we estimated a biomass of $0.35\,\mathrm{g\,C/m^2}$ and the highest macroalgal P/B of 25.4/y.

4.6 OTHER PRIMARY PRODUCERS

4.6.1 Saltmarsh plants

Since saltmarsh plants were not listed as members of community assemblages within the modelled area (D. Freeman, DOC, unpubl. data), we did not include these primary producers as trophic groups in the model. Where these plants do need to be included, production rates can be obtained from Silva et al. (2005).

4.6.2 Seagrass

Seagrass (*Zostera capricorni*) was recorded at low abundance during intertidal reef monitoring surveys: 5% and 1% maximum recorded percentage cover at two locations outside the marine reserve (Makorori and Turihaua, respectively), and no seagrass was recorded in the intertidal reserve locations. Seagrass is not present in the relatively exposed soft-sediment beach habitats. Due to its relatively low abundance (intertidal areas represent only 3% of the total model area, and seagrass is a very small proportion of the biomass within these areas), we expected that seagrass would have no substantial contribution to model dynamics. Therefore, we did not include it as a trophic group in the model. Where these plants do require inclusion in other models, estimates of production can be obtained from Schwarz (2004) and Nelson & Waaland (1997). Estimates of epiphyte biomass on seagrass can be found in Orth & van Montfrans (1984), Nelson & Waaland (1997), and Klumpp et al. (1992).

4.7 ZOOPLANKTON

Zooplankton were considered as two trophic categories based on their assumed trophic role and varying energetics:

1. Micro- and nanozooplankton ($< 200\,\mu m$): These are primarily ciliates and heterotrophic flagellates.

2. Meso- and macrozooplankton ($> 200\,\mu m$): Mesozooplankton are likely to be dominated by copepods. Macrozooplankton are assumed to be primarily euphausids, decapods and amphipods, but salps and other gelatinous macrozooplankton are also included here.

There is no local information on the biomass of these groups. Therefore, we estimated total zooplankton biomass using measurements from around New Zealand, and estimated the proportion of each zooplankton group from previous coastal modelling work on the Chatham Rise and Southern Plateau (Bradford-Grieve et al. 2003; M. Pinkerton, NIWA, unpubl. data). However, since biochemical conditions in the plankton are likely to vary substantially with location, even on small scales, we would recommend that some seasonal, local measurements of zooplankton biomass be carried out in the study area in the future to validate these estimates.

We calculated a geometric mean of zooplankton biomass per m^3 from detailed zooplankton information at Kaikoura and in western Cook Strait, which estimated ranges of zooplankton concentration to be 10–$400\,mg\,WW/m^3$ and 72–$240\,mg\,WW/m^3$, respectively (Bradford 1972; Bradford-Grieve et al. 1993). We assumed a mixed layer depth of 25 m for the study area to convert from volumetric (m^3) to depth-averaged (m^2) measurements. We converted wet weights to g C using empirical relationships for crustacean zooplankton ($1\,g\,WW = 0.209\,g\,DW$; $1\,g\,DW = 0.416\,g\,C$; Brey 2001). Hence, we estimated the total zooplankton biomass in the study region to be $0.267\,g\,C/m^2$.

We assumed that the zooplankton biomass is divided into proportions of 17% heterotrophic flagellates, 9% ciliates, 57% mesozooplankton and 17% macrozooplankton, following Bradford-Grieve et al. (2003). Zooplankton

biomass in the coastal study region was hence estimated to be 0.069 g C/m^2 nano/microzooplankton, and 0.198 g C/m^2 meso/macrozooplankton. Zooplankton surveys at Farewell Spit gave similar percentage compositions of copepods (mesozooplankton) ranging from 80% to 97% (Foster & Battaered 1985).

As a check of our zooplankton biomass estimate, we compared phytoplankton and zooplankton biomass. The annual average biomass of heterotrophic plankton is generally related to autotrophic biomass, though it is clear that there are significant variations by region, depth and season. The ratio of total zooplankton biomass to phytoplankton biomass has been reported as 1.7 (Southern Plateau New Zealand; Bradford-Grieve et al. 2003), 1.5 (Golden Bay, New Zealand; Jiang & Gibbs 2005), 1.1 (Ross Sea; Pinkerton et al. 2006), 0.77 (Gulf of Mexico; Arreguin-Sanchez et al. 2002), and 0.64 (Tongoy Bay, Chile; Wolff 1994). These values, across a range of systems, suggest an average heterotrophic:autotrophic plankton ratio of 1.11, which is the same as the zooplankton:phytoplankton ratio from our estimates.

We took production and consumption rates for zooplankton from Bradford-Grieve et al. (2003). Annual productivities (P/B y^{-1}) were: 290 (heterotrophic flagellates), 88 (ciliates), 20 (mesozooplankton), and 10 (macrozooplankton). Assimilation efficiencies were estimated to be in the narrow range of 0.30 (macrozooplankton) to 0.35 (ciliates and flagellates). Assuming zooplankton in the coastal study area have similar productivities and efficiencies to those offshore, P/B = 220/y and Q/B = 620/y for micro/nanozooplankton, and P/B = 18/y and Q/B = 52/y for meso/macrozooplankton. These values are comparable with previous studies (e.g. James 1989; Shushkina et al. 1998).

Nano/microzooplankton consume bacteria and phytoplankton, but the proportions of these in the diet can only be estimated. Trophic composition of mesozooplankton diet in western Cook Strait was estimated as 16–40% herbivorous copepods, 55–84% omnivorous copepods, and 0–5% carnivorous copepods (Bradford-Grieve et al. 1993), but this is likely to vary with food availability. The diet of macrozooplankton may include phytoplankton, microzooplankton and mesozooplankton, with copepods dominating the diet (Barange et al. 1991). Based on Bradford-Grieve et al. (2003), we suggest a diet composition for meso/macroplankton of 20% meso/macrozooplankton, 70% microzooplankton and 10% phytoplankton. For nano/microzooplankton, we suggest a diet composition of 10% nano/microzooplankton, 65% phytoplankton and 25% bacteria.

4.8   MACRO- AND MICROINVERTEBRATES

We combined phytal, macro- and microinvertebrates such as amphipods, isopods, microcrustacea, polychaetes and infaunal bivalves into one trophic compartment, due to minimal local information on the biomass of each group, and similar sizes of taxa represented across different sub-habitats. Phytal invertebrates are all macro- and microinvertebrate species living within macroalgae, while benthic macroinvertebrates (macrofauna) and microinvertebrates (meiofauna) live within or upon soft sediments. Most available information in the literature on the biomass of these groups is in terms of numbers of individuals, rather than separating out smaller and larger fauna to give more representative approximations of biomass, further supporting our choice to group these together into one trophic compartment.

4.8.1 Phytal invertebrates

Phytal invertebrates include all epifauna living in or on macroalgae. Microcrustaceans (amphipods, isopods and harpacticoid copepods) are dominant in terms of total number of individuals, but larger taxa such as gastropods and isopods are also included. Numerous reports detail phytal invertebrate abundance and productivity in New Zealand waters, primarily at Leigh (Kingsford & Choat 1985; Taylor & Cole 1994; Williamson & Creese 1996; Taylor 1998 a, b, c).

Phytal invertebrate biomass on macroalgae tends to be measured in two ways: as number of individual invertebrates or as total phytal invertebrate weight. As there are huge variations in individual size and weight (phytal harpacticoid copepods typically weigh less than 1% of ostracods), any measurements of individual numbers should also include enough information to estimate total biomass and convert biomass to g C. Production rates vary considerably with individual size, so that information on the taxonomy (at a coarse level at least) of phytal invertebrates is required to estimate P/B for the group. A further complication is that different studies measure phytal abundance either per unit wet weight of macroalgae or per unit ground area. Comparing these different measurements requires information on macroalgal biomass per unit area. Densities also vary with habitat type.

Dry weights of different phytal taxa have been measured from *C. maschalocarpum* and *C. torulosa* communities from a rocky reef off Kaikoura (Table 11; C. Duffy, DOC, unpubl. data). We used average individual weights for various taxa in Western Australia from Edgar (1990) combined with the biovolume conversion method of Donovaro et al. (2002) to estimate biomass from numbers of individuals (Table 11). Annual production values given by Donovaro et al. (2002) and Edgar (1990) for selected phytal invertebrates were combined using the relative abundances from raw data.

TABLE 11. ABUNDANCE, INDIVIDUAL SIZES AND PRODUCTIVITIES OF SELECTED PHYTAL INVERTEBRATE TAXA.

Values follow Edgar (1990) and Donovaro et al. (2002), and are based on phytal invertebrate abundance and weights obtained by C. Duffy (DOC, unpubl. data). Proportion of the total is given relative to total number of individuals (N), total biomass (B), and total production (P).

TAXON	INDIVIDUAL WEIGHT (μg C)	P/B (PER YEAR)	PROPORTION (%) BY:		
			N	B	P
Acari	1.2	10.4	1.18	0.02	0.08
Amphipoda	20.7	5.0	11.73	4.02	6.86
Foraminifera	0.7	11.9	0.03	0.00	0.00
Gastropoda	291.9	2.7	6.32	30.55	28.01
Harpacticoida	0.7	15.0	63.95	0.74	3.80
Insecta	1.2	10.4	0.01	0.00	0.00
Isopoda	585.7	3.4	0.30	2.88	3.34
Nematoda	0.7	10.1	0.98	0.01	0.04
Ostracoda	291.9	2.7	11.69	56.56	51.86
Platyhelminthes	3.1	6.6	0.47	0.02	0.05
Polychaeta	36.6	4.8	2.49	1.51	2.50
Tanaidacea	262.8	2.7	0.84	3.67	3.46

The average individual weight of phytal invertebrates based on data in Table 11 and weighted by abundance is 0.89 mg WW. This is of a similar magnitude to other estimates, e.g. 1.63 mg WW, estimated by Edgar (1990). As we were concerned that our estimate might be biased low, we converted phytal abundance into phytal wet weights using an average of our estimate and Edgar's estimate, i.e. 1.3 mg WW per individual.

Wet weights were converted to g C using empirical relationships for amphipods and isopods taken from Brey (2001): 1 g WW = 0.2 g DW; 1 g DW = 0.72 and 0.64 g AFDW for amphipods and isopods respectively; 1 mg AFDW = 22.7 J, and 1 mg C = 45.7 J. These imply that 1 g WW = 0.068 g C, and 1 g AFDW = 0.50 g C.

Some measurements of habitat-specific phytal abundances in New Zealand are given in Table 12. Taylor (1998a) measured habitat-specific density, biomass and productivity of epifaunal invertebrates at Leigh for four habitat types: *Carpophyllum* forest, *Ecklonia* forest, urchin barrens and coralline turfs. A second study at Leigh gave algal-specific densities of mobile epifaunal invertebrates per wet weight of three algal species (*Carpophyllum maschalocarpum*, *C. flexuosum* and *Ecklonia radiata*) (Taylor & Cole 1994). Taylor (1998b) recorded seasonal variations at Leigh in epifauna on three large brown algal species (*Carpophyllum maschalocarpum*, *C. flexuosum*, and *Ecklonia radiata*). Hicks (1977) detailed harpacticoid copepod abundance on various algal species in Wellington Harbour. Another study detailed phytal invertebrate abundance for ten subtidal brown algal species (Taylor & Cole 1994). Anderson et al. (2005) calculate phytal invertebrate abundance in kelp holdfasts.

TABLE 12. ABUNDANCE OF PHYTAL INVERTEBRATES FOR VARIOUS ALGAL SPECIES (HICKS 1977; TAYLOR & COLE 1994; WILLIAMSON & CREESE 1996; ANDERSON ET AL. 2005).

SPECIES	TYPE	ABUNDANCE PER 100 g WW	VARIATION IN ABUNDANCE
Carpophyllum plumosum	Brown canopy	735[a]	200–2000 (median 300)[c]
C. flexuosum	Brown canopy	102[a]	
C. maschalocarpum	Brown canopy	82[a]	40–110 (median 50)[c]
Ecklonia radiata	Brown canopy	61[a]	10–75 (median 40)[c]
Ecklonia radiata	Holdfast	572 (per 120 mL holdfast volume)[b]	
Cystophora retroflexa	Large brown	874[a]	
Cystophora torulosa	Large brown	332[a]	
Lessonia variegata	Large brown	13[a]	
Landsburgia quercifolia	Large brown	85[a]	
Sargassum sinclairii	Large brown	69[a]	
Xiphophora chondrophylla	Large brown	222[a]	5–40 per 10 cm^2 = c. 100 g based on 10 g/cm^{2} [d]
Zonaria turneriana	Brown foliose		10–80 per 10 cm^2 = c. 24.8 g[d]
Pterocladia capillacea	Red foliose		10–60 per 10 cm^2 = c. 100 g[d]
Corallina officinalis	Coralline/crustose		100–600 per 10 cm^2 = c. 15 g[d]
Pseudolithoderma sp.	Brown crustose		75–175 per 25 cm^2 = c. 9 g based on 0.35 g/cm^{2} [e]

[a] Taylor & Cole 1994.
[b] Anderson et al. 2005.
[c] Taylor 1998b.
[d] Hicks 1977.
[e] Williamson & Creese 1996.

We used two methods to estimate phytal invertebrate biomass: based on macroalgal-specific abundance of phytal invertebrates, and based on habitat-specific estimates of abundance of phytal invertebrates, extrapolated over the study area. We averaged the results of both methods to determine our estimate of phytal invertebrate biomass.

1. **Method 1—Macroalgal biomass:** We first estimated abundance of these smaller invertebrates as their density relative to the total biomass of each macroalgal trophic group, as calculated in section 4.5.1. Averaging over many studies gives a mean subtidal abundance of phytal invertebrates per g WW of algae of 1.02 for *Carpophyllum flexuosum*, 0.66 for *Carpophyllum* spp., 0.51 for *Ecklonia radiata*, 0.82 for other large brown algae, 0.25 for red foliose algae, 0.53 for green foliose algae, 0.53 for turfing algae, and 16.3 for crustose algae. For intertidal habitats, we related phytal invertebrate abundance to the three algal trophic groups as 5.0 individuals per g algae for large brown algae (using phytal invertebrate abundance of *Cystophora* spp. as the primary intertidal large brown alga in the model area), 1.0 individuals per g algae (wet weight) for foliose/turfing algae and 10 individuals per g for crustose/coralline algae. For each habitat, wet weight of algae per m^2 was obtained using conversions from g C and AFDW, as outlined in section 4.5.1.

2. **Method 2—Habitat-specific biomass:** As a second method of estimating phytal invertebrate abundance, we used the habitat-specific abundances in Table 12 to extrapolate phytal invertebrate abundance across all subtidal habitats in the marine reserve (Fig. 8K). Similar to Method 1, phytal density was estimated for each macroalgal species, averaging across published studies. Here we used number of individual macroalgae or percentage cover, as calculated in section 4.5.1, and converted phytal invertebrate estimates to g WW phytal invertebrate per algal individual (or percentage cover). Phytal invertebrate abundance was then converted into habitat-specific abundances based on the average number of individuals or percentage cover of macroalgae in each habitat type as per the habitat classifications and macroalgal abundance estimates in Table 4 (Table 13).

TABLE 13. DENSITY OF PHYTAL INVERTEBRATES FOR VARIOUS SUBTIDAL HABITATS.

Habitats are as in Table 4; estimated from various data sources (e.g. Hicks 1977; Taylor & Cole 1994; Williamson & Creese 1996; Anderson et al. 2005).

	SUBTIDAL HABITAT TYPE	DENSITY (g WW/m^2)
1	Deep reef/sponge garden	0.1
2	EckCaul	5.1
3	EckCflex	10.2
4	EckCor	4.9
5	EckFolred	7.3
6	MixedBr	35.3
7	CorCovReef	4.3
8	DeepCobbles	1.1
9	Sand	0.0

These values compare well with those from Taylor (1998a), where he weighed all epifauna (phytal invertebrates) in his survey. In his study, total phytal biomass was estimated at 27.2 g WW/m^2 (*Carpophyllum* forest, comparable to our mixed algae (MixedBr) habitat), 11.2 g WW/m^2 (*Ecklonia* forest), and 4.7 g WW/m^2 (urchin barren, comparable to our coralline-covered reef habitat).

Production

Using values from Table 11, we estimated an average P/B of 2.9/y for the phytal invertebrate assemblage.

Consumption

There is limited information available on conversion factors for estimating phytal consumption. Food consumption by phytal invertebrate assemblages is estimated using a factor that accounts for the food required to provide the estimated production after respiration, i.e. P/Q values. Often these factors are based on a small number of measurements that do not take into account temporal variability in metabolism and food availability. Commonly used P/Q factors for small invertebrates in the literature are: 32.5%, based on direct metabolic measurements (Warwick et al. 1979); 30–40%, based on measurements of respiration rates (Herman et al. 1984); and 10%, based on the Lindeman concept of energy flow through trophic levels (Lindeman 1942; Bouvy 1988). Here we assumed a P/Q of 25% for phytal invertebrates, giving a Q/B of 11.6/y. We note that this is considerably (more than an order of magnitude) smaller than the Q/B of 125/y suggested by Okey et al. (2004) for microcrustaceans from a Chilean temperate reef ecosystem model. However, we feel our estimate, which is more closely related to direct metabolic measurements, is more reliable.

Diet

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

4.8.2 Macrobenthic infauna and epifauna

This trophic group includes all those fauna living on or in the soft sediments of the study region that have an individual size of more than 0.5 mm. The group includes small infauna and epifauna, including amphipods, isopods and cumaceans, as well as larger fauna such as infaunal bivalves.

Local macrofaunal samples were available within the reserve at a location directly adjacent to the intertidal reef at shallow depths of approximately 2 m. Nine core samples (10-cm-diameter cores to 10 cm depth, surface area 78 cm^2, sieved on a 500 micron mesh) were taken, and invertebrates were identified to the extent practicable. A total of 555 individuals and 32 species were collected, with an average of 62 individuals and 11 taxa per core (7900 individuals/m^2) (Table 14). Most taxa were small, including most of the bivalves enumerated (primarily *Nucula hartvigiana* and *Arthritica bifurca*, both of which are approximately 5 mm long as adults). Polychaetes and oligochaetes comprised over half of the total number of individuals (Table 14).

TABLE 14. NUMBER OF MACROFAUNAL INVERTEBRATES BY TAXA FROM NINE CORE SAMPLES (10 cm DIAMETER) TAKEN FROM SOFT SEDIMENTS ADJACENT TO THE INTERTIDAL ROCK REEF PLATFORM INSIDE THE MARINE RESERVE.

| TAXON | TOTAL NUMBER | | AVERAGE NO. |
	SPECIES	INDIVIDUALS	INDIVIDUALS PER CORE
Amphipods	6	16	3.2
Bivalves	3	85	9.4
Decapods	1	20	2.2
Anemones	1	1	0.1
Gastropods	1	9	1.0
Isopods	4	67	7.4
Polychaetes	11	146	16.2
Barnacles	1	1	0.1
Oligochaetes	1	181	20.1
Ostracods	2	25	2.8
Tanaids	1	4	0.4

TABLE 15. TYPICAL WEIGHTS OF SOME SOFT-SEDIMENT BENTHIC INFAUNA AND EPIFAUNA. DEGREE OF MEASUREMENT ACCURACY AS REPORTED IN EDGAR (1990).

TAXON	SPECIES	TYPICAL WEIGHT (mg WW)
Amphipod	*Gammarus macronatus*	0.169
Amphipod	*Corophium insidiosum*	0.021
Amphipod	*Lembos websteri*	0.551
Amphipod	*Unciola inermis*	2.02
Amphipod	*Parkyale basrensis*	5.4
Amphipod	*Ampelisca macrocephala*	1.32
Amphipod	*Haustorius Canadensis*	3.0
Amphipod	*Pontoporeia femorata*	2.25
Amphipod	*Amphiporeia lawrenciana*	0.056
Isopod	*Cyathura carinata*	0.52
Polychaete	*Pectinaria koreni*	13.8
Polychaete	*Nephtys hambergi*	2.3
Polychaete	*Nereis diversicolor*	0.027

There have been few other studies of soft sediment infauna and epifauna within the Gisborne region, and most of these were associated with sewage outfall or port activities (Cole et al. 1999; Keeley et al. 2002). One Poverty Bay study gave densities of 76.8–518.3 individuals/m^2 for subtidal benthos offshore of the Gisborne sewage outfall (Keeley et al. 2002). Another macrofaunal survey included polychaetes, amphipods and cumaceans, but relatively few bivalves compared with some other locations on the east coast of the North Island (Cole et al. 1999). While macrofaunal abundance was much lower in these surveys than in our local estimates, this is not surprising due to these sites likely surveying locally stressed communities, as well as the use of a larger mesh size (1 mm), which does not reliably sample smaller taxa such as polychaetes and oligochaetes that were abundant in the local samples.

Intertidal beach fauna have been surveyed at Ohope Beach, Castlepoint and Napier (Fincham 1977), with average densities of 76, 184 and 56/m^2, respectively, of primarily amphipods, isopods and cumaceans. Another study at Wainui Beach reported densities of 480/m^2 (Stephenson 1993).

We expect macrofaunal abundance to vary with habitat within the model area, with higher densities in shallow areas that are in close proximity to the reef areas like that for which we have local samples, and lower densities in exposed beaches and subtidal soft sediments. As most of the soft-sediment habitat in the model area is comprised of subtidal areas and unlikely to have the high densities found near the reef, the typical density of macrofauna on subtidal and intertidal soft sediment within the reserve area is thus estimated to be the geometric mean of the available measurements, i.e. c. 150/m^2.

Edgar (1990) gave data on typical weights of amphipods, isopods and polychaetes (Tables 11 & 15). Amphipods have a median wet weight of about 1 mg, and polychaetes of about 2.3 mg; AFDW is taken to be about 19% of wet weight for these fauna (Brey 2001). In contrast, the AFDW of bivalves is much higher, with two estuarine bivalves (*Macomona liliana* and *Austrovenus stutchburyi*) having a mean individual AFDW estimated as 0.046 g and 0.044 g, respectively (Cummings et al. 1997). Thus, the biomass of soft-sediment fauna in the study region is highly dependent on the ratio of smaller fauna (amphipods, isopods, polychaetes) compared with the much larger bivalves. Based on the core data, we assumed that soft-sediment fauna around Te Tapuwae o Rongokako Marine

Reserve is dominated in terms of individual animal densities by the smaller groups (100:1).

Carbon content of benthic macrofauna is assumed to be similar to that of gammarid amphipods, i.e. 1 g AFDW is equivalent to c. 0.50 g C (Brey 2001). Soft sediment makes up 70% (outside reserve) to 80% (inside reserve) of the study regions. These data allowed us to estimate average macrobenthic infaunal and epifaunal biomass density for the reserve and non-reserve areas as approximately 0.03 g C/m^2.

Growth rates are available for some New Zealand surf clams, including *Spisula equilatera*, *Mactra murchisoni*, *M. discors*, *Dosinia anus* and *Paphies donacina* (Cranfield & Michael 2001), but little information is available for most of the dominant infaunal taxa found in New Zealand soft sediments. The paucity of energetic information on soft-sediment fauna is typical for most trophic models worldwide. Edgar (1990) and Donovaro et al. (2002) gave estimates of production for some small invertebrates, though few are for genera found within New Zealand (Table 11). Some comparisons of P/B by taxa range from 1.4–2.2/y (P = 33–300) for infaunal bivalves, 0.8/y for an infaunal isopod, 1.5–5.6/y for infaunal amphipods, and 3.5–29.7/y for polychaetes (Edgar 1990). We used literature estimates from other ecosystem models for heterotrophic benthos to estimate parameters required by the model for infaunal taxa. Literature values for heterotrophic benthos in temperate systems range between 1/y and 5/y for P/B (Q/B = 10–30/y). Here we initialised the model with estimates of P/B = 3/y and Q/B = 12/y for heterotrophic benthos based on Polovina (1984).

Soft-sediment fauna take food from the water column (zooplankton, phytoplankton and water column bacteria) and from the benthos (meiobenthos, macrobenthos, benthic bacteria and microphytobenthos). The proportions of these items in the diet of this group are not known.

4.8.3 Meiofauna

Meiofauna are microinvertebrates (infauna 63 μm–0.5 mm) living within soft sediments. Common taxa include copepods, nematodes and ostracods. Meiofaunal biomass in the soft-sediment region of Te Tapuwae o Rongokako Marine Reserve is likely to be dominated by nematodes. No information on meiofaunal biomass for the study region is available. We estimated meiobenthos biomass based on macrofaunal consumption requirements, assuming meiofauna are 20% of the diet of macrofauna (meiobenthos biomass = macrobenthic biomass × macrobenthic consumption × proportion of macrobenthic diet divided by meiobenthic production) (see section 4.8.2 for macrofaunal parameter estimates). This gave a starting value of approximately 0.01 g C/m^2.

Annual P/B ratios of meiofauna vary considerably (c. 2.5–15/y), with values of between 4/y and 10/y often being taken as typical values (Probert 1986; Feller & Warwick 1988). We assumed an annual P/Q ratio of 0.31 as in Bradford-Grieve et al. (2003), and thus a typical Q/B for benthic meiofauna of c. 35/y and P/B of 7/y.

The prime source of food for the meiobenthos is assumed to be bacteria, with some cannibalistic contribution from other meiobenthos.

4.8.4   Summary—Macro- and microinvertebrates

We estimated a biomass of $0.232\,\mathrm{g\,C/m^2}$, P/B of 2.9/y, and Q/B of 11.6/y for phytal invertebrates, based on estimates of macroalgal biomass in our model region. Assuming most macrofauna are found in subtidal soft sediments in the model region, we estimated a macrofaunal biomass of $0.026\,\mathrm{g\,C/m^2}$, P/B of 3/y, and Q/B of 12/y. We estimated a meiofaunal biomass of $0.009\,\mathrm{g\,C/m^2}$, P/B of 7/y, and Q/B of 35/y.

To estimate trophic parameters for this entire trophic compartment (phytal invertebrates, macrofauna and meiofauna combined), we summed biomass, production and consumption of each of the three groups as calculated above, and divided production and consumption by total biomass to estimate P/B and Q/B. Final estimates were B of $0.267\,\mathrm{g\,C/m^2}$, P/B of 3.05/y, and Q/B of 12.0/y, showing dominance of this group by phytal invertebrates. Diet components were reconciled across the three groups via weighting over both biomass and consumption rates, based on known diet components for each group, but also acknowledging high uncertainty in their relative proportion. We suggest an initial diet composition of 25% large canopy algae (and associated detritus), 25% phytoplankton, 25% microphytobenthos and 25% bacteria.

4.9   ENCRUSTING INVERTEBRATES

4.9.1   Sponges (Porifera)

Since sponges have a high relative biomass compared with other encrusting invertebrates, we include 'sponges' as a separate trophic group. Sponges also differed substantially from other encrusting invertebrates in their percentage cover-biomass (AFDW) relationships, again suggesting their inclusion as a separate trophic group.

The presence of 24 sponge species was documented in the initial Te Tapuwae o Rongokako Marine Reserve application (DOC & Ngati Konohi 1998). Characteristic species of the inshore reef and deep reef slope were listed as *Ancorina alata*, *Stelleta* sp., *Ircinia* sp., *Geodia* sp., *Raspailia* sp., *Callyspongia* spp. and *Cliona celata*. Sponges have highly variable morphology. Large massive sponges (e.g. *Ancorina alata*, *Stelleta maori*, *Cliona celata*) can grow up to 1–3 kg WW (approximately $300 \times 250 \times 250$ mm). In contrast, a review of 11 New Zealand thinly encrusting sponges showed a size range of 0.03–0.37 (mean 0.14) $\mathrm{g/cm^2}$ WW and 0.02–0.16 (mean 0.06) $\mathrm{g/cm^2}$ DW, with mean patch size of 7.8–151.8 (mean 41.7) $\mathrm{cm^2}$ (Ayling 1983).

As we had no data on sponge size and/or species distributions within the study area, sponge biomass was calculated using estimates of sponge percentage cover from Shears & Babcock (2004b), extrapolating over all habitat types as outlined in section 3.2.2 and assuming that the average estimates of biomass relative to percentage sponge cover were representative of the various growth forms found within the study region. The habitat identified as 'sponges and other encrusting invertebrates' was assumed to be made up of 75% sponges (typified as *Cliona celata*) and 25% non-sponges, as sponges are found to dominate the area coverage (C. Duffy, DOC, pers. comm.).

Percentage cover-biomass (AFDW) relationships for sponges were estimated using relationships available in Shears & Babcock (2004b) (Table 16), who obtained AFDWs by drying shell-free invertebrate samples to a constant weight at 80°C and then incinerating at 500°C. Converted biomass estimates were then extrapolated across habitat types using triangulation, as outlined in section 3 (Fig. 8I). Carbon was assumed to comprise c. 50% of AFDW (Brey 2001).

About 95% of New Zealand sponges are endemic. Their growth rates are generally not well known and productivity estimates are not available for most New Zealand taxa. Ayling (1983) listed normal growth rates for 11 thinly encrusting species as ranging from –0.01 to 0.28 mm² per cm border per day (mean 0.084 mm² per cm border per day). Normal growth rates for the globular sponge *Polymastia croceus* were calculated as a 22% increase in size over 2 months, while damaged sponges showed a wide range from negative growth to a 260% increase in size (Bell 1998). *Spongia* (*Heterofibria*) *manipulatus* exhibited average growth rates in culture of 28.5% over 9 months (Handley et al. 2003). Another study has shown growth for thinly encrusting sponges increasing by 22–2900 times in response to simulated grazing pressure by kina *Evechinus chloroticus* (Ayling 1983). It is also thought that sponges in New Zealand rocky reef ecosystems can enter a low-consumption state in some circumstances (C. Duffy, DOC, pers. comm.), but details of this 'shutdown' state are not well understood. If typical changes in sponge diameter per year are assumed to be independent of sponge size (Duckworth & Battershill 2001), an appropriate P/B value will be approximately 4/T, where T is the age of

TABLE 16. CONVERSIONS FROM PERCENTAGE COVER TO BIOMASS FOR ENCRUSTING INVERTEBRATES (FROM SHEARS & BABCOCK 2004b).

TAXON	STRUCTURAL GROUP	SPECIES	% COVER	BIOMASS (g AFDW)
Ascidians	Compound ascidian	*Didemnum* sp.	1	1.6
	Solitary ascidian	*Asterocarpa* sp.	1	6.4
	Stalked ascidian	*Pseudodistoma* sp.	1	2.2
	Sea tulip	*Pyura pachydermatina*	1	15.0
Barnacles	Barnacles	*Balanus* sp.	1	1.8
Mollusca	Oyster	*Crassostrea* sp.	1	5.0
	Large mussels	*Perna canaliculus*	1	26.0
	Small mussels	*Xenostrobus pulex*	1	8.9
Brachiopod	Brachiopod		0.25	0.4
Bryozoans	Branched bryozoan	*Cribricellina cribraria*	1	3.5
	–	*Bugula dentata*	1	0.7
	Encrusting bryozoan	*Membranipora* sp.	1	0.5
Coelenterates	Colonial anemone	*Anthothoe albocincta*	1	2.3
	Large solitary anemone	*Phlyctinactis* sp.	1	4.0
	Cup coral	*Monomyces rubrum*	0.25	0.3
	Soft coral	*Alcyonium* sp.	1	3.1
Hydrozoa	Hydroid turf	Unknown hydroid	0.25	0.4
	–	*Amphisbetia bispinosa*	1	8.1
	Hydroid tree	*Solanderia ericopsis*	1	10.0
Porifera	Encrusting sponge	*Cliona celata*	1	11.4
	Finger sponge	*Raspailia topsenti*	1	44.9
	Massive sponge	*Polymastia croceus*	1	22.2
	–	*Ancorina alata*	1	64.7

the oldest individual sponge. Smith & Gordon (2005) gave ages of 10–20 years for sponges of 150–200 mm, and maximum ages of 80 years for larger sponges with a diameter of 1 m. These figures suggest a P/B of 0.05–0.4/y. Therefore, we used 0.2/y as a best estimate for sponges.

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

Sponges are filter feeders. The diet of *Polymastia croceus* has been estimated as primarily consisting of picoplankton and ultraplankton (< 5 microns) (Bell 1998). Reiswig (1971) suggested that the diet of a tropical sponge community was composed of 80% bacteria and particulate organic matter (POM). While exact diet composition is unknown with respect to species preferences, size-selectivity for filter feeding, and seasonal variations in abundance of different prey items, we divided diet composition among the three trophic groups most likely to contribute to sponge diet composition. We estimated a diet composed of 30% microzooplankton, 40% phytoplankton and 30% bacteria.

4.9.2   Other encrusting invertebrates

Biomass of encrusting invertebrates other than sponges was estimated for subtidal reef areas using subtidal reserve monitoring data as described in section 3.2.2. Non-sponge encrusting invertebrates included ascidians, barnacles, mussels, bryozoans and hydrozoa, as well as various other encrusting taxa. We used percentage cover estimates by habitat type to calculate the biomass of encrusting invertebrate species (Shears & Babcock 2004b) (Table 4). The habitat identified as 'sponges and other encrusting invertebrates' is assumed to be made up of 25% non-sponge species (C. Duffy, DOC, pers. comm.). Percentage cover estimates for encrusting invertebrates were extrapolated across all subtidal habitats (Fig. 8L).

Intertidal encrusting invertebrates were assumed to be comprised solely of barnacles. Intertidal barnacles comprised 1.2% of the intertidal habitat (Table 6). Intertidal barnacle cover was converted to biomass using the conversion rates in Table 16, and then extrapolated over the intertidal area.

As green lip mussels (*Perna canaliculus*) do not form a substantial portion of the biomass in the region, we group them with other encrusting epifauna. In other systems, researchers may find it useful to include mussels as a separate trophic group, as mussels can be both major influencers of phytoplankton abundance and contributors to benthic detritus (see, for example, aquaculture impacts of long-line mussel culture; Jiang & Gibbs 2005). Mussels are also a major component in the diet of lobsters at many locations in New Zealand (S. Kelly, Auckland Regional Council, unpubl. data). Where mussels do require inclusion as a separate trophic group in other models, a general review for this species is available in Jeffs et al. (1999). Growth rates, respiration rates, filtration rates, diet and relative contributions of mussel faeces to benthic detritus can be found in Hickman (1979), James et al. (2001), Christensen et al. (2003) and Zeldis et al. (2004).

Production and consumption rates were not available for encrusting invertebrates within the study area. Other ecosystem models in temperate systems give a range for P/B of 1–4/y and Q/B of 12–17/y (Ortiz & Wolff 2002; Okey et al. 2004). Similarly, Edgar (1990) gave a P/B of 1.1/y for *Mytilus edulis*, an encrusting intertidal mussel. In our model, we used a P/B of 1.5/y, and calculated a Q/B of 6/y, assuming a P/Q of 0.25 based on literature estimates of P/Q for macroinvertebrates.

Limited information on diet composition is available for sessile invertebrates. Most sessile invertebrates are filter feeders (e.g. barnacles, tunicates, bryozoans and mussels). The diet of bryozoans appears to entirely consist of phytoplankton (Bullivant 1967). We assumed that the diet of heterotrophic encrusting invertebrates consists of phytoplankton, water column bacteria and zooplankton. While the exact composition is unknown due to taxon-specific feeding preferences and seasonality of prey availability, we estimated that diet was similar to that of sponges, and composed of 30% microzooplankton, 40% phytoplankton and 30% bacteria.

4.10   SEA CUCUMBERS

Sea cucumbers (holothuroids) are deposit feeders on benthic detritus. No local abundance information was available on holothuroids in the subtidal model area. Due to their relatively low abundance, no sea cucumbers were recorded in quadrat surveys of Gisborne subtidal reefs (Shears & Babcock 2004b). Surveys of rocky reef assemblages in the Hauraki Gulf estimated an average abundance of *Stichopus mollis* of $0.15/m^2$, with lower abundances of $0.05/m^2$ in the outer Gulf (Smith 2003). We assumed that sea cucumbers are present only in the subtidal reef area, and that no sea cucumbers are present in intertidal regions, as they were not recorded during intertidal monitoring surveys.

Average individual size of *Stichopus mollis* in northeastern New Zealand was calculated as 16.64 cm and 107.85 g (Sewell 1990). We converted wet weight to g C using conversion factors given in Brey (2001) of 0.112 g WW/g AFDW, 22.95 J/mg AFDW, and 45.7 J/mg C. These figures imply that carbon is approximately 5.6% wet weight (cf. approximately 10% for fish). This leads to estimates of average biomass density of sea cucumbers for the reserve as $0.31\,g\,C/m^2$ for subtidal areas (0.30 averaged over the entire study area, assuming no sea cucumbers were found in intertidal areas).

We used literature estimates of trophic parameters for holothuroids in temperate systems of P/B = 0.6/y and Q/B = 3.4/y (Okey et al. 2004).

4.11 MOBILE PREDATORY INVERTEBRATES

This trophic group includes crabs, octopuses, seastars, whelks, brittlestars, carnivorous polychaetes, and nudibranchs. Lobsters are included as a separate trophic group.

4.11.1 Crabs

We estimated crab abundance in the study region based on densities of two generic crab types (hermit crabs—Paguroidea, and rock crabs—*Plagusia* sp.) in three habitats (intertidal reef, subtidal reef and subtidal soft sediment). Twenty-four hermit crab species and *Plagusia* sp. were counted by Shears & Babcock (2004b) in their subtidal surveys of four hard-substrate sites ($75\,m^2$) near Gisborne, resulting in an estimated density of 0.32 crabs/m^2. Lower crab densities (0.06/m^2) were measured in depth transects from the shallow subtidal region to the reef edge at the same location (N. Shears, University of Auckland, unpubl. data). Higher densities of hermit crabs (0.6–0.8/m^2) have been reported from subtidal reef surveys of offshore Hauraki Gulf islands (Smith 2003). We used the observed value of 0.32/m^2 for the subtidal reef portion of the study area. Although crab abundance on subtidal soft sediments in the region is not known, we assumed that it is similar to neighbouring hard substrates (0.3/m^2) and composed exclusively of hermit crabs. Intertidal monitoring surveys showed similarly low densities in the reserve and non-reserve areas (0.24 and 1.65/m^2, respectively) (Table 17), with most individuals (approximately 75%) being hermit crabs in both subtidal and intertidal reef surveys.

TABLE 17. DENSITY (INDIVIDUALS/ m^2) OF MOBILE INVERTEBRATES FOUND DURING INTERTIDAL REEF MONITORING SURVEYS.

TAXON	DENSITY	
	RESERVE	NON-RESERVE
Crabs	0.24	1.65
Predatory gastropods	0.71	2.25
Other predatory invertebrates	0.33	1.70
Grazing gastropods	1.01	1.77
Chitons	4.21	6.43
Pupu	2.91	15.12
Limpets	4.00	0.61

One *Plagusia* sp. was measured in subtidal surveys as being 15 mm long (0.32 g; Table 18). Taylor (1998a) gave mean length as 20 mm for hermit crabs and 35 mm for *Plagusia* sp. Length-weight conversions result in an average individual biomass of 0.14 g AFDW for hermit crabs and 3.8 g AFDW for *Plagusia* sp. (Table 18). We converted from g AFDW to g C using relationships for decapods given in Brey (2001).

Taylor (1998a) estimated that P = 0.52 g AFDW m^{-2} y^{-1} and B = 0.55 g AFDW/m^2 for brachyuran crabs and P = 0.36 g AFDW m^{-2} y^{-1} and B = 0.22 g AFDW/m^2 for hermit crabs at Leigh. He estimated that crabs made up 2.57% of the total biomass of the rocky reef system. Average P/B from a variety of crab species has been calculated as 3.6/y (Edgar 1990). This study included two congeners of New Zealand species, *Macrophthalmus latifrons* and *Halicarcinus australis*, which had individual biomasses of 14.3 mg and 45.5 mg, and P/B of 5.2/y and 4.7/y, respectively (Edgar 1990). In Chile, ecosystem parameters for temperate crab species ranged from 0.5/y to 18/y for P/B and 4.5/y to 7/y for Q/B (Wolff 1994; Ortiz & Wolff 2002). For our model, we estimated that P/B = 0.95/y and

TABLE 18. LENGTH-WEIGHT RELATIONSHIPS FOR MOBILE INVERTEBRATES.

$W = aL^b$, where W = ash free dry weight (AFDW; g), L = linear body dimension (mm), and a and b are constants (Taylor 1998a).

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

Q/B = 4.75/y for rock crabs, and P/B = 1.6/y and Q/B = 6.4/y for hermit crabs. Q/B was estimated assuming a P/Q of 0.2 for rock crabs and 0.25 for hermit crabs.

Crab diet varies with species, with herbivorous, detrivorous and carnivorous species occurring in New Zealand. McLay (1988) stated that *Plagusia chabrus* (red rock crab) is an opportunistic feeder on limpets, chitons, gastropods, mussels, barnacles, brown algae and coralline turf, and is also cannibalistic and will eat carcasses (including seabirds). *Ovalipes catharus* (paddle crab), which is found mostly on soft sediments, is an opportunistic predator, whose diet in a Hawke's Bay survey included 65% bivalves, 12% polychaetes, 12% crustaceans and 9% other crabs (Wear & Haddon 1987), which are qualitatively similar to the results of McLay (1988). In contrast, *Notomitrax ursus* (hairy seaweed crab) is a herbivorous crab that eats primarily calcareous algae (*Corallina officinalis*), though it will ingest other algal species (Woods 1993). Extrapolating across these many studies, we suggest a diverse omnivorous diet composition for crabs of 5% crabs, 2% octopuses, 25% grazing invertebrates, 5% predatory invertebrates, 8% macrobenthos, 15% encrusting invertebrates, 10% phytal invertebrates, 10% large brown algae, 5% crustose algae, 5% foliose algae and 10% carcasses.

4.11.2 Octopuses

No estimates of octopus biomass were available for the study area, and this solitary predator was not observed during any of the intertidal and subtidal surveys. In Tasmania and South Australia, lobster fishermen record the number of dead lobsters and octopuses caught as bycatch (Brock & Ward 2004; Hunter et al. 2005). As these Australian species (*Jasus edwardsii* and *Pinnoctopus* (*Octopus*) *maorum*) are the same that occur in New Zealand (O'Shea 1999), we used estimates of the proportion of the abundance of octopuses to the abundance of rock lobsters to estimate octopus biomass in the region. On average, 4% of landings are lost to octopus predation in lobster traps in South Australia, with a range of 2–6% in Tasmania; an early report also estimated a 10% loss to octopuses in Hokianga, New Zealand, in 1972 (Brock & Ward 2004; Hunter et al. 2005). A similar percentage of octopus predation in lobster pots has been recorded

for octopuses captured in pot lifts during the lobster tagging programme in Te Tapuwae o Rongokako (D. Freeman, DOC, pers. comm.).

The total number of pot lifts in the commercial fishing region near the reserve is approximately 280 000/y based on numbers estimated in section 4.13. Tagging data from the reserve monitoring programme showed that a total of 1235 octopuses were captured in pot lifts during 2003–2005 (about 400 octopuses captured/y). We assumed that this is roughly 20% of the total annual biomass of octopuses, based on literature estimates of sustainable rates of bycatch of octopuses in lobster fisheries (Brock & Ward 2004), and thus estimated that there are 2300 octopuses in the model region (and thus 576 octopuses (approximately 3000 kg WW) in the reserve area). As an alternative approach, using rough estimates from the Australian lobster bycatch studies, 1/27 of total commercial landings were eaten by octopuses in pots, and the ratio of lobster to octopus mortality (bycatch) was approximately 3:1. Thus for the model region, using an average annual lobster fishery catch of 140 t, 1/81 of the total catch is 2 t or 2000 kg (approximately 400 octopuses) of octopus bycatch in the lobster fishery. Again, assuming 20% of octopuses are caught as bycatch, we estimated roughly 2000 octopuses in the study area. While clearly these estimates are not independent of lobster catch and effort data (pot lifts), we used these techniques (which gave similar results) in the absence of other information to estimate octopus abundance.

The total length of *Pinnoctopus maorum* ranges from 900 mm to 2064 mm, and its weight ranges from 1.5 kg to 9.2 kg in the outer Hauraki Gulf (mean = 1446 mm (7 kg) for males and 1167 mm (2 kg) for females) (Anderson 1999). Two smaller species in New Zealand reach sizes of 5 kg (*Octopus tetricus*) and 60 g (*Octopus warringa*). In this survey, the proportion of male to female octopuses was about 2/3 male (23 of 33 individuals captured). As no information is available in the Gisborne area, we assumed a similar sex ratio and an average individual weight of 5.3 kg, to extrapolate from individual octopus weight to total biomass in the marine reserve.

We assumed that the carbon:wet weight ratio for octopus is similar to that of squid, which has been estimated to be c. 8.3% (Brey 2001). This is consistent with work by Vlieg (1988), who found arrow squid dry weight to be 22.5% of wet weight, and ash to be 6.2% of dry weight; if ash-free dry material is made of material in carbohydrate proportions ($C_6H_{12}O_6$), then carbon is c. 40% ash-free dry weight or c. 9% wet weight. Vinogradov (1953) gave similar data for Cephalopoda, with dry weight ranging from 13% to 30% of wet weight and ash ranging from 0.9% to 2.4% of wet weight.

Trophic parameters were not available for octopuses in New Zealand. Therefore, we used values presented in an ecosystem model of a Chilean temperate reef, which reported values of P/B = 1.1/y and Q/B = 7.3/y (Okey et al. 2004). These give a P/Q of 0.15, which is reasonable.

The common octopus (*Pinnoctopus cordiformis*) is a selective feeder on New Zealand reefs, consuming mainly crustaceans (especially crabs and lobsters), bivalves, fish and other invertebrates (Sewell 2005). There is also evidence of some size-dependent cannibalism. In the absence of better information, we assumed an initial diet composition for octopuses of 50% crustaceans (20% lobster and 30% crab), 10% kina, 25% fish (15% benthic reef fish and 10% herbivorous reef fish) and 15% macrozooplankton.

4.11.3 Seastars, predatory gastropods and other mobile predatory invertebrates

Intertidal biomass estimates were calculated from intertidal monitoring surveys of the study area. Density estimates for intertidal predatory gastropods (mostly *Lepsiella scobina*) were 0.71 individuals/m^2 inside the reserve and 2.25/m^2 outside the reserve. Density estimates for other predatory invertebrates (seastars, polychaetes, brittlestars and nudibranchs) were 0.33/m^2 within the intertidal reserve area and 1.70/m^2 outside the reserve (Table 17). Since no size information was available from intertidal surveys, abundance estimates could not be converted to biomass.

Predatory invertebrates observed during subtidal surveys in the Gisborne area include the gastropod *Dicathais orbita* and the seastar *Astrostole scaber* (Shears & Babcock 2004b). Based on surveys of 75 m^2 of subtidal habitat, we estimated a density of mobile predatory invertebrates (excluding crabs and octopuses) of 0.09/m^2 (six *Dicathais* and one *Astrostole*). Depth-transects from the shallow subtidal region to the reef edge at the same locations showed a slightly higher predatory invertebrate density of 0.23/m^2, composed of three species of predatory whelks counted in 55 m^2 of habitats surveyed (N. Shears, University of Auckland, unpubl. data). Seastars were not present in quadrats at the four Gisborne sites in this survey, though one *Astrostole* was counted in quadrats at the neighbouring Mahia site. These estimates match other observations of very few mobile invertebrates on Gisborne reefs (N. Shears, pers. comm.). Other New Zealand surveys of mobile invertebrates have indicated higher numbers, with the average density of all mobile epifauna in the Hauraki Gulf being estimated at 14.1/m^2 (including grazing and predatory gastropods, crabs, sea cucumbers, pupu, limpets, paua and kina) (Smith 2003). In an earlier review of New Zealand reef habitats, Choat & Schiel (1982) indicated densities of all gastropod species of 5–38/m^2. For our model, we used the low density estimate of 0.09/m^2 for seastars and predatory gastropods, assuming that 70% of the individuals are predatory gastropods.

Taylor (1998a) gave the relationships between AFDW and linear body dimensions for many common rocky reef invertebrates (Table 18). The average size of *Dicathais orbita* ($n = 6$) in subtidal surveys was 43 mm, or 1.97 g AFDW per individual (Table 18). For *Buccinulum* sp., a smaller predatory gastropod, we estimated an average individual biomass of 0.24 g AFDW (Table 18). For all predatory gastropods in both intertidal and subtidal reef areas, we estimated an average individual biomass of 1.97 g AFDW/individual, as most of the biomass in surveys was of the larger gastropod. For seastars, we estimated an average biomass of 30 g WW.

Little information on trophic parameters is available for this group. Taylor (1998a) calculated P = 0.01 g AFDW m^{-2} y^{-1} and B < 0.01 g AFDW/m^2 for suspension-feeding gastropods, and P = 0.47 g AFDW m^{-2} y^{-1} and B = 0.21 g AFDW/m^2 for neogastropods. Based on these values, we estimated that P/B = 2.24/y for predatory gastropods. Using this value and assuming a ratio of 0.25 for P/Q, we calculated Q/B = 8.95/y. For seastars, we estimated P/B = 1.6/y and P/Q = 0.25; thus, Q/B = 6.4/y.

There are numerous studies on diet composition of predatory invertebrates, particularly in the intertidal region in New Zealand. Predation studies

show that the gastropods *Neothais scalaris* and *Lepsiella scobina* feed on intertidal barnacles (Luckens 1975). Predatory whelks in soft-sediment areas consume intertidal bivalves, particularly cockles (*Austrovenus stutchburyi*) (Stewart & Creese 2004). A 1970s study of diet preferences of the seastar *Astrostole scabra*, a generalist intertidal predator in Kaikoura, recorded diet composition as 68% molluscs (mostly grazing gastropods), 10.8% crustaceans (including more than 60 genera) and 15.4% unidentified (Town 1980). The grazing gastropods were further broken down into 19.9% trochid molluscs (*Cantharidus purpureus*, *Trochus viridus*), 16.9% chitons, 7.6% Rissoidae, 6% Turbinidae (*Cookia sulcata*) and 4.48% Littorinidae, including our trophic categories of both 'pupu/limpets' and 'other grazing invertebrates' (Town 1980). *Astrostole scabra* has also been reported as the primary predator of paua (McShane & Naylor 1995). We estimated percentage composition of this trophic group as being roughly 25% seastars and other large predators and 75% predatory gastropods (whelks), and estimated a diet composition for these predatory mobile invertebrates of 1% encrusting invertebrates, 75% grazing invertebrates, 15% crabs and 9% other predatory invertebrates.

4.11.4 Summary—Mobile predatory invertebrates

For crabs, we estimated a biomass of $0.018\,g\,C/m^2$, P/B of 0.95/y and Q/B of 4.75/y for rock crabs, and a biomass of $0.002\,g\,C/m^2$, P/B of 1.6/y and Q/B of 6.4/y for hermit crabs. For octopuses, we estimated a biomass of $0.011\,g\,C/m^2$, P/B of 1.1/y and Q/B of 7.3/y. For predatory gastropods, we estimated a biomass of $0.39\,g\,C/m^2$, P/B of 2.24/y and Q/B of 8.95/y. Finally, for seastars and other predatory invertebrate taxa not listed in the previous sub-groups, we estimated a combined biomass of $0.036\,g\,C/m^2$, P/B of 1.6/y and Q/B of 6.4/y.

For the purpose of our model, we reconciled biomass, production, consumption and diet composition across all mobile predatory invertebrates, weighting parameters over both biomass and consumption rates of each sub-group; minor diet components ($<5\%$) were removed to aid model balancing. Combined estimates were B of $0.106\,g\,C/m^2$, P/B of 1.67/y and Q/B of 7.15/y. We estimated a diet composition of 10% lobsters, 30% mobile grazing invertebrates, 5% sponges, 15% other encrusting invertebrates and 15% planktivorous fish.

4.12 MOBILE GRAZING INVERTEBRATES

Common mobile grazing invertebrates include paua, kina, pupu (grazing gastropods: *Cookia sulcata*, *Melagraphia* sp. and *Turbo* sp.), ngakihi (limpets), chitons and other grazing gastropods. We discuss paua, kina, pupu and ngakihi separately to enable the placement of these kaimoana species into separate trophic groups should this be preferable, though we combine all grazing invertebrates into one trophic group for our model.

4.12.1 Paua

Paua (*Haliotis australis* and *H. iris*) intertidal biomass was estimated from monitoring surveys for the reserve (Freeman 2006). Both species are present in the reserve, though *H. iris* was more abundant in intertidal monitoring surveys.

There are two recognised habitats for paua in the reserve: within the intertidal channels in the rock platform and associated with the Mixed Brown Algae habitat.

Paua abundance in the marine reserve was measured by walking transects. Densities of paua in the intertidal channels were calculated based on the length of channel, assuming a constant channel width of 1 m. Paua abundance in intertidal channels was relatively consistent, with a mean density of $0.036/m^2$. From aerial photos, intertidal channels were estimated to make up about 5% of the total area of the reef platforms.

Subtidal biomass was calculated from quadrat counts of paua that were made during the January 2002 survey of four sites in the Gisborne region (Shears & Babcock 2004b). Abundance data are available for two subtidal sites within the reserve, Pouawa South and Pouawa North (20 1-m^2 quadrats per site), and two subtidal sites outside the reserve, Baldy Reef and Makorori (20 and 15 1-m^2 quadrats, respectively). Six paua were recorded in 75 m^2 of surveyed subtidal habitat ($0.08/m^2$), occurring in quadrat samples at two of the four sites (Pouawa North and Baldy Reef) but only at the shallowest subtidal depth surveyed (< 2 m). Depth transects from the shallow subtidal region to the reef edge in the same locations gave similar estimates of paua density of $0.1/m^2$ (N. Shears, University of Auckland, unpubl. data). Paua density generally varies with depth, with highest densities at shallow depths (< 2 m). In Te Tapuwae o Rongokako Marine Reserve, higher paua densities of $0.2/m^2$ were normal, but only within subtidal habitats of Mixed Brown Algae less than 5 m deep (C. Duffy, DOC, pers. comm.). This habitat makes up about 2% of the total reserve area.

These figures suggest that there are 82 000 paua in the reserve area, with over 95% of these in the subtidal habitat. To convert abundance to biomass for both subtidal and intertidal paua, we required an estimate of size. As mean length was not measured by Shears & Babcock (2004b), we used estimates of mean length from length-frequency data obtained during intertidal monitoring surveys, where it was found that mean shell length was 61.6 mm inside the reserve and 32.4 mm outside the reserve. There is no quantitative stock assessment for paua fishery area PAU2 (east coast North Island), so we used the length-weight (mm-g) relationship of Schiel & Breen (1991) for D'Urville Island, Marlborough Sounds ($a = 2.59 \times 10^{-5}$, $b = 3.322$). Since the relationship between length and weight is non-linear, instead of calculating average individual weight based on mean length, we calculated average weights from weights per individual and the entire size-frequency distribution. This gave an average paua weight inside the reserve of 62 g WW. Assuming that carbon makes up approximately 6.7% of the wet weight of paua, as for other grazing gastropods, these figures lead to an overall paua biomass density of 0.015 g C/m^2 for the reserve.

To estimate growth rates for various sizes of paua, we used von Bertalanffy growth characteristics of paua from McShane & Naylor (1995) in conjunction with the length-weight relationship of Schiel & Breen (1991). Small paua grow faster than large paua, so to calculate an appropriate value for the population as a whole we estimated the annual growth-based production for each paua sampled. Average production due to growth was estimated to be 0.76/y. We assumed that production due to reproductive output is approximately twice production due to individual growth, giving an overall P/B of about 1.5/y. This value is similar to,

but lower than, previous estimates for molluscs in shallow temperate systems, where P/B = 1.9–2.8/y (Wolff 1994; Okey et al. 2004).

Consumption rates from laboratory studies range from 8–18.7% body weight/d for juveniles, and 2–7% body weight/d for adult paua (Marsden & Williams 1996). Using 4% body weight/d as an average value results in a Q/B of c. 15/y. This consumption rate is slightly higher than that given by Rybarczyk & Elkaim (2003), who gave Q/B = 7.5/y for 'benthic deposit feeders', Arreguin-Sanchez et al. (2002), who gave Q/B = 8.8/y for 'molluscs', and Wolff (1994), who gave Q/B = 9.9/y for 'bivalves > 10 mm'; and is slightly lower than that given by Jiang & Gibbs (2005), who suggested Q/B = 20/y for 'other shellfish' based on unpublished data. We expect that the laboratory paua studies with constant food supply are over-estimating consumption rate relative to *in situ* consumption; therefore, we conservatively estimated that Q/B = 8.0/y for paua in the reserve.

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

Fishery take of paua from inside the reserve is assumed to be zero. While paua is an important component of traditional and recreational fisheries outside the reserve, no information is available to estimate landings for non-commercial fisheries in PAU2. Commercial landings of paua in PAU2 are available in Ministry of Fisheries annual plenary reports (e.g. Sullivan et al. 2006).

4.12.2   Kina

Kina (*Evechinus chloroticus*) intertidal biomass was estimated from monitoring surveys for the reserve (Freeman 2006). Kina are found associated with two habitats in the reserve: within the intertidal channels in the rock platform and associated with the subtidal Mixed Brown Algae habitat. The average size of kina differed between the two habitats, with mean test diameter of 35 mm in intertidal habitats and 128 mm in subtidal habitats. We assumed that no kina occur off the reef areas, on soft sediments, or in water deeper than 12 m.

Walking transects gave a geometric mean of kina density in the intertidal channels of $1.3/m^2$. We note that the data at different sites vary by over two orders of magnitude. Nevertheless, these kina densities are well within the range observed throughout New Zealand.

While subtidal, habitat-specific estimates of kina abundance were available based on New Zealand habitat surveys (Shears et al. 2004; Table 4), we did not use these estimates in the model, as kina abundance in the region has been observed to be lower than at other New Zealand locations with similar habitat features (N. Shears, University of Auckland, pers. comm.). Instead, subtidal biomass was calculated from quadrat counts made during a survey of four sites in the Gisborne region in January 2002 (Shears & Babcock 2004b). Abundance data were available from two subtidal sites within the reserve, Pouawa South and Pouawa North (20 $1-m^2$ quadrats per site), and two subtidal sites outside the reserve, Baldy

Reef and Makorori (20 and 15 1-m^2 quadrats, respectively). In general, kina were very rare on subtidal reefs at Gisborne, with only 17 individuals (16 exposed, 1 cryptic) recorded in 75 m^2 of surveyed subtidal habitat (0.23/m^2). Kina density varied with depth, with peak density at mid-depths of 7–9 m. We used data from Pouawa North as the best representation of kina abundance within the model region (mean density = 0.23/m^2, with maximum density in depth ranges 7–9 m). Mean test diameter for subtidal kina measured during diver surveys was 128 mm, with a range of 70–170 mm.

We hence estimated that there are 240 000 kina in the reserve, with 78% of these in the subtidal area. We estimated an average weight as follows. First, we calculated a weight for kina with test diameters between 10 mm and 170 mm at 10-mm increments using the length-weight relationships from Taylor (1998a) (Table 18). The geometric mean of these values (140 g WW) was taken as an estimate of the average weight in the population. We converted WW to AFDW using a factor of 0.049 (Brey 2001). We then converted AFDW to carbon, assuming 6% of wet weight is carbon, as for benthic epifauna. Thus, we estimated a kina biomass of 0.078 g C/m^2 for the reserve.

Although the biology and ecology of kina have been extensively studied (e.g. Barker 2001), little is known about kina energetics (consumption and production rates). Lamare & Mladenov (2000) estimated that kina grow 8–10 mm in their first year of life. Growth rates vary considerably depending on local conditions, but kina may take 8–9 years to reach 100 mm TD (Lamare & Mladenov 2000), with *K* (von Bertalanffy) between 0.28/y and 0.39/y. The annual average growth rate for the population depends on the natural mortality (and hence age-frequency structure) of the population, which is likely to vary with region and is generally poorly known. For a natural mortality of c. 0.2/y, the average age in the population would be c. 5 y, and the annual biomass growth rate would be c. 0.27/y. Assuming that reproductive productivity is about three times as great as the growth production, we estimated that kina P/B = 1.1/y.

Consumption rates of kina are likely to be of the order of 5–10/y (here taken as 7.5/y), though no reliable local data exist for this parameter. Other ecosystem models in shallow temperate systems report P/B = 1.4/y and Q/B = 2.8–9.7/y for echinoid species (Okey et al. 2004).

Kina are grazing herbivores that preferentially consume drift algae from large canopy species (*Ecklonia radiata* and *Carpophyllum* spp.), but also consume live adult and juvenile plants (Schiel 1982; Barker 2001). They have also been observed eating crustose coralline algae and encrusting sponges (Ayling 1978). We suggest a diet composition of 60% large brown canopy algae, 15% foliose algae, 15% crustose algae, 5% encrusting invertebrates and 5% microphytobenthos in the model.

4.12.3 Kaimoana: pupu (gastropods) and ngakihi (limpets)

Pupu (gastropods) and ngakihi (limpets) are included as a separate group of gastropods, as these species are targeted in traditional fisheries in New Zealand. Pupu are grazing gastropods: *Turbo smaragdus* (cat's eye), *Melagraphia aethiops* and *Cookia sulcata*.

Based on surveys of 75 m^2 of subtidal habitat (Shears & Babcock 2004b), we estimated a density of pupu of 0.61/m^2 (based on observations of only *Cookia*

sulcata) for subtidal reef habitats. Depth transects from the shallow subtidal region to the reef edge also found low pupu densities of $0.23/m^2$, and also only detected *Cookia sulcata* in the $55\,m^2$ surveyed at four Gisborne sites (N. Shears, University of Auckland, unpubl. data). To estimate average biomass, we used a density of $0.61/m^2$ and converted abundance to AFDW based on an average size (biomass) of 38 mm (0.88 g) for *Cookia sulcata*, as obtained from subtidal surveys (Shears & Babcock 2004b), and using the length-weight relationships from Taylor (1998a) (Table 18).

Density estimates from intertidal monitoring surveys were 2.91 and 15.12 pupu/m^2 and 4.00 and 0.61 limpets/m^2 in reserve and non-reserve sites, respectively. Most limpets were very small individuals. Average sizes were obtained for the limpets *Cellana* spp. (9.4 mm), and pupu *Cookia sulcata* (22 mm) and *Turbo smaragdus* (16 mm) in the intertidal area. We converted these to individual biomass estimates of 0.004, 0.18 and 0.09 g WW/individual, respectively, based on length-weight conversions (Table 18; Taylor 1998a). We assumed that *Melagraphia* had a similar relationship to *Cookia* and that carbon makes up approximately 6.7% of the wet weight of grazing gastropods. Percentage composition of pupu in the reserve was 76% *Turbo*, 16% *Melagraphia* and 8% *Cookia*. Outside the reserve, percentage composition was 63% *Turbo*, 37% *Melagraphia* and 0.001% *Cookia*.

We suggest that P/B = 2.35/y (range 1.9–2.8/y) and Q/B = 9.75/y (range 5.5–14/y) based on parameter ranges for molluscs from ecosystem models of other shallow temperate systems (Wolff 1994; Okey et al. 2004). Other production estimates for limpets include 1.8–4.7/y (Edgar 1990).

Production, consumption and diet of pupu/limpets are discussed concurrently with diet for grazing gastropods in section 4.12.4.

4.12.4 Other grazing gastropods

Other herbivorous gastropods observed during subtidal surveys in the Gisborne area include the gastropods *Cantharidus purpureus*, *C. opalas*, *Modelia granosa* and *Trochus viridis*, and the chiton *Eudoxochiton nobilis* (Shears & Babcock 2004b). Based on surveys of $75\,m^2$ of subtidal habitat, we estimated a density of $0.93/m^2$ mobile grazing invertebrates ($0.73/m^2$ *Trochus viridis*) for subtidal reef habitats. Note that subtidal surveys likely counted only the larger mobile invertebrates. We converted abundance to biomass (Table 18) based on an average size (biomass) of 23 mm (0.38 g) for *Trochus viridis* and 25 mm (0.14 g) for *Cantharidus purpureus*, which we also used to represent the other less abundant gastropods for which we did not have size estimates.

Intertidal monitoring surveys resulted in density estimates of 4.21 and 6.43 chitons/m^2, and of 1.01 and 1.77 grazing gastropods/m^2 in reserve and non-reserve sites, respectively. Most grazing gastropods in the intertidal were *Zeacumantus subcarinatus*, *Trochus viridis* and other smaller species. Four chiton species were also observed: *Amaurochiton glaucus*, *Chiton pelliserpentis*, *Ischnochiton maorianus* and *Onithochiton neglectus*. The average size of these four species was 17–20 mm length. We estimated an average individual AFDW of small grazing gastropods of 0.01 g, based on the average AFDW of various grazing species including *Cantharidus purpureus* and *Trochus viridis* at 10 mm length.

Higher densities of mobile invertebrates were found during other New Zealand surveys, with estimates of all mobile epifauna in the Hauraki Gulf of $14.1/m^2$ (including grazing and predatory gastropods, crabs, sea cucumbers, pupu, limpets, paua and kina) (Smith 2003). Species-specific grazer densities were $1.6/m^2$ for *Trochus viridis*, $0.15/m^2$ for *Cookia sulcata*, and $0.01/m^2$ for the chiton *Cryptoconchus proposus* (Smith 2003). Choat & Schiel (1982) indicated densities of $5-38/m^2$ for all gastropod species in an early review of New Zealand reef habitats. A study of rocky reef productivity at Leigh indicated a density of 30.28 grazing gastropods/m^2 on the seafloor and an additional $12.49/m^2$ on seaweeds, with a total biomass of $8.27\,g\,AFDW/m^2$ and an estimated (combined) productivity of $5.31\,g\,AFDW\,m^{-2}\,y^{-1}$ (Taylor 1998a).

Taylor (1998a) estimated production and biomass for these species at Leigh: $P = 4.70\,g\,AFDW\,m^{-2}\,y^{-1}$ and $B = 7.01\,g\,AFDW/m^2$ for grazing gastropods on the seafloor, and $P = 0.61\,g\,AFDW\,m^{-2}\,y^{-1}$ and $B = 1.26\,g\,AFDW/m^2$ for grazing gastropods on seaweeds. He also estimated that grazing gastropods made up 28% of the total faunal biomass in the system ($8.48\,g\,AFDW/m^2$), and contributed roughly 12% of the total production. Ecosystem models of other shallow temperate systems have given $P/B = 1.9-2.8/y$ and $Q/B = 5.5-14/y$ as parameter ranges for molluscs (Wolff 1994; Okey et al. 2004). Brey & Hain (1992) gave a P/B of $0.305/y$ for the Antarctic benthic mollusc *Lissarca notorcadensis*, but production rates are likely to be higher for the warmer waters of Te Tapuwae o Rongokako Marine Reserve. We initialised the model with $P/B = 1.8$ and $Q/B = 9.75$ for chitons and other grazing gastropods.

Most intertidal grazing gastropods are generalist herbivores (Creese 1988). Gut contents are often difficult to quantify as the guts contain large amounts of unidentifiable material, and the contribution of microalgae is rarely measured. A review of grazing studies on New Zealand rocky reefs indicated that *Turbo smaragdus* eats foliose red and fucoid brown algae, *Amaurochiton glaucus* eats coralline algae, *Siphonaria zelandica* (a limpet) eats *Ralfsia* (a crustose brown alga), and *Zeacumantus subcarinatus* eats primarily *Ulva lactuca* (sea lettuce) (Creese 1988). A functional group analysis of intertidal grazing molluscs at Leigh and Otago sites listed the gut contents of chiton species and *Turbo* as including articulated coralline, leathery and filamentous algae; limpets eat crustose corallines, with additional components of filamentous and foliose algae; and other gastropods were associated with filamentous and foliose algae (Raffaelli 1985). Most gastropod guts also contained small amounts of various encrusting invertebrate species in this study. A detailed study of gut contents of *Cookia sulcata*, *Trochus viridis* and *Cantharidus purpureus* at Leigh showed the majority to consist of detritus composed of *Ecklonia* fragments, unicellular algae, diatoms, fine sediment, sponge spicules, crustacean appendages, foraminifera, bryozoans, and filamentous and coralline algae (Freeman 1998), implying that these gastropods are functionally detritivores, grazing primarily on the decaying tissue on distal parts of kelp, with some contribution of epiphytes and benthic sources. As about 80% of grazing gastropods in the intertidal region of our study area were chitons, we incorporated a high fraction of coralline algae into the diet.

We suggest a diet composition for chitons and *Trochus* of 15% large brown algae, 30% foliose and turfing algae, 45% crustose and coralline algae, 5% microphytobenthos, and 5% encrusting invertebrates. For pupu and limpets, we suggest 30% large brown algae, 40% foliose and turfing algae, 20% crustose and coralline algae, 5% microphytobenthos, and 5% encrusting invertebrates.

4.12.5 Summary—Mobile grazing invertebrates

We estimated a paua biomass of $0.015\,\text{g}\,\text{C/m}^2$, P/B of 1.5/y and Q/B of 8.0/y, and a kina biomass of $0.078\,\text{g}\,\text{C/m}^2$, P/B of 1.1/y and Q/B of 7.5/y. For kaimoana (pupu), we estimated a biomass of $0.008\,\text{g}\,\text{C/m}^2$, P/B of 2.35/y and Q/B of 9.75/y for edible gastropods, and a biomass of $0.00004\,\text{g}\,\text{C/m}^2$, P/B of 2.35/y, and Q/B of 9.75/y for limpets. For other grazing gastropods, we estimated a biomass of $0.005\,\text{g}\,\text{C/m}^2$, P/B of 1.8/y and Q/B of 9.75/y for *Trochus*, and a biomass of $0.005\,\text{g}\,\text{C/m}^2$, P/B of 1.8/y and Q/B of 9.75/y for chitons.

To estimate trophic parameters for all mobile grazing invertebrates combined, we summed biomass, production and consumption of each taxon as calculated above, and divided production and consumption by total biomass to estimate P/B and Q/B. Diet components were reconciled across the three groups via weighting over both biomass and consumption rates, and minor diet components were removed to aid model balancing. Combined estimates were B of $0.112\,\text{g}\,\text{C/m}^2$, P/B of 1.31/y and Q/B of 7.94/y. We estimated average diet composition of this trophic group as 35% large canopy algae (and associated detritus), 20% foliose and turfing algae, 20% crustose and coralline algae, and 25% microphytes.

4.13 LOBSTERS

The red rock lobster *Jasus edwardsii* is a key species in New Zealand coastal marine ecosystems. The biomass of subtidal reef-associated lobsters was estimated from subtidal monitoring surveys (D. Freeman, DOC, unpubl. data) and extrapolated across habitat types, as described in section 3 (Fig. 9A). The mean size of lobster, as calculated from size-frequency data from tagging programmes, was 57 mm tail width, and the average weight of lobsters captured in potlifts from 2003 to 2005 was 0.6 kg. Average size was converted to biomass using rate conversions from fishery reports: females, $w = 1.30\text{E}{-}5 {*} \text{TW}^{2.5452}$; Males, $w = 4.16\text{E}{-}6 {*} \text{TW}^{2.9354}$; where w is the wet weight (kg) and TW is tail width (mm) (Haist et al. 2005). We assumed that carbon makes up approximately 5.6% of the wet weight of lobsters (Brey 2001). Alternatively, the formula presented by Taylor (1998a) ($a = 7.551 \times 10^{-4}$ and $b = 2.5291$ (Table 18)) could have been used to convert length to dry weight; Taylor also gives von Bertalanffy relationships as $L_{\text{inf}} = 187$ mm and $K = 0.09$ for males, and $L_{\text{inf}} = 117$ mm and $K = 0.16$ for females. We assumed that lobsters are not permanent residents of intertidal areas, and calculated biomass of this trophic group based solely on abundance in subtidal areas.

Population rate of increase has been estimated as 25% increase in lobster abundance over 3 years (2000 to 2003) following reserve implementation, with an increase in average lobster size of 1.14 mm/y (D. Freeman, DOC, unpubl. data). Other rates of increase in marine reserves after implementation are 38% over 3 years and 2.3 mm/y in Te Angiangi Marine Reserve (D. Freeman, DOC, unpubl. data), 4.4% per year in Tonga Island Marine Reserve (Davidson et al. 2002), and 6.7% per year averaged over marine reserves in northeastern New Zealand (Kelly et al. 2000).

Annual growth rates of adult lobsters have been calculated as 4.8 mm from tag returns in Gisborne (Annala 1978), and 5.9–12.2 mm/y for males and 2.9 mm/y

Figure 9. Estimated lobster and fish abundance over the study region obtained by triangulation of data based on diver surveyed abundance (2000–2003 surveys) and habitat type. Each plot is scaled according to the colour bar shown at the bottom of the figure. Maximum values for each taxon correspond to red on the colour bar; blue and purple colours indicate lower estimated values. Maximum values (number/m^2) are as follows: A. lobster (0–26.6/m^2); B. blue moki (0–0.63/m^2); C. butterfish (0–0.19/m^2); D. goatfish (0–0.50/m^2); E. john dory (0–0.048/m^2); and F. spotty (0–11.0/m^2).
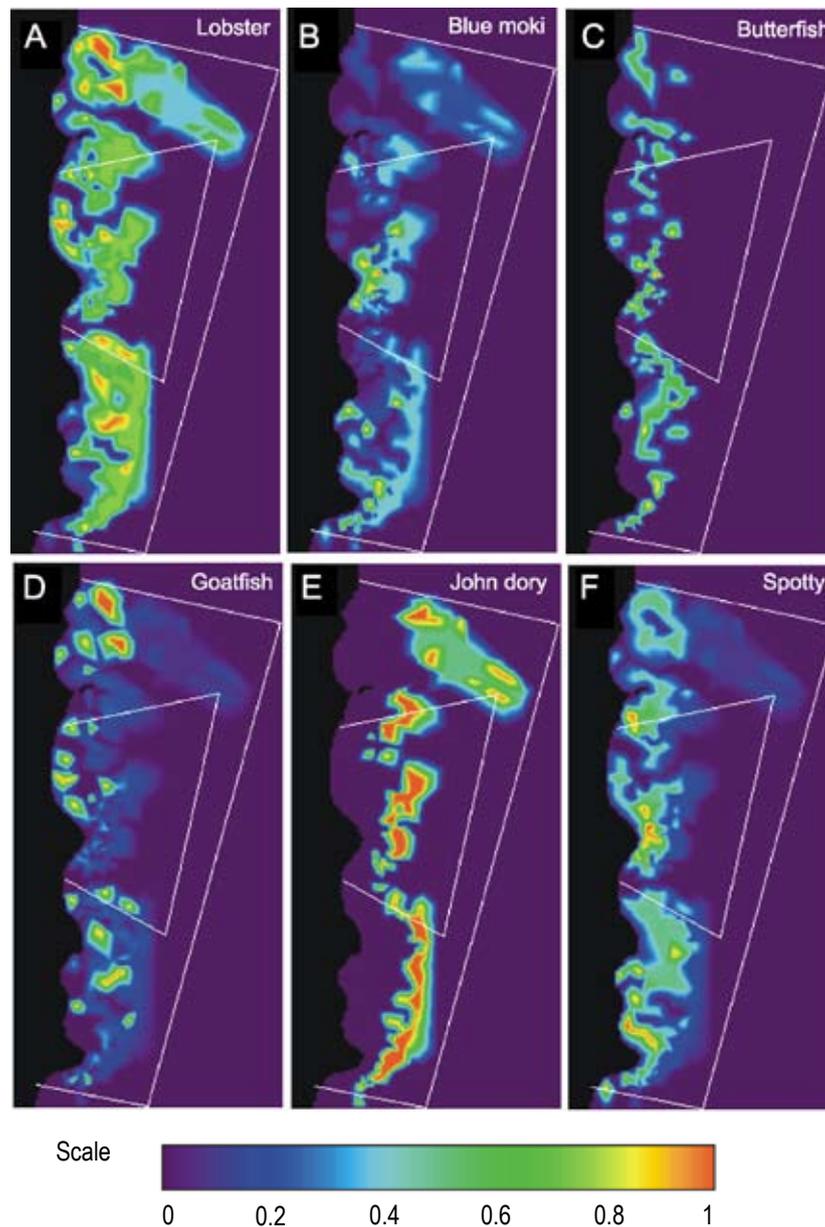
for females from size-frequency data in Gisborne (Annala 1980). Recent evidence has shown that lobster growth rates are higher in the reserve than outside it, probably due to indirect effects of fishing (D. Freeman, DOC, pers. comm.). While the data presented here include only the reserve area, larger areas that include both reserve and non-reserve areas could be modelled with different growth rates (and thus lobster production) to examine potential implications of different lobster growth rates inside and outside the reserve on model dynamics. At Leigh, Taylor (1998a) estimated that spiny lobsters contribute 2.37% of the total faunal biomass in the system, with $P = 0.05 \, g \, AFDW \, m^{-2} \, y^{-1}$ and $P/B = 0.07/y$, and make a very small relative contribution (0.10%) to total production. Comparable lobster trophic parameters were used in a Chilean temperate reef ecosystem model, where $P/B = 0.45/y$ and $Q/B = 7.4/y$ (Okey et al. 2004). Production of the spiny lobster *Panulirus homarus* in South Africa has been estimated at $47.6 \, kJ \, m^{-2} \, y^{-1}$ ($P/B = 0.42/y$) (Berry & Smale 1980). We initialised the model with $P/B = 0.5/y$ and $Q/B = 7.4/y$.

Movement of lobsters in the area has been studied in great detail from tag returns, with estimates that fewer than 5% of lobsters move greater than 5 km (Annala 1981; Booth 1997, 2003; Kendrick & Bentley 2003). Seasonal migrations of lobsters from reef to soft-sediment offshore habitats have been documented in other lobster populations (Kelly et al. 2002), though it is assumed in this model that these seasonal migrations are within the model boundaries as per data from the tagging study (D. Freeman, DOC, unpubl. data). Tagging studies suggest that most lobsters in the reserve do not move off the reef, and only the large males forage seasonally on the soft sediments, which are within the model boundaries. Unfortunately, little is known about diet composition during these seasonal excursions. For this initial trophic model, we assumed that lobsters remain within the model region.

The diet composition of lobsters is remarkably similar between sites that are separated by c. 550 km (Leigh and Wellington), and although there have been marked changes in the community composition of reefs over a period of 20-25 years (due to protection as marine reserve), these do not appear to have had a significant influence on *J. edwardsii* diet (S. Kelly, Auckland Regional Council, unpubl. data). Diet composition studies have shown that lobsters are a mix of opportunistic and selective predators, with a diet that includes 35-45% molluscs, 15-30% crustaceans (decapods, amphipods, ostracods and barnacles), 5-15% polychaetes, 0-10% algae (Phaeophyta, Chlorophyta, Rhodophyta and *Corallina* sp.), 8-13% echinoids (*Evechinus chloroticus* and ophiuroids), 0-5% encrusting benthos, and 0-3% fish. Mollusc species in guts were represented by 46 gastropod, 22 bivalve and 8 chiton species; trochid gastropods (e.g. *Cantharidus purpureus, Trochus viridus*) were most common, while the family Turbinidae (e.g. *Cookia sulcata*) was extremely rare in guts, despite being abundant in lobster habitats. Lobsters very rarely eat sponges (M. Kelly, NIWA, pers. comm.).

For the purposes of the initial model parameters detailed in this report, which are based solely on the reserve area with no lobster fishing, we do not include harvest or bait input from the lobster fishery in the model (management area CRA3, statistical area 910 which is 100 km of coastline incorporating the entire study area including the marine reserve), as no lobsters are fished from the reserve. If fisheries are to be included, Ministry of Fisheries stock assessments are published regularly with commercial landings, estimates of recreational, traditional and illegal landings, catch per unit effort (CPUE), and average weight per lobster (e.g. Haist et al. 2005). CPUE is usually given as the number of pot lifts, which can be used to estimate bait input (e.g. each pot is stocked with c. 2 kg of baitfish).

Fishes were divided into five groups. Cryptic reef fishes were first separated from larger species, and then the non-cryptic fishes were divided according to feeding preference: invertebrate feeders, piscivores, planktivores and herbivores. Extensive examination of the stomach contents of commercially important pelagic, demersal and reef-associated fish species in New Zealand underpins this division (e.g. Thompson 1981; Clark 1985; Clark et al. 1989), but for some species we note that the appropriate group is not unambiguous. For example, trevally (*Caranx georgianus*) is usually a midwater (planktivorous) feeder, but occasionally feeds by grubbing in the bottom sediments (Thompson 1981). In such cases, we assigned the fish to the trophic group that encompasses the largest proportion of the diet.

The abundance of large, reef-associated species was estimated from subtidal monitoring surveys, as described in section 3.2.2, and extrapolated across the subtidal habitat in the study area. Cryptic fish were not documented during subtidal reef fish monitoring. We used abundance estimates from other North Island locations to estimate cryptic reef fish abundance for intertidal and subtidal habitats. Demersal and pelagic fish abundance was estimated using research trawls and aerial surveys in the surrounding region to estimate biomass over soft sediments within the model region.

4.14.1 Biomass

Reef-associated fishes

The abundance of exposed (non-cryptic) reef-associated fish species was estimated based on diver transect surveys (Freeman 2005). Fish abundances were summarised by habitat type, as given in Table 3, and extrapolated across the entire model region (Fig. 9B–F). Surveys inside the reserve were assumed to apply to the entire reserve area. Similarly, all diver fish survey data outside the reserve but inside the larger model region were 'pooled' and assumed to apply to this whole 'outside reserve' study area.

There were 85 diver transects inside the reserve and 66 transects outside the reserve. These covered all habitat types except 'Deep Cobbles' and 'Sand'. We assumed that fish abundance over 'Deep Cobbles' was 20% of that over 'Deep Reef'.

Demersal fishes

To estimate demersal fish biomass over soft-sediment regions of the study area, we used trawl surveys of demersal fish abundance. Common species captured during inshore trawl surveys in the East Cape region included anchovy *Engraulis australis*, barracouta *Thyrsites atun*, carpet shark *Cephaloscyllium isabellum*, elephant fish *Callorhinchus milii*, frostfish *Lepidopus caudatus*, gurnard *Chelidonichthys kumu,* john dory *Zeus faber*, jack mackerel *Trachurus novaezelandiae*, kahawai *Arripis trutta*, red cod *Pseudophycis bachus*, rough skate *Dipturus nasutus*, school shark *Galeorhinus galeus*, snapper *Pagrus auratus*, spiny dogfish *Squalus acanthias*, rig *Mustelus lenticulatus*, tarakihi *Nemadactylus macropterus*, trevally *Pseudocaranx dentex* and warehou *Seriolella brama* (Ministry of Fisheries Research Trawl Survey database). No

trawl data were available within the study area; thus we used data from all trawls on the continental shelf within 100 km of the model area.

To estimate biomass of the demersal fish trophic group, we calculated average biomass (kg) per trawl over the area covered by each trawl (approximated by the average trawl distance × the average gear wing width) (Table 19). For simplicity, we did not make any corrections for gear inaccuracies in total amount of area covered. Species distributions differed with increasing depth, with snapper, trevally, gurnard, spiny dogfish and kahawai being the most common species in the shallow depths surveyed (Table 20). We did not incorporate catchability into our estimates, as this information is unknown, and assumed that trawl catches are representative of demersal fish biomass in the area.

TABLE 19.   AVERAGE BIOMASS (kg WW) OF DEMERSAL FISHES (OBTAINED FROM THE MINISTRY OF FISHERIES RESEARCH TRAWL DATABASE), AVERAGED BY DEPTH FROM TRAWLS NEAR THE MODEL AREA.

Area covered approximated by average trawl distance × average gear wing width.

DEPTH RANGE (m)	BIOMASS (kg)	DISTANCE n.m.	DISTANCE m	WING WIDTH (m)	ESTIMATED AREA COVERED m^2	ESTIMATED AREA COVERED kg/m^2
30–40	86.00	3.46	6398.66	20.00	127973.2	0.000672
40–50	397.01	3.59	6639.42	20.25	134448.3	0.002953
75–90	144.34	3.46	6403.80	20.33	130210.7	0.001109
100+	203.97	3.38	6265.93	18.67	116964.1	0.001744

TABLE 20.   TOP TEN MOST ABUNDANT DEMERSAL FISH SPECIES AND SPECIES-SPECIFIC BIOMASSES (kg WW) AVERAGED OVER DEPTH CATEGORIES FROM TRAWLS NEAR THE MODEL REGION.

Data taken from Ministry of Fisheries Research Trawl database. Anc = anchovy, Bar = barracouta, Car = carpet shark, Fro = frostfish, Gur = gurnard, Jdo = john dory, Jmn = jack mackerel, Kah = kahawai, Rco = red cod, Rsk = rough skate, Sch = school shark, Sna = snapper, Spd = spiny dogfish, Spo = rig, Tar = Tarakihi, Tre = trevally, and War = warehou. Scientific names are listed in section 4.14.1.

DEPTH (m)	SPECIES/ BIOMASS	1	2	3	4	5	6	7	8	9	10
30–40	Species	Sna	Tre	Gur	Spd	Kah	Anc	Jmn	Bar	Ele	Spo
	Biomass	28.1	25.2	10.0	8.9	3.5	2.2	2.0	1.7	1.2	1.0
40–50	Species	Rco	Kah	Gur	Sna	Bar	Tre	Jmn	War	Sch	Spo
	Biomass	89.3	85.6	54.5	44.3	33.3	23.3	17.7	7.9	6.5	6.4
75–90	Species	Bar	Sna	Jdo	Gur	Jmn	Car	Rco	Rsk	Fro	Tre
	Biomass	36.0	24.8	11.7	10.7	9.5	7.7	7.0	6.5	5.8	4.3
100+	Species	Tar	Sch	Fro	Bar	Sna	Jmn	Car	Jdo	Gur	Tre
	Biomass	79.3	33.7	28.3	18.9	8.3	7.6	5.4	3.8	3.3	3.2

Pelagic fishes

To estimate pelagic fish biomass over soft-sediment regions of the study area, we used aerial surveys of pelagic fish abundance and fishery stock assessments. Aerial surveys are rare in the East Cape region. We used aerial survey data for the five most abundant pelagic fish species in the area (kahawai *Arripis trutta*, jack mackerel (primarily *Trachurus novaezelandiae*), blue mackerel *Scomber australasicus*, kingfish *Seriola lalandi*, and skipjack tuna *Katsuwonus pelamis*) to generate estimates of abundance of each species. Note that three of these species were also caught in demersal (bottom) trawls, as these species are occasionally found near the bottom as well as being observed schooling near the surface. Some species were also occasionally observed (transient individuals, usually) in reef fish transects.

To estimate abundance of single species and mixed schools of the abundant species, we used aerial sitings from survey square #202 (centroid 38°45′S, 178°15′E) (30 × 30 n.m.), which is the square incorporating the model region, using only pilot #9 to minimise variability between observers. Most effort in the area, and thus most of the sitings, were in the 1986–1988 period, during the months of October, November and December. Data are given in the form of pelagic aggregate of tonnage sited, and we calculated average abundance by year as tonnes sited per hour based on the number of 15-min periods spent in the survey square (approximately equating to the number of visits). Aerial surveys indicated that the annual minimum absolute abundance for the pelagic fish component of square #202 is 3890–7880 t (P. Taylor, NIWA, pers. comm.). These are totals of observed sightings and we have no way, at this stage anyway, of estimating variance. Combining data for kahawai, jack mackerel, blue mackerel, kingfish and tuna, we estimated a pelagic fish biomass of 4739 t in the reserve area and 1968 t outside the reserve.

Pelagic fish are landed in commercial fisheries off East Cape; however, their contribution to landings in the study area is small, if not zero. Data are not available to define the proportion of landings (if any) that occur within the study area. Some recreational fishing does occur, including very small amounts of beach casting for snapper and kahawai. As our preliminary model is based only on the marine reserve, we assumed that no commercial, recreational or illegal fishing occurs within the model area.

Cryptic reef fishes—microcarnivores

Cryptic fishes were not counted during subtidal reef surveys in the study area. Therefore, we used studies in rocky reef habitats in northeastern North Island (Hauraki Gulf) (Smith 2003) to estimate biomass of subtidal cryptic reef fishes, using the average density of cryptic fishes found at Great Barrier Island (Aotea Island) and Coromandel offshore islands, as Department of Conservation staff suggested that these had the most similar reef community assemblage to the study region. Fish were counted over ten contiguous 5-m^2 quadrats along a 50-m transect, resulting in an average abundance of 3.28 cryptic fish/m^2. The most abundant species in these surveys included *Notoclinops segmentatus* (blue-eyed triplefin), *Forsterygion varium* (variable triplefin), *Forsterygion malcolmi* (mottled triplefin), *Forsterygion flavonigrum* (yellow-black triplefin), *Obliquichthys maryannae* (oblique-swimming triplefin) and *Pempheris adspersus* (big eye).

Willis & Anderson (2003) made similar estimates of cryptic fish abundance in northeastern rocky reefs, with 40 and 15 fish per 9-m^2 plot (4.44 and 1.67/m^2) in kelp forests in non-reserve and reserve areas, respectively, and 35 and 30 fish per 9-m^2 plot (3.89 and 3.33/m^2) in urchin barrens in non-reserve and reserve areas, respectively. The most common subtidal species in this study were *F. lapillum*, *Dellitchthys morelandii*, *F. varium* and *Ruanoho whero*. For our model, we averaged over all studies to arrive at an estimate of 3.32 cryptic reef fish/m^2 in subtidal habitats. We used an average size of 1 g per fish to calculate biomass.

Intertidal rock pool fish abundance was estimated from abundance and biomass information in central Hawke's Bay (Glassey 2002). The nine most abundant intertidal fish were *Grahamina capito*, *Ericentrus rubrus*, *Acanthoclinus fuscus*, *Bellaspiscus medius*, *Forsterygion lapillum*, *Trachelochismus melobesia*, *Notolabrus celidotus*, *Dellichthys morelandi* and *Lissocampus filum*. Across all species, mean fish weight was 1.03 g per individual, and mean abundance and biomass of fish (standardised to pool surface area) was 10 individuals and 10 g/m^2 (Glassey 2002). Fish abundance has also been estimated for subtidally fringing macroalgal habitats (Duffy 1989). Densities of 0.86 and 0.54 fish per kg of macroalgae were calculated for *Carpophyllum maschalocarpum* and *C. plumosum*, respectively (Duffy 1989). We extrapolated the estimated abundance of 10 fish/m^2 in intertidal rock pools across the intertidal area, assuming that 20% of the intertidal reef area is rock pools suitable for permanent occupation by cryptic fish.

Fish weights

To convert fish abundance to biomass it is necessary to estimate the average weight of a fish in the population. Since this has not been measured in Te Tapuwae o Rongokako Marine Reserve it must be estimated.

We attempted to estimate average fish weight for each species present in the marine reserve by two methods:

1. **Method 1—Based on observed average weights in Leigh marine reserve:** Average and maximum fish lengths and average and maximum fish weights have been reported for many reef-associated fish species found in Cape Rodney to Okakari Point Marine Reserve (hereafter referred to as Leigh) by Thompson (1981). Many of the species are common to Te Tapuwae o Rongokako Marine Reserve and are likely to have similar size distributions. Data from Leigh indicate that the median of the length as a proportion of maximum length of fish is 0.67 (range 0.43–0.93). Median weight as a proportion of maximum weight of fish in Leigh is 0.42 (range 0.13–0.99). We would expect the median weight in our model region to be lower due to the shorter time since implementation of reserve status compared to Leigh.

2. **Method 2—Based on maximum weight adjusted by a factor:** Maximum weights were calculated for each species from maximum lengths of fish using a length-weight relationship (wet weight). Maximum fish lengths were taken from Ministry of Fisheries plenary reports on New Zealand fish (e.g. Sullivan et al. 2006); maximum lengths of fish in Leigh (Thompson 1981); and data from miscellaneous New Zealand publications from the online resource 'Fishbase' (Froese & Pauly 2005). The maximum lengths of fish reported in Sullivan et al. (2006) agreed relatively well with those given in Thompson (1981) (median absolute differences were 21%).

Length-weight relationships for many New Zealand fish are available in Sullivan et al. (2006) and Taylor & Willis (1998); some are also given in Fishbase (Froese & Pauly 2005). Relationships between length and weight may also be inferred from data given by Thompson (1981). Where no length-weight conversion was available for a particular species, we used a log-log regression based on all available data for other species. The regression was relatively robust ($n = 111$ and $R^2 = 0.81$): $W = 0.171 * L^{2.40}$, where W = weight (g WW) and L = length (cm). The length data spanned 9–430 cm, and the weight data covered 0.016–16 kg.

Divers estimated fish lengths for six species of fish in Te Tapuwae o Rongokako Marine Reserve (blue cod *Parapercis colias*, red moki *Cheilodactylus spectabilis*, blue moki *Latridopsis ciliaris*, butterfish *Odax pullus*, snapper *Pagrus auratus* and tarakihi *Nemadactylus macropterus*) during subtidal reef fish surveys. Most of the fish sampled were blue cod (49%) or red moki (36%). These were estimated in three, or sometimes four, size categories: e.g. snapper < 100 mm, 100–400 mm and > 400 mm. Fish were assumed to be equally distributed within these length groups, between a minimum fish length (assumed to be 10 mm) and the maximum lengths of fish. Mean lengths were estimated to be 0.46 (0.33–0.56) of the maximum fish lengths. Note that the average weight of a fish is not the weight of a fish of average length, because the relationship between length and weight is non-linear. We hence used the length-weight relationships for each species to estimate an average weight for the six observed fish species in the marine reserve. The results indicate that the mean weight for these six species in the marine reserve is 0.28 (0.19–0.46) of the maximum weight.

For the model, the ratio of average weight to maximum weight was assumed to be equal to the average of the two ratios calculated in Methods 1 and 2. As mentioned previously, average weight as a proportion of maximum weight of fish based on fish at Leigh using Method 1 was 0.42 (0.13–0.99). This higher value is consistent with fish being larger relative to their maximum size in Leigh than in Te Tapuwae o Rongokako Marine Reserve (average length ratio for Te Tapuwae o Rongokako Marine Reserve : Leigh is 0.68) due to the longer time since reserve establishment at Leigh. In contrast, our calculation for Te Tapuwae o Rongokako only includes six species; other species that are not targeted in commercial and recreational fisheries might be expected to be larger on average relative to their maximum weight. Thus, we expect the actual factor to be between the estimates calculated by both methods. The factor used in the model was hence 0.33 (average of 0.42 and 0.28).

We used this factor to convert the abundance of fish over the reef landscape into biomass (wet weight) (Table 21). Biomass (wet weight) was converted to g C/m^2 using a ratio of carbon to wet weight of fish of 8.3%. Literature ranges of fish biomass (wet weight) to g C are 5.3% and 12.5% based on values from Ikeda (1996), Parsons et al. (1984), McLusky (1981) and Cohen & Grosslein (1987).

4.14.2   Production

The most accurate way of estimating annual production of a fish is to use an age-structured population model. In the absence of necessary information to do this, an empirical relationship that relates the maximum weight of the fish to P/B can be used, with small fish having generally higher production rates per unit weight than larger fish. Annual P/B ratios for non-cryptic fish were calculated from the

Biomass (g C/m²) is given as a proportion of the group biomass, and abundance (number of fish per m²)
is given as a proportion of the abundance of all the non-cryptic fish. P/B = production/biomass;
Q/B = consumption/biomass.

COMMON NAME	SCIENTIFIC NAME	BIOMASS (% GROUP)	ABUNDANCE (% TOTAL)	P/B (y⁻¹)	Q/B (y⁻¹)
Invertebrate feeder					
Red moki	*Cheilodactylus spectabilis*	33.0	1.6	0.32	2.7
Scarlet wrasse	*Pseudolabrus miles*	17.8	9.8	0.60	4.6
Leatherjacket	*Parika scaber*	14.0	2.4	0.44	2.9
Blue moki	*Latridopsis ciliaris*	9.2	0.5	0.33	3.4
Porae	*Nemadactylus douglasi*	8.6	0.8	0.37	5.1
Snapper	*Pagrus auratus*	5.8	0.3	0.32	3.8
Spotty	*Notolabrus celidotus*	5.2	4.5	0.67	4.9
Banded wrasse	*Notolabrus fucicola*	3.4	0.9	0.49	3.8
Goatfish	*Upeneichthys lineatus*	1.6	0.3	0.45	5.0
Piscivore					
Kahawai	*Arripis trutta*	35.3	2.6	0.42	3.9
Rock cod	*Lotella rhacinus*	27.9	2.7	0.36	2.4
Blue cod	*Parapercis colias*	27.9	2.7	0.45	2.9
Kingfish	*Seriola lalandi*	5.2	0.3	0.38	6.8
Spiny dogfish	*Squalus acanthias*	1.7	0.0	0.31	2.7
Red-banded perch	*Hypoplectrodes huntii*	0.4	0.4	0.81	5.8
Jack mackerel	*Trachurus novaezelandiae*	0.4	0.1	0.50	3.9
Planktivore					
Sweep	*Scorpis lineolatus*	35.8	28.3	0.52	7.9
Trevally	*Pseudocaranx dentex*	37.7	21.0	0.47	6.0
Blue maomao	*Scorpis violceus*	13.6	10.6	0.52	4.9
Butterfly perch	*Caesioperca lepidoptera*	12.8	11.2	0.53	4.6
Herbivore					
Marblefish	*Aplodactylus arctidens*	86.8	0.4	0.40	9.4
Butterfish	*Odax pullus*	13.2	0.1	0.43	10.1

equations given by Haedrich & Merrett (1992), where P/B = 2.4M$^{-0.26}$, M being
the maximum wet weight (g) of the fish species. This relationship gives similar
results to that of Banse & Mosher (1980). Work on the Chatham Rise suggests
that these regressions tend to overestimate production values by a factor of
c. 2.3. However, it is not known whether this result, which was based on open
ocean middle-depth and deep-water species, is applicable to the shallow-water
ecosystem of Te Tapuwae o Rongokako Marine Reserve. Hence, we have not
reduced the P/B values estimated by the regression of Haedrich & Merrett (1992)
at this stage.

For non-cryptic fish species of Te Tapuwae o Rongokako, production was estimated
to be between 0.32/y and 0.81/y (median = 0.45/y) (Table 21). For cryptic fish,
we estimated a P/B of 2.4/y. This is generally higher than for mid- and deep-water
species, as expected. In comparison, Bradford-Grieve et al. (2003) estimated a
P/B of 0.32/y for southern blue whiting and 0.36/y for hoki. P/B values for each
fish trophic group were weighted by the biomass of each species within each
fish trophic group (piscivorous fish, herbivorous fish, etc.).

4.14.3 Consumption

The amount of food consumed by fish is a function of their size, prey 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:

$$Q/B = 3 \cdot W_W{}^{-0.2} \cdot T^{0.6} \cdot A_R{}^{0.5} \cdot 3\,e^{Ft} \qquad (5)$$

where W_W = asymptotic weight, T = temperature (°C), A_R = aspect ratio of tail, and F_t = food type (0 for carnivores, 1 for herbivores). Tail shape was taken from photographs of adult fish in FishBase (Froese & Pauly 2005), average water temperature in the study region was assumed to be 10°C and maximum fish weights were estimated as described previously. For the adults of non-cryptic species in the study region, this method gave Q/B values of 1.8–7.9/y for all carnivores, including piscivores, planktivores and invertebrate feeders, and 9.4–10.1/y for herbivores (Table 21); these values are similar to those used in other trophic models (e.g. Bradford-Grieve et al. 2003). For cryptic fish, we estimated a Q/B of 15.7/y.

As for P/B, the Q/B values for each fish trophic group were weighted by the biomass of each species within each fish trophic group (piscivorous fish, herbivorous fish, etc.).

4.14.4 Diet composition

Diet composition is available for many common New Zealand reef fish. Most data on fish diet are from northeastern North Island (particularly the Hauraki Gulf) (e.g. Russell 1983; Jones 1988). Of the 44 reef species examined by Russell (1983), 82% were carnivores, 11% were herbivores and 7% were omnivores. For cryptic fish, Duffy (1989) recorded the percentage frequency of various prey in the gut contents of cryptic fish, observing that phytal invertebrates, crabs, gastropods, heterotrophic benthos, other cryptic fish and some algae were present at the highest frequencies in these diets.

In New Zealand, there have been over 20 years of research surveys and extensive examination of stomach contents of commercially important pelagic and demersal fish species (e.g. Clark 1985; Clark et al. 1989). The data from more than 27 scientific papers on fish diets around New Zealand have recently been summarised by Stevens (NIWA, unpubl. data). However, much of this work provides only limited qualitative information on diet composition, usually in terms of the presence/absence of material in the fish stomachs, and there are few studies assessing how much of the energy intake of fish comes from different sources. Also, few of the studies have looked specifically at fish species living in waters shallower than 30 m or at areas near to the study region.

In this work, we assumed that pelagic fish are predominantly plankton feeders, taking zooplankton from the water column in addition to fish. Macrobenthic epifauna may also be a significant part of the diet of pelagic fish in shallow waters. Demersal fish are assumed to be opportunistic feeders that feed mainly on benthic invertebrates, but also take demersal fish, and meso- and macrozooplankton from the water column; we assumed that they will also scavenge for any available suitable material on the sea-bed.

We compiled information on fish diet into diet categories that approximate the trophic groups used in the model (Table 22). Often data were available as either percentage of individuals (rather than percentage volume) or as presence/absence in guts, limiting our ability to determine the relative values of each diet component for trophic consumption. Only small sample sizes were available for analysis for most fish species, and crustaceans and gastropods were likely over-represented due to the presence of hard parts that decompose slowly relative to other invertebrate taxa. Therefore, we modified the final diet composition data to more accurately represent known diet components based on personal observations. Diet composition was then averaged based on the relative biomass of each species within each fish trophic group.

4.15   BIRDS — SHOREBIRDS AND SEABIRDS

Numerous bird species have been observed feeding in the model area, including New Zealand dotterels, variable oystercatchers, banded dotterels, white-faced herons, pied shags, little blue penguins, black-backed gulls and godwits (Table 23). Less common species include sooty shearwaters, grey-faced petrels, fluttering shearwaters, Hutton shearwaters *Puffinus huttoni*, Cook's petrels *Pterodroma cookii*, black-winged petrels *Procellaria parkinsoni*, Australasian gannets *Morus serrator*, albatrosses *Diomedea epomophora sanfordi* and mollymawks *Thalassarche bulleri* and *T. cauta*. In addition, red-billed gulls *Larus novaehollandiae*, black-billed gulls *Larus bulleri*, Caspian terns *Sterna caspia* and white-fronted terns *Sterna striata* are occasionally seen (A. Bassett, DOC, pers. comm.; Bert Lee, Charter Fishing, pers. comm.).

Typical weights for individual birds were taken from Heather & Robertson (1986). Carbon to weight ratios for seabirds were taken as 10%, the same carbon content as fish (Vinogradov 1953), following previous trophic modelling work (e.g. Bradford-Grieve et al. 2003).

Most bird species do not live or feed exclusively within Te Tapuwae o Rongokako Marine Reserve. Therefore, to estimate bird biomass and consumption for the model it was necessary to estimate the average proportion of each individual's life that can be considered to take place within the study area for each species. These estimates were based on published information on the foraging areas of the various species, and seasonal migration patterns of the birds (if relevant). Obviously, there will be no consumption of food from the study area when the bird is outside the study region.

The model takes these factors into account by reducing the biomass of each species in the study region proportionately, according to Equation 6 (see Table 23 for values):

$$B = \frac{N \cdot W \cdot C}{A} \cdot \left(\frac{S}{100}\right) \cdot \left(\frac{M}{12}\right) \tag{6}$$

where B = effective average annual biomass density (g C/m^2), N = number of birds in local population, W = average weight of bird (g WW), C = carbon:wet weight ratio, 0.1 g C/g WW, A = study area (m^2), S = proportion of foraging area covered by the study region (%), and M = months spent in the foraging area per year (months).

TABLE 22.   PERCENTAGE DIET COMPOSITION OF FISH SPECIES AND AVERAGE DIET COMPOSITION BY FISH TROPHIC GROUPS IN THE MODEL.

Fish = fish, gast = gastropod, paua = paua, kina = kina, cuc = sea cucumber, graz = other grazing invertebrates, octo = octopus, crab = crab, phyt = phytal invertebrates, encr = encrusting invertebrates, ben = heterotrophic benthos, zoo = zooplankton, brown = brown algae, red = red algae, green = green algae, det = detritus, spo = sponge.

COMMON NAME	SCIENTIFIC NAME	FISH	GAST	PAUA	KINA	CUC	GRAZ	OCTO	CRAB	PHYT	ENCR	BEN	ZOO	BROWN	RED	GREEN	DET	SPO
Herbivorous fishes																		
Marblefish	*Aplodactylus arctidens*	0	0	0	0	0	0	0	0	0	0	0	0	15	80	5	0	0
Parore	*Girella tricuspidata*	0	0	0	0	0	0	0	0	0	0	0	0	47	53	0	0	0
Butterfish	*Odax pullus*	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0
Invertebrate feeders																		
Red cod	*Cheilodactylus macropterus*	0	0	0	0	0	0	0	33	0	33	0	34	0	0	0	0	0
Red moki	*Cheilodactylus spectabilis*	0	0	0	8	0	10	0	13	40	29	0	0	0	0	0	0	0
Scarlet wrasse	*Cheilodonichthys kumu*	0	20	0	0	0	0	0	60	0	0	20	0	0	0	0	0	0
Hiwihiwi	*Chironemus marmoratus*	0	10	0	5	0	50	0	25	0	10	0	0	0	0	0	0	0
Blue moki	*Latridopsis ciliaris*	0	0	0	6	0	10	0	30	40	7	0	0	0	7	0	0	0
Porae	*Nemadactylus douglasi*	2	0	0	10	0	4	0	5	16	57	0	0	0	6	0	0	0
Spotty	*Notolabrus celidotus*	0	0	0	5	0	3	0	40	5	47	0	0	0	0	0	0	0
Banded wrasse	*Notolabrus fucicola*	0	25	0	10	0	3	0	60	0	2	0	0	0	0	0	0	0
Snapper	*Pagrus auratus*	10	9	4	5	0	3	0	31	0	17	10	11	0	0	0	0	0
Leatherjacket	*Parika scaber*	0	0	0	10	0	0	0	0	0	41	0	0	0	12	0	0	37
Scarlet wrasse	*Pseudolabrus miles*	0	20	0	0	0	0	0	53	0	27	0	0	0	0	0	0	0
Bastard red cod	*Pseudophycis barbata*	0	0	0	0	0	0	0	45	40	15	0	0	0	0	0	0	0
Scorpionfish	*Scorpaena cardinalis*	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0
Goatfish	*Upeneichthys lineatus*	0	0	0	0	0	0	0	65	30	5	0	0	0	0	0	0	0
Piscivores																		
Kahawai	*Arripis trutta*	67	0	0	0	0	0	0	0	0	0	0	33	0	0	0		
Elephant fish	*Callorhynchus milii*	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Opalfish	*Hemerocoetes monopterygius*	60	0	0	0	0	0	0	0	0	0	0	40	0	0	0	0	0
Red-banded perch	*Hypoplectrodes huntii*	60	0	0	0	0	0	0	35	0	0	5	0	0	0	0	0	0
Rock cod	*Lotella rhacinus*	50	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0
Rig	*Mustelus lenticulatus*	60	5	0	0	0	0	0	30	0	0	10	0	0	0	0	0	0
Blue cod	*Parapercis colias*	55	0	0	5	0	0	0	30	0	5	0	0	0	0	0	0	0
Kingfish	*Seriola grandis*	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spiny dogfish	*Squalus acanthias*	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 22—continued

COMMON NAME	SCIENTIFIC NAME	DIET COMPONENTS																
		FISH	GAST	PAUA	KINA	CUC	GRAZ	OCTO	CRAB	PHYT	ENCR	BEN	ZOO	BROWN	RED	GREEN	DET	SPO
Barracouta	*Thyrsites atun*	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jack mackerel	*Trachurus novaezelandiae*	80	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0
John dory	*Zeus faber*	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Planktivores																		
Butterfly perch	*Caesioperca lepidoptera*	0	0	0	0	0	0	0	0	0	0	8	92	0	0	0	0	0
Demoiselle	*Chromis dispilus*	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0
Anchovy	*Engraulis australis*	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0
Slender roughy	*Optivus elongatus*	0	0	0	0	0	0	0	40	0	0	0	60	0	0	0	0	0
Trevally	*Pseudocaranx dentex*	0	0	0	0	0	0	0	0	50	0	0	50	0	0	0	0	0
Sweep	*Scorpis lineolatus*	0	0	0	0	0	0	0	0	10	0	0	80	0	0	0	10	0
Blue maomao	*Scorpis violaceus*	0	0	0	0	0	0	0	0	0	0	0	90	0	0	0	10	0
Common warehou	*Seriolella brama*	20	0	0	0	0	0	0	20	0	0	0	60	0	0	0	0	0
Cryptic reef fishes																		
Conger eel	*Conger verreauxi*	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0
Urchin clingfish	*Dellichthys morelandi*	0	0	0	90	0	0	0	0	10	0	0	0	0	0	0	0	0
Spectacled triplefin	*Ruanoho whero*	0	6	0	0	0	7	0	30	30	27	0	0	0	0	0	0	0
Moray eel	*Gymnothorax prasinus*	15	0	0	0	0	0	0	85	0	0	0	0	0	0	0	0	0
Twister	*Helcogramma medium*	0	30	0	0	0	8	0	0	60	0	0	0	0	0	2	0	0
Crested blenny	*Parablennius laticlavius*	0	5	0	0	0	0	0	0	5	35	0	53	0	7	0	0	0
Striped clingfish	*Trachelochismus melobesia*	0	0	0	0	0	5	0	0	95	0	0	0	0	0	0	0	0
Blue-eyed triplefin	*Notoclinops segmentatus*	0	10	0	0	0	5	0	0	60	25	0	0	0	0	0	0	0
Common triplefin	*Tripterygion capito*	0	0	0	5	0	30	0	25	40	0	0	0	0	0	0	0	0
Yellow and black triplefin	*Forsterygion flavonigrum*	0	0	0	0	0	0	0	0	45	55	0	0	0	0	0	0	0
Oblique swimming triplefin	*Obliquichthys maryannae*	0	0	0	0	0	0	0	0	20	0	0	80	0	0	0	0	0
Variable triplefin	*Forsterygion varium*	0	10	0	0	0	5	0	25	50	10	0	0	0	0	0	0	0
Yaldwyn's triplefin	*Notoclinops yaldwyni*	0	0	0	0	0	0	0	10	80	10	0	0	0	0	0	0	0

Weight = average wet weight; B = biomass; Q/B = consumption/biomass.

COMMON NAME	SCIENTIFIC NAME	WEIGHT (g)	NUMBER OF BIRDS*	B (g C)	Q/B (y^{-1})
New Zealand dotterel	*Charadrius obscurus*	160	12	192	149
Variable oyster catcher	*Haematopus unicolor*	725	20	1450	98
Banded dotterel	*Charadrius bicinctus*	60	14	84	195
White-faced heron	*Ardea novaehollandiae*	550	14	770	106
Pied shag	*Phalocrocorax varius*	2000	30	6000	74
Little blue penguin	*Eudyptula minor*	1100	5	550	87
Black-backed gull	*Larus dominicanus*	950	40	3800	91
Bar-tailed godwit	*Limosa lapponica*	325	15	488	122
Sooty shearwater	*Puffinus griseus*	800	20	1600	95
Grey-faced petrel	*Pterodroma macroptera gouldi*	550	20	1100	106
Fluttering shearwater	*Puffinus gavia*	300	20	600	125
N Bullers mollymawk	*Thalassarche bulleri*	3000	2	600	66

* Adjusted for estimated proportion of time birds spend in the region and estimated proportion of food that is from the marine system, i.e. this is the equivalent number of birds that could be assumed to feed solely from the marine system, all year round.

This simple linear approach implicitly assumes that the flows of energy to and from each species are steady through the year. If individuals of a particular species of bird consume food or die at very different rates depending on whether they are inside or outside the study region, our estimates will be biased in the model. This could be accommodated readily in future work by estimating an import or export of material from the system as a result of the migrations.

Medway (2000) gave dietary information for many of these species. Most shorebirds feed in upper intertidal areas, both on sandy and rocky substrates, while seabirds feed primarily on small surface-feeding fish and zooplankton. Variable oystercatchers feed mostly on molluscs, worms, crabs and other small invertebrates, and also occasionally on various terrestrial insects. New Zealand dotterels similarly feed on crustaceans, small molluscs and other small invertebrates and fish. Banded dotterels feed opportunistically on both coastal and near-coastal invertebrates. Seasonal waders include primarily the eastern bar-tailed godwit. Godwits feed on intertidal mudflats and sandflats and occasionally on saltmarshes, mainly consuming worms, molluscs and crabs. Black-backed gulls are opportunistic foragers, with diets including marine invertebrates, small fish, and dead fish and other carcasses, as well as terrestrial food sources and eggs of other species. Of the less common species, diet information is available for red-billed gulls (primarily planktonic crustaceans, though they are also opportunistic feeders in some seasons); Caspian and white-fronted terns (small surface fish); and black-billed gulls (invertebrates and small fish).

The benthic biomass required to feed shorebirds has been calculated for three species (South Island pied oystercatcher, wrybill godwit and lesser knot) in two locations (Firth of Thames and Manukau Harbour) based on diets composed of

the bivalves *Macomona liliana* and *Austrovenus stutchburyi* (Cummings et al. 1997; Lundquist et al. 2004). Gross Food Intake (GFI) was calculated as:

$$GFI = C^{-1} * DEE \qquad (7)$$

where GFI = g AFDW per bird per day, C = calorific content, and DEE = daily energy expenditure (kcal per bird per day), estimated as a fixed multiple of the standard metabolic rate (SMR). We used an average value for sediment-dwelling bivalves of C = 5.01 kcal/g AFDW (Hughes 1970; Chambers & Milne 1975). Daily energy expenditure was estimated as:

$$DEE = A^{-1} * k * SMR \qquad (8)$$

where A = assimilation efficiency (% of intake), estimated as 80% (Castro et al. 1989); SMR = standard metabolic rate (kcal bird^{-1} d^{-1}); and k is a temperature-dependent multiple of SMR. We estimated k as 2.5. SMR was calculated using the formula from Lasiewski & Dawson (1967):

$$SMR = 78.3 * W^{0.723} \qquad (9)$$

where W = average wet weight of bird (kg).

Gross food intake (GFI = g AFDM/d) for South Island pied oystercatchers, bar-tailed godwits and lesser knots was thus estimated as 33.06, 17.93 and 11.17, respectively, for average body masses (kg) of 0.583, 0.250 and 0.130, respectively (Cummings et al. 1997; Lundquist et al. 2004). Carbon content of prey (assuming prey consists of primarily benthic macrofauna) was calculated using 1 g AFDW = c. 0.50 g C (Brey 2001). We estimated average consumption/biomass (Q/B) of birds in the marine reserve as 104, 132 and 158 for these three species. We assumed that these estimates are representative of New Zealand shorebirds of three varying body weights and thus used these relationships to estimate Q/B for all bird species found in the study area (including those that eat primarily fish). After weighting each species according to its predicted abundance, we estimated that Q/B = 90/y for birds.

This annual Q/B value for seabirds and shorebirds in the study area (90/y) is comparable to but slightly higher than previous work (e.g. 62/y for northern Chile seabirds (Wolff 1994); 58.4/y for Italian lagoon cormorants (Brando et al. 2004)). Work in the Ross Sea suggested that different species of birds have Q/B values between 38/y and 189/y, with larger birds having smaller Q/B values (Pinkerton et al. 2006). Therefore, since most of the birds in the study region are small, this higher Q/B value is reasonable.

Production rates (P/B) of bird populations in the Ross Sea (Pinkerton et al. 2006) were estimated to be c. 0.03/y. This is lower than estimated by previous studies. For example, Wolff (1994) used 0.07/y for northern Chile seabirds, and Brando et al. (2004) used 0.04/y for Italian cormorants. This difference could be a result of the difficult environmental and food-limited Southern Ocean system. Bradford-Grieve et al. (2003) suggested a P/B of 0.30/y for seabirds south of the Chatham Rise, though this seems high. In the absence of measurements to the contrary, we propose using a P/B of 0.10/y for birds in the study region.

Marine mammals are mostly transient in the area and do not feed locally. Although fur seals have haul-out sites in the area, they feed off the continental shelf in deeper waters than those modelled here (Harcourt et al. 2002). Feeding studies of female scat samples in Otago showed primary prey species to include arrow squid and myctophids in summer and autumn, with more diverse diets in winter also including ahuru (pink cod), mackerel and barracouta (Harcourt et al. 2002). As their feeding is unlikely to be within the study area, we did not include marine mammals in our preliminary model.

5.   Diet fraction modelling

Diet fractions, that is the proportion of various prey items in the diet of a consumer, were estimated for each of the consumer trophic groups identified above. These values should not be considered exact for a number of reasons including:

- Many of the diet studies used here to estimate diets of consumers in Te Tapuwae o Rongokako Marine Reserve were carried out in other areas, where the relative abundances of various prey items are likely to differ. This may well alter the diet fractions for predators in the study area.

- Studies of consumer diets are often short and localised, and may not represent the actual spatial and temporal variability in diets. There may also be significant variation in diets between individuals in a population in a given area at a given time. This variation will only be recognised if the sample sizes used in the diet study are sufficiently large.

- Studies of consumer diets are often only semi-quantitative, with prey abundance being measured in terms of presence/absence, percentage occurrence in diet, or by wet weight. The values of diet fraction used in the model here are strictly proportions in weight of organic carbon.

- Methods used to correct for the relative rates of digestion of different organisms are uncertain, so that there may be a bias in diet studies towards prey items that are slowly digested, or contain hard parts that are readily identified in stomach analysis. For example, hard macrozooplankton such as krill tend to remain identifiable in stomachs longer than gelatinous zooplankton such as salps, and this may mean diet studies estimate erroneously high proportions of the former compared to the latter. Some particularly digestible prey items may be missed altogether by diet studies.

The high measurement uncertainty and intrinsic large variability in diet fractions means that studies often give wide ranges of the proportions of various prey items in the diets of consumers. It is essential that an ecosystem model allows for variability in diet fractions. For example, if a predator consumes ten different prey items and half of these are removed from the system, it is unreasonable to assume that it will not consume more of the remaining prey items. The NIWA trophic model used to balance the dataset presented here allows diet fractions to be varied as part of the balancing procedure, while Ecopath does not.
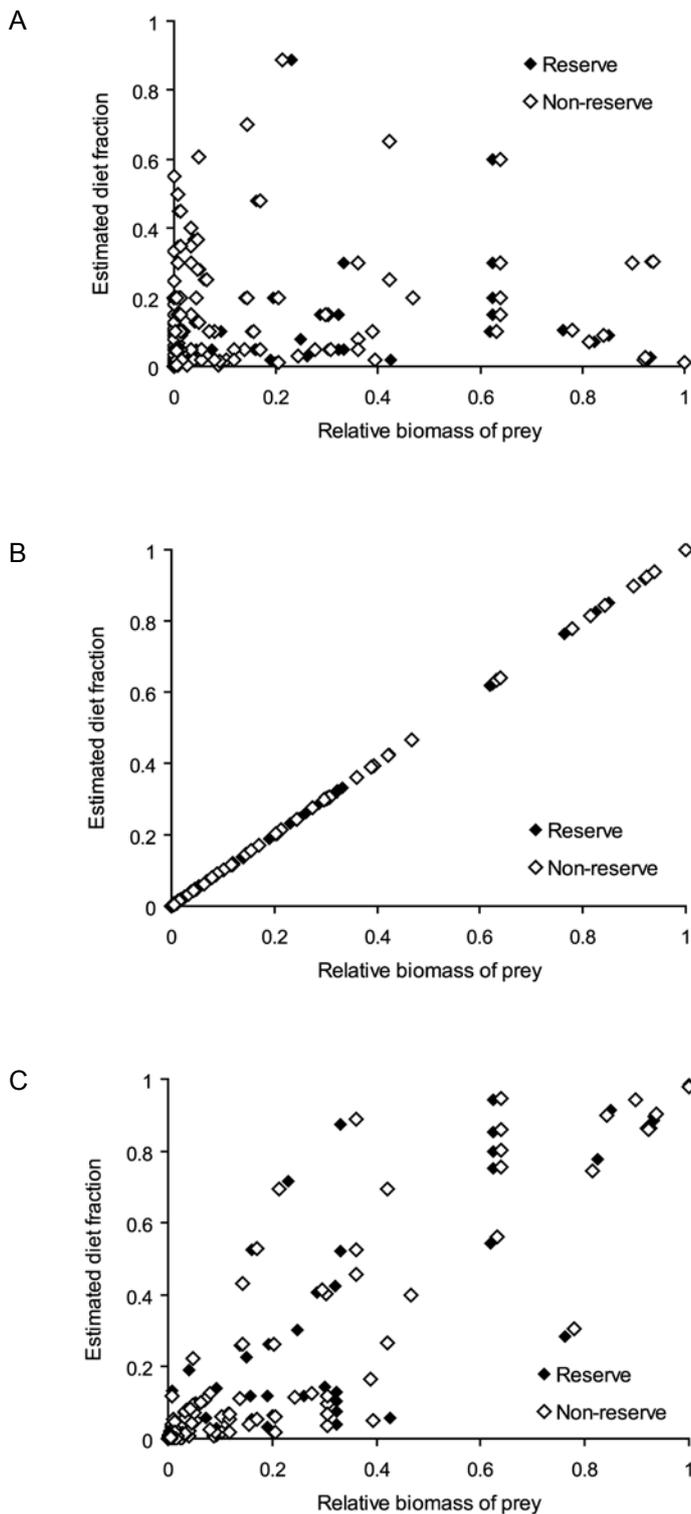
Figure 10. Diet fractions for predator groups in Te Tapuwae o Rongokako system estimated by three different methods: A. Method 1—using values from the scientific and grey literature; B. Method 2—assuming predators have no preference for prey amongst possible prey items; C. Method 3—assuming that literature values indicate preferences for different prey items, but that relative prey abundance also affects diet composition of predators. See text for more details. In all cases, diet fractions are shown as a function of the relative biomass of the various prey items.

Below, we outline three ways to obtain a feasible solution for diet compositions:

1. Use the diet fraction values estimated for each trophic group in section 4. The relationship between the diet fractions estimated in this way and the relative abundances of prey items is shown in Fig. 10A. This method assumes that diet does not vary with relative abundance of prey taxa.

2. Use the diet fraction values estimated in section 4 to identify potential prey items, and assume that predators have no preference between these prey items. Instead, prey items are selected based on their relative abundance. In this case, diet fractions will be equal to the relative biomass of the potential prey items (shown in Fig. 10B).

3. Use the diet fraction values estimated in section 4 to identify potential prey items for each predator, and assume that the proportions of these prey items in the diet reflect both the relative abundance of prey item, and the preference of the predator if all potential prey items were equally abundant. The actual diet fractions are then estimated to be proportional to the product of the preference value and the biomass of the prey item. For example, if a predator is reported in the literature as consuming 75% prey A and 25% prey B, we assume that if prey A and B were equally abundant, these would be the proportions in the diet of the predator. We refer to these values as 'electivities', E_{ij} (where i = predator, j = prey). However, if prey B is twice as abundant as prey A then the actual diet fractions can be calculated to be 60% prey A and 40% prey B using Equation 10:

$$DF_{ij} = \frac{E_{ij} \cdot B_j}{\sum_{all\,k}(E_{ik} \cdot B_k)} \qquad (10)$$

This reflects the assumption that the predator would rather consume A than B, but that B is more abundant. The result of this for Te Tapuwae o Rongokako is shown in Fig. 10C.

Method 2 is unlikely to be a good approach except for predators that are completely opportunistic feeders, as most fauna would be expected to show some preference between potential prey items. Method 1 would be preferred if we had measurements of diet made in the study area for most of the predators. However, this is not the case. Instead, most of the estimates of diet given in the preceding sections were from areas other than Te Tapuwae o Rongokako Marine Reserve, and often the quality of the estimates is not known. If we believe the estimates are reasonable, the decision of whether Method 1 or Method 3 is a more appropriate starting point depends on whether the relative abundances of prey items in the various regions used to estimate the diet fractions are similar to Te Tapuwae o Rongokako. We tried to use diet fractions from studies around New Zealand, so the question is: how similar are relative prey abundances between different New Zealand 'rocky-reef' regions? Certainly, the preliminary stable isotope samples indicate that the abundance of prey items for lobsters in the reserve potentially differ from that found in diet studies at Wellington and Leigh (S. Kelly, unpubl. data). Whether other animals exhibit site-specific differences in diet will likely depend primarily on whether they are generalist or specialist predators.

We recommend that Method 3 be used to obtain starting values for diet fractions because we believe that many of the estimates of diet fractions are not reliable. Combining these diet-based estimates with relative biomass values for prey items is likely to give diet fractions that are more reasonable than the diet-based estimates alone. This assumption requires further testing, however, because Method 1 and Method 3 lead to very different diet fraction estimates. As the overall conclusions of trophic models depend significantly on the diet fractions at the balance point, it is important to address the issue of sensitivity of model balancing to initial diet fractions.

6. Discussion

We present the complete dataset of trophic parameters and diet composition based on the Te Tapuwae o Rongokako Marine Reserve in Appendix 1 (trophic parameters: Table A1.1; diet matrix: Table A1.2). The development of this model dataset will serve three useful purposes:

- It forces the assembly of data on all components of the ecosystem in a form where they may be combined to develop a trophic ecosystem model. Such a model can test whether our current understanding of the ecosystem structure and function is complete and consistent. In assessing completeness, the model (and data collation) will allow us to identify critical gaps in our knowledge, data or approach. In testing consistency, assembling the model will help to identify priorities for future work.

- It formalises our conceptual model of ecosystem interconnectedness. The conceptual model should be viewed as a straw-man for discussion by researchers, managers and other stakeholders for a particular region. For example, it may help to determine whether there are bottlenecks of energy flow through the system, or key species on which the system depends.

- Balanced trophic models based on this dataset will allow system-level comparison with other ecosystems around the world that have different top-down and bottom-up regulation of ecosystem processes.

6.1 CHARACTERISATION OF TE TAPUWAE O RONGOKAKO MARINE RESERVE ECOSYSTEM

The data collected (prior to model balancing) indicate that the biomass of primary producers in Te Tapuwae o Rongokako Marine Reserve ecosystem is dominated by canopy macroalgae (88%), with other significant contributions from foliose macroalgae (8%) and microphytes (8%), and minor contributions (< 1%) from phytoplankton and crustose macroalgae. The biomass of consumers is dominated by sponges (65%) and other encrusting/sessile invertebrates (12%), with only a few other groups contributing more than 1% to the total biomass of consumers in the system, including planktivorous fish (7.5%), invertebrate-feeding fish (3.1%), sea cucumbers (2.6%), phytal/microinvertebrates (2.3%), meso/macrozooplankton (1.7%), lobsters (1.4%,) and piscivorous fish (1.1%). Bacteria are excluded from this comparison. The data are further resolved into a balanced model in Pinkerton et al. (in press) to determine feasible biomass estimates based on energetic parameters and diet composition.

We are relatively confident that our conceptual model (and associated data presented here) is accurately representing the structure and function of the ecosystem. Obviously, there are many trophic groups for which better information would improve model reliability, e.g. sponges and encrusting invertebrates, which constitute over two-thirds of the consumer biomass in the system. Phytal invertebrates and microphytes should also be afforded high priority in data collection in the future. The pelagic system appears to be significant within the

ecosystem, and some water sampling, if only basic measurements of seasonal chlorophyll concentration and zooplankton biomass, would be useful to check if the model representation of these groups is realistic. Determining the relative contribution of kelp-derived organic carbon to the food web also should be given high priority.

6.2   STATUS OF THE TROPHIC MODEL PARAMETERS

This project has brought together a considerable amount of monitoring data from Te Tapuwae o Rongokako Marine Reserve and presents a dataset of biomass, diet composition and trophic parameters based on a conceptual model of the structure of trophic flows within the ecosystem (Appendix 1). Values are based on data averaged over the reserve area only. The next step is to create a balanced quantitative trophic model based on the data presented here; this is published elsewhere (Pinkerton et al. in press), and elucidates additional information about the structure and functioning of this coastal ecosystem.

To balance the trophic model based on our dataset, we will probably need to quantify and/or reduce uncertainty in the data more than has been possible within this project. Although a large amount of high-quality data on the Te Tapuwae o Rongokako Marine Reserve ecosystem has been collected over a number of years, unsurprisingly there is considerable uncertainty in much of the data used in the model. Much of this uncertainty arises from scaling up point measurements to the whole of the Te Tapuwae o Rongokako study area. More point or small-scale measurements would help to address this issue, but uncertainties will always remain unless a method is developed for the large-scale census of the biomass of many marine organisms within a rocky reef ecosystem. It is recommended that the development of such a methodology (based, for example, on spatial modelling with habitat constraints such as is used in soft-sediment systems) be pursued in the future.

The initial parameters were obtained from local survey information, published research from a nearby rocky reef marine reserve and, where necessary, the scientific literature. It is important to note that biomass measurements in the study area are generally incomplete with respect to space, time and species; for example, most monitoring surveys are generally performed only in summer. There is also huge variation in the magnitude of flows of energy through different trophic groups. Given that all ecological models are developed from a position of limited information, modelling approaches need to be able to handle parameters that have variable and often high uncertainties.

It is likely to be necessary to significantly adjust many of the trophic parameters from their initial estimates to obtain a balanced model. In particular, parameters associated with bacteria often need to be substantially changed to balance trophic models. Many coastal trophic models do not explicitly include either water column or benthic bacteria as separate trophic groups, often with the rationale that the appropriate parameters for these groups are poorly known (e.g. Jarre-Teichmann et al. 1997; Arreguin-Sanchez et al. 2002; Rybatczyk & Elkaim 2003; Jiang & Gibbs 2005). Although we have included bacteria and detrital groups, the lack of information on biomass, production, consumption

and the trophic role of bacteria and detritivores makes it disputable whether we will derive any benefit from having the additional detrital-bacterial closure constraints. We expect a model to also have difficulty in balancing the sponge, sea cucumber and phytoplankton groups, which have poorly quantified productions and biomass in the study region, and generally weak direct predation pressure.

Initial estimates of the diets of many groups are likely to need changing for model balancing. Little is known about the long-term diet composition of most reef species. We suggest that diet may vary considerably between different rocky reef ecosystems because of changes in relative prey abundance and suitable habitats for different groups. Stable isotope analysis of a number of larger, more abundant species was carried out and has been useful in informing possible diets of lobsters (Appendix 2). The stable isotope data could be expanded to be of further use; the inclusion of more species, more samples and more consistent methodology can increase the value of information obtained by this approach. It is emphasised, however, that diets for ecosystems such as that discussed here will generally be poorly known, implying that modelling methods need to allow diet fractions to vary.

6.3   RECOMMENDATIONS FOR FUTURE RESEARCH

A combination of modelling, field studies and experience show that the indirect effects of fishing on ecosystems can be substantial, but that these effects are difficult to predict (e.g. Brose et al. 2005). The development of an ecosystem model for the region is an important part of exploring the implications of various management strategies on the marine ecosystem community dynamics. Obviously, predicting how an ecosystem will change in the future in response to various management actions (commercial, recreational, traditional fisheries, tourism, etc.) that may affect the relative abundance of different trophic groups (e.g. predatory lobsters and reef fish), as well as environmental changes (interannual variability, El Niño Southern Oscillation (ENSO), climate change, etc.) requires additional information. In particular, we need to understand what controls the abundance of various organisms in the ecosystem at the present time. To address this question, we need to understand the relative importance of factors such as food availability, habitat quality and quantity, reproductive success (e.g. larval supply, larval attachment and recruitment), predation pressure, and environmental controls (e.g. currents and temperature). Numerical models that assume that trophic interactions (i.e. predator-prey relationships) are the only factor affecting population levels are simplistic; however, they can be used to develop testable predictions that can be measured in field experiments that incorporate variability in other factors that regulate the abundance of organisms in coastal marine ecosystems. To reliably predict how the ecosystem will change over time, we need to understand the interplay of all the factors given above.

To test the model assumptions and determine the 'realism' of trophic models, we need to identify and fill gaps in our knowledge of trophic parameters for this system. It is important to note that the amount of information available for Te Tapuwae o Rongokako Marine Reserve, particularly with respect to the intertidal and subtidal reef habitats for this region, is extensive compared with what is typically available for New Zealand marine ecosystems. Selection of this

region as the focus of the Ministry of Research, Science and Technology (MoRST) Cross Departmental Research Pool (CDRP) project 'Maori Methods and Indicators of Marine Protection', and more specifically this project, allowed us to utilise the substantial datasets collected in the monitoring of the marine reserve and in other local marine surveys to develop a baseline understanding of the ecological interactions defining this coastal marine ecosystem. However, the marine reserve monitoring programme was not designed with this purpose in mind, and thus does not collect information on all trophic groups. Particular datasets that require better resolution to resolve trophic ecosystem models include:

1. Diet of major consumers within the area, including spatial (reserve, non-reserve) and temporal (seasonal and inter-annual) variability

2. Abundance of groups that are not specifically monitored within the reserve, such as encrusting and phytal invertebrates

3. Biomass and production of micro-producers (microphytes and phytoplankton)

4. Relative contribution of kelp-derived organic detritus to the food web

Building on the existing monitoring programme, we recommend continued regular monitoring of key ecosystem indicators at Te Tapuwae o Rongokako Marine Reserve for the long term. Ecosystem indicators can include the biomass of key harvest species (such as lobster, paua and kina, all of which are currently monitored within and outside of the reserve area), as well as key species directly linked in a trophic sense to them (especially encrusting invertebrates and phytal invertebrates), for which a balanced model might predict changes under various management or environmental scenarios. Information from diet studies (e.g. from stable isotope analysis) could also be included as ecosystem indicators. Target values related to ecosystem indicators could be given in terms of the density of an organism (fish, lobster, paua, etc.), total biomass, a trend in an indicator (e.g. lobster populations constant from year to year within 10%), or a more complex indicator (e.g. diet of an organism shown to be stable over time).

Many of these key ecosystem indicators have already been identified (Gibson 2006; Wilson et al. 2007), and a regular programme for monitoring some of these (lobster, reef fish, paua and kina) was initiated in 2000 and is used to monitor the state of Te Tapuwae o Rongokako Marine Reserve. A time series of data will help to distinguish interannual variability and long-term trends. Similar monitoring of key ecosystem indicators in nearby locations with different management regimes (e.g. the proposed mataitai, and areas open to commercial and recreational fishing) would allow comparison with Te Tapuwae o Rongokako Marine Reserve, which is in theory protected from harvest to allow the ecosystem to recover to its 'natural' state (though the timeframe of this recovery process is unknown). In addition, monitoring of key ecosystem indicators in non-reserve locations can allow interpretation of marine community changes due to different management regimes, which can be simulated using trophic models to develop and test predictions of expected changes in community structure and functioning. Some monitoring is already in place outside the marine reserve, and the ecosystem model based on parameters developed here can be further used to select additional valuable ecosystem indicators to inform and test model predictions.

A methodology should also be developed to allow the large-scale assessment of biomass of key organisms in coastal marine ecosystems such as Te Tapuwae o Rongokako Marine Reserve. If possible, this should be used to collect information seasonally over at least 1 year. More complete measurements of the biomass of groups should be obtained, taking account of seasonal and spatial variations. Data should particularly be collected on the biomass of organisms within the encrusting invertebrate and phytal invertebrate groups, as well as potential harvest species, such as paua, kina and lobster. In addition, better information on phytoplankton and zooplankton in the vicinity of the reef would be useful, since the pelagic ecosystem was found to be important to Te Tapuwae o Rongokako Marine Reserve in the current model.

7. Acknowledgements

8. References

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Appendix 1

COMPLETE DATASET OF TROPHIC PARAMETERS
AND DIET COMPOSITION BASED ON
TE TAPUWAE O RONGOKAKO MARINE RESERVE

TABLE A1.1. TROPHIC GROUP PARAMETERS FOR TE TAPUWAE O RONGOKAKO MARINE RESERVE ESTIMATED FROM LOCAL DATA AND LITERATURE, AS EXPLAINED IN THE TEXT.

B = Biomass, P = Production, Q = Consumption, E = Ecotrophic efficiency, A = Accumulation, X = Export and fishery, U = Unassimilated consumption. N/A = not applicable. Estimated value and range is listed for each parameter.

NO.	GROUP	B (g C/m²)	P/B (y⁻¹)	Q/B (y⁻¹)	E	A (g C m⁻² y⁻¹)	X (g C m⁻² y⁻¹)	U
1	Birds	0.00022 (0.00017–0.00028)	0.10 (0.08–0.12)	89.8 (71.8–107)	1	0	0	0.20 (0.16–0.24)
2	Lobster	0.16 (0.12–0.20)	0.17 (0.13–0.20)	1.74 (1.39–2.09)	1	0	0	0.30 (0.24–0.36)
3	Mobile_inverts_herb	0.11 (0.08–0.13)	1.30 (1.04–1.56)	7.94 (6.35–9.52)	1	0	0	0.30 (0.24–0.36)
4	Mobile_inverts_carn	0.106 (0.070–0.11)	1.67 (1.41–2.12)	7.15 (5.97–8.96)	1	0	0	0.30 (0.24–0.36)
5	Cucumber	0.29 (0.22–0.37)	0.60 (0.48–0.72)	3.40 (2.72–4.08)	1	0	0	0.30 (0.24–0.36)
6	Phytal_inverts	0.26 (0.20–0.33)	3.05 (2.44–3.67)	12.0 (9.66–14.4)	1	0	0	0.30 (0.24–0.36)
7	Sponge	7.45 (5.59–9.32)	0.20 (0.08–0.24)	0.80 (0.64–0.96)	1	0	0	0.30 (0.24–0.36)
8	Sessile_inverts	1.37 (1.03–1.72)	1.50 (1.20–1.80)	6.00 (4.80–7.20)	1	0	0	0.30 (0.24–0.36)
9	Fish_cryptic	0.064 (0.048–0.080)	2.40 (1.92–2.88)	15.6 (12.5–18.7)	1	0	0	0.30 (0.24–0.36)
10	Fish_invert	0.35 (0.26–0.44)	0.41 (0.33–0.50)	3.59 (2.87–4.30)	1	0	0	0.30 (0.24–0.36)
11	Fish_pisc	0.12 (0.09–0.16)	0.43 (0.34–0.51)	3.62 (2.90–4.35)	1	0	0	0.30 (0.24–0.36)
12	Fish_plank	0.86 (0.64–1.08)	0.50 (0.40–0.60)	6.33 (5.06–7.59)	1	0	0	0.30 (0.24–0.36)
13	Fish_herb	0.013 (0.0094–0.016)	0.40 (0.32–0.48)	9.52 (7.61–11.4)	1	0	0	0.30 (0.24–0.36)
14	Microphytes	8.52 (6.39–10.6)	21.0 (16.8–25.2)	N/A	1 (0–1)	0	0	N/A
15	Macroalgae_canopy	132 (99.1–165)	2.87 (2.29–3.44)	N/A	1 (0–1)	0	26.4 (19.8–33)	N/A
16	Macroalgae_foliose	8.76 (6.57–10.9)	13.0 (10.4–15.7)	N/A	1 (0–1)	0	1.8 (1.3–2.2)	N/A
17	Macroalgae_crustose	0.35 (0.26–0.44)	25.4 (20.3–30.5)	N/A	1 (0–1)	0	0.07 (0.05–0.09)	N/A
18	Zooplankton	0.19 (0.14–0.24)	17.7 (14.1–21.2)	51.5 (41.2–61.8)	1	0	0	0.30 (0.24–0.36)
19	Microzooplankton	0.069 (0.051–0.086)	220 (176–264)	624 (499–749)	1	0	0	0.30 (0.24–0.36)
20	Phytoplankton	0.23 (0.17–0.29)	324 (129–389)	N/A	1	0	0	N/A
21	Bacteria	0.60 (0.19–1.80)	100 (80.0–120)	400 (320–480)	1	0	0	0

TABLE A1.2. DIET MATRIX ESTIMATED FROM LOCAL DATA AND LITERATURE, SHOWING MEAN AND RANGE FOR EACH TROPHIC GROUP. PREY GROUPS ARE LISTED AS ROW HEADINGS, AND PREDATOR GROUPS (NUMBERS ONLY) ARE LISTED AS COLUMN HEADINGS.

NO.	GROUP	1	2	3	4	5	6	7	8	9	10	11	12	13	18	19	21
1	Birds				0.01 (0.00–0.20)												
2	Lobster				0.10 (0.01–0.50)												
3	Mobile_inverts_ herb	0.25 (0.10–1.00)	0.26 (0.05–0.70)		0.29 (0.10–1.00)						0.16 (0.10–1.00)						
4	Mobile_inverts_ cam	0.30 (0.10–1.00)	0.14 (0.05–0.50)		0.24 (0.10–1.00)						0.30 (0.10–1.00)						
5	Sea cucumber				0.01 (0.00–0.20)												
6	Phytal_inverts	0.35 (0.10–1.00)	0.28 (0.05–1.00)							0.64 (0.10–1.00)	0.17 (0.10–1.00)						
7	Sponge				0.10 (0.01–0.50)						0.04 (0.01–0.50)						
8	Sessile_inverts				0.14 (0.10–1.00)					0.21 (0.10–1.00)	0.32 (0.10–1.00)						
9	Fish_cryptic	0.10 (0.01–0.50)										0.09 (0.01–0.50)					
10	Fish_invert				0.06 (0.01–0.50)							0.21 (0.10–1.00)					
11	Fish_pisc											0.09 (0.01–1.00)					
12	Fish_plank				0.07 (0.01–0.50)							0.53 (0.10–1.00)	0.22 (0.10–1.00)				

Table A1.2—continued

NO.	GROUP	1	2	3	4	5	6	7	8	9	10	11	12	13	18	19	21
13	Fish_herb											0.09 (0.01–0.50)					
14	Microphytes			0.25 (0.10–1.00)			0.25 (0.10–1.00)										
15	Macroalgae_ canopy		0.19 (0.05–0.70)	0.35 (0.10–1.00)			0.25 (0.10–1.00)							0.24 (0.10–1.00)			
16	Macroalgae_ foliose			0.20 (0.10–1.00)										0.66 (0.10–1.00)			
17	Macroalgae_ crustose		0.13 (0.05–1.00)	0.20 (0.10–1.00)										0.09 (0.01–0.50)			
18	Meso/macro-zooplankton									0.15 (0.10–1.00)			0.72 (0.10–1.00)		0.20 (0.10–1.00)		
19	Micro-zooplankton							0.30 (0.10–1.00)	0.30 (0.10–1.00)						0.70 (0.10–1.00)	0.10 (0.01–0.50)	
20	Phytoplankton						0.25 (0.10–1.00)	0.40 (0.10–1.00)	0.40 (0.10–1.00)						0.10 (0.01–0.50)	0.65 (0.10–1.00)	
21	Bacteria					1.00 (1.00–1.00)	0.25 (0.10–1.00)	0.30 (0.10–1.00)	0.30 (0.10–1.00)				0.06 (0.01–0.50)			0.25 (0.10–1.00)	0.50 (0.10–1.00)
22	Detritus																0.50 (0.10–1.00)

Appendix 2

STABLE ISOTOPE ANALYSIS OF LOBSTER DIET

A2.1   Introduction

Stable isotopes can give additional information on the assimilation of prey from various sources. A preliminary stable isotope analysis of various species from within the study area was completed on samples collected in 2006 (Table A2.1). We used 'IsoSource', a source-apportioning isotopic-mixing model (Phillips & Gregg 2003), to attempt to determine likely diets of some species within the study area. Here we describe preliminary results from this analysis, detailing relevant information from this preliminary dataset. Additional samples have been collected and not yet analysed (D. Freeman, DOC, unpubl. data); these will be analysed in more detail elsewhere. It should be noted that these samples were not collected for the purpose of informing the trophic model, so some diet components that would be valuable for determining trophic linkages for the entire ecosystem and validating the diet fractions chosen for the model are not available. In addition, sampling was performed on various tissues (gonad tissue, muscle tissue, and whole animals with and without shell), making this preliminary analysis challenging for our purpose of informing diet composition for a trophic model. We have omitted outliers from the dataset that likely represent sampling error (e.g. mussels were dropped from the analysis as the isotopic signature clearly showed that shell tissue was included and no acidification step was performed). However, we feel that some preliminary conclusions were validated with the available data, and present them here.

We limit our specific discussion to lobsters, for which we felt confident that enough prey groups had been sampled to resolve a preliminary balanced diet. It is important to note that not all trophic groups included in the model were sampled; thus the diet analysis of the system is incomplete. For example, detritus, phytoplankton, phytal invertebrates and encrusting invertebrates were not sampled. As these groups are potentially important prey items within a trophic model of the system, any definitive conclusions based on stable isotope analysis would require a complete sample of all trophic groups that comprise components of the ecosystem.

A2.2   Evaluation of lobster diet

Isotopic signatures of lobsters and food sources were averaged where appropriate to reduce the number of sources in the IsoSource modelling and maximise our ability to make preliminary conclusions. Analyses were performed separately on reserve and non-reserve samples. We chose likely sources of diet components based on lobster diet studies by S. Kelly (Auckland Regional Council, unpubl. data). It was assumed that the lobster flesh did not include substantial carbonate content, though the data source implies that all samples were processed on legs including shells.

We used the IsoSource mixing model to estimate the proportion of each prey type in the diet of lobster within the Te Tapuwae o Rongokako marine reserve. The IsoSource mixing model determines the isotopic balance of the food sources

SPECIES	TYPE	SAMPLE ANALYSED	RESERVE	OUTSIDE RESERVE
Primary producers				
Carpophyllum maschalocarpum	Subtidal brown alga	Whole plants	x	x
Coralline turf	Coralline turf	Whole plants	x	x
Cystophora torulosa	Subtidal brown alga	Whole plants	x	x
Ecklonia radiata	Subtidal brown alga	Whole plants	x	x
Hormosira banksii	Intertidal brown alga	Whole plants	x	x
Nongeniculate corallines	Coralline paint	Whole plants	x	x
Porphyra columbina	Red alga	Whole plants	x	x
Pterocladia capillacea	Red alga	Whole plants	x	
Zostera capricorni	Seagrass	Whole plants		x
Grazers				
Amaurochiton glaucus	Chiton	Whole animals, including shell	x	
Cellana ornata	Gastropod	Whole animals, minus shell	x	x
Chiton pelliserpentis	Chiton	Whole animals, minus shell	x	x
Cookia sulcata	Gastropod	Whole animals	x	x
Evechinus chloroticus	Kina	Gonad tissue only	x	x
Haliotis iris	Paua	Whole animals, minus shell and gut	x	x
Melagraphia aethiops	Gastropod	Whole animals including shell for reserve, minus shell for fished	x	x
Trochus viridis	Gastropod	Whole animals, minus shell	x	x
Turbo smaragdus	Gastropod	Whole animals, minus shell	x	x
Filter feeders				
Ophionereis spp.	Brittlestar	Whole animals	x	
Xenostrobus pulex	Mussel	Whole animals, including shell	x	
Carnivores				
Polychaetes	Polychaetes	Whole animals	x	
Jasus edwardsii	Lobster	Legs only, including shell	x	x
Pagurus novaezelandiae	Crab	Whole animals	x	x
Plagusia chabrus	Crab	Whole animal (one animal only)	x	x
Latridopsis ciliaris	Predatory fish	Muscle tissue only		x
Nemadactylus macropterus	Predatory fish	Muscle tissue only		x
Pagrus auratus	Predatory fish	Muscle tissue only		x
Polyprion oxygeneios	Predatory fish	Muscle tissue only		x
Triplefins	Triplefins	Whole animals	x	

required to match the tissue of the consumer but does not automatically correct for isotopic fractionation. For this reason, the isotopic values of the consumer tissue must be corrected by subtracting one level of fractionation, i.e. –3.5‰ of N and –1‰ of C from each isotope (Newsome et al. 2004; Benstead et al. 2006).

The IsoSource analysis, using the lobster tissue isotopic values corrected for isotopic fractionation, produced a diet that is consistent with the opportunistic scavenging and predatory feeding behaviour of the lobster. The statistical means of the feasible solutions suggest that chitons, the brown algae *Ecklonia* and coralline turf were the major components of the diet of lobsters in the reserve (Table A2.2). These three components comprise about 90% of the lobster diet in the reserve, with small amounts of all other potential sources being possible. We note the large range of possible solutions (Table A2.2), implying that a large range of diet items and proportion is feasible for lobsters.

TABLE A2.2. LOBSTER DIET IN THE RESERVE (CORRECTED FOR ISOTOPIC FRACTIONATION). STATISTICAL MEAN FEASIBLE PROPORTION OF THE TESTED FOOD SOURCES IN THE LOBSTER DIET.

FOOD SOURCE	MEAN FEASIBLE PROPORTION (%)	RANGE (%)
Predatory fish (Fished)	0.3	0–4
Crab (Reserve)	1.1	0–10
Chiton (minus shell) (Reserve)	36.9	0–64
Coralline turf (Reserve)	20.5	0–80
Ecklonia (Reserve)	34.3	14–48
Urchin gonad (Reserve)	3.2	0–20
Subtidal gastropod *Trochus* (minus shell) (Reserve)	1.8	0–12
Triplefins (Reserve)	0.6	0–6
Polychaete (Reserve)	1.4	0–10

The same analysis was repeated for lobsters collected outside the reserve area to determine whether there were differences in diet associated with reserve status (Table A2.3). The large number of solutions and broad range of potential food sources that appear at a mean proportion of more than 2% suggest that these lobsters outside the reserve have an omnivorous diet and are scavenging and foraging as opportunists. While there is the possibility that some component of their diet is missing, the main diet components are essentially the same as in the reserve but at lower proportions and with additional major components at >8%. These results are comparable with those used to define lobster diet for the trophic model, except that the isotope data predict a much larger diet contribution of algae (*Ecklonia* and coralline turf: almost 40% compared to the 4% calculated by volume for lobsters in Wellington and Leigh from gut contents alone; S. Kelly, Auckland Regional Council, unpubl. data).

TABLE A2.3. LOBSTER DIET OUTSIDE THE RESERVE (CORRECTED FOR ISOTOPIC FRACTIONATION). STATISTICAL MEAN FEASIBLE PROPORTION OF THE TESTED FOOD SOURCES IN THE LOBSTER DIET.

FOOD SOURCE	MEAN FEASIBLE PROPORTION (%)	RANGE (%)
Predatory fish (Fished)	3.8	0–22
Crab (Fished)	8.0	0–46
Chiton (minus shell) (Fished)	14.8	0–50
Coralline turf (Fished)	19.9	0–60
Subtidal brown algae *Ecklonia* (Fished)	18.6	0–52
Urchin gonad (Fished)	10.9	0–42
Subtidal gastropod *Trochus* (minus shell) (Fished)	9.9	0–52
Triplefins (Reserve)	5.2	0–30
Polychaete (Reserve)	8.8	0–50

A2.3   Future research

The isotope analysis supports our prior knowledge with respect to the omnivorous diet of lobsters, though additional information would assist in further resolving diet of lobsters and other important trophic groups. Scavenging species such as lobsters often change their diet depending upon prey availability, and thus may have different diets inside and outside the marine reserve. This analysis could be improved if samples were taken at multiple times of year to resolve potentially important seasonal differences in data, and if the tissue sampled was consistent across taxa, e.g. using solely muscle tissue, or analysing both short- and long-term tissues to determine short- and long-term influences on diet. In addition, an acidification step would be valuable to reconcile contributions of shell or other carbonate components (e.g. in coralline algae) to isotopic signatures and make carbon isotope samples comparable across taxa.

What data do you need to create a coastal marine ecosystem model?

Ecosystem models can inform us about how New Zealand marine coastal ecosystems function and the effect of different management strategies on them. We present the data required to build a balanced ecosystem model for Te Tapuwae o Rongokako Marine Reserve. We consolidate species into 22 groups, chosen to represent the major interactions within the model region. For each group, we present estimates of biomass, production rates, consumption rates and diet preferences. Although other coastal marine ecosystems are likely to require different types of data, this information should enable others to develop a balanced model in their own region.

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