

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

Carolyn J. Lundquist and Matt H. Pinkerton

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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

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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:

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

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 inputted, 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:

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

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 n th) 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:

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

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:

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

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.

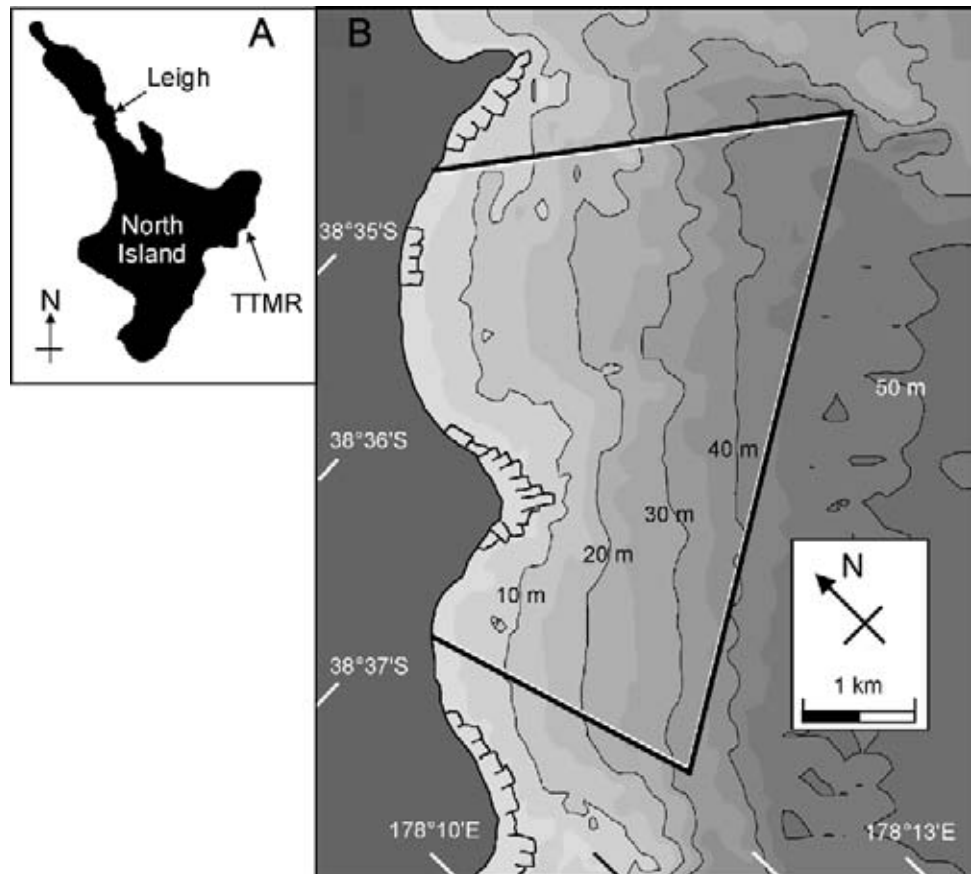
3.1.1 Defining the model region

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 $\text{g C m}^{-2} \text{y}^{-1}$ 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 $38.6117^\circ\text{S } 178.1836^\circ\text{E}$, $38.6407^\circ\text{S } 178.1974^\circ\text{E}$, $38.6021^\circ\text{S } 178.2689^\circ\text{E}$ and $38.5783^\circ\text{S } 178.2200^\circ\text{E}$ (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	
Phytoplankton, 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, hiwihiki
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, marbled wrasse, 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 understory 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 m ²) 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-m ² depth-stratified quadrats at two reserve sites, 35 1-m ² quadrats at two adjacent sites	Additional 28 1-m ² quadrats (reserve) and 27 1-m ² 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 <i>Caulerpa articulata</i> meadows.	Sponge flats	100% sponge garden
2 EckCaul	<i>Ecklonia radiata</i> forest with conspicuous understorey of <i>Caulerpa</i> , primarily <i>C. articulata</i> , with some <i>C. geminata</i> .	50% <i>Ecklonia</i> forest, 50% <i>Caulerpa</i> mats	50% <i>Ecklonia</i> forest, 50% mixed algae
3 EckCflex	Mixed forest of <i>Ecklonia radiata</i> and <i>Carpophyllum flexuosum</i> —'stands' of tall <i>C. flexuosum</i> .	Mixed algae	50% <i>Carpophyllum</i> , 50% <i>Ecklonia</i> forest
4 EckCor	<i>Ecklonia radiata</i> forest with coralline turf/Crustose Coralline Algae (CCA) understorey. No/few conspicuous foliose algae beneath kelp canopy.	50% <i>Ecklonia</i> forest, 50% urchin barrens	100% <i>Ecklonia</i> forest
5 EckFolred	<i>Ecklonia radiata</i> forest with conspicuous understorey of foliose red algae, primarily <i>Plocamium</i> spp. and <i>Osmundaria colensoi</i> .	50% <i>Ecklonia</i> forest, 50% red foliose algae	50% <i>Ecklonia</i> forest, 50% mixed algae
6 MixedBr	Shallow (< 5 m) mixed brown macroalgae—primarily <i>Carpophyllum maschalocarpum</i> and <i>C. flexuosum</i> , with some <i>Ecklonia radiata</i> .	Shallow <i>Carpophyllum</i>	75% <i>Carpophyllum</i> , 25% mixed algae, 5% <i>Ecklonia</i> 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:

- 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 m²) 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 understory 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 m²) 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/m²)									
<i>Ecklonia radiata</i>	0	8.7	3.9	8.6	8.9	1.7	0	0	0
<i>Carpophyllum</i> spp. (<i>C. maschalocarpum</i> , <i>C. plumosum</i> , <i>C. angustifolium</i>)	0	1.2	12.6	0.25	1.75	87.7	0.1	0	0
<i>Carpophyllum flexuosum</i>	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
<i>Caulerpa</i> 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

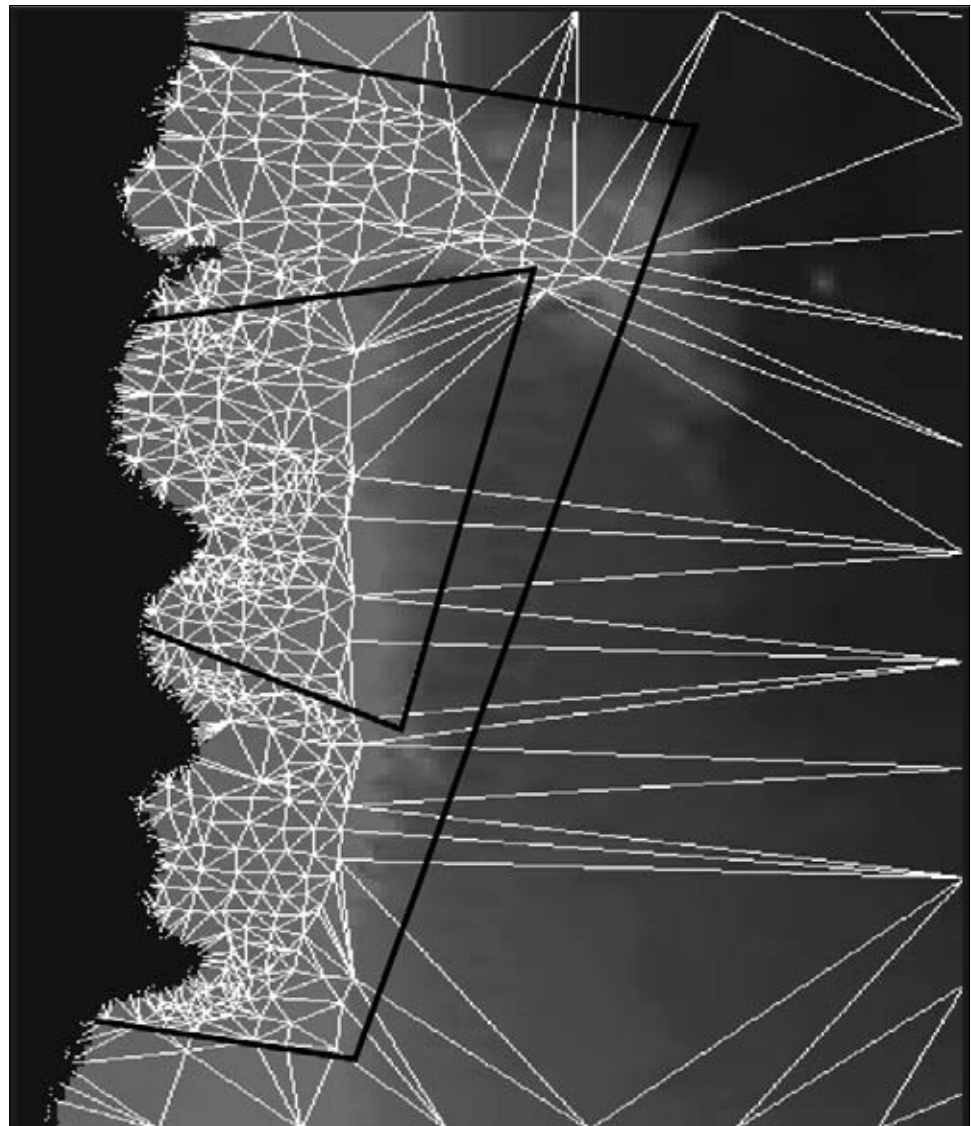
* See Table 3 for definitions of these habitat types.

† 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 Delaunay 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.

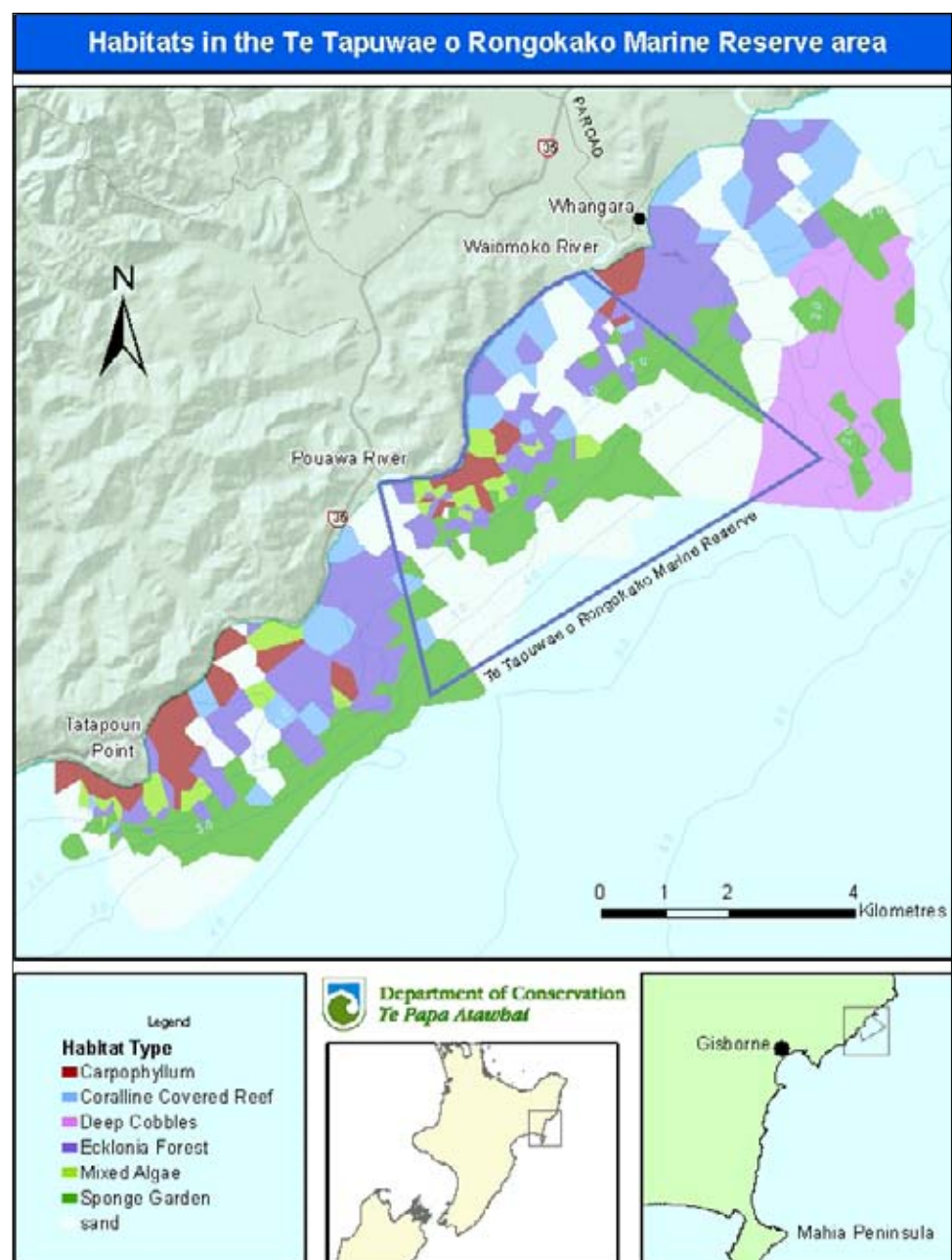


3.2.3 Method 2—GIS habitat maps

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 m². 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
<i>Hormosira banksii</i>	4.0	MixedAlgae
<i>Cystophora</i> 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/m² 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/m², 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/m² (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/m², 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 km² (Fig. 4).