

biomass in the coastal study region was hence estimated to be 0.069 g C/m² nano/microzooplankton, and 0.198 g C/m² 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 gC. 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 ($\mu\text{g C}$)	P/B (PER YEAR)	PROPORTION (%) BY:		
			<i>N</i>	<i>B</i>	<i>P</i>
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 = 22.7J, and 1 mg C = 45.7J. 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
<i>Carpophyllum plumosum</i>	Brown canopy	735 ^a	200–2000 (median 300) ^c
<i>C. flexuosum</i>	Brown canopy	102 ^a	
<i>C. maschalocarpum</i>	Brown canopy	82 ^a	40–110 (median 50) ^c
<i>Ecklonia radiata</i>	Brown canopy	61 ^a	10–75 (median 40) ^c
<i>Ecklonia radiata</i>	Holdfast	572	
		(per 120 mL holdfast volume) ^b	
<i>Cystopbora retroflexa</i>	Large brown	874 ^a	
<i>Cystopbora torulosa</i>	Large brown	332 ^a	
<i>Lessonia variegata</i>	Large brown	13 ^a	
<i>Landsburgia quercifolia</i>	Large brown	85 ^a	
<i>Sargassum sinclairii</i>	Large brown	69 ^a	
<i>Xiphopbora chondrophylla</i>	Large brown	222 ^a	5–40 per 10 cm ² = c. 100 g based on 10 g/cm ² ^d
<i>Zonaria turneriana</i>	Brown foliose		10–80 per 10 cm ² = c. 24.8 g ^d
<i>Pterocladia capillacea</i>	Red foliose		10–60 per 10 cm ² = c. 100 g ^d
<i>Corallina officinalis</i>	Coralline/crustose		100–600 per 10 cm ² = c. 15 g ^d
<i>Pseudolithoderma</i> 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 m² 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/m² (*Carpophyllum* forest, comparable to our mixed algae (MixedBr) habitat), 11.2 g WW/m² (*Ecklonia* forest), and 4.7 g WW/m² (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 detritivorous; 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. podocericid 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 cm², 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/m²) (Table 14). Most taxa were small, including most of the bivalves enumerated (primarily *Nucula bartvigiana* 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	<i>Gammarus macronatus</i>	0.169
Amphipod	<i>Corophium insidiosum</i>	0.021
Amphipod	<i>Lembos websteri</i>	0.551
Amphipod	<i>Unciola inermis</i>	2.02
Amphipod	<i>Parkyale basrensis</i>	5.4
Amphipod	<i>Ampelisca macrocephala</i>	1.32
Amphipod	<i>Haustorium Canadensis</i>	3.0
Amphipod	<i>Pontoporeia femorata</i>	2.25
Amphipod	<i>Amphiporeia lawrenciana</i>	0.056
Isopod	<i>Cyathura carinata</i>	0.52
Polychaete	<i>Pectinaria koreni</i>	13.8
Polychaete	<i>Nephtys bambergi</i>	2.3
Polychaete	<i>Nereis diversicolor</i>	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/m² 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/m², respectively, of primarily amphipods, isopods and cumaceans. Another study at Wainui Beach reported densities of 480/m² (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/m².

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/m².

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 Donovano 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/m².

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 g C/m², 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 g C/m², P/B of 3/y, and Q/B of 12/y. We estimated a meiofaunal biomass of 0.009 g C/m², 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 g C/m², 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*, *Stellela* sp., *Ircinia* sp., *Geodia* sp., *Raspailia* sp., *Callyspongia* spp. and *Cliona celata*. Sponges have highly variable morphology. Large massive sponges (e.g. *Ancorina alata*, *Stellela maori*, *Cliona celata*) can grow up to 1–3 kg WW (approximately 300 × 250 × 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) g/cm² WW and 0.02–0.16 (mean 0.06) g/cm² DW, with mean patch size of 7.8–151.8 (mean 41.7) cm² (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	<i>Didemnum</i> sp.	1	1.6
	Solitary ascidian	<i>Asterocarpa</i> sp.	1	6.4
	Stalked ascidian	<i>Pseudodistoma</i> sp.	1	2.2
	Sea tulip	<i>Pyura pachydermatina</i>	1	15.0
Barnacles	Barnacles	<i>Balanus</i> sp.	1	1.8
Mollusca	Oyster	<i>Crassostrea</i> sp.	1	5.0
	Large mussels	<i>Perna canaliculus</i>	1	26.0
	Small mussels	<i>Xenostrobus pulex</i>	1	8.9
Brachiopod	Brachiopod		0.25	0.4
Bryozoans	Branched bryozoan	<i>Cribricellina cribraria</i>	1	3.5
	-	<i>Bugula dentata</i>	1	0.7
	Encrusting bryozoan	<i>Membranipora</i> sp.	1	0.5
Coelenterates	Colonial anemone	<i>Anthoobothoe albocincta</i>	1	2.3
	Large solitary anemone	<i>Pblyctimactis</i> sp.	1	4.0
	Cup coral	<i>Monomyces rubrum</i>	0.25	0.3
	Soft coral	<i>Alcyonium</i> sp.	1	3.1
Hydrozoa	Hydroid turf	Unknown hydroid	0.25	0.4
	-	<i>Amphisbetia bispinosa</i>	1	8.1
	Hydroid tree	<i>Solanderia ericopsis</i>	1	10.0
Porifera	Encrusting sponge	<i>Cliona celata</i>	1	11.4
	Finger sponge	<i>Raspailia topsenti</i>	1	44.9
	Massive sponge	<i>Polymastia croceus</i>	1	22.2
	-	<i>Ancorina alata</i>	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/m², with lower abundances of 0.05/m² 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 gC 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/m² 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).

4.1.1 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 m²) near Gisborne, resulting in an estimated density of 0.32 crabs/m². Lower crab densities (0.06/m²) 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/m²) have been reported from

TABLE 17. DENSITY (INDIVIDUALS/m²) 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

subtidal reef surveys of offshore Hauraki Gulf islands (Smith 2003). We used the observed value of 0.32/m² 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/m²) 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/m², respectively) (Table 17), with most individuals (approximately 75%) being hermit crabs in both subtidal and intertidal reef surveys.

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 $P = 0.52 \text{ g AFDW m}^{-2} \text{ y}^{-1}$ and $B = 0.55 \text{ g AFDW/m}^2$ for brachyuran crabs and $P = 0.36 \text{ g AFDW m}^{-2} \text{ y}^{-1}$ and $B = 0.22 \text{ g AFDW/m}^2$ 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)
<i>Buccinulum</i> spp.	Predatory gastropod	Aperture length	3.964×10^{-5}	2.9096	11–23
<i>Cantbaridus purpureus</i>	Grazing gastropod	Height	1.774×10^{-5}	2.7903	7–25
<i>Cellana</i> spp. (data for <i>C. stellifera</i>)	Grazing limpet	Length	2.149×10^{-6}	3.3899	13–40
<i>Cookia sulcata</i>	Pupu (grazing gastropod)	Length	2.153×10^{-5}	2.9192	18–85
<i>Dicathais orbita</i>	Predatory gastropod	Aperture length	8.596×10^{-6}	3.2809	16–50
<i>Evechinus chloroticus</i>	Kina	Test diameter	6.550×10^{-4}	2.1835	13–95
<i>Jasus edwardsii</i>	Lobster	Carapace length	7.551×10^{-4}	2.5291	50–188
Paguroidea	Hermit crab	Shell length	7.208×10^{-5}	2.2261	13–45
<i>Plagusia chabrus</i>	Predatory crab	Carapace width	1.162×10^{-4}	2.9224	8–58
<i>Trochus viridis</i>	Grazing gastropod	Width	9.473×10^{-8}	4.8496	14–23
<i>Turbo smaragdus</i>	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, detritivorous 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/m² inside the reserve and 2.25/m² outside the reserve. Density estimates for other predatory invertebrates (seastars, polychaetes, brittlestars and nudibranchs) were 0.33/m² within the intertidal reserve area and 1.70/m² 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 m² of subtidal habitat, we estimated a density of mobile predatory invertebrates (excluding crabs and octopuses) of 0.09/m² (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/m², composed of three species of predatory whelks counted in 55 m² 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/m² (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/m². For our model, we used the low density estimate of 0.09/m² 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 $P=0.01 \text{ g AFDW m}^{-2} \text{ y}^{-1}$ and $B<0.01 \text{ g AFDW/m}^2$ for suspension-feeding gastropods, and $P=0.47 \text{ g AFDW m}^{-2} \text{ y}^{-1}$ and $B=0.21 \text{ g AFDW/m}^2$ for neogastropods. Based on these values, we estimated that $P/B=2.24/\text{y}$ for predatory gastropods. Using this value and assuming a ratio of 0.25 for P/Q , we calculated $Q/B=8.95/\text{y}$. For seastars, we estimated $P/B=1.6/\text{y}$ and $P/Q=0.25$; thus, $Q/B=6.4/\text{y}$.

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 (*Cantbaridus 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/m², P/B of 0.95/y and Q/B of 4.75/y for rock crabs, and a biomass of 0.002 g C/m², 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/m², 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/m², 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/m², 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/m², 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/m². 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-m² quadrats per site), and two subtidal sites outside the reserve, Baldy Reef and Makorori (20 and 15 1-m² quadrats, respectively). Six paua were recorded in 75 m² of surveyed subtidal habitat (0.08/m²), 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/m² (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/m² 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/m² 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-m² quadrats, respectively). In general, kina were very rare on subtidal reefs at Gisborne, with only 17 individuals (16 exposed, 1 cryptic) recorded in 75 m² of surveyed subtidal habitat (0.23/m²). 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/m², 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/m² 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 m² of subtidal habitat (Shears & Babcock 2004b), we estimated a density of pupu of 0.61/m² (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 $0.23/\text{m}^2$, 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 $0.61/\text{m}^2$ 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 $P/B = 2.35/\text{y}$ (range 1.9–2.8/y) and $Q/B = 9.75/\text{y}$ (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. opalae*, *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 $0.93/\text{m}^2$ mobile grazing invertebrates ($0.73/\text{m}^2$ *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 *Onitochiton 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 $14.1/\text{m}^2$ (including grazing and predatory gastropods, crabs, sea cucumbers, pupu, limpets, paua and kina) (Smith 2003). Species-specific grazer densities were $1.6/\text{m}^2$ for *Trochus viridis*, $0.15/\text{m}^2$ for *Cookia sulcata*, and $0.01/\text{m}^2$ for the chiton *Cryptoconchus propodus* (Smith 2003). Choat & Schiel (1982) indicated densities of $5\text{--}38/\text{m}^2$ 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 $12.49/\text{m}^2$ on seaweeds, with a total biomass of 8.27 g AFDW/ m^2 and an estimated (combined) productivity of 5.31 g AFDW $\text{m}^{-2} \text{y}^{-1}$ (Taylor 1998a).

Taylor (1998a) estimated production and biomass for these species at Leigh: $P=4.70$ g AFDW $\text{m}^{-2} \text{y}^{-1}$ and $B=7.01$ g AFDW/ m^2 for grazing gastropods on the seafloor, and $P=0.61$ g AFDW $\text{m}^{-2} \text{y}^{-1}$ 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 $P/B=1.9\text{--}2.8/\text{y}$ and $Q/B=5.5\text{--}14/\text{y}$ as parameter ranges for molluscs (Wolff 1994; Okey et al. 2004). Brey & Hain (1992) gave a P/B of $0.305/\text{y}$ 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 g C/m^2 , P/B of 1.5/y and Q/B of 8.0/y, and a kina biomass of 0.078 g 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 g 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 g 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 g C/m^2 , P/B of 1.8/y and Q/B of 9.75/y for *Trochus*, and a biomass of 0.005 g 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 g 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.

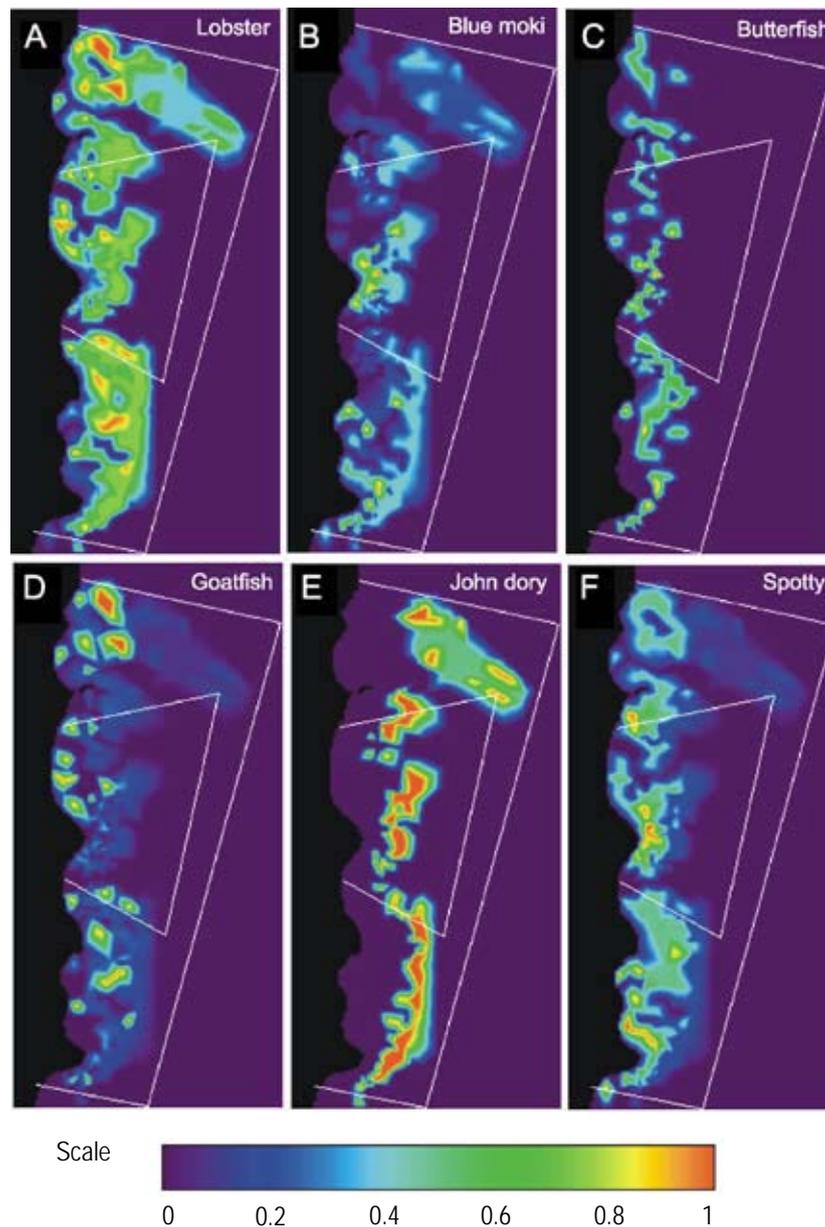
4.13 LOBSTERS

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 $L_{\text{inf}} = 187 \text{ mm}$ and $K = 0.09$ for males, and $L_{\text{inf}} = 117 \text{ mm}$ 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/m²) are as follows: A. lobster (0–26.6/m²); B. blue moki (0–0.63/m²); C. butterfish (0–0.19/m²); D. goatfish (0–0.50/m²); E. john dory (0–0.048/m²); and F. spotty (0–11.0/m²).



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 $P = 0.05 \text{ g AFDW m}^{-2} \text{ y}^{-1}$ and $P/B = 0.07/\text{y}$, 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 $P/B = 0.45/\text{y}$ and $Q/B = 7.4/\text{y}$ (Okey et al. 2004). Production of the spiny lobster *Panulirus homarus* in South Africa has been estimated at $47.6 \text{ kJ m}^{-2} \text{ y}^{-1}$ ($P/B = 0.42/\text{y}$) (Berry & Smale 1980). We initialised the model with $P/B = 0.5/\text{y}$ and $Q/B = 7.4/\text{y}$.

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).

4.14 FISHES

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 *Callorhynchus 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 *Seriotelella 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		WING WIDTH (m)	ESTIMATED AREA COVERED	
		n.m.	m		m ²	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-m² quadrats along a 50-m transect, resulting in an average abundance of 3.28 cryptic fish/m². 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 adpersus* (big eye).

Willis & Anderson (2003) made similar estimates of cryptic fish abundance in northeastern rocky reefs, with 40 and 15 fish per 9-m² plot (4.44 and 1.67/m²) in kelp forests in non-reserve and reserve areas, respectively, and 35 and 30 fish per 9-m² plot (3.89 and 3.33/m²) 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 *Ruanobo wbero*. For our model, we averaged over all studies to arrive at an estimate of 3.32 cryptic reef fish/m² 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*, *Trachelobismus 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/m² (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/m² 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/m² 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

TABLE 21. BIOMASS AND TROPHIC PARAMETERS FOR COMMON FISHES IN TE TAPUWAE O RONGOKAKO MARINE RESERVE.

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

$$Q/B = 3 \cdot W_w^{-0.2} \cdot T^{0.6} \cdot A_R^{0.5} \cdot 3 e^{F_t} \quad (5)$$

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. Macro-benthic 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 buttoni*, 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):

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

where B = effective average annual biomass density (g C/m²), 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 (m²), 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 = kina, kina = kina, cuc = sea cucumber, graz = other grazing invertebrates, octo = octopus, crab = crab, phyt = phytal invertebrates, ben = heterotrophic benthos, zoo = zooplankton, brown = brown algae, red = red algae, green = green algae, det = detritus, spo = sponge.

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

Continued on next page

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	<i>Thyrsites atun</i>	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jack mackerel	<i>Trachurus novaezelandiae</i>	80	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0
John dory	<i>Zeus faber</i>	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Planktivores																		
Butterfly perch	<i>Caesioperca lepidoptera</i>	0	0	0	0	0	0	0	0	0	0	8	92	0	0	0	0	0
Demoiselle	<i>Chromis dispilus</i>	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0
Anchovy	<i>Engraulis australis</i>	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0
Slender roughy	<i>Opitius elongatus</i>	0	0	0	0	0	0	0	40	0	0	0	60	0	0	0	0	0
Trevally	<i>Pseudocaranx dentex</i>	0	0	0	0	0	0	0	0	50	0	0	50	0	0	0	0	0
Sweep	<i>Scorpius lineolatus</i>	0	0	0	0	0	0	0	0	10	0	0	80	0	0	0	10	0
Blue maomao	<i>Scorpius vitokeus</i>	0	0	0	0	0	0	0	0	0	0	0	90	0	0	0	10	0
Common warehou	<i>Serioteleia brama</i>	20	0	0	0	0	0	0	20	0	0	0	60	0	0	0	0	0
Cryptic reef fishes																		
Conger eel	<i>Conger verreauxi</i>	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0
Urchin clingfish	<i>Deltichthys morelandi</i>	0	0	0	90	0	0	0	0	10	0	0	0	0	0	0	0	0
Spectacled triplefin	<i>Ruanoho whero</i>	0	6	0	0	0	7	0	30	30	27	0	0	0	0	0	0	0
Moray eel	<i>Gymnothorax prasinus</i>	15	0	0	0	0	0	0	85	0	0	0	0	0	0	0	0	0
Twister	<i>Helcogramma medium</i>	0	30	0	0	0	8	0	0	60	0	0	0	0	0	2	0	0
Crested blenny	<i>Parablennius laticlavus</i>	0	0	0	0	0	0	0	0	5	35	0	53	0	7	0	0	0
Striped clingfish	<i>Trachelobdismus melobesia</i>	0	5	0	0	0	0	0	0	95	0	0	0	0	0	0	0	0
Blue-eyed triplefin	<i>Notoclinops segmentatus</i>	0	10	0	0	0	5	0	0	60	25	0	0	0	0	0	0	0
Common triplefin	<i>Tripterygion capito</i>	0	0	0	5	0	30	0	25	40	0	0	0	0	0	0	0	0
Yellow and black triplefin	<i>Forsterygion flavonigrum</i>	0	0	0	0	0	0	0	0	45	55	0	0	0	0	0	0	0
Oblique swimming triplefin	<i>Obliquibhys maryannae</i>	0	0	0	0	0	0	0	0	20	0	0	80	0	0	0	0	0
Variable triplefin	<i>Forsterygion varium</i>	0	10	0	0	0	5	0	25	50	10	0	0	0	0	0	0	0
Yaldwyn's triplefin	<i>Notoclinops yaldwyni</i>	0	0	0	0	0	0	0	10	80	10	0	0	0	0	0	0	0

TABLE 23. SEABIRD AND SHOREBIRD ABUNDANCE ESTIMATES IN TE TAPUWAE O RONGOKAKO MARINE RESERVE.

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	<i>Charadrius obscurus</i>	160	12	192	149
Variable oyster catcher	<i>Haematopus unicolor</i>	725	20	1450	98
Banded dotterel	<i>Charadrius bicinctus</i>	60	14	84	195
White-faced heron	<i>Ardea novaehollandiae</i>	550	14	770	106
Pied shag	<i>Phalacrocorax varius</i>	2000	30	6000	74
Little blue penguin	<i>Eudyptula minor</i>	1100	5	550	87
Black-backed gull	<i>Larus dominicanus</i>	950	40	3800	91
Bar-tailed godwit	<i>Limosa lapponica</i>	325	15	488	122
Sooty shearwater	<i>Puffinus griseus</i>	800	20	1600	95
Grey-faced petrel	<i>Pterodroma macroptera gouldi</i>	550	20	1100	106
Fluttering shearwater	<i>Puffinus gavia</i>	300	20	600	125
N Bullers mollymawk	<i>Thalassarche bulleri</i>	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 liliiana* and *Austrovenus stutchburyi* (Cummings et al. 1997; Lundquist et al. 2004). Gross Food Intake (GFI) was calculated as:

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

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:

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

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):

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

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

Gross food intake (GFI = g AFDW/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.

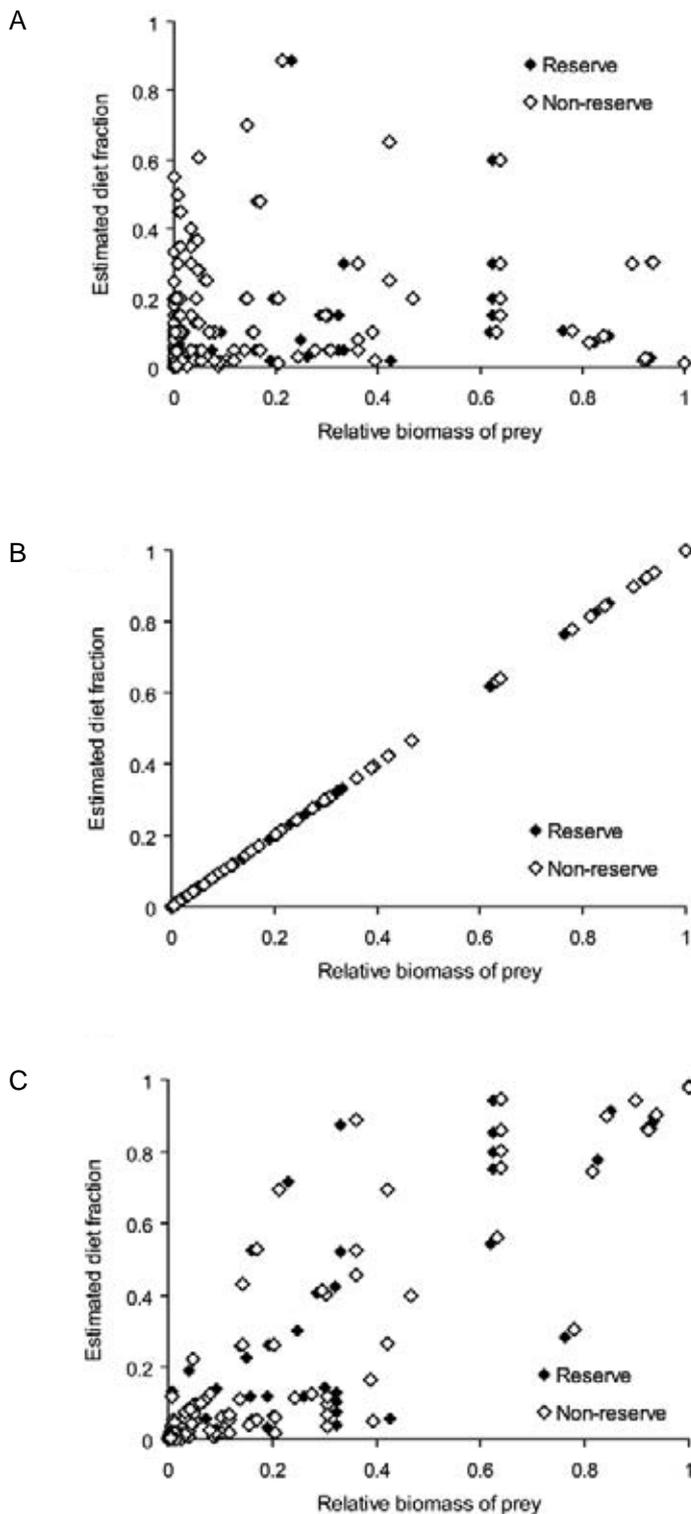


Figure 10. Diet fractions for predator groups in Te Tapuwae o Rongokako system estimated by three different methods: A. Method 1—using values from the scientific and grey literature; B. Method 2—assuming predators have no preference for prey amongst possible prey items; C. Method 3—assuming that literature 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:

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

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

This work was funded by the Ministry of Research, Science & Technology, New Zealand (CDRP project 'Maori Methods and Indicators of Marine Protection'), the Department of Conservation (Science Investigation No. 3765), and the Foundation for Research, Science and Technology, New Zealand ('Ocean Ecosystems: Their Contribution to New Zealand Marine Productivity'; 'Sustainability and Enhancement of Coastal Reef Fisheries of Economic and Cultural Importance'). We thank many individuals and organisations for access to and interpretation of unpublished data: Ministry of Fisheries, Department of Conservation, NIWA, Clinton Duffy, Debbie Freeman, James Holborow, Andy Bassett, Franz Smith, Shane Kelly, Richard Taylor, Nick Shears, Alison MacDiarmid, John Leathwick, Paul Taylor, Michelle Kelly and Malcolm Francis. We thank Max Gibbs (NIWA) for providing the preliminary stable isotope analysis. We thank two anonymous reviewers for helpful comments on the manuscript. We especially thank the NIWA library staff for providing access to thousands of reports, journal articles and student theses that provided the background information underlying the model.

8. References

- Anderson, M.J.; Diebel, C.E.; Blom, W.M.; Landers, T.J. 2005: Consistency and variation in kelp holdfast assemblages: spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. *Journal of Experimental Marine Biology and Ecology* 320: 35–56.
- Anderson, T.J. 1999: Morphology and biology of *Octopus maorum* Hutton 1880 in northern New Zealand. *Bulletin of Marine Science* 65(3): 657–676.
- Andrew, N.L. 1986: The interaction between diet and density in influencing reproductive output in the echinoid *Evechinus chloroticus* (Val.). *Journal of Experimental Marine Biology and Ecology* 97: 63–79.
- Ankar, S. 1977: The soft bottom ecosystem of the northern Baltic proper with special reference to the macrofauna. *Contributions from the Asko Laboratory* 19. University of Stockholm, Sweden. 62 p.
- Annala, J.H. 1978: Mortality estimates for the New Zealand rock lobster, *Jasus edwardsii*. *Fisbery Bulletin* 77(2): 471–480.
- Annala, J.H. 1980: Mortality estimates for the rock lobster, *Jasus edwardsii*, near Gisborne, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 14(4): 357–371.
- Annala, J.H. 1981: Movements of rock lobsters (*Jasus edwardsii*) tagged near Gisborne, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 15: 437–443.
- Arreguin-Sanchez, F.; Arcos, E.; Chavez, E.A. 2002: Flows of biomass and structure in an exploited benthic ecosystem in the Gulf of California, Mexico. *Ecological Modelling* 156: 167–183.
- Ayling, A.L. 1978: The relation of food availability and food preferences to the field diet of an echinoid *Evechinus chloroticus* (Valenciennes). *Journal of Experimental Marine Biology and Ecology* 33: 223–235.
- Ayling, A.L. 1983: Growth and regeneration rates in thinly encrusting Demospongiae from temperate waters. *Biological Bulletin* 165: 343–352.
- Banse, K.; Mosher, S. 1980: Adult body mass and annual production/biomass relationships of field populations. *Ecological Monographs* 50(3): 355–379.
- Barange, M.; Gibbons, M.J.; Carola, M. 1991: Diet and feeding of *Euphausia hanseni* and *Nematoscelis megalops* (Euphausiacea) in the northern Benguela Current: ecological significance of vertical space partitioning. *Marine Ecology Progress Series* 73: 173–181.
- Barker, M.F. 2001: The ecology of *Evechinus chloroticus*. Pp. 251–260 in Lawrence, J.M. (Ed.): Edible sea urchins: biology and ecology. Elsevier Science.
- Behrenfeld, M.J.; Falkowski, P.G. 1997: Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography* 42(1): 1–20.
- Bell, A.H. 1998: The feeding dynamics of the sponge *Polymastia croceus* (Porifera: Demospongiae: Hadromerida) and implications for its ecology and aquaculture. Unpublished MSc thesis, University of Auckland, Auckland, New Zealand. 93 p.
- Benstead, J.P.; March, J.G.; Fry, B.; Ewel, K.; Pringle, C.M. 2006: Testing IsoSource: stable isotope analysis of a tropical fishery with diverse organic matter sources. *Ecology* 87(2): 326–333.
- Berry, P.F.; Smale, M.J. 1980: An estimate of production and consumption rates in the spiny lobster *Panulirus homarus* on a shallow littoral reef off the Natal Coast, South Africa. *Marine Ecology Progress Series* 2: 337–343.
- Booth, J.D. 1997: Long-distance movements in *Jasus* spp. and their role in larval recruitment. *Bulletin of Marine Science* 61(1): 111–128.
- Booth, J.D. 2003: Research sampling design for rock lobsters in Te Tapuwae o Rongokako Marine Reserve. *DOC Science Internal Series* 128. Department of Conservation, Wellington, New Zealand. 25 p.

- Booth, W.E. 1986: Photosynthetic activity of an epiphytic diatom, *Gomphonema novo-zelandicum*, and its *Carpophyllum* (Phaeophyta) hosts. *New Zealand Journal of Marine and Freshwater Research* 20: 615-622.
- Bouvy, M. 1988: Contribution of the bacterial and microphytobenthic microflora in the energetic demand of the meiobenthos in an intertidal muddy sediment (Kerguelen Archipelago). *PSZN I: Marine Ecology* 9: 109-122.
- Boyd, P.W. 2002: The role of iron in the biogeochemistry of the Southern Ocean and equatorial Pacific: a comparison of in situ iron enrichments. *Deep-Sea Research II* 49(9-10): 1803-1821.
- Bradford, J.M. 1972: Systematics and ecology of New Zealand central east coast plankton sampled at Kaikoura. *New Zealand Oceanographic Institute Memoir No. 54*. 89 p.
- Bradford, J.M.; Heath, R.A.; Chang, F.H.; Hay, C.H. 1982: The effect of warm core eddies on oceanic productivity off northeastern New Zealand. *Deep-Sea Research* 29(12A): 1501-1516.
- Bradford-Grieve, J.M.; Chang, F.H.; Gall, M.; Pickmere, S.; Richards, F. 1997: Size-fractionated phytoplankton standing stocks and primary production during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31: 201-224.
- Bradford-Grieve, J.M.; Murdoch, R.C.; Chapman, B.E. 1993: Composition of macrozooplankton assemblages associated with the formation and decay of pulses within an upwelling plume in greater Cook Strait, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 27: 1-22.
- Bradford-Grieve, J.M.; Probert, P.K.; Nodder, S.D.; Thompson, D.; Hall, J.; Hanchet, S.; Boyd, P.; Zeldis, J.; Baker, A.N.; Best, H.A.; Broekhuizen, N.; Childerhouse, S.; Clark, M.; Hadfield, M.; Safi, K.; Wilkinson, I. 2003: Pilot trophic model for sub Antarctic water over the Southern Plateau, New Zealand: a low biomass, high transfer efficiency system. *Journal of Experimental Marine Biology and Ecology* 289: 223-262.
- Brando, V.E.; Ceccarelli, R.; Libralato, S.; Ravagnan, G. 2004: Assessment of environmental management effects in a shallow water basin using mass-balance models. *Ecological Modelling* 172: 213-232.
- Brey, T. 2001: Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. www.thomas-brey.de/science/virtualhandbook (viewed 12 June 2008).
- Brey, T.; Hain, S. 1992: Growth, reproduction and production of *Lissarca notorcadensis* (Bivalvia: Phyllobryidae) in the Weddell Sea, Antarctica. *Marine Ecology Progress Series* 82: 219-226.
- Brock, D.J.; Ward, T.M. 2004: Maori octopus (*Octopus maorum*) bycatch and southern rock lobster (*Jasus edwardsii*) mortality in the South Australian rock lobster fishery. *Fisbery Bulletin* 102: 430-440.
- Brose, U.; Berlow, E.L.; Martinez, N.D. 2005: Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters* 8(12): 1317-1325.
- Bullivant, J.S. 1967: The rate of feeding of the bryozoan, *Zoobotryon verticillatum*. *New Zealand Journal of Marine and Freshwater Research* 2: 111-134.
- Bustamante, R.H.; Branch, G.M. 1995: Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102: 189-201.
- Bustamante, R.H.; Branch, G.M. 1996: The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *Journal of Experimental Marine Biology and Ecology* 196: 1-28.
- Cahoon, L.B.; Safi, K.A. 2002: Distribution and biomass of benthic microalgae in Manukau Harbour, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 36: 257-266.
- Castro, G.; Stoyan, N.; Myers, J.P. 1989: Assimilation efficiency in birds: a function of taxon or food type? *Comparative Biochemistry and Physiology* 3: 271-278.
- Chambers, M.R.; Milne, H. 1975: The production of *Macoma balthica* (L.) in the Ythan Estuary. *Estuarine and Coastal Marine Science* 3: 443-455.

- Chisholm, J.R.M. 2003: Primary productivity of reef-building crustose coralline algae. *Limnology and Oceanography* 48(4): 1376-1387.
- Choat, J.H.; Schiel, D.R. 1982: Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *Journal of Experimental Marine Biology and Ecology* 60: 129-162.
- Christensen, P.B.; Glud, R.N.; Dalsgaard, T.; Gillespie, P. 2003: Impacts of longline mussel farming on oxygen and nitrogen dynamics and biological communities of coastal sediments. *Aquaculture* 218: 567-588.
- Christensen, V.; Pauly, D. 1992: The ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61: 169-185.
- Christensen, V.; Walters, C.J. 2004: Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 172: 109-139.
- Christensen, V.; Walters, C.J.; Pauly, D. 2005: Ecopath with Ecosim: a user's guide. Fisheries Centre, University of British Columbia, Vancouver, Canada. 154 p.
- Clark, M.R. 1985: The food and feeding of seven fish species from the Campbell Plateau, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 19: 339-363.
- Clark, M.R.; King, K.J.; McMillan, P.J. 1989: The food and feeding relationships of black oreo, *Allocyttus niger*, smooth oreo, *Pseudocyttus maculatus*, and eight other fish species from the continental slope of the south-west Chatham Rise, New Zealand. *Journal of Fish Biology* 35: 465-484.
- Close, M.E.; Davies-Colley, R.J. 1990: Baseflow water chemistry in New Zealand Rivers 2. Influence of environmental factors. *New Zealand Journal of Marine and Freshwater Research* 24: 343-356.
- Cohen, E.B.; Grosslein, M.D. 1987: Production on Georges Bank compared with other shelf ecosystems. Pp. 387-391 in Backus, R.H.; Bourne, D.W. (Eds): Georges Bank. MIT Press, Cambridge.
- Cole, R.G.; Tindale, D.; Richards, L.; Glasby, C.; Grange, K. 1999: Benthic fauna of the offshore dumpground in Poverty Bay. NIWA Client Report #PGL90401 prepared for Port Gisborne Ltd. 40 p.
- Cranfield, H.J.; Michael, K.P. 2001: Growth rates of five species of surf clams on a southern beach, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 35: 909-924.
- Creese, R.G. 1988: Ecology of molluscan grazers and their interactions with marine algae in north-eastern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* 22: 427-444.
- Cummings, V.J.; Schneider, D.C.; Wilkinson, M.R. 1997: Multiscale analysis of aggregative responses of mobile predators to infaunal prey. *Journal of Experimental Marine Biology and Ecology* 216: 211-227.
- D'Antonio, C. 1985: Epiphytes on the rocky intertidal red algae *Rhodomela larix* (Turner) C. Agardh: negative effects on the host and food for herbivores. *Journal of Experimental Marine Biology and Ecology* 86: 197-218.
- Davidson, R.J.; Villouta, E.; Cole, R.G.; Barrier, R.G.F. 2002: Effects of marine reserve protection on spiny lobster (*Jasus edwardsii*) abundance and size at Tonga Island Marine Reserve, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12: 213-227.
- DOC (Department of Conservation) 2003: Te Tapuwae o Rongokako Marine Reserve operational plan. Department of Conservation Publication, East Coast/Hawke's Bay Conservancy, New Zealand.
- DOC (Department of Conservation); Ngati Konohi 1998: Te Tapuwae o Rongokako Marine Reserve application: a joint application by Ngati Konohi and the Director-General of Conservation and Ministry for the Environment. East Coast/Hawke's Bay Conservancy, Department of Conservation, Gisborne, New Zealand. 68 p.

- Donovaro, R.; Gambi, C.; Mirto, S. 2002: Meiofaunal production and energy transfer efficiency in a seagrass *Posidonia oceanica* bed in the western Mediterranean. *Marine Ecology Progress Series 234*: 95-104.
- Duckworth, A.R.; Battershill, C.N. 2001: Population dynamics and chemical ecology of New Zealand Demospongiae *Latrunculia* sp. nov. and *Polymastia croceus* (Poecilosclerida: Latrunculiidae: Polymastiidae). *New Zealand Journal of Marine and Freshwater Research 35*: 935-949.
- Duffy, C.A.J. 1989: The fish fauna of subtidally fringing macroalgae sampled at Wairepo Flats, Kaikoura: species composition, distribution and abundance. Unpublished MSc thesis, University of Canterbury, Christchurch, New Zealand. 137 p.
- Duggins, D.O.; Simenstad, C.A.; Estes, J.A. 1989: Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science 245*: 170-173.
- Dunn, J.R.; Ridgway, K.R. 2002: CARS 2000: mapping ocean properties in regions of complex topography. *Deep Sea Research 49(3)*: 591-604.
- Edgar, G.J. 1990: The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *Journal of Experimental Marine Biology and Ecology 137*: 195-214.
- Feller, R.J.; Warwick, R.M. 1988: Energetics. Pp. 181-196 in Higgins, R.P.; Thiel, H. (Eds): Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, DC.
- Fincham, A.A. 1977: Intertidal sand-dwelling peracarid fauna of North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research 11(4)*: 677-696.
- Foster, B.A.; Battaered, W.R. 1985: Distribution of zooplankton in a coastal upwelling in New Zealand. *New Zealand Journal of Marine and Freshwater Research 19*: 213-226.
- Freeman, D. 1998: Ecological interactions between three herbivorous gastropods and *Ecklonia radiata* (Laminariales) in northeastern New Zealand kelp forests. Unpublished MSc thesis, University of Auckland, Auckland, New Zealand. 159 p.
- Freeman, D. 2005: Reef fish monitoring Te Tapuwae o Rongokako Marine Reserve. Unpublished report held by East Coast/Hawke's Bay Conservancy, Department of Conservation, Gisborne, New Zealand. 26 p.
- Freeman, D. 2006: Intertidal paua and kina monitoring: Te Tapuwae o Rongokako Marine Reserve. *East Coast/Hawke's Bay Technical Support Series No. 26*. East Coast/Hawke's Bay Conservancy, Department of Conservation, Gisborne, New Zealand. 23 p.
- Froese, R.; Pauly, D. 2005: FishBase: concepts, design and data sources. ICLARM, Los Baños, Laguna, Philippines. www.fishbase.org/home.htm (viewed 8 February 2008).
- Fu, G.; Baith, K.S.; McClain, C.R. 1998: SeaDAS: the SeaWiFS Data Analysis System. Pp. 73-79 in: Proceedings of the 4th Pacific Ocean Remote Sensing Conference, Qingdao, China, 28-31 July 1998.
- Gibson, P. (on behalf of Ngati Konohi) 2006: Maori methods and indicators for marine protection: a process to identify tohu (marine indicators) to measure the health of the rohe moana of Ngati Konohi. Department of Conservation and Ministry for the Environment, New Zealand. 55 p.
- Gillespie, P.A.; Maxwell, P.D.; Rhodes, L.L. 2000: Microphytobenthic communities of subtidal locations in New Zealand: taxonomy, biomass, production, and food-web implications. *New Zealand Journal of Marine and Freshwater Research 34*: 41-53.
- Glasse, N.J. 2002: The composition and resilience of rockpool fish assemblages on the Central Hawke's Bay coast, New Zealand. Unpublished MSc thesis, Massey University, Palmerston North, New Zealand. 128 p.
- Haedrich, R.L.; Merrett, N.R. 1992: Production/biomass ratios, size frequencies, and biomass spectra of deep-sea demersal fishes. Pp. 157-182 in Rowe, G.T.; Pariente, V. (Eds): Deep-sea food chains and the global carbon cycle. Kluwer Academic Publishers, Dordrecht.
- Haist, V.; Breen, P.A.; Kim, S.W.; Starr, P.J. 2005: Stock assessment of red rock lobsters (*Jasus edwardsii*) in CRA 3 in 2004. New Zealand Fisheries Assessment Report No. 2005/38. 126 p.

- Handley, S.; Kelly, S.; Kelly, M. 2003: Non-destructive video image analysis method for measuring growth in sponge farming: preliminary results from the New Zealand bath-sponge *Spongia (Heteroibria) manipulatus*. *New Zealand Journal of Marine and Freshwater Research* 37: 613-621.
- Harcourt, R.G.; Bradshaw, C.J.A.; Dickson, K.; Davis, L.S. 2002: Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology Progress Series* 227: 11-24.
- Heather, B.; Robertson, H. 1986: The field guide to the birds of New Zealand. Penguin Books, New York. 432 p.
- Herman, P.M.J.; Vranken, G.; Heip, C. 1984: Problems in meiofauna energy-flows studies. Pp. 21-28 in Heip, C. (Ed.): Biology of meiofauna. International Meiofauna Conference, Gent (Belgium), 16-20 August 1983.
- Hickman, R.W. 1979: Allometry and growth of the green-lipped mussel *Perna canaliculus* in New Zealand. *Marine Biology* 51: 311-327.
- Hicks, G.R.F. 1977: Species associations and seasonal population densities of marine phytoplankton harpacticoid copepods from Cook Strait. *New Zealand Journal of Marine and Freshwater Research* 11: 621-643.
- Hooker, S.B.; Esaias, W.E.; Feldman, G.C.; Gregg, W.W.; McClain, C.R. 1992: An overview of SeaWiFS and Ocean Colour, NASA Technical Memo 194566, Volume 1. Pp. 1-24 in Hooker, S.B.; Firestone, E.R. (Eds): NASA Goddard Space Flight Center, USA.
- Hughes, R.N. 1970: An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (da Costa). *Journal of Animal Ecology* 39: 357-381.
- Hunter, C.M.; Haddon, M.; Sainsbury, K.J. 2005: Use of fishery-dependent data for the evaluation of depensation: case study involving the predation of rock lobster (*Jasus edwardsii*) by octopus (*Octopus maorum*). *New Zealand Journal of Marine and Freshwater Research* 39: 455-469.
- Ikeda, T. 1996: Metabolism, body composition, and energy budget of the mesopelagic fish *Maurolicus muelleri* in the Sea of Japan. *Fishery Bulletin* 94: 49-58.
- James, M.R. 1989: Role of zooplankton in the nitrogen cycle off the west coast of the South Island, New Zealand, winter 1987. *New Zealand Journal of Marine and Freshwater Research* 23: 507-518.
- James, M.R.; Weatherhead, M.A.; Ross, A.H. 2001: Size-specific clearance, excretion, and respiration rates, and phytoplankton selectivity for the mussel *Perna canaliculus* at low levels of natural food. *New Zealand Journal of Marine and Freshwater Research* 35: 73-86.
- Jarre-Teichmann, A.; Brey, T.; Bathmann, U.V.; Dahm, C.; Dieckmann, G.S.; Gorny, M.; Klages, M.; Pagés, F.; Plötz, J.; Schnack-Shiel, S.B.; Stiller, M. 1997: Trophic flows in the benthic shelf community of the eastern Weddell Sea, Antarctica. Pp. 118-134 in Battaglia, B.; Valencia, J.; Walton, D.W.H. (Eds): Antarctic communities, species, structure and survival. University Press, Cambridge.
- Jarre-Teichmann, A.; Shannon, L.J.; Moloney, C.L.; Wickens, P.A. 1998: Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. *South African Journal of Marine Science* 19: 391-414.
- Jeffs, A.G.; Holland, R.C.; Hooker, S.H.; Hayden, B.J. 1999: Overview and bibliography of research on the greenshell mussel, *Perna canaliculus*, from New Zealand waters. *Journal of Shellfish Research* 18: 347-360.
- Jiang, W.; Gibbs, M.T. 2005: Predicting the carrying capacity of bivalve shellfish culture using a steady, linear food web model. *Aquaculture* 244: 171-185.
- Jones, G.P. 1988: Ecology of rocky reef fish of north-eastern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* 22: 445-462.
- Keeley, N.; Barter, P.; Robertson, B. 2002: Assessment of ecological effects on the seabed surrounding the Gisborne wastewater outfall: winter 2002. Cawthron Institute Report #735 prepared for the Gisborne District Council. 40 p.

- Kelly, S.; Scott, D.; MacDiarmid, A.B. 2002: The value of a spillover fishery for spiny lobsters around a marine reserve in northern New Zealand. *Coastal Management* 30: 153-166.
- Kelly, S.; Scott, D.; MacDiarmid, A.B.; Babcock, R.C. 2000: Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biological Conservation* 92: 359-369.
- Kendrick, T.H.; Bentley, N. 2003: Movements of rock lobsters (*Jasus edwardsii*) tagged by commercial fishers around the coast of New Zealand from 1993. New Zealand Fisheries Assessment Report No. 2003/55. 48 p.
- Kingsford, M.J.; Choat, J.H. 1985: The fauna associated with drift net algae captured with a plankton-mesh purse seine net. *Limnology & Oceanography* 30(3): 618-630.
- Kirk, J.T.O. 1994: Light and photosynthesis in aquatic ecosystems, second edition. Cambridge University Press. 509 p.
- Kirkman, H. 1984: Standing stock and production of *Ecklonia radiata* (C.Ag.) J. Agardh. *Journal of Experimental Marine Biology and Ecology* 76: 119-130.
- Klumpp, D.W.; Salita-Espiosa, J.S.; Fortes, M.D. 1992: The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. *Aquatic Botany* 43: 327-349.
- Lamare, M.D.; Mladenov, P.V. 2000: Modelling somatic growth in the sea urchin *Evechinus chloroticus* (Echinoidea: Echinometridae). *Journal of Experimental Marine Biology and Ecology* 243: 17-43.
- Lamare, M.D.; Wing, S.R. 2001: Calorific content of New Zealand marine macrophytes. *New Zealand Journal of Marine and Freshwater Research* 35: 335-341.
- Langlois, T.J.; Ballantine, W.J. 2005: Ecological research using fully-protected marine reserves: conclusions from northern New Zealand. *Conservation Biology* 19: 1763-1770.
- Larkum, A.W.D. 1986: A study of growth and primary production in *Ecklonia radiata* (C. Ag.) J. Agardh (Laminariales) at a sheltered site in Port Jackson, New South Wales. *Journal of Experimental Marine Biology and Ecology* 96: 177-190.
- Lasiewski, R.C.; Dawson, W.R. 1967: A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13-23.
- Lefevre, N.; Taylor, A.H.; Gilbert, F.J.; Geider, R.J. 2003: Modeling carbon to nitrogen and carbon to chlorophyll a ratios in the ocean at low latitudes: evaluation of the role of physiological plasticity. *Limnology and Oceanography* 48(5): 1796-1807.
- Lindeman, R.L. 1942: The trophic-dynamic aspect of ecology. *Ecology* 23(4): 399-418.
- Littler, M.M.; Arnold, K.E. 1982: Primary productivity of marine macroalgal functional-form groups from southwestern North America. *Journal of Phycology* 18: 307-311.
- Luckens, P.A. 1975: Predation and intertidal zonation of barnacles at Leigh, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 9(3): 355-378.
- Lundquist, C.; Chiaroni, L.; Halliday, J.; Williston, T. 2004: Identifying areas of conservation value in the Waikato coastal marine environment. NIWA Client Report #HAM2004-039 prepared for the Department of Conservation. 98 p.
- Marsden, I.D.; Williams, P.M.J. 1996: Factors affecting the grazing rate of the New Zealand abalone *Haliotis iris* Martyn. *Journal of Shellfish Research* 15(2): 401-406.
- McLay, C.L. 1988: Crabs of New Zealand. Leigh Laboratory Informal Bulletin 25/33-3002. 463 p.
- McLusky, D.S. 1981: The estuarine ecosystem. Blackie Press, Glasgow. 150 p.
- McShane, P.E.; Naylor, J.R. 1995: Small-scale spatial variation in growth, size at maturity, and yield-and egg-per-recruit relations in the New Zealand abalone *Haliotis iris*. *New Zealand Journal of Marine and Freshwater Research* 29: 603-612.
- Medway, D.G. 2000: The Reed field guide to common New Zealand shorebirds. Reed Publishing (NZ) Ltd, Auckland. 155 p.

- Murphy, R.J.; Pinkerton, M.H.; Bradford-Grieve, J.M.; Boyd, P.W. 2001: Phytoplankton distributions around New Zealand derived from SeaWiFS remotely-sensed ocean colour data. *New Zealand Journal of Marine and Freshwater Research* 35: 343-362.
- Nelson, T.A.; Waaland, R.J. 1997: Seasonality of eelgrass, epiphyte, and grazer biomass and productivity in subtidal eelgrass meadows subjected to moderate tidal amplitude. *Aquatic Botany* 56: 51-74.
- Newell, R.C.; Field, J.G. 1985: The contribution of bacteria and detritus to carbon and nitrogen flow in a benthic community. *Marine Biology Letters* 4: 23-36.
- Newsome, S.D.; Phillips, D.L.; Culleton, B.J.; Guilderson, T.P.; Koch, P.L. 2004: Dietary reconstruction of an early to middle Holocene human population from central California coast: insights from advanced stable isotope mixing models. *Journal of Archaeological Sciences* 31: 1101-1115.
- Novaczek, I. 1984: Development and phenology of *Ecklonia radiata* at two depths in Goat Island Bay, New Zealand. *Marine Biology* 81: 189-197.
- Okey, T.A.; Banks, S.; Born, A.F.; Bustamante, R.H.; Calvopina, M.; Edgar, G.J.; Espinoza, E.; Farina, J.M.; Garske, L.E.; Reck, G.K.; Salazar, S.; Shepherd, S.; Toral-Granda, V.; Wallem, P. 2004: A trophic model of a Galapagos subtidal rocky reef for evaluating fisheries and conservation strategies. *Ecological Modelling* 172: 383-401.
- Orth, R.J.; van Montfrans, J. 1984: Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. *Aquatic Botany* 18: 43-69.
- Ortiz, M.; Wolff, M. 2002: Spatially explicit trophic modelling of a harvested benthic ecosystems in Tongoy Bay (central northern Chile). *Aquatic Conservation: Marine and Freshwater Ecosystems* 12: 601-618.
- O'Shea, S. 1999: The marine fauna of New Zealand: Octopoda (Mollusca: Cephalopoda). *NIWA (National Institute of Water & Atmospheric Research Ltd) Biodiversity Memoir* 112. 280 p.
- Paine, R.T.; Vadas, R.L. 1969: Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. *Marine Biology* 4: 79-86.
- Palomares, M.L.D.; Pauly, D. 1998: Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine and Freshwater Research* 49: 447-453.
- Parsons, T.R.; Takahashi, M.; Hargrave, B. 1984: Biological oceanographic processes. Pergamon Press Ltd, Oxford. 332 p.
- Phillips, D.L.; Gregg, J.W. 2003: Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136: 261-269.
- Pinkerton, M.H.; Hanchet, S.; Bradford-Grieve, J.; Cummings, V.; Wilson, P.; Williams, M. 2006: Modelling the effects of fishing in the Ross Sea. Final Report to Ministry of Fisheries, Project ANT2004-05. 169 p.
- Pinkerton, M.H.; Lundquist, C.J.; Duffy, C.A.J.; Freeman, D. in press: Trophic modelling of a New Zealand rocky reef ecosystem using simultaneous adjustment of diet, biomass and energetic parameters. *Journal of Experimental Marine Biology and Ecology*.
- Polovina, J.J. 1984: Model of a coral reef ecosystem. Part I: the ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* 3: 1-11.
- Pomeroy, L.R. 1979: Secondary production mechanisms of continental shelf communities. Pp. 163-186 in Livingston, R.J. (Ed.): *Ecological processes in coastal and marine systems*. Plenum Press, New York.
- Press, W.H.; Teukolsky, S.A.; Vetterling, W.T.; Flannery, B.P. 1992: Linear programming and the Simplex method. Pp. 430-444 in: *Numerical recipes in C*. Second Edition. Cambridge University Press.
- Probert, P.K. 1986: Energy transfer through the shelf benthos off the west coast of South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 20: 407-417.

- Raffaelli, D.R. 1985: Functional feeding groups of some intertidal molluscs defined by gut content analysis. *Journal of Molluscan Studies* 51: 233-239.
- Reiswig, H.M. 1971: Particle feeding in natural populations of three marine Demosponges. *Biological Bulletin* 141: 568-591.
- Richardson, K.M.; Pinkerton, M.H.; Image, K.; Snelder, T.; Boyd, P.W.; Gall, M.P.; Zeldis, J.; Oliver, M.D.; Murphy, R.J. 2002: SeaWiFS data from around New Zealand: validation and an application. COSPAR, World Space Congress, 10-19 October 2002, Houston, USA.
- Ridgway, K.R.; Dunn, J.R.; Wilkin, J.L. 2002: Ocean interpolation by four-dimensional least squares. Application to the waters around Australia. *Journal of Atmospheric and Oceanic Technology* 19(9): 1357-1375.
- Russell, B.C. 1983: The food and feeding habits of rocky reef fish of north eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 17: 121-145.
- Rybarczyk, H.; Elkaim, B. 2003: An analysis of the trophic network of a macrotidal estuary: the Seine Estuary (Eastern Channel, Normandy, France). *Estuarine, Coastal and Shelf Science* 58: 775-791.
- Schiel, D. 2005: Common kelp and giant kelp. Pp. 64-79 in Andrew, N.; Francis, M. (Eds): The living reef: the ecology of New Zealand's rocky reefs. Craig Potton Publishing, Nelson, New Zealand.
- Schiel, D.R. 1982: Selective feeding by the echinoid, *Evechinus chloroticus*, and the removal of plants from subtidal algal stands in northern New Zealand. *Oecologia* 54: 379-388.
- Schiel, D.R.; Breen, P.A. 1991: Population structure, ageing and fishing mortality of the New Zealand abalone *Haliotis iris*. *Fisbery Bulletin* 89: 681-691.
- Schwarz, A.-M. 2004: Contribution of photosynthetic gains during tidal emersion to production of *Zostera capricorni* in a North Island, New Zealand estuary. *New Zealand Journal of Marine and Freshwater Research* 38: 809-818.
- Sewell, M.A. 1990: Aspects of the ecology of *Stichopus mollis* (Echinodermata: Holothuroidea) in north-eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 24: 97-103.
- Sewell, M. 2005: Mobile invertebrates. Pp. 92-99 in Andrew, N.; Francis, M. (Eds): The living reef: the ecology of New Zealand's rocky reefs. Craig Potton publishing, Nelson, New Zealand.
- Shears, N.T.; Babcock, R.C. 2003: Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series* 246: 1-16.
- Shears, N.T.; Babcock, R.C. 2004a: Indirect effects of marine reserve protection on New Zealand's rocky coastal marine communities. *DOC Science Internal Series* 192. Department of Conservation, Wellington, New Zealand. 48 p.
- Shears, N.T.; Babcock, R.C. 2004b: Quantitative classification of New Zealand's shallow subtidal reef communities. *Science for Conservation* 245. Department of Conservation, Wellington, New Zealand. 65 p.
- Shears, N.T.; Babcock, R.C. 2007: Quantitative description of mainland New Zealand's shallow subtidal reef communities. *Science for Conservation* 280. Department of Conservation, Wellington, New Zealand. 126 p.
- Shears, N.T.; Babcock, R.C.; Duffy, C.A.J.; Walker, J.W. 2004: Validation of qualitative habitat descriptors commonly used to classify subtidal reef assemblages in north-eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 38: 743-752.
- Shushkina, E.A.; Vinogradov, M.E.; Lebedeva, L.P. 1998: Biotic balance in the ocean and estimation of the organic matter flux from epipelagic zones on the basis of satellite and expeditionary data. *Oceanology* [translated from *Okeanologiya*] 38(5): 628-635.
- Silva, J.; Santos, R.; Calleja, M.L.; Duarte, C.M. 2005: Submerged versus air-exposed intertidal macrophyte productivity: from physiological to community-level assessments. *Journal of Experimental Marine Biology and Ecology* 317: 87-95.

- Smith, B.D.; Cabot, E.L.; Foreman, R.E. 1985: Seaweed detritus versus benthic diatoms as important food sources for two dominant subtidal gastropods. *Journal of Experimental Marine Biology and Ecology* 92: 143-156.
- Smith, F. 2003: Marine environment classification: physical influences on rocky reef assemblages in the Hauraki Gulf. Consultancy report prepared for the Department of Conservation. 62 p.
- Smith, F.; Gordon, D. 2005: Sessile invertebrates. Pp. 80-91 in Andrew, N.; Francis, M. (Eds): The living reef: the ecology of New Zealand's rocky reefs. Craig Potton Publishing, Nelson, New Zealand.
- Sorokin, Y.I. 1981: Microheterotrophic organisms in marine ecosystems. Pp. 293-342 in Longhurst, A.R. (Ed.): Analysis of marine ecosystems. Academic Press, London.
- Stephens, S.; Haskew, R.; Lohrer, D.; Oldman, J. 2004: Larval dispersal from the Te Tapuwae o Rongokako Marine Reserve: numerical model simulations. NIWA Client Report HAM2004-088 prepared for the Department of Conservation. 50 p.
- Stephenson, G. 1993: Macrofauna of Wainui beach south of Hamanatua stream: an assessment of changes associated with beach erosion. *Conservation Advisory Science Notes* 38. Department of Conservation, Wellington, New Zealand. 21 p.
- Stewart, M.J.; Creese, R.G. 2004: Feeding ecology of whelks on an intertidal sand flat in north-eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 38: 819-831.
- Strickland, J.D.H.; Parsons, T.R. 1972: A practical handbook of sea water analysis. Fisheries Research Board of Canada. 310 p.
- Sullivan, K.J.; Mace, P.M.; Smith, N.W.McL.; Griffiths, M.H.; Todd, P.R.; Livingstone, M.E.; Harley, S.J.; Key, J.M.; Connell, A.M. 2006: Report from the Fishery Assessment Plenary, May 2005: stock assessments and yield estimates. Unpublished report held in NIWA library, Wellington. Ministry of Fisheries, Wellington, New Zealand. 792 p.
- Taylor, A.H.; Geider, R.J.; Gilbert, F.J.H. 1997: Seasonal and latitudinal dependencies of phytoplankton carbon-to-chlorophyll a ratios: results of a modelling study. *Marine Ecology Progress Series* 152: 51-66.
- Taylor, M.W.; Taylor, R.B.; Rees, T.A.V. 1999: Allometric evidence for the dominant role of surface cells in ammonium metabolism and photosynthesis in northeastern New Zealand seaweeds. *Marine Ecology Progress Series* 184: 73-81.
- Taylor, R.B. 1998a: Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. *Marine Ecology Progress Series* 172: 37-51.
- Taylor, R.B. 1998b: Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal brown seaweeds in northeastern New Zealand. *Hydrobiologia* 361: 25-35.
- Taylor, R.B. 1998c: Short-term dynamics of a seaweed epifaunal assemblage. *Journal of Experimental Marine Biology and Ecology* 227: 67-82.
- Taylor, R.B.; Cole, R.G. 1994: Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand. *Marine Ecology Progress Series* 115: 271-282.
- Taylor, R.B.; Willis, T.J. 1998: Relationships amongst length, weight and growth of north-eastern New Zealand reef fishes (note). *Marine & Freshwater Research* 49: 255-260.
- Thompson, S. 1981: Fish of the marine reserve: a guide to the identification and biology of common coastal fish of north eastern New Zealand. *Leigh Laboratory Bulletin No. 3*. University of Auckland, New Zealand. 364 p.
- Town, J.C. 1980: Diet and food preference of intertidal *Astrostele scabra* (Asteroidea: Forcipulata). *New Zealand Journal of Marine and Freshwater Research* 14(4): 427-435.
- Vinogradov, A.P. 1953: The elementary chemical composition of marine organisms. Memoir of the Sears Foundation for Marine Research, Yale University, New Haven II. 647 p.
- Vlieg, P. 1988: Proximate composition of New Zealand marine finfish and shellfish. Biotechnology Division, DSIR, Palmerston North, New Zealand. 52 p.

- Warwick, R.M.; Joint, I.R.; Radford, P.J. 1979: Secondary production of the benthos in an estuarine environment. Pp. 429–450 in Jefferies, R.L.; Davey, A.J. (Eds): Ecological processes in coastal environments. Blackwell Scientific Publications, Oxford.
- Wear, R.G.; Haddon, M. 1987: Natural diet of the crab *Ovalipes catbarus* (Crustacea, Portunidae) around central and northern New Zealand. *Marine Ecology Progress Series* 35: 39–49.
- Williamson, J.E.; Creese, R.G. 1996: Small invertebrates inhabiting the crustose alga *Pseudolithoerma* sp. (Ralfsiaceae) in northern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 30: 221–232.
- Willis, T.J.; Anderson, M.J. 2003: Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Marine Ecology Progress Series* 257: 209–221.
- Willis, T.J.; Millar, R.B.; Babcock, R.C. 2003: Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology* 40: 214–227.
- Wilson, C.; Freeman, D.; Hogan, K.; Thompson, K. 2007: Maori methods and indicators for marine protection: summary of research findings. Ngati Kere, Ngati Konohi, Ministry for the Environment and Department of Conservation, New Zealand. 59 p.
- Wolff, M. 1994: A trophic model for Tongoy Bay—a system exposed to suspended scallop culture (Northern Chile). *Journal of Experimental Marine Biology and Ecology* 182: 149–168.
- Woods, C.M. 1993: Natural diet of the crab *Notomitbrax ursus* (Brachyura: Majidae) at Oaro, South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 27: 309–315.
- Zeldis, J.; Robinson, K.; Ross, A.; Hayden, B. 2004: First observations of predation by New Zealand Greenshell mussels (*Perna canaliculus*) on zooplankton. *Journal of Experimental Marine Biology and Ecology* 311(2): 287–299.
- Zemke-White, W.L.; Speed, S.; McClary, D. 2004: Beach cast seaweed review: environmental impacts of harvesting beach-cast seaweeds in New Zealand. Kingett-Mitchell Ltd. 39 p.

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/m ²)	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	Phytopl_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 A.1.2. 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)		0.22 (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)					

Continued on next page

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							0.40 (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

TABLE A2.1. SAMPLES AVAILABLE FOR STABLE ISOTOPE ANALYSIS, PLANT/ANIMAL TISSUE ANALYSED AND COLLECTION LOCATION OF SAMPLES.

SPECIES	TYPE	SAMPLE ANALYSED	RESERVE	OUTSIDE RESERVE
Primary producers				
<i>Carpophyllum maschalocarpum</i>	Subtidal brown alga	Whole plants	x	x
Coralline turf	Coralline turf	Whole plants	x	x
<i>Cystophora torulosa</i>	Subtidal brown alga	Whole plants	x	x
<i>Ecklonia radiata</i>	Subtidal brown alga	Whole plants	x	x
<i>Hormosira banksii</i>	Intertidal brown alga	Whole plants	x	x
Nongeniculate corallines	Coralline paint	Whole plants	x	x
<i>Porphyra columbina</i>	Red alga	Whole plants	x	x
<i>Pterocladia capillacea</i>	Red alga	Whole plants	x	
<i>Zostera capricorni</i>	Seagrass	Whole plants		x
Grazers				
<i>Amaurochiton glaucus</i>	Chiton	Whole animals, including shell	x	
<i>Cellana ornata</i>	Gastropod	Whole animals, minus shell	x	x
<i>Chiton pelliserpentis</i>	Chiton	Whole animals, minus shell	x	x
<i>Cookia sulcata</i>	Gastropod	Whole animals	x	x
<i>Evechinus chloroticus</i>	Kina	Gonad tissue only	x	x
<i>Haliotis iris</i>	Paua	Whole animals, minus shell and gut	x	x
<i>Melagraphbia aethiops</i>	Gastropod	Whole animals including shell for reserve, minus shell for fished	x	x
<i>Trochus viridis</i>	Gastropod	Whole animals, minus shell	x	x
<i>Turbo smaragdus</i>	Gastropod	Whole animals, minus shell	x	x
Filter feeders				
<i>Opbionereis</i> spp.	Brittlestar	Whole animals	x	
<i>Xenostrobus pulex</i>	Mussel	Whole animals, including shell	x	
Carnivores				
Polychaetes	Polychaetes	Whole animals	x	
<i>Jasus edwardsii</i>	Lobster	Legs only, including shell	x	x
<i>Pagurus novaezelandiae</i>	Crab	Whole animals	x	x
<i>Plagusia chabrus</i>	Crab	Whole animal (one animal only)	x	x
<i>Latridopsis ciliaris</i>	Predatory fish	Muscle tissue only		x
<i>Nemadactylus macropterus</i>	Predatory fish	Muscle tissue only		x
<i>Pagrus auratus</i>	Predatory fish	Muscle tissue only		x
<i>Polyprion oxygeneios</i>	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
<i>Ecklonia</i> (Reserve)	34.3	14–48
Urchin gonad (Reserve)	3.2	0–20
Subtidal gastropod <i>Trochus</i> (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 <i>Ecklonia</i> (Fished)	18.6	0–52
Urchin gonad (Fished)	10.9	0–42
Subtidal gastropod <i>Trochus</i> (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.

Lundquist, C.J.; Pinkerton, M.H. 2008: Collation of data for ecosystem modelling of Te Tapuwae o Rongokako Marine Reserve. *Science for Conservation* 288. 103 p.