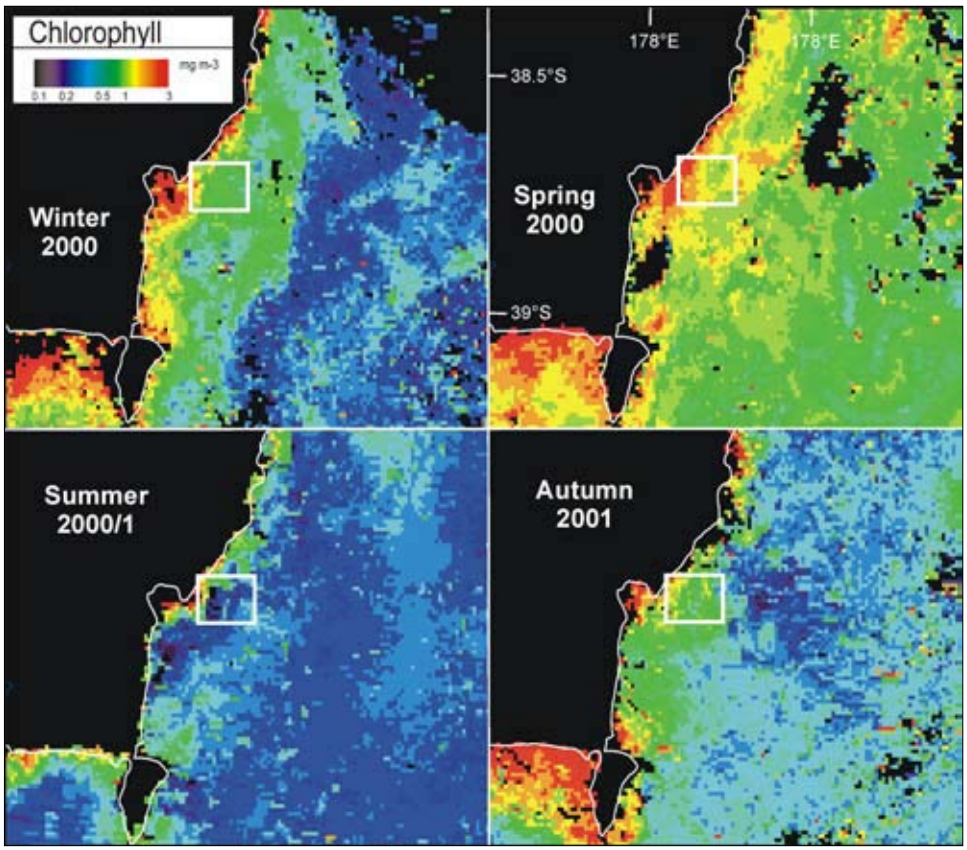


Figure 4. Example of 1-km-resolution surface chlorophyll-*a* concentrations from the SeaWiFS ocean colour sensor over an annual cycle. The white boxes indicate the region from which data were extracted.

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

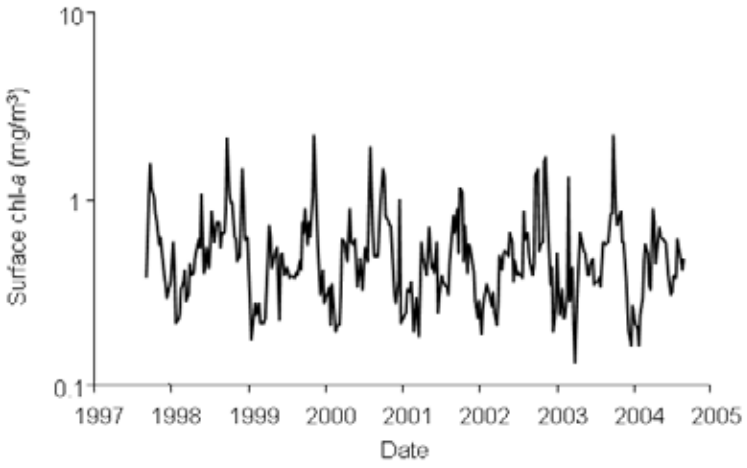


Figure 5. Seven years of measurements of chlorophyll-*a* concentration in the box offshore from Te Tapuwae o Rongokako Marine Reserve, taken from measurements of ocean colour by the SeaWiFS satellite sensor. Median values are shown.

Note that it is possible that phytoplankton biomass, chlorophyll concentration and phytoplankton primary production are different nearer the shore than offshore for a number of reasons:

- Average light levels received by the phytoplankton in the water column may be higher in shallower than deeper waters, even allowing for the fact that higher suspended sediment concentrations near-shore may result in greater light attenuation than offshore. We corrected for this effect as described below in section 4.3.3.
- Nutrients recycled from the sea floor may be available to phytoplankton in the water column. We have no information on this, but the effect is likely to be relatively small.
- Macronutrient (nitrate, phosphate, silicate) input from land run-off may result in higher production than in offshore waters. However, Close & Davies-Colley (1990) characterised rivers in the vicinity of the reserve as having relatively low nutrient loads (< 100 mg/m^3 nitrate).
- Grazing pressure/predation on phytoplankton may be different by region. There are no data available to compare grazing rates of phytoplankton between the reserve and offshore region, but we assume that this effect is small.

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

4.3.2 Water column phytoplankton biomass

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

1. **Total depth of water:** The average depth in Te Tapuwae o Rongokako Marine Reserve is calculated to be 11 m.
2. **Distribution of phytoplankton vertically through the water column:** There are no vertical measurements of chlorophyll or water column structure in the study region. In shallow coastal waters with limited freshwater inflow like the study region, it is unlikely that there is persistent vertical stratification. Thus, we assumed phytoplankton was uniformly distributed over the whole depth.
3. **Carbon-to-chlorophyll ratio for phytoplankton:** The ratio of carbon to chlorophyll-*a* in marine phytoplankton has been found to vary considerably, from 20 to > 200 g C/g Chl-*a* (Taylor et al. 1997; Lefevre et al. 2003). In subtropical waters near New Zealand, work suggests a seasonal variation in C:Chl-*a* values of approximately 50 before the spring bloom, 40 during the spring bloom, and 60 after the bloom (Boyd 2002; P. Boyd, NIWA, unpubl. data). A linear interpolation between these latter values was used to estimate C:Chl-*a* ratios through the year.

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

4.3.3 Net primary production

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

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

Two further effects were also considered when using offshore values to estimate net primary production by phytoplankton in Te Tapuwae o Rongokako Marine Reserve. First, the depth of production is much less near the shore, because the depth of water (10 m) is less than the depth of the photic zone (c. 50 m). Second, average light levels in the photic zone will tend to be greater in shallow waters than in deep waters. Bio-optical work by NIWA in many regions around

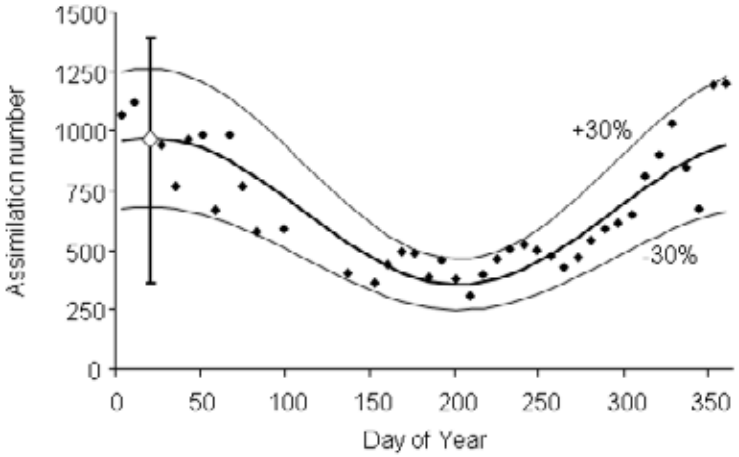
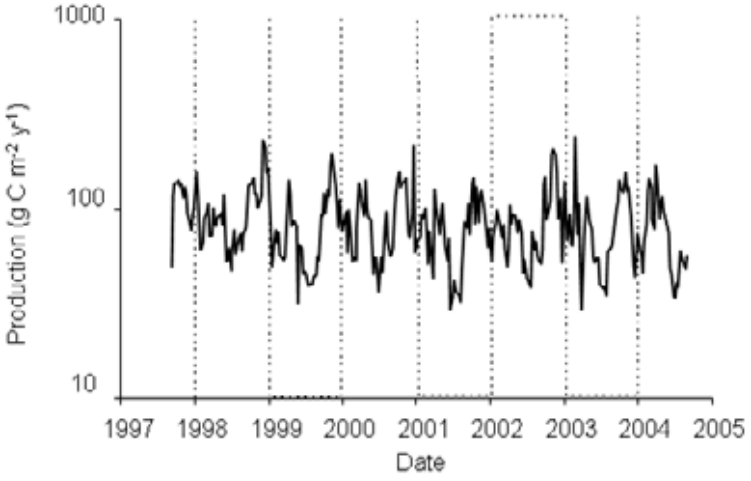


Figure 6. Assimilation numbers (water column integrated photosynthesis per unit surface chlorophyll concentration (mg C d^{-1} m^{-2}) (mg Chl-*a* m^{-3})$^{-1}$ for the area immediately offshore from Te Tapuwae o Rongokako Marine Reserve. The open diamond and error bars indicate the 25th–75th percentile range for assimilation numbers measured in 1976 (Bradford et al. 1982). The black diamonds show modelled net primary production during the year 2000 (Behrenfeld & Falkowski 1997), which have been scaled to reconcile them with *in situ* measurements. A sinusoid was fitted to these values, and the ±30% ranges are shown (solid lines).

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

Figure 7. Net primary production by phytoplankton in Te Tapuwae o Rongokako Marine Reserve, based on modelled data as described in the text.



This value of net primary production by phytoplankton is somewhat less than was measured offshore by Bradford-Grieve et al. (1997), who reported values of 360 g C m^{-2} y^{-1} during spring in the Subtropical Front. This difference is reasonable, given the range of uncertainty related to the factors explained above.

4.3.4 Production to biomass ratio

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

4.3.5 Summary—Phytoplankton

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

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

4.3.6 Further work

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

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

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

4.4 MICROPHYTOBENTHOS AND EPIPHYTAL ALGAE

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

4.4.1 Microphytobenthos

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

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

4.4.2 Epiphytic algae (macrophytes and microphytes)

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

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

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

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

4.4.3 Summary—Microphytobenthos and epiphytal algae

To calculate average biomass for this trophic group, we summed biomass over both epiphytic algae and microphytobenthos. We estimated a microphytobenthos biomass of 1.6 g C/m^2 and P/B of 40/y, and an epiphytic algae biomass (including macrophytes and microphytes) of 5% of the total macroalgal biomass (calculated in section 4.5) and P/B of 14/y. Summing biomass of these groups gave an estimate of 8.52 g C/m^2. A weighted average of production across relative biomass of these groups gave a P/B of 21.0/y.

4.5 MACROALGAE

4.5.1 Biomass

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

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

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

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

For canopy algae, average densities (individuals/m^2) combined over all habitats were converted into wet weights using length-weight relationships from Shears & Babcock (2004b) (Table 8). We calculated average plant lengths and ash-free dry weights (AFDW) averaged across all habitats using size-frequency measurements of *Ecklonia radiata*, *Carpophyllum maschalocarpum*, *C. flexuosum* and *Sargassum sinclairii* (other large brown algae) from transects taken within the study region (Shears & Babcock 2004b). Dry weight estimates were converted into AFDW by multiplying them by 0.91, based on the assumption that the proportion of $CaCO_3$ and inorganic materials is c. 9% of the dry weight of New Zealand algal species (R.B. Taylor, University of Auckland, unpubl. data, as cited in Shears & Babcock 2004b) (Table 8). Additional length-weight relationships for algal species not common in the study area can be found in Appendix 3 of Shears & Babcock (2004b). Where multiple relationships were available, we used relationships based on data from the closest location to the study area; most often these were from northeastern New Zealand, and more specifically the Hauraki Gulf.

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

For intertidal habitats, we converted average percentage cover of intertidal algal species to AFDW using conversions described below (averaged across the foliose/turfing and crustose/coralline macroalgal groupings), and extrapolated biomass to the total intertidal reef area. For intertidal large brown algae, there was no information available on conversions from percentage cover to biomass or on average length of the primary species (*Cystophora torulosa*, *C. retroflexa* and *Hormosira banksii*) from the subtidal Gisborne surveys (Shears & Babcock

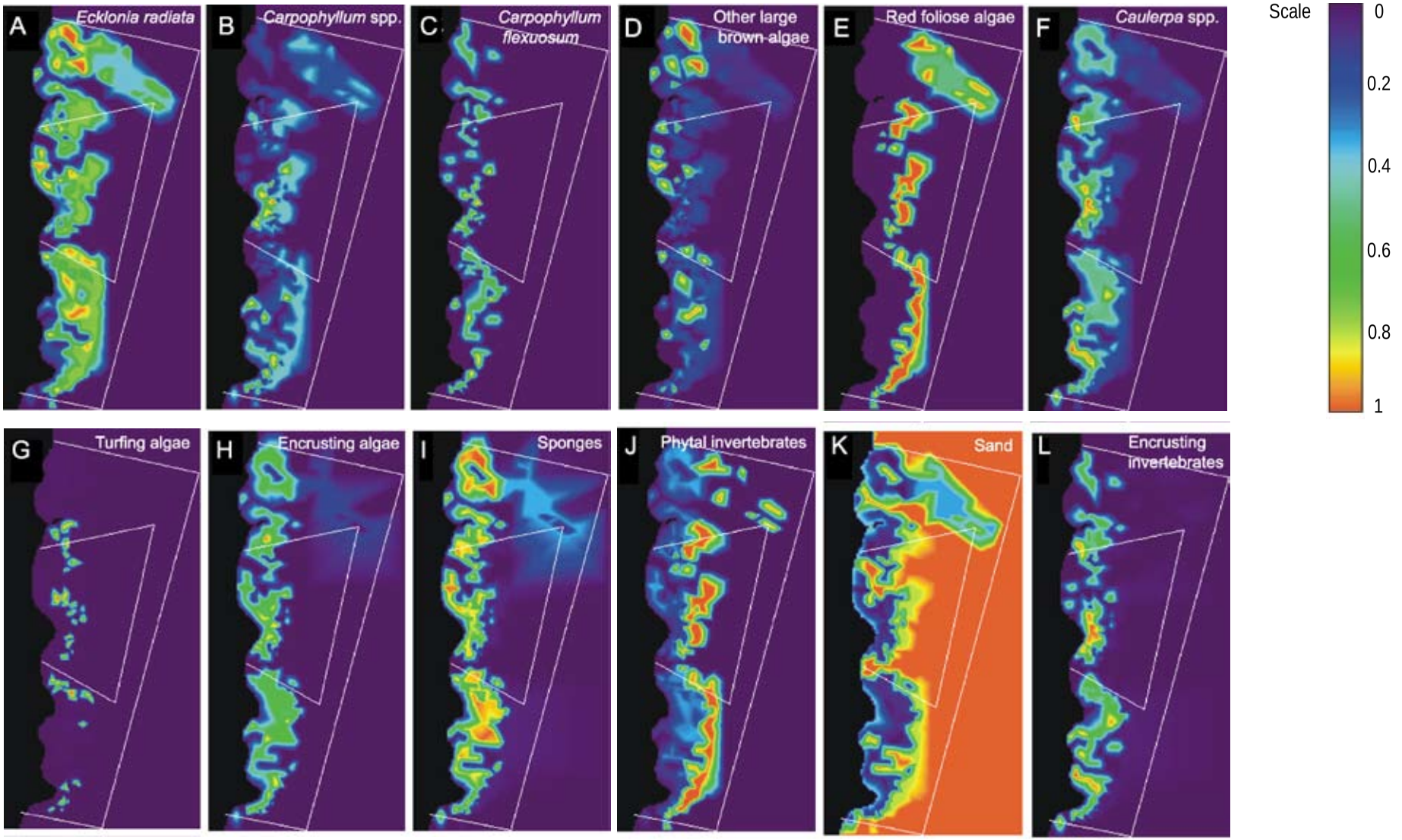


Figure 8. Spatial distribution of selected taxa over the study region obtained by triangulation of data as explained in the text. Each plot is scaled according to the colour bar shown at the right-hand side of the figure. Maximum values for each taxon correspond to red on the colour bar; blue and purple colours indicate lower estimated values. To aid interpretation of values, we plotted density of individuals for large canopy-forming macroalgae; percentage cover for foliose and encrusting algae, encrusting invertebrates, and sediment; and wet weight for phytal invertebrates, as described for each taxon in the text. Maximum values are as follows: A. *Ecklonia radiata* (0–8.9/m^2); B. *Carpophyllum* spp. (0–87.7/m^2); C. *Carpophyllum flexuosum* (0–3.0/m^2); D. other large brown algae (0–11.6/m^2); E. red foliose algae (0–20.0% cover); F. *Caulerpa* spp. (0–30.4% cover); G. turfing algae (0–15.7% cover); H. encrusting algae (0–66.8% cover); I. sponges (0–14.5% cover); J. soft sediment and/or sand (0–100% cover); K. phytal invertebrates (0–35.3 g WW/m^2); L. encrusting invertebrates (0–19.2% cover). The white lines indicate the reserve area and larger study region used here.

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

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

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

* The proportion of $CaCO_3$ in *Corallina officinalis* has been estimated as 45% of the dry weight. Therefore, the value given is 55% of the total dry weight.

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

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

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

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

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

4.5.2 Production

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

1. Stipe elongation rates

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

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

2. Monthly growth measurements

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

3. Net production measurements

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

TABLE 10. RATES OF PRODUCTION (P) FOR COMMON NEW ZEALAND SPECIES OF MACROALGAE (SHEARS & BABCOCK 2004a).

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

SPECIES	TYPE	PRODUCTION ($\mu mol\ O_2\ hr^{-1}\ g\ DW^{-1}$)	
		PHOTOSYNTHESIS	RESPIRATION*
Carpophyllum maschalocarpum	Brown canopy	41.2	
C. plumosum	Brown canopy	72.1	
C. flexuosum	Brown canopy	68.8	
C. angustifolium	Brown canopy	38.1	
Ecklonia radiata	Brown canopy	95.3	
Cystophora torulosa	Large brown	74.0	10.6*
Landsburgia quercifolia	Large brown	78.1	
Lessonia variegata	Large brown	65.8	
Sargassum sinclairii	Large brown	139.6	
Xiphophora chondrophylla	Brown foliose	68.8	5.9*
Zonaria turneriana	Brown foliose	88.2	19.2*
Melanthalia abscissa	Red foliose	75.8	8.6*
Osmundaria colensoi	Red foliose	118.0	10.1*
Pterocladia capillacea	Red foliose	108.8	22.0*
Caulerpa flexilis	Green foliose	245.7	
Ulva sp.	Green foliose	493.0*	39.0*
Enteromorpha sp.	Green foliose	361.0*	24.5*
Distromium scottsbergii	Brown turfing	143.0	
Laurencia distichophylla	Red turfing	279.8	
Hymenema variolosa	Red turfing	235.0	
Crustose coralline spp.	Crustose/coralline	307.8	
Corallina officinalis	Crustose/coralline	295.6	20.7*

Summary—Macroalgal production

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

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

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

4.5.3 Export

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

4.5.4 Summary—Macroalgae

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

4.6 OTHER PRIMARY PRODUCERS

4.6.1 Saltmarsh plants

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

4.6.2 Seagrass

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

4.7 ZOOPLANKTON

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

1. Micro- and nanozooplankton (< 200 µm): These are primarily ciliates and heterotrophic flagellates.
2. Meso- and macrozooplankton (> 200 µm): Mesozooplankton are likely to be dominated by copepods. Macrozooplankton are assumed to be primarily euphausids, decapods and amphipods, but salps and other gelatinous macrozooplankton are also included here.

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

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

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

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