Return to previous file: dsis192.pdf

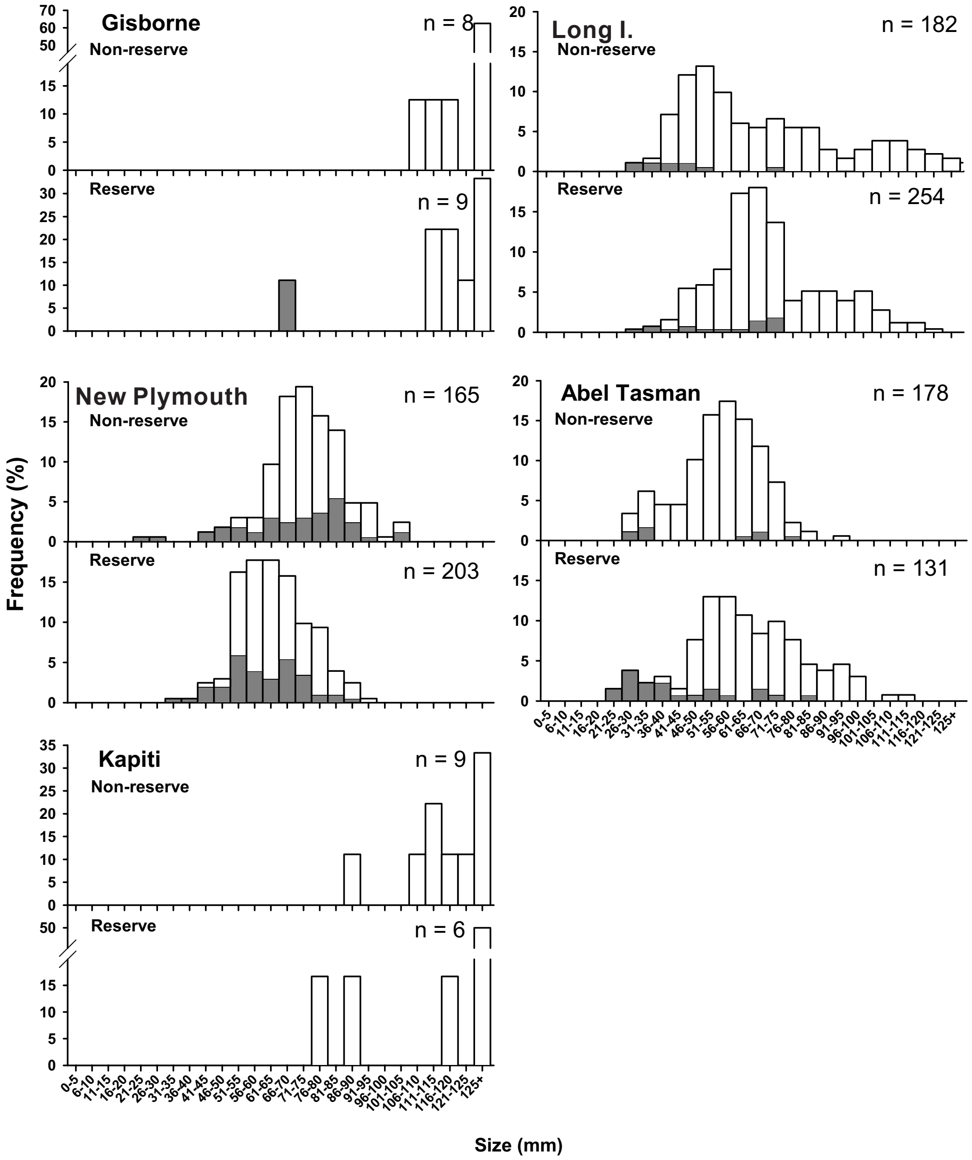


Figure 4 (continued). Size frequency distribution of *E. chloroticus* populations for non-reserve sites (left) and reserve sites (right) at other New Zealand locations. Shaded bars indicate the proportion of cryptic individuals, while open bars indicate the proportion of exposed individuals.

there were significant differences between reserve and non-reserve population structures (K–S $(d_{max})_{0.05,20,100} > 12$, $p < 0.05$). The modal size of adult sea urchins at New Plymouth reserve sites was smaller than at non-reserve sites, while at Abel Tasman and Long I. the modal size of adults tended to be larger inside the reserves. Juvenile sea urchins (< 40 mm test diameter) were more cryptic at reserve sites than non-reserve sites at Abel Tasman.

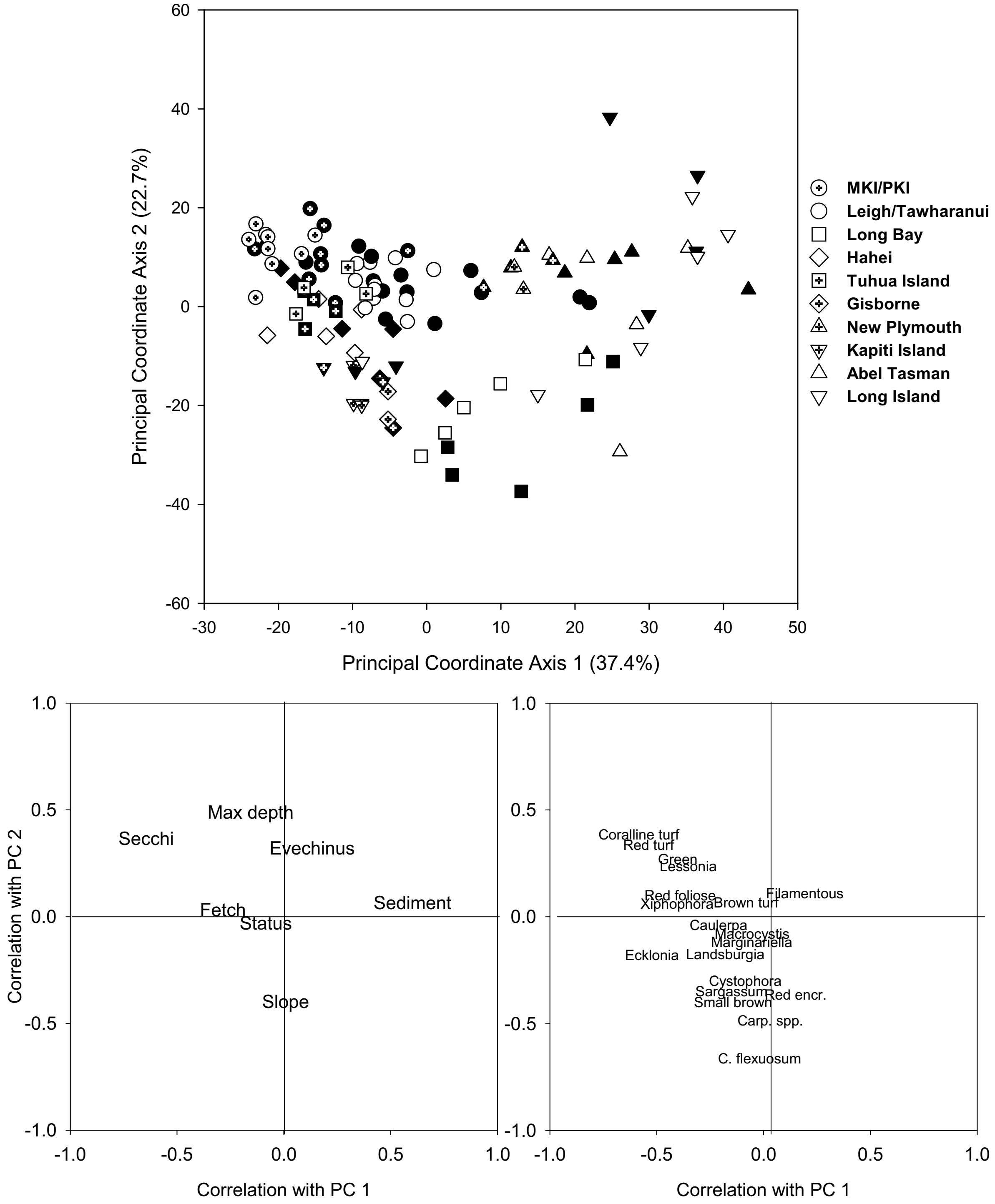


Figure 5. Patterns in algal community structure for reserve (open symbols) and non-reserve (shaded symbols) sites among locations named. Principal coordinates analysis of algal biomass data and correlations between the first two principal coordinates axes and the environmental variables, and also the original species variables. The relationship between reserve status and the principal coordinates axes is also shown.

3.4 ALGAL COMMUNITY STRUCTURE

There was high variation in algal assemblages among sites within and between locations, and overall, no clear differences were apparent between reserve and non-reserve sites (Fig. 5, Table 3). This variability in algal assemblages appeared

TABLE 3. RESULTS FROM MULTIVARIATE MULTIPLE REGRESSION ON THE RELATIONSHIP BETWEEN ALGAL COMMUNITY STRUCTURE, RESERVE STATUS AND ENVIRONMENTAL VARIABLES.

Based on fourth-root transformed quadrat-level data, Bray–Curtis dissimilarities, and restricted permutation of raw data with 4999 permutations. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

	EFFECT	PERCENTAGE VARIATION
Status	$F_1 = 0.47$	
Environmental variables		
Secchi	$F_1 = 25.67$***	19.4
Sediment	$F_1 = 18.10$***	14.5
Max depth	$F_1 = 9.61$***	8.2
Slope	$F_1 = 6.79$***	6.0
Fetch	$F_1 = 5.80$***	5.1
Exposed *E. chloroticus*	$F_1 = 3.59$**	3.3
All env. variables	$F_1 = 10.28$***	37.7

highly related to site-specific environmental conditions (Fig. 5). There was a significant relationship between algal communities and all the environmental variables measured (Table 3). These variables were highly interrelated and in total explained 37.7% of the variation in the similarity matrix. This was reflected in the negative and positive correlations between secchi depth (turbidity) and sediment cover, respectively, with principal coordinates axis 1. This highlighted the general gradient in algal communities along principal coordinates axis 1 from sites with clear water (high secchi reading, e.g. Poor Knights, Mokohinau, and Tuhua), to more turbid sites with higher levels of sediment at locations such as Long Bay, Long I., and Abel Tasman. In contrast, maximum depth and exposed *E. chloroticus* density were positively correlated, and reef slope negatively correlated, with principal coordinates axis 2 (Fig. 5). This axis therefore corresponds to the gradient from sites with gradually sloping reefs, low sea urchin densities and typically characterised by high biomasses of *C. flexuosum*, e.g. some sites from Long Bay, Gisborne, Kapiti I., and Hahei, to steeper reefs where sea urchins are typically more abundant, e.g. Mokohinau Is and Long I. The large variation among sites within some locations, e.g. Long I. and Hahei, demonstrated that algal community structure can vary considerably across environmental gradients over relatively small spatial scales (< 5 km). Differences at the quadrat-level between reserve and non-reserve sites were investigated separately for each location (Figs 6, 7), and the effect of environmental variables in explaining these differences were tested (Tables 4, 5).

Northeastern New Zealand locations

Algal communities at Leigh only differed between reserve and non-reserve sites in the 4–6 m depth range (Table 4). This depth corresponds to the zone where sea urchins were most abundant (Fig. 3) and overgraze algae at non-reserve sites. For the other depth strata sampled, sea urchins were rare and large brown algae dominated, and consequently there was no difference between reserve and non-reserve sites (Table 4). Among the other coastal locations, Tawharanui and Hahei exhibited the same pattern as Leigh, and significant differences

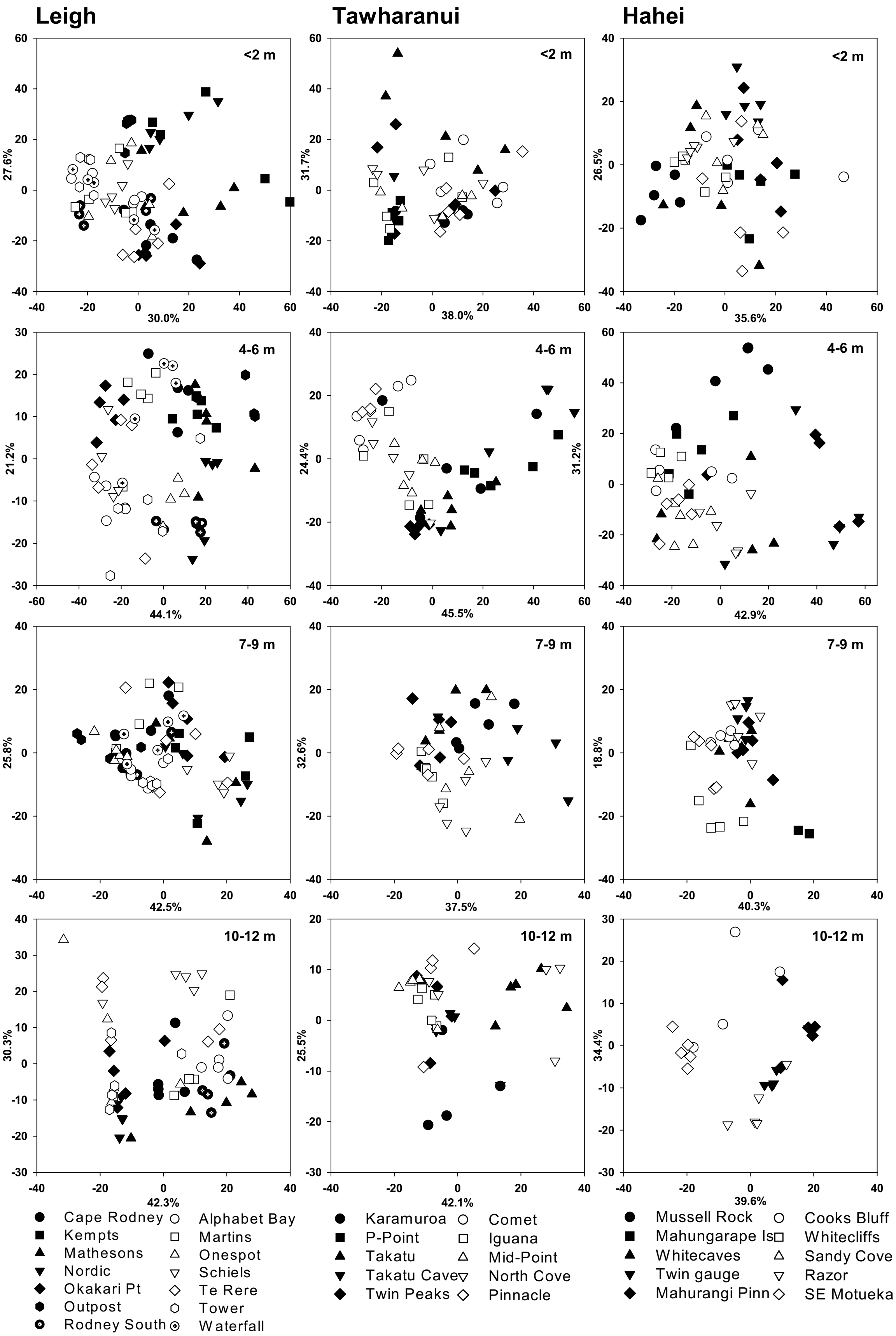


Figure 6 (above and opposite). Principal coordinates analysis on quadrat-level algal biomass data for reserve (open symbols) and non-reserve (closed symbols) sites for northeasternNew Zealand locations. Axis labels give proportion of variation explained by Principal Coordinates Axis 1 (x-axis) and Principal Coordinates Axis 2 (y-axis).

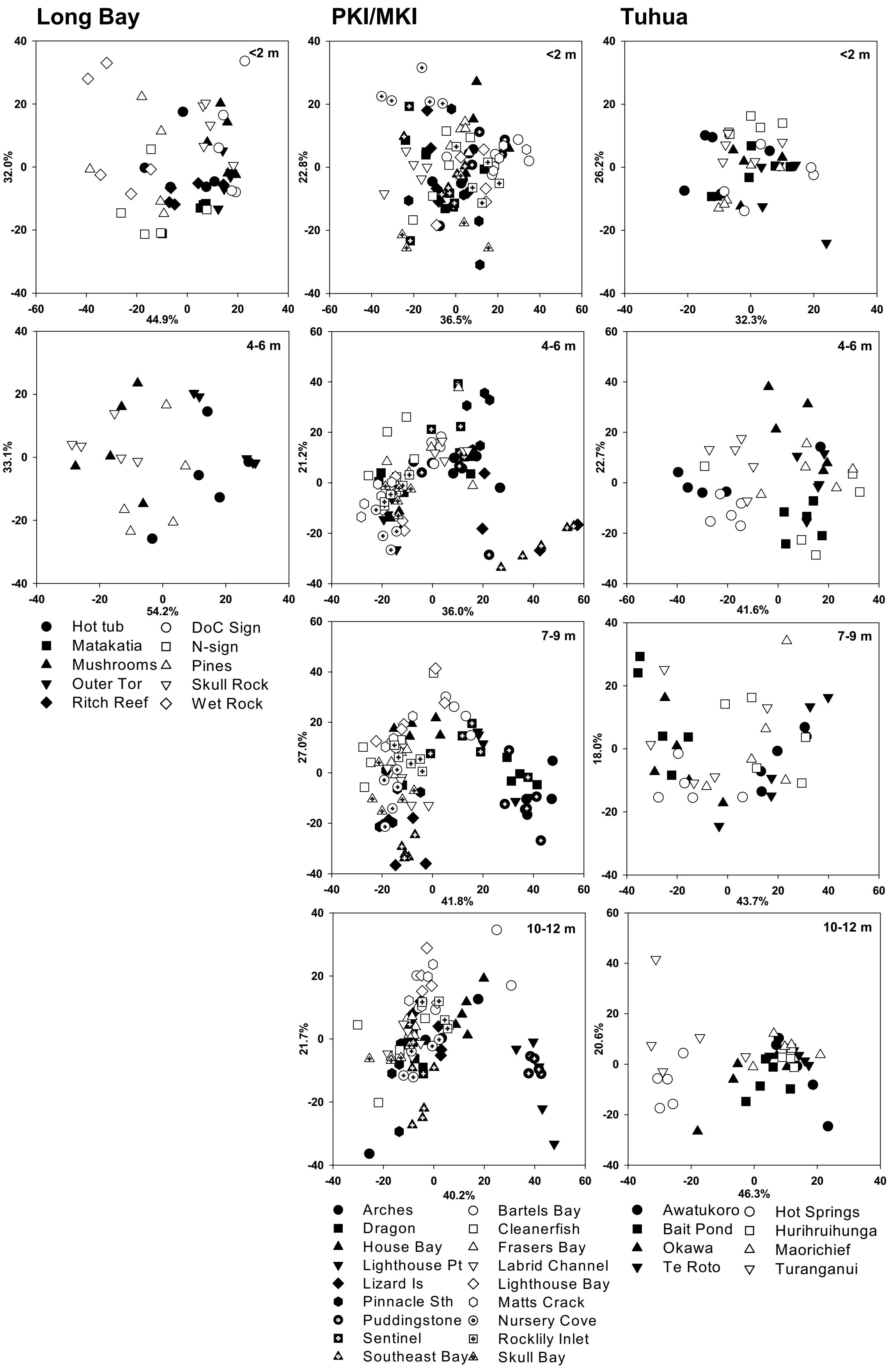


Figure 6 (continued).

TABLE 4. DIFFERENCES IN ALGAL COMMUNITY STRUCTURE BETWEEN RESERVE AND NON-RESERVE SITES FOR NORTHEASTERN LOCATIONS, EFFECT OF ENVIRONMENTAL VARIABLES ON ALGAL COMMUNITIES, AND EFFECT OF RESERVE STATUS GIVEN THE EFFECT OF ENVIRONMENTAL VARIABLES.

Analyses based on fourth-root transformed quadrat-level data, Bray-Curtis dissimilarities and restricted permutation of raw data with 4999 permutations. $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$.

DEPTH ZONE (m)	STATUS	SITE (STATUS)	ENV. VARIATIONS	STATUS + ENV. VARIATIONS
Leigh				
< 2	$F_1 = 2.12$	$F_{12} = 6.72^{***}$	$F_5 = 3.29^{***}$ (20.4%)	-
4–6	$F_1 = 3.92^{*}$	$F_{12} = 6.17^{***}$	$F_5 = 2.02^{*}$ (13.6%)	$F_1 = 6.03^{***}$ (7.5%)
7–9	$F_1 = 0.63$	$F_{12} = 4.57^{***}$	$F_5 = 2.79^{***}$(17.9%)	-
10–12[a]	$F_1 = 1.76$	$F_9 = 6.71^{***}$	$F_5 = 4.36^{***}$ (30.8%)	-
Tawharanui				
< 2	$F_1 = 0.73$	$F_8 = 3.40^{***}$	$F_5 = 2.16^{**}$ (19.7%)	-
4–6	$F_1 = 6.22^{**}$	$F_8 = 3.98^{***}$	$F_5 = 4.76^{***}$ (35.1%)	$F_1 = 8.46^{***}$ (10.7%)
7–9	$F_1 = 2.61$	$F_6 = 3.31^{***}$	$F_5 = 2.41^{**}$ (26.2%)	-
10–12	$F_1 = 1.05$	$F_6 = 3.42^{***}$	$F_5 = 4.73^{***}$ (41.0%)	-
Long Bay[b]				
< 2	$F_1 = 1.64$	$F_8 = 5.68^{***}$	$F_4 = 4.88^{***}$ (30.3%)	-
4–6[#]	$F_1 = 1.14$	$F_3 = 5.04^{***}$	$F_4 = 3.99^{***}$ (44.4%)	-
Hahei				
< 2	$F_1 = 0.98$	$F_8 = 4.14^{***}$	$F_5 = 4.23^{***}$ (32.5%)	-
4–6	$F_1 = 3.17^{*}$	$F_8 = 6.40^{***}$	$F_5 = 9.87^{***}$ (52.9%)	$F_1 = 2.94^{*}$ (3.0%)
7–9	$F_1 = 1.28$	$F_6 = 7.12^{***}$	$F_5 = 5.35^{***}$ (44.1%)	-
10–12[a]	$F_1 = 1.62$	$F_3 = 8.95^{***}$	$F_5 = 9.08^{***}$ (70.5%)	-
Mokohinau/Poor Knights Is[b]				
< 2[a]	$F_1 = 1.42$	$F_{15} = 5.08^{***}$	$F_4 = 6.24^{***}$ (23.8%)	-
4–6	$F_1 = 3.10^{*}$	$F_{16} = 9.10^{***}$	$F_4 = 9.49^{***}$ (30.9%)	$F_1 = 7.29^{***}$ (5.5%)
7–9	$F_1 = 5.01^{**}$	$F_{16} = 9.38^{***}$	$F_4 = 5.16^{***}$ (19.6%)	$F_1 = 21.98^{***}$ (16.7%)
10–12	$F_1 = 2.86^{*}$	$F_{16} = 8.99^{***}$	$F_4 = 6.69^{***}$ (24.0%)	$F_1 = 8.18^{**}$ (6.8%)
Tuhua[b]				
< 2	$F_1 = 1.43$	$F_6 = 3.13^{***}$	$F_4 = 2.87^{***}$ (24.7%)	-
4–6	$F_1 = 0.21$	$F_6 = 5.23^{***}$	$F_4 = 3.60^{***}$ (29.1%)	-
7–9	$F_1 = 0.39$	$F_6 = 4.67^{***}$	$F_4 = 1.55$	-
10–12	$F_1 = 1.23$	$F_6 = 6.88^{***}$	$F_4 = 3.84^{***}$ (30.5%)	-

[a] Effect of Status and Site (Status) calculated by coding the unbalanced ANOVA design using DISTLM.

[b] Turbidity estimates were not included in the analyses for these locations as the measurement was the same at all sites.

between reserve and non-reserve sites were only detected in the 4–6 m stratum. At Hahei, there was substantial variation in algal communities at 4–6 m among non-reserve sites, with clear separation between sites East (Twin gauge and Mahurangi Pinnacle) and West (Mussell Rock and Mahungarape I.) of the reserve (Fig. 6). At Long Bay there was no difference between reserve and non-reserve sites at any depth (Table 4).

Algal community structure at the offshore island locations did not differ between reserve and non-reserve sites at Tuhua, but did for the Poor Knights/

TABLE 5. DIFFERENCES IN ALGAL COMMUNITY STRUCTURE BETWEEN RESERVE AND NON-RESERVE SITES FOR OTHER LOCATIONS, EFFECT OF ENVIRONMENTAL VARIABLES ON ALGAL COMMUNITIES, AND EFFECT OF RESERVE STATUS GIVEN THE EFFECT OF ENVIRONMENTAL VARIABLES.

Analyses based on fourth-root transformed quadrat-level data, Bray-Curtis dissimilarities and restricted permutation of raw data with 4999 permutations. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

DEPTH ZONE (m)	STATUS	SITE (STATUS)	ENV. VARIATIONS	STATUS + ENV. VARIATIONS
Gisborne[b]				
< 2	$F_1 = 0.85$	$F_2 = 2.43^{*}$	$F_4 = 2.36^{**}$ (38.7%)	-
4–6	$F_1 = 0.38$	$F_2 = 3.41^{**}$	$F_5 = 1.75^{0.05}$ (38.5%)	-
7–9	$F_1 = 1.51$	$F_2 = 4.03^{*}$	$F_5 = 5.69^{***}$ (67.0%)	-
10–12[a]	$F_1 = 1.61$	$F_2 = 1.12$	$F_5 = 1.11$	-
New Plymouth[b]				
< 2[a]	$F_1 = 1.88$	$F_4 = 5.70^{***}$	$F_4 = 10.07^{***}$ (61.7%)	-
4–6[a]	$F_1 = 0.50$	$F_4 = 20.64^{***}$	$F_5 = 7.83^{***}$ (62.0%)	-
7–9[a]	$F_1 = 1.25$	$F_4 = 13.62^{***}$	$F_5 = 11.34^{***}$ (70.3%)	-
10–12[a]	$F_1 = 2.01$	$F_4 = 8.34^{***}$	$F_5 = 6.51^{***}$ (57.5%)	-
Kapiti I.				
< 2	$F_1 = 0.23$	$F_4 = 4.71^{***}$	$F_4 = 3.59^{***}$ (36.5%)	-
4–6	$F_1 = 0.41$	$F_4 = 9.91^{***}$	$F_5 = 5.62^{***}$ (53.9%)	-
7–9	$F_1 = 0.34$	$F_4 = 6.09^{***}$	$F_6 = 3.92^{***}$ (50.5%)	-
10–12[a]	$F_1 = 0.43$	$F_3 = 5.95^{***}$	$F_6 = 3.43^{***}$ (53.3%)	-
Long I.				
< 2	$F_1 = 0.66$	$F_{10} = 7.30^{***}$	$F_6 = 7.04^{***}$ (44.3%)	-
4–6	$F_1 = 0.21$	$F_{10} = 24.65^{***}$	$F_6 = 23.87^{***}$ (73.0%)	-
7–9	$F_1 = 0.61$	$F_{10} = 38.91^{***}$	$F_6 = 25.89^{***}$ (74.6%)	-
10–12	$F_1 = 1.18$	$F_8 = 14.77^{***}$	$F_6 = 15.32^{***}$ (65.7%)	-
Abel Tasman				
< 2	$F_1 = 1.36$	$F_8 = 4.21^{***}$	$F_6 = 3.19^{***}$ (30.8%)	-
4–6	$F_1 = -0.01$	$F_8 = 10.35^{***}$	$F_6 = 1.94^{0.05}$ (21.3%)	-
7–9	$F_1 = 2.08$	$F_8 = 7.12^{***}$	$F_6 = 1.96^{*}$ (21.5%)	-
10–12	$F_1 = 0.07$	$F_6 = 6.67^{***}$	$F_6 = 5.45^{***}$ (43.2%)	-

[a] Effect of Status and Site (Status) calculated by coding the unbalanced ANOVA design using DISTLM.

[b] Turbidity estimates were not included in the analyses for these locations as the measurement was the same at all sites.

Mokohinau Is comparison (Table 4). Despite the high degree of overlap between reserve and non-reserve sites (Fig. 6), a significant difference between the Mokohinau and Poor Knights Is was found at all depths except in the < 2 m stratum, where *E. chloroticus* are generally rare. Sampling sites within both of these locations were located across a range of exposure conditions, which may explain the variability seen among sites and potentially confound comparisons between these two locations.

At all locations, for each depth range (except 7–9 m at Tuhua), there was a significant relationship between algal communities and the environmental variables, sediment cover, wind fetch, turbidity, slope and maximum depth

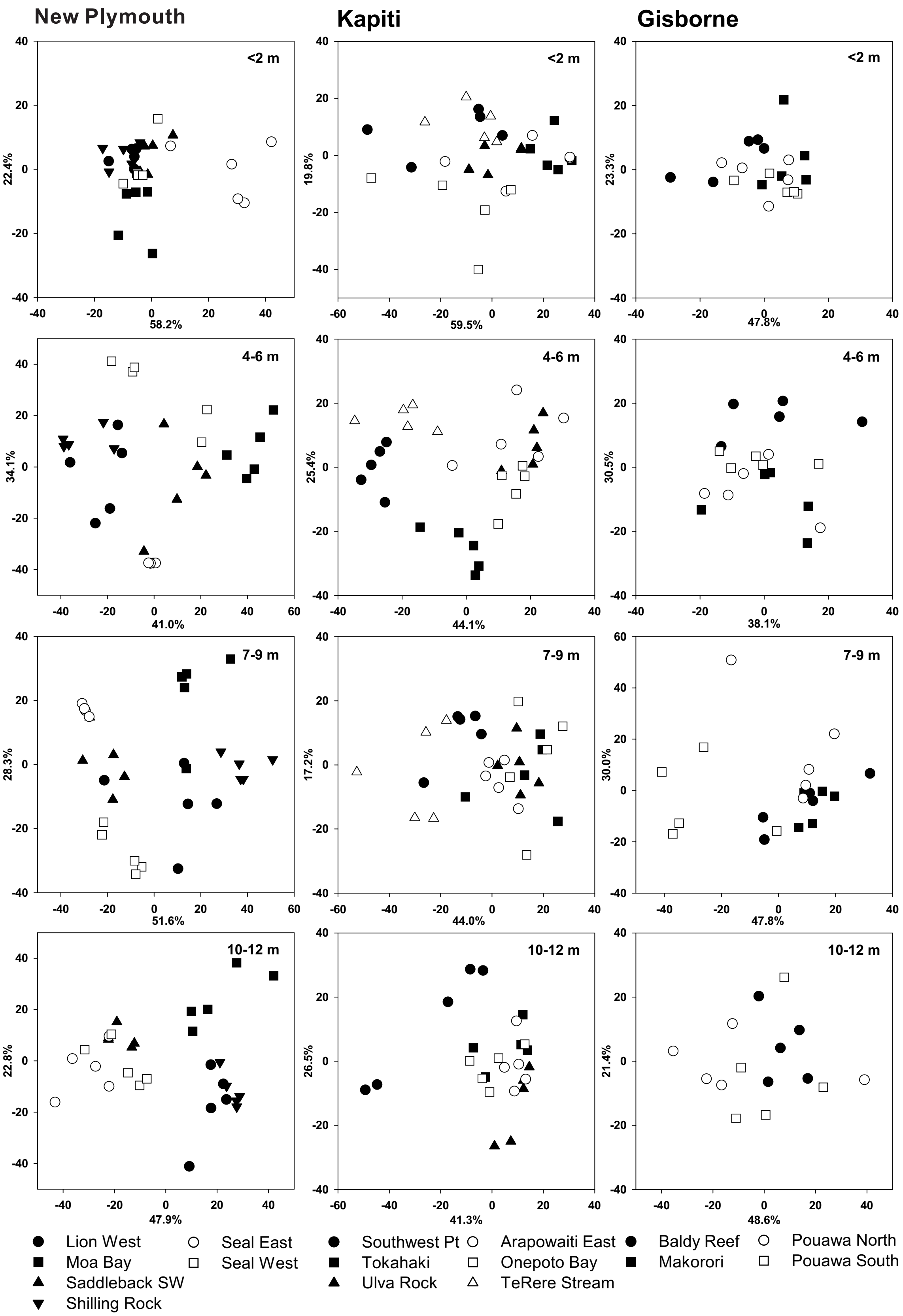


Figure 7 (above and opposite). Principal coordinates analysis on quadrat-level algal biomass data for reserve (open symbols) and non-reserve (closed symbols) sites for other New Zealand locations. Axis labels give proportion of variation explained by Principal Coordinates Axis 1 (x-axis) and Principal Coordinates Axis 2 (y-axis).

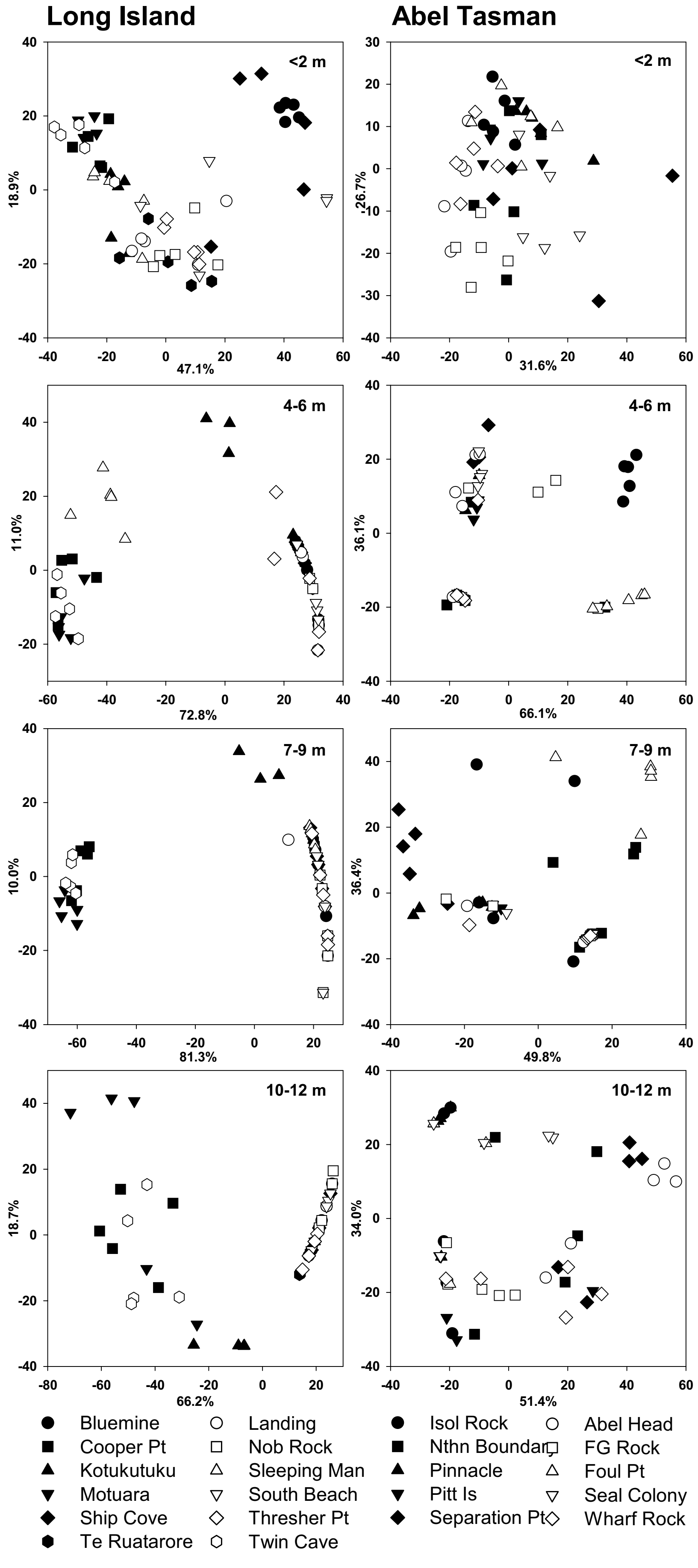


Figure 7 (continued).

(Table 4). These variables explained 13.6% to 70.5% of total variation in algal communities. Hahei was the location at which environmental variables contributed the most to site-level variation in algal communities. The effect of status at 4–6 m remained significant ($p = 0.044$) despite this environmental variability, but it only explained an additional 3% of the variation (Table 4). Therefore, while the majority of variation in algal communities between reserve and non-reserve sites at Hahei was attributable to different environmental condi-tions, there still appeared to be an effect of reserve status. At Leigh, Tawharanui, and MKI/PKI, the effect of status remained significant when the environmental variables were set as co-variables (Table 4), suggesting that the difference between reserve and non-reserve sites was not due to local patterns in the environmental variables measured.

Other New Zealand locations

No significant differences in algal assemblage structure were found between reserve and non-reserve sites for any of the other locations examined (Table 5, Fig. 7). Algal assemblages were significantly related to the six environmental variables measured for all locations and at all depths, except for the 10–12 m depth stratum at Gisborne. This is probably a result, however, of only three sites being sampled at Gisborne in this depth stratum (Fig. 5). Algal communities at Gisborne and also Kapiti I. were generally dominated by *Carpophyllum* *maschalocarpum*, *C. flexuosum* and *Ecklonia radiata*, and there were no clear differences between reserve and non-reserve sites. At Kapiti I., however, algal community structure differed between sites on the eastern side of the island (Te Rere Stream and Southeast Point, left-hand side of the ordinations (Fig. 7), compared with the remaining sites on the northwestern side of the island. This pattern was most apparent in the 4–6 m, 7–9 m and 10–12 m depth strata where the environ-mental variables explained c. 50 % of the variation in algal community structure.

Algal community structure at the two reserve sites at New Plymouth was generally quite different from that found at the four non-reserve sites, particularly at 7–9 m and 10–12 m, but this was not significant (Fig. 7). This was probably due to these sites being located on a small offshore reef (Seal Rocks) situated in relatively clear water, while the majority of the other sites were closer to the mainland coast and generally more turbid. The Saddleback SW site, however, is also located offshore and the algal communities at this site were most similar to the reserve sites. These patterns are reflected by the large amount of variation explained by the environmental variables (between 58% and 70%, Table 5).

There was also large variation in algal communities among sites at Long I. (Fig. 7). Northern sites located towards the entrance of Queen Charlotte Sound (northern end of Long I.), e.g. Motuara I., Twin Cave, Sleeping Man, and Cooper Pt, were clearly separated from the remaining sites, although this was not apparent in the shallow stratum (< 2 m). Northern sites were typified by deep algal stands (mainly *C. flexuosum* and to a lesser extent *E. radiata*), while the sites located further into the Sound were dominated by crustose coralline algae, hence the high degree of similarity among these samples. Similar patterns were observed at Abel Tasman, but only one site had deep *C. flexuosum* stands (Foul Point). In general, there was less variability among sites at Abel Tasman, probably a result of the environmental conditions among the sites being more uniform due to the relatively straight nature of the coastline. Subsequently, the environmental variables explained less of the variation in algal communities at Abel Tasman compared with Long I. (Table 5).

3.5 MACROALGAL BIOMASS AND PRODUCTIVITY

Differences in macroalgal biomass and productivity between reserve and non-reserve sites (Table 6, Fig. 8) were generally found at locations and depths where differences in macroalgal community structure were identified (Table 4). At Leigh, Tawharanui, and Hahei, the differences between reserve and non-reserve were depth-specific with total macroalgal biomass at 4–6 m depth being 2.9 (CL_{95} = 1.4, 6.1), 3.8 (CL_{95} = 2.5, 5.7), and 3.3 (CL_{95} = 1.4, 7.5) times higher at reserve sites than non-reserve sites, while maximum productivity was 2.3 (CL_{95} = 1.1, 5.0), 2.5 (CL_{95} = 1.7, 3.7), and 3.8 (CL_{95} = 2.5, 5.7) times higher. For the MKI/PKI there was an overall effect of reserve status (difference between the two locations) although it did vary significantly with depth (Table 6). Algal

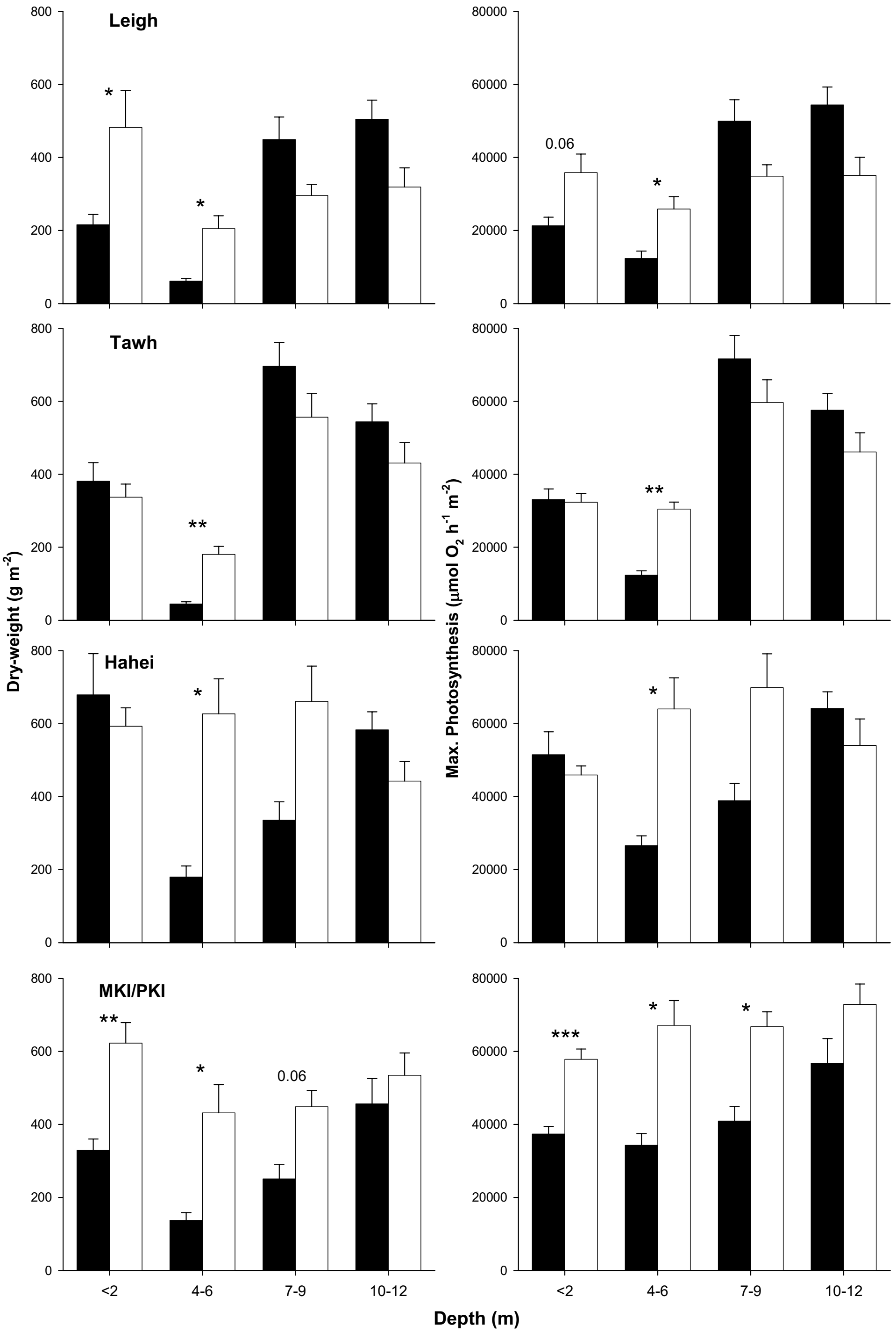


Figure 8. Total macroalgal biomass and productivity for non-reserve sites (shaded bars) and reserve sites (open bars). * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

Tawh = Tawharanui, MKI/PKI = Mokohinau/Poor Knights Is.

TABLE 6. MIXED MODEL ANALYSIS OF MACROALGAL BIOMASS AND PRODUCTIVITY FROM QUADRAT SAMPLING AT RESERVE AND NON-RESERVE SITES.

Model back-fitted by removing non-significant interaction terms. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

	FIXED EFFECTS			COVARIANCE PARAMETER ESTIMATE
Location	Status	Depth	Status•Depth	Site
Macroalgal biomass				
Leigh	$F_{1,13} = 2.26$	$F_{3,254} = 17.40^{***}$	$F_{3,254} = 13.54^{***}$	0.09^{*}
Tawh	$F_{1,8} = 1.15$	$F_{3,164} = 44.55^{***}$	$F_{3,164} = 7.94^{***}$	$0.04^{0.08}$
Hahei	$F_{1,8} = 3.43$	$F_{3,149} = 6.97^{***}$	$F_{3,149} = 9.73^{***}$	$0.10^{0.07}$
MKI/PKI	$F_{1,16} = 11.85^{**}$	$F_{3,331} = 11.35^{***}$	$F_{3,331} = 5.07^{**}$	0.12^{*}
Macroalgal productivity				
Leigh	$F_{1,13} = 0.88$	$F_{3,254} = 19.96^{***}$	$F_{3,254} = 10.43^{***}$	0.07^{*}
Tawh	$F_{1,8} = 1.08$	$F_{3,164} = 58.50^{***}$	$F_{3,164} = 10.95^{***}$	$0.03^{0.07}$
Hahei	$F_{1,8} = 3.26$	$F_{3,149} = 2.75^{*}$	$F_{3,149} = 9.06^{***}$	$0.07^{0.06}$
MKI/PKI	$F_{1,16} = 11.75^{**}$	$F_{3,331} = 8.53^{***}$	$F_{3,331} = 2.83^{*}$	0.07^{**}

biomass at the Poor Knights Is was generally higher than at the Mokohinau Is across all depths (Fig. 8), although it was not significant at 10–12 m. In the shallower strata (< 2 m, 4–6 m, and 7–9 m) algal biomass was 1.8 (CL_{95} = 1.3, 2.7), 2.9 (CL_{95} = 1.3, 6.1), and 2.2 (CL_{95} = 1.1, 4.7) times higher at the Poor Knights Is, while the productivity was 1.6 (CL_{95} = 1.3, 1.9), 2.0 (CL_{95} = 1.2, 3.2) and 1.8 (CL_{95} = 1.1, 2.8) times higher, compared with the Mokohinau Is.

3.6 ABUNDANCE AND SIZE-STRUCTURE OF OTHER GRAZER SPECIES

The densities of herbivorous gastropod species were variable among sites and with depth, and in general, no clear patterns emerged between reserve and non-reserve sites (Fig. 9, Table 7). Data for Kapiti I. and Gisborne are not presented as herbivorous gastropods were very rare at these locations.

The limpet *Cellana stellifera*, tended to be slightly more abundant in particular depth ranges at non-reserve sites from Leigh, Abel Tasman, and Long I. (significant interaction between status and depth). There were, however, clear differences in its size distribution between reserve and non-reserve sites at a number of locations (Fig. 10). *C. stellifera* populations at reserve sites at Hahei, Leigh, and Tawharanui were characterised by small individuals whereas non-reserve populations comprised larger individuals (Fig. 10). At Abel Tasman and Long I. *C. stellifera* tended to be less abundant at reserve sites, particularly in the mid-size range (15–30 mm).

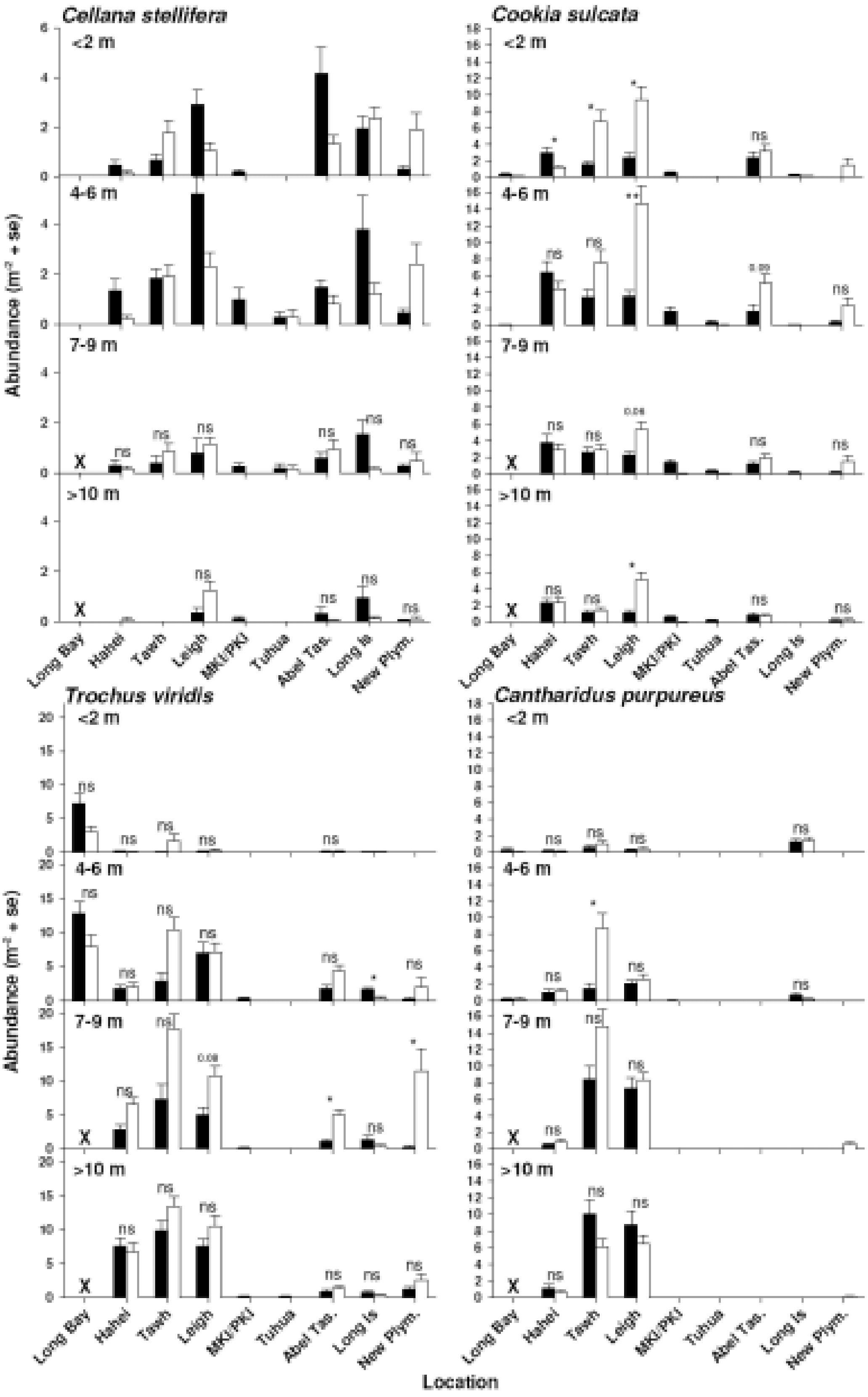


Figure 9. Mean density of herbivorous gastropod species at reserve (open bars) and non-reserve sites (shaded bars). * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

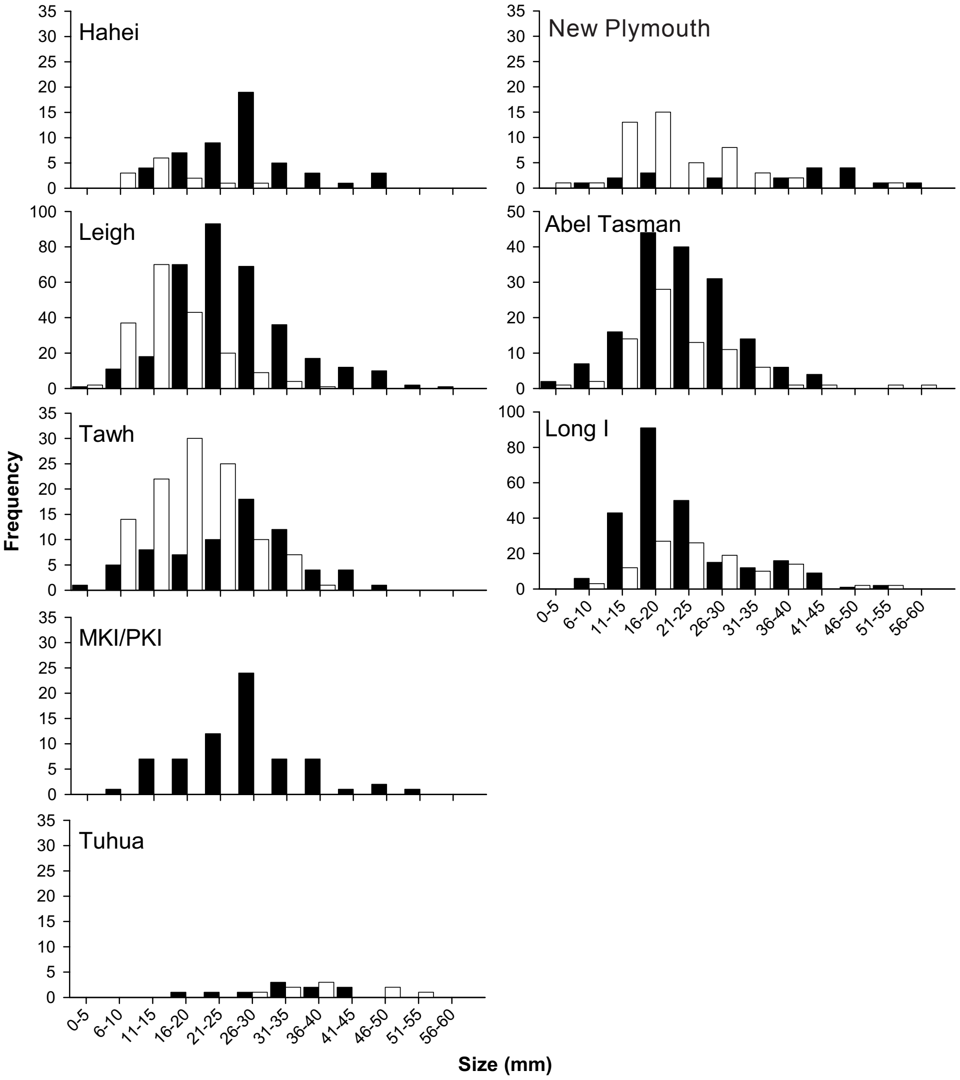
TABLE 7. MIXED MODEL ANALYSIS ON GASTROPOD DENSITY FROM QUADRAT SAMPLING AT RESERVE AND NON-RESERVE SITES FOR EACH LOCATION.

Model back-fitted by removing non-significant interaction terms. Analysis excludes depth strata where urchins were absent or very rare. $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$.

	FIXED EFFECTS			COVARIANCE PARAMETER ESTIMATE
Location	Status	Depth	Status•Depth	Site
Cellana stellifera				
Leigh	$F_{1,13} = 0.15$	$F_{3,254} = 9.70^{***}$	$F_{3,254} = 2.79^{*}$	0.43^{*}
Tawh (excl. 10–12 m)	$F_{1,8} = 0.37$	$F_{2,128} = 7.11^{**}$		0.48
Hahei (excl. 10–12 m)	$F_{1,8} = 1.53$	$F_{2,128} = 6.75^{**}$		$1.80^{0.08}$
New Plymouth	$F_{1,4} = 1.16$	$F_{3,111} = 5.41^{**}$		1.72
Abel Tasman	$F_{1,8} = 1.74$	$F_{3,184} = 8.68^{***}$	$F_{3,184} = 2.60^{*}$	$0.31^{0.07}$
Long I.	$F_{1,10} = 0.60$	$F_{3,217} = 9.88^{***}$	$F_{3,217} = 6.55^{***}$	1.79^{*}
Cookia sulcata				
Leigh	$F_{1,13} = 14.49^{**}$	$F_{3,257} = 23.44^{***}$		0.36^{*}
Tawh	$F_{1,8} = 1.68$	$F_{3,164} = 14.62^{***}$	$F_{3,164} = 4.05^{**}$	$0.38^{0.05}$
Hahei	$F_{1,8} = 2.43$	$F_{3,1.52} = 9.74^{***}$		$0.19^{0.07}$
Abel Tasman	$F_{1,8} = 1.75$	$F_{3,187} = 12.07^{***}$		$0.38^{0.05}$
Long I.	-	-	-	-
New Plymouth	$F_{1,4} = 1.10$	$F_{3,111} = 2.98^{*}$		1.16
Trochus viridis				
Leigh	$F_{1,13} = 0.88$	$F_{3,257} = 13.70^{***}$		0.36^{*}
Tawh	$F_{1,8} = 4.16^{0.076}$	$F_{3,164} = 7.45^{***}$	$F_{3,164} = 2.85^{*}$	$0.69^{0.08}$
Hahei	$F_{1,8} = 0.20$	$F_{3,149} = 15.50^{***}$	$F_{3,149} = 2.73^{0.046}$	0.12
Abel Tasman	$F_{1,8} = 12.51^{**}$	$F_{3,187} = 15.51^{***}$		0.13
Long I.	$F_{1,10} = 2.43$	$F_{3,220} = 6.98^{***}$		1.11^{*}
New Plym (excl. < 2 m)	$F_{1,4} = 6.77^{0.06}$	$F_{2,80} = 2.26$	$F_{2,80} = 6.43$	0.64
Cantharidus purpureus				
Leigh	$F_{1,13} = 0.09$	$F_{3,257} = 46.73^{***}$		0.45^{*}
Tawh	$F_{1,8} = 3.79^{0.087}$	$F_{3,164} = 21.34^{***}$	$F_{3,164} = 8.71^{***}$	0.09
Hahei	$F_{1,8} = 0.14$	$F_{3,152} = 5.70^{***}$		0.30
Abel Tasman	-	-	-	-
Long I. (excl. 10–12 m)	$F_{1,10} = 0.00$	$F_{2,166} = 19.51^{***}$		$1.28^{0.065}$
New Plymouth	-	-	-	-
Turbo smaragdus				
Long Bay	$F_{1,9} = 0.22$	$F_{1,62} = 31.09^{***}$	$F_{1,62} = 8.34^{**}$	1.12^{*}
Abel Tasman	$F_{1,8} = 6.90^{*}$	$F_{3,184} = 24.23^{***}$	$F_{3,184} = 2.89^{*}$	$0.92^{0.056}$
Long I.	$F_{1,10} = 0.11$	$F_{3,217} = 72.59^{***}$	$F_{3,217} = 6.09^{***}$	2.38^{*}

In contrast, the turbinid gastropod *Cookia sulcata* was more abundant at reserve sites at Leigh and Tawharanui, particularly at shallow depths (Fig. 9, Table 7). This pattern was not apparent, however, at any of the other reserves examined. While reserve sites at New Plymouth tended to have higher abundances of *Cellana stellifera*, *Cookia sulcata,* and *Trochus viridis* (Fig. 9),

Figure 10. *Cellana stellifera* size-frequency distribution at reserve (open bars) and non-reserve (shaded bars) sites for each location.



this was probably associated with the higher abundance of *E. chloroticus* (Fig. 3) and was not significant.

Both *Cantharidus purpureus* and *Trochus viridis* were more abundant at coastal locations in northeastern New Zealand than in other parts of the country, but in general there were no clear trends between reserve and non-reserve sites (Fig. 9, Table 7). *Turbo smaragdus* was the most abundant gastropod at Long Bay, but was highly variable among sites and with depth (Table 7). At Long Island and Abel Tasman, *Turbo* was also common, but found to be more abundant at non-reserve sites. The small sea urchin *Pseudechinus* sp. was only found at a few sites outside the Long Island marine reserve.

Paua, *Haliotis iris*, were rare at the majority of sites sampled in this study (Fig. 11). Among all the marine reserve sites examined, only the Flea Bay marine reserve had densities of paua greater than 1 per m^2 (excluding the South Beach site in Long I. reserve, which had 1.4 ± 0.5 m^{-2} in the < 2 m depth stratum). Compared to sites sampled on the northern side of Banks Peninsula, *Haliotis iris* at Flea Bay were larger with a higher proportion of the population being over minimum legal size (Fig. 11(a)). Densities at Long I. were generally too low to make such comparisons (Fig. 11 (b)).

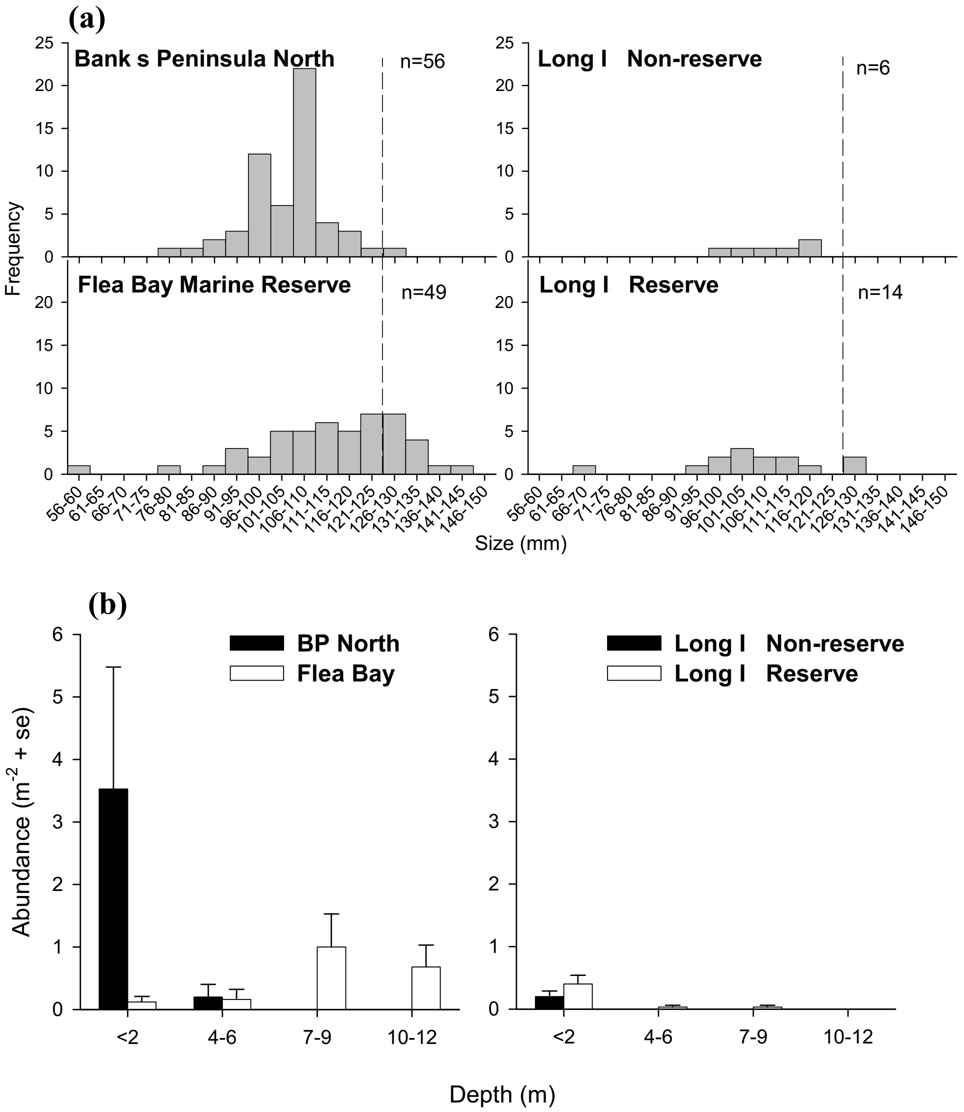


Figure 11. *Haliotis iris* size-frequency distribution (a) and mean abundance (b) at Banks Peninsula and Long Island. Dashed line equals minimum legal size.

4. Discussion

Throughout New Zealand the positive effect of marine reserves on exploited fish populations, primarily snapper, blue cod, and spiny lobster, has been conclusively demonstrated (Cole et al. 2000; Kelly et al. 2000; Willis et al. 2000, 2003; Davidson, 2001; Davidson et al. 2002; Denny et al. 2003, 2004). The increase in these predatory species associated with the cessation of fishing activities has been shown to have a cascading effect on benthic community structure in New Zealand's two oldest marine reserves at Leigh and Tawharanui (Babcock et al. 1999; Shears & Babcock 2002). While this pattern was clearly evident in the current study, from comparisons between reserve and non-reserve sites at Leigh in 1999, there was a subsequent decline in *E. chloroticus* numbers at some long-term monitoring sites outside the Leigh Marine Reserve between 1999 and 2001 due to mechanisms other than predation (Shears & Babcock 2003). Despite this, surveys carried out in 2003 demonstrate that the contrasting habitat states between reserve and non-reserve sites remain consistent with the present study, and *E. chloroticus* is common at non-reserve sites (2–6 exposed *E. chloroticus* per m^2 at 3–6 m depth) and rare at marine reserve sites (< 1 exposed sea urchin per m^2) (N. Shears unpubl. data). The present study, based on comparisons of sea urchin populations and algal communities at reserve and non-reserve sites at 13 locations throughout New Zealand, demonstrates that this trophic cascade is not universal across all subtidal reefs throughout New Zealand, and such effects are likely to differ across environmental gradients within and among locations. While many of the reserves examined may be too young to show such effects, the absence of trophic cascade effects is not solely attributable to reserve age.

4.1 SEA URCHIN POPULATIONS

The urchin barrens habitat is a common feature of shallow subtidal reefs in northeastern New Zealand, but is generally less common around most other parts of the country (Schiel 1990; Schiel & Hickford 2001), with the exception of the northern coast of the South Island (e.g. Long I. and Nelson in the present study). Consequently, at a number of locations examined in this study, such as Kapiti I., Gisborne, and Banks Peninsula, urchin barrens were very rare and, in general, *E. chloroticus* was found at very low densities. In northeastern New Zealand, the extent of urchin barrens habitat and the abundance of sea urchins have been found to decrease with increasing shelter from wave action (Grace 1983; Walker 1999; Shears & Babcock 2004). This was reflected in the absence of the urchin barrens habitat and very low sea urchin densities recorded at Long Bay, the most sheltered location examined. Conversely, sea urchins occurred at greater depths at the more exposed offshore island locations. In general, the extent of urchin barrens habitat, as well as the density and size structure of sea urchin populations, varied considerably among the locations sampled. The extent of urchin barrens only differed significantly between reserve and non-reserve sites at the two oldest reserves, Leigh and Tawharanui. This was consistent with previously described patterns (Babcock et al. 1999; Shears & Babcock 2003), with urchin barrens being less extensive at reserve sites in these locations. The Poor Knights Is also tended to have less extensive urchin barrens habitat than its unprotected locality-pair, the Mokohinau Is. However, at Tuhua and Hahei there was no difference in the extent of urchin barrens between reserve and non-reserve sites. This demonstrates that contrasting habitat states between reserve and non-reserve sites are not consistent throughout northeastern New Zealand. Urchin barrens were extensive at Abel Tasman and Long I., but there was no difference between reserve and non-reserve sites. In the small reserve at New Plymouth, which has been protected since 1986, urchin barrens tended to be more extensive than at the non-reserve sites sampled. This is probably because the protected area is a small offshore island situated in clean water, compared with the reference sites, which were closer to the mainland and appeared to have higher levels of sedimentation. In general, *E. chloroticus* occur at high densities at offshore islands on the west coast, but are rare at coastal sites (N. Shears unpubl. data).

Differences in densities of exposed sea urchins between reserve and non-reserve sites were greatest at the oldest reserves (Leigh and Tawharanui); in the 4–6 m depth stratum they were about six and three times higher at reserve sites for Leigh and Tawharanui, respectively. The lower densities, higher crevice occupancy at larger sizes, and strongly bimodal population structure at reserve sites in these locations are consistent with higher levels of predation in these reserves (Shears & Babcock 2002). Such patterns were not clearly apparent at the other reserves examined, which were all younger. Although the New Plymouth reserve has been no-take since 1986, there was no difference in sea urchin densities. This reserve may not be large enough to protect sufficient numbers of predators to impact on sea urchin populations. At Hahei, while there was high variation in sea urchin densities, exposed sea urchin densities tended to be lower in the reserve. Subsequent sampling at Hahei in 2000 (Shears et al. unpubl. 2000), found higher crevice occupancy at reserve sites and a significant difference in sea urchin numbers between reserve and non-reserve sites. This may be due to the higher abundance of snapper (Willis et al. 2003), and in particular spiny lobster (Kelly et al. 2000), in the Hahei reserve compared with outside. If so, these differences in sea urchin populations may become more pronounced over time. No differences in sea urchin densities were found at Abel Tasman and Long I. between reserve and non-reserve sites, although subtle differences in population structure were apparent. Both of these reserves had been protected for six years at the time of sampling. In the Long I. marine reserve, blue cod, *Parapercis colias*, are larger and more abundant than at nearby unprotected areas (Davidson 2001), while at both the Long I. and Tonga I. (Abel Tasman) marine reserves, *J. edwardsii* have increased in both size and density (Davidson et al. unpubl. 2002, R.J. Davidson unpubl. data). Given this increase in predator abundance, there is potential for changes in sea urchin populations to occur in these reserves over time.

The density of exposed sea urchins was approximately twice as high at the Mokohinau Is as at the Poor Knights Is. This, however, was due to a higher proportion of adult sea urchins being cryptic at the Poor Knights Is, as there was no overall difference in total numbers of sea urchins between these island groups. Predation pressure on large sea urchins at the Poor Knights Is is likely to be low, as spiny lobster are scarce (MacDiarmid & Breen 1993) and snapper tend to feed on smaller sea urchins (Shears & Babcock 2002). Furthermore, the area had only been completely no-take for less than one year prior to the sampling, therefore, differences in sea urchin crevice-occupancy between Poor Knights Is and Mokohinau Is are likely to be due to factors other than increased predation resulting from marine reserve protection. In California, Harrold & Reed (1985) demonstrated that sea urchins abandoned open microhabitats for crevices when sufficient drift algae were present. Therefore, higher availability of food at the Poor Knights Is may explain why a large proportion of sea urchins remain cryptic at larger sizes. At Tuhua, sea urchin densities and size distributions were similar inside and outside the reserve after seven years of protection. Within the Tuhua reserve there has been very little recovery of both crayfish and snapper populations (Kelly et al. 2001; Shears & Usmar 2004). High levels of illegal fishing in the Tuhua reserve have been suggested as a major factor responsible for the lack of recovery of snapper in this reserve (Shears & Usmar 2004).

At the offshore islands in northeastern New Zealand, sea urchin populations at both protected and unprotected sites exhibited a bimodal population structure, similar to that seen at reserve sites at Leigh and Tawharanui. This may be related to the high abundance of large wrasses, which are important predators of small benthic invertebrates, including juvenile sea urchins (Francis 1996, C. Denny unpublished data) at offshore islands (Denny et al. 2003). These species are generally not targeted by fishermen and therefore occur at similar densities at both protected and unprotected offshore islands (Denny et al. 2003). Another potential explanation for the bimodal population structure of sea urchins is increased size-specific growth rates (Ebert et al. 1993). At offshore islands, increased growth rates may occur when sea urchins move from a cryptic to an exposed lifestyle (40–60 mm size class). This may be facilitated by higher food availability at offshore islands where there were more ephemeral algae (e.g. *Ulva* sp.) than at coastal locations (Shears & Babcock 2004).

4.2 ALGAL COMMUNITIES

Large variation in algal community structure was found within and among locations, and, overall, there was no clear difference between reserve and non-reserve sites. In general, algal communities were strongly correlated with the environmental variables measured, in particular turbidity (secchi disc) and sediment cover. Algal communities differed significantly between reserve and non-reserve sites at specific depths at Leigh, Tawharanui, Hahei, and Poor Knights Is. Differences in algal communities were generally only found at depths where exposed sea urchin density varied between reserve and non-reserve sites. Differences in algal communities at Leigh and Tawharanui only occurred in the 4–6 m stratum where non-reserve sites had a low algal biomass due to high numbers of *E. chloroticus*, while *Ecklonia* and *C. maschalocarpum* dominated at reserve sites. These patterns were consistent with the greater extent of macroalgal habitats in these reserves and with the long-term decline in urchin barrens in the Leigh reserve (Babcock et al. 1999; Shears & Babcock 2003). In the present study, however, analysis of the effect of several environmental variables (wave exposure, sediment, turbidity, reef slope, and maximum depth) revealed that these differences between reserve and non-reserve sites were not due to differing environmental conditions and could be attributed to reserve status. Furthermore, primary productivity of macroalgal assemblages at 4–6 m was estimated (based on macroalgal standing stock) as being 2.3 and 2.5 times higher at reserve sites for Leigh and Tawharanui, respectively. This strengthens previous findings based on the comparison of reserve and non-reserve sites at these localities.

Algal communities also differed between reserve and non-reserve sites in the 4–6 m stratum at Hahei, with productivity being 3.8 times higher at reserve sites. However, this difference was most likely due to differing environmental conditions between reserve and non-reserve sites. This does not mean that trophic cascades do not occur, or will not develop, but rather that differences detected from direct comparisons between reserve and non-reserve 'control' sites must be interpreted cautiously (Stewart-Oaten & Bence 2001). Similarly, for the Poor Knights–Mokohinau Is comparison, differences in algal communities occurred at 4–6 m but also at greater depths (7–9 m and > 10 m). This apparent effect of reserve status remained significant despite a significant effect of environmental variables on algal communities. However, macroalgal productivity tended to be higher than that at the Mokohinau Is across all depths. While this difference is consistent with the lower abundance of exposed sea urchins at the Poor Knights Is at these depths, it is argued that this is likely to be due to mechanisms other than a top-down predator effect for a number of reasons. Firstly, there was no difference in overall sea urchin density between Poor Knights Is and Mokohinau Is. Secondly, the Poor Knights Is had only been totally protected for approximately one year at the time of sampling. Finally, these areas are separated by about 50 km and the algal communities at the Mokohinau Is were found to be intermediate between those of other offshore islands (Poor Knights Is and Tuhua) and coastal locations (Shears & Babcock 2004). It is therefore likely that the differences found are due to other environmental variables that differ between these two locations. This may be explained by a stronger influence of the warm East Auckland Current at Poor Knights Is, and possibly also Tuhua, than at Mokohinau Is. A number of other oceanographic features may influence these islands in different ways. For example, both upwelling (Black et al. 2000) and internal waves (Stewart 2001) occur at the Poor Knights Is and may be important mechanisms for driving nutrient and larval supply. It is likely that such bottom-up processes result in high algal recruitment and growth, allowing sea urchins to lead a more cryptic lifestyle (cf. Harrold & Reed 1985).

4.3 EFFECTS OF RESERVES ON OTHER GRAZERS

The blackfoot paua, *Haliotis iris*, forms the basis of a large fishery in New Zealand, and therefore previously fished populations are likely to recover in marine reserves. However, while we were not specifically targeting sites with ideal habitat for abalone, very few *H. iris* were recorded in the present study. Legal sized *H. iris* were only recorded in the Flea Bay marine reserve. This reserve, however, had only been protected for one year at the time of sampling. A subsequent study by Davidson et al. (unpubl. 2001) found paua to be significantly larger at sites inside this reserve than those at nearby control sites. Creation of reserves in the South Island, in particular, could play an important role in protecting this species.

There are generally strong associations between sea urchins and other smaller invertebrate grazers (Choat & Andrew 1986). Consequently, changes in the density of invertebrate grazers may be expected to occur in response to changes in the density of sea urchins, but also directly from increased predation on these grazers in reserves. Differences in size structure of the limpet *Cellana stellifera* between reserve and non-reserve sites at Leigh, Tawharanui and Hahei (and possibly also Abel Tasman and Long I.) may be due to higher levels of predation in reserves and/or a result of reduced sea urchin density leading to changes in available microhabitat (Andrew & Choat 1982, N. Shears unpubl. data). In contrast, the higher abundance of *Cookia sulcata* at reserve sites at Leigh and Tawharanui may be a result of an increased abundance of a more favourable habitat (coralline turf) (Shears & Babcock 2003). At Abel Tasman and

Long I., while there were no clear differences in sea urchin densities between reserve and non-reserve sites, both *C. stellifera* and *Turbo smaragdus* tended to occur at lower densities in the reserves than outside. This may be related to the higher abundances of large blue cod in these reserves (Davidson 2001).

4.4 ENVIRONMENTAL VARIABILITY AND TROPHIC CASCADES

Menge & Sutherland (1987) suggest that the importance of biotic interactions changes across environmental gradients and that food-web complexity decreases with increasing stress. If this is true, trophic cascade effects will differ over environmental gradients and only occur under certain environmental conditions. For example, in locations like Long Bay and Gisborne where there is high environmental stress (e.g. high sedimentation, turbidity and fresh water run-off), bottom-up processes are likely to be very weak (e.g. low sea urchin recruitment, low benthic primary productivity), and consequently sea urchins occur at low numbers and do not have an important role in structuring algal communities. Under such circumstances, habitat-level changes or trophic cascades are not likely to occur as a result of marine reserve protection. Similar mechanisms may prevent sea urchins from overgrazing kelps at depths greater than 4–6 m at Leigh and Tawharanui (Andrew & Choat 1985). These locations are typical of moderately exposed locations in northeastern New Zealand (Choat & Schiel 1982; Shears & Babcock 2004) and trophic cascade effects appear to be restricted to between approximately 3 and 7 m depth under such environ-mental conditions.

High wave action is another environmental stressor that prevents sea urchins from overgrazing kelp (Lissner 1980; Cowen et al. 1982; Dayton 1985). This is particularly evident at shallow depths in northeastern New Zealand, where sea urchins are restricted to crevices and there are no differences in algal communities between reserve and non-reserve sites. In other parts of New Zealand, high wave action may restrict sea urchins to greater depths and prevent trophic cascade effects, e.g. on exposed reefs at Cape Reinga (Shears & Babcock 2004), Three Kings Is (Choat & Schiel 1982), Chatham Is, and southern New Zealand (Schiel & Hickford 2001). *E. chloroticus* has, however, been shown to have an important structuring influence on algal communities in some more sheltered areas of the South Island (e.g. Dusky Sound, Villouta et al. 2001), and also appears to overgraze macroalgae at other southern locations (e.g. Paterson Inlet, Abel Tasman, Nelson, and Marlborough Sounds, N. Shears unpubl. data). In such locations, large-scale changes in community structure may occur after longer periods of marine reserve protection. Furthermore, *E. chloroticus* has been shown to influence species composition in habitats dominated by large brown algae (Villouta et al. 2001). Under such circumstances, an increase in predators is likely to result in more subtle trophic effects. Similar effects may occur in locations such as Poor Knights Is (and to a lesser extent Tuhua) where strong bottom-up processes (e.g. high nutrients and clear water) may result in high algal production regardless of sea urchin abundance.

From this study, the relative importance of top-down and bottom-up processes appears to be important in determining the strength of trophic cascade effects, and this is likely to vary across environmental gradients. However, a more convincing assessment of this hypothesis in our system will only be possible after sufficient time has passed to allow trophic cascade effects to manifest themselves at all locations. It took approximately 15 years before any habitat-level effects were detected in the Leigh Marine Reserve (R. Babcock pers. comm.) and these are still happening after 25 years (Shears & Babcock 2003). With the exception of Leigh and Tawharanui, all of the reserves examined in the present study were younger than 15 years old. A better understanding of how sea urchin–algal interactions change over environmental gradients in other systems may also help explain the generality of such trophic cascade effects (cf. Foster & Schiel 1988).

5. Conclusions

Evidence from New Zealand's two oldest marine reserves, at Leigh and Tawharanui, suggest that the recovery of predators following marine reserve protection results in declines in sea urchins, large-scale changes in habitats including increased macroalgal biomass and productivity, and changes in other smaller grazer species. However, these trophic cascade effects were not as apparent at the other reserves examined in this study. There are three key explanations for this. Firstly, the other reserves are much younger and trophic cascades may not yet have occurred. Secondly, some reserves may be too small to protect large populations of mobile predators such as snapper and blue cod (e.g. the reserve at New Plymouth). Thirdly, the abundance of sea urchins and algal community structure vary considerably across environmental gradients both within and among locations. Therefore, while differences in sea urchin population structure and density are likely to occur as a result of increased predation, only under certain environmental conditions are these changes likely to result in cascading effects on algal communities. At locations where sea urchins do not play an important structuring role and overgraze macroalgae (e.g. Long Bay, Gisborne, Kapiti I., and large parts of the South Island), such trophic changes are not likely to occur. Whereas at sites where sea urchins are abundant and appear to overgraze macroalgae (e.g. Long I. and Abel Tasman), large-scale changes in habitats may be expected in marine reserves after sufficient lengths of protection. This study clearly demonstrates the importance of taking environmental variation into account when assessing trophic cascade effects using spatial comparisons between reserve and non-reserve sites.

6. Acknowledgements

We are extremely grateful to a large number of DOC staff throughout the country who provided their time, resources and local knowledge to this project. Clinton Duffy, Robert Russell, Natalie Managh, Jarrod Walker, and Debbie Freeman all provided invaluable diving assistance during the study. Additional thanks must go to Clinton Duffy for providing advice throughout, as well as organising local area support and the logistics of trips around the country. Eduardo Villouta provided the initiative for this project, valuable technical advice, and software for calculating wind fetch. Thanks also to the staff of the Leigh Marine Laboratory, to Marti Anderson for providing statistical support, and to Bionda Morelissen for carrying out photosynthetic measurements. This study was funded by DOC Science & Research Unit, under Science Investigation No. 2481.

7. References

Anderson, M.J. 2001: A new method for non-parametric multivariate analysis of variance. *Australian Ecology 26*: 32–46.

Anderson, M.J. 2002: DISTLM v2: a FORTRAN computer program to calculate a distance based multivariate analysis for a linear model. Department of Statistics, University of Auckland.

Andrew, N.L.; Choat, J.H. 1982: The influence of predation and conspecific adults on the abundance of juvenile *Evechinus chloroticus* (Echinoidea: Echinometridae). *Oecologia 54*: 80–87.

Andrew, N.L.; Choat, J.H. 1985: Habitat related differences in the growth and survivorship of juvenile echinoids. *Marine Ecology Progress Series 27*: 155–161.

Babcock, R.C. 2003: The New Zealand marine reserve experience: the science behind the politics. Pp. 108–119 in Hutchings, P.; Lunney, D. (Eds): Conserving marine environments. Out of sight out of mind? Royal Zoological Society of New South Wales, Mosman, NSW.

Babcock, R.C.; Kelly, S.; Shears, N.T.; Walker, J.W.; Willis, T.J. 1999: Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series 189*: 125–134.

Benedetti-Cecchi, L.; Airoldi, L.; Abbiati, M.; Cinelli, F. 1996: Estimating the abundance of benthic invertebrates: A comparison of procedures and variability between observers. *Marine Ecology Progress Series 138*: 93–101.

Bennett, B.A.; Attwood, C.B. 1991: Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa. *Marine Ecology Progress Series 75*: 173–181.

Black, K.P.; Bell, R.G.; Oldman, J.W.; Carter, G.S.; Hume, T.M. 2000: Features of 3-dimensional barotropic and baroclinic circulation in the Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research 34*: 1–28.

Botsford, L.W.; Castilla, J.C.; Peterson, C.H. 1997: The management of fisheries and marine ecosystems. *Science 277*: 509–515.

Chapman, A.R.O.; Johnson, C.R. 1990: Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. *Hydrobiologia 192*: 77–121.

Choat, J.H.; Andrew, N.L. 1986: Interactions among species in a guild of subtidal benthic herbivores. *Oecologia 68*: 387–394.

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.

Cole, R.G. 1993: Distributional relationships among subtidal algae, sea urchins and reef fish in northeastern New Zealand. PhD thesis, University of Auckland.

Cole, R.G.; Ayling, T.M.; Creese, R.G. 1990: Effects of marine reserve protection at Goat Island, northern New Zealand. *New Zealand Journal of Marine and Freshwater Research 24*: 197–210.

Cole, R.G.; Keuskamp, D. 1998: Indirect effects of protection from exploitation: patterns from populations of *Evechinus chloroticus* (Echinoidea) in northeastern New Zealand. *Marine Ecology Progress Series 173*: 215–226.

Cole, R.G.; Villouta, E.; Davidson, R.J. 2000: Direct evidence of limited dispersal of the reef fish *Parapercis colias* (Pinguipedidae) within a marine reserve and adjacent fished areas. *Aquatic Conservation: Marine and Freshwater Ecosystems 10*: 421–436.

Cowen, R.K.; Agegian, C.R.; Foster, M.S. 1982: The maintenance of community structure in a central California giant kelp forest. *Journal of Experimental Marine Biology and Ecology 64*: 189–201.

Davidson, R.J. 2001: Changes in population parameters and behaviour of blue cod (*Parapercis colias*; Pinguipedidae) in Long Island Kokomohua Marine Reserve, Marlborough Sounds, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems 11*: 417–435.

Davidson, R.J.; Barrier, R.; Pande, A. 2001: Biological Monitoring of Pohatu Marine Reserve, April 2001. Report to Department of Conservation, Wellington, New Zealand (unpublished). 35 p.

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.

Dayton, P.K. 1985: The structure and regulation of some South American kelp communities. *Ecological Monographs 55*: 447–468.

Denny, C.M.; Willis, T.J.; Babcock, R.C. 2003: Effects of Poor Knights Islands marine reserve on demersal fish populations. *Department of Conservation Science Internal Series 142*: 1–34. Department of Conservation, Wellington, New Zealand.

Denny, C.M.; Willis, T.J.; Babcock, R.C. 2004: Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. *Marine Ecology Progress Series 272*: 183–190.

Ebert, T.A.; Schroeter, S.C.; Dixon, J.D. 1993: Inferring demographic processes from size-frequency distributions: effect of pulsed recruitment on simple models. *Fishery Bulletin 91*: 237–243.

Edgar, G.J.; Barrett, N.S. 1997: Short term monitoring of biotic change in Tasmanian marine reserves. *Journal of Experimental Marine Biology and Ecology 213*: 261–279.

Edgar, G.J.; Barrett, N.S. 1999: Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology* 242: 107–144.

Elner, R.W.; Vadas, R.L. 1990: Inference in ecology: the sea urchin phenomenon in the northwestern Atlantic. *American Naturalist 136*: 108–125.

Estes, J.A.; Duggins, D.O. 1995: Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. *Ecological Monographs 65*: 75–100.

Foster, M.S. 1990: Organisation of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia 192*: 21–33.

Foster, M.S.; Schiel, D.R. 1988: Kelp communities and sea otters: keystone species or just another brick in the wall? Pp. 92–108 in VanBlaricom, G.R.; Estes, J.A. (Eds): The community ecology of sea otters. Springer-Verlag, Berlin.

Francis, M. 1996: Coastal fishes of New Zealand: an identification guide. Reed Books, Auckland.

Grace, R.V. 1983: Zonation of sublittoral rocky bottom marine life and its changes from the outer to the inner Hauraki Gulf, northeastern New Zealand. *Tane 29*: 97–108.

Harrold, C.; Reed, D.C. 1985: Food availability, sea urchin grazing, and kelp forest community structure. *Ecology 66*: 1160–1169.

Heath, R.A. 1985 A review of the physical oceanography of the seas around New Zealand – 1982. *New Zealand Journal of Marine and Freshwater Research 19*: 79–124.

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.

Larson, G.L.; Buktenica, M.W. 1998: Variability of secchi disk readings in an exceptionally clear and deep Caldera Lake. *Archiv fur Hydrobiologie 141*: 377–388.

Laur, D.R.; Ebeling, A.W.; Coon, D.A. 1988: Effects of sea otter foraging on subtidal reef communities off central California. Pp. 151–168 in: VanBlaricom, G.R.; Estes, J.A. (Eds): The community ecology of sea otters. Springer-Verlag, Berlin.

Lissner, A.L. 1980: Some effects of turbulence on the activity of the sea urchin *Centrostephanus coronatus* Verill. *Journal of Experimental Marine Biology and Ecology 48*: 185–193.

Littell, R.C.; Milliken, G.A.; Stroup, W.W.; Wolfinger, R.D. 1996: SAS system for mixed models. SAS Institute Inc., North Carolina.

MacDiarmid, A.B.; Breen, P.A. 1993: Spiny lobster population change in a marine reserve. Pp. 47–56 in Battershill, C.N.; Schiel, D.R.; Jones, G.P.; Creese, R.G.; MacDiarmid, A.B. (Eds): Proceedings of the Second International Temperate Reef Symposium, 7–10 January 1992, Auckland, New Zealand. NIWA Marine Wellington, New Zealand.

McClanahan, T.R. 1994: Kenyan coral reef lagoon fish – effects of fishing, substrate complexity, and sea urchins. *Coral Reefs 13*: 231–241.

McClanahan, T.R. 2000: Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biological Conservation 94*: 191–198.

McClanahan, T.R.; Arthur, R. 2001: The effect of marine reserves and habitat on populations of east African coral reef fishes. *Ecological Applications 11*: 559–569.

McClanahan, T.R.; Muthiga, N.A.; Kamukuru, A.T.; Machano, H.; Kiambo, R.W. 1999: The effects of marine parks and fishing on coral reefs of northern Tanzania. *Biological Conservation 89*: 161–182.

McClanahan, T.R.; Shafir, S.H. 1990: Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia 83*: 362–370.

Menge, B.A.; Sutherland, J.P. 1987: Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist 130*: 730–757.

Pauly, D.; Christensen, V.; Dalsgaard, J.; Froese, R.; Torres, F.J. 1998: Fishing down marine food webs. *Science 279*: 860–863.

Russ, G.R.; Alcala, A.C. 1996: Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecological Applications 6*: 947–961.

Sala, E.; Boudouresque, C.F.; Harmelin-Vivien, M. 1998: Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos 82*: 425–439.

Sala, E.; Zabala, M. 1996: Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Marine Ecology Progress Series 140*: 71–81.

Scheibling, R.E. 1996: The role of predation in regulating sea urchin populations in eastern Canada. *Oceanologica Acta 19*: 421–430.

Schiel, D.R. 1990: Macroalgal assemblages in New Zealand: structure, interactions and demography. *Hydrobiologia 192*: 59–76.

Schiel, D.R.; Hickford, M.J.H. 2001: Biological structure of nearshore rocky subtidal habitats in southern New Zealand. *Science for Conservation 182*. Department of Conservation, Wellington, New Zealand.

Shears, N.T.; Babcock, R.C. 2002: Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia 132*: 131–142.

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. 2004: Community composition and structure of shallow subtidal reefs in northeastern New Zealand. *Science for Conservation 245*. Department of Conservation, Wellington, New Zealand. 65 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 northeastern New Zealand. *New Zealand Journal of Marine and Freshwater Research 38*: 743–752.

Shears, N.T.; Usmar, N.R. 2004: Response of reef fish to partial and no-take protection at Tuhua (Mayor) Island. Unpublished report to the Department of Conservation, Wellington, New Zealand. 30 p.

Shears, N.T.; Walker, J.W.; Babcock, R.C. 2000: Te Whanganui a Hei Marine Reserve Benthic Community Monitoring Program – 1999/2000. Unpublished report to Department of Conservation, Wellington, New Zealand. 40 p.

Stewart, C.L. 2001: Aspects of the physical oceanography of the Poor Knights region, north-east New Zealand. MSc thesis, University of Auckland

Stewart-Oaten, A.; Bence, J.R. 2001: Temporal and spatial variation in environmental impact assessment. *Ecological Monographs 71*: 305–339.

Taylor, M.W. 1998: The physiology and biochemistry of ammonium assimilation in New Zealand seaweeds. MSc thesis, University of Auckland.

Tegner, M.J.; Dayton, P.K. 2000: Ecosystem effects of fishing in kelp forest communities. *ICES Journal of Marine Science 57*: 579–589.

Thomas, M.L.H. 1986: A physically derived exposure index for marine shorelines. *Ophelia 25*: 1–13.

Vadas, R.L.; Steneck, R.S. 1995: Overfishing and inferences in kelp-sea urchin interactions. Pp. 509–524 in Skjoldal, H.R.; Hopkins, C.; Erickstad, K.E.; Leinaas, H.P. (Eds): Ecology of fjords and coastal waters. Elsevier Science, B.V., Amsterdam.

Villouta, E.; Chadderton, W.L.; Pugsley, C.W.; Hay, C.H. 2001: Effects of sea urchin (*Evechinus chloroticus*) grazing in Dusky Sound, Fiordland, New Zealand. *New Zealand Journal of Marine and Freshwater Research 35*: 1007–1024.

Walker, J.W. 1999: Subtidal reefs of the Hauraki Gulf. MSc thesis, University of Auckland.

Ward, N. 2002: Survey of the relative abundance of snapper (*Pagrus auratus*) in the Long Bay–Okura Marine Reserve by baited underwater video. Leigh Marine Laboratory unpublished report, 16 p.

Wharton, W.G.; Mann, K.H. 1981: Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American Lobster, *Homarus americanus*, on the Atlantic Coast of Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences 38*: 1339–1349.

Willis, T.J.; Millar, R.B.; Babcock, R.C. 2000: Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series* 198: 249–260.

Willis, T.J.; Millar, R.B.; Babcock, R.C. 2003: Protection of exploited fishes 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.

Appendix 1

Site names, codes and positions for each sampling location

R/N indicates whether sites were located inside (R) or outside (N) reserves.

SITE	CODE	R/N	NORTHING	EASTING
Poor Knights Is				
Bartels' Bay	BAR	R	6634747	2668554
Cleanerfish Bay	CLN	R	6636866	2668059
Frasers Bay	FRA	R	6633668	2669024
Labrid Channel	LAB	R	6633083	2668543
Lighthouse Bay	LHB	R	6637499	2668637
Matt's Crack	MTC	R	6634467	2668846
Nursery Cove	NUR	R	6634558	2668452
Rock Lily Inlet	RLI	R	6636787	2668741
Skull Bay	SKB	R	6636118	2668289
Mokohinau Is				
Arches	ACH	N	6585467	2700220
Dragon South	DRA	N	6585296	2700547
HouseBay	HSE	N	6586216	2701287
Lighthouse Pt	LHP	N	6586156	2701840
Lizard I	LIZ	N	6585652	2701371
Pinnacle South	PST	N	6584844	2699726
Puddingstone I	PUD	N	6586008	2700557
Sentinel South	STS	N	6584921	2700385
Southeast Bay	SEB	N	6585531	2700666
Leigh				
Alphabet Bay	ABC	R	6546767	2671853
Cape Rodney	CRO	N	6545535	2674152
Kempts Beach	KEM	N	6547458	2669136
Martins Rock	MAR	R	6546565	2670741
Mathesons	MAT	N	6542562	2672272
Nordic	NOR	N	6543630	2673093
Okakari	OKA	N	6547541	2669323
Onespot	ONE	R	6545795	2673503
Outpost	OUT	N	6544131	2673923
Rodney South	RST	N	6545146	2674176
Schiels Pool	SCH	R	6546990	2671943
Te Rere	TER	R	6546945	2670114
Ti Pt	TIP	N	6540956	2672136
Tower	TOW	R	6546361	2672527
Waterfall Reef	WFR	R	6546526	2672183
Gisborne				
Pouawa South	PRS	R	6274453	2963647
Pouawa North	PRN	R	6274642	2963796
Baldy Reef	BDR	N	6272250	2961200
Makorori Reef	MRS	N	6269378	2958008

SITE	CODE	R/N	NORTHING	EASTING
New Plymouth				
Lion West	LIW	N	6238943	2598866
Mower Bay	MWB	N	6239076	2599112
Saddleback SW	SSW	N	6239366	2597835
Shilling Rock	SHS	N	6237742	2597679
Seal West	SEW	R	6238252	2596816
Seal East	SEE	R	6238202	2596933
Abel Tasman				
Seal Colony	SEC	R	6035029	2515763
Wharf Rock	WHR	R	6036413	2515494
Foul Pt	FLP	R	6033097	2515324
Separation Pt	SPP	N	6047167	2509748
Isol Rock	ISR	N	6044518	2511057
Nthn Boundary	NTB	N	6039465	2513845
Pinnacle I	PNI	N	6030807	2515568
FG Rock	FGR	R	6037996	2515200
Abel Head	ABH	R	6038883	2514836
Pitt I	PTI	N	6028741	2515648
Doubtful Sound				
Hubs Spur	HSP	N	5533804	2029146
Sail Rock	SOR	N	5530768	2032513
Jamieson	JAM	N	5528830	2030626
Hut Bay	HUB	R	5528325	2036333
Renown Rock	RNR	N	5527670	2037523
Joseph Pt	JSP	N	5525670	2037307
Tern Rock	TRC	R	5703134	2511478
Tawharanui				
Comet	COM	R	6535612	2674920
Iguana	IGU	R	6535671	2677210
Karamuroa	KAR	N	6537667	2672542
Mid-Pt	MID	R	6535623	2676710
North Cove	NCO	R	6535619	2676045
P-Pt	PPT	N	6536649	2673550
Takatu	TAK	N	6535969	2677683
Takatu Cave	TCA	N	6535511	2678192
Pinnacle	PNN	R	6535904	2677435
Twin Peaks	TWP	N	6535722	2678018

SITE	CODE	R/N	NORTHING	EASTING
Long Bay				
DoC sign	DOC	R	6499909	2667199
Hot tub	HOT	N	6505648	2668514
Matakatia	MTK	N	6506334	2668858
Mushrooms	MSH	N	6498879	2667662
N-sign	NSI	R	6501120	2666782
Outer Tor	TOR	N	6498445	2667497
Pines	PNS	R	6502553	2666811
Ritch Reef	RIT	N	6506036	2668964
Skull Rock	SKR	R	6499835	2667364
Wet Rock	WET	R	6501912	2666661
Hahei				
Cooks Bluff	CKS	N	6483105	2757571
Mahungarape	MAH	N	6486296	2755919
Mussel Rock	MUS	N	6482939	2756861
Mahurangi Pinn	MPN	N	6481256	2761755
Razor Rocks	RAZ	R	6483166	2760471
Sandy Cove	SAN	R	6482610	2758899
SE Motueka	SEM	R	6482908	2760416
Twin gauge	TWI	R	6481777	2762066
Whitecaves	WCA	N	6479881	2761731
Tuhua				
Awatukoro Pt	AWA	N	6430789	2796796
Bait pond	BPO	N	6431457	2797426
Hot Springs	HTS	R	6431789	2800658
Hurihurihunga	HUR	R	6431942	2799367
Maorichief	MAO	R	6431898	2798268
Okawa	OKW	N	6430305	2800838
Te Roto	TRT	N	6429485	2800658
Turanganui	TUR	R	6431404	2800918

SITE	CODE	R/N	NORTHING	EASTING
Kapiti I				
Onepoto Bay	OPB	R	6040573	2671952
Arapawaiti East	AWE	R	6040876	2672338
Tokahaki	TKH	N	6041217	2673377
Ulva Rock	ULR	N	6037336	2670003
Te Rere Stream	TRS	R	6038374	2673278
Southeast Pt	SEP	N	6033916	2669541
Long I				
Nob Rock	NBR	R	6009413	2618257
Thresher Pt	THP	R	6007500	2616432
Te Ruatarore	TRT	N	6008622	2614687
Bluemine I	BLI	N	6002125	2614507
Landing	LND	R	6010010	2619057
South Beach	SOB	R	6007974	2616600
Ship Cove	SHC	N	6012282	2614745
Sleeping Man	SLM	R	6009865	2617956
Twin Cave	TWC	R	6010290	2619136
Motuara I	MTI	N	6012835	2617543
Cooper Pt	COP	N	6009053	2620483
Kotukutuku	KTK	N	6008099	2619512
Banks Peninsula – North				
Lubchenco	LBC	N	5736088	2493316
Godley North	GDN	N	5736235	2493891
Little Akaloa	LAK	N	5728539	2511739
Banks Peninsula – Flea Bay				
Outer West	OUW	N	5703426	2511002
Rock Pool Pt	RPP	R	5703669	2510731
Flea East	FLE	R	5703958	2510793
Hectors wall	HEW	R	5703579	2511360
Tern Rock	TRC	R	5703134	2511478

Appendix 2

Biomass equations for major algal species and groups

Length-weight and/or percentage cover-weight relationships for major algal species and groups. y = dry weight (g), x = total length, SL = stipe length, LL = laminae length.

GROUP/SPECIES	EQUATION	R^2	n	COLLECTED
Ecklonia radiata	$\ln(y) = 2.625\ln(x) - 7.885$	0.97	21	Cape Reinga
Stipe	$\ln(y) = 1.671\ln(SL) - 3.787$	0.97	46	Leigh
Rest	$\ln(y) = 1.177\ln(SL \times LL) - 3.879$	0.94	55	Leigh
Carpophyllum flexuosum	$\ln(y) = 1.890\ln(x) - 4.823$	0.91	22	Long Bay
	$\ln(y) = 2.049\ln(x) - 5.251$	0.90	52	Tawharanui
	$\ln(y) = 1.792\ln(x) - 4.538$	0.89	59	Mokohinau Is
Other *Carpophyllum* spp.				
C. angustifolium [a]	$y = 0.068x - 0.27$	0.92	23	Leigh
	$\ln(y) = 1.131\ln(x) - 3.522$	0.89	117	Mokohinau Is
C. maschalocarpum	$\ln(y) = 2.078\ln(x) - 5.903$	0.88	116	Long Bay
	$\ln(y) = 1.764\ln(x) - 4.311$	0.72	46	Leigh
	$\ln(y) = 1.567\ln(x) - 4.204$	0.96	38	Mokohinau Is
C. plumosum	$\ln(y) = 1.472\ln(x) - 3.850$	0.66	62	Leigh
	$y = 1.638x - 4.413$	0.92	31	Hahei
	$\ln(y) = 1.517\ln(x) - 4.778$	0.69	60	Mokohinau Is
Cystophora spp.				
C. torulosa	$\ln(y) = 1.551\ln(x) - 2.6282$	0.79	12	Nelson
C. retroflexa	$\ln(y) = 1.560\ln(x) - 3.9486$	0.90	14	Nelson
Lessonia variegata	$\ln(y) = 1.677\ln(x) - 5.537$	0.83	9	Mokohinau Is
Landsburgia quercifolia	$\ln(y) = 1.971\ln(x) - 5.058$	0.83	19	Cape Reinga
Macrocystis pyrifera	$\ln(y) = 1.7997\ln(x) - 5.672$	0.79	42	Stewart I.
Marginariella boryana	$\ln(y) = 2.1691\ln(x) - 6.4778$	0.95	21	Kaikoura
Sargassum sinclairii	$y = 0.075x + 0.124$	0.58	25	Cape Reinga
Xiphophora chondrophylla	$y = 1.786x - 4.171$	0.62	18	Hahei
	$\ln(y) = 2.01\ln(x) - 5.377$	0.75	33	Mokohinau Is
Red foliose				
Osmundaria colensoi	$\ln(y) = 1.720\ln(x) - 3.3791\% = 22.93$g	0.70	143	Mokohinau Is
Pterocladia lucida	$\ln(y) = 1.963\ln(x) - 5.0761\% = 10$g	0.73	473	Leigh
Melanthalia abscissa	$\ln(y) = 1.775\ln(x) - 4.247$	0.64	22	Leigh
Plocamium spp.	$\ln(y) = 2.649\ln(x) - 8.812$	0.80	34	Mokohinau Is
Euptilota formosissima	$\ln(y) = 1.616\ln(x) - 4.971$	0.78	13	Mokohinau Is
Placentophora colensoi	$\ln(y) = 2.582\ln(x) - 6.392$	0.87	23	Cape Reinga
Red turfing	1% = 1.74g		3	Mokohinau Is
Coralline turf[b]	1% = 1.5g		3	Mokohinau Is
Crustose corallines[b]	1% = 0.35g		3	Leigh
Brown turfing	1% = 1.74g		3	Mokohinau Is
Small browns				
Carpomitra costata	$\ln(y) = 1.735\ln(x) - 5.856$	0.43	18	Mokohinau Is
Zonaria turneriana	$\ln(y) = 2.587\ln(x) - 6.4431\% = 2.48$g	0.83	273	Mokohinau Is
Caulerpa spp.				
Caulerpa flexilis	1% = 5.81g		3	Mokohinau Is
Other greens				
Codium spp.	1% = 4.68g		3	Mokohinau Is
Ulva spp.	1% = 1.71g		3	Mokohinau Is

---

[a] From Choat & Schiel (1982).

[b] The proportion of $CaCO_3$ in *Corallina officinalis* has been estimated as 45% of the dry-weight. Therefore, the value given is the total dry-weight of samples less 45%

Appendix 3

Algal productivity rates

SPECIES	MAX. RATE OF PHOTOSYNTHESIS μmol O_2 H^{-1} g DW^{-1}	SE	*n*
Large brown algae			
Carpophyllum maschalocarpum	41.2	3.0	7
C. plumosum	72.1	4.4	6
C. flexuosum	68.8	8.6	6
C. angustifolium	38.1	5.6	6
*Cystophora torulosa**	74.0	12.9	
Ecklonia radiata	95.3	10.3	9
Lessonia variegata	65.8	2.4	6
Sargassum sinclairii	139.6	14.3	6
Xiphophora chondrophylla	68.8	4.4	6
Landsburgia quercifolia	78.1	3.6	6
Small brown algae			
Zonaria turneriana	88.2	7.6	6
Brown turfing algae			
Distromium scottsbergii	143.0	19.6	4
Red foliose algae			
Pterocladia lucida	108.8	16.5	8
Osmundaria colensoi	118.0	22.8	7
Melanthalia abscissa	75.8	1.9	3
Red turfing algae			
Laurencia distichophylla	279.8	43.2	7
Hymenena variolosa	235.0	15.7	4
*Corallina officinalis**	295.6	45.9	3
Red encrusting			
Crustose coralline	307.8	55.2	8
Green algae			
Ulva sp.	469.2	55.7	7
Caulerpa flexilis	245.7	17.0	11

* Rate from Taylor (1998)