REEF-ASSOCIATED PREDATORS INFLUENCE ADJACENT SOFT-SEDIMENT COMMUNITIES

Timothy J. Langlois,[1,3] Marti J. Anderson,[2] and Russell C. Babcock[1,4]

[1]*Leigh Marine Laboratory, University of Auckland, P.O. Box 349, Warkworth, New Zealand*
[2]*Department of Statistics, Tamaki Campus, University of Auckland, Private Bag 92019, Auckland, New Zealand*

Abstract. Marine reserves provide a large-scale manipulation of predator densities, which provides a means to investigate the potential effects of predation. The effects of reef-associated predators were examined in northeastern New Zealand by comparing soft-sediment assemblages at sites having different densities of large predators. Large rock lobsters (*Jasus edwardsii*) were 3.8 times more abundant, and large snapper (*Pagrus auratus*) 12 times more abundant, on average, at reserve sites compared with non-reserve sites. The overall structure of infaunal communities differed between areas with high predator densities (reserve) and those with lower densities (fished). Sites with consistently higher densities of snapper and lobster were found to have a lower biomass of two bivalve species, and the greatest decreases were found near the reef edge (2–5 m). For several fauna a strong gradient in their density with distance from the reef was observed at both reserve and non-reserve sites. The hermit crab *Pagurus novizelandiae* occurred more frequently near the reef edge, while the heart urchin *Echinocardium cordatum* and bivalve *Dosinia subrosea* occurred more frequently farther away from the reef. The results suggest that certain species in this assemblage are affected differently by a combination of physical and biological forces. We conclude that, where reef predators are removed by fishing pressure, a resultant indirect effect is an increase in prey species in adjacent soft-sediment assemblages.

Key words: bivalves; community structure; effects of fishing; macrofauna; marine reserves; New Zealand; predation; subtidal infauna.

Introduction

In ecology, "halos" have been described in many contexts (Suchanek 1978, Fairweather 1988) and generally are thought to result from a predator or herbivore foraging given distances from a "shelter habitat" out into a "food habitat." Studies in temperate marine ecosystems have found "infaunal halos," areas of decreased density of soft-sediment fauna adjacent to reefs, at a variety of scales: 0–30 m (Davis et al. 1982), and 0–70 m (Posey and Ambrose 1994). Various models have been proposed to explain these patterns, including bioturbation (Suchanek 1983, Dahlgren et al. 1999), physical disturbance (DeFelice and Parrish 2001), recruitment (Watzin 1986), infaunal predation (Ambrose 1991), and predation by reef fauna (Posey and Ambrose 1994). The model suggesting that reef-associated predators are responsible for halos is supported by studies of gut contents of fish on temperate reefs (Lindquist et al. 1994). However, convincing demonstrations of predators causing halos of prey in these systems have been hampered due to limited rep-

lication of caging studies (Posey and Ambrose 1994) and the lack of large-scale manipulations (Thrush et al. 2000).

The most conspicuous predators associated with reefs in northeastern New Zealand are the sparid fish *Pagrus auratus* (snapper) and the rock lobster *Jasus edwardsii*. Snapper occur across the continental shelf from estuarine habitats to depths >100 m (Paul 1976) and are generalist predators that take primarily large (>4 mm) invertebrate prey from both soft-sediment and rocky reefs (Babcock et al. 1999). Studies have shown that rock lobster, although commonly assumed to spend the majority of their time on rocky reefs, do forage up to 1 km over adjacent sandy areas (Kelly et al. 1999).

Snapper and rock lobster are both heavily fished in northeastern New Zealand's coastal areas. They occur at higher densities inside no-take marine reserves: greater than legal-sized snapper (>270 mm fork length) and rock lobster (>100 mm carapace length) are 14 times and 3.7 times respectively more abundant inside compared to outside no-take reserves (Babcock et al. 1999). In this region the influence of predators on rocky reefs has been examined using the existing large-scale experimental framework provided by marine reserves (Babcock et al. 1999, Shears and Babcock 2002). Using this approach, it is possible to examine the potential role of large reef-associated predators in structuring adjacent soft-sediment communities, by contrasting the densities of predators and prey found inside vs. outside

[3] E-mail: timothy.langlois@gmail.com
[4] Present address: CSIRO Marine Research Floreat, Private Bag Number 5, Wembley, Western Australia 6913 Australia.
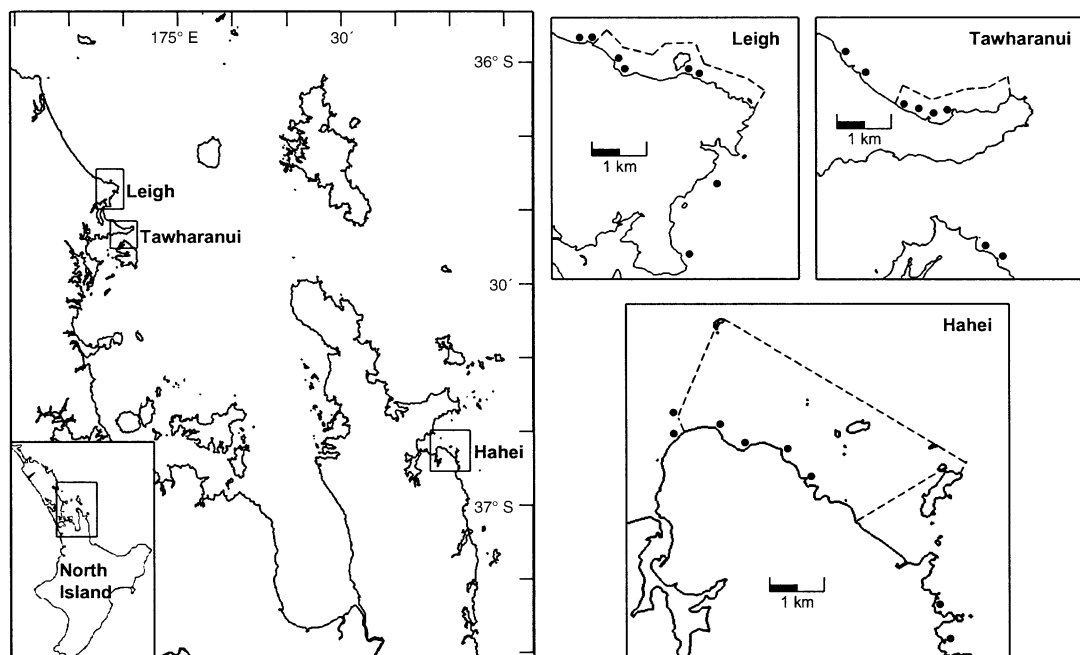
Fig. 1. Map of Hauraki Gulf, New Zealand, and environs, showing the location of the three reserves surveyed in this study (left). The right-hand panels show the reserve boundaries (dashed lines) and survey sites (solid circles) at the three locations.

several no-take areas. At these locations several other large macro-invertebrate predators, including rays (*Dasyatis brevicaudata* and *Myliobatis tenuicaudatus*) and octopus (*Octopus maorum*), associate with the reef/soft-sediment interface but have not been observed to occur at higher densities within reserves.

Unlike a before/after, control/impact (BACI) designed study, a potential problem with studies of established marine reserves is that evidence of a negative relationship between predator densities and densities of prey does not eliminate other potential models (Hurlbert 1984, Underwood et al. 2000). Results might be confounded by other factors that may structure the soft-sediment community (e.g., wave action, sediment grain-size distributions, organic matter, infaunal interactions). Due to the complex nature of soft-sediment marine communities, it has been recognized that to investigate patterns and processes, large-scale and long-term studies are needed to avoid problems associated with making erroneous inferences from short-term manipulations (Thrush et al. 2000). In addition, the inclusion of several scales of sampling and replication at larger scales can be used to unravel these issues and to test hypotheses concerning the generality of patterns and processes (Underwood 1997).

In this study we used three marine reserves as part of a large-scale experiment with replication at various scales. The hypothesis was that predation by large reef-associated predators would result in lower densities of large (>4 mm) soft-sediment macrofauna inside reserves compared to outside reserves (*Results: Predator*

model). A further hypothesis was that predation would decrease with increasing distances from the reef, resulting in a "halo" pattern in the community (Posey and Ambrose 1994), i.e., an increase in prey densities with increasing distances from the reef edge (*Results: Distance model*).

METHODS

Study sites and sampling methods

New Zealand's northeastern bioregion contains eight reserves, three of which are considered broadly comparable biotype replicates (Shears 2003, Willis et al. 2003*a*). This study was carried out between January and March of 2002, using these three locations as a random factor to explicitly test the generality of any potential differences in the effects of marine reserve status (as in Beck 1997). The Cape Rodney to Okakari Point (Leigh) Marine Reserve (36°16′ S, 174°48′ E) was gazetted in 1975, the Tawharanui Marine Park (36°22′ S, 174°50′ E) was declared a no-take area in 1981, and the Te Whanganui a Hei (Hahei) Marine Reserve (36°50′ S, 175°49′ E) was gazetted in 1993 (Fig. 1). At each location eight sites of similar wave exposure and reef/soft-sediment interfaces were chosen, four inside and four outside each marine reserve. To ensure interspersion, in each case, two of the non-reserve sites were located north and the other two located south of the reserve (see Fig. 1). The use of three locations and the interspersion of sites on either side of each reserve area was also to mitigate the potential

confounding influence of other environmental variables (such as recruitment or food supply). Within each site, sampling was done at each of four distances from the reef edge: 2, 5, 15, and 30 m. These distance strata were comparable to previous studies of infaunal halos (Posey and Ambrose 1994) and within the likely foraging ranges of snapper (Parsons et al. 2003) and rock lobster (MacDiarmid et al. 1991). At each distance, six replicate samples were obtained using box quadrats measuring 0.5 m² (1 × 0.5 m) × 13 cm deep (0.065 m³). Sediment was excavated by hand with a metal scoop and sieved in the field using a sieve with a 4-mm mesh. Other studies from different systems (Ambrose 1991, Lindquist et al. 1994, Posey and Ambrose 1994, Dahlgren et al. 1999) have focused on smaller infauna (>0.5 mm) where the corresponding reef-associated predators were also smaller. In the present study, we focused on larger infauna (>4 mm), corresponding to the larger reef-associated predators found within reserves (snapper are ~316 mm mean total length and rock lobster are ~109.9 mm mean carapace length inside reserves; Babcock et al. 1999). Pilot studies showed that large (>4 mm) fauna in the soft sediment around the chosen locations were relatively patchy in their spatial distribution, thus requiring a sampling unit area of 0.5 m². Organisms retained on the sieve were preserved in 5% formalin and later transferred to 70% ethanol. All organisms were identified to the lowest taxonomic resolution possible. Dry mass biomass estimates were made for all infauna, with the shells of bivalves being excluded from such measurements.

Environmental variables

Physical environmental variables measured at each distance stratum at each site included replicate measurements of grain size ($n = 3$) by dry sieving (with a focus on the proportion of coarse sediments), organic content ($n = 3$) by ignition at 550°C, bed form measurements ($n = 4$), and wave exposure. Wave exposure was estimated using an index of potential fetch (Thomas 1986). The index was calculated by summing the potential fetch for each 10° sector of the compass rose. For open sectors of water the radial distance was arbitrarily set to be 300 km. Estimates of the density of snapper at the reef edge were obtained using baited underwater video (BUV) ($n = 4$) during April and May 2002 as part of an ongoing monitoring program. BUV is a relatively new method, which has been shown to provide better measures of relative abundances of snapper than underwater visual censuses by divers in these systems (Willis et al. 2000). Estimates of the density of lobster at the reef edge were obtained by underwater visual census (UVC) of 25-m² quadrats ($n = 10$) during February and March 2002, and the sizes of lobster were estimated using a visual method as described by Mac-Diarmid (1991). The time discrepancy between the estimates of snapper and rock lobster are not likely to

confound any comparison given the relative stability in the temporal variation of these species over summer (Kelly 2001, Willis et al. 2003a). Densities of octopus and other species known to be predators of soft-sediment fauna were also looked for during rock lobster census dives. From the samples of the infaunal assemblages, the densities of infaunal bioturbators and infaunal predators were also recorded. A list and brief description of the environmental variables measured and subsequently included in analyses are given in Appendix A.

Statistical analyses

The overall experimental design consisted of four factors: location (random with three levels, Leigh, Tawharanui, and Hahei), status (fixed with two levels, inside vs. outside a marine reserve), site (random with four levels, nested within location × status), and distance (fixed with four levels, 2, 5, 15, or 30 m from the reef edge). Although location was treated as a random factor in order to examine the hypothesis of generality, we were also interested in examining the sources of any inconsistencies detected when effects of either status or distance varied among locations. Thus, separate individual comparisons at each location were sometimes warranted.

To test for any obvious confounding in the study design preliminary analyses of several individual physical and biological predictor variables (see Appendix A) were done using univariate analysis of variance (ANOVA). These variables were abundant enough to be analyzed using univariate ANOVA on either raw or transformed values, except for the density of large snapper and rock lobster, which were analyzed using a log-linear GLM model with overdispersed Poisson errors. All ANOVA analyses were preceded by Cochran's test for homogeneity of variance (see Underwood 1981, Winer 1991). Where the test showed significant heterogeneity, variables were transformed to $x' = \ln(x + 1)$. Analyses of variance were followed by a posteriori Student-Newman-Keuls tests (SNK tests) on appropriate terms of the model found to be significant with $P < 0.05$.

To investigate effects on the infaunal assemblage as a whole, the entire experimental design was analyzed using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001a, McArdle and Anderson 2001). All tests used 4999 permutations of the raw data or appropriate units as required by the design (see Anderson 2001b). Significant terms and interactions were investigated using a posteriori pairwise comparisons with the PERMANOVA t statistic and 999 permutations. All multivariate analyses were done on the untransformed abundance data of soft-sediment taxa using Gower's dissimilarity measure, including double zeros, calculated between every pair of cores. Double zeros were not excluded because in this study

of potential predatory effects joint absences were considered to increase similarity among cores.

Overall patterns of variation in the community were visualized with metric multidimensional scaling (mMDS) plots. To examine the nature of significant community effects, canonical analysis of principal coordinates (CAP, Anderson and Robinson 2003) was used. In addition, the particular taxa that might be responsible for any group differences seen in the CAP plots were investigated by calculating correlations with canonical ordination axes (Anderson and Willis 2003). The relationship between the entire set of measured environmental variables (all of those listed in Appendix A) and the community assemblage was investigated using distance-based redundancy analysis (dbRDA, Legendre and Anderson 1999, McArdle and Anderson 2001).

To estimate effects on individual taxa, the biomass data for each of the most conspicuous and abundant fauna were analyzed with separate univariate analyses. These data contained a great many zeros and were too overdispersed to consider using either a GLM or a traditional ANOVA on either raw or transformed values. Therefore, we assumed only additivity of effects and exchangeability of errors and used an ANOVA to partition the variability and obtain F statistics on the original raw data, but all P values were obtained using 4999 permutations of the appropriate exchangeable units (Anderson and ter Braak 2003). This avoided making any particular distributional assumptions, apart from exchangeability, for these analyses.

RESULTS

Examination of potential confounding factors

The following results are from the preliminary analyses of individual physical and biological factors to test for obvious confounding in the design with the factors of either distance or reserve status. If higher densities of large predators were not found inside reserves, there would be no basis for subsequent comparisons. Also, if any of the other measured environmental variables displayed a similar or inverse pattern to the density of large predators, such variables would confound the interpretation of results.

Large rock lobster were found to be consistently and significantly more abundant at reserve sites of all locations (Fig. 2a, $\chi^2_{1,2} = 54.47$, $P < 0.001$). The estimated effect was a 3.8-fold higher density in greater-than-legal-size rock lobster at reserve sites compared to non-reserve sites (with 95% confidence bounds of 2.4–5.9). No octopuses or rays were seen during the censuses of rock lobster. Large snapper were also more abundant at the reserve sites of all locations (Fig. 2b, $\chi^2_{1,2} = 15.07$, $P < 0.001$). The estimated effect was a 12-fold higher density in greater-than-legal-size snapper at reserve sites compared to non-reserve sites (with 95% confidence bounds of 2.7–53.2).
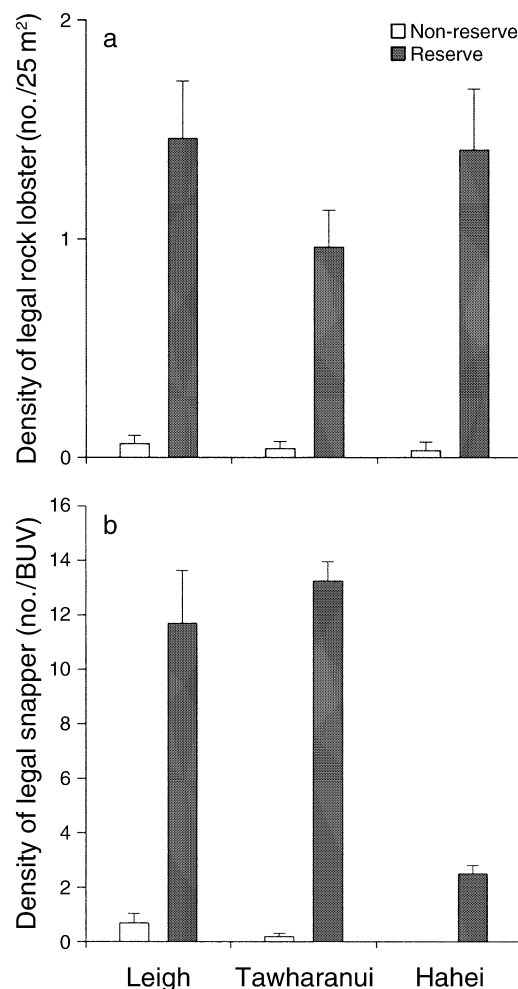

FIG. 2. Density (mean + SE) of legal-sized (a) rock lobster (*Jasus edwardsii*) and (b) snapper (*Pagrus auratus*) per baited underwater video (BUV) deployment at reserve and non-reserve sites of each location.

There was an apparent negative relationship between the average abundance of all predatory infauna (Appendix B) and the percentage of coarse sediments (Appendix C). However, there were no consistent patterns in the proportions of coarse sediments or in the distribution of potential infaunal predators (Morton and Miller 1968), with a significant interaction between location and status in each case (Appendices C and D, Table D1, $F_{2,18} = 6.52$, $P < 0.01$, and $F_{2,18} = 5.9$, $P < 0.05$, respectively). The most abundant bioturbator was the heart urchin *Echinocardium cordatum*. This species is an important prey item for snapper associating with soft-sediments (Colman 1972) and so could potentially confound any comparison of the effects of bioturbation and predation. The abundance of all infaunal bioturbators was significantly different among locations (Appendices C and D, Table D1, $F_{2,18} = 5.34$, $P > 0.05$), with lower average abundances at Leigh. The lack of any consistent patterns in these variables indicated that
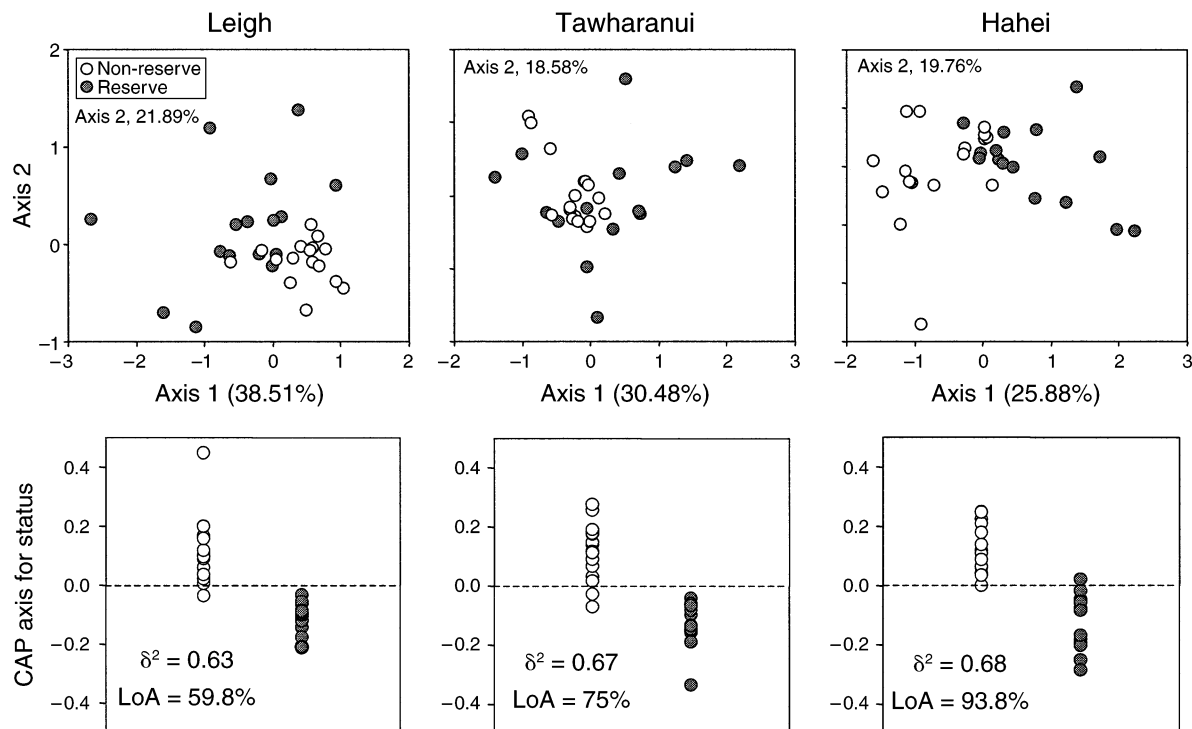
FIG. 3. Top panels show unconstrained metric MDS plots and bottom panels show constrained canonical (CAP) plots of the effect of reserve status at Leigh (37 taxa), Tawharanui (41 taxa), and Hahei (49 taxa) (with $n = 6$ replicates pooled). The percentage of total variation explained by the first two axes of the metric MDS analyses is given. The CAP panels also report squared correlation coefficients (δ^2) and results of leave-one-out allocation (LoA) success.

comparisons of soft-sediment assemblages inside vs. outside these reserves would not be confounded in any systematic way with these physical and biological factors.

Multivariate analyses

Distance-based redundancy analysis.—The first three axes from the dbRDA explained 30.1% of the variability in the fitted relationship between the ecological and environmental variables and 10.5% of the overall variability in the ecological data. In the biplot of the first two dbRDA axes (Appendix E), lobster density was positively correlated with the first axis. Variation in sediment characteristics, from fine to coarse grain sizes (see Appendix A), correlated strongly with the second axis. However, there was no distinct separation of reserve and non-reserve observations along this axis. A biplot of the first and third dbRDA axes (Appendix E) showed a fairly clear separation between the reserve and non-reserve observations, mainly on the third axis, which correlated strongly with lobster density and, to a lesser extent, snapper density. There was no strong correlation between predatory or bioturbating infauna and any of the first three dbRDA axes. These results indicated that although variation in sediment texture explained a large portion of the variability in the biota, any effects of status on the com-

munity would likely be due to densities of large predators.

Predator model.—In total there were 61 taxa from seven phyla obtained from 576 box quadrats in this study (Appendix F). The interaction found in the multivariate analysis between location and status (Appendix G, $F_{2,18} = 2.44$, $P < 0.01$) indicated that analyses of status should be done separately for each location. There were significant differences between assemblages at sites inside the reserves vs. those at non-reserve sites for each location: Leigh ($t_{24} = 2.88$, $P < 0.001$), Tawharanui ($t_{24} = 1.95$, $P < 0.001$), and Hahei ($t_{24} = 2.37$, $P < 0.001$). There was a significant multivariate interaction between distance and site ($F_{54, 480} = 1.37$, $P < 0.01$), indicating small-scale variability in the structure of the assemblages from site to site at different distances from the reef.

Patterns in the assemblage shown in the mMDS ordinations for each location (Fig. 3, top) indicated that communities at Leigh and Hahei differed between reserve and non-reserve sites but no clear effect was evident at Tawharanui. The effect at Leigh largely appeared to be caused by greater variability (dispersion) of the assemblages within the reserve. Canonical analyses for Tawharanui and Hahei (Fig. 3, bottom) showed a strong separation between reserve and non-reserve assemblages with an allocation success of 75% for Ta-

wharanui and 93.8% for Hahei. The canonical plot for status effects at Leigh also appeared to show a strong effect (good separation), but the allocation success was only 59.4% suggesting reserve effects were not as clear for Leigh as for the other two locations. (Note that with two groups, an allocation success of 50% or less would suggest that any separation of groups seen in the CAP plot was purely arbitrary.) Correlations of individual species with the canonical axis for status indicated that only a few individual taxa were responsible for the separation between reserve and non-reserve sites (Table 1).

Distance model.—There were significant differences among assemblages located different distances from the reef (Appendix G, $F_{3,6} = 2.25$, $P < 0.05$). The lack of any significant interaction between distance and either location or status suggested that the effect of distance from the reef edge on the soft-sediment fauna was consistent at larger scales, although variable at individual sites. Results of pairwise a posteriori comparisons found communities that were 2 and 5 m from the reef edge did not differ significantly from each other, but were significantly different from communities either 15 or 30 m away from the reef edge (Appendix H).

The multivariate distance by site interaction (Appendix G) was also illustrated in the mMDS ordination of distance strata where no consistent pattern could be discerned (Appendix I). However, the canonical correlation of the assemblage data with distance from the reef edge showed some slight evidence of a gradient in community structure ($\delta^2 = 0.27$) from 2 to 30 m (Appendix I). The correlations of the individual species with the canonical axis for distance from the reef showed this gradient to be due to variation in both relative abundances and species composition (Table 2).

Univariate analyses of prominent taxa

Correlation of species with the canonical axis for reserve status suggested that the bivalves *Dosinia subrosea* and *Myadora striata*, the third and fifth most abundant taxa, consistently occurred with greater abundance at sites outside reserves (Table 1). These bivalves showed the strongest influence of status with a consistent pattern of greater average biomass outside reserves (Appendix D, Fig. 4a, *D. subrosea*, $F_{1,2} = 21.09$, $P < 0.05$; Fig. 4b, *M. striata*, $F_{1,2} = 8.84$, $P < 0.05$). *D. subrosea* had a mean density of 0.56 m^{-2} inside reserves and 1.3 m^{-2} outside reserves. Correlation of species with the canonical axis for distance from the reef also suggested that *D. subrosea* occurred in greater average abundance away from the reef edge (Table 2). However, there was a pattern of increasing biomass of *D. subrosea* with distance from the reef at Tawharanui but not at Hahei or Leigh, resulting in a significant interaction between location and distance ($F_{6,54} = 2.64$, $P < 0.05$). *M. striata* exhibited a pattern of low biomass within the reserves and a pattern of increasing biomass

with distance from the reef outside the reserves but not inside, producing a significant interaction of St × Di ($F_{3,6} = 2.64$, $P < 0.05$), with a mean density of 0.16 m^{-2} inside reserves and 7.2 m^{-2} outside reserves. In addition, the gastropod *Philine angasi* occurred more frequently at sites inside reserves but at a lower abundance compared to other taxa (Table 1).

For the other most abundant species, the opistobranch *Amalda novaezelandiae*, the hermit crab *Pagurus novizelandiae*, and the heart urchin *Echinocardium cordatum*, there were no consistent effects of reserve status but some evidence of effects of distance from the reef. *A. novaezelandiae* occurred with greater abundance within reserve sites at Tawharanui and Hahei, but at non-reserve sites at Leigh (Table 1), *P. novizelandiae* occurred with greater frequency near the reef edge (Table 2) and *E. cordatum* occurred with greater frequency further away from the reef edge. The most abundant species, *A. novaezelandiae*, was responsible for the strong negative correlation between the mean density of predatory infauna and the percentage of coarse sediments (Appendix C). That is, the biomass of *A. novaezelandiae* (Fig. 4c, Appendix D) had a positive relationship with the percentage of fine sediments. The biomass of *P. novizelandiae* and *E. cordatum* were not found to have any consistent effects due to significant small-scale variability at the site level (Fig. 4d,e, Appendix D).

DISCUSSION

Sites with consistently higher densities of snapper and lobster were found to have lower biomass of several bivalve species, including the third and fifth most abundant taxa: *Dosinia subrosea* and *Myadora striata*. This result was consistent across several locations separated by 100s of kilometers. In contrast, the biomass of the three other most abundant species, the heart urchin *Echinocardium cordatum*, the hermit crab *Pagurus novizelandiae* and the opistobranch *Amalda novaezelandiae*, did not show any consistent pattern with predator density.

Comparison of sites with different densities of predators was not confounded in any systematic way with other measured environmental variables, including sediment characteristics, bioturbating or predatory infauna. There was a consistent pattern of decreased biomass of bivalves with increased lobster and snapper density inside reserves, in contrast with the inconsistent distribution of grain size and other variables. This suggests that large predators have an important ecological influence on the distributions of these bivalves. The difference in the community inside and outside the reserves was also driven by the gastropod *Philine angasi* that was found to be more abundant inside reserves.

The distribution of certain components of the community is apparently driven more by sediment texture, regardless of reserve status (Appendix E). For example, the most abundant species, the opistobranch *A. novae-*

TABLE 1. Correlations of individual species (r) with canonical axis for reserve status for each of the three locations, as shown in Fig. 3 (bottom panels).

| | | | Leigh | |
| | | | Mean (SE) | |
Species and correlation	Class/order	r	Fished	Reserve
a) Positive correlation (non-reserves)				
Myadora striata	Bivalvia	0.71	0.37 (0.07)	0
Dosinia subrosea	Bivalvia	0.61	0.95 (0.12)	0.04 (0.02)
b) Negative correlation (reserves)				
Philine angasi	Gastropoda	−0.44	0.01 (0.01)	0.06 (0.03)
Contrasting patterns				
c) −Leigh, +Tawharanui, and +Hahei				
Scalpomactra scalpellum	Bivalvia	−0.18	0	0.01 (0.01)
d) +Leigh, −Tawharanui, and −Hahei				
Amalda novaezelandiae	Gastropoda	0.61	1.9 (0.19)	0.4 (0.08)
Marginella pygmaea	Gastropoda	0.23	0.21 (0.06)	0.03 (0.02)
Pagurus novizelandiae	Decapoda	0.47	1.49 (0.04)	0.4 (0.08)
e) −Leigh, −Tawharanui, and +Hahei				
Sigalion capense	Polychaeta	−0.56	0	0.12 (0.04)
Ovalipes catharus	Decapoda	−0.42	0.01 (0.01)	0.06 (0.03)

Notes: For each location, the abundance (mean and 1 SE) of species from non-reserve (fished) and reserve sites is shown. A positive correlation (a) indicates species associated with non-reserve sites, while a negative correlation (b) indicates species associated with reserve sites. Several species (c–e) displayed strong patterns of contrasting positive (+) and negative (−) correlations at different locations. Species are given in decreasing order of the absolute value of their average for the correlation across the three locations. Species that occurred at fewer than six sites (out of a total of 24) and with an average absolute value of the correlation among locations <0.25 were not included.

zelandiae, appeared to have a positive relationship with the percentage of fine sediments. In contrast, the abundances of other prominent taxa in the assemblage (i.e., the bivalves *D. subrosea* and *M. striata*) were driven by predator density and were primarily responsible for the detected effects of reserve status.

There were also some differences in the magnitude of the effects detected at each location, with the greatest response being shown by *D. subrosea* at Hahei, having a mean density of 0.08 m^{-2} inside reserves and 1.88 m^{-2} outside reserves. High small-scale variability detected in all locations could have been due to patchiness in foraging (Connell and Kingsford 1998). However, there was a consistent overall pattern in the community response to the large-scale manipulative experiment provided by marine reserve status. The greater community variability in the reserve sites at Leigh could be due to greater levels of disturbance, as the highest densities of predators were observed there.

Several other studies have found bivalve populations to be susceptible to predation. For example, sea otters have been found to dramatically reduce some bivalve species through predation and disturbance (Kvitek et al. 1992), and spiny lobster (*Panulirus interruptus*) have been shown to control intertidal mussel populations (Robles et al. 1990).

A pattern of increasing abundance with increasing distance from reefs (halos) was observed in several species, in particular *D. subrosea* and *E. cordatum*, but the reverse pattern was also observed, particularly in the hermit crab *P. novizelandiae*. The pattern of in-creasing abundance with increasing distance from reefs occurred at sites both inside reserves, with high relative densities of predators, and at non-reserve sites, with relatively low densities of predators.

Posey and Ambrose (1994) found significantly decreased abundances of polychaetes, bivalves, isopods, and scaphopods up to 75 m away from the edge of an offshore reef near Wrightsville Beach, North Carolina (depth ~30 m). In that study, no leveling off in the increase of infaunal abundance with increasing distance from the reef edge was observed. In our study, at non-reserve sites (areas with low densities of reef-associated predators), several bivalve taxa exhibited a trend of increasing abundance with increasing distance from the reef edge. This suggests that subtle predation effects or other, perhaps physical (DeFelice and Parrish 2001), factors are important in influencing the distribution of infauna in relation to distance from the reef edge. A study of the stomach contents of reef-associated fishes in North Carolina's Onslow Bay by Lindquist et al. (1994) indicated that feeding by these fish might play a major role in creating infaunal halos. However, a study by Dahlgren et al. (1999) at the same location suggested that in this system bioturbation is of sufficient magnitude to influence infaunal abundances close to the reef, and may work concurrently with predation to produce observed infaunal abundance patterns. The dominant bioturbator found in our study has been shown to be an important component of the diet of snapper in offshore soft-sediment areas (Godfriaux 1970). However, their abundance was not found to cor-

TABLE 1. Extended.

| | Tawharanui | | | Hahei | | |
| | | Mean (SE) | | | Mean (SE) | |
r	Fished	Reserve	r	Fished	Reserve
0.29	0.34 (0.07)	0.22 (0.06)	0.58	0.38 (0.07)	0.02 (0.02)
0.04	0.77 (0.13)	0.72 (0.16)	0.25	0.24 (0.07)	0.08 (0.04)
−0.22	0.01 (0.01)	0.06 (0.04)	−0.26	0.04 (0.02)	0.14 (0.04)
0.59	0.37 (0.07)	0	0.46	0.19 (0.05)	0.03 (0.02)
−0.24	0.99 (0.12)	1.19 (0.14)	−0.58	0.15 (0.04)	1.81 (0.03)
−0.56	0.13 (0.03)	1.44 (0.22)	−0.2	0	0.03 (0.02)
−0.07	0.45 (0.11)	0.43 (0.1)	−0.23	0.5 (0.09)	0.88 (0.14)
−0.1	0.05 (0.02)	0.07 (0.04)	0.29	0.09 (0.03)	0.02 (0.02)
−0.17	0	0.01 (0.01)	0.23	0.02 (0.02)	0

relate with snapper and lobster density in this study, suggesting that the influence of bioturbators is not confounded by the abundance of large predators. Dahlgren et al. (1999) found a very different distribution of their dominant infaunal bioturbator, the holothurian *Holothuria princeps*, compared with the present study. Dahlgren et al. (1999) found significantly higher densities close to the reef edge (1 m) compared to further away (10–25 m), whereas in the present study we found the distribution of infaunal bioturbators increased with increasing distance from the reef edge, in particular for *E. cordatum*. Our study dealt with the responses of animals >4 mm and these larger organisms may, by virtue of their size, be less affected by bioturbation than small infauna.

No-take marine reserves provide a strong and consistent large-scale contrast in the density of previously exploited predators and this has enabled us to investigate the potential role of reef-associated predators in soft-sediment communities. Another approach to demonstrating such roles is to conduct smaller scale caging experiments. Such experiments are useful in that they can reduce or remove concerns relating to confounding environmental effects at larger scales. However, these will only be successful if there are significant levels of predation in the "uncaged" treatment.

CONCLUSIONS

Long-term and large-scale manipulations, such as the establishment of marine reserves, are necessary to ap-

TABLE 2. Correlations of individual species (r) with the canonical axis for distance from the reef, as shown in Appendix I.

| | | Distance from the reef edge | | | |
Species and correlation	r	2 m	5 m	15 m	30 m
Positive correlation (near)					
Pagurus novizelandiae	0.34	0.83 (0.11)	0.86 (0.1)	0.48 (0.08)	0.59 (0.1)
Lophopagurus cristatus	0.24	0.06 (0.04)	0.06 (0.03)	0.02 (0.02)	0.01 (0.01)
Philine angasi	0.22	0.01 (0.01)	0.14 (0.04)	0.03 (0.02)	0.03 (0.01)
Marginella pygmaea	0.22	0.58 (0.13)	0.36 (0.09)	0.2 (0.08)	0.08 (0.03)
Nemertea spp.	0.20	0.07 (0.02)	0.08 (0.02)	0.06 (0.02)	0.06 (0.02)
Negative correlation (far)					
Echinocardium cordatum	−0.49	0.10 (0.03)	0.03 (0.02)	0.34 (0.07)	0.49 (0.09)
Dosinia subrosea	−0.46	0.27 (0.05)	0.34 (0.06)	0.45 (0.09)	0.81 (0.12)
Dosinia anus	−0.40	0.01 (0.01)	0.01 (0.01)	0.1 (0.03)	0.22 (0.06)
Amalda depressa	−0.30	0.01 (0.01)	0	0.01 (0.01)	0.04 (0.02)
Paguristes setosus	−0.26	0.13 (0.05)	0.09 (0.03)	0.24 (0.07)	0.41 (0.13)
Amalda australis	−0.24	0.03 (0.01)	0	0.06 (0.02)	0.03 (0.02)

Notes: The abundance (mean with SE in parentheses) of species from each distance stratum is shown. Species are grouped by positive correlation (near to the reef) and negative correlation (far from the reef) and are given in decreasing order of the absolute value of their correlation. Species that occurred at fewer than six sites (out of a total of 24) and with an average absolute value of the correlation among locations <0.2 were not included.
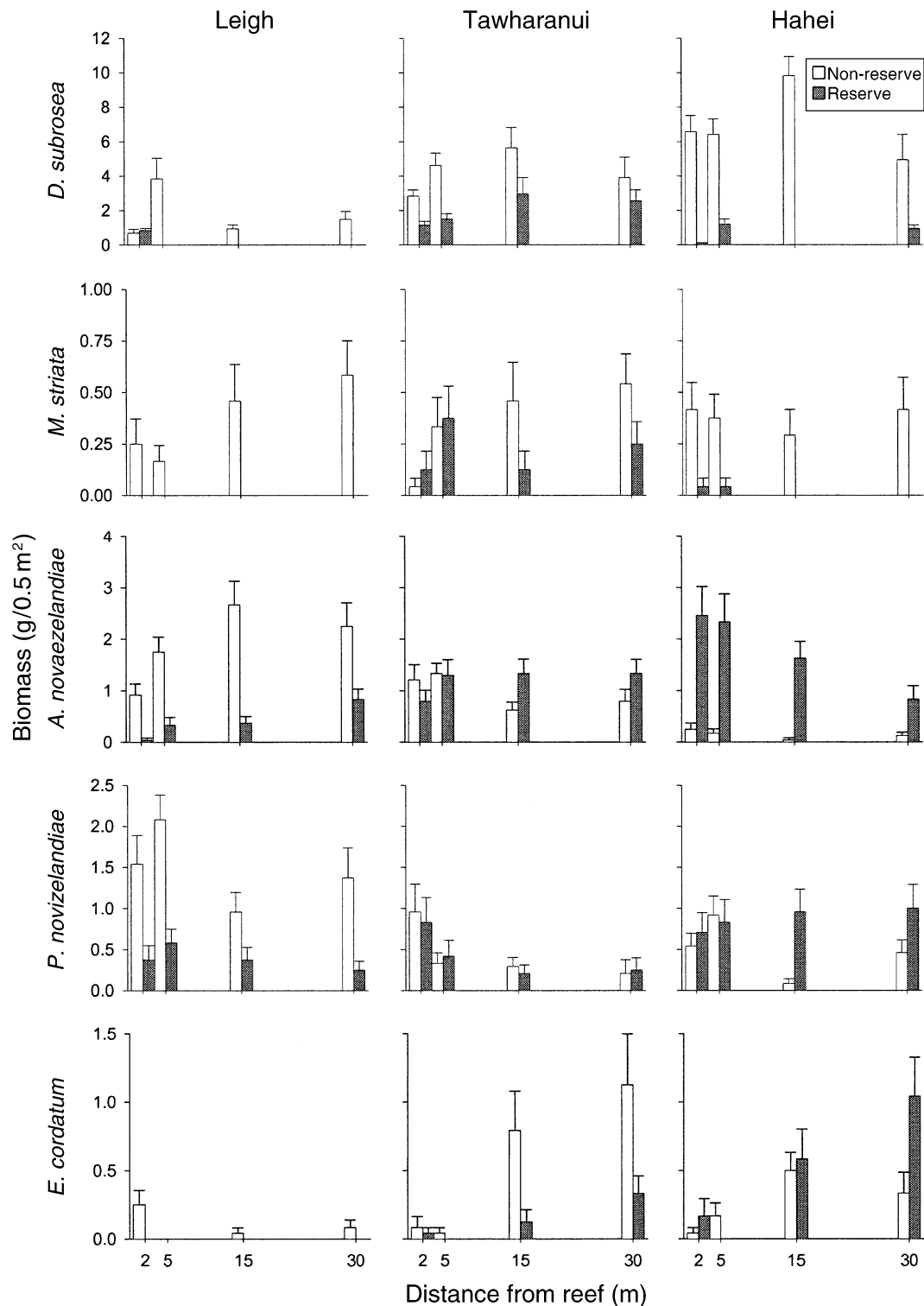
FIG. 4. Biomass (mean + SE) of *Dosinia subrosea*, *Myadora striata*, *Amalda novaezelandiae*, *Pagurus novizelandiae*, and *Echinocardium cordatum* at each distance stratum, reserve status, and location (sites and replicates pooled).

preciate fully the impacts of fishing (Dayton et al. 1998). They can also allow us to investigate how the removal of top-level predators from the ecosystem affects other trophic levels. Direct effects of fishing on soft-sediment communities due to the impacts of trawling and dredging have been described in several studies (Watling 1991, Jennings and Kaiser 1998, Thrush et al. 2001). Secondary effects have also been documented where, in the wake of bottom trawling activities, the diet of benthivorous fishes has changed to reflect changes in the soft-sediment community (Frid and Hall 1999). Our study suggests that the exploitation of predatory fauna can have important indirect effects on soft-sediment communities, where the fishing pressure on snapper and rock lobster results in positive effects on their prey species. No-take marine reserves provide a release from fishing pressure allowing the investigation of indirect harvesting effects. Caging manipulations (with controls and replication inside and outside reserves) are needed to establish that large snapper and rock lobster are indeed causing observed effects. There have not been, to our knowledge, any previous studies of the effects of predatory fauna on soft-sediment systems using marine reserves.

Marine reserves have provided us with new insights into ecosystem function and the pervasiveness of the indirect effects of fishing (Shears and Babcock 2003, Willis et al. 2003b). Marine reserves are ecosystems that are generally less disturbed by humans, but this study shows that they do not necessarily result in increases in the abundance, biomass, and diversity of all communities as suggested in recent meta-analyses by Halpern and Warner (2002, 2003). The indirect effects of fishing uncovered by this study emphasise the importance of a ''system-level'' approach to the modeling and investigation of marine reserves (Agardy 2000).

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APPENDIX A

A table listing environmental variables used in the multivariate models is available in ESA's Electronic Data Archive: *Ecological Archives* E086-081-A1.

APPENDIX B

A table listing predatory and bioturbating infauna found in the study that were used as environmental variables in multivariate models is available in ESA's Electronic Data Archive: *Ecological Archives* E086-081-A2.

APPENDIX C

A figure showing the percentage of coarse sediments, abundance of infaunal predators, and abundance of infaunal bioturbators at each distance stratum, reserve status, and location (sites and replicates pooled) is available in ESA's Electronic Data Archive: *Ecological Archives* E086-081-A3.

APPENDIX D

Results of four-factor ANOVA examining: (1) percentage of coarse sediment by mass, abundance of infaunal predators, and bioturbators; (2) biomass of *Dosinia subrosea* and *Myadora striata*; (3) biomass of *Amalda novaezelandiae*, *Pagurus novizelandiae*, and *Echinocardium cordatum* at each distance stratum, reserve status, and location (sites and replicates pooled) are available in ESA's Electronic Data Archive: *Ecological Archives* E086-081-A4.

APPENDIX E

Figures showing (a) distance-based RDA ordination of first and second fitted axes relating the environmental variables to the faunal data and (b) distance-based RDA as in (a), but showing the first and third axes are available in ESA's Electronic Data Archive: *Ecological Archives* E086-081-A5.

APPENDIX F

A table listing 61 taxa from seven phyla obtained from 576 box quadrats in our study is available in ESA's Electronic Data Archive: *Ecological Archives* E086-081-A6.

APPENDIX G

Results of four-factor nonparametric multivariate analysis of variance (PERMANOVA) of soft-sediment fauna are available in ESA's Electronic Data Archive: *Ecological Archives* E086-081-A7.

APPENDIX H

Results of pairwise a posteriori comparisons of soft-sediment communities among the four distance strata are available in ESA's Electronic Data Archive: *Ecological Archives* E086-081-A8.

APPENDIX I

(a) Metric MDS ordination and (b) canonical (CAP) analysis of the correlation of soft-sediment fauna with distance from the reef edge are available in ESA's Electronic Data Archive: *Ecological Archives* E086-081-A9.