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Fine-scale habitat change in a marine reserve, mapped using radio-acoustically positioned video transects

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Abstract. Large-scale changes in subtidal reef habitats have occurred within the Leigh Marine Reserve (New Zealand) since its establishment in 1976. To determine the extent of habitat change within Goat Island Bay, video transects positioned by a radio acoustic positioning telemetry (RAPT) system were used to map habitats within a Geographic Information System (GIS) framework. This map was compared to a map of the same area constructed 22 years earlier in 1978. Visual categorisation of habitats was consistent with the quantification of habitat-forming species within quadrats, justifying the creation of a map based on visually interpreted video footage. Furthermore, the large-scale changes in habitats were consistent with smaller-scale changes in community structure identified at permanent sites located in the study area. The most obvious changes were the total disappearance of 'urchin barrens' across all depths and the recovery of kelp forest in water <8 m, caused by a trophic cascade related to predator recovery. In water >12 m, the extent of kelp forest and sponge flats was found to decrease by 25 and 33%, respectively, while turfing algal habitat had increased by 50%. This increase in turfing algal habitat had not been previously documented due to the spatial scale of traditional sampling methods.

Extra keywords: benthic habitat change, habitat mapping, north-eastern New Zealand, radio acoustic positioning telemetry, subtidal temperate reef.

Introduction

Subtidal reefs are an extremely important and dynamic coastal environment. It is therefore important that marine environment classification systems recognise the array of biological habitats found on them. Furthermore, understanding and hence management of subtidal reef systems requires the study of reefs at a variety of spatial scales (Underwood et al. 2000). Small-scale quantitative sampling methods are most commonly used to monitor changes in subtidal reef habitats and these are usually stratified by depth (Shears and Babcock 2003) or habitat type (Underwood et al. 1991). However, such techniques will only observe changes at the spatial scale of the quadrat, or within the targeted strata. Bias due to small errors in accuracy or precision can translate to errors of large magnitude when results of small stratified samples are used to produce large-scale estimates at the ecosystem level. Methods such as belt transects have been used to assess changes that may occur at larger scales, and integrate changes across several strata (Babcock et al. 1999). An alternative method of investigation involves the construction of a habitat map that could then act as a baseline for monitoring.

In north-eastern New Zealand changes in benthic habitats have been documented in New Zealand's oldest marine reserve, the Cape Rodney to Okakari Point (CROP) Marine Reserve (Babcock et al. 1999; Shears and Babcock 2003). The large-scale decline in the extent of urchin grazed barrens habitat is consistent with higher predation levels on sea urchins (Shears and Babcock 2002) and increased abundances of previously targeted predator species in the marine reserve associated with the cessation of fishing, e.g. snapper Pagrus auratus (Willis et al. 2003) and spiny lobster Jasus edwardsii (Kelly et al. 2000). Anecdotal reports gathered by Dromgoole (1964) suggest that at many sites throughout north-eastern New Zealand, urchin 'barrens' replaced areas of kelp forest sometime after 1950, which coincides with a sudden increase in snapper landings and a drop in spawning stock biomass (Gilbert et al. 2000). This suggests that reserve status has allowed this section of coast to return to a state similar to that which may have existed before high fishing pressure with few sea urchins and high macroalgal abundance. While these changes have been recorded at several sites throughout the CROP Marine Reserve (Babcock et al. 1999; Shears and Babcock 2003), the spatial variability and extent of these changes is unknown.

Such changes in benthic habitats have important management and scientific implications and their detection has only

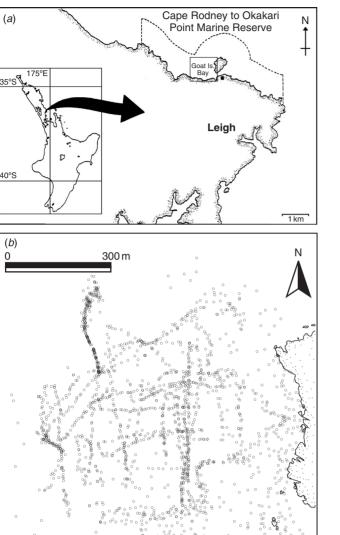


Fig. 1. (*a*) Location map of New Zealand's North Island (inset) and the Cape Rodney to Okakari Point Marine Reserve. Square indicates the Goat Island Bay study area. (*b*) Map of Goat Island Bay and the locations (empty circles) where habitat information was collected for the 2000 map.

been made possible by comparison with extensive baseline data collected when the CROP reserve was established. This included quantification of benthic communities at permanent sites (Ayling 1978) and construction of a map of subtidal reef habitats for the entire reserve (Ayling *et al.* 1981). The map was based on diver-transects that classified benthic habitats in subtidal reef areas in the CROP Marine Reserve (Ayling *et al.* 1981). The opportunity to resurvey a section of this map was brought about through the use of a radio acoustic positioning and telemetry (RAPT) system within the reserve. This system was designed to follow the movements of fish (Parsons *et al.* 2003) but proved just as effective at locating the position of a diver conducting video transect surveys.

Mapping of seafloor habitats is increasingly being used in coastal management for monitoring programmes and impact assessment (Donoghue et al. 1994; Sheppard et al. 1995; Sanderson 2001; Vallega 2002). However, due to the nature of the marine environment the use of traditional remote sensing techniques is restricted. Aerial photographs have been used but these are only suitable for shallow habitats in areas of clear water (Andrew and O'Neill 2000) or where subtidal algae form surface canopies (Fyfe et al. 1999). Several other techniques have been developed for mapping the seabed, e.g. side-scan sonar (Rosenberg et al. 2003), seafloor acoustic discrimination (QTC View, Quester Tangent Corporation, Sidney, Canada; Morrison et al. 2001) and laser line scan (Carey et al. 2003). While these techniques have been used extensively for management and conservation of soft sediment environments their application to reef systems is limited due to their inability to distinguish between biologically meaningful habitats.

The objective of this paper was to determine the aerial extent of changes in habitats within Goat Island Bay in the CROP Marine Reserve (Fig. 1*a*), and to assess the suitability of RAPT monitored video transects for mapping subtidal habitats. First, a classification system of habitat types was established and tested. These classifications were then used to construct a habitat map that used the RAPT mapping method, which was then compared to the 1978 map (Ayling *et al.* 1981). To verify findings at this larger scale, patterns were compared to findings from permanent sites in the same area that have been quantitatively assessed over the same temporal scale (Shears and Babcock 2003). Findings were also compared with long-term demographic studies of the kelp *Ecklonia radiata* in Goat Island Bay (T. R. Haggitt, unpublished data).

Materials and methods

Habitat classification

A classification system of habitat types (Table 1) was determined *a priori* based on those described previously for reefs in the Leigh area (Ayling 1978; Choat and Schiel 1982; Taylor 1998; Shears 2002). These were essentially comparable to the habitat definitions used to produce the original habitat map of the CROP Marine Reserve (Ayling *et al.* 1981). The reliability of any broad-scale habitat survey rests on the accuracy with which individual habitat units can be classified. Therefore, to determine if the habitats could be reliably categorised visually and whether there were actual differences in the abundance of habitat-forming organisms between habitat types, benthic communities were quantified within each habitat type in the field. Transects were run perpendicular to the shore from mean low water spring to the bottom of the reef or a maximum distance of 100 m, whichever came first. Quadrats (1 m²) were placed at 5 m intervals along the transect. A habitat type was assigned visually to each quadrat and the abundances of dominant organisms were recorded.

Habitat type	Depth range (m)	Habitat description			
Shallow Carpophyllum spp.	<3	High numbers of <i>Carpophyllum</i> spp. (>20 plants m ⁻²). <i>Ecklonia radiata</i> and <i>Pterocladia lucida</i> common. Urchins low in abundance and usually cryptic. Adapted from Choat and Schiel (1982) and Shears and Babcock (2000).			
Mixed algae	2–10	Mixture of large brown macroalgae such as: <i>Carpophyllum</i> spp., <i>Sargassum sinclairii</i> and <i>Echlonia radiata</i> with no clear dominance of any one species. Underlying substratum covered b crustose or turfing coralline algae. Urchins may be common. Combined with <i>Carpophyllum</i> zon forms Ayling's (1978) shallow broken rock habitat.			
Urchin barrens	4–12	Absence of large brown algae, rock covered by crustose coralline algae and some sponges. Average urchin density $3-7 \text{ m}^{-2}$. Synonymous with the rock flats habitat of Ayling (1978).			
Turfing algae	<16	High coverage of coralline turf (>30% cover), low numbers of brown algae. Sand/sedimen often trapped in turf. Urchins low in abundance. Presence of sponges and sediment increase with depth. Sediment layer can be centimetres thick at depths greater than 10 m. This habitat i synonymous with the sediment flats habitat of Ayling <i>et al.</i> (1981).			
Kelp forest	0–18	Almost entirely mono-specific stands of <i>Ecklonia radiata</i> (>4 adult plants m^{-2}). Underlyin substratum covered by coralline algae, bryozoans, hydroids, sponges and ascidians. Urchins rar			
Sponge flats	>15	Thick layer of sand/sediment overlying rock. Higher coverage of sponges than sediment including: <i>Ancorina alata</i> , <i>Cliona celata</i> , <i>Polymastia granulose</i> , <i>P. fusca</i> , <i>Raspailia</i> sp., <i>Caly gia ramose</i> , <i>Cinachyra uteoides</i> , <i>Aapotos aaptos</i> , <i>Stelleta crater</i> and <i>S. hauraki</i> . Urchins This habitat is patchy and transitional (Ayling 1978).			
Deep reef	>18	<i>Ecklonia radiata</i> sparse with sponges being abundant and urchins rare. Similar to kelp fore the bottom of its depth range.			
Sand/gravel	All	Areas of sand or aggregations of small rock fragments and gravel.			
Cobbles	All	Drifts of small boulders and cobbles that are unstable due to movement, dominated by crustose coralline algae.			

Table 1. Habitat classification system used for construction of the 2000 habitat map

Counts of organisms that were considered to be the typical habitat formers in north-eastern New Zealand were made. These included Ecklonia radiata (>25 cm total length), fucalean algae (>25 cm total length) and the sea urchin Evechinus chloroticus (exposed individuals; cf. Cole and Keuskamp 1998). In addition the percentage cover of sponges, coralline turf and sediment were visually estimated. Transects were sampled at seven sites around Leigh in April 2000. The concordance between the communities recorded and the habitat type assigned to each quadrat was analysed using the PRIMER software package (Clarke and Warwick 1994). Non-metric multidimensional scaling (MDS) of log(x + 1) was used to transform species abundance data using the Bray-Curtis similarity measure. This technique was used to assess the similarity in communities among quadrats assigned to each habitat type. To test for differences in communities between habitat types a one-way analysis of similarity (ANOSIM; Clarke 1993) was carried out to ensure that visual classifications reflected actual differences in community types.

Habitat map construction

Data used to construct the habitat map were acquired from a variety of different sources. The coastline of this map was digitised from the original Goat Island Habitat Map (Ayling *et al.* 1981). Ground control points (>50), obtained with a differential global positioning system (dGPS), were then used to correct inaccuracies in the original map by using rubber sheeting within ArcView version 3.2 (ESRI 1999).

The majority of the habitat and depth data were obtained by application of the RAPT system (O'Dor *et al.* 1998). This involved the attachment of an acoustic tag to a scuba diver who swam transects while recording the substratum on a digital video camera. Transects were organised in a grid formation where parallel transects were separated by ~ 20 m. Habitat types were extracted from the video by matching the time displayed on the video camera with the position of the diver's tag, calculated by the RAPT system. These positions are accurate within 1-2 m at the centre of the tracking system (O'Dor et al. 1998). The habitat type of each recorded position was then defined, using the classification scheme described in Table 1. A depth for each position was obtained from a depth gauge mounted in view of the video camera. These depths were later adjusted to account for the height of the diver above the substratum (~ 1.5 m) and the height of the tide at that time using SimTide version 1 (Gowens 1999). Because the RAPT tracking system does not work well in shallow waters (<4 m) with high relief topography, additional habitat points were also obtained through the hull of a 'glass bottom' boat. Depths were recorded from a depth sounder and geographic locations were obtained with a dGPS. The locations of all habitat information collected can be seen in Fig. 1b. An area with a high density of data points was used to form a map. No interpolations concerning the habitat type or depth were made outside this area. The habitat type and depth were then defined by assigning the proximity to the habitat and depth data points using ArcView version 3.2 (ESRI 1999).

The resultant map was then compared to the equivalent area on the 1978 map (Ayling *et al.* 1981), which was digitised using ArcView version 3.2 (ESRI 1999). The percentage of each habitat type within this region and the depth range over which each habitat was distributed were calculated for both maps. The total area of reef was found to be similar (<2% change) on both maps, so the proportion of total reef area they occupied defined habitats.

Quantitative changes at permanent sites

Data from seven 10×10 m permanent sites within Goat Island Bay (Ayling 1978; Babcock *et al.* 1999; Shears and Babcock 2003) were used to quantitatively validate the changes observed by comparing habitat maps. Two of the permanent sites were shallow (<4 m, classified as 'rock flats/shallow broken rock' in 1978), three occurred between 6 and

8 m (originally classified as 'rock flats' or urchin barrens), and the final two occurred at 12 m depth (originally classified as kelp forest). For the purpose of this study only the numbers of *E. chloroticus*, adult *E. radiata* (>10 cm stipe length) and fucaleans are presented (see Shears and Babcock 2003 for further details). Temporal data of *E. radiata* biomass

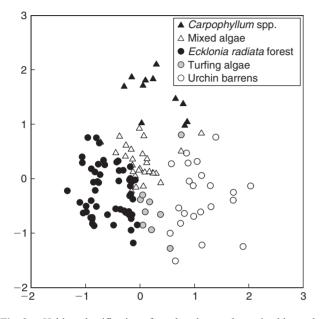


Fig. 2. Habitat classification of quadrat data as determined by multidimensional scaling ordination (stress = 0.18). Symbols refer to the *in situ* visual assessment of habitat in each quadrat.

from five permanent 1 m^2 quadrats, nested within a larger $10 \times 10 \text{ m}$ area of *E. radiata* forest were used to validate changes in habitats at depths > 12 m (Haggitt and Babcock 2003).

Results

Habitat classification

There was good agreement between the quantitatively defined benthic communities and the habitat classifications given for each quadrat, with quadrats of the same habitat type grouping closely on the MDS ordination (Fig. 2). Despite some overlap between habitats on the MDS ordination, ANOSIM showed that there was an overall significant difference between habitats (sample statistic r = 0.63, P < 0.01%) and pair-wise comparisons revealed significant differences (P < 0.01%) between all habitats with the value of the sample statistic rranging from 0.32 to 0.99. These analyses support the habitat classification system used, and demonstrate that these habitat types can be reliably categorised visually (Table 1).

Large-scale habitat change

Direct visual comparison between the 2000 habitat map and the 1978 map illustrated extensive changes in the distribution and extent of reef habitats (Fig. 3). In addition, the map produced by Ayling *et al.* (1981) contained larger continuous areas of uniform habitat type. The boundaries between these habitats were smooth curves generated by visual interpolation. In contrast, the map constructed in the present study was

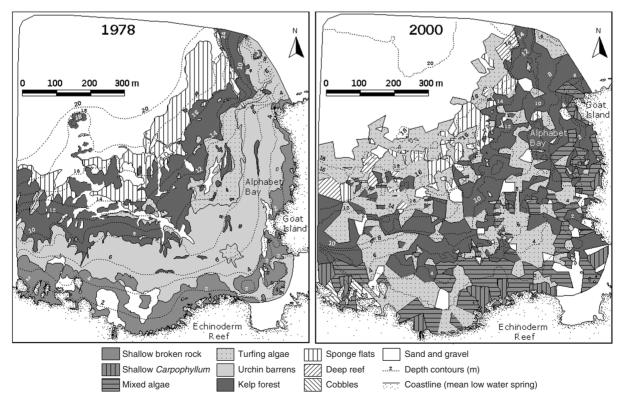


Fig. 3. Subtidal habitats of Goat Island Bay in 1978 (adapted from Ayling et al. (1981)) and 2000.

generated by a proximity algorithm in ArcView version 3.2 (ESRI 1999), and had smaller patches of individual habitat types separated by straight lines. The total number of habitat patches for each map was 113 for 1978 and 274 for 2000. The resolution of data points within the mapped area was such that 74% of the area mapped in 2000 was within 20 m of a data point. The north-west corner of the map could account for nearly all of the remaining 26% where data points were >20 m apart. This part of the map was well away from the reef edge on soft sediment where habitat gradients were low. Therefore, the reef areas of the map, where habitats varied over smaller scales, had a much higher density of data points.

The percentage of kelp forest in 2000 (35.2%) was about the same as it was in 1978 (35.5%; Table 2). The cover of urchin barrens had declined from around 26% of the mapped reef area in 1978 to being non-existent in 2000, conversely turfing algae increased from around 6% cover to a total coverage within reef areas of almost 38%. Areas of shallow broken rock (defined as Carpophyllum zone and mixed algae habitats combined for the 2000 map) increased from 13 to 18%, while sponge flats decreased from 18 to 4%. Further inspection of the distribution of habitat types within different depth strata provided a better indication of how habitats had changed between 1978 and 2000 (i.e. which habitats were replaced by other habitats; Fig. 4). The largest change observed was in the extent of urchin barrens. This habitat covered >87% of the reef in the 4-8 m depth range in 1978 but was absent in 2000. Within this depth range kelp forest increased from 5 to 50% and shallow broken rock also increased from 4 to 14%. At shallow depths (0-4 m) kelp forest also increased from 0 to 17% coverage, while shallow broken rock and urchin barrens decreased from 72 to 54% and from 27 to 0%, respectively. Within the 8-12 m depth range again the urchin barrens habitat disappeared while kelp forest appeared to be stable, decreasing by less than 3%. At depths greater than 12 m kelp forest decreased from 49 to 24%, and sponge flats decreased from 47 to 14% while turfing algae increased from 2 to 52%.

Quantitative changes at permanent sites

The temporal patterns in the abundance of the dominant species at permanent sites in Goat Island Bay closely reflected the habitat changes identified from the habitat mapping. Relative to 1978 values, the density of urchins had decreased substantially, primarily within the permanent sites located in the mid-depth range (4–8 m), and subsequently the abundance of *Ecklonia radiata* and fucaleans had increased (Fig. 5). These changes were consistent with the large-scale change at 4–8 m from barrens in 1978 to kelp forest in 2000 (Fig. 3). This pattern has remained stable since 1994 and the abundance of *E. radiata* actually peaked in 2000. For the shallow permanent sites (<4 m depth) the abundance of *Evechinus chloroticus* has been variable since 1978 although there has been some increase in the density of *E. radiata* and fucaleans. This can be explained by the fact that most of the urchins recorded in 1999 and 2000 were cryptic (crevice bound) and may not play an important grazing role (N. Shears, unpublished data). No such data on urchin crevice occupancy exist from the time of the initial survey (Ayling 1978). The deeper permanent sites (~12 m depth) have remained dominated by

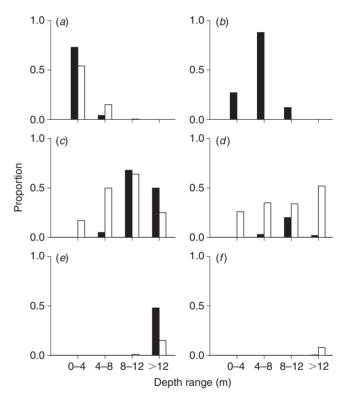


Fig. 4. Proportional cover of reef habitat types by depth range within Goat Island Bay for 1978 (solid bars) and 2000 (empty bars). (*a*) Shallow broken rock, (*b*) urchin barrens, (*c*) kelp forest, (*d*) turfing algae, (*e*) sponge flats, (f) deep reef.

 Table 2. Percentage of each habitat type within all depth ranges in 1978 and 2000

 Shallow broken rock is a combination of the shallow Carpophyllum spp. and mixed algae habitat as defined in Table 1

Habitat	Shallow	Urchin	Kelp	Turfing	Sponge	Deep	Cobbles
(year)	broken rock	barrens	forest	algae	flats	reef	
1978	13.06	26.69	35.50	5.99	18.62	0.09	0.05
2000	18.90	0.00	35.22	37.68	4.90	2.62	0.68

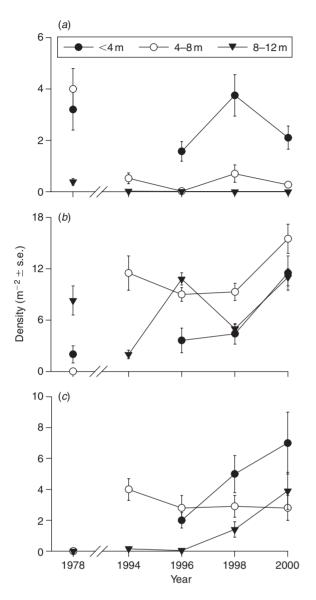
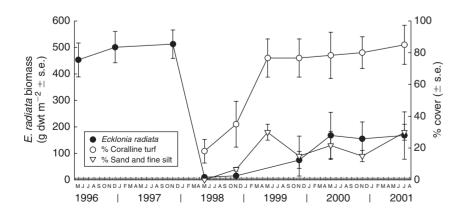


Fig. 5. Long-term data from permanent quadrats in Goat Island Bay established by Ayling (1978). (*a*) *Evechinus chloroticus*, (*b*) *Ecklonia radiata*, (*c*) fucalean algae.



E. radiata with very low urchin densities since 1978. Adult *E. radiata* densities in the 8–12 m stratum were reduced in 1994 after a large-scale (km) dieback during the austral 1992–1993 summer (Cole and Babcock 1996) and again in 1998 after a smaller-scale (tens of metres) dieback (T. R. Haggitt, unpublished data; Fig. 5). At depths >12 m, *E. radiata* stands were also affected by dieback in 1993 and 1998 but in contrast to shallower populations have not shown a complete recovery since 1998 (Fig. 6). In three of the five permanent quadrats sampled at a depth of 13 m the cover of coralline turf and sediment has increased since 1998 (Fig. 6). This decline in *E. radiata* forest and increase in turfing algal habitat at depths >12 m, is consistent with changes seen from the habitat maps.

Discussion

Mapping of subtidal habitats within Goat Island Bay in the Leigh Marine Reserve revealed large-scale changes in the distribution of habitats since the area was last mapped in 1978. In general, these large-scale changes are consistent with quantitative changes described previously at smaller spatial scales (Babcock *et al.* 1999; Shears and Babcock 2003). However, investigation of change at the habitat-scale revealed several previously undocumented changes in community structure and provides a baseline for future monitoring projects.

The combination of methodologies used in this study was the key to achieving meaningful results. The concordance between visual and quantitative assessment of habitats confirmed that visual categorisation of habitats, and maps produced from such methods, can provide an accurate representation of benthic community structure. This validates the analysis of differences between the map produced in this study and that of Ayling *et al.* (1981) to assess changes in the abundance and distribution of subtidal species and habitats in Goat Island Bay. In fact, without mapping, significant habitat changes would probably not have been detected.

Despite this advantage, large-scale mapping of habitats is the most time-consuming and expensive method of

Fig. 6. Mean *Ecklonia radiata* biomass and percentage cover of coralline turf and sand within five permanent 1 m^2 quadrats > 12 m depth at Alphabet Bay, May 1996 to July 2001.

documenting habitats, and realistically can only be applied at low frequencies. It is worth noting that under such circumstances the annualised cost of mapping is perhaps no greater than that for smaller scale sampling. Consequently it may be best suited to detecting long-term trends. However, confidence in the mapping data can only be achieved and maintained with adequate validation from smaller scale and more intensive sampling. For example, if average values from the permanent sites are used to classify the habitats present, the changes between 1978 and 2000 were consistent with changes described by map-based classifications. However, in 1978 the permanent sites were not stratified by depth as well as habitat type. Therefore, major habitat changes (*Ecklonia*-turf transition at >12 m depth) may not have been detected without mapping. While in some circumstances small-scale sampling, such as, quadrats or transects may have limited power to detect unanticipated changes, it is well-suited to targeted application and hypothesis testing. Therefore a combination of mapping and more intensive but spatially limited quantitative sampling is not only desirable but ultimately necessary.

It should be noted that the two habitat maps were made using different methodologies. Because Ayling *et al.* (1981) did not have access to any accurate form of position estimation their map might have been prone to inaccuracies and therefore a lower resolution. Second, Ayling *et al.* (1981) used many voluntary divers, yet in the current study the same observer carried out all interpretation of habitats. Whatever the inaccuracy or error associated with either mapping method, the final habitat map represents an estimate of the proportion of the different habitats that were present in the specified area. It is this estimate of the area covered by each habitat that is relevant to this study.

The different methods of mapping did undoubtedly have an effect on some aspects of the maps, such as, the patchy nature of the habitats in the 2000 map. The computerised interpolation method used here was more likely to produce patches than the more subjective manual contouring method used in 1978. Given the level of accuracy in positioning available to Ayling in 1978, the smoothing used in the construction of the 1978 habitat map was probably prudent and conservative. This being said, urchin barrens outside of the reserve are generally continuous between depths of 3–7 m because the rock is grazed bare of any habitat-forming algae (Shears and Babcock 2003). A decline of urchins in the reserve could therefore have resulted in increased spatial heterogeneity of habitats.

Perhaps the most ecologically significant change was the total reduction of urchin barrens between 1978 and 2000 (26–0%). These changes were consistent with previous findings (Babcock *et al.* 1999; Shears and Babcock 2003) but demonstrate that barrens have now been totally eliminated from Goat Island Bay. This supports the idea that top down regulation of herbivores can result from reserve protection and

are consistent with Estes and Duggins (1995), who observed large-scale habitat change when otters returned to the Alaskan coast.

Given the decline in urchin barrens, the lack of change in the overall proportion of kelp forest since 1978 was surprising. However, when the proportion of kelp forest is considered by depth, the results presented are consistent with those of Babcock et al. (1999) who recorded large increases in the proportion of kelp forest at shallow depths (<8 m). This change is most likely due to the reduced urchin abundances inside the CROP Marine Reserve (Shears and Babcock 2002). Between depths of 8–12 m both the current study and that of Babcock et al. (1999) found kelp forest to be stable since 1978. This was not unexpected, as *Ecklonia radiata* typically dominates these depths, with low densities of urchins, throughout northeastern New Zealand (Choat and Schiel 1982). The current study does, however, produce results that were not observed by Babcock et al. (1999) at both ends of the depth spectrum. This could be an artefact of the impracticality of using quadrats at these depths and reflect the advantage of using a mapping approach.

In shallow waters, <4 m, a decrease in the area of shallow broken rock and an increase in kelp forest was observed. It is possible that with urchins almost entirely absent from the mapped area, E. radiata, which is a preferred food of Evechinus chloroticus (Schiel 1982; Cole and Haggitt 2001), obtains a competitive advantage over fucalean species. At depths >12 m, there were large decreases in the extent of kelp forest and sponge flats and corresponding increases in turfing algae. Rapid declines in E. radiata below 10 m depth in Goat Island Bay have previously been attributed to reduced photo-irradiance resulting from phytoplankton blooms (Cole and Babcock 1996). During one such bloom in 1993 mortalities of sponges were also noted in Goat Island Bay (C. Battershill, personal communication). In general E. radiata populations at 8-12 m depth appear to be stable, and recover quickly from short-term mortality events. However, at greater depths other mechanisms may have prevented the recovery of E. radiata. For example, the increased cover of sediment, sand and coralline turf seen at some permanent quadrats in Goat Island Bay may prevent the recovery of E. radiata populations. The presence of a covering layer of sediment has been shown to inhibit recruitment of laminarian algae (Devinney and Volse 1978).

The reduction in the extent of sponge flats observed here has not been previously documented but can also potentially be linked to increased sedimentation. Indeed Battershill (1987) suggested that the sponge communities of Goat Island Bay, which occur on low-profile reefs at the reef/sand boundary, were vulnerable to increased levels of sedimentation. The fact that both *E. radiata* forest and sponge flats have decreased at the expense of turfing algae, a habitat characterised by a covering layer of sediment, gives further credence to this conclusion.

Hume et al. (2000) modelled the transport of sand around Cape Rodney. One of the conclusions from this study was that the majority of sand moving south from Pakiri bypasses Goat Island at >20 m depth and that the 'sponge garden' habitats of Goat Island Bay are unaffected by sand movement. However, their study also indicated that in times of low swell energy, sand moving south accumulated on the reefs of Goat Island Bay before being removed by storms. This indicated that accumulation of sediment in the deeper areas of Goat Island Bay could be a naturally occurring but episodic process, potentially related to a decrease in the average surge height recorded at Leigh, New Zealand during the past 25 years (J. Evans, unpublished data). Additionally, increased terrestrial erosion and run-off could contribute to increased turbidity and sedimentation levels. The catchment of Goat Island Bay was predominantly pasture in 1978 and remains the same today. It is not known if sedimentation from elsewhere may influence both turbidity and sedimentation within Goat Island Bay. From these observations it would seem reasonable to suggest that habitat changes in the deeper areas (>12 m) have been brought about by: (i) a natural increase in mass sand movement; or (ii) a human-induced increase in coastal run-off that may result in increased turbidity and sedimentation. Anecdotal evidence suggests that on a regional basis there has been an increase in turbidity. Changes of this nature may explain the decrease in the lower-limit of macroalgae (e.g. Gorostiaga et al. 1998). It is likely that a combination of these factors is operating but these explanations are speculative and further work would be required to demonstrate that such increases in sedimentation have actually occurred and that they explain the observed habitat changes.

Previous estimates of productivity changes in the CROP Marine Reserve flowing from trophic cascade effects since 1978 may need to be revised on the basis of changes revealed here by habitat mapping. Babcock et al. (1999) assumed that the lower extent of the kelp forest had been stable at the same depth at which it existed in the original 1978 surveys. Consequently their calculation for total productivity of kelp forest is likely to have been an overestimate. Alternatively, areas that had not converted to kelp forest were assumed to have remained as low productivity urchin barrens (Babcock et al. 1999) while the 2000 habitat map shows that these areas are now comprised of algal turf habitats, which are highly productive (Littler and Arnold 1982). Consequently, while it is clear that the sources of primary productivity have changed, determining the magnitude of any change and whether it has been positive, negative or static, is a question that remains to be answered. While the overall cover of kelp forest area has remained more or less constant, the fact that it now occupies shallower, better-illuminated water, suggests that kelp forest productivity is likely to have increased (Novaczek 1984). Increases in the extent of algal turf areas in shallow strata also suggest increased productivity.

The habitat change that occurred in Goat Island Bay appeared to fall into two classes: (i) recovery of algal assemblages in shallow water due to decreased herbivory; and (ii) decline of sponge and algal communities in deep water potentially due to the persistence of sand on reef areas, increased sedimentation and/or turbidity. While the changes in shallow water algal assemblages are consistent with the cessation of fishing within the reserve, increased sedimentation may be due to either natural or human-induced change. This suggests that while a return to natural processes can revert community structure to its original state, in other circumstances an alternative stable state may persist. Whatever the causes of change, visual categorisation and the existence of a longterm dataset from a protected area allowed the observation of large-scale changes in community structure that were not previously revealed by other methods.

Acknowledgments

We would like to thank B. Flaim, B. Muller and P. Stokes for extensive help with data collection, H. Acosta and J. Evans for perseverance with map construction, I. Blackwell for use of the 'glass bottom' boat and G. Jackson and R. O'Dor for loan of equipment. Numerous student volunteers also assisted with data collection. We thank A. Ayling and B. Ballantine for comments on the original map and R. Taylor, N. Tolimieri for comments on the manuscript. This project was made possible through Department of Conservation funding and financial aid from the Vice-Chancellor's Committee, University of Auckland.

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Manuscript received 19 November 2003; revised 4 March 2004; and accepted 12 March 2004.