
C S I R O P U B L I S H I N G

Marine & Freshwater Research

Volume 51, 2000
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A journal for the publication of original contributions
in physical oceanography, marine chemistry,
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Large-scale patterns in habitat structure on subtidal rocky reefs in New South Wales

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Abstract. Aerial photography was used to estimate the representation of shallow subtidal habitats in New South Wales. Sixty sites, each between 4 and 5 hectares, were mapped with Geographical Information Systems software using ortho-rectified images digitized from 1:8000-scale photographs and 'ground truthed' in the field by divers. Barrens habitat covered an estimated 50% (s.e. = 3.9) of nearshore reefs between Port Stephens and Disaster Bay. Coverage of barrens habitat was greatest in Disaster Bay (68%, s.e. = 6.7) and least south of Disaster Bay (1%, s.e. = 0.3). There were clear differences among localities in the area of reef within the mapped sites; those at Cape Howe, Nadgee, and Turingal were significantly smaller in area than all others. There was no clear latitudinal trend in these differences but there was evidence of sand inundation at a site at Nadgee, where the reef was small. Differences in the densities and size-structure of the sea urchin *Centrostephanus rodgersii* at 27 of the mapped sites provide a basis for testing relationships between the demography of this species and the persistence of the barrens habitat. The extensive coverage of the barrens habitat in New South Wales is likely to limit the productivity of the abalone industry. The development of a sea urchin fishery may have large impacts on habitat representation on nearshore reefs.

Introduction

A major challenge for ecologists is to link species and ecosystems in a framework that both accommodates the variability found in the study of individuals and their interactions and allows the broad predictions required by natural resource managers. Central to this problem is the extrapolation of the hard-won knowledge from studies of small-scale phenomena to larger scales (Dayton and Tegner 1984; Rastetter *et al.* 1992; Schneider 1994; Petersen *et al.* 1997). A necessary step in scaling up such understanding is to describe patterns at larger spatial and temporal scales. This requires sampling places increasingly far apart and for longer periods and increasing the grain and extent of sampling (Wiens 1989). As new patterns emerge from such sampling, small-scale heterogeneity will, necessarily, be averaged out. Whether this small-scale heterogeneity is important is a vexing issue – the 'problem of relevant detail' (Levin 1992; Ludwig *et al.* 1993; C. G. Jones and Lawton 1995). At the very least, knowledge of patterns apparent at different scales will promote the development of more complex and useful models of community dynamics.

Examples of analogous issues may be found in the fisheries literature. Fisheries management is increasingly required to accommodate the ecological impacts of fisheries (see Dayton *et al.* 1995, Langton and Auster 1999 for recent discussions). Typically, however, management is based on assessment models that simulate the dynamics of single species and are already challenged by a paucity of data; adding the complexity of ecological relationships will be difficult (e.g. Yodzis 1994). In considering these issues, fisheries biologists must decide which of the many interactions among harvested species and their ecosystems are important and determine appropriate scales at which to 'manage' these processes.

In New South Wales, a fishery for the roe of sea urchins is likely to cause major changes in habitat structure on shallow subtidal reefs. There are large areas of shallow subtidal reef with high but variable densities of sea urchins and no large brown algae, known as the barrens habitat (Fletcher 1987; Andrew and Underwood 1989, 1993; Andrew 1991, 1993, 1994; G. P. Jones and Andrew 1990; Andrew *et al.* 1998). The extent and persistence of patches of barrens have important implications for the ecology of many species of algae, fishes and commercially important invertebrates such as abalone (Shepherd 1973; Holbrook *et al.* 1994; Andrew and Underwood 1992).

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Sea urchins compete with abalone in New South Wales (Andrew and Underwood 1992; Andrew 1994; Andrew *et al.* 1998). The effect of a sea urchin fishery on the abalone fishery will depend, in part, on the areal extent of the barrens habitat. The objective of this study is to provide a large-scale description of habitat structure, and particularly the extent of the barrens habitat, at sites over a wide geographic range. Aerial photographs are used to generate maps of 60 sites along the New South Wales coast. These maps both facilitate testing hypotheses about the effect of spatial structure on community processes at a variety of spatial scales and provide a basis for managing abalone and sea urchin fisheries in New South Wales.

Materials and methods

Twelve localities were selected between Port Stephens and the Victorian border (Fig. 1). They had a wide geographic spread and were separated by an average straight-line distance of 46.5 km (s.d. 49.4). Localities were concentrated in the south of the State where the abalone fishery is largest. Selection thereafter was limited by the presence of rocky reefs (only 33% of the NSW coastline is rocky reef, Fairweather 1990) and availability of adequate aerial photographs. Sea conditions and the

topography of the reefs caused some stretches of coast to be excluded. For example, reefs in front of Jervis Bay were in water too deep to be photographed adequately and, in the far south of the State, poor quality of the photographs excluded stretches of coast between Bermagui and Tathra, and between Mowarry Rock and Green Cape. Five sites, each between 4 and 5 hectares in area, were mapped per locality. Within the limits provided by the availability of adequate photographs, sites were selected haphazardly by applying the following criteria: (1) sites were separated by a minimum of 200 m along the coast or around headlands, (2) sites were no closer than 100 m from a beach, and (3) offshore islands and estuaries were excluded. The average straight-line distance between sites within localities was 2.4 km (s.d. 3.6).

The reef at each site was mapped out to 150 m from the nearest point in the intertidal zone visible at the time the photograph was taken (hereafter defined as nearshore reef). This boundary was chosen because features of the reef could be seen at least 150 m from shore in all images. Contiguous reef extended beyond 150 m from shore in 40% of the 60 sites mapped. As a result of these limitations in sampling, the *Ecklonia* forest and Deep Reef habitats were under-represented at sites where the reef extended beyond 150 m (Underwood *et al.* 1991).

Aerial photographs were taken within 2 h of low tide on days with low swell and calm sea surface conditions at times of the year or day with low sun angle (to avoid reflections off the sea). These constraints limited the number of appropriate days and this was compounded by the long length of coastline; hence, it was impossible to satisfy these conditions for the whole coast on a single day. The photographs were taken between July and August 1996 and between April and October 1997 with a Wild RC10 camera and 214 mm lens. All photographs were taken at a scale of 1:8000, except those in Sydney, which were taken at 1:8500 because of flight restrictions in the vicinity of Sydney International Airport.

Contact prints were digitized at 400 dpi to produce 24-bit colour TIFF files. The contrast in the resultant images was improved by Gaussian enhancement in DIMPLE image-processing software (Process Software Solutions Pty Ltd). Each image was geo-rectified to the Australian Map Grid by use of a minimum of three ground-control points. Mapping was done in ArcView (Environmental Systems Research Institute Inc.) by on-screen digitizing of boundaries of different patches of habitat. All such maps from all sites were 'ground-truthed' (checked against the actual sites) by divers and revised as necessary. In a few instances, patches of reef covered with large brown algae appeared the same in photographs but were, in fact, different habitats. Boundaries with the barrens habitat were always unambiguous. The exact location of boundaries between patches of different habitat, and the depth at which they occurred could not be assessed without differential GPS. This was beyond the logistic capacity of the present study. The mapped location of boundaries was therefore assumed to be correct and the ground-truthing was used to assign habitat categories to the patches.

The maps were ground-truthed as soon as possible after the creation of the preliminary maps but sometimes up to 11 months after the photograph was taken. The high degree of congruence between the preliminary maps and the patterns observed during the ground-truthing suggests that there was little change in habitat structure during the intervening period. One exception to this was at Nadgee where sand inundated much of a site in the six months between the photography and the ground-truthing (see below).

The seven habitat types recognized by Underwood *et al.* (1991) were used in the present study: *Pyura*, Fringe, *Phyllospora* forest, Barrens, *Ecklonia* forest, Turf and Deep Reef. Detailed descriptions of these habitats are provided by Underwood *et al.* (1991; see also Andrew 1999 for photographs of the major habitat types). An additional habitat type, *Durvillaea* forest, was recognized in the present study because the bull kelp *Durvillaea potatorum* formed dense bands in the low intertidal and immediate subtidal zone of many reefs in the far south of the State. The Turf habitat, as defined by Underwood *et al.* (1991), was largely characterized by a high percentage cover of articulated coralline algae (typi-

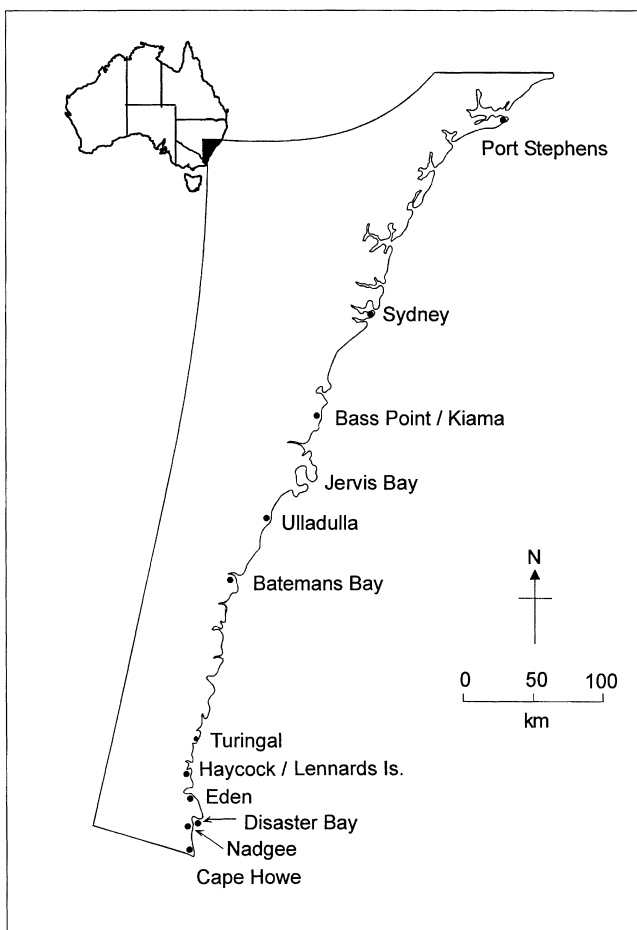


Fig. 1. Locations of mapped sites along the coast of New South Wales.

cally species in the genera *Corallina* and *Amphiroa*), the absence of *Phyllospora comosa*, and low densities of large brown algae such as *Ecklonia radiata*, *Sargassum* spp., and *Cystophora moniliformis*. The Turf habitat was differentiated from habitats dominated by large brown algae by the absence of a canopy.

A subset of the 60 sites mapped as part of this study was further sampled as the basis of a long-term study of the processes underlying the persistence of the Barrens habitat. The abundance and size structure of populations of *C. rodgersii* were quantified in patches of Barrens habitat at three sites at each of nine of the localities (Port Stephens, Sydney, Bass Point–Kiama, Ulladulla, Batemans Bay, Haycock–Lennards Island, Eden, and Disaster Bay). Turingal, Nadgee and Cape Howe were excluded because of the absence or rarity of Barrens habitat at the sites surveyed. The three sites used at each locality were randomly selected from the five sites mapped. At each site, sea urchins were counted in 15 transects, each 10 × 1 m. Fibre-glass tape measures were haphazardly laid out and start positions for the transects randomly chosen along either side of the tape measure. In the same area as the transects, the test diameters (TD) of at least 150 *C. rodgersii* were measured. The sea urchins were found by careful searching but without disturbing the substratum.

Differences in the area of reef and proportional representation of the major habitats among localities were analysed by single-factor analyses of variance on arcsin-transformed data. Differences among localities and sites in the density of *C. rodgersii* were analysed by a two-factor nested analysis of variance with the factor Site nested within Locality. The results of these tests are reported in the text along with pairwise *a posteriori* tests (Ryan's tests with $P < 0.05$) of differences among means following significant *F* ratios.

Results

Within the 150 m boundary used, the reef was significantly smaller at the two southernmost localities (Cape Howe and Nadgee) and Turingal than at any other locality (Fig. 2, $F_{(11,48)} = 12.13$, $P < 0.001$, Ryan's tests). There were no significant differences among all other localities in the area of reef within 150 m from shore (Ryan's tests). The reef gave way to sand within 150 m of shore at 60% or 36 of the 60 sites mapped. The recorded representation of habitats at these sites is, therefore, representative of all habitats found. The reef ended within 150 m from shore in at least one site at all localities except Sydney and Disaster Bay. At those sites where the

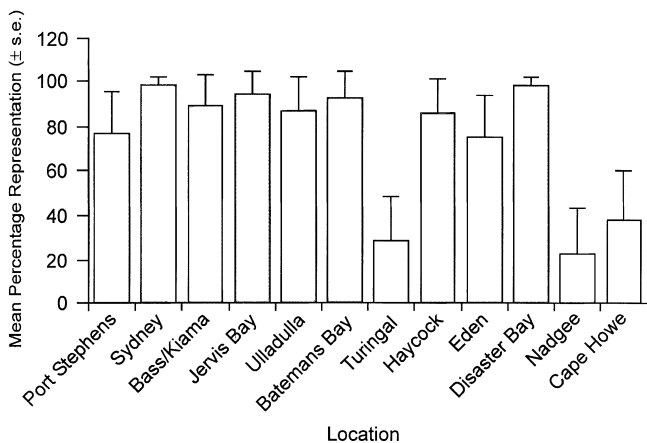


Fig. 2. Mean (± s.e.) percentage representation of nearshore subtidal rocky reef at 12 localities along the NSW coast.

reef extended beyond 150 m from shore, inspection of photographs revealed that the reefs outside 150 m comprised a range of habitats, including extensions of the Barrens habitat. In addition to the Barrens habitat, the Deep Reef, *Ecklonia* forest and Turf habitats are likely to be under-represented at these sites. At several sites at Cape Howe extensive offshore reefs were isolated from those mapped inshore.

At Nadgee Site 5, 0.89 ha of the reef present when the photograph was taken on 9 April 1997 had been inundated with sand before 29 September 1997. Although the total area of reef at this site was small (1.35 ha), the area inundated represented 65% of the reef present ~6 months previously. The reef at this site, as at all sites at Cape Howe and Nadgee, was of low relief and covered with a veneer of sediment. There was no evidence of sand inundation at any other site.

There was a significantly greater representation of Fringe habitat at Cape Howe and Nadgee than at any other locality (Fig. 3a, $F_{(11,48)} = 5.06$, $P < 0.001$, Ryan's tests). At most sites at Cape Howe and Nadgee, the Fringe habitat extended from the intertidal zone to the sand. Where this was not the case, the *Phyllospora* habitat dominated the reef, particularly at sites at Nadgee where the entire reef at two sites was covered

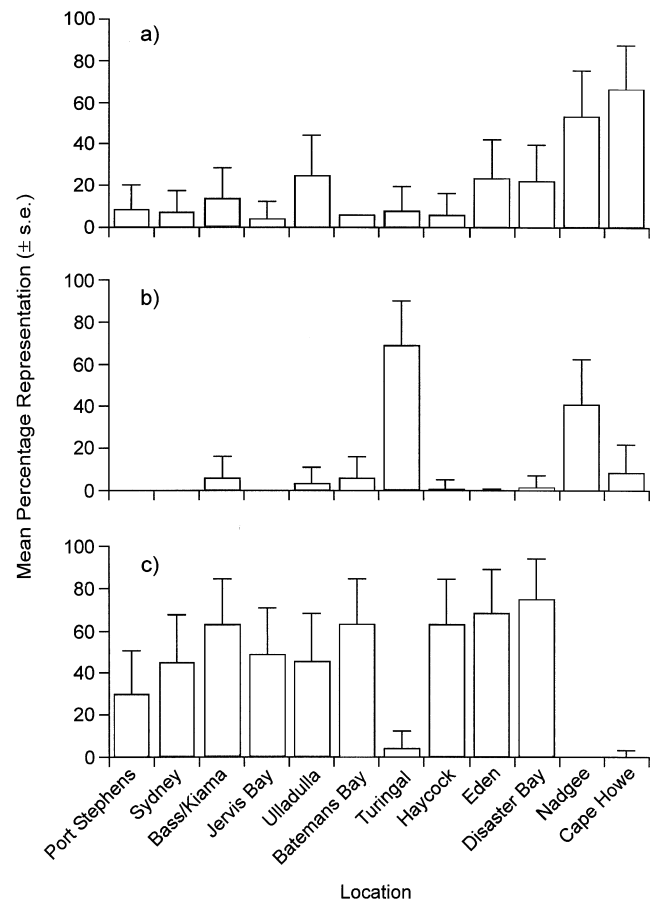


Fig. 3. Mean percentage representation (± s.e.) of habitats on nearshore reefs: (a) Fringe habitat, (b) *Phyllospora* forest, and (c) Barrens habitat at 12 localities along the New South Wales coast.

with a dense *P. comosa* forest (Fig. 3b). The *Ecklonia radiata* found at Nadgee and Cape Howe had an unusual (for New South Wales) growth form, in that the primary laminae and laterals were elongate and smooth (see fig. 120A in Womersley 1987). There was a clear decline in the range of estimated areas of Fringe habitat with decreasing latitude (Fig. 4a). At latitudes greater than 36°S there was a wide range in the representation of Fringe habitat, but between 32 and 33°S it always covered <20% of the nearshore reef.

The *Phyllospora* habitat was most represented at Turingal and Nadgee where it covered a mean of 62% (s.e. = 17) and 40% (s.e. = 21) of the reefs respectively (Fig. 3b). This representation was significantly greater than at any other locality ($F_{(11,48)} = 7.13$, $P < 0.001$, Ryan's tests). There was no significant difference among all other localities in the percentage rep-

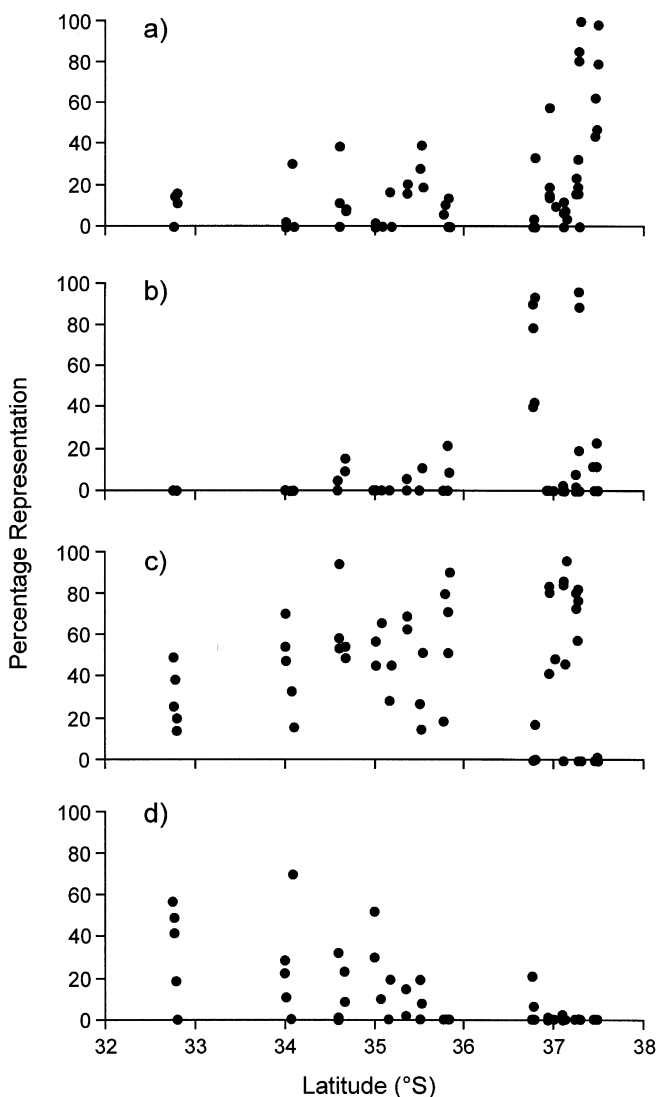


Fig. 4. Scattergrams of percentage representation of: (a) Fringe habitat, (b) *Phyllospora* forest, (c) Barrens habitat and (d) *Ecklonia* forest as a function of latitude at 60 sites along the New South Wales coast.

resentation of the *Phyllospora* habitat (Ryan's tests). This habitat was absent from the two northernmost localities although individual plants were observed at one site in Port Stephens and two sites in Sydney. These latter localities are close to the northern limit of distribution for this species. When all 60 sites were plotted as a function of latitude (Fig. 4b), there was a clear decline in the maximum representation of the *Phyllospora* habitat at localities north of 36°S.

The Barrens habitat covered an estimated 50% (s.e. = 3.9) of nearshore reefs at sites between Port Stephens and Disaster Bay. Coverage was greatest in Disaster Bay where 68% (s.e. = 6.7) of nearshore reef was Barrens Habitat (Fig. 3c). Although there were extensive areas of Deep Reef and Turf Habitat in deeper water further from shore at sites in Disaster Bay (Andrew, personal observation), these were beyond the mapped reef. At the northernmost locality, Port Stephens, Barrens covered only 30% (s.e. = 15) of the nearshore reef and was absent from some sites. South of Disaster Bay, at Nadgee and Cape Howe, only 1% (s.e. = 0.3) of nearshore reefs were Barrens habitat (Fig. 3c). These localities and Turingal had significantly less Barrens habitat than any other locality ($F_{(11,48)} = 7.79$, $P < 0.001$, Ryan's tests).

With the exception of Turingal, Nadgee and Cape Howe, where the nearshore reefs were small, there was a trend toward increasing mean representation of Barrens habitat with increasing latitude (Fig. 3c). However, when all 60 sites were plotted against latitude, there was no significant correlation between latitude and representation of the Barrens habitat ($r_{(58)} = -0.18$, ns, Fig. 4c). There was a significant positive correlation between the proportional representation of Barrens habitat and the area of nearshore reef ($r_{(58)} = 0.68$, $P < 0.05$).

The mean representation of *Ecklonia* forest at localities declined with increasing latitude (Fig. 5a). At sites between 32 and 34°S, a wide range of coverage of *Ecklonia* forest was recorded; however, in the far south of the State, large areas of canopy-forming forest were not recorded (Fig. 4d). There was significantly greater representation of the *Ecklonia* forest habitat at Port Stephens than at any other locality ($F_{(11,48)} = 5.06$, $P < 0.001$, Ryan's tests). *Ecklonia* forests were absent from all mapped sites at Nadgee and Cape Howe and from four of the five sites at each of Batemans Bay, Disaster Bay and Haycock–Lennards I. Although *E. radiata* plants were present at all localities and sites, densities were usually not sufficient to form a canopy (Andrew, personal observation). Although the representation of *Ecklonia* forest may be found in more sheltered waters in the south of the State (e.g. in Twofold Bay, Eden; Andrew, personal observation). Because all the mapped sites were exposed to the open coast, care is needed in generalizing the biogeographic patterns described in this study.

There were no significant differences among localities in the representation of the Turf habitat (Fig. 5b, $F_{(11,48)} = 1.27$, ns). Although the Turf habitat was extensive at some sites,

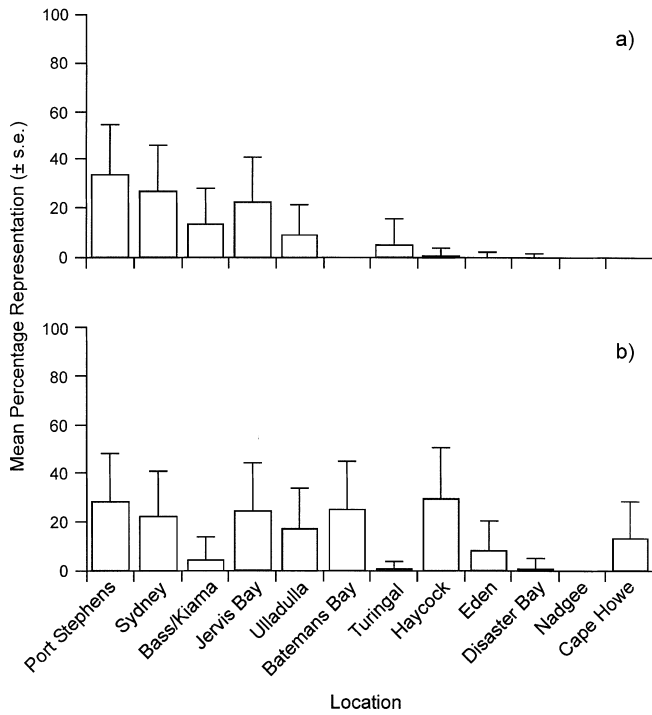


Fig. 5. Mean percentage representation (\pm s.e.) of habitats on nearshore reefs: (a) *Ecklonia* forest and (b) Turf habitat at 12 localities along the New South Wales coast.

there was considerable variability among sites within localities. Large brown algae such as *Cystophora moniliformis*, *Ecklonia radiata* and *Sargassum* spp. were common in patches of Turf habitat. By definition, *Phyllospora comosa* and *Pyura* spp. were absent.

In addition to those described above, two additional habitats were recorded but generally formed a minor proportion of the coverage of nearshore reefs. The *Pyura* habitat was recorded at 3 of the 60 sites (at Bass Point, Jervis Bay, and Turingal). This habitat was most represented at Turingal where it accounted for 57% of the small area of reef present at one site. At Bass Jetty (Bass Point) and Mary Cove (Jervis Bay) it accounted for <5% of the reef area. The *Pyura* habitat dominates many reefs between Nadgee and Disaster Bay, at sites not mapped during the present study (Andrew personal observation).

The bull kelp *Durvillaea potatorum* was present at most sites south of Turingal and was found either at high densities in a narrow band in the immediate subtidal zone or as scattered plants on the tops of ridges and places with greatest wave exposure. The *Durvillaea* forest habitat was recognized at sites in Turingal, Disaster Bay, Nadgee and Cape Howe. At all sites this habitat accounted for <2% of the total nearshore reef area.

The abundance and size–frequency structure of *C. rodgersii* was estimated at nine of the mapped localities (a total of 27 sites). At these localities, sea urchins were most abundant at Bass Point–Kiama where, at several sites, densities exceeded 75 per 10 m² (Fig. 6). There were significant differences in

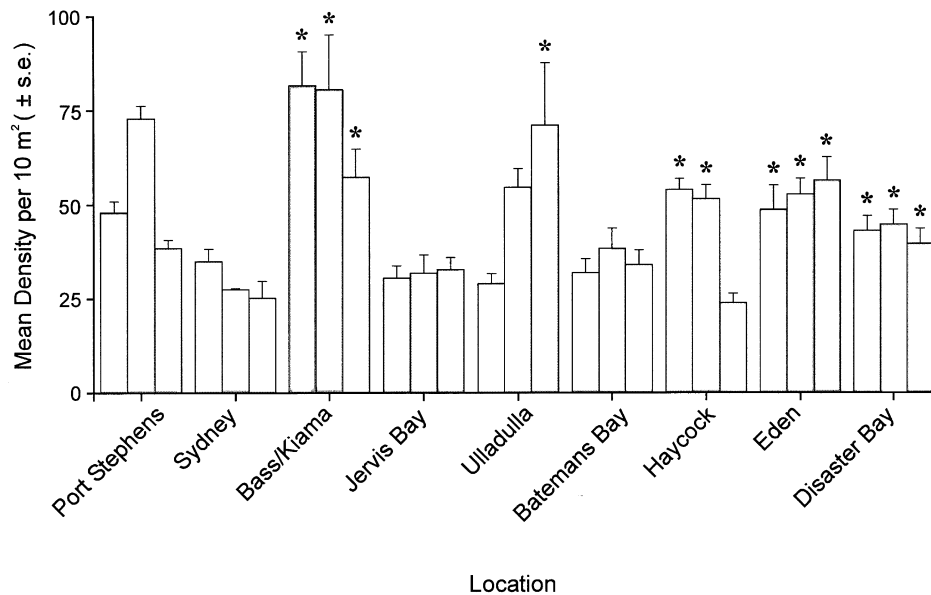


Fig. 6. Mean density (\pm s.e.) of *Centrostephanus* per 10 m² at 27 sites at 12 localities in New South Wales. Asterisks indicate those sites at which urchins were observed outside shelters during the day.

the density of *C. rodgersii* among localities ($F_{(8, 18)} = 3.91$, $P < 0.01$) and sites within localities ($F_{(18, 378)} = 3.91$, $P < 0.001$). There was no north–south trend in mean density among localities (Fig. 6), nor was there a significant correlation between latitude and the mean density of *C. rodgersii* at sites ($r_{(25)} = 0.11$, ns).

Sea urchins were observed outside shelters, such as gutters or the spaces under boulders, at sites at Bass Point–Kiama, Ulladulla, Haycock–Lennards I., Eden and Disaster Bay (Fig. 6). These sea urchins were commonly but not always aggregated in tight groups. Exposed sea urchins were observed only at sites with densities > 30 per 10 m^2 , but not all sites with such densities had exposed urchins (Fig. 6).

There was considerable variability among sites in the size–frequency structure of populations of *C. rodgersii* (Fig. 7). At 24 of the 27 sites sampled, sea urchins between 65 and 85 mm TD dominated the populations. At Anna Bay Site 1 (Port

Stephens) the population was dominated by large individuals, with a modal size class of 90 mm TD, whereas the population at an adjacent site (Site 2) comprised much smaller urchins, with a modal size of 65 mm TD (Fig. 7). In Sydney and Eden, there was little difference among sites in population size–structure but there was a wide range of sizes of urchins present at all sites (Fig. 7). For the 24 sites with unimodal size–frequency distributions, there was a significant negative correlation between the mean density of sea urchins at a site and the modal size of individuals ($r_{(22)} = 0.53$, $P < 0.05$). The smallest sea urchins observed were between 40 and 45 mm TD. Urchins < 50 mm TD were found at all three sites in Sydney, but rarely at other sites.

Discussion

With several noteworthy exceptions, the results of this study broadly support the habitat descriptions and estimates of rep-

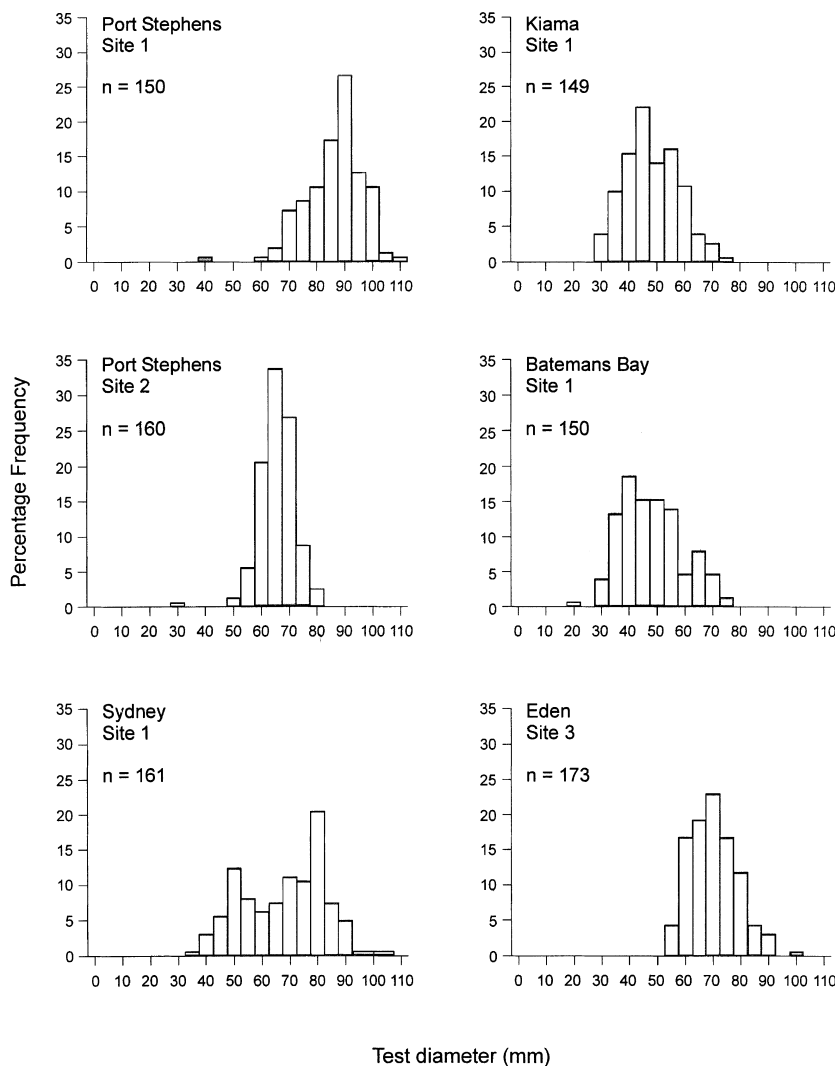


Fig. 7. Size–frequency distributions of *Centrostephanus* at six sites in New South Wales. Sample sizes as indicated on each graph.

resentation reported by Underwood *et al.* (1991). The addition of the *Durvillaea* habitat reflects the extended range of study to more southern reefs. The *Pyura* habitat was recorded in Underwood *et al.* (1991) only at the two most northern sites, at Southwest Rocks and Charlotte Head. In the present study, this habitat, although relatively rare, was also found in the far south of the State but in both studies was strongly associated with sites where the reef extended only a short distance into the subtidal zone before disappearing into sand.

The differing methods used to quantify habitat representation in Underwood *et al.* (1991) and the present study allow insights into the patchy nature of habitats on New South Wales nearshore reefs. There are clear limitations to both methods, which differ in grain, extent and intensity of sampling (Wiens 1989, 1990 and references therein). The sampling grain (the lower limit of resolution in the sampling) using the digitized aerial photographs was an individual pixel, which represented approximately 0.5 m² of reef. In practice, the smallest 'patch' distinguished in creating the maps was larger, because of uncertainties in interpreting the images and in locating patches on the map during ground-truthing. These operational facts meant that small-scale heterogeneity (<2 m²) was averaged out. The effect of this on estimates of area obtained varied among localities and habitats. The boundaries between the barrens habitat and those dominated by patches of foliose algae were always clear (see also Andrew 1993, 1994) and the interpretations of the images unambiguous. The mosaic of fringe, *Phyllospora* and turf habitats in the immediate subtidal zone made detecting patches of these habitats more difficult and the loss of heterogeneity at scales smaller than approximately 2 m² was inevitable.

Although the estimates of habitat representation derived from transects used in Underwood *et al.* (1991) were at a finer grain, the sampling was both less extensive (covered a smaller overall area – 80 m of coastline per site) and less intense (the actual area quantified was small – the points under four tape measures <100 m long). Given the complex way different habitats were arranged in space, sampling four transects normal to the shore may not have been sufficiently intense to reliably quantify habitat representation. Large differences were observed in the proportional representation of some habitats both among transects within surveys and between surveys separated by 4–5 months. It is improbable that such large changes would occur over this time period, because the large brown algae and sea urchins that define these habitats recruit and grow to a size that would cause habitat change over much longer periods. The observed differences are more likely to reflect artifacts associated with sampling transects in such reticulated reefs.

The representation of the barrens habitat at Merimbula reported in the present study and in Underwood *et al.* (1991) similarly differed, suggesting either a dramatic change in one habitat type only or inconsistency in the definition of this habitat. Because sea urchins and crustose coralline algae may

be abundant in the deep reef habitat (Underwood *et al.* 1991), the latter cause is more probable.

The predominance of the barrens habitat on reefs throughout the range of the NSW abalone fishery and the known negative association between this habitat and the abundance of abalone (Shepherd 1973; Andrew and Underwood 1992; Andrew *et al.* 1998) suggests that sea urchins may limit the productivity of the abalone fishery. The development of a fishery for sea urchin roe in New South Wales (Andrew *et al.* 1998) offers the potential to enhance the abalone fishery by reducing the abundance of sea urchins on reefs.

It is probable that the development of a large-scale fishery for sea urchins will have a profound impact on the habitat structure of subtidal reefs in New South Wales. Although such a fishery is likely to concentrate on sea urchins from the fringe habitat in the first instance, expansion into other habitats may follow. This expansion is likely to come about through more sophisticated management and possibly the enhancement of roe quality as the densities of sea urchins decline. Small-scale experiments (Andrew and Underwood 1993) indicate that there is likely to be a non-linear relationship between the abundance of *C. rodgersii* and the area of barrens on a reef. As densities decline after fishing we hypothesize that patches of barrens habitat will fragment and that densities within these patches will decline at a slower rate than the overall abundance of sea urchins at a site. The indirect effects of such reductions in density and consequent changes to the size and arrangement of habitat patches are difficult to predict. Reductions in sea urchin density over large areas of reef may cause significant changes in the relative abundance of invertebrates and fish that respond to the landscape provided by sea urchin herbivory.

The differences in size structure and abundance of sea urchins observed in the patches of barrens described in this study provide a basis for testing hypotheses (such as those above) about the link between the demography of *C. rodgersii* and habitat structure. The implications of differences in the demography of sea urchins to the long-term persistence of the barrens habitat are unclear. In particular, the absence of small sea urchins (<40 mm TD and 2 years old, Andrew 1991) at all but a few sites suggests either sporadic recruitment to populations of long-lived urchins or the potential for a greater degree of unpredictability in the extent and persistence of different habitat types than was previously thought (e.g. Andrew and Underwood 1989; Andrew 1993).

In contrast to studies around Sydney (e.g. Fletcher 1987; Andrew and Underwood 1989; Andrew 1993), *C. rodgersii* was observed in the open during daylight at some localities, particularly south of Merimbula and at sites at Bass Point–Kiama. Although data were not collected on the proportion of sea urchins in the open at each site, it appeared that they were greatest in areas with highest densities and/or relatively little shelter (Andrew personal observation). There was no evidence, at least from their daytime patterns of distribution and

dispersion, that these aggregations were mobile and that the urchins were foraging outside the barrens habitat. The underlying causes of these differences in shelter usage remain unclear; there are insufficient data on the relative abundance of predators such as fish, lobsters and octopus along the New South Wales coast. The long-term consequences of these differences in abundance and dispersion of sea urchins to the persistence of patches of barrens remain unknown.

This study is restricted to a description of pattern on and at a broad scale and a consideration of the management implications of harvesting sea urchins. The related issue of the generality of causal processes (Foster 1990) underlying patterns evident at different scales should be approached in future studies. In considering this problem, the heterogeneity evident in so many ecological systems is likely to confound development of simple scaling rules (e.g. Schneider *et al.* 1997). Heterogeneity may arise from different processes operating within patches of habitat. Aggregating these patterns and processes is therefore likely to be difficult. A possible way forward is to develop models that integrate habitat information with data on the demography of key species (Paine and Levin 1981; Sousa 1984; Levin 1992; Dunning *et al.* 1995; C. G. Jones and Lawton 1995; Burrows and Hawkins 1998). This approach has been instructive in applied disciplines such as conservation biology (e.g. Hanski and Thomas 1994; Possingham and Davies 1995).

Acknowledgments

Grateful thanks to Mark Malady for completing the long task of image processing, and John Marthick and the School of Geosciences Spatial Analysis Laboratory for support. Thanks to BHP Land Technologies, particularly Mal Henschel and Bruce Adie, for completing an unusual and difficult photographic contract so well. Laurie Derwent, Peter Gibson, Kate Hodgson, Brett Loudon, Will Macbeth, David Ward and Duncan Worthington assisted in the field. Thanks also to Rowan Chick and Craig Blount for help in the field and in preparing the manuscript, and Penny Brett for assisting in all other phases of the study. Comments by Paul Breen improved the manuscript. This study was partially funded by the Fisheries Research and Development Corporation (Project 93/108) and the NSW commercial abalone industry.

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Manuscript received 1 February 1999; revised and accepted 22 November 1999