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Validation of qualitative habitat descriptors commonly used to classify subtidal reef assemblages in north-eastern New Zealand

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Abstract On shallow temperate subtidal reefs, habitat types are usually defined subjectively by the dominance or presence of major macroalgal species. Many of these habitat types (e.g., urchin barrens, kelp forest) are frequently used in the literature but little attempt has been made to quantitatively define these habitats. A survey of shallow subtidal reefs in north-eastern New Zealand identified a number of commonly occurring "habitat types". In this paper the abundances of habitat-forming species within each of these habitats are quantified and the validity of the subjective classification system is tested. In addition to previously-described reef habitats from north-eastern New Zealand a number of other habitat types were encountered and described in this study (e.g., "mixed algae", "red foliose algae", and "*Caulerpa* mats"). The algal communities within each habitat were biologically distinct and there was strong concordance between the grouping of samples from cluster analysis and the subjective habitat type assigned to each. The habitat classification system was reliable and canonical analysis of principal coordinates revealed an overall classification success of 81%. This provides strong evidence that the habitat classifications used in this study are biologically meaningful based on the abundances of habitat-forming algal groups. Furthermore, this demonstrates that these habitat types can be reliably categorised visually, which has important applications in classification and mapping of the marine environment.

Keywords habitat classification; kelp forest; macroalgal assemblages; temperate reefs; urchin barrens

INTRODUCTION

Identifying and describing the distribution of habitat types at broad spatial scales is an important step in understanding the underlying processes responsible for patterns (Andrew & Mapstone 1987; Underwood et al. 2000). Subtidal temperate reefs are no exception to this generalisation and although they are frequently characterised by high heterogeneity in community structure (Schiel & Foster 1986; Steneck et al. 2002), a number of commonly occurring habitat types are frequently referred to. Macroalgae are generally the dominant structural components on shallow temperate reefs and therefore the defining feature of habitat types is typically the species composition of macroalgae. For example, "kelp forest" typically comprises large stands of laminarian kelps, whereas "urchin barrens" lack large brown algae resulting from the grazing activity of sea urchins. These two broad habitat types are regularly encountered in the ecological literature (Lawrence 1975).

The classification and mapping of large-scale habitats is a fundamental tool in managing a range

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of marine ecosystems (e.g., Mumby & Harborne 1999; Andrew & O'Neill 2000). Large-scale mapping of habitats provides baselines necessary to detect change in their spatial extent (e.g., Babcock et al. 1999; Parsons et al. 2004), is fundamental to extrapolating productivity estimates (e.g., Taylor 1998; Babcock et al. 1999), and is also essential for calculating habitat-stratified estimates of total abundance (e.g., McCormick & Choat 1987). Accurate and reliable classification of meaningful habitat types based on clear criteria is therefore a prerequisite for such applications. The advantage of standardised qualitative classification systems over purely quantitative descriptions for describing community structure is that they can be applied rapidly over large areas, and that ecological processes can be scaled by the area of habitat (e.g., Taylor 1998).

In north-eastern New Zealand, subtidal reef communities have been described and studied over the last 40 years (Berguist 1960; Ayling 1981; Choat & Schiel 1982). Ayling described a number of habitat types for subtidal reefs in the Cape Rodney to Okakari Point (CROP) marine reserve at Leigh, and these habitat classifications have been widely used in subsequent studies (e.g., Taylor 1998; Babcock et al. 1999). Although these habitat types are generally based on the dominant species characterising the communities, the biological distinctness of these habitats has never been quantitatively tested. Furthermore, despite many qualitative descriptions there have been few attempts to provide quantitative descriptions of rocky subtidal habitat types in north-eastern New Zealand.

This study is part of a large project aimed at describing patterns in shallow subtidal reef communities at a number of locations throughout north-eastern New Zealand (Shears 2002). At each location the benthos was quantitatively sampled, and each sample was subjectively assigned to a habitat type *in situ*. The habitat types used were broadly based on previous descriptions of habitats in the CROP (Leigh) marine reserve (Ayling 1978) to ensure continuity with previous studies, and enable the assessment of long-term habitat changes. The validity of these habitat types was tested by analysing the concordance between the abundance of dominant algal species or groups and the habitat type assigned to each sample. Here we present the results of those analyses and propose a standardised set of habitat descriptors that could be used to reliably classify shallow subtidal reef habitats in north-eastern New Zealand.

METHODS

Analyses were carried out on line transect data collected between April 1999 and March 2000 at Cape Reinga (172º41′E, 34º25′S; *n* = 2), Cape Karikari (173º25′E, 34º50′S; *n* = 8), Long Bay (174º45′E, 36º40′S; *n* = 10), and Tuhua Island (176º16′E, 37º16′S; *n* = 8) (see Shears 2002 for site locations). These four locations were chosen for this analysis because they spanned the full geographic range sampled, and include sheltered, exposed, and offshore island locations. Furthermore, many of the habitat types in question have previously been described from the moderately exposed coastline around Leigh, so these locations were chosen to determine the applicability of the habitat types to different wave exposure regimes and other parts of north-eastern New Zealand. At each site within these locations, a single line transect was run perpendicular to the shore from mean low water spring tide level to a maximum depth of 12 m or the edge of the reef, whichever came first. Quadrats (1 m^2) were placed at 5–m intervals along the transect, the habitat in which each quadrat was placed was recorded (Table 1), and the abundance of habitat-forming species was recorded. This included counts of adult large brown algae (>30 cm total length (TL)) and visual estimates of the percent covers of foliose, turfing, and encrusting algae, sediment, and encrusting invertebrates. The number of sea urchins, *Evechinus chloroticus*, found openly grazing the substratum (i.e., exposed, not occupying crevices) was also recorded.

Habitat types were categorised according to the list in Table 1. It is important to note, however, that the abundance or percentage cover (m^{-2}) values given in the definitions (Table 1) are indicative only. It is not practical to have specific densities of species that separate habitats because of variation in size, biomass, and morphologies both within and among seaweed species. Instead, habitats were categorised in a subjective manner based on the visual dominance of particular species.

As a result of sampling quadrats along line transects, an uneven number of quadrats was sampled for each habitat at each site. Sample sizes were balanced by randomly selecting 30 quadrats from each habitat type. Both "*Caulerpa* mats" and "red foliose algae" habitats were rarely recorded, so only 10 quadrats of each of these habitats were available for analysis. "Cobbles", "encrusting invertebrates", and "sponge flats" habitats were not included in the analysis as very few quadrats were assigned to these classes. The following algal species

Table 1 Description of habitat types used in this study. Figures in the descriptions are indicative only, mean abundances of dominant species are presented in Table 2. Habitats were determined by subjective assessment of dominant species.

Habitat	Typical depth range (m)	Description
Shallow *Carpophyllum*[†]	<3	Dominated by high abundances (≥20 adult plants m^{-2}) of *Carpophyllum maschalocarpum*, *C. plumosum*, and *C. angustifolium*. *Ecklonia radiata* and the red algae *Pterocladia lucida*, *Osmundaria colensoi*, and *Melanthalia abscissa* also common. Sea urchin *Evechinus chloroticus* occurs at low numbers and generally occupies crevices.
Ecklonia forest[*]	>5	Generally monospecific stands of mature *Ecklonia* form a complete canopy (≥4 adult plants m^{-2}), occasional *C. flexuosum* plants. Urchins at low numbers (<1 exposed urchins m^{-2}) and usually occupy crevices.
Carpophyllum flexuosum forest	3–12	*C. flexuosum* plants dominate (≥4 adult plants m^{-2}), on sheltered reefs plants are large and associated with high levels of sediment. On more exposed reefs plants are short and generally associated with *Evechinus*.
Mixed algae[†]	2–10	Mixture of large brown algal species. No clear dominance of one particular species, usually only partial canopy (≥4 adult plants m^{-2}) and urchins may also occur at low numbers (<2 exposed urchins m^{-2}).
Red foliose algae	2–9	Substratum predominantly covered (>40%) by red foliose algae such as *P. lucida* or *O. colensoi*. Low numbers of large brown algae (<4 adult plants m^{-2}).
Turfing algae[*‡]	3–12	Substratum predominantly covered by turfing algae (e.g., articulated corallines and other red turfing algae) (>30% cover). Low numbers of large brown algae (<4 adult plants m^{-2}) and urchins may be common.
Caulerpa mats	3–12	Green algae, usually *Caulerpa flexilis*, form dense mats over the substratum (>40%). Urchins and large brown algae rare.
Urchin barrens[*§]	3–9	Very low numbers of large brown algae present (<4 adult plants m^{-2}), substratum typically dominated by crustose coralline algae. Usually associated with grazing activity of *Evechinus* (>2 exposed urchins m^{-2}), which leaves the substratum relatively devoid of macroalgae. *C. flexuosum* and *Sargassum sinclairii* may occur.
Cobbles		Reef comprises cobbles (c. <0.5 m diam.), unstable and subject to high levels of agitation from wave exposure. Crustose coralline algae are dominant along with a high cover of bare rock and sand. Large brown algae are generally absent.
Encrusting invertebrates		Usually vertical walls, substratum predominantly covered by community of encrusting ascidians, sponges, hydroids, and bryozoans. Large brown algae rare.
Sponge flats	>10	Sponges visually dominant, high cover of sediment. Usually occurs on the reef-sand interface. Low numbers of *Ecklonia* may be present (<4 adult plants m^{-2}).

[*] Habitat types described by Ayling (1978).

[†] Shallow *Carpophyllum* and mixed algae are both components of the "Shallow broken rock" habitat described in Ayling (1978).

[‡] Turfing algae are analogous to "sediment flats" in Ayling (1978).

[§] Urchin barrens are analogous to "rock flats" in Ayling (1978).

or groups were used for analyses as these were considered to be the major habitat-formers: counts of adult *Ecklonia radiata*, *Carpophyllum flexuosum*, other *Carpophyllum* spp. (*C. angustifolium*, *C. maschalocarpum*, and *C. plumosum*), other large brown algae, and the percentage cover of red turfing algae (including articulated coralline algae), red foliose algae, and the green alga *Caulerpa flexilis*. For *Carpophyllum* species, counts of all blades greater than 30 cm TL were made, as it is often difficult to discern between individual plants (cf. Choat & Schiel 1982).

To investigate the concordance between algal communities and the subjective habitat type assigned to each quadrat, hierarchical cluster analysis was carried out using the statistical package PRIMER (Clarke & Warwick 1994). The analysis was based on a Bray-Curtis dissimilarity matrix calculated using untransformed quadrat data. The relative weights of different species or groups in the similarity matrix differed because some species were recorded as abundances and some as percentage covers. Although the Bray-Curtis dissimilarity technique is designed for counts there is nothing to prevent its use with "mixed" data provided scales are comparable (e.g., Anderson & Underwood 1994). In this instance the scales associated with the counts and percentage covers were similar with few counts greater than 100. Analysis of similarity (ANOSIM; Clarke 1993) was carried out to test for differences in algal communities between the habitat types.

Canonical analysis of principal coordinates (CAP) (Anderson & Willis 2003) was also used to test the validity of the assigned habitat types as well as the classification success. In addition to a traditional unconstrained ordination (principal coordinates analysis), this technique performs a constrained ordination with reference to a specific *a priori* hypothesis, in this instance, no difference among habitat types. CAP chooses the axes that best separate the designated groups (habitat types) in multivariate space and carries out a permutation test for differences among groups. In addition, CAP provides misclassification errors by carrying out a leave-one-out allocation of observations to groups (habitat types), thus indicating the success of the classification system. This analysis was also based on a Bray-Curtis similarity matrix calculated from untransformed quadrat data. The original species variables were also correlated with principal coordinate axes 1 and 2, and CAP axes 1 and 2, to identify which species were responsible for the multivariate pattern produced by the respective ordinations.

RESULTS

Habitat types recorded

The present study covered a large range of locations throughout north-eastern New Zealand and a number of previously unreported habitat types were identified (Table 1). In general, the most common habitat types have previously been described, e.g., "*Ecklonia* forest", "shallow *Carpophyllum*" (also termed "shallow broken rock", "shallow mixed weed zone", or "*Carpophyllum* forest"), "*C. flexuosum* forest", "turfing algae", and "urchin barrens". An additional "mixed algae" habitat was defined. This incorporated samples that did not clearly fall into one of the other habitat types, e.g., where both *Ecklonia* and *Carpophyllum* species were abundant. Other less common habitats identified included a red foliose algae habitat and mats of the green alga *Caulerpa flexilis*, termed *Caulerpa* mats. Both of these habitats occurred at Tuhua, Cape Karikari, and Cape Reinga. Cobbles, encrusting invertebrates, and sponge flats were also occasionally recorded. The latter is analogous to Ayling's (1978) "sponge garden". The encrusting invertebrates habitat was generally only recorded on vertical walls at offshore islands.

Quantitative description of habitat types

The averages and ranges of density or percentage cover of the dominant species within each habitat are given in Table 2. The abundance of dominant algal species within each habitat closely reflected the habitat descriptions and classification criteria (Table 1). For example, *Ecklonia* forest was dominated by adult *Ecklonia* with very low numbers of other large brown algae and a high cover of encrusting algae (predominantly crustose coralline algae), whereas the shallow *Carpophyllum* habitat was characterised by very high densities of *Carpophyllum* species (excluding *C. flexuosum*) and low numbers of other large browns. Conversely, the mixed algae habitat had, on average, moderate densities of all large brown algae and a high cover of coralline turf. The main difference between urchin barrens and turfing algae, which were both relatively devoid of large brown algae, was the cover of coralline turf, encrusting algae, and the abundance of exposed *Evechinus*. Exposed *Evechinus* were generally rare in all other habitats.

Large brown algae also occurred in low numbers in the red foliose algae and *Caulerpa* mats habitats. The red foliose algae habitat was characterised by a high cover of both red foliose algae and turfing algae, whereas the dominance of *Caulerpa flexilis* distinguished the *Caulerpa* mats habitat. Both algae and invertebrates were rare in the cobbles habitat, presumably as a result of the mobile nature of the substratum. Crustose coralline algae and sediment dominated this habitat. Sediment as well as sponges characterised the sponge flats habitat. Among the habitats dominated by large brown algae, sediment cover was highest in the *Carpophyllum flexuosum* forest.

Habitat classification success

Quadrats assigned to different habitat types generally clustered into separate groups (Fig. 1). The mixed algae habitat however did not form its own large cluster, instead it was predominantly classified with the shallow *Carpophyllum* and *C. flexuosum* forest habitats. Similarly a number of quadrats assigned as urchin barrens were also grouped with turfing algae and *C. flexuosum* forest. Despite this overlap, algal communities were significantly different among habitats (ANOSIM, Global *R*: 0.753, significance level: 0.1%, 999 permutations). Furthermore, pairwise tests revealed highly significant differences between all habitat types (*R*: >0.3, significance level: <0.2%, 999 permutations).

CAP analysis also found a highly significant difference in algal assemblages among habitat types (P = 0.001 for both test statistics using 999 permutations). Although differences among habitat types were apparent on the principal coordinates (unconstrained) plot (Fig. 2A), there was much clearer separation of habitats on the constrained ordination (Fig. 2B). The grouping of habitats in both ordinations was strongly reflected in the correlations between species variables with either the principal coordinates or CAP axes. For the constrained ordination (Fig. 2B), CAP axis 1 was positively correlated with *Ecklonia* and negatively correlated with *Carpophyllum* spp., representing the division between shallow *Carpophyllum* habitat and deeper *Ecklonia* forest with mixed algae in the middle. In contrast, CAP axis 2 was positively correlated with large brown algal species (*Ecklonia* and *Carpophyllum* spp.) and negatively correlated with coralline turf and *Caulerpa*, reflecting the gradient from large brown algal dominated habitats to urchin barrens and to turfing algae and *Caulerpa* mats.

CAP analysis revealed a high classification success (82%) across all habitat types (i.e., only 18% misclassification error). The six principal coordinate axes used for the CAP analysis explained 81% of the variability in the original dissimilarity matrix and achieved the maximum number of correct allocations. The success of classifications for the constrained analysis was lowest (60%) for both the mixed algae and red foliose algae habitats (Table 2). The low success for red foliose algae is probably a result of the low sample size ($n = 10$). In all instances these were misclassified by the leave-one-out allocation procedure as turfing algal habitat. For mixed algae the low classification success is not surprising given the "mixed" nature of the habitat, these were most commonly misclassified as shallow *Carpophyllum* (10%), *C. flexuosum* forest (13%), and urchin barrens (10%).

DISCUSSION

The habitat classification system presented in this study describes biologically meaningful and distinct habitat types that can be reliably categorised visually for subtidal reef communities in north-eastern New Zealand. Subjective categorisation of habitats relies on a rapid visual assessment of which species are dominant, or share dominance (cf. mixed algae), therefore the high multivariate classification success of habitats (82%) demonstrates that the habitat classes described here are appropriate for classifying shallow subtidal reef communities in north-eastern New Zealand. The classification success calculated is based on counts or percentage covers of dominant species, and does not take into account differences in size or morphology. It may, therefore, underestimate an observer's ability to categorise habitats. For example, the grouping of some urchin barrens quadrats in the *C. flexuosum* forest group is probably because of the occurrence of small, exposed growth forms of *C. flexuosum* in the urchin barrens habitat at some sites (Cole et al. 2001). This also explains the separation of urchin barrens into two groups, one being urchin barrens with *C. flexuosum* present, the other being those without it (Fig. 1, 2A). Similarly, the distinction between turfing algae and urchin barrens is largely dependent on a subjective assessment of the dominance of coralline turf, which may explain why some urchin barrens quadrats are grouped with turfing algae. Ultimately, no classification system can be expected to be 100% consistent as all habitat types intergrade from one to another. Such a continuum must result in at least some intermediate conditions that will complicate a multiple state classification.

The habitat types described are broadly consistent with those originally described in the CROP marine reserve (Ayling 1978). However, in some instances Ayling's classifications have been refined and names changed to allow generalisation to the larger geographic area examined in this study. For example, Ayling's urchin-grazed "rock flats" habitat is referred to as the more widely used term "urchin barrens", as this habitat occurs over a variety of rocky substratum types from relatively flat bedrock to large boulders. For similar reasons, Ayling's "shallow broken rock" habitat was changed to "shallow *Carpophyllum*". This habitat includes high

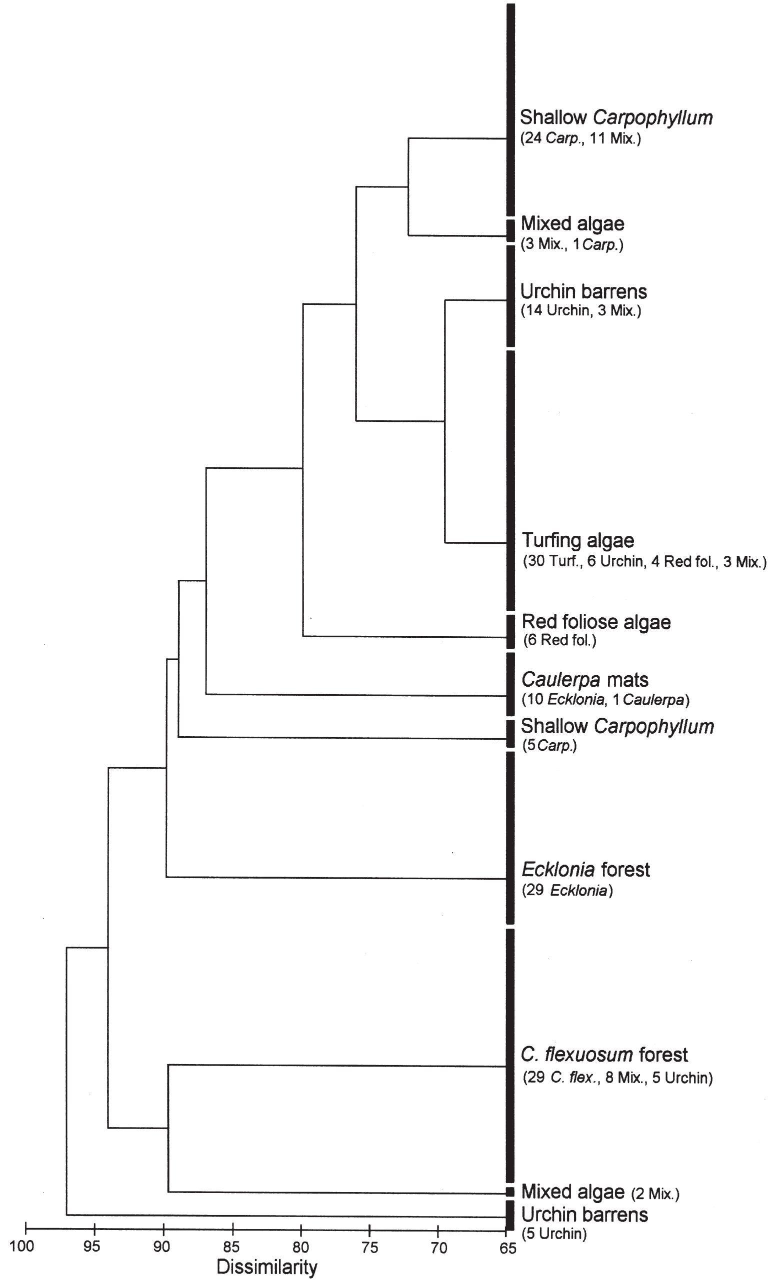

Fig. 1 Dendrogram from hierarchical cluster analysis of untransformed quadrat data. Relationship of this grouping to subjectively determined habitat types is given by labels at right. Clusters are named according to the dominant habitat within each. Values in parentheses indicate the number of quadrats of each habitat type assigned in the field within each cluster (*Carp.*, shallow *Carpophyllum*; mix., mixed algae; urchin, urchin barrens; turf., turfing algae; red fol., red foliose algae; *Caulerpa*, *Caulerpa* mats; *Ecklonia*, *Ecklonia* forest; *C. flex.*, *C. flexuosum* forest).

densities of fucalean algae and is analogous to the "fringe habitat" of New South Wales (Underwood et al. 1991). Ayling's shallow broken rock habitat was, however, further refined with the addition of a "mixed algae" habitat. This habitat generally occurred at intermediate depths between the shallow *Carpophyllum* and *Ecklonia* forest where *Evechinus* occurred in low numbers (Shears 2002). Choat & Schiel (1982) also described a similar zone for reefs in north-eastern New Zealand. The mixed algae habitat may now be more conspicuous in the CROP marine reserve than it was in the 1970s as a result

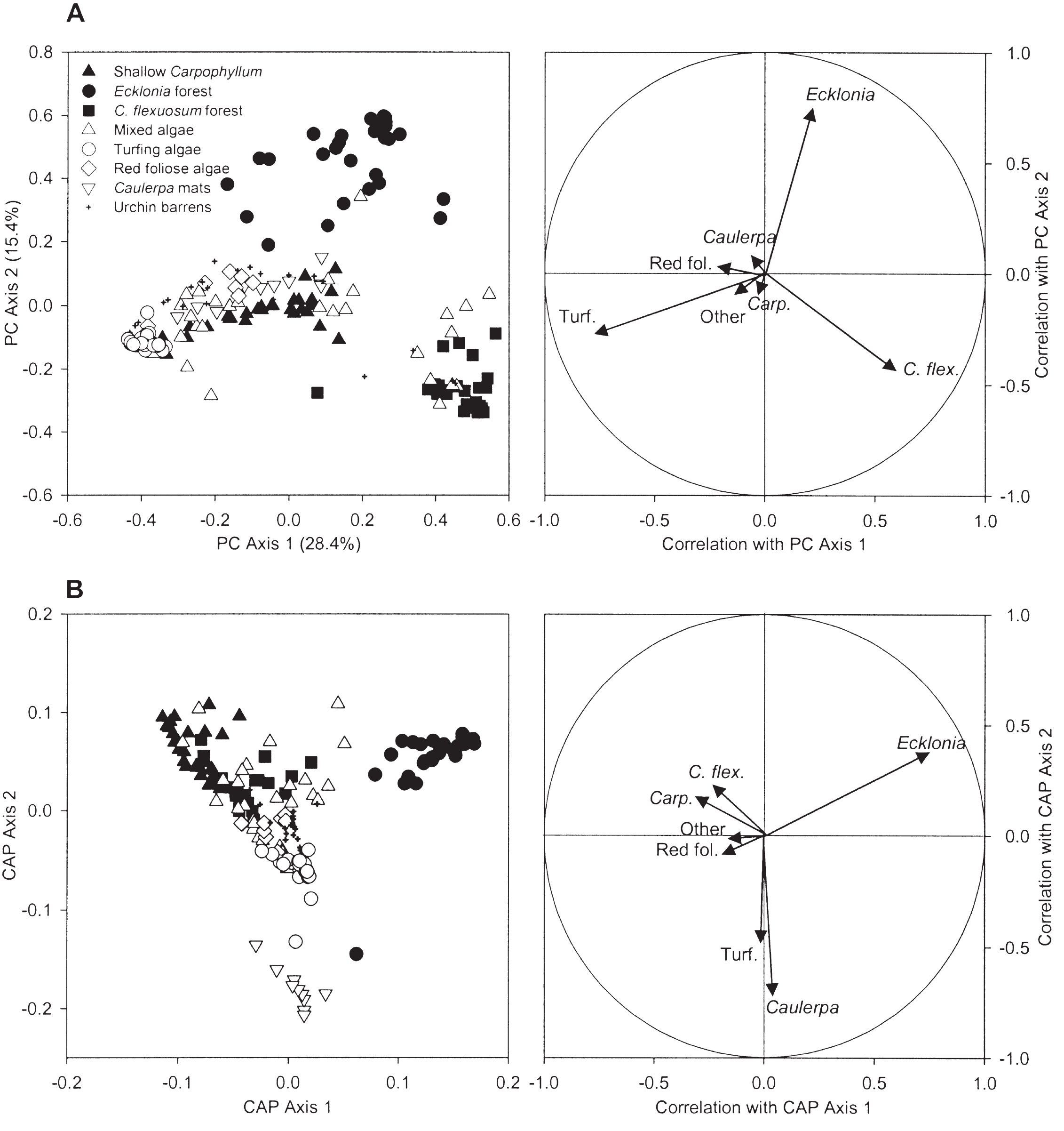

Fig. 2 Habitat classifications for north-eastern New Zealand. **A**, Unconstrained (principal coordinates analysis) and **B**, constrained (CAP) ordination of algal assemblages from quadrat sampling. Each symbol represents one quadrat and indicates the habitat type it was assigned to in the field. Bi-plots show correlations between the original species variables and **A**, the two principal coordinate axes, and **B**, the two CAP axes.

of the decline in urchin barrens and increase in large brown algal habitats (Babcock et al. 1999; Shears & Babcock 2003).

The *Caulerpa* mats and red foliose algae habitats are previously undescribed in north-eastern New Zealand although Bergquist (1960) reported a zone of red foliose algae in the upper subtidal on exposed reefs at Spirits Bay. These habitat types generally did not form distinct zones and were more likely to be found in patches ranging in size from 2 to 20 m^2, particularly at offshore islands and northern localities such as Cape Karikari. The red foliose algae habitat

Table 2 Habitat specific abundance ($m^{-2} \pm SE$, minimum and maximum in parentheses) of dominant species and classification success (cross-validation of habitat types from CAP analysis using leave-one-out technique). (CAP, Canonical analysis of principal coordinates.)

		Algal species/groups used in analysis						
Habitat	*n*	*Ecklonia radiata*	*Carpophyllum* spp.*	*C. flexuosum*	Other large browns	Red foliose (%)	*Caulerpa* spp. (%)	Turfing algae (%)
Shallow *Carpophyllum*	63	1.7 ± 0.5 (0, 20)	87.7 ± 12.5 (17, 608)	0.2 ± 0.1 (0, 3)	4.6 ± 1.0 (0, 33)	7.6 ± 1.4 (0, 44)	0.0 ± 0.0 (0, 1)	8.3 ± 1.4 (0, 40)
C. flexuosum forest	29	0.6 ± 0.2 (0, 4)	1.2 ± 0.5 (0, 10)	17.7 ± 2.0 (5, 40)	1.0 ± 0.3 (0, 8)	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)	0.6 ± 0.5 (0, 15)
Mixed algae	102	3.9 ± 0.9 (0, 77)	12.6 ± 1.9 (0, 129)	3.0 ± 0.7 (0, 50)	11.6 ± 1.9 (0, 153)	1.6 ± 0.5 (0, 31)	0.3 ± 0.3 (0, 30)	14.4 ± 1.7 (0, 70)
Ecklonia forest	61	17.2 ± 1.2 (4, 52)	0.4 ± 0.2 (0, 14)	0.9 ± 0.3 (0, 8)	0.7 ± 0.2 (0, 7)	1.6 ± 0.4 (0, 15)	0.6 ± 0.5 (0, 30)	8.5 ± 1.8 (0, 60)
Red foliose algae	10	0.6 ± 0.3 (0, 2)	3.1 ± 2.1 (0, 16)	0.0 ± 0.0 (0, 0)	0.3 ± 0.2 (0, 2)	38.5 ± 5.2 (13, 65)	0.2 ± 0.2 (0, 2)	22.9 ± 5.7 (5, 50.5)
Caulerpa mats	10	0.2 ± 0.2 (0, 2)	2.0 ± 1.5 (0, 15)	0.0 ± 0.0 (0, 0)	0.4 ± 0.3 (0, 3)	3.6 ± 1.2 (0, 10)	60.2 ± 5.7 (40, 90)	10.1 ± 3.2 (0, 30)
Turfing algae	47	0.1 ± 0.0 (0, 2)	1.2 ± 0.4 (0, 10)	0.1 ± 0.1 (0, 4)	1.7 ± 0.4 (0, 13)	2.1 ± 0.7 (0, 20)	0.7 ± 0.4 (0, 20)	56.9 ± 2.7 (30, 95)
Urchin barrens	60	0.0 ± 0.0 (0, 1)	0.1 ± 0.1 (0, 4)	0.9 ± 0.3 (0, 11)	0.5 ± 0.2 (0, 13)	0.0 ± 0.0 (0, 2)	0.2 ± 0.2 (0, 10)	10.4 ± 1.3 (0, 40)
Cobbles†	5	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)	2.2 ± 1.2 (0, 5)
Sponge flats†	2	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)	0.5 ± 0.5 (0, 1)	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)

		Other species/groups				
Habitat	*n*	Encrusting algae (%)	Exposed *Evechinus*	Sponges (%)	Sediment/sand (%)	Classification success (%)
Shallow *Carpophyllum*	63	55.7 ± 3.0 (0, 95)	1.4 ± 0.4 (0, 13)	1.7 ± 0.5 (0, 25)	7.5 ± 1.5 (0, 40)	86.7
C. flexuosum forest	29	65.8 ± 2.7 (40, 98)	1.7 ± 0.9 (0, 23)	2.0 ± 0.9 (0, 20)	22.1 ± 2.8 (0, 50)	86.2
Mixed algae	102	44.3 ± 2.7 (0, 100)	1.1 ± 0.4 (0, 31)	1.6 ± 0.5 (0, 30)	21.9 ± 2.2 (0, 75)	60.0
Ecklonia forest	61	54.0 ± 3.3 (8, 99)	0.3 ± 0.1 (0, 7)	3.9 ± 0.7 (0, 25)	18.4 ± 2.5 (0, 75)	93.1
Red foliose algae	10	28.5 ± 5.0 (15, 50)	2.2 ± 1.4 (0, 13)	1.8 ± 0.8 (0, 8)	2.2 ± 1.1 (0, 10)	60.0
Caulerpa mats	10	13.5 ± 3.1 (3, 30)	1.0 ± 0.5 (0, 4)	1.1 ± 1.0 (0, 10)	7.5 ± 2.9 (0, 20)	80.0
Turfing algae	47	18.9 ± 2.0 (0, 50)	4.7 ± 1.0 (0, 37)	0.7 ± 0.2 (0, 4.5)	12.1 ± 3.1 (0, 60)	100.0
Urchin barrens	60	66.8 ± 2.1 (30, 93)	6.4 ± 0.9 (0, 37)	5.0 ± 1.0 (0, 30)	5.9 ± 1.2 (0, 50)	66.7
Cobbles†	5	23.0 ± 3.4 (15, 35)	0.0 ± 0.0 (0, 0)	0.0 ± 0.0 (0, 0)	37.0 ± 11.4 (5, 70)	–
Sponge flats†	2	2.5 ± 2.5 (0, 5)	0.0 ± 0.0 (0, 0)	14.5 ± 0.5 (14, 15)	82.5 ± 2.5 (80, 85)	–

* Excluding *C. flexuosum*.

† These habitats were not included in analyses because of the low number of records.

generally occurred in shallow water (<6 m) and was dominated by the red algae *Osmundaria colensoi* and *Pterocladia lucida* (Shears 2002). *Caulerpa* mats were typically found at greater depths (>6 m), particularly at the reef-sand interface. This may be related to the highly opportunistic life-history characteristics of this genus (Vroom & Smith 2001). In north-eastern New Zealand *C. flexilis* is the dominant species forming this habitat (Shears 2002).

Although this classification system has been developed for rapid visual assessment by divers, it is also suitable for use with a range of other habitat mapping techniques such as side-scan sonar, aerial photographs, drop camera, and towed video survey methods. Many of these methods have the advantage of covering a larger spatial scale and also providing a permanent visual record accessible to future workers. However, they may not be able to distinguish between habitats that are structurally or spectrally similar (e.g., urchin barrens and turfing algae appear the same in aerial photographs). It is important that survey or mapping methodologies have the resolution to differentiate between different biological habitats, as they are ecologically and functionally very different. For example, Taylor (1998) found considerable variation in secondary productivity among four of the habitats (shallow *Carpophyllum* > turfing algae > *Ecklonia* forest > urchin barrens). These habitats also play different roles in the distribution, feeding ecology, and behaviour of many reef species (e.g., Kingett & Choat 1981; Andrew & Choat 1985; Choat & Ayling 1987).

Reliable classification of habitats is essential for describing large-scale patterns in communities (Underwood et al. 2000; Solan et al. 2003; Parsons et al. 2004), detecting large-scale changes in habitats over time (Babcock et al. 1999; Shears & Babcock 2003), and understanding the mechanisms responsible (Shears & Babcock 2002). This requires standardisation of descriptors to ensure that studies carried out by different observers are compatible, thus reducing the chance of inconsistencies in definitions being interpreted as changes in habitat types over time (contrast Underwood et al. 1991; Andrew & O'Neill 2000). Application of the habitat classification scheme described in this study to benthic monitoring programmes, or the creation of subtidal habitat maps, can therefore produce reliable and repeatable results from which clear inferences and management decisions can be made. Although this study describes habitats for north-eastern New Zealand they appear to be applicable to most of the northern mainland New Zealand biogeographic region (Babcock & Shears 2003). This region includes the entire North Island except for the Wellington and Wairarapa coasts, and also includes the northern coast of the South Island (e.g., Marlborough Sounds, Nelson, and Abel Tasman). Although analogs of the habitats described may occur at localities further south, a different suite of species generally characterises shallow subtidal reefs in these localities (Babcock & Shears 2003), thus requiring a different habitat classification.

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