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Biogeographical and ecological context for managing threats to coral and rocky reef communities in the Lord Howe Island Marine Park, south-western Pacific

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ABSTRACT

1. Quantitative subtidal surveys of fishes, macro-invertebrates and sessile organisms at 33 sites within the Lord Howe Island Marine Park revealed a rich fauna and flora, including 164 fishes, 40 mobile invertebrate taxa, 53 coral and other sessile invertebrate taxa, 32 algal taxa, and two seagrasses. The biota in this newly-zoned marine park was overwhelmingly tropical when species lists were tabulated; however, species with distributions centred on temperate coasts of eastern Australia and New Zealand occurred in disproportionately high densities compared with the tropical species.

2. Lord Howe Island reefs were generally in good condition. Virtually no bleached coral was observed (0.2% of the reef surface; 0.8% of total hard coral cover). Living scleractinian coral comprised the predominant group of organisms growing on reef surfaces, with 25.5% cover overall. Other major taxa observed were brown algae (18.8% cover) and red algae (16.9% cover).

3. Three distinctive community types were identified within the marine park—coral reefs, macroalgal beds and an offshore/open coast community. The distribution of these community types was strongly related to wave exposure, as indicated by an extremely high correlation with the first principal coordinates axis for biotic data ($R^2 = 0.80$).

4. The close (<3 km) proximity of tropical coral and temperate macroalgal community types off Lord Howe Island is highly unusual, with localized patterns of nutrient enrichment suggested as the primary cause. The macroalgal community type is only known from a small area off the south-western coast that is not protected from fishing. This community is considered highly susceptible to threats because of potential impacts of global warming and the possibility of expansion of sea urchin barrens. Coral bleaching and ocean acidification associated with global climate change also threaten the coral reef community, which includes relatively high numbers of endemic and near endemic fish species.

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INTRODUCTION

Marine biota associated with isolated oceanic islands include a disproportionate concentration of global biodiversity (Allen, 2007). Such biota are also subjected to a disproportionately high level of threat because of the small ranges of endemic taxa, and the possibility that stochastic climatological or human-induced disturbance events can lead to species extinction. Accordingly, conservation management of small oceanic islands is arguably more critical and also more difficult than elsewhere – management actions need to account for strong interactions between biogeographical processes at the regional level, ecological processes at the local level, and anthropogenic threats.

In the present study, Lord Howe Island is used as a case example of how information on biogeography, ecology and

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*Correspondence to: Graham J. Edgar, Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Private Bag 49, Hobart, Tasmania, 7001 Australia. E-mail: g.edgar@utas.edu.au human activity can improve conservation decision-making. Two questions are addressed: What are the major marine conservation values of Lord Howe Island in global and regional contexts? Are these values adequately safeguarded at the within-island scale using the current marine protected area (MPA) zoning scheme and other local management processes?

Lord Howe Island lies approximately 600 km east of the northern NSW coast at latitude 31°50′S. With several small satellite islands, it sits on the western margin of the basaltic Lord Howe Rise, an isolated north–south trending underwater volcanic ridge (Woodroffe *et al*., 2006). The island rises to 800 m height and is crescent shaped, 11 km long and slightly less than 3 km wide, with a shallow, sheltered, coral-fringed lagoon extending for *c*.6 km off the western coast.

Oceanographically, the island lies on a boundary between tropical (Coral Sea) and temperate (Tasman Sea) water masses, commonly referred to as the Tasman Front. This front oscillates in a north–south direction, thereby contributing to seasonally alternating cooler and warmer waters in the region (Nilsson and Cresswell, 1981). Water temperatures vary from *c*.17°C in winter to *c*.25°C in late summer (Hutton, 1986), although temperatures up to 28°C have been recorded in the sheltered lagoon (Allen *et al*., 1976).

The alternating influences of warm and cool currents have created an oceanic transition zone in the region between temperate and tropical biomes (Kennedy *et al*., 2002). As a consequence, waters surrounding Lord Howe Island possess rich and unusual biodiversity, and are globally important in several respects (Environment Australia, 2000).

The high conservation significance of the region was recognized by its inclusion on the UNESCO World Heritage List in 1982 (Environment Australia, 2000). Values that contributed to the World Heritage listing and are specific to the marine environment included:

- the unusual combination of tropical and temperate taxa of marine flora and fauna, including many species at their distributional limits, reflecting the extreme latitude of coral reef ecosystems, which comprise the southernmost true coral reef in the world;
- the high diversity of marine benthic algae, fishes and marine invertebrates and associated high levels of endemicity.

The richness of the Lord Howe Island marine biota is shown by the ichthyofauna, which includes over 490 recorded species (Allen *et al*., 1976; Francis, 1993; Parker, 1993). Of the 433 known inshore fish species, the majority are wide-ranging tropical forms, while *c*.10% are found only at Lord Howe Island, southern Australia and/or New Zealand (Allen *et al*., 1976). Approximately 4% (15 species) of the shore fishes are endemic to the Lord Howe region (including Norfolk Island) and 32% are restricted to the south-western or southern Pacific Ocean (Allen *et al*., 1976).

At least 110 species of echinoderms have been identified at Lord Howe Island, including nine (8%) endemic species. Combined with an additional 22 species known from the nearby Elizabeth and Middleton Reefs, the echinoderm fauna of the region include 72% tropical species, 22% species endemic to the Tasman Sea, and 6% associated with warm temperate Australian coasts (Hoggett and Rowe, 1988). On the basis of several early papers and summaries of common intertidal species (Hedley and Hull, 1912; Iredale, 1940; Iredale and Allan, 1940; Allen and Paxton, 1974), Lord Howe Island supports over 1500 species of molluscs, including several endemic species (Parker, 1993).

In total, 86 species of coral from 33 genera in 11 families have also been recorded (Harriott *et al*., 1993, 1995; Harriott and Banks, 2002; Bullard, 2003). While this number is low compared with tropical reefs, it indicates a relatively high diversity considering the island's latitude, small reef size and isolation from other major coral communities. Lord Howe Island coral communities include populations of tropical species at the southern limits of their distribution, as well as subtropical species that are rare or absent on tropical reefs (Harriott *et al*., 1995).

Algal assemblages at Lord Howe Island are diverse and abundant compared with tropical reefs, with macroalgal species dominant over corals at many sites (Harriott *et al*., 1995). Approximately 320 species of benthic algae are present, comprising 76 green algae, 68 brown algae and 174 red algae, and with 47 (15%) endemic species (Millar and Kraft, 1993, 1994a, b; Kraft, 2000; Millar, 2004; Millar and Freshwater, 2005). The most common genera are the brown algae *Dictyota*, *Sargassum* and *Lobophora*, and the green algae *Caulerpa*, *Ulva*, *Codium* and *Chlorodesmis* (Harriott *et al*., 1995). Lord Howe Island is also important because it sits at the extreme latitudinal limit of many algal species and genera. Among the green algae, it holds the world's highest latitude populations for the genera *Neomeris*, *Boodlea*, *Valoniopsis*, *Ventricaria* and *Trichosolen* (Millar and Kraft, 1994a).

In order to protect the various marine biological values associated with Lord Howe Island, the New South Wales Government proclaimed the Lord Howe Island Marine Park (LHIMP) in 1999; however, negotiations with stakeholders were protracted, and a zoning scheme only came into force on 1 December 2004 (Figure 1). The zoning scheme partitioned coastal waters to allow different human uses while minimizing threats to marine conservation values, and included restrictions on fishing. The objectives of the zoning scheme were: (a) to conserve marine biological diversity and marine habitats; (b) to maintain ecological processes; and (c) where consistent with the preceding, to provide for ecologically sustainable use of fish and marine vegetation, and (d) to provide opportunities for public appreciation, understanding and enjoyment (*Marine Parks Act 1997*). The majority (73%) of the marine park consists of large *Habitat Protection Zones*, which allow most forms of fishing, including charter boat trips and recreational fishing other than spearfishing. Seven *Sanctuary Zones* (27% of LHIMP waters) are also included, where fishing, anchoring and other activities that harm marine life are banned.

Fishing pressure on waters surrounding Lord Howe Island, both before and after declaration of LHIMP, has been low compared with that experienced in mainland Australian waters, with almost all fish taken by handline. Fishing practices recognized as most environmentally harmful — including gill-netting, dredging and trawling — are banned. While no commercial fishing licences currently exist, operators of several recreational charter vessels sell captured animals of value through the local restaurant trade.

Prior to declaration of LHIMP, areas most heavily fished included waters off the northern coast out to the Admiralty

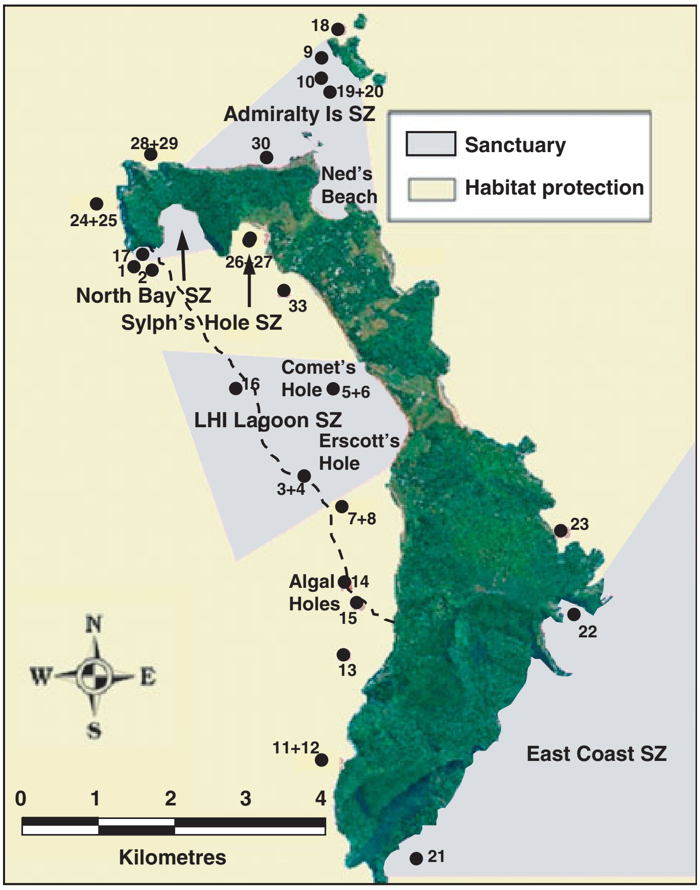

Figure 1. Locations of biodiversity survey sites investigated (note that sites 31 and 32, which are located 25 km south-west near Balls Pyramid, are not included in this figure). The dashed line indicates outer reef edge of the lagoon.

Islands, and the northern, southern and outer lagoonal regions off the west coast. Three locations (Comet's Hole, Ned's Beach and Erscott's Hole) have acted as de facto sanctuary zones for over 40 years, following recognition by local residents that these sites possess much greater value for tourism than for their fishery resources (Gary Crombie, pers. commun.).

Patterns of biodiversity in nearshore marine habitats within LHIMP were surveyed and are described here, with an assessment of how well the present zoning scheme reflects the distribution of community types and threats. At the time that LHIMP was declared, little ecological information was available to aid in the design of the zone network (Lindsay *et al*., 2008). Field methods utilized here were based on those applied widely in marine park monitoring along the temperate Australian coast and tropical island systems to allow broad scale comparisons through the long term (Edgar *et al*., 1997, 2004a; Edgar and Barrett, 1999). Quantitative surveys were undertaken for fishes, mobile macro-invertebrates, sessile invertebrates and benthic macroalgae.

METHODS

Sites studied

Field surveys were conducted from 12 to 28 February 2006. A total of 33 sites were investigated, including two sites near Balls Pyramid, an isolated rock spire emerging from the ocean 25 km to the south-west that is also included within LHIMP. A total of 16 sites were located in Sanctuary Zones, where no fishing is allowed, and 17 sites in Habitat Protection Zones, where limited fishing is permitted (Figure 1). Sites were selected to encompass the range of environmental variation on reefs at Lord Howe Island, and also to cover all six sanctuary zones with shallow reef (Admiralty Islands, North Bay, Sylph's Hole, Lord Howe Island Lagoon, East Coast and Observatory Rock, which lies offshore of Balls Pyramid) plus adjacent sites in habitat protection zones that could be used as reference sites. Each 'site' included transects for fishes, mobile macro-invertebrates and sessile biota undertaken at two different depths.

Three environmental variables were quantified at each site — depth, underwater visibility, and wave exposure. The depth of each transect line was recorded from scuba gauges. Underwater visibility was estimated as the maximum distance sighted by divers along transect lines set underwater. Wave exposure was estimated at each site using a five point scale — 1: highly sheltered conditions with little wave or wind energy; 2: sheltered conditions in lagoonal and other protected environments with little oceanic swell but wind-driven waves; 3: sheltered coast open to limited swell; 4: coast open to moderate swell; and 5: coast open to full oceanic swell from prevailing east and south swell directions.

Species recorded on transects were categorized within six distributional categories: (i) species endemic to Lord Howe Island, Norfolk Island, and Elizabeth and Middleton

Reefs; (ii) near endemic species confined to these islands and/or New Caledonia and the Kermadec Islands; (iii) insular species predominantly found at Lord Howe Island and associated islands but with vagrant individuals recorded from the eastern NSW coast and/or northern New Zealand; (iv) species with largely subtropical distributions to the southern Great Barrier Reef, Kermadec Islands, Rapa and/or Easter Island but not further north; (v) tropical species occurring widely across the Indo-West Pacific region; and (vi) species with largely warm temperate distributions in eastern Australia and/or northern New Zealand.

Underwater visual census techniques

Densities of fishes, mobile macro-invertebrates and sessile organisms were separately estimated using Reef Life Survey (http://www.reeflifesurvey.com) methods. The fish censusing protocol at each site involved a diver laying the 50 m transect line along the depth contour then recording the number and estimated size-category of all fishes sighted within 5 m of the deeper side of the transect line. The transect block thus encompassed a total reef area of 50 m × 5 m. The diver next censused the adjacent shallower replicate block by swimming back parallel to the initial transect. This up and back procedure was repeated at a second depth contour, generating duplicate transect block data for each of two depths at each site (1000 m^2 total). For sites 1–13, transect data were not duplicated by return swim at the shallowest transect level at the site because of insufficient dive time. Estimated fish lengths were binned in size intervals of 25 (i.e. 0 – 37.4), 50 (37.5 – 62.5), 75, 100, 125, 150, 200, 250, 300, 350, 375, 400, 500, 625, 750 and 875 mm. Lengths of fish >1 m length were individually estimated.

Fish abundance counts and size estimates were converted to biomass estimates using length–weight relationships outlined for each species (in some cases genus and family) in Fishbase (http://www.fishbase.org/). In cases where length–weight relationships were described in Fishbase in terms of standard length or fork length rather than total length (as recorded by divers), additional equations provided in Fishbase allowed conversion between different length metrics. For improved accuracy in biomass assessments, the bias in divers' perception of fish size underwater was additionally corrected using relationships presented in Edgar *et al.* (2004b). Estimates of fish abundance made by divers can be greatly affected by fish behaviour for many species (Edgar *et al.*, 2004b), hence biomass determinations, like abundance estimates, are compared only in a relative sense (i.e. for comparisons with data collected using the same methods) rather than considered to provide an accurate absolute estimate of fish biomass for a patch of reef.

Fishbase was also used to subdivide fish species into four trophic categories — herbivore, planktivore, benthic carnivore and higher carnivore. Benthic carnivores were distinguished from higher carnivores on the basis of whether their diet predominantly consisted of molluscs, amphipods, isopods and polychaetes rather than other fishes, squid and decapods.

Cryptic fishes (i.e. inconspicuous species closely associated with the seabed that were likely to be overlooked during primary fish surveys) and large macro-invertebrates (large molluscs, echinoderms and crustaceans) were censused along the transect lines set at two depths per site for baseline fish surveys. A diver swam along the lower side of the transect, counting all macro-invertebrates and cryptic fishes within 1 m of the line, then returned along the other side of the line counting animals within the adjacent 50 m × 1 m block. For the four sites studied on the first day (sites 1 to 4), data collected along the shallowest transect were not duplicated (i.e. the diver did not undertake a return count along the upper side of the line) because of insufficient dive time.

Habitat characteristics along the subtidal transect lines set for fish and invertebrate censuses were recorded by taking digital photoquadrats using a Nikon D70 6.4 megapixel camera in underwater housing with fill-in flash. Photo images were taken vertically-downward each 5 m along each transect line from a height sufficient to encompass at least a 0.5 m × 0.5 m area. The scale of each quadrat is evident from centimetre markings along the transect line. No photoquadrats were taken at Site 8 (Erscott's Passage South).

The percentage cover of different macroalgal, coral, sponge and other attached invertebrate species was digitally quantified from the photo images. A grid of 50 points was superimposed on the quadrat image, and species present under each grid point identified to the highest taxonomic level possible and counted. Substratum classes (e.g. rock, rubble, sand) were also recorded when no living organism was evident under a particular grid point.

Statistical analyses

Differences between sites and depths were assessed statistically using analysis of covariance (ANCOVA), where mean values for transects undertaken at two depths at 33 sites were analysed. The factor site was regarded as a random categorical factor and the factor depth as a continuous factor. Following graphical assessment of the distribution of residuals, abundance data were log transformed to reduce heteroscedasticity in ANCOVAs: log $(x+1)$ was used for transformation of data sets with zero values. Log transformations were also used in ANOVAs where effects of marine park zone type were compared.

The significance of differences between sanctuary zones and habitat protection zones was assessed using two-way ANOVAs, with MPA zone type (two levels; sanctuary zone and habitat protection zone) and MPA location (six levels, each comprising sites within a single sanctuary zone plus nearby fished reference sites in habitat protection zones; Admiralty Islands, North Bay, Sylph's Hole, Lord Howe Island Lagoon, East Coast and Observatory Rock Sanctuary Zones) as fixed factors. While location is often regarded as a random factor in models of MPA effects, in the case of MPA location here, all six inshore areas zoned as sanctuary zones were surveyed. Thus, the test related to variation between the six sanctuary zones and adjacent locations, with sites within locations used as replicates. The mean value for transects within a site provided one replicate data point.

Patterns of community structure in the region were initially analysed using Principal Coordinates Analysis (PCA), as run by the CAP program (Anderson, 2003; Anderson and Willis, 2003). Data for all three raw data sets (fishes, macro-invertebrates and sessile biota) were initially combined into a total site-by-abundance matrix, which was then converted to a Bray–Curtis similarity matrix relating paired sites after performing double root transformation of data. Counts for different depths and transects within each site were aggregated to provide a single number for each site-by-species combination. Species recorded from only one site were excluded.

In order for the combined analysis to reflect equally fishes, mobile macro-invertebrates and sessile biota, the three raw data sets were combined after data in each had been standardized to a similar range in abundance. This was done by multiplying each count in the macro-invertebrate data set by the maximum number of any fish species recorded at a site (i.e. 1850) and dividing by the maximum number of any invertebrate species recorded at a site (i.e. 512). The same process was used to standardize the sessile biota data set to the same maximum value as for fishes and macro-invertebrates. No photoquadrats were taken at Site 8, hence this site was excluded from the analysis of the total biota, and 32 sites in total were investigated.

Possible environmental influences on community structure were identified by relating the three major environmental variates investigated (wave exposure, depth and underwater visibility) to each of the first two principal coordinates using Pearson correlation. Associations of common species with different community types were also assessed by calculating analogous correlations using species abundance data for each site and species.

RESULTS

Fishes

Lord Howe Island possesses a rich fish fauna compared with other regions surveyed using the same transect technique (Edgar and Stuart-Smith, 2009), with an average of 16 species recorded per 50 m × 5 m transect block, and 161 taxa recognized during all fish transects. One additional fish species (*Gymnothorax annasona*) was recorded during cryptic fish searches. Amongst the 150 fishes identified to species, four species (*Aluterus scriptus*, *Chrysiptera flavipinnis*, *Gymnothorax thyrsoideus*, *Monotaxis grandoculis*) had not previously been reported from Lord Howe Island.

The most abundant fish species sighted were the three planktivorous damselfishes *Chromis hypsilepis*, *Chrysiptera notialis* and *Neoglyphidodon polyacanthus*, followed by the carnivorous wrasse *Pseudolabrus luculentus*, planktivorous cardinalfish *Ostorhinchus norfolcensis* and three herbivorous damselfishes *Parma polylepis, Stegastes gascoynei* and *Stegastes fasciolatus* (Table 1). *Chromis hypsilepis* was also the biomass dominant within the fish fauna. Four of the top seven biomass dominants were herbivores — *Prionurus maculatus*, *Parma polylepis*, *Girella cyanea* and *Kyphosus gibsoni.* These species were only moderately abundant but possessed large mean body size. Other biomass dominants were the abundant damselfish *Neoglyphidodon polyacanthus* and the wrasse *Pseudolabrus luculentus* (Table 1).

Table 1. Total abundance, biomass (kg) and number of sites recorded for fish species sighted at 10 or more sites over a total surveyed transect area of 29,750 m^2.

Species	Sites	Number	Biomass	Trophic	Range
Parma polylepis	33	1436	229.63	h	st
Pseudolabrus luculentus	33	2708	138.24	b	wt
Stegastes gascoynei	32	1298	77.75	h	st
Chaetodon tricinctus	29	355	68.31	b	e
Chrysiptera notialis	28	4744	104.90	p	st
Coris bulbifrons	28	117	103.54	b	in
Stegastes fasciolatus	28	1119	74.47	h	t
Chromis hypsilepis	27	13180	281.73	p	wt
Thalassoma lutescens	26	608	43.28	b	t
Anampses elegans	25	269	30.09	b	st
Neoglyphidodon polyacanthus	24	2751	176.93	p	t
Labroides dimidiatus	23	159	1.67	b	t
Plagiotremus tapeinosoma	21	68	0.26	b	t
Ostorhinchus norfolcensis	19	1968	97.14	p	ne
Parupeneus signatus	19	252	62.73	b	t
Notolabrus inscriptus	19	86	19.52	b	wt
Cheilodactylus ephippium	17	66	36.72	b	wt
Chaetodon flavirostris	17	118	17.49	b	t
Cirrhitus splendens	16	58	12.53	b	in
Girella cyanea	15	226	143.81	h	wt
Trachypoma macracanthus	15	21	2.90	c	t
Coris picta	15	44	1.62	b	wt
Centropyge tibicen	14	31	2.07	b	t
Amphiprion maccullochi	12	269	18.79	h	e
Ostorhinchus flavus	12	163	16.23	p	st
Stethojulis bandanensis	12	47	1.51	b	t
Gomphosus varius	12	65	1.32	b	t
Prionurus maculatus	11	252	274.68	h	t
Kyphosus sydneyanus	11	113	87.05	h	wt
Chaetodon melannotus	11	56	7.41	b	t
Kyphosus gibsoni	10	160	116.99	h	t
Plectroglyphidodon dickii	10	49	5.16	b	t
Pseudanthias squamipinnis	10	109	0.80	p	t

Trophic category (p: planktivore, c: higher carnivore, b: benthic carnivore, h: herbivore) and distributional range (e: endemic to Lord Howe and Norfolk islands, ne: near endemic, t: tropical, st: subtropical, wt, warm temperate, w: widespread) are also shown

No introduced fish species, nor fish species listed under the IUCN Red List (IUCN, 2006), Australian *Environmental Protection and Biodiversity Conservation Act* or the New South Wales (NSW) *Threatened Species Conservation Act*, were sighted during surveys, although an Endangered green turtle (*Chelonia mydas*) was recorded on a transect at site 18. A single black cod (*Epinephelus daemelii*) was sighted at site 20. Black cod have been totally protected in NSW waters since 1983, and are listed as 'Vulnerable' under the NSW *Fisheries Management Act* and by Pogonoski *et al.* (2002) in their threat assessment of Australian fishes. Two wrasses that are common at Lord Howe Island, *Anampses elegans* and *Coris bulbifrons*, are also protected species in NSW waters in accordance with the *Fisheries Management Act* because of concern about their conservation status (*C. bulbifrons* is protected from spearfishing only).

A total of 110 (74%) of the identified fish species are widely distributed across the tropical Pacific (Table 2). Fishes with other distribution patterns included (i) three species endemic to Lord Howe Island and Norfolk Island (*Chaetodon tricinctus*, *Amphiprion maccullochi* and *Gymnothorax annasona*), (ii) three 'near endemic' species confined to these two islands and/or New Caledonia and the Kermadecs (*Genicanthus semicinctus*, *Cheilodactylus francisi* and *Ostorhinchus norfolcensis*), (iii) three 'insular' species predominantly found at Lord Howe Island and associated islands but with vagrant individuals recorded from the eastern NSW coast and/or northern New Zealand (*Coris bulbifrons*, *Amphiprion latezonatus* and *Cirrhitus splendens*), (iv) 11 species with largely subtropical distributions (e.g. *Anampses elegans*, *Ostorhinchus capricornis* and *Chaetodontoplus conspicillatus*), and (v) 20 species

Table 2. Total number of species, abundance and biomass of fishes recorded over a total transect area of 29 750 m^2 at 33 sites, with fishes categorized by different distributional ranges

Category	Species	Abundance	Biomass (kg)
Endemic*	2 (1.3%)	624 (1.7%)	87 (2.9%)
Near endemic	3 (2.0%)	1979 (5.5%)	98 (3.3%)
Insular	3 (2.0%)	176 (0.5%)	116 (3.9%)
Subtropical	11 (7.4%)	8019 (22.2%)	485 (16.4%)
Tropical	110 (73.8%)	8687 (24.1%)	1314 (44.5%)
Warm temperate	20 (13.4%)	16633 (46.1%)	853 (28.9%)
Total	149	36118	2953

*An additional endemic fish species (*Gymnothorax annasona*) was recorded during cryptic fish searches.

Table 3. Total number of species, abundance and biomass (kg) of fishes recorded over a total transect area of 29 750 m^2 at 33 sites, with fishes categorized by major trophic groups

Category	Species	Abundance	Biomass (kg)
Benthic carnivore	73 (49.0%)	6043 (16.7%)	712 (24.1%)
Higher carnivore	24 (16.1%)	245 (0.7%)	332 (11.2%)
Herbivore	29 (19.5%)	5156 (14.3%)	113 (38.6%)
Planktivore	23 (15.4%)	24674 (68.3%)	770 (26.1%)
Total	149	36118	2954

Table 4. Results of analysis of covariance with random categorical factor 'site' (df = 32/32) and continuous factor 'depth' (df = 1/32)

Taxon	Site			Depth			Error
	MS	F	P	MS	F	P	MS
Fishes							
Species richness	19.99	1.45	0.151	2.12	0.15	0.698	13.82
Density	0.63	2.74	0.003	0.14	0.60	0.445	0.23
Biomass	0.42	1.00	0.504	0.98	2.33	0.137	0.42
Benthic carnivore density	0.22	1.20	0.308	0.20	1.10	0.303	0.18
Higher carnivore density	0.53	1.32	0.217	1.55	3.89	0.057	0.40
Herbivore density	0.42	1.83	0.047	1.92	8.29	0.007	0.23
Planktivore density	2.53	3.67	<0.001	0.20	0.29	0.594	0.69
Macro-invertebrates							
Invertebrate species richness	5.97	5.22	<0.001	20.44	17.89	<0.001	1.14
Centrostephanus density	3.81	13.61	<0.001	0.02	0.08	0.784	0.28
Heliocidaris density	3.70	20.65	<0.001	0.54	2.99	0.093	0.18
Sessile biota							
Hard coral cover	319.8	5.02	<0.001	117.1	1.84	0.185	63.74
Soft coral cover	88.3	6.16	<0.001	6.2	0.43	0.515	14.32
Crustose coralline algal cover	43.8	4.37	<0.001	25.6	2.54	0.121	10.05
Brown algal cover	792.2	7.51	<0.001	80.9	0.77	0.388	105.55
Green algal cover	43.9	4.37	<0.001	25.6	2.54	0.121	10.05
Red algal cover	298.9	7.36	<0.001	30.9	0.76	0.390	40.61

Mean-square values, F-values and probability values associated with F-tests are shown. Interaction terms were tested and subsequently excluded from models because of a lack of significance.

with largely warm temperate distributions to eastern Australia and/or northern New Zealand (e.g. *Chromis hypsilepis*, *Cheilodactylus vestitus*, *Aplodactylus etheridgii* and *Atypichthys latus*).

Many species with tropical distributional ranges were sighted infrequently and are apparently vagrants to the region. As a consequence, tropical species contributed a much lower proportion of total fish abundance and biomass than their proportion of the total species list would suggest (Table 2). By contrast, most warm temperate and subtropical species sighted were observed on many occasions, and these groups contributed relatively high proportions of total fish abundance and biomass.

Almost half of all fish species sighted during transects were categorized trophically as benthic carnivores; however, this trophic category contributed only 17% of total abundance and 24% of total biomass (Table 3). Herbivorous fishes as a trophic group contributed the greatest proportion of total biomass of fishes (38.6%). In terms of abundance, planktivorous fishes dominated the fish community (68% of total). Although the total number of planktivorous fishes sighted on transects was one hundred times greater than the total number of higher carnivorous fishes, total biomass of planktivorous fishes (770 kg) was only just over twice that estimated for higher carnivorous fishes (332 kg).

Results of analysis of covariance based on mean values at two depths at 33 sites (Table 4) indicated that major community metrics associated with fishes were highly stable between sites. No significant differences between sites were evident for fish species richness or fish biomass, nor did these two metrics or fish density vary significantly between depths. The density of fishes counted per transect did, however, vary significantly between sites ($P = 0.003$). Among the different trophic level consumers, the densities of fish planktivores and herbivores both varied between sites, while herbivores also showed a significant decline with depth (Table 4). Mean herbivore biomass per 250 m^2 transect declined from *c.*12 kg at 4 m depth to *c.*5 kg at 14 m.

Little systematic geographic variation is evident in the distribution of fish biomass belonging to different trophic level feeders around the island (Figure 2). Benthic carnivores and planktivores were widely distributed. The biomass of higher carnivores was much higher at sites 5 and 6 (Comet's Hole) than elsewhere, due primarily to the presence of numerous large individuals of the spangled emperor *Lethrinus nebulosus* and morwong *Cheilodactylus ephippium*. The biomass of herbivorous fishes at sites 14 and 15 (Algal Holes) was double that of any other site as a result of schools of large spotted surgeonfish *Prionurus maculatus* and bluefish *Girella cyanea*.

Macro-invertebrates

A total of 40 macro-invertebrate taxa and seven cryptic fish taxa were recorded during 50 m × 1 m transects. The most common macro-invertebrate species encountered were the sea urchins *Centrostephanus rodgersii*, *Heliocidaris tuberculata* and *Echinostrephus aciculatus*, which comprised 38%, 22% and 11% of total invertebrate abundance, respectively.

The majority of identified invertebrate species sighted during transects possessed tropical Pacific distributions (21 of 28 species; 75% of total); however, in terms of

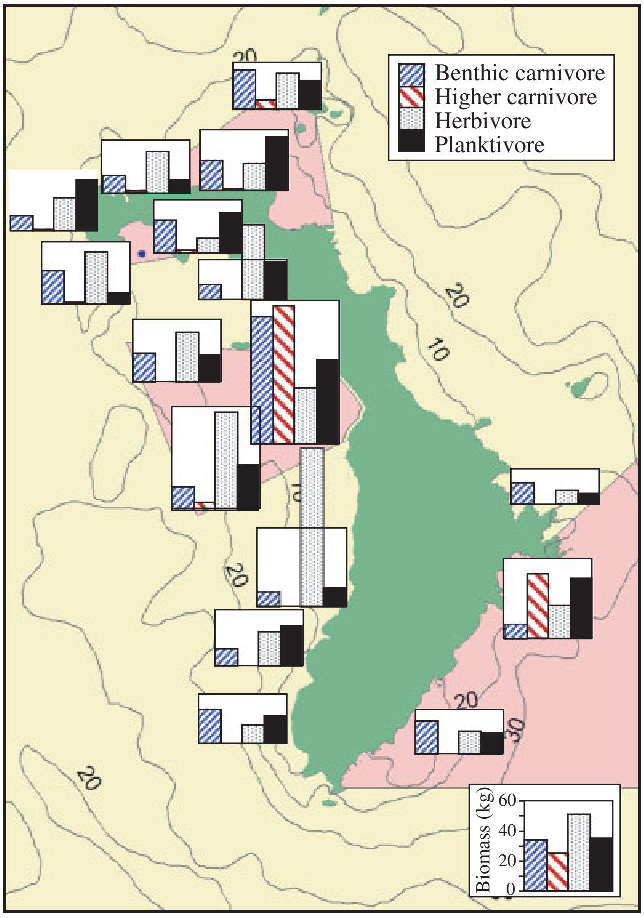

Figure 2. Mean fish biomass per 1000 m^2 belonging to different trophic level feeders around Lord Howe Island. Data from sites surveyed within 500 m of each other have been aggregated as a mean value. Data shown at bottom right relate to sites near Balls Pyramid. Sanctuary zones are more darkly shaded.

abundance, the four warm temperate species (*Centrostephanus rodgersii*, *Heliocidaris tuberculata*, *Morula nodulifera* and *Octopus tetricus*) predominated (3425 of 4910 individuals; 70% of total). Although two species with 'insular' distributions that are centred on Lord Howe Island were recorded (*Astrostole rodolphi* and *Turbo cepoides*), no endemic, near endemic or subtropical invertebrate species were sighted on transects.

The number of benthic invertebrate species recorded in transects varied greatly with depth and between sites (analysis of covariance, $P<0.001$; Table 4). An average of two species were sighted per transect block at 2 m depth, increasing to approximately five species per transect below 8 m depth. Sites located in lagoon holes (Sylph's Hole and Comet's Hole) possessed almost no macro-invertebrates. Densities of the two dominant urchin species did not show significant relationships with depth when assessed using ANCOVA, but varied greatly between sites (Table 4).

Sessile biota

The sessile flora and fauna present in photoquadrats taken at the 32 sites surveyed were classified into a total of 84 different taxa. Living scleractinian coral comprised the predominant group in terms of both number of taxa recognized (40) and percentage of total cover (25.5%). Other major taxa observed were brown algae (18.8% average cover), red algae (16.9%), soft corals (6.3%), green algae (4.0% cover) and seagrasses (0.9% cover). Virtually no bleached coral was recorded in photoquadrats (0.2% of the reef surface; 0.8% of total hard coral cover).

The majority of taxa recorded from photoquadrats were grouped at a level of classification higher than species. A total of 25 of 84 taxa comprised species level categories. Recognized species contributed 35% of total biotic percentage cover, and included 14 of the 40 hard coral taxa. Most of the identified corals were tropical species (79%) with the remainder subtropical, whereas only 4 of 10 macroalgal species identified (40%) possessed tropical distributions and no macroalga was regarded as subtropical. The two corals *Acropora palifera* (6.4% mean reef cover across all sites) and *Porites heronensis* (5.8% cover) were the most important sessile faunal species observed, while the dominant macroalgal taxa were *Dictyota* spp. (4.7%) and *Asparagopsis taxiformis* (3.5%). Approximately 25.6% of the reef substratum comprised rubble, rock, dead coral and sand, with a fine layer of filamentous algae in places.

The percentage cover of different sessile components varied greatly between sites, but not with depth (Table 4). Coral occurred in highest density at sites 3 to 8 in the central section of the lagoon (Figure 3). Macroalgae covered most of the reef surface towards the outer edge of the lagoon, north-west Lord

Howe Island, and the vicinity of the Admiralty Islands. Large areas of bare rock and rubble were common off the south-east coast and northern lagoon.

Biotic patterns associated with LHIMP zoning scheme

Although the mean number of species, density and biomass of fishes per site tended to be higher in no-fishing 'sanctuary' zones than 'habitat protection' zones, which are open to fishing, the differences in mean values were not great (<30%), nor were differences found to be significant using two-way ANOVA (Table 5). Within 'habitat protection' zones, a mean (±SE) of 15.0 (±0.5) species was recorded per 50 m × 5 m transect block compared with 17.8 (±1.3) species per block in sanctuary zones. Comparable means for fish density per site were 275 (±37) and 348 (±40), and for biomass 23 (±3) kg and 30 (±6) kg, for habitat protection zones and sanctuary zones, respectively. Total species richness and fish biomass did, however, both show significant regional variation between the six different MPA sanctuary zones in the Lord Howe Island Marine Park (including nearby reference regions) (Table 5), with highest richness and biomass both located in the Lord Howe Island Lagoon Sanctuary Zone.

When the fish fauna is subdivided into trophic categories, only one fish metric – the biomass of herbivorous fishes – showed significant differences between sanctuary and habitat protection zones (Figure 4, Table 5). The mean biomass of higher carnivores appeared many times higher in sanctuary zones than habitat protection zones (Figure 4); however, this result was caused by anomalously high carnivore biomass at the two Comet's Hole sites (see Figure 2), an outcome that contributed substantially to variation between sites but not variation between zone types. The species richness, density and biomass of herbivore species all varied significantly with MPA location, while the biomass of herbivores also showed a significant interaction, indicating that differences between sanctuary zones and habitat protection zones varied on a regional basis.

No significant differences were evident in mean species richness or density of macro-invertebrates per site in the two major MPA zone types (Table 5). Although the mean number of *Heliocidaris tuberculata* per site in habitat protection zones was five times greater than in sanctuary zones, this difference was not statistically significant because of the high level of variation between sites. Densities of *Centrostephanus rodgersii* also did not significantly differ between the two management zone types, although pronounced regional variation in density was evident. The total density of macro-invertebrates showed a significant 'MPA zone type × location' interaction (Table 5).

The mean cover of hard corals in sanctuary zones (27%) was much higher than in habitat protection zones (16%), a statistically significant outcome (Figure 5, Table 5). Green algae also covered significantly more of the reef surface in

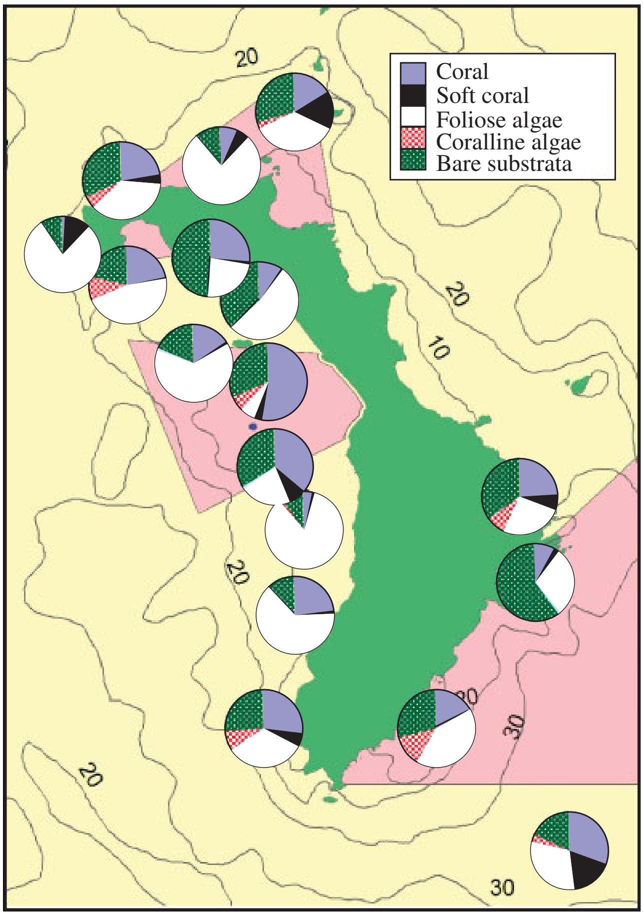

Figure 3. Variation in percentage cover of hard corals, soft corals, foliose algae, coralline algae and bare substrata around Lord Howe Island. Data from sites surveyed within 500 m of each other have been aggregated. The category bare substrata includes rock, sand and dead coral rubble. Data shown at bottom right relate to sites near Balls Pyramid. Sanctuary zones are more darkly shaded.

Table 5. Results of two-way ANOVAs for different metrics with MPA zone type (2 levels; sanctuary zone and habitat protection zone) and MPA location (six levels) as fixed factors

Trophic level	MPA type		MPA location		Interaction		Error
	MS	F	MS	F	MS	F	MS
Fish species richness							
Benthic carnivores	217.6	3.40	150.0	2.35	74.8	1.17	64.0
Higher carnivores	7.11	1.38	3.45	0.67	4.18	0.81	5.14
Herbivores	3.35	0.40	36.87	4.45**	23.93	2.89*	8.29
Planktivores	1.80	0.12	12.73	0.87	13.14	0.89	14.69
Total	424.0	3.09	379.0	2.76*	157.0	1.14	137.3
Fish density							
Benthic carnivores	0.26	1.96	0.18	1.42	0.15	1.14	0.13
Higher carnivores	1.44	1.26	0.74	0.64	1.56	1.36	1.15
Herbivores	0.07	0.31	0.75	3.29*	0.14	0.63	0.23
Planktivores	0	0	1.75	1.59	0.76	0.69	1.10
Total	0.07	0.24	0.46	1.61	0.12	0.43	0.28
Fish biomass							
Benthic carnivores	1.55	3.90	0.19	0.47	0.45	1.13	0.40
Higher carnivores	14.73	3.00	3.02	0.62	2.38	0.48	4.91
Herbivores	1.32	5.54*	1.91	8.00***	0.70	2.92*	0.24
Planktivores	0.53	0.42	1.19	0.94	0.52	0.42	1.26
Total	0.07	0.34	1.03	4.76**	0.09	0.43	0.22
Macro-invertebrates							
Species richness	4.26	0.12	194.4	5.45**	43.79	1.23	35.6
Total density	0.79	1.11	6.7	9.41***	3.19	4.47**	0.7
Centrostephanus density	0.24	0.15	13.6	8.25***	0.56	0.34	1.6
Heliocidaris density	2.30	0.62	4.5	1.22	3.44	0.93	3.7
Sessile biota cover							
Hard Coral	617.2	4.53*	176.7	1.30	209.7	1.54	136.3
Soft coral	50.1	1.24	147.9	3.67*	14.0	0.35	40.3
Brown algae	532.5	6.19*	213.4	2.48	112.7	1.31	86.0
Green algae	17.4	5.21*	14.7	4.41**	13.9	4.17**	3.3
Red algae	608.5	1.48	491.4	1.20	642.6	1.56	410.9
Encrusting coralline algae	20.4	1.14	62.9	3.50*	14.7	0.82	18.0
Bare substratum	82.0	0.44	233.1	1.26	38.7	0.21	184.9

***$P<0.001$; ** $0.001<P<0.01$; * $0.01<P<0.05$. Degrees of freedom for F-tests are 1/5, 5/21 and 5/21 for MPA type, MPA location and the factor interaction, respectively.

sanctuary zones. By contrast, brown algae showed significantly higher cover in habitat protection zones than in sanctuary zones. Other major indices of substratum cover showed no significant differences between different management zone types ($P>0.05$). The cover of soft coral, green algae and encrusting coralline algae all varied significantly between zone locations (Table 5), while green algae also showed significant interaction between MPA zone type and location.

Community relationships

Principal Coordinates Analysis based on the total data set (192 taxa after taxa recorded from a single site were excluded) for fishes, macro-invertebrates and sessile biota indicated that three distinctive community types exist around the island, with a degree of mixing of these major community types at most locations (Figure 6(A)).

The three primary Lord Howe Island community types comprised: (i) a sheltered coral reef community, as apparent in Sylph's Hole and Comet's Hole; (ii) a macroalgal community, as most evident at the Algal Holes; and (iii) an 'offshore' rocky reef community present off islands and along open coasts with good water clarity. In Figure 6, six regional community types are shown, comprising the three primary types described above plus (iv) a lagoonal community composed of a mixture of coral and macroalgal communities; (v) a north channel entrance community that includes a predominance of macroalgae but also with elements of the offshore and coral communities; and (vi) a southern coast wave-exposed community that comprises a mixture of algal and offshore community types. Somewhat surprisingly because of the distant separation, the biotic communities near Balls Pyramid grouped very closely with the offshore Admiralty Islands sites.

Wave exposure was highly negatively correlated with the first coordinate axis ($R=0.89$), indicating that the primary difference between community types was strongly associated with wave exposure or a correlate. Both depth and underwater visibility were also highly negatively correlated with the first coordinate axis ($R=0.70$, 0.64, respectively), indicating that these three environmental variates were closely related (Figure 6(B)). Transects were generally undertaken at greatest depth at sites with high wave exposure and good water clarity.

Species with abundances highly correlated with the first two coordinate axes subdivided without exception into three very tightly defined groups (Figure 6(B)), which each typified one of the three major community types. Almost half of the species with highest correlations to the first two PCA axes were fish and coral species associated with coral habitat (Table 6). The herbivorous kyphosid *Girella cyanea* was highly associated with macroalgal habitat, which was also closely associated with the algae *Asparagopsis taxiformis*, *Sarcodia ciliata*, *Pterocladia lucida* and 'other red algae'. Offshore reef communities were characterized by species belonging to a wide variety of taxonomic groups, including echinoderms (e.g. *Ophidiaster confertus*), fishes (e.g. *Chromis hypsilepis*, *Amphichaetodon howensis* and *Cirrhitus splendens*), encrusting sponges, hydroids, corals (e.g. *Montastrea curta*), ascidians (e.g. *Herdmania grandis*) and macroalgae (e.g. *Dasya pilosa*).

The species richness, density and biomass of fishes at different trophic levels tended to be very stable between sites within a community type, with a low level of site-to-site variation (see standard deviations in Table 7). Fish species richness was also consistent for each of the trophic feeder groups regardless of community type, with the exception that benthic carnivores were disproportionately rich in species in the coral community (Table 7).

Planktivorous fishes overwhelmingly dominated the offshore community numerically (density data; Table 7). Most planktivorous fishes possessed relatively small body sizes, reducing the biomass of planktivores to levels comparable with benthic carnivores and herbivores in the offshore community. By contrast, many herbivores were large bodied animals, causing the biomass of herbivores present within the macroalgal community to be five times higher than for all other fishes

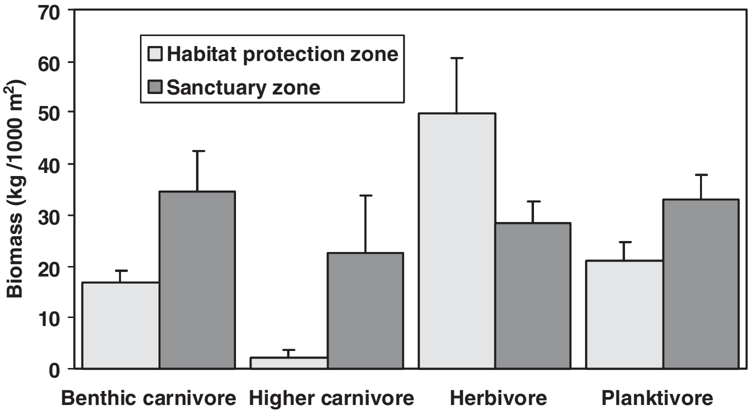

Figure 4. Biomass of fish species belonging to different trophic level feeders recorded per site (adjusted per $1000\,m^2$; ±SD of site means) in two major management zone types.

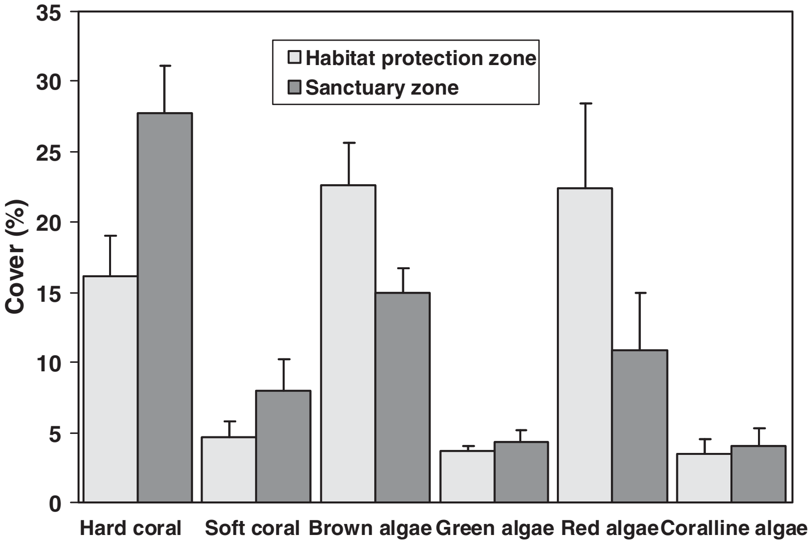

Figure 5. Mean cover (±SE) of hard corals, soft corals, brown algae, green algae and red algae per site in the two major management zone types.

combined. A relatively high biomass of herbivores was also encountered in the lagoon community. The coral community included a very high biomass of carnivorous fishes, with higher carnivores particularly well represented among coral communities compared with other community types.

The numbers of fish species with different biogeographic affinities did not vary greatly between the major community types, with the exception of tropical species, which were much more highly represented in the coral community than elsewhere (Table 8). In communities other than coral, the number of tropical species was about double the number of subtropical and warm temperate species, and the number of endemic, insular and near endemic species was low.

In terms of fish density, warm temperate species tended to predominate at the most wave-exposed areas (particularly offshore and south exposed community types; Table 8), while tropical species predominated in more sheltered areas (particularly coral, lagoon and North Passage community types). The coral reef community type was most important for endemic and near endemic fish species, with the lagoon community type also important. Densities of endemic and near endemic fishes were an order of magnitude greater in these habitat types than elsewhere.

Patterns of distribution of fish biomass among species with different biogeographic affinities were broadly similar to patterns in fish density (Table 8); however, the biomass of warm temperate species in the macroalgal community type was disproportionately high, while the proportionate biomass of warm temperate species in offshore communities was much lower than for the density data set.

Macro-invertebrate abundance and species richness varied greatly between community types (Table 9), with highest numbers found in the two community types exposed to oceanic wave action (offshore and southern). Sites sampled within the sheltered coral community types possessed negligible macro-invertebrate numbers.

Not surprisingly, coral communities possessed the highest percentage cover of hard corals, and also the highest amount

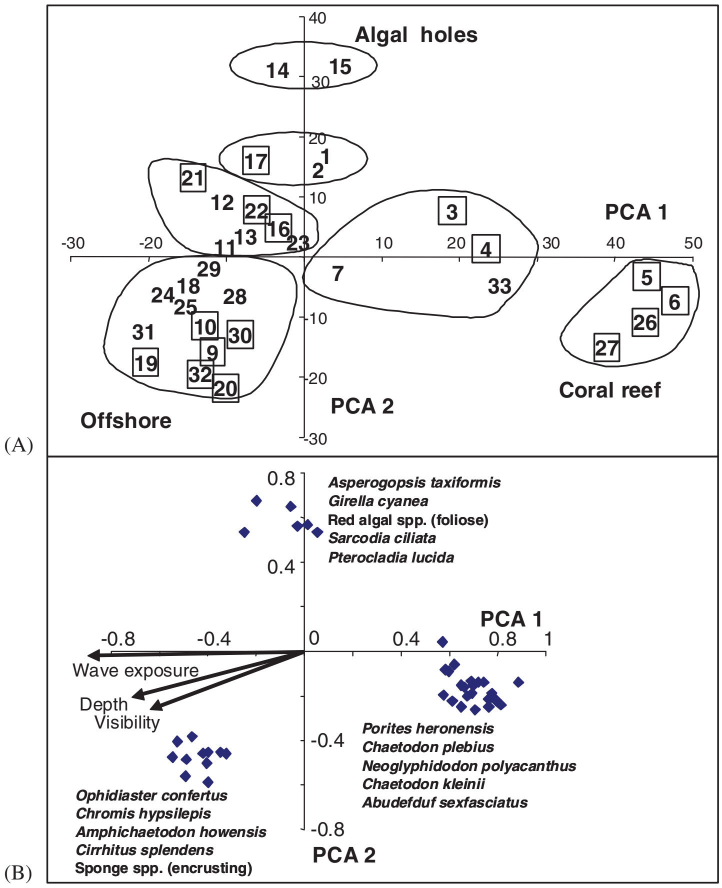

Figure 6. Results of principal coordinates analysis using data combined from the three survey methods. (A) Distribution of sites along first two principal components. (B) Correlation coefficients with PCA1 and PCA2 for 40 species with highest correlations (diamonds) and environmental variates (wave exposure, depth and underwater visibility). Species names are shown for the five taxa most highly correlated with generated groups (see Table 6 for correlation coefficients for these and additional species). Sites labels are as shown in Figure 1, with labels of sanctuary zone sites surrounded by box.

Table 6. Taxa most highly correlated with first two principal coordinate axes of PCA, with associated correlation coefficients

Taxon	Group	PCA1	PCA2	Taxon	Group	PCA1	PCA2
Coral community				Algal community			
Porites heronensis	Coral	0.885	−0.138	*Asparagopsis taxiformis*	Algae	−0.199	0.677
Chaetodon plebius	Fish	0.813	−0.243	*Girella cyanea*	Fish	−0.059	0.650
Neoglyphidodon polyacanthus	Fish	0.793	−0.221	*Foliose red algae*	Algae	−0.248	0.536
Chaetodon kleinii	Fish	0.763	−0.252	*Sarcodia ciliata*	Algae	0.013	0.567
Abudefduf sexfasciatus	Fish	0.775	−0.189	*Pterocladia lucida*	Algae	−0.029	0.561
Centropyge tibicen	Fish	0.764	−0.215	*Stethojulis bandanensis*	Fish	0.080	0.546
Stylophora pistillata	Coral	0.743	−0.138	*Dilophus* spp.	Algae	−0.211	0.472
Chaetodon auriga	Fish	0.707	−0.262				
Chaetodon flavirostris	Fish	0.719	−0.141	Offshore community			
Chaetodon lunulatus	Fish	0.696	−0.188	*Ophidiaster confertus*	Asteroid	−0.496	−0.559
Chaetodon tricinctus	Fish	0.698	−0.152	*Chromis hypsilepis*	Fish	−0.546	−0.477
Amphiprion maccullochi	Fish	0.672	−0.202	*Amphichaetodon howensis*	Fish	−0.399	−0.602
Thalassoma lunare	Fish	0.688	−0.134	*Cirrhitus splendens*	Fish	−0.490	−0.484
Dascyllus aruanus	Fish	0.649	−0.249	Encrusting sponges	Sponge	−0.528	−0.407
Chaetodon melannotus	Fish	0.662	−0.160	*Pseudanthias squamipinnis*	Fish	−0.404	−0.503
Pterois volitans	Fish	0.649	−0.152	Hydroids	Hydroid	−0.420	−0.457
Chaetodon speculum	Fish	0.611	−0.224	*Zanclus cornutus*	Fish	−0.401	−0.454
Canthigaster valentini	Fish	0.621	−0.059	*Montastrea curta*	Coral	−0.467	−0.382
Amblygobius phalaena	Fish	0.577	−0.196	*Dasya pilosa*	Algae	−0.347	−0.456
Lethrinus nebulosus	Fish	0.597	−0.091	*Herdmania grandis*	Ascidian	−0.352	−0.432
Parupeneus ciliatus	Fish	0.585	−0.080	*Plagiotremus tapeinosoma*	Fish	−0.467	−0.293
Pocillopora damicornis	Coral	0.518	−0.263	*Pseudolabrus luculentus*	Fish	−0.474	−0.271
Zebrasoma scopas	Fish	0.569	0.042	*Comanthus wahlbergi*	Crinoid	−0.344	−0.420
Seriatopora hystrix	Coral	0.517	0.000	*Stylaster* spp.	Coral	−0.304	−0.448
				Thamnaconus analis	Fish	−0.334	−0.392
				Cantherines pardalis	Fish	−0.376	−0.348
				Chrysiptera notialis	Fish	−0.450	−0.233

Table 7. Total fish species richness, density and biomass (kg) per 50 m × 5 m transect block for different trophic level feeders in different community types. Standard deviation of site means shown in parentheses

Community	Benthic carnivore	Higher carnivore	Herbivore	Planktivore	Total
Species richness					
Offshore	8.1 (1.0)	0.8 (0.6)	3.7 (0.3)	2.9 (0.8)	15.4 (1.1)
North Passage	9.2 (0.8)	0.2 (0.3)	4.8 (1.8)	3.5 (0.3)	17.6 (2.1)
Lagoon (Erscott's)	7.4 (1.9)	0.5 (0.2)	4.6 (1.0)	3.7 (1.1)	16.1 (2.0)
Coral	13.4 (2.0)	1.5 (0.7)	4.7 (0.7)	4.1 (0.7)	23.7 (3.7)
Southern exposed	6.3 (1.3)	0.5 (0.2)	3.2 (0.5)	3.4 (1.0)	13.4 (2.3)
Macroalgal	7.9 (1.6)	0 0	4.6 (1.2)	2.5 (1.4)	15.0 (1.4)
Overall	8.3 (2.4)	0.6 (0.6)	4 (0.9)	3.3 (0.9)	16.3 (3.6)
Density					
Offshore	45 (15)	1 (2)	29 (14)	300 (158)	376 (156)
North Passage	44 (7)	0 (0)	38 (28)	37 (13)	119 (22)
Lagoon (Erscott's)	37 (14)	0 (0)	53 (16)	139 (78)	228 (72)
Coral	74 (22)	10 (9)	47 (7)	127 (25)	257 (20)
Southern exposed	41 (16)	1 (0)	46 (21)	161 (127)	248 (144)
Macroalgal	54 (14)	0 (0)	60 (18)	63 (24)	176 (8)
Overall	47 (18)	2 (4)	41 (19)	187 (146)	277 (142)
Biomass					
Offshore	5.1 (3.2)	1.7 (3.6)	6.8 (4.8)	5.8 (3.7)	19.4 (9.4)
North Passage	4.6 (0.3)	0.1 (0.2)	7.2 (4.6)	1.7 (0.2)	13.5 (4)
Lagoon (Erscott's)	3.5 (1.6)	1 (2)	15.2 (9.8)	7.1 (1.9)	26.8 (11.4)
Coral	13.1 (8.8)	11.5 (14.9)	5.7 (4.8)	10.2 (4.2)	40.6 (29.8)
Southern exposed	4.3 (2.5)	1.6 (4.1)	4.6 (2.2)	5.1 (2.7)	15.6 (7.4)
Macroalgal	2.2 (0.7)	0 (0)	27.1 (2)	3 (2.7)	32.3 (0)
Overall	5.4 (4.6)	2.5 (6.4)	8.8 (7.6)	5.8 (3.7)	22.5 (14.6)

Table 8. Total species richness, density and biomass (kg) per 50 m × 5 m transect block for fishes with different biogeographic origins in different community types. Standard deviation of site means shown in parentheses

Community	Endemic	Near endemic	Insular	Subtropical	Tropical	Warm temperate	Total
Species number							
Offshore	0.5 (0.3)	0.1 (0.2)	1.1 (0.3)	3.2 (0.4)	6.5 (1.1)	3.6 (0.6)	15.4 (1.1)
North Passage	0.5 (0)	0.3 (0.3)	0.8 (0.3)	3.4 (0.6)	7.9 (0.8)	3.8 (0.5)	17.6 (2.1)
Lagoon (Erscott's)	1.1 (0.5)	1.0 (0.3)	0.5 (0.4)	3.0 (0.8)	7.5 (2.2)	2.8 (1.2)	16.1 (2.0)
Coral	1.7 (0.1)	1.0 (0)	0.3 (0.3)	2.1 (0.3)	14.7 (2.6)	3.1 (1.3)	23.7 (3.7)
Southern exposed	0.6 (0.3)	0.8 (0.5)	0.5 (0.2)	3.0 (0.3)	5.1 (1.3)	3.3 (0.6)	13.4 (2.2)
Macroalgal	0.4 (0.2)	0.3 (0.4)	0.3 (0)	3.3 (0.4)	6.6 (1.6)	4.1 (0.2)	15.0 (1.4)
Average	0.8 (0.5)	0.5 (0.5)	0.7 (0.4)	3.0 (0.6)	7.5 (3.2)	3.4 (0.8)	16.3 (3.6)
Density							
Offshore	2 (3)	11 (36)	2 (1)	82 (66)	42 (35)	236 (131)	376 (156)
North Passage	2 (0)	1 (1)	2 (1)	28 (7)	55 (20)	27 (5)	119 (22)
Lagoon (Erscott's)	5 (3)	33 (26)	1 (1)	42 (18)	102 (62)	44 (44)	228 (72)
Coral	22 (14)	37 (13)	1 (1)	17 (5)	148 (17)	20 (12)	257 (20)
Southern exposed	2 (1)	7 (7)	1 (2)	84 (62)	38 (18)	116 (109)	248 (144)
Macroalgal	1 (1)	1 (1)	0 (0)	38 (2)	68 (3)	69 (3)	176 (8)
Average	5 (8)	15 (27)	1 (1)	61 (55)	66 (50)	126 (128)	277 (142)
Biomass							
Offshore	0.3 (0.2)	0.1 (0.1)	1.2 (2.3)	4 (1.9)	7.4 (7.1)	6.4 (2.7)	19.4 (9.4)
North Passage	0.2 (0.1)	0 (0)	0.7 (0.3)	4.5 (1.9)	4.2 (1.8)	3.7 (1.7)	13.5 (4)
Lagoon (Erscott's)	0.5 (0.3)	2.3 (1.8)	0.4 (0.4)	3.5 (1.6)	15.4 (12.8)	4.5 (3.2)	26.8 (11.4)
Coral	3.4 (2.7)	2.3 (2.4)	0.2 (0.4)	1.7 (0.6)	22.8 (14.8)	9.7 (11.3)	40.6 (29.8)
Southern exposed	0.2 (0.2)	0.4 (0.5)	1.4 (2.2)	4.1 (1.8)	4.2 (5)	5.2 (2.6)	15.6 (7.4)
Macroalgal	0.1 (0.1)	0 (0)	0 (0)	3.3 (0.5)	15.1 (6.5)	13.8 (6.9)	32.3 (0)
Average	0.7 (1.3)	0.7 (1.4)	0.9 (1.7)	3.7 (1.7)	10.0 (10.2)	6.5 (5)	22.5 (14.6)

of bare substratum in the form of dead coral rubble (Table 10). Together, these two substratum categories covered 80% of the sea bed among coral communities. Macroalgal communities, on the other hand, possessed almost 80% cover of foliose red algae. Sites in other community types possessed a range of different substratum types.

Table 9. Total number of species and abundance of benthic invertebrates, *Centrostephanus rodgersii* and *Heliocidaris tuberculata* per site for different community types. Standard deviation of site means shown in parentheses

Community	Invertebrate species	Invertebrate density	*Centrostephanus* density	*Heliocidaris* density
Offshore	20.1 (6.8)	242.8 (144.8)	93.8 (98.8)	14.2 (32.5)
North Passage	7.7 (5.5)	118.3 (118.4)	67.7 (69.4)	46.0 (47.0)
Lagoon (Erscott's)	11.4 (6.0)	159 (227.3)	5 (6)	138.4 (218.5)
Coral	3.0 (3.5)	4.8 (5.6)	0 (0)	0 (0)
Southern exposed	20.7 (4.8)	171.3 (29.3)	96.1 (52.4)	14.6 (27.6)
Macroalgal	12.0 (1.4)	77.0 (76.4)	14.5 (16.3)	46.0 (65.1)
Average	15.2 (8.4)	164.7 (145.1)	62.3 (77.1)	36.2 (94.0)

Table 10. Mean cover (%) of major sessile invertebrate taxa, macroalgal taxa and bare substrata for different community types. Standard deviation of site means shown in parentheses

Community	Hard corals	Soft corals	Brown algae	Green algae	Red algae	Coralline algae	Bare substrata
Offshore	16.9 (10.7)	12.1 (9.0)	22.0 (9.4)	4.7 (3.0)	15.7 (16.3)	2.4 (2.3)	23.7 (11.2)
North Passage	22.6 (10.7)	0.4 (0.2)	17.4 (9.3)	5.2 (1.5)	22.2 (12.0)	10.2 (7.0)	22.0 (3.1)
Lagoon (Erscott's)	29.7 (14.8)	5.7 (4.2)	24.1 (15.2)	3.6 (2.3)	1.0 (1.1)	0.2 (0.4)	35.7 (8.1)
Coral	39.4 (15.7)	2.1 (2.8)	12.4 (10.7)	1.0 (1.4)	0.1 (0.1)	3.7 (4.9)	40.9 (12.7)
Southern exposed	21.0 (10.2)	3.1 (2.8)	18.7 (9.5)	4.8 (2.4)	16.7 (14.5)	5.7 (6.4)	30.0 (15.6)
Macroalgal	3.9 (1.3)	1.2 (1.7)	3.8 (3.6)	1.7 (0.7)	78.3 (3.2)	1.5 (0.8)	9.6 (1.5)
Average	22.0 (13.8)	6.3 (7.4)	18.8 (10.8)	4.0 (2.7)	16.7 (21.5)	3.7 (4.8)	27.7 (13.3)

DISCUSSION

Regional biogeographic influences on biota

A characteristic feature of Lord Howe Island is the relatively large number of endemic marine plants and animals, particularly when defined to include the broader region encompassing Norfolk Island, Elizabeth Reef and Middleton Reef. The endemic biota represents *c.*4% of total fish (Allen *et al.*, 1976; Francis, 1991; 1993), 8% of echinoderms (Pollard and Burchmore, 1985; Hoggett and Rowe, 1988), and 15% of macroalgal species (Millar and Kraft, 1993, 1994a, b; Kraft, 2000). Moreover, the recent description of the endemic Lord Howe Island sea horse *Hippocampus colemani* (Kuiter, 2003), a charismatic species that had formerly been overlooked because of cryptic habits, affirms the likelihood that future studies will identify additional endemic species. Yet while new endemic taxa will undoubtedly be added to the island's species list through the future, the proportion of island endemics may not change greatly because other species now considered endemic will presumably prove be more widely distributed than currently known.

Lord Howe Island lies at a marine biogeographic crossroad with a biotic mix of different distributional elements, including endemic, insular, tropical, subtropical and warm temperate species. The contributions of these different biogeographic elements vary between taxonomic groups and location, and also depend on whether species richness or abundance is considered.

Tropical species dominate the subtidal reef fauna at Lord Howe Island in terms of species numbers. The percentage contribution of tropical species to the total fauna was consistently around 75%, regardless of whether fishes, mobile macro-invertebrates or sessile invertebrates were assessed. Allen *et al.* (1976) also found tropical species comprised *c.*75% of inshore fishes recorded for the region. On the basis of the small sample size of species identified, a lesser proportion of the subtidal flora appears to be tropical (*c.*40%).

Although tropical species tend to dominate Lord Howe Island faunal lists, warm temperate species were numerically abundant and contributed disproportionately to the total density and biomass of reef communities (Table 2). Of the 110 tropical fish species recorded here, 20 species were observed only as single individuals, while less than 10 individuals were observed for over half of the tropical fish species. The proportionate abundances of warm temperate fish and macro-invertebrate species were 46% and 70%, respectively, whereas these groups contributed only 13% and 18% of total species numbers. Fish species with subtropical affinities also occurred in disproportionately high numbers, with the 11 subtropical species contributing approximately the same number of individuals observed as the 110 tropical species (Table 2).

The difference in contribution of the various biogeographic elements, depending on whether presence or abundance data are used, has both scientific and management implications. For broad-scale planning purposes, and for identifying biogeographic patterns at oceanic basin scales, presence – absence data as compiled in species lists provide a good representation of geographic variation. By contrast, abundance and biomass data more closely reflect local environmental conditions (Steinitz *et al.*, 2005), thereby providing a better basis for understanding ecological processes and for discerning finer-scale patterns at the within-island scale.

Tropical fish species present at Lord Howe Island have lower conservation significance as a group than subtropical, warm-temperate or endemic taxa. Their low abundances indicate that population strongholds are largely elsewhere, and that few possess significant functional roles in local ecosystems. Most tropical species presumably drift south with the East Australian Current as vagrants and lack a self-sustaining population on the island. The East Australian Current, which forms the most important transport vector for tropical planktonic organisms arriving at the island (Harriott, 1995; Harriott and Banks, 1995), flows from the north along the eastern seaboard of the Australian continent and then swings offshore in pulses from about September to December (Nilsson and Cresswell, 1981).

Biogeographic patterns for corals are similar to those for fishes, with the majority of species possessing populations centred in the tropics and with very low densities at Lord Howe Island. Most tropical coral species presumably settle episodically without establishing self-recruiting populations (Harriott *et al*., 1993). Notable exceptions to this generalization are the tropical corals *Acropora palifera*, *Porites lichen* and *Pocillopora damicornis*, which, together with the subtropical corals *Acropora glauca* and *Porites heronensis*, locally dominate coral communities and generate important habitat structure (Harriott *et al*., 1995).

Habitat provided by coral is highly significant from a conservation perspective, in part because of its value for endemic taxa. A mean of 2.7 endemic and near-endemic fish species were sighted per transect amongst the coral community type, compared with 0.7 and 0.6 species among the macroalgal and offshore community types, respectively (Table 8). Biomass of endemic and near endemic fish showed even greater differentiation, with over an order of magnitude higher biomass in the coral community type compared with macroalgal and offshore community types.

The percentage of the known Lord Howe Island marine fauna of tropical origin is likely to disproportionately increase with additional sampling (Francis, 1991), given that the pool of tropical species in nearby regions is much larger than in temperate regions, and that tropical species tend to be more widely distributed than temperate taxa because of the prevalence of long-distance dispersing larvae (Hutchins *et al*., 1991; Randall, 1999; Ayre and Hughes, 2000; Harriott and Banks, 2002). This prediction is supported by the four new fishes records reported here, all species with wide tropical distributions. It is also consistent with the trend in recent taxonomic studies of fish at Lord Howe Island to add new records for the island based on a few individuals of widespread Indo-Pacific species (Francis and Randall, 1993). Coral studies indicate substantial turnover of species at Lord Howe Island, with apparent loss of some uncommon species and recruitment of others at decadal scales (Harriott *et al*., 1995; Harrison *et al*., 1995).

By contrast, warm temperate and subtropical species present on Lord Howe Island reefs tend to have much larger population sizes. Many probably possess self-recruiting populations on the island, as indicated by analysis of chemical otolith markers for the warm temperate wrasse *Coris picta* (Patterson and Swearer, 2007). About half of all individuals of this species examined at Lord Howe Island had apparently recruited from the New South Wales coast, while the other half derived through local breeding and self-recruitment mechanisms.

Larval connectivity with the New South Wales coast probably occurs through advection in eddies derived from the East Australian Current (Patterson and Swearer, 2007). This ecological pathway possibly operates in both directions, as several abundant fish species at Lord Howe Island (e.g. *Aplodactylus etheridgii*, *Amphichaetodon howensis* and *Cirrhitus splendens*) occur in low numbers on the mainland NSW coast (Kuiter, 1993), probably as vagrant larval settlers.

Maintenance of all self-recruiting populations should comprise a long-term management goal for the island. The small total population sizes of endemic, near endemic species and some insular species such as the wrasse *Coris bulbifrons* (Patterson and Swearer, 2007) make them important conservation targets (Edgar *et al*., 2008). Many would in fact qualify under IUCN Red List Criteria (IUCN, 2001) as threatened if formally assessed on grounds of small range size, low total population numbers, and existence of stochastic threats. For wider ranging species, self-recruiting populations at Lord Howe Island expand the range of genotypic variation within species (Ayre and Hughes, 2004; Miller and Ayre, 2004), thus providing some adaptive insurance for changing environmental conditions across the broader distributional range (Baums, 2008).

Local distributional patterns

Coral and macroalgal communities observed in this study were broadly similar to those reported in 1977, 1992–1994, 1999 and 2002 (Veron and Done, 1979; Harriott *et al*., 1993, 1995; Harrison *et al*., 1995; Harrison and Carroll, 2002; Bullard, 2003), with the same genera and species of corals and macroalgae generally dominant. Previous studies had, however, reported change in coral dominance at particular sites between 1977 and 1992 (Pollard and Burchmore, 1985; Harrison *et al*., 1995), including a change in dominant coral in the northern lagoon at Sylph's Hole from *Pocillopora damicornis* to *Porites* species. In 2006 surveys, sites 26 and 27 at Sylph's Hole remained dominated by *Porites*, with 23% average cover of that genus compared with 2% cover for *Pocillopora.*

Surveys undertaken during the current study included a much broader spatial and taxonomic coverage than had previously been attempted around the island, albeit with less detail on the distribution of corals at individual sites. No previous investigation had quantitatively reported on the distribution of mobile macro-invertebrates or fishes, other than surveys specifically directed at the crown-of-thorns sea star *Acanthaster planci* (DeVantier and Deacon, 1990; Harriott *et al*., 1993; Harriott, 1995; Harrison *et al*., 1995) and a recent survey of reef fishes (Lindsay *et al*., 2008).

Among sites sampled, the coral community occurred most characteristically at Sylph's Hole (sites 26 and 27) and Comet's Hole (sites 5 and 6) within the lagoon. With the likely addition of Erscott's Hole, which was not surveyed but is also known to be very coral rich (Harrison and Carroll, 2002), these lagoon holes comprise a distinctive geomorphological feature that is unlikely to be replicated elsewhere at Lord Howe Island. Moreover, no other known locations in the region possess macroalgal communities as rich and productive as those at Algal Holes at the southern end of the lagoon, so this community type is also unlikely to be duplicated elsewhere.

The distinctive coral and macroalgal community types present in LHIMP can be regarded in many respects as displaced tropical and warm temperate communities, respectively. The coral community type possessed most features typical of coral reefs, including (i) a substratum dominated by reef corals that overlay a framework of coral rubble, (ii) negligible mobile macro-invertebrates, (iii) a predominance of tropical fishes and invertebrate species, and (iv) a high biomass of predatory fish species. By contrast, temperate characteristics predominated in the macroalgal community, including (i) foliose macroalgae dominating almost all (84%) of the substratum, (ii) warm temperate species comprising a relatively high proportion (43%) of biomass of all fishes present, (iii) an exceptionally high biomass of herbivorous fishes, and (iv) macrobenthic invertebrate fauna dominated by the warm temperate sea urchin species *Centrostephanus rodgersii* and *Heliocidaris tuberculata*.

The close (<3 km) proximity of tropical and temperate community types in the waters surrounding Lord Howe Island represents an anomalous biotic feature in a global sense. Other locations worldwide that possess temperate macroalgal-dominated and tropical coral ecosystems in close proximity (e.g. Abrolhos Islands, Solitary Islands, Galapagos Islands — Johannes *et al.*, 1983; Hatcher *et al.*, 1987; Harriott *et al.*, 1994; Harriott and Banks, 1995; Edgar *et al.*, 2004a) tend to have patchy interspersion of coral with macroalgae at scales <1 m rather than reefs with $>80\%$ coral and coral rubble cover immediately adjacent to beds with $>80\%$ macroalgal cover, as observed here.

The close interspersion of ecosystem types at Lord Howe Island provides an opportunity to identify functional mechanisms underlying the development of coral reefs and macroalgal beds. In particular, much scientific attention has focused on the primary factors responsible for coral versus macroalgal dominance (Lirman, 2001; McCook *et al.*, 2001; Jompa and McCook, 2002), and tropical to temperate gradients in species diversity (Rohde, 1978; Mora and Robertson, 2005; Kerswell, 2006)–two topics that still remain largely unresolved. With careful planning, the relative importance of predation, herbivory, competition and environmental influences could be disentangled at Lord Howe Island where coral and macroalgal community types have access to the same regional species pool.

At present we can only speculate on the factors contributing to the separate development of these two adjacent community types. In the Principal Coordinates Analysis (PCA), the overriding factor affecting Lord Howe Island biotic communities was wave exposure or a close correlate. The extremely high correlation between PCA axis 1 and wave exposure ($R^2 = 0.80$) was in fact unexpected, given the semi-quantitative ranks used to classify wave exposure and associated error thereby introduced. With respect to biotic differences between coral and macroalgal community types, the separation between these groups was partly related to the wave exposure gradient indicated by PCA axis 1, but was more related to unknown factors related to PCA axis 2 (Figure 6).

Among the major factors suggested elsewhere to contribute to algal dominance over corals – reduced herbivory, reduced predation rates, reduced aragonite saturation rates, differential larval settlement, reduced water temperatures, decreased solar radiation, and increased nutrient levels (Tanner, 1995; Barber *et al.*, 2001; Harriott and Banks, 2002; Yap and Molina, 2003) – local nutrient enrichment seems the most likely causal factor at Lord Howe Island. Perhaps rainfall captured on the high wet peaks of southern Lord Howe Island percolates through soil and humus, and is then channelled via gullies and aquifers to the Algal Holes area. An understanding of local hydrological processes is needed to manage optimally the conservation values of this site.

Management of human impacts

Reef ecosystems within LHIMP appeared in good condition in 2006, with little indication of recent coral mortality or disease. This assessment is similar to the previous assessments (Harrison and Carroll, 2002; Bullard, 2003); nevertheless, the marine environment remains subject to a variety of potential and actual threats, including climate change, introduced and invasive species, fishing, nutrification and sedimentation, and diving impacts.

Climate change clearly poses the largest potential threat to Lord Howe Island marine ecosystems. This island is particularly susceptible to changing ocean climate because of its location on the seasonally-varying Tasman Front. A relatively small increase in global water temperatures will likely push the Tasman Front southward, leading to continual tropical conditions, as is presently the case 200 km north at Elizabeth and Middleton Reefs. Conversely, a relatively small decrease in temperatures would lead to prolonged temperate conditions. In either case, conditions would become unsuitable for a major component of local biodiversity and a major component of the biota could be lost.

The sensitivity of local biota to changing environmental conditions is indicated by the historical extirpation of beds of the fucoid alga *Hormosira banksii*. This species was once a dominant organism on intertidal shores of the lagoon; however, beds declined rapidly during the 1930s (Lucas, 1935), and the species has since been regarded as regionally extinct (Millar and Kraft, 1994b). Endemic algal species are likely threatened by similar processes, particularly as temperatures warm globally.

Coral reef communities at Lord Howe Island are also threatened by climate change, through bleaching associated with thermal stress (Graham *et al.*, 2006; Carpenter *et al.*, 2008), and by the more pervasive effects of ocean acidification and reduced saturation of carbonate relative to bicarbonate (Orr *et al.*, 2005; Poloczanska *et al.*, 2007). In March and April 1998, significant coral bleaching occurred at Lord Howe Island, with up to 80% of corals reportedly bleached at some sites. Subsequent surveys in July 1998 indicated that most corals had recovered from bleaching (Harrison and Carroll, 2002), and only 2% of corals remained in bleached condition at that time (P. Harrison and T. Kitchener unpub. data, cited in Harrison and Carroll, 2002). Only 0.8% of live coral was observed to be bleached in the current study. While it could be argued that the highly variable oceanographic climate and the rapid recovery of corals from the 1998 bleaching event indicate that Lord Howe corals are pre-adapted to thermal anomalies, the local magnitude of coral bleaching in 1998 (80%) is a major counter-indication. Any increase in the period of bleaching, as can be expected under future climate change scenarios (Poloczanska *et al.*, 2007), will likely lead to substantially higher coral mortality.

Although no introduced marine species have been detected at Lord Howe Island (Aquenal, 2006), the threat to marine biodiversity posed by invasive species is also potentially huge (Molnar *et al.*, 2008). Once exotic species such as invasive algae establish, they can alter ecosystems in fundamental ways (Occhipinti-Ambrogi and Savini, 2003; Smith, 2003; Millar, 2004). Ongoing monitoring and prompt response to any incipient outbreaks are important management goals. Programmes to eradicate introduced species are generally impossible or economically unfeasible once species are well established, although the small size of Lord Howe Island will greatly assist any eradication programme if deemed necessary.

In addition to introduced marine pests, explosive outbreaks of native species can also compromise local biodiversity values. Three echinoderm species are of particular concern at Lord Howe Island — crown-of-thorns sea star (*Acanthaster planci*), hollow-spined urchin (*Centrostephanus rodgersii*), and the white urchin (*Tripneustes gratilla*).

The risk of *Acanthaster* outbreaks has long been recognized, with surveys specifically targeted at this species (DeVantier and Deacon, 1990; Harriott, 1995). Despite an apparent increase from initial surveys in 1984 to the late 1990s

(Harriott, 1995; Maniwavie *et al*., 2000), few examples of recent coral mortality were evident in surveys and numbers of *A. planci* were low. In the present study, only a single *A. planci* was recorded on transects (site 24 at 20 m depth) while a second individual was observed at the same site, off transect.

By contrast, densities of *C. rodgersii* were very high, with small urchin 'barrens' present in some areas, most notably in the Admiralty Islands region and at offshore and coastal sites exposed to oceanic swell. A major expansion of urchin barrens could potentially cause island-wide declines in biodiversity.

Macroalgal communities have suffered catastrophic decline elsewhere through sea urchin overgrazing, including off eastern Australia, Tasmania and the oceanic Galapagos archipelago (Andrew and O'Neil, 2000; Johnson *et al*., 2005; Sonnenholzner *et al*., 2009). The threat posed by urchin barren formation appears to be facilitated by increasing influences of warm currents, which stress native communities and contribute to larval dispersal (Tegner and Dayton, 1991, 2000; Pederson and Johnson, 2006), and overfishing of urchin predators. Fishers primarily target large predatory fishes and lobsters, with their removal allowing urchin numbers to increase and urchin barrens to form, which in turn adversely affects macroalgal beds and associated species (Tegner and Dayton, 1999; Ling, 2008).

The possibility that urchin barren expansion at Lord Howe Island could cause species extinction is greater than on continental coasts because of the island's small size, the relatively large number of endemic macroalgae and invertebrates, and habitat-modifying behaviour and life-history attributes of local urchin species. *Centrostephanus rodgersii* is a broad-scale spawner that releases hundreds of thousands of eggs, possesses a larval stage of 3–4 months, and utilizes long-distance episodic recruitment (Huggett *et al*., 2005; Banks *et al*., 2007; Ling, 2008; Ling *et al*., 2009).

Tripneustes gratilla is another potentially invasive sea urchin. Although absent from most sites, this urchin has been reported elsewhere as a destructive grazer (Alcoverro and Mariani, 2002) and observations in 2008 indicate a huge increase in numbers since the 2006 surveys (G. Edgar, J. Valentine, unpublished data). Populations of *C. rodgersii*, *T. gratilla* and the red urchin *Heliocidaris tuberculata* should be specific targets of reef monitoring programmes through the long term, in order to track changes in population density, the distribution of urchin barrens, and changes to other reef organisms at sites with increasing urchin density. If urchin barrens threaten the conservationally important macroalgal habitat, then manual removal of sea urchins should be considered (McClanahan *et al*., 1996). Diver removals are, however, only likely to be effective at scales < 1 km^2 because of high cost.

Although most marine habitats in the lagoon and elsewhere around the island showed little apparent impact of human activity, localized habitat degradation was evident at a few locations. Divers noted patchy growth of epiphytic cyanobacteria and filamentous algae at shallow subtidal sites in the north-eastern section of the lagoon, primarily in seagrass beds, although also on some coral heads. This growth probably reflected elevated levels of nutrients or a paucity of herbivores, or a combination of these two factors (McCook, 1999; Szmant, 2002; Fabricius *et al*., 2005). Epiphyte growth was most evident at Signal Point (site 33) near the central township, suggesting one or more of the following causes: (i) seepage of nutrient enriched groundwater; (ii) ineffective management of waste from nearby premises; or (iii) disposal of wastes from moored boats.

While impacts of nutrification can be regarded as a localized threat to marine biodiversity, potential sources of nutrients require active management to prevent more widespread degradation. Studies of relationships between nutrient enrichment, sediment smothering, algal overgrowth of corals and seagrasses, and habitat change in the local environment should be encouraged and supported. Targeted studies aimed at quantifying the magnitude and distribution of three other localized threats to marine habitats — propeller scraping in seagrass, anchor damage, and seabed contact by divers — would also usefully inform management.

Compared with the situation in eastern Australia, fishing pressure within LHIMP is low. All fishing is prohibited in sanctuary zones that cover 27% of the marine park, and no fishing for export is undertaken in other zones. The Lord Howe Island marine environment is also free of the most damaging fishing practices, which include trawling, dredging, long-lining and gill net fishing. The impacts of fishing most likely to affect biodiversity are secondary impacts associated with removal of top predators in fished habitat protection zones.

Quantification of ecological patterns in different park zones generated two major benefits for LHIMP managers: (i) the collection and archiving of baseline data against which ecological changes in different management zones can be compared through time, and (ii) description of the distribution of marine biodiversity, which allows the representativeness and comprehensiveness of the current zoning scheme to be assessed. The process used between 1999 and 2004 to delineate management zones in LHIMP was aimed at maximizing representation of the various local habitat classes within sanctuary zones; however, few ecological data were available at the time. Zones were defined on the basis of habitat data obtained through coral surveys concentrated in the Lagoon region, habitat boundaries visually delineated from aerial maps, and anecdotal information provided by local divers (Lindsay *et al*., 2008).

Biotic differences across LHIMP are strongly related to the wave exposure gradient. The current zoning scheme captures this variation well. The most sheltered habitats are contained within the Lord Howe Island Lagoon, North Bay and Sylph's Hole Sanctuary Zones, the most wave exposed habitats within the East Coast, Observatory Rock and South East Rock Sanctuary Zones (the latter two located adjacent to Balls Pyramid), and habitats with intermediate levels of wave exposure in the majority of sanctuary zones, which are generally zoned out from the coast into water depths >20 m.

Of the three major community types identified in the present study (Figure 6), (i) the offshore community is well represented within most sanctuary and habitat protection zones, (ii) the coral community is only known from two sanctuary zones (Sylph's Hole and Lord Howe Island Lagoon), and (iii) the macroalgal community is represented only in one habitat protection zone. The lack of protection from fishing of any representative component of the macroalgal community is a serious concern given the potential threat to macroalgal communities posed by urchin barren expansion, fishing and climate change.

In addition to biodiversity conservation issues, the biased distribution of sanctuary zones around Lord Howe Island with respect to the three fundamental community types complicates scientific assessment of the ecological effectiveness of the current zoning scheme. In statistical comparisons through time, coral community sites in sanctuary zones are compared with reference sites with somewhat different characteristics in habitat protection zones, and macroalgal community sites in habitat protection zones are compared with somewhat different sites in sanctuary zones. In both cases, optimal reference sites for macroalgal and coral community comparisons are either not locally available or not known.

Additional survey work is needed to determine whether an example of the macroalgal community type exists within a sanctuary zone for inclusion in the monitoring programme. If no comparable site exists, then the MPA zoning plan should be amended if possible to include the Algal Holes within a sanctuary zone. Such a change in the zoning plan would help protect the macroalgal community type from expansion of urchin barrens. From the perspective of scientific monitoring, the establishment of at least one coral monitoring site within a habitat protection zone is also desirable.

Overall, the experimental design applied in this study will allow changes in biotic variates following protection from fishing to be adequately detected at the scale of populations across LHIMP, although not at the scale of coral and macroalgal community types. Mean values for most biotic variates were similar in sanctuary and habitat protection zones when calculated across the full extent of LHIMP, with differences in mean values generally small and non-significant.

Variates that differed significantly between habitat protection and sanctuary zones in 2006 comprised coral cover and green algal cover, which were highest in sanctuary zones, and herbivore biomass and brown algal cover, which were highest in habitat protection zones. These differences probably reflected site-to-site differences at the locations studied rather than an effect of protection from fishing in sanctuary zones. This is particularly likely for coral cover given that coral community sites were all located in sanctuary zones, and also for brown algal cover given that macroalgal community sites were confined to habitat protection zones.

The short time span since gazetting of the marine park zones makes it unlikely that fishing protection has already led to a substantial increase in the abundance and biomass of fish predators at the island scale (Edgar *et al*., 2009). Sites 5 and 6 (Comet's Hole) nevertheless possessed de facto sanctuary status for about four decades prior to declaration of LHIMP due to the local desire to safeguard Comet's Hole for glass-bottom boat viewing and snorkel tourism. These lagoonal sites notably possessed extremely high abundances of carnivorous fishes (Figure 2), which contributed to elevated densities of this trophic group in sanctuary zones relative to habitat protection zones overall (Figure 4). Comparisons between results of future monitoring surveys and baseline survey data described here should help clarify ecological changes associated with different zones, and the extent to which local site issues including historical de facto protection, has affected populations of predatory and herbivorous fishes.

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