

Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants

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Abstract

The reef biota in four Tasmanian marine reserves and at associated unprotected reference sites was investigated over a 6-year period following protection from fishing. The largest reserve at Maria Island (7 km coastline length) proved the most effective at achieving species conservation and resource enhancement. The number of fish, invertebrate and algal species, the densities of large fishes (> 325 mm length), bastard trumpeter (*Latridopsis forsteri*) and rock lobsters (*Jasus edwardsii*), and the mean size of blue-throated wrasse (*Notolabrus tetricus*) and abalone (*Haliotis rubra*), all increased significantly within the Maria Island reserve relative to external reference sites. Increases of an order of magnitude in the biomass of rock lobsters and two orders of magnitude in the abundance of trumpeter were particularly noticeable. Small abalone declined in density within the reserve, while large abalone became more numerous. The effectiveness of marine reserves corresponded with reserve size. Changes in species richness of fishes, invertebrates or plants were not detected in any of the three smaller reserves, other than an increase in number of fish species greater than 325 mm size within the Tinderbox marine reserve (2 km reserve length). Although patterns were partly obscured by the low power of statistical tests, trends were generally evident at the Tinderbox reserve for increasing densities of large fishes and rock lobsters, and for increases in the mean size of rock lobsters, abalone and blue-throated wrasse. Most of these trends were not apparent in the reserves with small reef areas at Governor Island (1 km reserve length) and Ninepin Point (1 km length). Rock lobsters above the legal size limit nevertheless became abundant in all reserves by the end of the study while remaining rare outside. Indirect changes to reef assemblages were also detected following the declaration of the Maria Island marine reserve. Accompanying the increase in macroalgal species richness was a change in predominant plant species from *Cystophora retroflexa* to *Ecklonia radiata*. Results of this study provide the first clear evidence that shallow Tasmanian reef ecosystems are overfished, and that unfished coastal ecosystems differ substantially from those where fishing occurs. The most

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noticeable changes caused by fishing were the virtual elimination of net-susceptible and heavily targeted species, which may otherwise be common, plus indirect changes to algal communities. We suggest that ecosystem change associated with fishing of shallow coastal reefs may be a widespread phenomenon worldwide. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Ecologically sustainable development of coastal ecosystems is now recognised by most government agencies to involve more than the management of individual species, because the exploitation of one resource will have effects on others. Consequently, an increasing number of marine reserves and other forms of marine protected area are being proclaimed around the world with the primary purpose of enhancing fishery stocks (Davis, 1981; Roberts and Polunin, 1991; Dugan and Davis, 1993; Attwood and Bennett, 1996). Marine reserves are also increasingly declared to conserve marine biodiversity, partly because the distribution and taxonomy of marine species is poorly known compared to terrestrial species, so single species management is more difficult and assemblage protection more desirable when dealing with marine communities (Roberts and Polunin, 1993; Sobel, 1993).

Most investigations of ecological interactions in the marine environment rely on manipulation of plant and animal densities at the scale of metres, such as the removal of particular grazers or predators from patches of shore. Processes operating at these small scales often differ from those operating at larger scales, so conclusions reached cannot be extrapolated to the more interesting larger domains without validation (Eberhardt and Thomas, 1991; Menge, 1992). The investigation of marine reserves offers one opportunity to carry out such validation because unfished areas are created that extend up to hundreds of square kilometres, and these areas can be compared with areas where resources are continuously removed (Walters and Holling, 1990). The establishment of marine reserves thus represents a manipulative removal experiment at a vast spatial scale.

Given the theoretical and practical benefits that result from research into the effects of marine reserves, the number of publications that present empirical data on this topic is surprisingly limited, particularly when compared with the number of reviews and desktop studies that make general recommendations (recent examples are Jones et al., 1993; Kenchington and Bleakley, 1994; McNeill, 1994; Gubbay, 1995; Attwood et al., 1997; Allison et al., 1998). Field investigations of subtidal marine reserves (most notably Bell, 1983; Buxton and Smale, 1989; Russ and Alcala, 1989, 1996a,b; Cole et al., 1990; Bennett and Attwood, 1991; Roberts, 1995; McClanahan and Kaunda-Arara, 1996; Rakitin and Kramer, 1996; Wantiez et al., 1997; McClanahan et al., 1999) also vary in quality, with studies generally confounded by intrinsic ecological differences between sites investigated inside and outside reserves, by a lack of site and reserve replication, or

by the absence of information about the biota existing at the time reserves were declared. Moreover, virtually no studies have investigated the effects of marine reserves across a range of taxa in order to assess indirect effects (but see McClanahan et al., 1999). Because of the ubiquity of secondary effects in marine ecosystems (see, for example, Menge, 1995), the tacit acceptance that resource enhancement aims are achieved with the declaration of marine reserves is questionable. Only a small proportion of exploited species may be adequately conserved in some marine reserves.

In the present study, changes to reef assemblages associated with four ‘no-take’ marine reserves are described for a 6-year period following protection from fishing. Results obtained during the first 2 years of the study were described in an earlier paper (Edgar and Barrett, 1997). The reserves investigated, at Governor Island, Maria Island, Tinderbox and Ninepin Point on the eastern and southeastern Tasmanian coasts (Fig. 1), were declared on 18 September 1991 for a variety of reasons. The largest reserve at Maria Island was primarily declared in order to conserve marine habitats representative of the Tasmanian east coast, the Ninepin Point reserve was declared to protect an unusual habitat, and the Tinderbox and Governor Island reserves were declared primarily for recreational purposes (Edgar, 1984b). Given that the recreational value of a marine reserve depends partly on numbers of large fishes and rock lobsters observed by divers, a common management objective of all four marine reserves was that numbers of exploited species return to undisturbed levels.

In addition to the major aim of determining whether protection from fishing within reserves leads to a predicted increase in abundance and mean size of exploited species, a second aim of the study was to identify any indirect effects of fishing on marine ecosystems. Indirect effects could not be predicted because of complicated chains of relationships between organisms associated with reefs. For example, in small-scale Australian and New Zealand studies, the removal of reef fish has been found to increase the survival of juvenile sea urchins (Andrew and Choat, 1982). High numbers of sea urchins can denude reefs of macroalgae (Choat and Andrew, 1986; Fletcher, 1987; Andrew and Underwood, 1993), while the presence of macroalgae can in turn affect densities of fishes (Choat and Ayling, 1987; Jones, 1992).

2. Methods

2.1. Sites examined

Biological changes that followed the declaration of marine reserves were quantified using underwater visual censuses at sites within reserves and at reference sites outside reserves that possessed a similar habitat type (Edgar and Barrett, 1997). The effects of reserves could only be distinguished from long term trends in Tasmanian coastal waters when changes in a reserve were found to be significantly larger or smaller than changes outside the reserve (Green, 1979). Historic data on unexploited population densities for reef-associated species in Tasmania are almost completely lacking.

The four Tasmanian marine reserves investigated varied substantially in size, with ≈ 7 km of coastline protected from fishing in the Maria Island Marine Reserve, 2 km

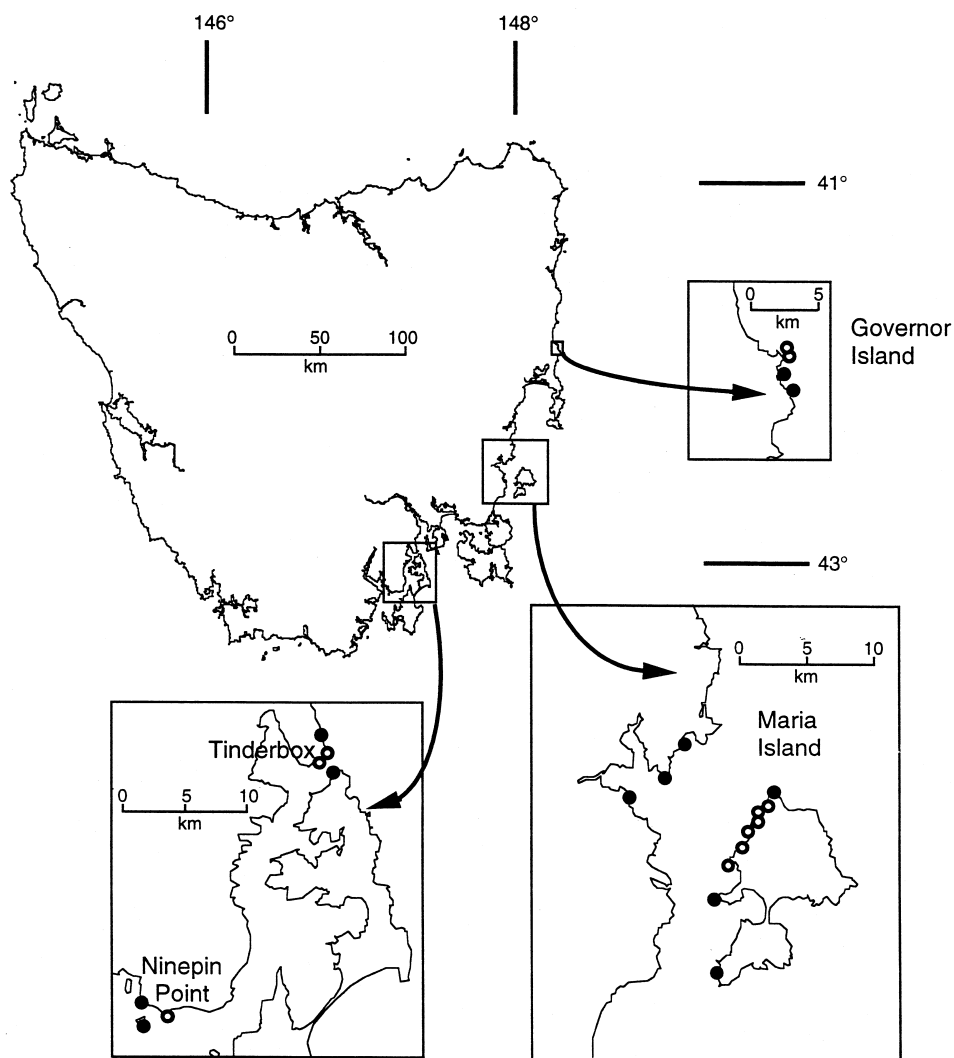


Fig. 1. Map showing distribution of study sites along the eastern Tasmanian coast. Sites with solid circles were located within reserves, open circles indicate external reference sites.

protected in the Tinderbox Marine Reserve, and ≈ 1 km in the Governor Island and Ninepin Point Marine Reserves. In order to maintain consistency of spatial scale, sites selected for monitoring (each ≈ 250 m across) were separated by a similar distance in all reserves (≈ 1 km between neighbouring sites). Approximately half of the total sampling effort was therefore concentrated at the large Maria Island reserve, where six sites in the reserve and six sites outside were monitored. Two sites were monitored both inside and outside the other reserves, except at Ninepin Point where the small region of

reef included sufficient area for only one site inside the reserve to be assessed. The locations of these monitoring sites are shown in Fig. 1.

External reference sites were selected at approximately equal-spaced distances as the best match of wave exposure and macroalgal communities to the reserve sites (Edgar and Barrett, 1997). A consequence of this procedure was that the spatial separation of reserve sites (1–7 km) was less than the spatial separation of associated reference sites (3–20 km). Multivariate analyses using MDS indicated that plant and animal assemblages at reference sites always corresponded more closely with associated reserve sites than with sites at other reserves (Edgar and Barrett, 1997).

Monitoring commenced at the Maria Island, Tinderbox and Ninepin Point marine reserves in March 1992 and at the Governor Island Marine Reserve in August 1992, with surveys undertaken each year in autumn until 1997 and in the spring of 1993, 1994 and 1997. The exception to this protocol was that no monitoring was conducted at Governor Island in 1995 or 1996. Although monitoring commenced almost 6 months after the reserves were proclaimed, little change occurred to fishing practices over the initial 6-month period because of a lack of signage and policing.

Spatial variability between sites was reduced by obtaining data only along the 5 m (± 1 m) depth contour, except on the deeper reef at Governor Island where single additional sites at 10 m inside and outside the reserve were monitored for rock lobsters. The depth of 5 m was considered optimal for monitoring because (i) few reefs in reserves other than Governor Island extended below 7 m, (ii) shallower habitats were difficult to sample because of near-vertical slopes in some areas and wave turbulence, (iii) diving times were not limited by decompression schedules, and (iv) reefs at 5 m are subjected to heavy fishing pressure from net and rock lobster fishers and divers.

Our study concentrated on species associated with reefs because this habitat type is the most heavily targeted by inshore fisheries, and because many reef-associated species are site-attached and so should recover relatively rapidly in marine reserves (Barrett, 1997). By contrast, most open water and soft-bottom fishes are unlikely to remain in small marine reserves for sufficient time to receive adequate protection.

2.2. *Census methodology*

Visual census techniques were used in the study because sampling needed to be non-destructive within reserves and a large amount of data was required on a range of species within the short seasonal survey periods. Three different census methods were used to obtain adequate descriptive information on reef communities over a range of spatial scales. These methods are described briefly below and in more detail elsewhere (Edgar and Barrett, 1997; Edgar et al., 1997).

At each reef site, the abundance and size structure of large fishes, the abundance of cryptic fishes and benthic invertebrates, and the percent cover of macroalgae were each censused separately. The densities of large fishes were estimated by laying four 50-m transect lines along the 5-m isobath and recording on waterproof paper the number and estimated size-class of fish within 5 m of each side of the line, as observed by a diver swimming up one side of the line and then back the other. Size-classes used in the study were 25, 50, 75, 100, 125, 150, 200, 250, 300, 350, 375, 400, 500, 625, 750, 875 and

1000 + mm. A total of four 10 × 50-m transects was thus censused for large fish at each site. The distance between ends of adjacent transects was small (0–5 m) relative to the length of transects (50 m), consequently the four transects at each site were considered subsamples, which indicate variability within the site, rather than as true randomly distributed replicates.

Cryptic fishes and megafaunal invertebrates (large molluscs, echinoderms, crustaceans) were next counted along the transect lines used for the fish survey by recording animals within 1 m of one side of the line (a total of four 1 × 50-m transects). The distance of 1 m was assessed using a stick carried by the diver. The maximum length of abalone and the carapace length of rock lobsters were measured underwater using vernier callipers whenever possible.

The area covered by different macroalgal species was then quantified by placing a 0.25 m² quadrat at 10-m intervals along the transect line and estimating the percent cover of the various plant species. Cover was assessed by counting the number of times each species occurred directly under the 50 positions on the quadrat at which perpendicularly placed wires crossed each other (a total of 1.25 m² for each of the 50-m sections of transect line).

To reduce variability in estimates attributable to different divers, all plant data and approximately 65% of fish and invertebrate data were obtained by the two authors. The remaining data were obtained by several other divers, with a single additional diver used in each season for both reserve and reference sites. Biases associated with different divers were almost evenly distributed between reserve and reference sites.

2.3. Statistical analyses

The effects of marine reserves were investigated using univariate data relating to (i) number of fish, invertebrate and plant species per 50-m transect, (ii) density and mean size of heavily exploited species, and (iii) density of abundant species. Individual species investigated included (i) all those that were common and exploited by fishers in the region, namely bastard trumpeter *Latridopsis forsteri* (Castelnau), blue-throated wrasse *Notolabrus tetricus* (Richardson), purple wrasse *Notolabrus fucicola* (Richardson), toothbrush leatherjacket *Penicipelta vittiger* (Castelnau), southern rock lobster *Jasus edwardsii* (Hutton), black-lip abalone *Haliotis rubra* Leach and sea urchin *Heliocidaris erythrogramma* (Valenciennes), and (ii) all those that occurred commonly at sites but are not exploited, namely senator wrasse *Pictilabrus laticlavius* (Richardson), hulafish *Trachinops caudimaculatus* (McCoy), the laminarian kelp *Ecklonia radiata* (C.Ag.) J.Ag. and the fucoid algae *Cystophora retroflexa* (Labill.) J.Ag. and *Sargassum fallax* Sonder. Total abundance of all fishes was also investigated, as was abundance of fishes larger than the 300-mm size class, the size at which local gill nets become effective (R. Murphy and J. Lyle, unpublished data).

Data relating to abundance of fishes and invertebrates were $\log(x + 1)$ transformed before analyses because multiplicative effects were considered more likely than additive effects, and in order to reduce skewness and heterogeneity of variances. Species richness, mean size and algal percent cover data were not transformed.

Data were initially analysed using a two-factor ANOVA to flag significant changes

that occurred within each reserve relative to outside, with ‘season’ (autumn/spring) and ‘reserve’ (inside/outside) fixed factors in this analysis. The difference between years (e.g. log abundance of rock lobsters in 1997 less log abundance of rock lobsters in 1992) for each site was calculated and used as the data value in ANOVAs (see Edgar and Barrett, 1997). Data associated with Governor Island were analysed for the period 1993–1997 because no data were available for autumn 1992. Data associated with the Ninepin Point Marine Reserve were not analysed using ANOVA because only a single site was censused within this reserve. An asymmetric ANOVA could have been conducted using Ninepin Point data (see Glasby, 1997); however, results would have been meaningless because of extremely low power.

Similarly, although a global three-factor ANOVA, with data from all Tasmanian marine reserves grouped by the four locations (a random factor), provided a much more interesting and general test of reserve effects, this analysis was not conducted because of the unbalanced design and extremely low statistical power, requiring an F -value = 17.4 ($df = 1/3$) for $\alpha = 0.05$. We considered it unrealistic to expect changes of similar magnitude, either additive or proportional, across all four reserves (see McKone and Lively, 1993).

A consequence of conducting separate ANOVAs for each of three reserves was that the number of statistical tests made was great, and several Type I errors (i.e. identifying a significant effect when none in fact occurred) could therefore be expected. Accordingly, the validity of results was assessed by investigating the time course of change. Significant changes that occurred in a consistent direction over time were considered reliable whereas changes that oscillated between years were considered doubtful.

The significance of long-term trends was assessed by calculating Spearman rank correlation coefficients relating sampling date (i.e. time since declaration of reserve) with the difference between mean values from reserve and reference sites. Thus, if the magnitude of difference between reserve and reference sites monotonically increased or decreased over the 6-year sampling period, then this change should be indicated by a significant Spearman rank correlation.

3. Results

3.1. Species richness

The numbers of fish, invertebrate and algal species recorded along transects in the Maria Island Marine Reserve all changed significantly over the 5-year period of monitoring within reserves relative to reference sites (Table 1). The average number of fish species recorded per transect at Maria Island increased by 5% within reserves and decreased by 23% outside, an overall increase of 29% relative to external reference sites (Fig. 2). Relative rather than absolute change is the important consideration here because change between years may occur as a result of different underwater visibility, slightly different time of sampling or the use of different divers in different years.

Part of the observed increase in fish species at Maria Island resulted from large fishes such as the bastard trumpeter *Latridopsis forsteri*, ling *Genypterus tigerinus* Klunzinger,

Table 1

Results of two-way ANOVAs (fixed factors: season and reserve) using data on difference at each site in number of species recorded along transects between 1992 and 1997 at Maria Island and Tinderbox, and between 1993 and 1997 at Governor Island; reserve \times season interaction was included as a factor in the models but results were non-significant ($P > 0.1$) in all cases so have not been shown; reserve and season factors both possess one degree of freedom

	Reserve			Season			Error	
	MS	F	P	MS	F	P	df	MS
<i>Fish species</i>								
Maria Island	26.04	7.757	0.011	0.010	0.003	0.956	20	3.357
Tinderbox	0.070	0.014	0.912	14.45	2.840	0.167	4	5.09
Governor Island	0.031	0.025	0.883	19.53	15.43	0.017	4	1.266
<i>Fish species > 325 mm</i>								
Maria Island	8.167	11.68	0.003	2.344	3.353	0.082	20	0.699
Tinderbox	2.258	3.568	0.132	0.945	1.494	0.289	4	0.633
Governor Island	0.031	0.400	0.561	4.500	57.60	0.002	4	0.078
<i>Invertebrate species</i>								
Maria Island	27.63	8.538	0.008	19.71	6.091	0.023	20	3.236
Tinderbox	1.320	0.772	0.429	9.570	5.594	0.077	4	1.711
Governor Island	1.531	0.367	0.577	1.125	0.270	0.631	4	4.172
<i>Algal species</i>								
Maria Island	66.67	7.260	0.014	88.17	9.601	0.006	20	9.183
Tinderbox	0.500	0.049	0.836	18.00	1.756	0.256	4	10.25
Governor Island	8.000	1.280	0.321	0.000	0.000	1.000	4	6.250

marblefish *Aplodactylus arcidens* Richardson and draughtboard shark *Cephaloscyllium laticeps* (Dumeril), which were originally rare, becoming more regularly recorded along transects. The number of species of large fish (> 325 mm length) observed at Maria Island increased significantly during the study (Fig. 2, Table 1).

The number of mobile invertebrate species recorded per transect at Maria Island increased by 25% at reserve sites and decreased by 7% at reference sites, an overall change of 31%. Algal species richness increased by 11% within the reserve and decreased by 5% outside (Fig. 2).

While fish species richness increased significantly within the reserve relative to outside between 1992 and 1997 (Table 1, Fig. 2), the interannual trend in autumn data was not gradual (Fig. 3). A clearer trend for increase was evident in the spring data, albeit with only three periods of sampling (Fig. 3). The number of fish species observed during spring censuses was substantially lower than the number recorded during autumn.

The number of invertebrate and plant species recorded along transects within the Maria Island reserve showed more consistent patterns of change over time relative to external sites (Fig. 3). Invertebrate species richness showed a slight decline in autumn at external sites and increased within the reserve. Macroalgal species richness generally showed an increasing trend within the reserve and a decrease outside.

Spearman rank correlation coefficients relating time since reserve declaration with

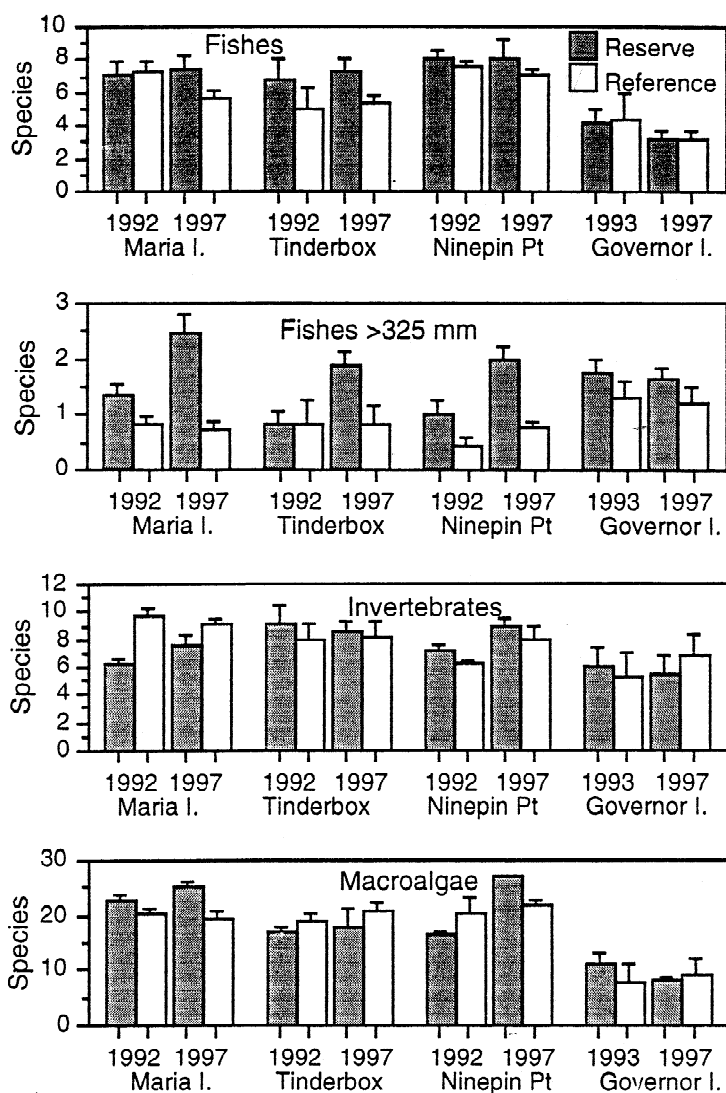


Fig. 2. Mean number of species of fishes, invertebrates and algae recorded per 50-m transect inside and outside reserves in 1992 (1993 at Governor Island) and 1997. Error bars indicate standard error of the means of different sites.

difference between reserve and reference sites in fish, invertebrate and algal species richness were relatively high for Maria Island (Table 2); however, these correlations were not found to be significant at the 5% level using two-tailed tests.

The number of fish, invertebrate and plant species recorded in the smaller reserves did not change significantly between the 1992 and 1997 periods of monitoring (Table 1). In the Tinderbox, Ninepin Point and Governor Island marine reserves, the mean number of

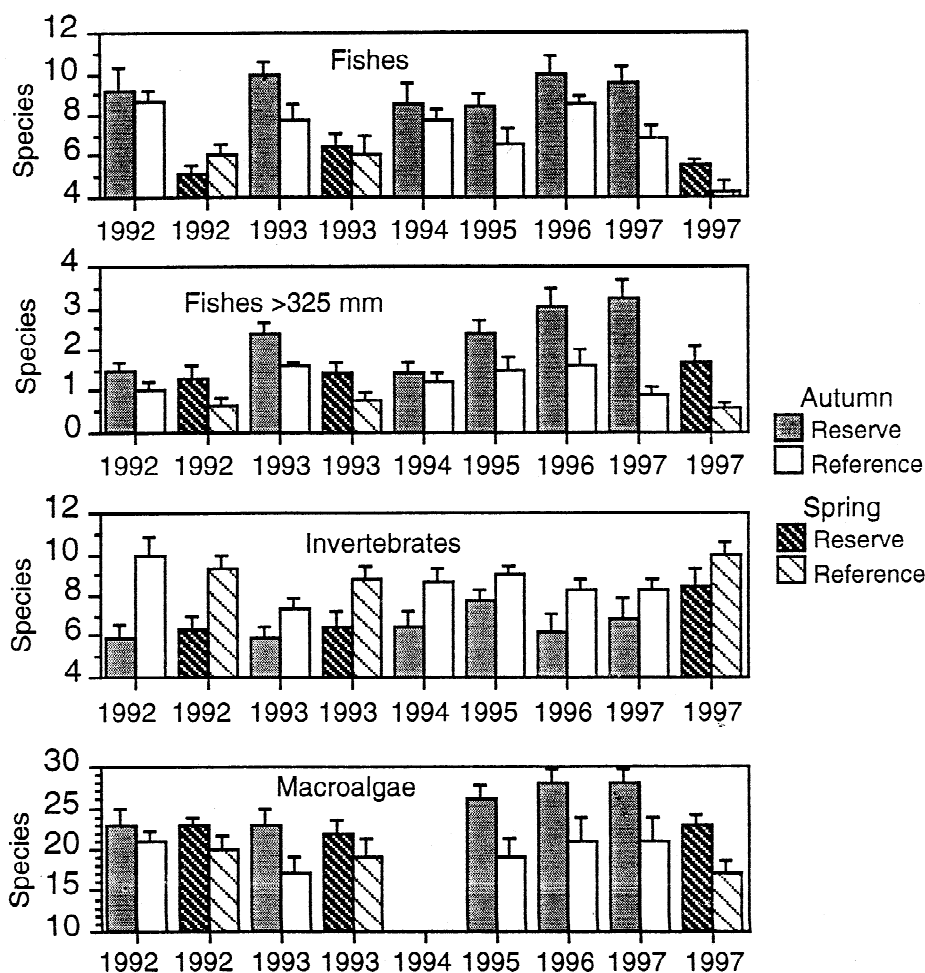


Fig. 3. Mean number of species recorded per transect inside and outside the Maria Island marine reserve at different census times. Error bars indicate standard error of site means.

fish species sighted per transect increased by 1, 7 and 15% relative to external reference sites, respectively. The number of invertebrate species decreased by 9, 4 and 46% relative to external reference sites at Tinderbox, Ninepin Point and Governor Island, respectively, while the corresponding changes for algal species richness were -2 , $+56$ and -35% .

A significant increase in number of large fish species (> 325 mm) was detected over time within the Tinderbox reserve, when assessed using Spearman rank correlation (Table 2). A substantial change in species richness was also detected for plants at Ninepin Point, albeit at a marginally non-significant level ($0.1 > P > 0.05$).

Table 2

Spearman rank correlation coefficients relating difference between reserve and reference sites with time since declaration of reserve; reserves were sampled on nine occasions (i.e. $n=9$), with the exception of plant data and Maria Island rock lobster size data, where $n=8$; data for the Governor Island reserve are not included because of the very small sample size ($n=6$) and lack of power for tests

	Maria Island	Tinderbox	Ninepin Point
<i>Species richness</i>			
Fishes	0.567	0.405	−0.119
Fishes >325 mm length	0.733*	0.778*	0.218
Invertebrates	0.600#	−0.268	−0.109
Plants	0.595	−0.254	0.661
<i>Density</i>			
Total fish	−0.700*	0.850**	−0.433
Total fish >325 mm	0.767*	0.644#	0.343
<i>Latridopsis forsteri</i> abundance	0.932***	0.395	
<i>Notolabrus tetricus</i> abundance	−0.367	0.126	0.728*
<i>Notolabrus fucicola</i> abundance	−0.050	−0.017	0.017
<i>Trachinops caudimaculatus</i> abundance	−0.767*	0.817*	−0.650
<i>Pictilabrus laticlavius</i> abundance	−0.251	−0.326	−0.233
<i>Penicipelta vittiger</i> abundance	−0.343	0.150	−0.449
Rock lobster abundance	0.803*	0.633#	−0.018
Abalone abundance	−0.767*	−0.235	0.025
Sea urchin abundance	0.017	0.317	−0.433
<i>Size</i>			
<i>Notolabrus tetricus</i> length	0.433	0.700*	0.100
Abalone length	0.633#	0.283	0.483
Rock lobster carapace length	0.667#	0.317	0.678#
<i>Plant cover</i>			
<i>Cystophora retroflexa</i>	−0.738*	−0.548	−0.102
<i>Ecklonia radiata</i>	0.976***	0.250	0.633
<i>Sargassumfallax</i>	−0.810*	−0.250	−0.100

^a Significance levels are based on two-tailed tests: #0.1> P >0.05, *0.05> P >0.01, **0.01> P >0.001, ***0.001> P .

3.2. Fishes

The densities of reef fish in different size-classes within the Maria Island reserve changed substantially during the study, primarily through large animals becoming much more common. While total abundance of fishes showed no significant change between 1992 and 1997 census periods, the number of large fish (> 325 mm length) observed per 500-m² transect increased significantly (Table 3). Mean numbers of large fish rose from an average of 2.6 to 9.2 within the reserve while remaining unchanged outside ($\bar{x}=1.0$), an overall increase of 243% between fished and unfished areas (Fig. 4). The trend for increased densities of large fish within the reserve was consistent over time (Table 2).

Analysis of the overall size-distribution of fish indicated that the Maria Island reserve

Table 3

Results of two-way ANOVAs (fixed factors: season and reserve) using data on difference in log-transformed density of fish species between 1992 and 1997 at Maria Island and Tinderbox, and between 1993 and 1997 at Governor Island; reserve×season interaction was included as a factor in the models but results were non-significant ($P>0.10$) in all cases so have not been shown; reserve and season factors both possess one degree of freedom; tests for *Trachinops caudimaculatus* and *Pictilabrus laticlavius* at Governor Island could not be undertaken because of a lack of data, tests for *Penicipelta vittiger* and *Trachinops caudimaculatus* should be treated with caution because of high variance heterogeneity

	Reserve			Season			Error	
	MS	F	P	MS	F	P	df	MS
<i>Total fish</i>								
Maria Island	0.001	0.007	0.936	0.033	0.2 16	0.647	20	0.151
Tinderbox	1.449	9.044	0.040	0.661	4.123	0.112	4	0.160
Governor Island	0.064	0.389	0.567	1.381	8.423	0.044	4	0.164
<i>Total fish >325 mm</i>								
Maria Island	0.816	8.251	0.009	0.117	1.185	0.289	20	0.099
Tinderbox	0.287	7.124	0.056	0.044	1.086	0.356	4	0.040
Governor Island	0.000	0.030	0.870	0.547	87.66	0.001	4	0.006
<i>Latridopsis forsteri abundance</i>								
Maria Island	1.813	15.95	0.001	0.057	0.504	0.486	20	0.114
Tinderbox	0.026	0.837	0.412	0.002	0.067	0.809	4	0.031
Governor Island	0.003	0.311	0.607	0.014	1.689	0.264	4	0.009
<i>Notolabrus tetricus abundance</i>								
Maria Island	0.002	0.036	0.852	0.039	0.893	0.356	20	0.044
Tinderbox	0.077	0.827	0.414	0.081	0.866	0.405	4	0.093
Governor Island	0.030	2.450	0.193	0.015	1.285	0.320	4	0.012
<i>Notolabrus fucicola abundance</i>								
Maria Island	0.010	0.113	0.740	0.133	1.569	0.225	20	0.085
Tinderbox	0.039	6.510	0.063	0.156	26.32	0.007	4	0.006
Governor Island	0.047	0.606	0.480	0.089	1.146	0.345	4	0.078
<i>Trachinops caudimaculatus abundance</i>								
Maria Island	0.680	1.479	0.238	0.832	1.809	0.194	20	0.460
Tinderbox	0.480	1.650	0.268	1.500	5.152	0.086	4	0.291
<i>Pictilabrus laticlavius abundance</i>								
Maria Island	0.001	0.008	0.929	0.075	1.123	0.302	20	0.067
Tinderbox	0.019	0.139	0.412	0.522	3.758	0.809	4	0.139
<i>Penicipelta vittiger abundance</i>								
Maria Island	0.014	0.047	0.83 1	0.122	0.422	0.524	20	0.290
Tinderbox	0.004	0.042	0.848	0.788	7.848	0.049	4	0.100
Governor Island	0.337	2.850	0.167	0.242	2.048	0.226	4	0.118

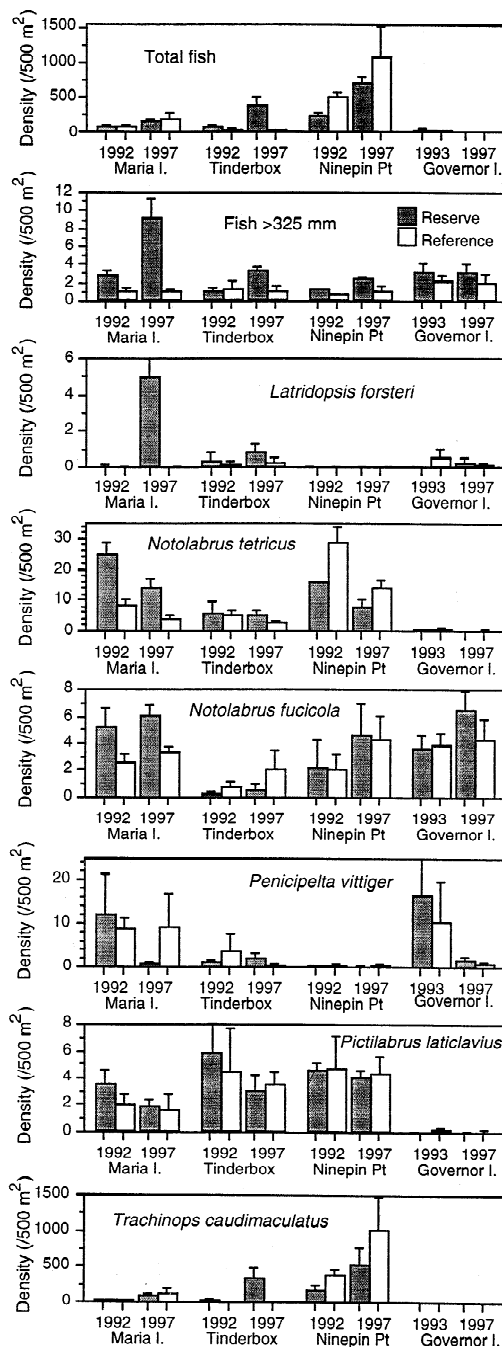


Fig. 4. Mean densities of reef-associated fish species observed along 500-m² transects within reserves and at external reference sites in 1992 (1993 at Governor Island) and 1997. Schooling pelagic fishes (carangids, centrolophids, arripids and clupeoids) were excluded from calculations of total fish and fish >325 mm length. Error bars indicate standard error of site means.

was effective at increasing the densities of fish in size classes greater than 300 mm (Fig. 5), with much of the increase occurring between 1996 and 1997. Densities within many length classes less than 300 mm decreased over the period of study both inside and outside the reserve.

Shifts in the overall size-distribution of fish were largely caused by changes in the size-structure of the abundant blue-throated wrasse *Notolabrus tetricus*, which increased significantly in mean size within the reserve compared with outside (Table 4). The mean length of blue-throated wrasse increased between 1992 and 1997 both inside and outside the reserve, with the more rapid increase occurring inside (Fig. 6).

The overall size-distribution of fish at Maria Island was also influenced by an enormous increase in the abundance of the bastard trumpeter *Latridopsis forsteri* (Table 3, Fig. 4). The density of trumpeter within the reserve increased two orders of magnitude, from an average of 0.04 to 4.9 per 500-m² transect, while outside the reserve no trumpeter were recorded at fished sites in 1992 or 1997 (Fig. 7). Trumpeter recruited irregularly within the reserve, with few animals recorded until a large cohort entered the reserve in 1994. Fish belonging to this cohort increased in size by ≈ 50 mm each year (Fig. 7).

An increase in density of fishes > 325 mm size also occurred in the Tinderbox reserve, and was of equivalent magnitude (300%) to that observed in the Maria Island reserve. The probability value associated with this change was just outside the 5% significance level using ANOVA with 1992 and 1997 data ($P = 0.056$, Table 3). A significant increase was, however, detected using mean data from all years and a one-tailed test ($r_s = 0.64$, $P = 0.04$, Table 3).

No clear increase in densities of large fish occurred at Governor Island, while overall trends in the Ninepin Point reserve were obscured by the lack of site replication and a single school of large long-fin pike *Dinolestes lewini* (Griffith). If pike are considered reef-associated, and so included in the data set, then fishes greater than 325 mm length show substantially increased abundance within the reserve relative to outside between 1992 and 1997. If pike are considered pelagic, and so removed from the data set, then no consistent size effects were evident. Pike occurred rarely in other reserves and their occasional presence did not affect analyses.

The general pattern of increase in abundance of large fishes was influenced by the patchy distribution of trumpeter, and probably also by distance from reserve boundary (Fig. 8). At Maria Island, trumpeter were regularly recorded at only four sites, including the two sites at greatest distance from the reserve boundary. Amongst the smallest three reserves, the greatest change in large fish abundance was detected at the site at greatest distance from the boundary (at Tinderbox).

In contrast to the substantial changes within reserves between 1992 and 1997 in numbers of large fishes, species that remain unexploited because of small size (*Pictilabrus laticlavius* and *Trachinops caudimaculatus*) were not found using ANOVA to change in abundance at reserve relative to reference sites between 1992 and 1997. However, tests using Spearman rank correlation indicate that *T. caudimaculatus* decreased significantly over time at Maria Island and increased over the same period at Tinderbox (Table 2). These trends are probably spurious, resulting from the disproportionate recruitment towards the end of the monitoring period of huge schools of

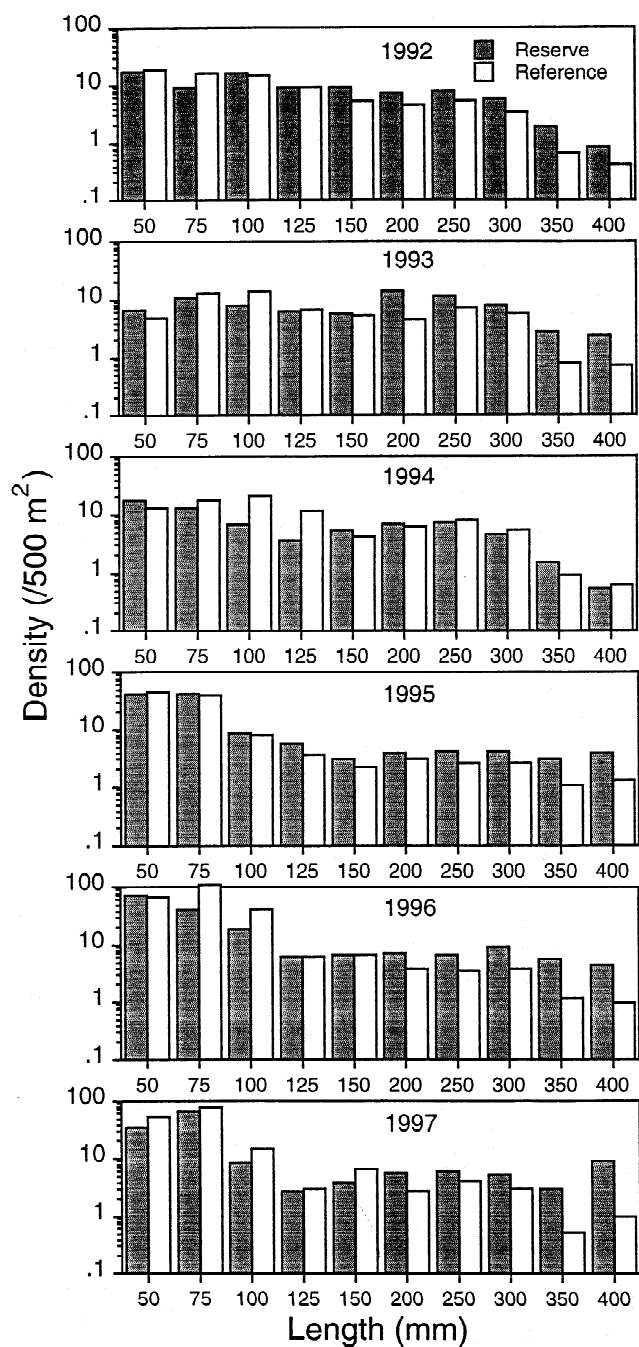


Fig. 5. Estimated densities of fish in different size classes at Maria Island in different years.

Table 4

Results of two-way ANOVAs (fixed factors: season and reserve) using data on difference in mean size of exploited species between 1992 and 1997 at Maria Island and Tinderbox, and between 1993 and 1997 at Governor Island; reserve \times season interaction was included as a factor in the models but results were non-significant ($P>0.10$) in all cases so have not been shown; reserve and season factors both possess one degree of freedom; tests for *Notolabrus tetricus* and rock lobster length at Governor Island, and abalone length at Tinderbox, have not been undertaken because of a lack of data

	Reserve			Season			Error	
	MS	F	P	MS	F	P	df	MS
<i>Notolabrus tetricus</i> length								
Maria Island	8.26	6.097	0.023	1.12	0.828	0.374	20	1.35
Tinderbox	14.92	4.702	0.096	6.28	1.981	0.232	4	3.17
<i>Rock lobster</i> carapace								
Maria Island	2.23	0.006	0.939	95.44	0.263	0.618	11	362.50
Tinderbox	4255.0	14.140	0.033	171.10	0.569	0.506	3	902.70
<i>Abalone</i> length								
Maria Island	1157.0	7.996	0.010	33.65	0.233	0.635	20	144.70
Governor Island	26.42	0.111	0.756	43.43	0.183	0.691	4	237.70

this planktivorous fish at single sites associated with each reserve (see Fig. 4). The presence of enormous numbers of *T. caudimaculatus*, which grows to a maximum length of only 100 mm (Last et al., 1983), also swamped tests for total fish abundance and caused significant change over time for that variable (Table 2). If *T. caudimaculatus* is removed from calculations, then total fish abundance shows negligible change over time ($r_s = -0.07$ at Maria Island and $r_s = -0.15$ at Tinderbox).

The two fish species examined that grow to moderate size, *Notolabrus fucicola* and *Penicipelta vittiger*, also showed no significant change over time. *N. fucicola* grew to a smaller size than its congener *N. tetricus* at the sites examined, with only 1% of the population exceeding 350 mm length compared to 6% of the *N. tetricus* population. Analysis of *P. vittiger* density was primarily affected by the heterogeneous presence of schools of juveniles.

3.3. Invertebrates

Rock lobster numbers increased significantly in the Maria Island reserve, from an average of 0.8 per 50-m² transect in 1992 to 2.8 per transect in 1997 (a 260% increase; Table 5, Fig. 9). Over the same period numbers outside the reserve increased by only 12% (from 1.3 to 1.5 per 50 m²). Changes in rock lobster densities were gradual over the monitoring period, with densities at reference sites fluctuating around 1.5 per 50 m² throughout the study but with densities within the reserve steadily increasing.

Rock lobster size data were not collected during spring 1992, hence the ANOVA design could only be used to analyse changes in mean size of animals between 1993 and 1997. Change that had already occurred presumably affected the result, which was not significant (Table 4) despite a 30% increase. However, consistent changes over time in

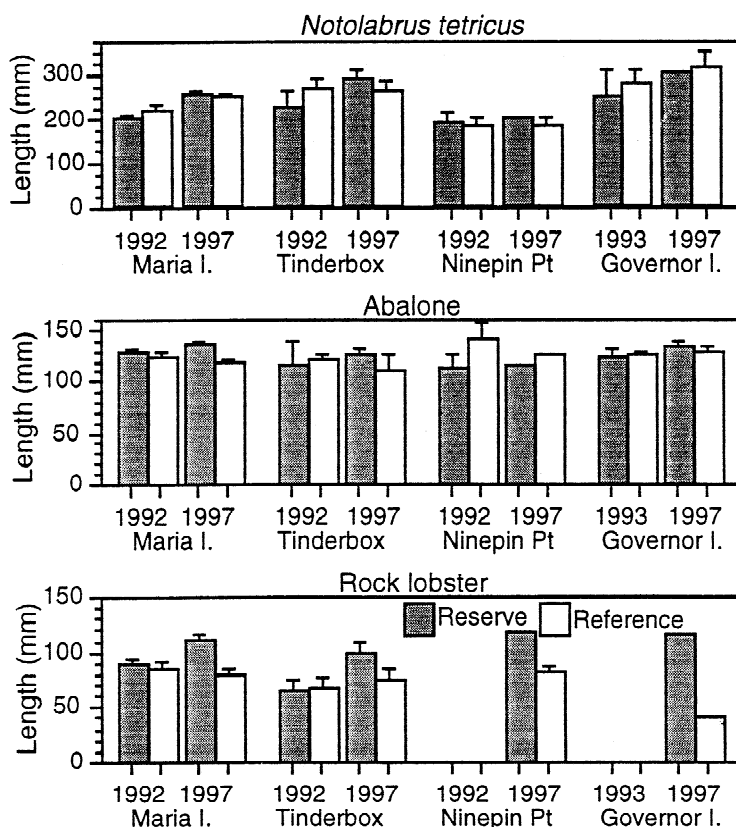


Fig. 6. Mean size of *Notolabrus tetricus*, rock lobster and abalone observed within reserves and at external reference sites in 1992 (1993 at Governor Island) and 1997. Error bars indicate standard error of site means.

the size distribution of rock lobsters at Maria Island were detected using Spearman rank correlation (Table 2).

While the numbers of rock lobster below 110 mm remained stable inside and outside the Maria Island reserve (Fig. 10), the largest animals encountered inside the reserve increased by ≈ 15 mm during each year of monitoring. During the 1992 surveys the largest animal observed in the reserve was 110 mm carapace length, while in the subsequent 5 years the largest animals observed were 129, 144, 150, 160 and 198 mm, respectively. Numerous animals between 110 and 200 mm carapace length were found within the reserve in 1997, whereas outside the reserve very few individuals exceeded the minimum legal size for the fishery (110 mm for males and 105 mm for females).

Data on rock lobster densities and sizes were converted to biomass using a regression equation that relates wet biomass (B ; in g) with carapace length (L , in mm) for rock lobsters on the Tasmanian east coast (S. Frusher, unpublished data): $B = 0.000271 * L^{3.135}$. Using these data, the total biomass of rock lobsters in the Maria Island reserve is estimated to have increased by more than an order of magnitude during the

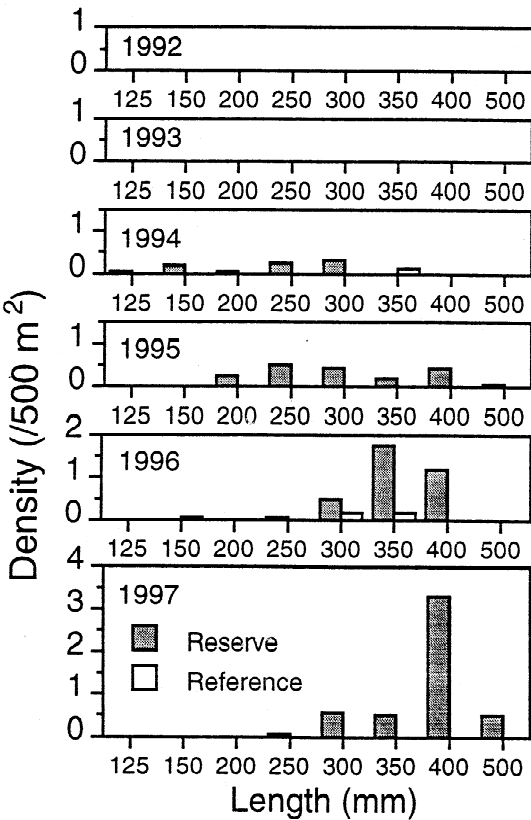


Fig. 7. Estimated densities of *Latridopsis forsteri* in different size-classes at Maria Island in different years.

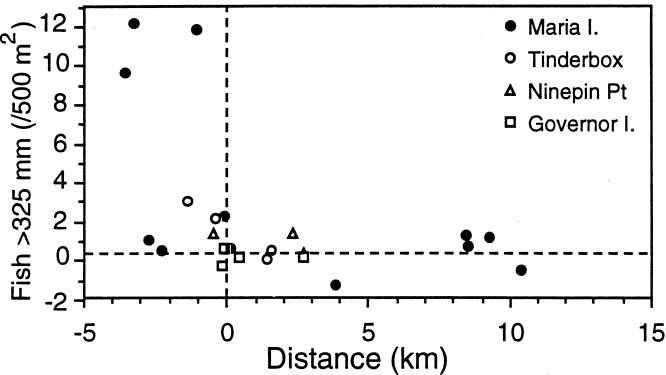


Fig. 8. Change in abundance of large fishes (>325 mm) between 1992 and 1997 versus distance from reserve boundary.

Table 5

Results of two-way ANOVAs (fixed factors: season and reserve) using data on difference in log-transformed density of exploited invertebrate species between 1992 and 1997 at Maria Island and Tinderbox, and between 1993 and 1997 at Governor Island; rock lobster analysis includes data from single 10 m deep sites inside and outside the reserve as well as data from 5 m sites; reserve \times season interaction was included as a factor in the models but results were non-significant ($P > 0.05$) in all cases so have not been shown; reserve and season factors both possess one degree of freedom

	Reserve			Season			Error	
	MS	F	P	MS	F	P	df	MS
<i>Rock lobster</i>								
Maria Island	0.610	11.280	0.003	0.004	0.068	0.797	20	0.054
Tinderbox	0.000	0.000	0.999	0.343	1.494	0.289	4	0.230
Governor Island	0.032	1.239	0.298	0.069	2.678	0.140	9	0.026
<i>Abalone</i>								
Maria Island	0.250	2.208	0.153	0.157	1.381	0.254	20	0.113
Tinderbox	0.080	1.395	0.303	0.199	3.468	0.136	4	0.057
Governor Island	0.038	0.321	0.601	0.018	0.153	0.716	4	0.117
<i>Sea urchin</i>								
Maria Island	0.092	1.545	0.228	0.161	2.699	0.116	20	0.060
Tinderbox	0.005	0.096	0.772	0.050	1.017	0.370	4	0.049
Governor Island	0.097	2.760	0.172	0.019	0.553	0.498	4	0.035

5-year period of protection (from 130 to 2200 g per 50-m² transect; Fig. 11), and the total biomass of rock lobsters above legal size is estimated to have increased over 20 times (from 80 to 1920 g). Outside the reserve, the biomass of rock lobsters remained stable at ≈ 270 g per 50-m² transect.

Using a regression that relates annual egg production of mature female rock lobsters to carapace length ($R = 0.1814 * L^{2.969}$; R. Kennedy, unpublished data) and the assumptions that the sex ratio was 1:1 and animals > 90 mm carapace length were mature, the estimated reproductive output of rock lobsters in the Maria Island reserve is calculated to also have increased an order of magnitude. Egg production per 50-m² transect is estimated to have risen from 34 200 to 343 000 within the reserve.

Similar trends were also evident in the three smaller reserves (Fig. 6), with the change in mean size within the Tinderbox reserve statistically significant (Table 4). This test could not be conducted for the Ninepin Point or Governor Island reserves because of a lack of early data, although the mean size of animals in these reserves was much greater inside than outside reserves at the end of the study (Fig. 6). Large rock lobsters became increasingly common inside all reserves but were virtually absent outside, resulting in enormous increases in biomass (Fig. 11) and reproductive output within the reserves.

The change in mean rock lobster size was consistent within as well as between reserves. With the exception of one site near the reserve boundary at Tinderbox, the mean carapace length of rock lobsters was ≈ 115 mm at reserve sites and between 65 and 105 mm at all external sites (Fig. 12). The change in rock lobster size occurred rapidly within 1 km of reserve boundaries.

Mean abalone size in the Maria Island marine reserve increased significantly during

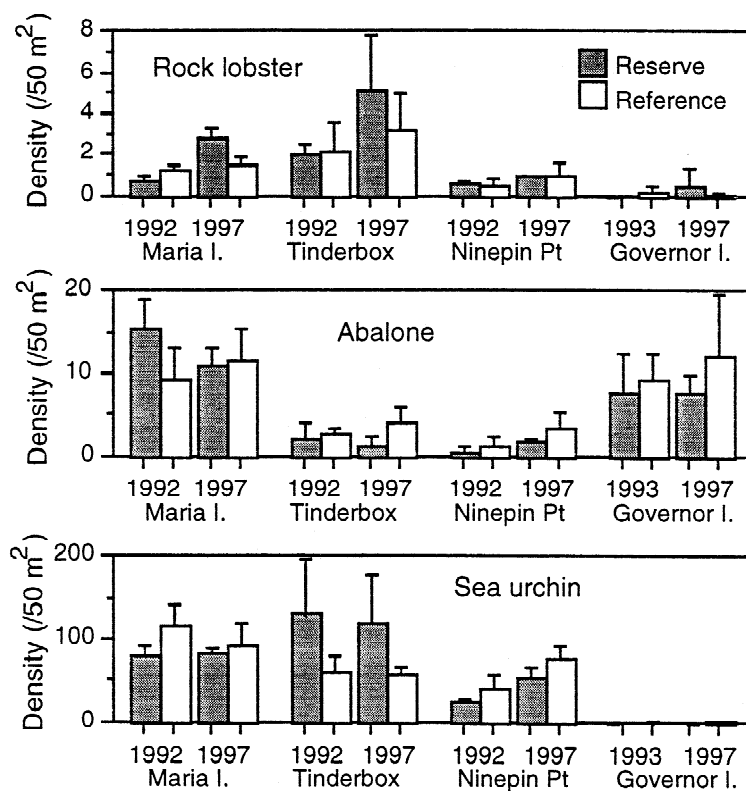


Fig. 9. Mean number of exploited invertebrate species observed along 50-m² transects within the four marine reserves and at external reference sites in 1992 (1993 at Governor Island) and 1997.

the study (Table 4), from 128 to 136 mm shell length, while average size outside the reserve declined from 125 to 118 mm (Fig. 6). Large individuals are now more abundant inside the reserve compared to outside although they comprise only a relatively small proportion of the total (Fig. 13). Total densities showed no significant change using ANOVA at Maria Island, nor at the smaller reserves. The mean size of abalone also showed no significant change in the three small reserves (Fig. 6), although animals larger than 160 mm were almost exclusively confined to reserves.

One trend common to all marine reserves in this study was that, relative to the reference sites, the number of abalone smaller than the legal size limit (132 mm) decreased during the study. At the commencement of the study animals between 100 and 120 mm length were considerably more abundant at reserve sites than at reference sites at Maria Island but this trend had reversed by 1997 (Fig. 13). To test the significance of this effect, animals were subdivided into those less than 145 mm and those greater than that size. Using similar two-way ANOVAs to those described in Table 4, the density of small abalone within the Maria Island reserve was found to significantly decrease ($MS=0.667$, $F=10.13$, $P=0.005$), and the density of large abalone to significantly

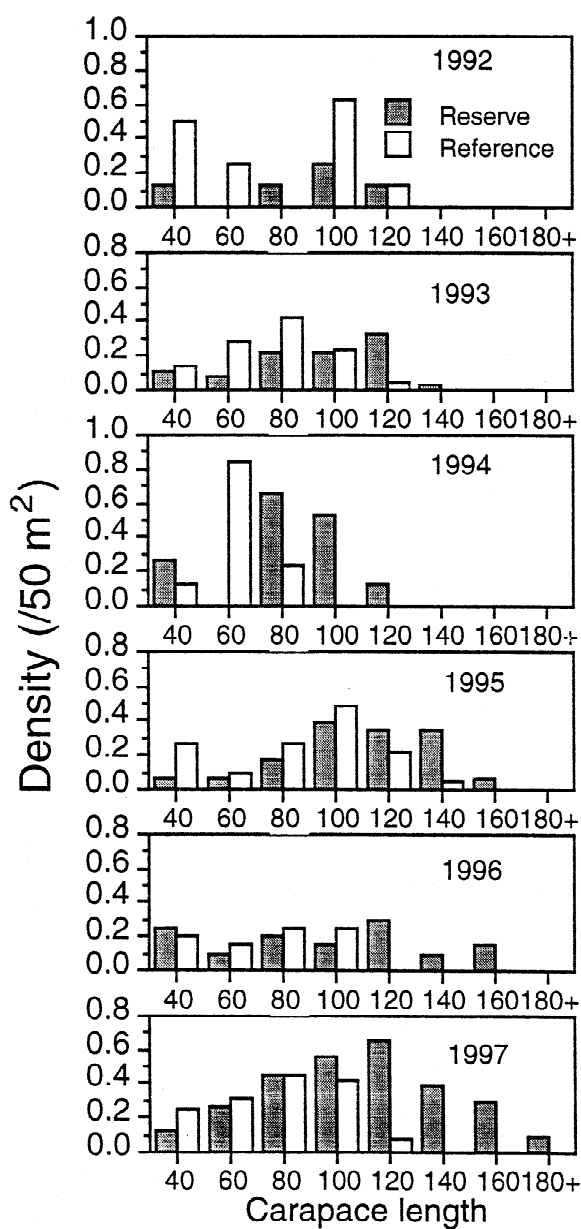


Fig. 10. Estimated densities of different size classes of rock lobsters at reserve and external reference sites at Maria Island in the various sampling seasons.

increase ($MS=0.313$, $F=4.262$, $P=0.045$). The large decline in number of juvenile abalone at Maria Island caused a significant overall decrease in total abalone numbers, when assessed using Spearman correlation (Table 2).

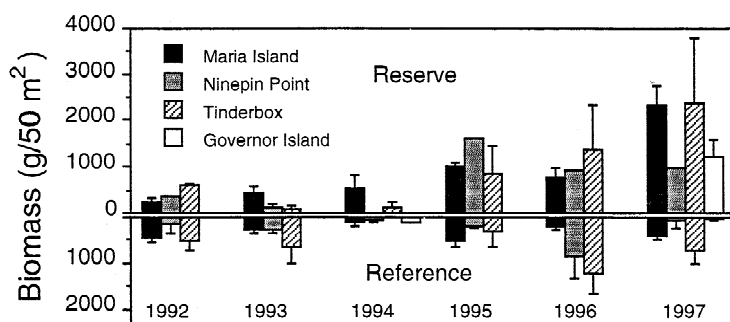


Fig. 11. Estimates of the biomass of rock lobsters in reserves and at external reference sites.

In contrast to the various effects of marine reserves detected for rock lobster and abalone populations, no change in density of sea urchins was found at Maria Island nor in any other reserve (Table 5).

3.4. Macroalgae

Changes between 1992 and 1997 in the percent cover of the most common macroalgae within the Maria Island reserve, *Ecklonia radiata*, *Cystophora retroflexa* and 'Sargassum fallax' are shown in Fig. 14. The taxon *Sargassum fallax* primarily includes that species, but may also include a few similar plants in the genus *Sargassum* that were misidentified during the autumn season when diagnostic reproductive fronds were lacking.

Substantial changes in mean plant cover occurred in the Maria Island reserve, with *E. radiata* significantly increasing in total cover relative to reference sites (Tables 2 and 6, Fig. 14). Although not found to be statistically significant using ANOVA, the large decreases in mean cover of *C. retroflexa* and *S. fallax* within the reserve over time were statistically significant using Spearman correlation (Table 2).

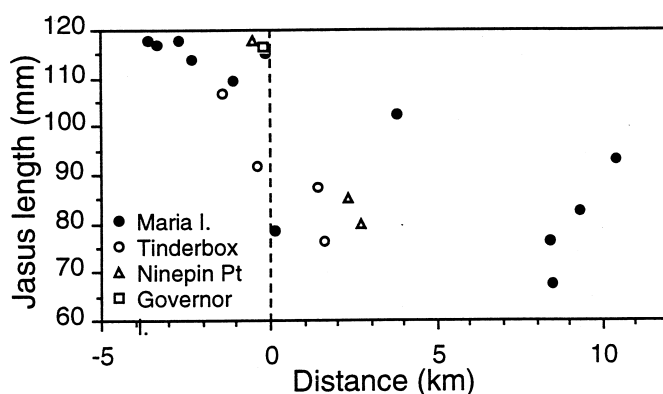


Fig. 12. Mean size of rock lobsters at sites versus distance from reserve boundary.

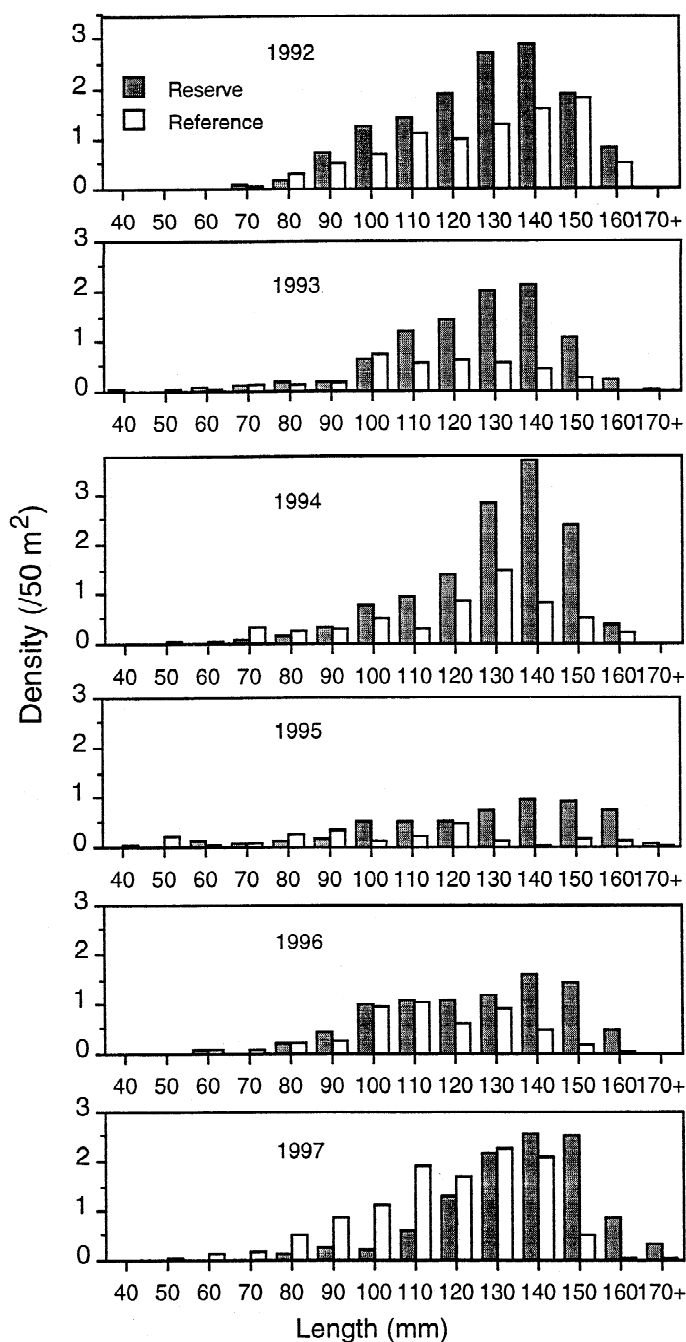


Fig. 13. Estimated densities of different size classes of abalone at reserve and external reference sites in 1992 and 1997.

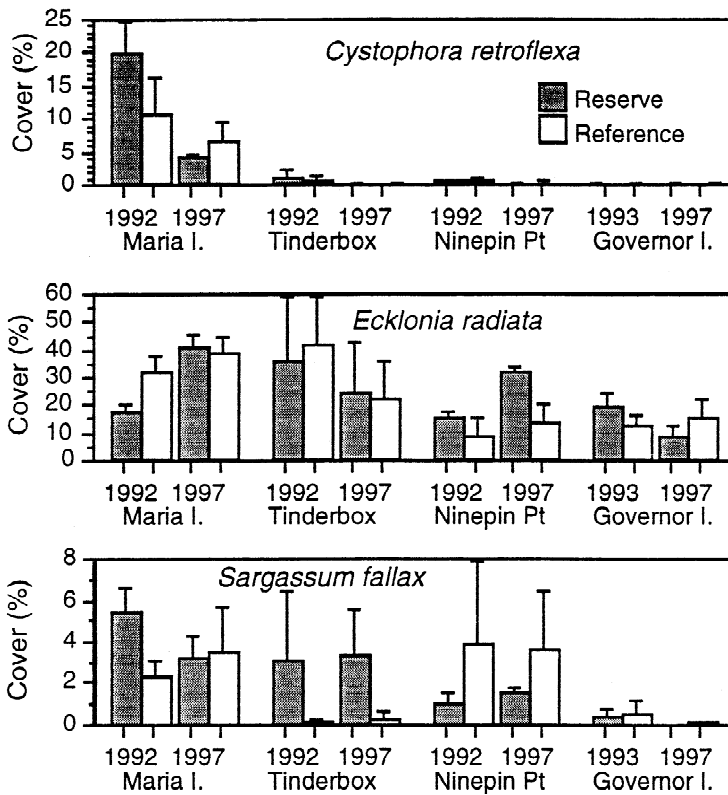


Fig. 14. Mean percent cover of common macroalgal species observed along transects within the four marine reserves and at external reference sites in 1992 (1993 at Governor Island) and 1997.

Changes over time in cover of *E. radiata* and *C. retroflexa* were clearly-defined and monotonic during the period of study at Maria Island reserve and reference sites (Fig. 15), with changes at the reserve sites considerably more rapid than outside. *C. retroflexa* decreased from 20 to 4% cover between 1992 and 1997 within the Maria Island reserve and from 11 to 6% cover at reference sites. *E. radiata* increased from 17 to 40% cover within the reserve and from 32 to 39% outside. A comparable increase in the cover of *E. radiata* occurred at Ninepin Point but not in the other two marine reserves studied (Fig. 14).

Sargassum fallax also showed a consistent interannual change at Maria Island, although seasonal growth of reproductive fronds resulted in much higher cover of plants during the spring months (Fig. 15). The mean cover of *S. fallax* increased from 2.3 to 3.5% within the reserve and decreased from 5.4 to 3.2% outside over the period of monitoring. Little change in this species occurred in other reserves. The introduced Japanese kelp *Undaria pinnatifida* (Harvey) Suringar became established in the Maria Island reserve during the first year of the study and increased from 0 to 4% cover by 1997. This kelp also increased in abundance at reference sites.

Table 6

Results of two-way ANOVAs (fixed factors: season and reserve) using data on difference in algal cover between 1992 and 1997 at Maria Island and Tinderbox, and between 1993 and 1997 at Governor Island; reserve \times season interaction was included as a factor in the models but results were non-significant ($P>0.05$) in all cases so have not been shown; reserve and season factors both possess one degree of freedom

	Reserve			Season			Error	
	MS	F	P	MS	F	P	df	MS
<i>Ecklonia radiata</i>								
Maria Island	1634	9.014	0.007	270.7	2.503	0.234	20	180.1
Tinderbox	117.0	0.923	0.391	56.18	0.443	0.542	4	126.8
Governor Island	399.0	4.411	0.102	199.0	2.200	0.212	4	90.46
<i>Sargassum fallax</i>								
Maria Island	73.50	2.505	0.129	8.882	0.303	0.588	20	29.35
Tinderbox	0.001	0.000	0.985	1.901	0.601	0.481	4	3.161
<i>Cystophora retroflexa</i>								
Maria Island	772.9	2.119	0.160	6.827	0.019	0.893	20	364.7
Tinderbox	0.211	0.106	0.761	3.781	1.894	0.241	4	1.996

4. Discussion

4.1. Errors, biases and caveats

Visual survey techniques, such as those used in this study, are widely used for estimating fish population sizes on reefs (e.g. Russell, 1977; Branden et al., 1986; McCormick and Choat, 1987), but are affected by a number of biases so cannot be used to estimate total densities without considerable caution (Brock, 1982; Thresher and Gunn, 1986; Lincoln-Smith, 1988, 1989; Cheal and Thompson, 1997). Visual census data have been used here to indicate relative rather than absolute differences between sites.

The major biases that may have affected our visual censuses were variability between different divers, underwater visibility, changed behaviour of fishes and habitat variability. These biases will principally affect estimates of fish density and fish size but should not greatly affect estimates of plant and slow-moving invertebrate densities (including abalone, rock lobsters and sea urchins).

In general, sampling biases should not greatly affect conclusions reached in the study, providing that they occurred systematically in both reserve and reference locations. For example, the use of different divers on different sampling occasions will add to variability and differences between years (see Thompson and Mapstone, 1997). It should not, however, greatly affect the most interesting tests of changes (those in reserves relative to those outside, expressed over time), unless one diver was used more for reserve rather than reference sites, or vice versa. For this reason, each diver was used approximately evenly inside and outside when censusing a particular reserve. Similarly, censuses conducted within a reserve and at associated reference sites were interspersed

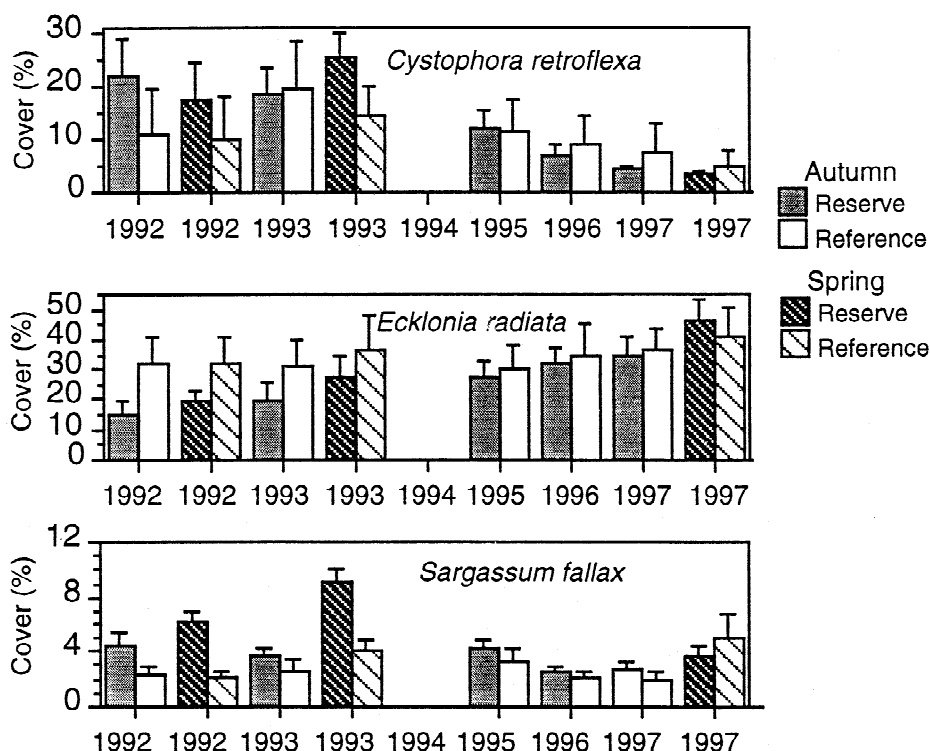


Fig. 15. Mean percent cover of the common macroalgal species *Cystophora retroflexa* and *Ecklonia radiata* at different census times within the Maria Island marine reserve and at external reference sites. Error bars indicate standard error of site means.

over time so that one region was not disproportionately sampled during a time of bad weather and poor underwater visibility.

Of greater concern are biases that potentially differ systematically between reserve and reference locations. The most important of these are behavioural effects (Kulbicki, 1998), because a number of fishes that normally avoid divers are known to modify their behaviour within marine reserves and approach divers (Cole, 1994). Any such behavioural change will lead to spuriously high density estimates within reserves.

The extent of such effects was not estimated in the present study, although diver observations provided no indication that fish behaviour changed within reserves. Wrasses, particularly *Notolabrus fucicola*, tended to follow divers both within reserves and outside, while trumpeter (*Latridopsis forsteri*) tended to remain in circumscribed areas of ≈ 25 m diameter. Spearfishing, an activity that would tend to reinforce avoidance behaviour in fishes, is not a common recreational activity in Tasmanian waters and is prohibited commercially. We are unaware of any instances of fish feeding by divers within reserves.

A second bias with potential to systematically affect the study relates to differences in visual census estimates in different habitats. A pronounced shift in the algal community

occurred within the Maria Island reserve over the period of study relative to reference sites, with the predominant plant changing from the fucoid alga *Cystophora retroflexa* to the laminarian kelp *Ecklonia radiata*. Such changes in algal cover can bias results if the visibility of particular fishes to divers differs between *Cystophora* and *Ecklonia* beds. While the extent of such biases remain unknown, they are unlikely to be great for fishes that generally swim well above the seabed, such as trumpeter and, to a lesser extent, species of *Notolabrus*, but could be of considerable importance for more cryptic fishes such as *Pictilabrus laticlavius*.

While systematic biases will have greatest impact on fish population estimates, they could also potentially affect estimates of the mean size of rock lobsters. Estimates of the density of rock lobsters are considered reliable because the antennae of animals were readily visible at the entrance to caves or under rocks; however, not all rock lobsters sighted could be captured by divers for size measurement. If large animals showed less resistance to capture within reserves compared to outside, then overall size estimates and tests would be biased. Nevertheless, given that the magnitude of change in the size-distribution of rock lobsters within reserves was great and that approximately half rock lobsters sighted were captured (e.g. 53% in 1997), any such bias should not be great.

Spatial confounding, caused by differences in the separation of reserve and reference sites, possibly caused some analytical errors in our study. Sites within reserves were separated by distances ranging from 1 to 7 km, while surrounding reference sites were separated by distances of 3 to 21 km. Spatial confounding is unavoidable in a study such as this unless only one internal and one reference site were to be associated with each reserve, a protocol that precludes replication of sites and does not allow effects at individual reserves to be examined. Grouping reference sites together at the same scale of separation as a similar number of reserve sites leads to much greater confounding because environmental factors may operate differently in the particular region where the reference sites are located. Substantially increasing the number of reference sites to accommodate a 1-km separation between all sites leads to an unbalanced statistical design with the majority of data collected outside reserves, and does not reduce the separation distance between the most distant reference sites.

Confounding caused by differences in the separation distances of reserve and reference sites nevertheless appears to have been relatively minor in our study, and is unlikely to have seriously affected most tests. Environmental factors that affect all sites in a marine reserve but only a subset of the more distantly separated reference sites should cause greater variability of response variables at reference sites than at reserve sites. This spatial confounding should therefore be evident in larger confidence intervals for reference sites than for reserve sites, but such effects were not generally seen (see Figs. 2, 4, 6, 9 and 14). The variables with consistently higher error bars associated with data collected outside reserves compared to inside were sea urchin density and *Cystophora retroflexa* and *Ecklonia radiata* cover. Interpretation of trends in these variables therefore need to be treated with a high degree of caution.

A related problem is the error introduced by conducting tests based on a random distribution of samples, when the sampling units used for tests (sites) were selected haphazardly rather than randomly. Ideally, a large set of sampling sites would initially

be identified and the particular sites to be sampled then selected using random numbers. In practice, the number of sites available to be sampled is normally very low, as in the present study, and the most suitable sites are used. The extent of site confounding may be large in field studies, but generally cannot be estimated.

Another aspect of spatial confounding is bias introduced by particular sites possessing disproportionately high density values, and therefore dominating mean data values for the region. This bias, which greatly affects statistical tests of F -values and correlations, is indicated by large confidence intervals and heterogeneous variances. At Maria Island, the densities of *Trachinops caudimaculatus* and *Penicipelta vittiger*, and cover of *Cystophora retroflexa*, were affected in this way, hence statistical tests for these variables are possibly unreliable. Large increases in density of *T. caudimaculatus* at a single reference site, for example, will result in a significant negative correlation when changes in reserves relative to reference sites are examined over time. Caution is also required in interpreting trends in trumpeter numbers because of the absence of that species from most reference sites and most 1992 reserve sites.

Analytical errors in our study probably also resulted from low power in many of the statistical tests used and consequent Type II errors (i.e. a difference between treatments was present but not detected). Such errors would be much more common for data collected at Tinderbox and Governor Island, where a total of only four sites were sampled, than at Maria Island, where 12 sites were sampled. Power analyses indicate that the ANOVA design used would, for example, detect an increase in fish species richness of 25% at Maria Island with a probability of 0.80 (viz. $\beta=0.8$, $\alpha=0.05$, no change at external sites), whereas an increase in species richness of $\approx 60\%$ would be needed for the same probability of detection at Tinderbox or Governor Island. The same α ($=0.05$) and β ($=0.80$) values for rock lobster density, mean abalone size and *Cystophora* cover would allow the detection of 96, 11 and 98% increase at Maria Island, respectively, but would require 410, 28 and 240% increase at the smaller reserves. Results of the present study generally agree with earlier calculations (Edgar and Barrett, 1997) that a doubling or halving in population numbers would be necessary to detect a significant change in density at Maria Island, but that much smaller changes of only $\approx 10\%$ would be required for significant change to be detected in mean body size.

4.2. Conservation value of marine reserves

Marine reserves are frequently cited to be amongst the most useful tools available to coastal managers for conserving marine biodiversity (e.g. Ballantine, 1991; Zann, 1995), a claim that relies almost entirely on a theoretical basis. Fishing is suggested to cause declines in biodiversity through reduction of heavily exploited species' populations to such low levels that they are effectively removed from the system (see Dayton et al., 1998), and through the indirect loss of species not adapted to the ecosystem perturbations caused by fishing.

The present study provides empirical evidence to support this hypothesis for subtidal temperate reefs. The large Maria Island marine reserve was effective at maintaining and enhancing the number of species of fishes, invertebrates and macroalgae at the scale of 50-m transects. The Tinderbox marine reserve also was effective at enhancing the

number of species of large fishes. By contrast, the two small reserves had no tangible effects on species richness.

The conservation effectiveness of the Maria Island and Tinderbox reserves relates primarily to the disproportionate presence of large fish species such as trumpeter, ling and draughtboard shark, which have been virtually eliminated from heavily fished reefs outside the reserve. While invertebrate and macroalgal species richness also significantly increased within the Maria Island reserve relative to outside, the changes in these groups were presumably indirect responses rather than direct responses to fishing. The only three invertebrate species widely exploited in eastern Tasmania (abalone, rock lobster and sea urchin) all occurred commonly on transects outside as well as inside reserves, hence no change in the number of exploited invertebrate species occurred.

Processes contributing to the increases in invertebrate and algal species richness at Maria Island remain uncertain; however, the changes probably relate to the general transformation in the algal community over the 5-year monitoring period. Fewer algal species are typically found associated with *Cystophora retroflexa* than *Ecklonia radiata* (see, for example, Edgar, 1983).

The factors responsible for the transformation in the algal community at Maria Island remain unknown, although it is notable that a similar direction of change in *E. radiata* and *C. retroflexa* (but not *S. fallax*) occurred outside the reserve, albeit at a slower rate. The detection of significant changes in algal species within the Maria Island reserve relative to outside may have resulted from spatial confounding (see previous section); however, it is more likely that interaction between fishing and long-term hydrological effects was responsible. A gradual increase in mean water temperature in excess of 1°C, and associated decreases in nutrient concentrations, have been documented in eastern Tasmanian waters over the past four decades (Harris et al., 1987; Crawford et al., 1999). Concurrent with these hydrological changes have been declines in pelagic fish catches and the extent of *Macrocystis pyrifera* beds, and a southern expansion of warm temperate species (Edgar, 1984a; Harris et al., 1992; Crawford et al., 1999).

Despite our results at Maria Island, changes in invertebrate and algal species richness following the declaration of marine reserves will rarely be predictable at the scale of transects unless habitat structure is damaged by fishing gear (Watling and Norse, 1998). In many situations, removal of fishing pressure may cause a decline in species richness because of unpredictable ecosystem changes or because particular species become dominant and exclude others. However, at spatial scales of tens to hundreds of kilometres, the presence of marine reserves should lead to increased species diversity because of increased ecosystem heterogeneity associated with fished and unfished areas. Major biodiversity conservation benefits of marine reserves therefore can be summarised as: (i) direct increases in the number of exploited species and bycatch species at reef scales, (ii) protection of habitats at reef scales from fishing gear damage, and (iii) increases in ecosystem heterogeneity at regional scales.

4.3. Fish propagation value of marine reserves

Prohibitions on fishing within the Maria Island and Tinderbox marine reserves significantly affected fish, invertebrate and macroalgal populations, particularly popula-

tions of the most heavily exploited species – rock lobster, abalone and large finfish. Densities of these three groups all increased for size-classes above the minimum legal size, while remaining stable or decreasing for size-classes below that size. The minimum legal sizes in Tasmania are 110 mm (male) and 105 mm (female) carapace length for rock lobster, 132 mm for abalone, and 330 mm for trumpeter.

Local fishery statistics indicate that rock lobster, abalone and large finfish account for nearly all of the inshore fishery catch in Tasmania. Approximately similar biomasses (≈ 2000 tonnes) of rock lobsters, abalone and finfish were taken by commercial fishers in 1996–1997 from inshore Tasmanian waters, with rock lobster and abalone most heavily targeted, together contributing 91% of the total Tasmanian wild fishery catch by value (Australian Bureau of Agricultural and Resource Economics, 1997).

The response of these three major fishery groups to protection from fishing was variable, with abalone responding in a different way to rock lobsters or large fishes. Rock lobster abundance increased by 250 and 100% at Maria Island and Tinderbox, respectively, and mean rock lobster carapace length increased substantially in all reserves. By contrast, a decrease in abalone density of at least 30% occurred within all reserves that was concurrent with an increase in mean abalone length. The cause of the abalone population decline can only be speculated on, but perhaps intraspecific competition occurred amongst abalone, with large individuals dominating the use of resources at the expense of small individuals. Alternatively, elevated densities of large fishes and rock lobsters within reserves may increase predation pressure on small abalone.

The number of large finfish increased consistently by $\approx 250\%$ within the Maria Island and Tinderbox reserves, with the population of bastard trumpeter at Maria Island increasing approximately 100-fold. Recovery of the trumpeter population at Maria Island was, however, strongly influenced by a single major recruitment event in 1994/95, hence data over a longer time span are required to determine whether this recovery is sustainable.

Given that the biomass of exploited stocks has substantially increased within the two larger marine reserves, the question of primary interest to fishers and managers is whether this increased biomass translates to increased production in adjacent regions. Increased production can occur through two processes – enhanced reproductive output of eggs and larvae, leading to a rise in juvenile recruitment outside reserves, or large individuals emigrating from marine reserves, inflating fish catches nearby.

Marine reserves at Maria Island, Tinderbox and, to a lesser extent, the two smaller Tasmanian locations now produce substantially higher numbers of eggs and larvae of heavily exploited species than similar areas of fished reef. Included amongst the species with more mature individuals and enhanced reproductive output are blue-throated wrasse, rock lobster and abalone. The Maria Island marine reserve should also contribute to increased reproductive output of bastard trumpeter, although trumpeter observed during the study had not reached the size of sexual maturity by 1997 (see Harries and Lake, 1985) and possibly move to deeper offshore reefs to spawn.

Increased reproductive output of exploited species is probably a general feature of marine reserves of adequate size because (i) higher population densities often occur inside reserves, (ii) the population inside reserves includes a greater proportion of large

animals that are sexually mature, and (iii) the large mature animals inside reserves produce more eggs and larvae than the relatively small mature animals outside. While these factors will not always operate together, when they combine huge increases in egg production can occur, such as the order of magnitude increase that was estimated for rock lobsters over the 6-year monitoring period at Maria Island. Whether this increased egg production leads to increased juvenile recruitment remains speculative.

The strength of linkages between egg production, juvenile recruitment and total fish catch presumably vary greatly between species, and also with location and ambient population densities. Relationships between egg production and recruitment are unlikely to be linear in most cases (Caputi, 1993; Hilborn, 1997), with declines in egg production closely related to declining recruitment only at low population densities (Myers et al., 1996). Marine reserves should provide effective propagation areas whenever the linkage between egg production and recruitment is close to linear, and also provide insurance against catastrophic stock collapses when a minimum density of spawning animals is required for successful recruitment (see Ballantine, 1991).

The extent to which adults emigrate from reserves, and so enhance fisheries nearby, also has not been assessed in the present study, so remains conjectural. Anecdotal information and the tendency for fishers to set nets and pots on reserve boundaries in Tasmania nevertheless suggest that considerable export of adult fish and rock lobster biomass occurs. Emigration of fish may well be enhanced by crowding in marine reserves. Increasing emigration rates with increasing densities have been documented for a number of marine species (e.g. Levinton, 1979).

4.4. Size of marine reserves versus effectiveness

Although generalisations are limited by the small number of reserves examined, effectiveness corresponded with reserve size in this study. The protected area at Maria Island, which extends along ≈ 7 km of coastline, has worked effectively for species conservation and fish propagation, followed by Tinderbox (2 km of coastline) and then the Ninepin Point and Governor Island reserves (both ≈ 1 km of coastline). Nevertheless, this size/effectiveness relationship may result solely from chance, with further work needed to determine whether the relationship is generally true or a consequence of particular conditions unrelated to size that particularly enhance the effectiveness of the Maria Island reserve.

The lack of detection of significant change in the smallest reserves presumably resulted partly from a lack of power in statistical tests. However, this does not explain why the magnitude of change of almost all the biological variables examined was greater at the large Maria Island reserve than at the two smallest reserves. Six of the variables found to increase significantly in the Maria Island Marine Reserve showed comparable increases at Tinderbox (large fish species richness, large fish abundance, mean blue-throated wrasse size, rock lobster density, mean rock lobster size, mean abalone size), while only rock lobster density (Governor Island), rock lobster size and abalone size (Ninepin Point) increased substantially in the small reserves.

A size/effectiveness relationship is consistent with information on the home ranges of large reef fishes, many of which move distances of several hundred metres over daily

and weekly periods. On Tasmanian reefs, where movements of six fish species have been studied, the wrasse *Notolabrus fucicola* and the monacanthids *Penicipelta vittiger* and *Meuschenia australis* were found to move distances exceeding 150 m across reefs during the day while *Pictilabrus latidivus* and *Notolabrus tetraodon* had smaller home ranges, usually 20–60 m (Barrett, 1997).

In small reserves of $\approx 1 \text{ km}^2$ where reef extends across the boundary, the average distance between location of any fish and the boundary is so small that few readily captured species can be expected to reach a large size. Such a situation prevails at Ninepin Point and Governor Island, where nets and rock lobster pots are routinely set in large numbers around the reserve boundary.

The effectiveness of marine reserves will depend largely on the mobility of target species, with the more sedentary animals such as abalone most likely to be protected in reserves of a small size. The present study indicates that rock lobsters, which grew to a large size even in the small Ninepin Point and Governor Island reserves, must also be highly site-attached and generally move distances of less than a kilometre over periods of several years. Any rock lobsters roaming out from Tasmanian reserves would have a high chance of capture.

One surprising result of the study was that trumpeter greatly increased in number at Maria Island, and so appear to rarely move between reefs despite swimming continuously well above the seabed. Unpublished tagging data obtained by Tasmanian Aquaculture and Fisheries Institute biologists R. Murphy and J. Lyle (personal communication) indicated that animals can move more than 140 km over a year period, but that the majority of tagged trumpeter associated with inshore reefs remained for several years within 5 km of the initial tagging site, the minimum resolution used in their study. Comparable results were found in a South African study of galjoen (*Coracinus capensis*), a species inferred to be polymorphic in its movements, with some individuals migrating large distances while other animals of a similar size are recaptured in a localised area (Attwood and Bennett, 1994; C. Attwood, personal communication).

The more sedentary individuals of trumpeter in Tasmania are possibly hindered in their longshore movement by sandy beaches, and so restricted to particular rocky headlands. The Maria Island reserve included relatively small headlands separated by several hundred metres of intervening sand.

Reserve designs clearly need to take into account what is known of the short and long term movement patterns of the species they are intended to protect. If the primary aim of a reserve is to conserve biological communities, then the presence of any potential barriers to movement, such as beaches that act as boundary fences, should be identified and used wherever possible, particularly if the reserve is small. If the primary function of a reserve is as a fish propagation area, then it may be desirable to have an open boundary with continuous reef that allows ready movement of animals out from the reserve.

4.5. Monitoring value of marine reserves

The present study revealed that Tasmanian coastal reef communities have changed

greatly in response to fishing pressure. This result is consistent with results of another long-term study of temperate reefs, the Californian study of Dayton et al. (1998), where the functional loss of numerous major predators was identified. Tasmanian coastal reefs appear capable of supporting much higher densities of rock lobsters and commercially important fishes but have been heavily overfished. In this context it is worth noting that data on the size-distribution of fishes and rock lobster, and cover of dominant macroalgae at Maria Island, showed little sign of having stabilised at the unfished state in 1997. The magnitude of the difference between undisturbed and fished reefs is therefore probably considerably greater than results currently indicate.

The major cause of large fish mortality on inshore Tasmanian reefs is probably trapping in gillnets, with these nets widely used by both recreational and commercial fishers in the state. Statistics for 1996 indicate that the 5614 licensed recreational net fishers in Tasmania set their 50 m long nets for approximately 120 000 'net days' per year (Anon, 1998). Trumpeter were the major target species, and comprised the main or second catch species for 47% of fishers (Anon, 1998). The mean length of trumpeter caught in the 108-mm mesh nets used was 320 mm, with a similar mean size (330 mm) of wrasse also taken (R. Murphy and J. Lyle, unpublished data).

The virtual absence of trumpeter at reference sites outside the Maria Island reserve indicates that current levels of fishing, which primarily target immature fish, are far in excess of maximum sustainable levels for the region. The catch history of this species also indicates substantial overfishing and a long-term decline. At the end of the nineteenth century, the two local trumpeter species, *Latridopsis forsteri* and *Latris lineata* (Bloch and Schneider), were the mainstay of the Tasmanian scalefish fishery. Following a substantial decline, catches of ≈ 50 tonnes were taken in the 1940s; however, by 1980 the total commercial catch had further declined to only ≈ 1 tonne (Harries and Croome, 1989). Commercial catches have risen since 1980 to ≈ 15 tonnes (J. Lyle, unpublished data) but remain many times lower than last century.

One major outcome of the present marine reserve study is that new avenues of fishery management are indicated, with potential to lead to increased total catches. Closure of small areas of coast from rock lobster fishing and reopening over cycles of several years, for example, should lead to increases in the overall biomass of rock lobsters caught. On the basis of Maria Island data on densities of animals in size-classes above 90 mm carapace length, the minimum size that should progress to the legal size during the next 12 months, re-opening a closed area similar to the Maria Island reserve after 5 years is estimated to allow ≈ 400 kg per hectare of legal sized rock lobsters to be harvested. This equates to a catch of 80 kg/hectare/year, compared with ≈ 40 kg/hectare/year that can be taken with no reserve. Without the declaration and monitoring of marine reserves, the overfished state of coastal reefs in Tasmania would remain unknown, and possible avenues for increasing fish catches remain unexplored.

In other temperate areas of the world, monitoring within marine reserves has also proved the most effective tool for identifying gross ecosystem effects of fishing. Continuous human harvesting of plants and animals in the marine environment has been most comprehensively investigated in Chile. To the surprise of Chilean investigators, the intertidal community that developed in an area protected from human foragers showed virtually no similarity to that previously considered as 'normal'. Species thought to

occur only in subtidal depths became prevalent in the intertidal, and species formerly rare became conspicuous and dominant (Castilla, 1989; Duran and Castilla, 1989).

Additionally, the investigation of marine reserves in South Africa led to the discovery that rock lobsters can play a pivotal role in structuring invertebrate assemblages associated with reefs. High densities of rock lobsters in an unexploited marine reserve were found to eliminate beds of mussels and other filter feeders, and therefore alter ecosystem functioning (Barkai and Branch, 1988). Monitoring the effects of marine reserves in other temperate regions may well show that ecosystem changes caused by overfishing are widespread.

Monitoring studies of marine reserves are thus an important tool for identifying general impacts of fishing and assessing the ‘health’ of coastal reefs. Monitoring of reference sites associated with marine reserves also provides valuable information on long-term trends in the coastal environment, including those related to global warming and introduced species (Edgar et al., 1997).

4.6. Scientific value of marine reserve studies

The present study of marine reserves, and others with similar design, represent orthodox scientific experiments in the Baconian tradition (see Popper, 1968). The general hypothesis investigated is that protection of areas from fishing leads to increased abundance of large size classes of exploited species. Amongst the specific predictions arising from this general hypothesis are that the density of large rock lobsters, trumpeter and abalone will increase within Tasmanian marine reserves, which in turn generates the testable null hypotheses that no change will occur in the density of large individuals of these species within reserves relative to reference sites. In the present study, the null hypotheses relating to rock lobster, trumpeter and abalone at Maria Island were rejected after statistical analyses, thereby providing empirical support for the general hypothesis.

In addition to structured hypothesis-testing, studies of the effects of marine reserves can also produce serendipitous results because predictions generally cannot be made about the indirect effects of fishing, or the influence of marine reserves on biodiversity of plants and invertebrates. Unexpected observations made in marine reserve studies may well prove more interesting than the outcomes of hypothesis-testing because they reveal aspects of ecosystem function at large scales that have previously been unrecognised – and therefore stimulate the formulation of new general hypotheses.

As an example, amongst the more interesting outcomes of the present study was the observation that increasing numbers of large abalone within reserves were accompanied by decreasing numbers of smaller individuals. This observation may result from a general pattern of exploitative competition for resources between different life-history stages of grazing species, an important hypothesis that deserves direct testing in future marine reserve studies. Considerable evidence to support this hypothesis is available from experiments at small spatial scales (e.g. Creese and Underwood, 1982; Quinn, 1988; Edgar, 1993; Edgar and Aoki, 1993); however, such experiments need to be expanded to larger domains.

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References

- Allison, G.W., Lubchenco, J., Carr, M.H., 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.* 8, S79–S92.
- Andrew, N.L., Choat, J.H., 1982. The influence of predation and conspecific adults on the abundance of juvenile *Evechinus chloroticus* (Echinoidea: Echinometridae). *Oecologia* 54, 80–87.
- Andrew, N.L., Underwood, A.J., 1993. Density-dependent foraging in the sea urchin *Centrostephanus rodgersii* on shallow subtidal reefs in New South Wales, Australia. *Mar. Ecol. Prog. Ser.* 99, 89–98.
- Anon, 1998. Recreational scalefish fishery, Department of Primary Industry and Fisheries, Hobart, Australia, Policy paper.
- Attwood, C.G., Bennett, B.A., 1994. Variation in dispersal of galjoen (*Coracinus capensis*) (Teleostei: Coracinidae) from a marine reserve. *Can. J. Fish. Aquat. Sci.* 51, 1247–1257.
- Attwood, C.G., Bennett, B.A., 1996. Modelling the effect of marine reserves on the recreation fishery of the South-Western Cape, South Africa. *S. Afr. J. Mar. Sci.* 16, 227–240.
- Marine Reserves Task Group, Attwood, C.G., Harris, J., Williams, A., 1997. International experience of marine protected areas with relevance to South Africa. In: *Towards A New Policy On Marine Protected Areas For South Africa*, SANCOR, Pretoria, South Africa, pp. 13–52.
- Australian Bureau of Agriculture and Resource Economics, 1997. *Australian Fisheries Statistics – 1997*, ABARE, Canberra, Australia.
- Ballantine, B., 1991. Marine Reserves for New Zealand. *Leigh Lab. Bull. Univ. Auckland* 25, 1–196.
- Barkai, A., Branch, G.M., 1988. The influence of predation and substratal complexity on recruitment to settlement plates: a test of the theory of alternate states. *J. Exp. Mar. Biol. Ecol.* 124, 215–237.
- Barrett, N.S., 1997. Short and long-term movement patterns of six temperate reef fishes (Families: Labridae and Monacanthidae). *J. Mar. Freshw. Res.* 46, 853–860.
- Bell, J.D., 1983. Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the northwestern Mediterranean Sea. *J. Appl. Ecol.* 20, 357–369.
- Bennett, B.A., Attwood, C.G., 1991. Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa. *Mar. Ecol. Prog. Ser.* 75, 173–181.
- Branden, K.L., Edgar, G.J., Shepherd, S.A., 1986. Reef fish populations of the Investigator Group, South Australia: a comparison of two census methods. *Trans. R. Soc. S. Aust.* 110, 69–76.
- Brock, R.E., 1982. A critique of the visual census method for assessing coral reef fish populations. *Bull. Mar. Sci.* 32, 269–276.
- Buxton, C.D., Smale, M.J., 1989. Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the southern Cape coast. *J. Appl. Ecol.* 26, 441–451.
- Caputi, N., 1993. Aspects of spawner–recruit relationships, with particular reference to crustacean stocks: a review. *Aust. J. Mar. Freshw. Res.* 44, 589–607.
- Castilla, J.C., 1989. Human exclusion from rocky intertidal of Las Cruces, central Chile: Effects on *Durvillaea antarctica* (Phaeophyta, Durvilliales). *Mar. Ecol. Prog. Ser.* 50, 203–214.

- Cheal, A.J., Thompson, A.A., 1997. Comparing visual counts of coral reef fish: implications of transect width and species selection. *Mar. Ecol. Prog. Ser.* 158, 241–248.
- Choat, J.H., Andrew, N.L., 1986. Interactions amongst species in a guild of subtidal benthic herbivores. *Oecologia* 68, 387–394.
- Choat, J.H., Ayling, T., 1987. The relationship between habitat structure and fish faunas on New Zealand reefs. *J. Exp. Mar. Biol. Ecol.* 110, 257–284.
- Cole, R.G., 1994. Abundance, size structure, and diver-oriented behaviour of three large benthic carnivorous fishes in a marine reserve in northeastern New Zealand. *Biol. Conserv.* 70, 93–99.
- Cole, R.G., Ayling, T.M., Creese, R.G., 1990. Effects of marine reserve protection at Goat Island, northern New Zealand. *New Zealand J. Mar. Freshw. Res.* 24, 197–210.
- Crawford, C.M., Edgar, G.J., Cresswell, G.R., 1999. The Tasmanian region. In: Sheppard, C. (Ed.), *Seas at the Millennium*, Elsevier, Oxford, In press.
- Creese, R.G., Underwood, A.J., 1982. Analysis of inter-and intra-specific competition amongst intertidal limpets with different methods of feeding. *Oecologia* 53, 337–346.
- Davis, G.E., 1981. On the role of underwater parks and sanctuaries in the management of coastal resources in the southeastern United States. *Environ. Conserv.* 8, 67–70.
- Dayton, P.K., Tegner, M.J., Edwards, P.B., Riser, K.L., 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecol. Appl.* 8, 309–322.
- Dugan, J.E., Davis, G.E., 1993. Introduction to the International Symposium on Marine Harvest Refugia. *Can. J. Fish. Aquat. Sci.* 50, 1991–1992.
- Duran, L.R., Castilla, J.C., 1989. Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Mar. Biol.* 103, 555–562.
- Eberhardt, L.L., Thomas, J.M., 1991. Designing environmental field studies. *Ecol. Monogr.* 61, 53–73.
- Edgar, G.J., 1983. The ecology of south-east Tasmanian phytal animal communities. I. Spatial organisation on a local scale. *J. Exp. Mar. Biol. Ecol.* 70, 129–157.
- Edgar, G.J., 1984a. General features of the ecology and biogeography of Tasmanian rocky reef communities. *Pap. Proc. R. Soc. Tasmania* 118, 173–186.
- Edgar, G.J., 1984b. Marine life and potential marine reserves in Tasmania. Part 2. *Natl. Parks Wildl. Serv. Tasmania, Occasional Papers* 7, 1–102.
- Edgar, G.J., 1993. Measurement of the carrying capacity of benthic habitats using a metabolic-rate based index. *Oecologia* 95, 115–121.
- Edgar, G.J., Aoki, M., 1993. Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*. *Oecologia* 95, 122–133.
- Edgar, G.J., Barrett, N.S., 1997. Short term monitoring of biotic change in Tasmanian marine reserves. *J. Exp. Mar. Biol. Ecol.* 213, 261–279.
- Edgar, G.J., Moverley, J.S., Barrett, D., Peters, N.S., Reed, C., 1997. The conservation-related benefits of a systematic marine biological sampling program: the Tasmanian bioregionalisation as a case study. *Biol. Conserv.* 79, 227–240.
- Fletcher, W.J., 1987. Interactions among subtidal Australian sea urchins, gastropods, and algae: Effects of experimental removals. *Ecol. Monogr.* 57, 89–109.
- Glasby, T.M., 1997. Analysing data from post-impact studies using asymmetrical analyses of variance: a case study of epibiota on marinas. *Aust. J. Ecol.* 22, 448–459.
- Green, R.H. (Ed.), 1979. *Sampling Design and Statistical Methods For Environmental Biologists*, Wiley, Chichester, p. 257.
- Gubbay, S. (Ed.), 1995. *Marine Protected Areas: Principles and Techniques For Management*, Chapman & Hall, London, p. 232.
- Harries, D.N., Croome, R.L., 1989. A review of past and present inshore gill netting in Tasmania with particular reference to the bastard trumpeter *Latridopsis forsteri* Castelnau. *Pap. Proc. R. Soc. Tasmania* 123, 97–110.
- Harries, D.N., Lake, P.S., 1985. Aspects of the biology of inshore populations of bastard trumpeter, *Latridopsis forsteri* (Castelnau, 1872) in Tasmanian waters. *Tas. Fish. Res.* 27, 19–43.
- Harris, G.P., Griffiths, F.B., Clementson, L.A., 1992. Climate and the fisheries off Tasmania – interactions of physics, food chains and fish. *S. Afr. J. Mar. Sci.* 12, 585–597.

- Harris, G.P., Nilsson, C.S., Clementson, L.A., Thomas, D.P., 1987. The water masses of the east coast of Tasmania: seasonal and interannual variability and the influence on phytoplankton biomass and productivity. *Aust. J. Mar. Freshw. Res.* 38, 569–590.
- Hilborn, R., 1997. Comment: recruitment paradigm for fish stocks. *Can. J. Fish. Aquat. Sci.* 52, 984–985.
- Jones, G.P., 1992. Interactions between herbivorous fishes and macro-algae on a temperate rocky reef. *J. Exp. Mar. Biol. Ecol.* 159, 217–235.
- Jones, G.P., Cole, R.C., Battershill, C.N., 1993. Marine reserves: do they work. In: Battershill, C.N., Schiel, D.R., Jones, G.P., Creese, R.G., MacDiarmid, A.B. (Eds.), *Proceedings of the 2nd International Temperate Reef Symposium NIWA, Wellington, New Zealand*, pp. 29–45.
- Kennington, R., Bleakley, C., 1994. Identifying priorities for marine protected areas in the insular Pacific. *Mar. Pollut. Bull.* 29, 3–9.
- Kulbicki, M., 1998. How acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *J. Exp. Mar. Biol. Ecol.* 222, 11–30.
- Last, P.R., Scott, E.O.G., Talbot, F.H. (Eds.), 1983. *Fishes of Tasmania*, Tasmanian Fisheries Development Authority, Hobart, p. 563.
- Levinton, J.S., 1979. The effects of density upon deposit-feeding populations: movement, feeding and floating of *Hydrobia ventrosa* Montagu (Gastropoda: Prosobranchia). *Oecologia* 43, 27–39.
- Lincoln-Smith, M.P., 1988. Effects of observer swimming speed on sample counts of temperate rocky reef fish assemblages. *Mar. Ecol. Prog. Ser.* 43, 223–231.
- Lincoln-Smith, M.P., 1989. Improving multispecies rocky reef fish censuses by counting different groups of species using different procedures. *Environ. Biol. Fishes* 26, 29–37.
- McClanahan, T.R., Kaunda-Arara, B., 1996. Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conserv. Biol.* 10, 1187–1199.
- McClanahan, T.R., Muthiga, N.A., Kamakuru, A.T., Machano, H., Kiambo, R.W., 1999. The effects of marine parks and fishing on coral reefs of northern Tanzania. *Biol. Conserv.* 89, 161–182.
- McCormick, M.I., Choat, J.H., 1987. Estimating total abundance of a large temperate-reef fish using visual strip transects. *Mar. Biol.* 96, 469–478.
- McKone, M.J., Lively, C.M., 1993. Statistical analysis of experiments conducted at multiple sites. *Oikos* 67, 184–186.
- McNeill, S.E., 1994. The selection and design of marine protected areas: Australia as a case study. *Biodivers. Conserv.* 3, 586–605.
- Menge, B.A., 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores. *Ecology* 73, 755–765.
- Menge, B.A., 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol. Appl.* 5, 21–74.
- Myers, R.A., Mertz, G., Barrowman, N.J. (Eds.), 1996. Invariants of spawner–recruitment relationship for marine, anadromous, and freshwater species, International Council for the Exploration of the Sea, Copenhagen, Denmark, p. 17. *ICES Council Meeting Papers*.
- Popper, K.R. (Ed.), 1968. *The Logic of Scientific Discovery*, Hutchinson, London, p. 480.
- Quinn, G.P., 1988. Effects of conspecific adults, macroalgae and height on the shore on recruitment of an intertidal limpet. *Mar. Ecol. Prog. Ser.* 48, 305–308.
- Rakitin, A., Kramer, D.L., 1996. Effects of a marine reserve on the distribution of coral reef fishes in Barbados. *Mar. Ecol. Prog. Ser.* 131, 97–113.
- Roberts, C.M., 1995. Rapid build up of fish biomass in a Caribbean marine reserve. *Conserv. Biol.* 9, 815–826.
- Roberts, C.M., Polunin, N.V.C., 1991. Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fish.* 1, 65–91.
- Roberts, C.M., Polunin, N.V.C., 1993. Marine reserves: Simple solutions to managing complex fisheries? *Ambio* 22, 363–368.
- Russ, G.R., Alcala, A.C., 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. *Mar. Ecol. Prog. Ser.* 56, 13–27.
- Russ, G.R., Alcala, A.C., 1996a. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Mar. Ecol. Prog. Ser.* 132, 1–9.

- Russ, G.R., Alcala, A.C., 1996b. Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecol. Appl.* 6, 947–961.
- Russell, B.C., 1977. Population and standing crop estimates for rocky reef fishes of north eastern New Zealand. *New Zealand J. Mar. Freshw. Res.* 11, 23–26.
- Sobel, J., 1993. Conserving marine diversity through marine protected areas. *Oceanus* 36, 19–26.
- Thompson, A.A., Mapstone, B.D., 1997. Observer effects and training in underwater visual surveys of reef fishes. *Mar. Ecol. Prog. Ser.* 154, 53–63.
- Thresher, R.E., Gunn, J.S., 1986. Comparative analysis of visual census techniques for highly mobile, reef-associated piscivores (Carangidae). *Environ. Biol. Fishes* 17, 93–116.
- Walters, C.J., Holling, C.S., 1990. Large-scale management experiments and learning by doing. *Ecology* 71, 2060–2068.
- Wantiez, L., Thollot, P., Kulbicki, M., 1997. Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. *Coral Reefs* 16, 215–224.
- Watling, L., Norse, E.A., 1998. Disturbance of the seabed by mobile fishing gear: A comparison to forest clearfelling. *Conserv. Biol.* 12, 1180–1197.
- Zann, L.P. (Ed.), 1995. Our sea, our future. Major findings of the state of the marine environment report for Australia, Great Barrier Reef Marine Park Authority, Townsville, Queensland, p. 112.