



Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection

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ABSTRACT

Densities of macrobenthic invertebrates and macro-algae in four Tasmanian 'no-take' marine protected areas (MPAs) were monitored annually for 10 years following MPA establishment, with changes compared to those at external (fished) reference locations. Fishing substantially influenced the population characteristics of many species, including altering the mean size and abundance of rock lobsters and the abundance of prey species such as urchins and abalone. Strong declines in abundances of purple urchins and abalone within the largest MPA at Maria Island indicate likely indirect effects related to protection of predators from fishing. The two smallest MPAs (ca. 1 km coastal span) generated few detectable changes. Our results affirm the importance of long-term monitoring and the value of MPAs, when sufficiently large, as reference areas for determining and understanding ecosystem effects of fishing in the absence of historical baseline data.

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1. Introduction

Scientific interest is increasingly focused on the use of marine protected areas (MPAs) as spatial management tools to counter anthropogenic impacts on inshore marine ecosystems (e.g. Mann, 1982 in Nova Scotia; Tegner and Dayton, 1991; Cowen, 1983 in California), and to ensure long-term sustainability of coastal ecosystems. In Australia, these aims are embodied in Oceans Policy (Commonwealth of Australia, 1998), with all States and Territories committed to the establishment of a National Representative System of Marine Protected Areas (ANZECC, 1998). While the primary purpose of these MPAs is conservation of biodiversity, other suggested benefits include the protection of fish spawner biomass, a source of recruits, insurance against stock collapse, and increased ecosystem resilience (for review see Roberts and Hawkins, 2000; Ward et al., 2001; Gell and Roberts, 2002; Edgar et al., 2007). MPAs also provide the opportunity to inform fisheries managers about natural growth and mortality rates, and the ecosystem effects of fishing.

Much of the literature on MPAs has focussed on target species (e.g. Bell et al., 1985; Buxton and Smale, 1989; Cole et al., 1990; Bennett and Attwood, 1991; Francour, 1994; Babcock et al., 1999; Chapman and Kramer, 1999; Cole et al., 2000; Paddock and Estes, 2000; Willis et al., 2003a), demonstrating an increase in size and abundance within MPAs relative to adjacent fished sites. More recent studies examine the secondary effects of the cessation of fishing, providing evidence of top-

down regulation of food chains that re-establish within MPAs (reviews by Pinnegar et al., 2000; Tegner and Dayton, 2000; Sumaila et al., 2000). Shears and Babcock (2002, 2003) demonstrated top-down control of community structure on temperate reefs in two north-eastern New Zealand marine reserves, where lobsters and predatory fishes at natural densities limit destructive overgrazing by urchins.

This study presents a long-term time series of data on the changes that have taken place following the establishment of four Tasmanian no-take reserves in 1991. The survey design provides the opportunity to test assumptions that led to declaration of these MPAs, including that fishing had substantially altered coastal biotic assemblages, particularly with regard to target and bycatch species. Importantly the study covers the period from the beginning of protection, examining the divergence of assemblages in protected and fished areas using an experimental "Before-After-Control-Impact" type design (*sensu* Green, 1979) with replicate sites within these. This design overcomes a major limitation with many studies that either do not have a "before" component, and therefore cannot readily differentiate between differences due to habitat and protection effects (discussed in Willis et al., 2003b), or lack generality as they are based on observations of a single MPA.

MPAs effectively provide a natural controlled manipulation, where the removal of fishing pressure is the treatment. Studies of changes in MPAs are thus large scale experiments where human predators are excluded from patches of coast (Walters and Holling, 1990). This type of experiment allows changes due to natural variability and environmental cycles to be distinguished from those due to anthropogenic effects. The availability of a long time series allows an examination of trends rather than differences between endpoints, greatly reducing the chance of Type 1 errors. Incorporating four Tasmanian MPAs

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allowed an examination across a range of habitats, reserve designs (including shape and size), and differing levels of fishing pressure. Although some interaction between these factors likely exists, the inclusion of a range of locations allows for interpretation of the most likely influences of change and a better understanding of the generality of observed differences at a regional scale.

The results presented here quantify changes in the megafaunal-invertebrate and macroalgal assemblages within the Tasmanian MPAs and associated reference areas as an annual time-series over the first 10-year period following protection. Changes within fish assemblages are detailed in an associated publication (Barrett et al., 2007). The specific aims of the study were to determine if there were any identifiable effects associated with the removal of fishing pressure within reserves on target species or the broader ecosystem over this ecologically significant timescale.

2. Methods

Four “no-take” MPAs, referred to hereafter as ‘marine reserves’, were declared in Tasmania in September 1991 and all are included in this

study (Fig. 1). Field surveys commenced in February 1992. Although these surveys were undertaken shortly after declaration, no policing or signage had been undertaken, hence the initial surveys are regarded as representing baseline (“before”) conditions. The reserves differ in their intended roles, their size and the assemblages they protect. The largest reserve, a marine extension to the Maria Island National Park (referred to hereafter as “Maria I”) on the Tasmanian east coast, is a regional conservation reserve protecting 7 km of sheltered coastline. Also on the central east coast, the smaller Governor Island Marine Reserve (referred to hereafter as Governor I) at Bicheno protects 950 m of exposed coastline. In south-eastern Tasmania, the Tinderbox Marine Reserve (referred to hereafter as Tinderbox) protects a 2-km stretch of sheltered coastline, while the Ninepin Point Marine Reserve (referred to hereafter as Ninepin Pt) protects 1 km of slightly to moderately exposed coastline where tannin-stained river waters overlies clearer marine water, resulting in an altered light environment and a unique assemblage of macro-algae and animals.

Site positions are shown in Fig. 1. All surveys were restricted to the 5-m depth contour to reduce depth-related variability in comparisons. For Maria I six sites were established within the reserve and six closely

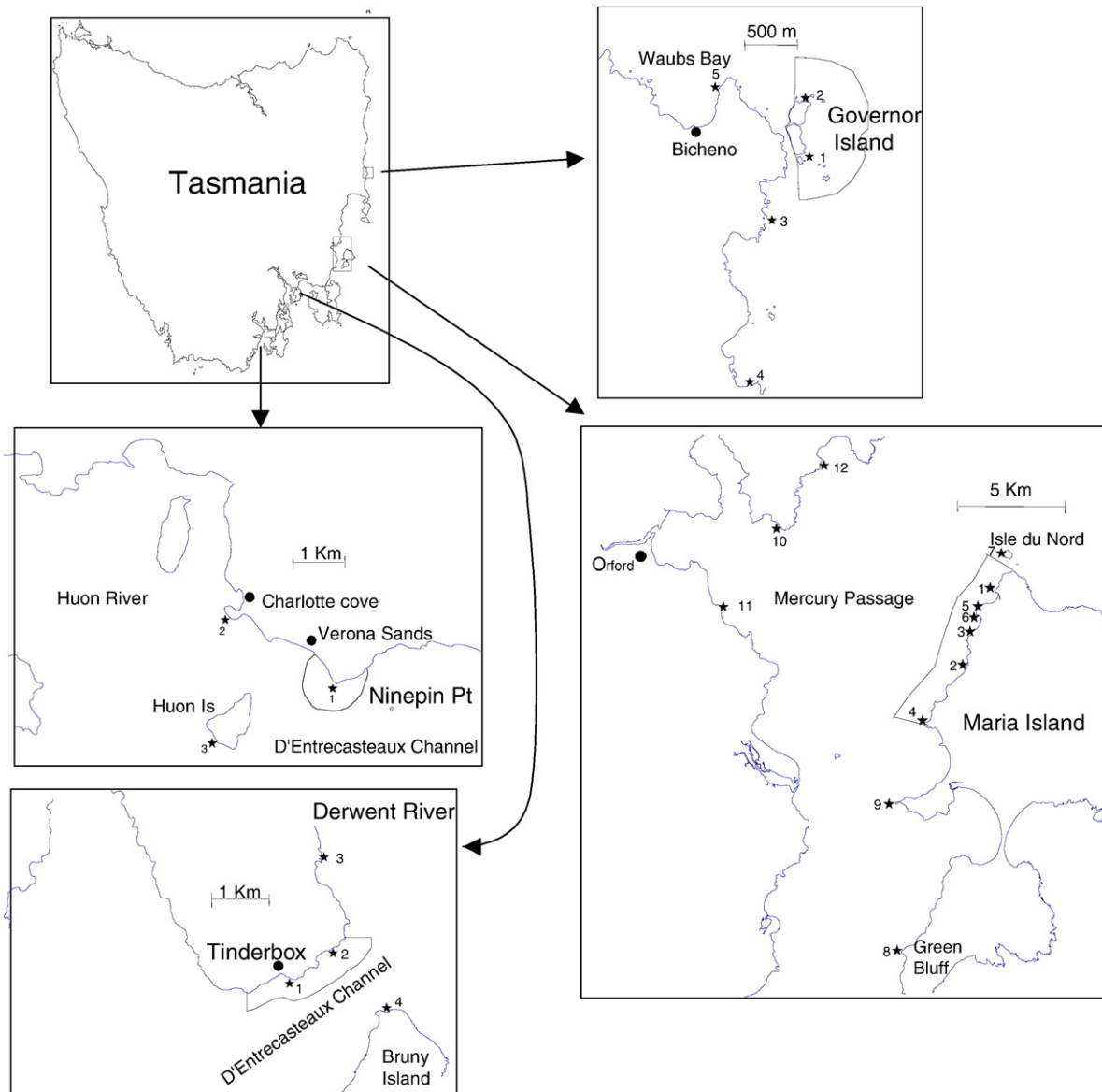


Fig. 1. Map showing location of reserves and sites surveyed.

matched reference sites were established nearby. The match of reserve and reference sites for all reserves was assessed by multivariate comparison of biological assemblage data collected during the initial design phase survey (Edgar and Barrett, 1997). Sites investigated within the reserve cover a substantial proportion of the total reef area, as much of the remaining area consists of sandy beaches or very shallow reef with little offshore extension.

At Tinderbox, only two sites were located within the reserve due to a scarcity of suitable habitat, and two reference sites were located in matching habitats nearby. The Ninepin Pt reserve contains one site internally and two reference sites. Like Tinderbox, insufficient reef was available for additional sites to be located within this reserve, but two reference sites could be established due to an abundance of similar habitat nearby. At Bicheno two sites were established within the Governor I reserve and at two closely matched external sites in close proximity.

The sampling periods were restricted to two “seasons” within each year. These periods were usually late February to late April for “Autumn” surveys and September for “Spring” surveys. Autumn and spring surveys of macroinvertebrates and macro-algae were undertaken in all reserves in 1992, 1993 and 1997, with less extensive surveys, in terms of reserves or seasons covered, undertaken in other years through to 2002, with emphasis on the Maria I reserve (Table 1).

At each site, a 200-m long transect line was laid along a fixed depth contour. While consisting of four 50-m blocks, these blocks were pooled as subsamples for analysis with “site” regarded as the lowest level of replication. For the invertebrate census, a diver thoroughly searched the seabed for a distance of 1-m on one side of the transect line, investigating all visible crevices and overhangs but not overturning boulders. The distance of 1-m was measured by a 1-m-length tube carried by each diver. The tube also aided in the capture of lobsters. Macro-algae were swept away from the transect to obtain a clear view of the substrate. Most mobile mega-faunal invertebrates (approximately >20 mm length) were counted, including decapod crustaceans (crabs, rock lobsters and hermit crabs), large gastropods (whelks, tritons, abalone, turbinids), asteroids, echinoids, crinoids and holothurians. Other invertebrates such as annelids, polyplacophorans, shrimps and ophiuroids were not counted as they were mostly cryptic and too numerous to be accurately censused in the time available per survey.

As abalone and lobsters are heavily exploited by both commercial and recreational fishers in Tasmania, and are subject to minimum size regulations, size data were collected for these species. For abalone, the maximum shell length of each animal was measured *in situ* to the nearest mm with calipers until at least 20 abalone had been measured in each 50-m section of the transect. The carapace length (C.L.) of lobsters was also measured where possible. Measurements were restricted to lobsters greater than 30 mm carapace length and to situations where the animals could be captured and handled without damage. Approximately half of the observed lobsters were captured for size and sex determination. Where lobsters could not be captured, estimates of carapace length were obtained by holding calipers as close to the lobsters as possible.

The percentage cover of macroalgal species was quantified by placing a 0.5 m×0.5 m quadrat at 10-m intervals along the 200-m transect and estimating the percent cover of all species in each

quadrat. Twenty quadrats were thus sampled per site. The quadrat was divided into a grid of 7×7 perpendicular wires, giving 50 points (including one corner) per sample position, under each of which the cover of the various species present was recorded. Initially the cover of over-storey species was recorded, and then these were swept aside to expose the understorey species for counting. Point-counts were recorded for each taxon, usually to species level but within higher categories for algae that could not be accurately identified *in situ*.

The experimental design for this study was based on a BACI design, with before and after comparisons made between reserve (impact) and fished (control) sites. Multiple sites were examined within each treatment to give generality to any observed response with time. In addition, because a 10-y time series was available where trends through time could be examined rather than just the endpoints, alternative approaches were explored to incorporate the significance of increasing divergence between treatments through time. We assessed trends using Spearman rank correlation because this test is directly focussed on the parameter of biological significance, i.e. an increasing divergence between the mean values within each treatment through time. The Spearman correlation coefficient was calculated between time since MPA establishment and the difference between the reserve site mean and the control site mean. As this is a non-parametric rank order test, it is not unduly influenced by non-linearity in the rate of divergence, and is suited to analysing biological systems where the rates and timing of divergence may be unpredictable. Two-tailed critical values of the Spearman rank correlation coefficient (r_s) were used with $n-2$ degrees of freedom, where n =the number of time points sampled. In analyses of single reserves we used means of site means in the Spearman tests, and for analyses of the combined reserves we used the mean of individual reserve means, thus giving equal weighting to each reserve in analysis of overall patterns observed.

The univariate parameters of interest in this study included the abundance (or percentage cover) per site of a wide range of invertebrate and algal species and broader species groupings, species richness per site, and the mean size per site of lobsters and abalone. While effort was focussed on common and exploited species, a large number of species were examined for significant trends because the ecological response within reserves following protection was not readily predictable. Common and exploited species include *Jasus edwardsii* (southern rock lobster), *Haliotis rubra* (black-lip abalone) and *Heliocidaris erythrogramma* (purple urchin). For macro-algae, the most common species were examined for evidence of long-term trends, including the dominant canopy-forming brown algal species *Ecklonia radiata*, *Cystophora retroflexa* and *Sargassum fallax*. Taxonomic authorities for species discussed are provided in Edgar (2008).

In addition to single species, several groupings of algae were also examined as these may respond more generally to changes, and result in alteration of ecological processes. Groupings of interest included total cover (influencing overall productivity), canopy cover (the cover of large brown algae that form an over-storey above other species, influencing structural complexity), red algal cover and the cover of *Sargassum* species. Red algal species were included as these may be particularly influenced by grazer species and the *Sargassum* species grouping was included as individual *Sargassum* species could not always be readily identified and growth of these species usually responds in a similar manner to environmental variation. In some

Table 1
Details of years surveyed during monitoring of Tasmanian marine reserves between 1992 and 2002 along 5 m depth strata

Location/Year	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Maria Island	AS	AS	A	A	A	AS	A	AS	AS	AS	A
Tinderbox	AS	AS	A	A	A	AS	–	AS	AS	AS	A
Ninepin Point	AS	AS	A	A	A	AS	–	A	A	A	A
Bicheno	–	AS	A	–	A	AS	–	AS	A	A	A

A denotes Autumn survey only, AS denotes both Autumn and Spring surveys were completed.

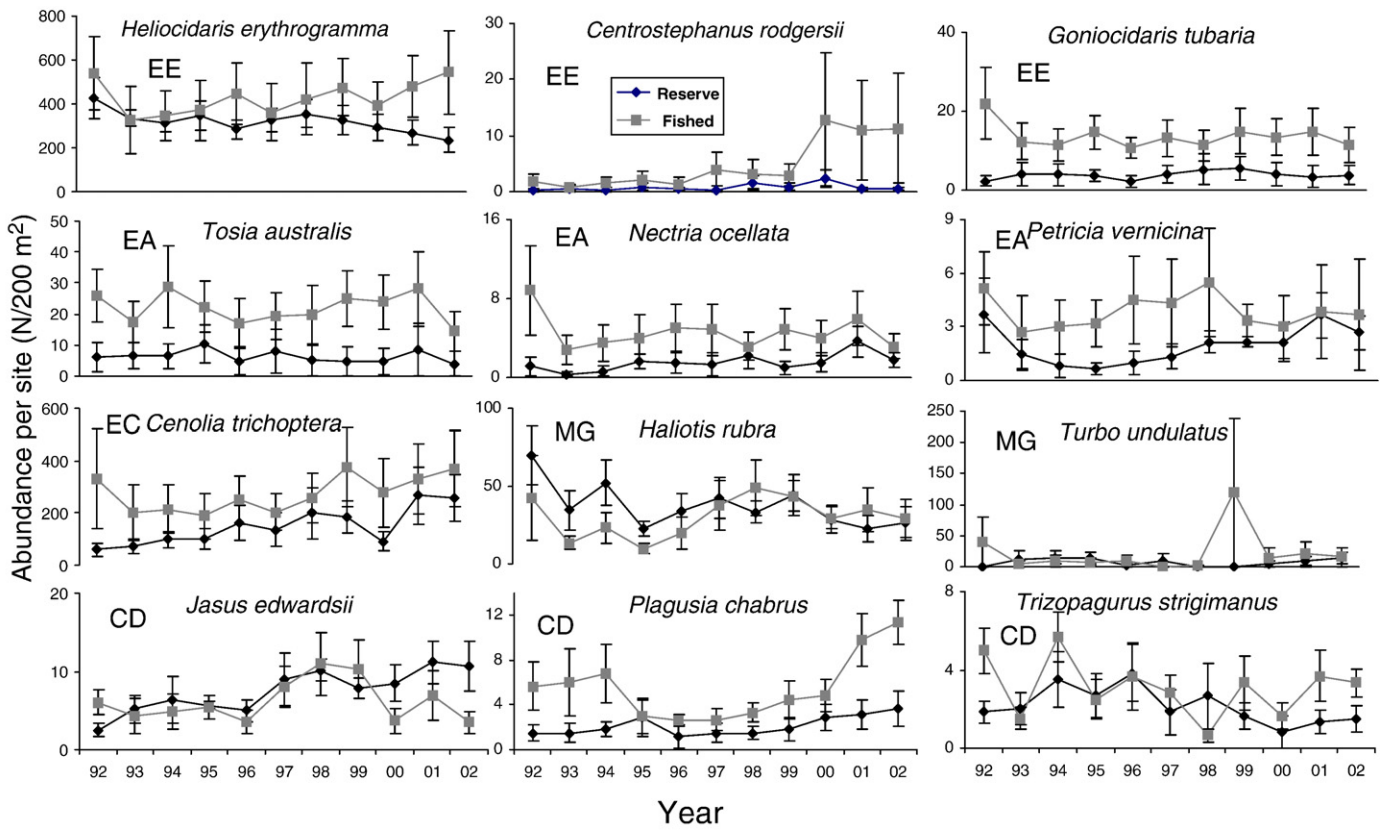


Fig. 2. Mean abundance per site (\pm SE) of mobile macro-invertebrates within the Maria I marine reserve and at fished reference sites during autumn surveys between 1992 and 2002. Species groupings for Figs. 2–5 are identified by the following codes: EE (Echinoderm, Echinoid), EA (Echinoderm, Asteroid), EC (Echinoderm, Crinoid), EH (Echinoderm, Holothuroid), MG (Mollusc, Gastropod), CD (Crustacean, Decapod).

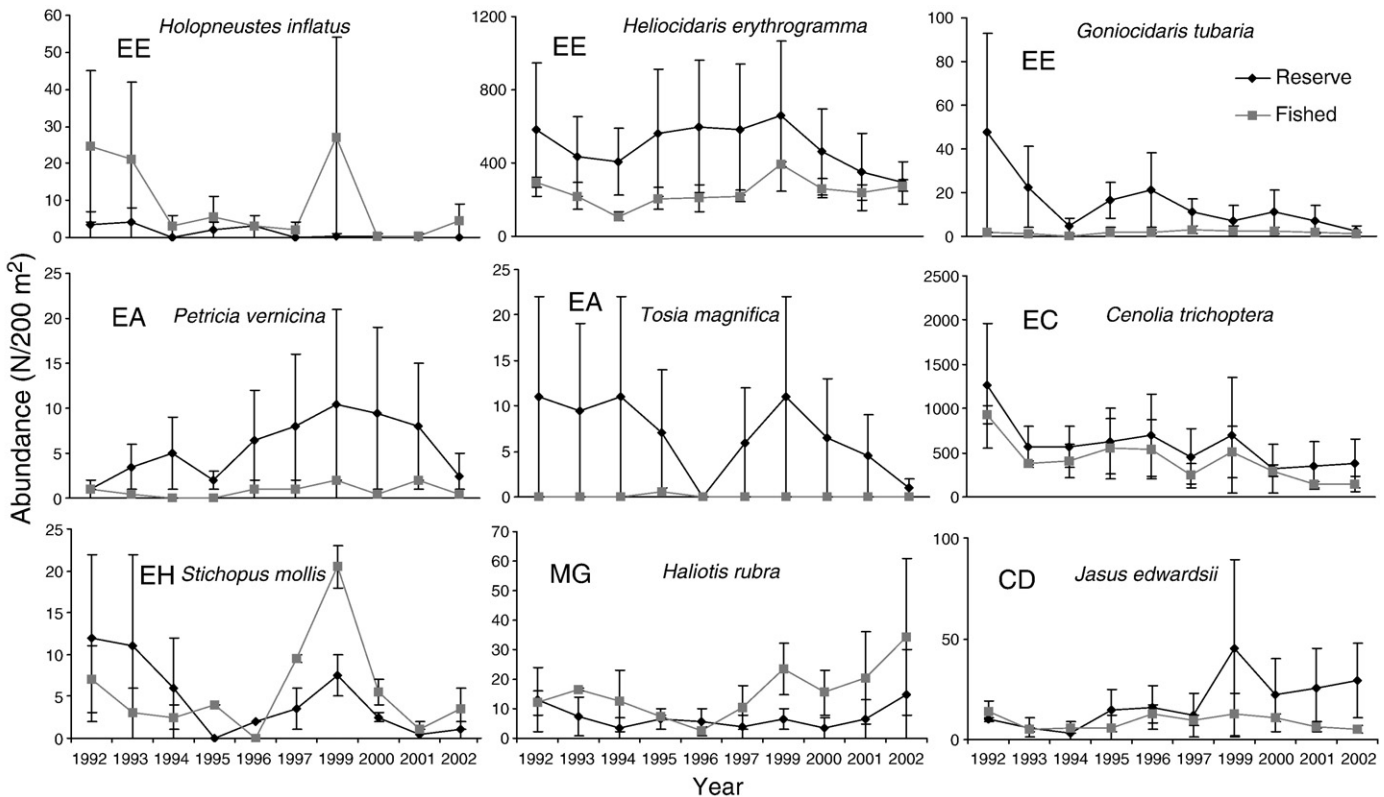


Fig. 3. Mean abundance per site (\pm SE) of mobile macro-invertebrates within the Tinderbox Marine Reserve and at fished reference sites between 1992 and 2002. Species code key is given in Fig. 2 caption.

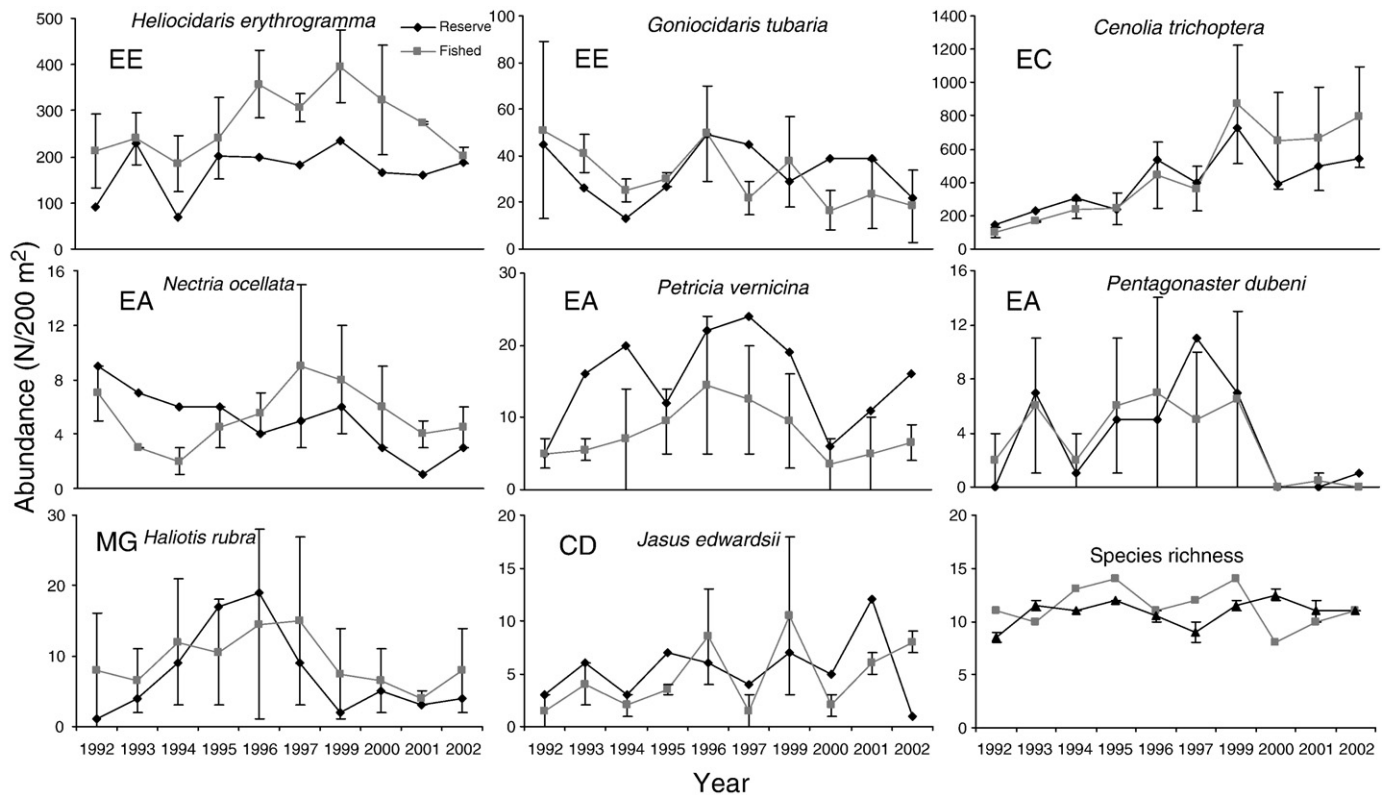


Fig. 4. Mean abundance per site (\pm SE) of mobile macro-invertebrates within the Ninepin Point marine reserve and at fished reference sites between 1992 and 2002. Species code key is given in Fig. 2 caption.

analyses the abundance data were separated into size categories on the basis of biological and fishery characteristics. *J. edwardsii* size classes were based on immature (35–87 mm C.L.), mature but sub-legal (88–112 mm C.L.), mature and legal (113 mm+ C.L.). The current minimum legal size for female lobsters is 105 mm C.L., and males 110 mm C.L. *H. rubra* size classes were based on small animals that may normally be cryptic (35–84 mm), non-cryptic but sub-legal (85–134 mm), non-cryptic and legal (>135 mm). The current minimum legal size for abalone is 132 mm.

Changes in the overall assemblages of invertebrates and macro-algae through time were examined for each reserve and associated control site. In this comparison we pooled abundance or percent cover data within treatments (reserve and fished) for each year to derive a Bray–Curtis similarity index matrix. Prior to analysis the data were fourth root transformed for invertebrate abundance and square root transformed for percentage cover of macro-algae. Similarity matrices were calculated using PRIMER, and this program was also used to graphically represent the resulting relationships using multi-

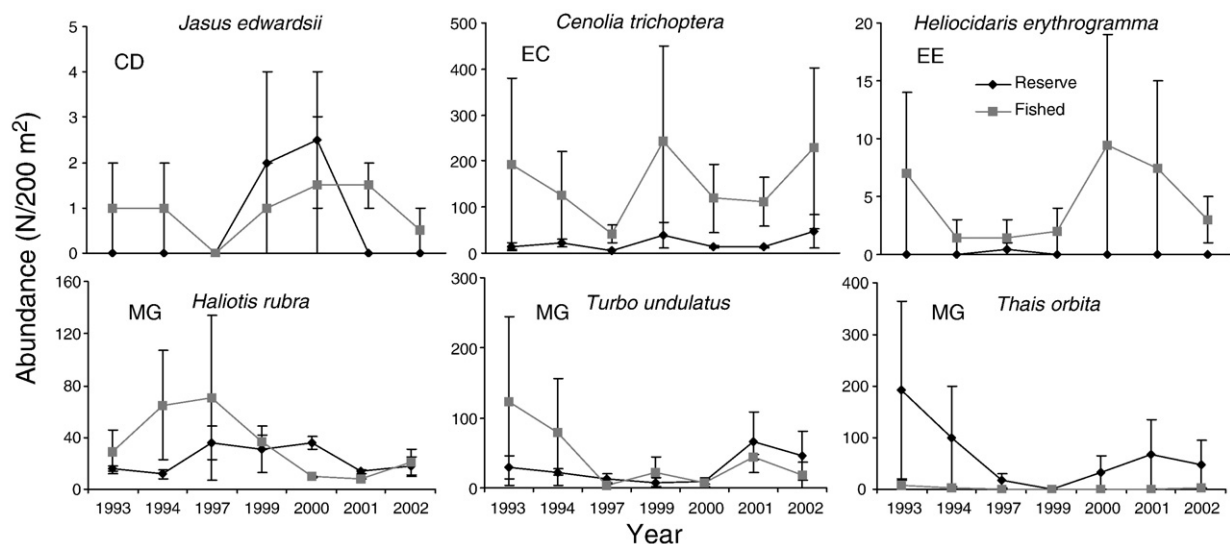


Fig. 5. Mean abundance per site (\pm SE) of mobile macro-invertebrates within the Governor I marine reserve and at fished reference sites between 1992 and 2002. Species code key is given in Fig. 2 caption.

dimensional scaling (MDS) for interpretation of assemblage changes through time.

3. Results

3.1. Invertebrate density

A total of 46, 40, 31 and 36 species of mobile invertebrates were recorded from MPAs and associated reference sites at Maria I, Tinderbox, Ninepin Point and Governor I, respectively. Many species were rarely encountered or had distribution restricted to a limited number of sites. These species were not examined individually.

The abundances of many of the common invertebrates encountered were relatively stable through time (Figs. 2–5), with no evidence of statistically significant convergence or divergence between reserve and fished sites (Table 2). At Maria I (Fig. 2), these included the sea stars *Tosia australis*, *Nectria ocellata* and *Petricia vernicina*, the feather star *Cenolia trichoptera*, and the sea urchin *Goniocidaris tubaria*. At

Table 2

Tests of convergence or divergence between mean survey values at reserve and fished sites

Species/location	Maria Island r_s (15)	Tinderbox r_s (13)	Ninepin Pt r_s (10)	Governor Island r_s (8)	All reserves r_s (15)
Invertebrates					
<i>Jasus edwardsii</i>	0.67**	0.73**	−0.09	0.16	0.69**
<i>Jasus</i> (115 mm+)	0.86***	0.76**	−0.06	0.10	0.72**
<i>Jasus</i> mean size	0.85***	0.39			
<i>Plagusia chabrus</i>	−0.18	−0.25		−0.09	
<i>Haliotis rubra</i>	−0.76***	−0.73**	0.04	0.10	−0.31
<i>Haliotis</i> (30–130 mm)	−0.76***			0.024	
<i>Haliotis</i> (> 135 mm)	0.01			0.18	
<i>Haliotis</i> mean size (> 135 mm)	0.83***				
<i>Pleuroploca australasia</i>	−0.12	−0.34			
Short-spined urchins (<i>Amblypneustes</i> spp. + <i>Holopneustes</i> spp.)		−0.15	−0.44	0.67	−0.03
<i>Centrostephanus rodgersii</i>	−0.64*			−0.19	
<i>Cenolia</i> spp.	0.32	−0.18	−0.72#	−0.34	−0.51
<i>Goniocidaris tubaria</i>	−0.12	−0.77**	0.34	−0.48	−0.33
<i>Heliocidaris erythrogramma</i>	−0.56#	−0.66*	−0.31	−0.58	−0.69**
<i>Nectria ocellata</i>	−0.04	−0.18	−0.64		−0.45
<i>Petricia vernicina</i>	−0.02	−0.37	0.22		0.30
<i>Tosia australis</i>	0.08	0.10			
<i>Tosia magnifica</i>		−0.57			
<i>Uniophora granifera</i>	0.07	−0.37			
Invertebrate species richness	−0.05	−0.68*	−0.39	−0.6	−0.71**
Algae					
<i>Acrocarpia panniculata</i>	0.37	0.72**	−0.1		
<i>Carpoglossum confluens</i>	−0.21	−0.12			
<i>Caulerpa brownii</i>	0.62#				
<i>Caulerpa trifaria</i>	−0.75**	0.16	0.18		
<i>Cystophora retroflexa</i>	−0.36				
<i>Durvillaea potatorum</i>				0.59	
<i>Ecklonia radiata</i>	0.86***	−0.07	−0.1	−0.66	−0.28
<i>Lessonia corrugata</i>				0.27	
<i>Macrocystis pyrifera</i>		0.13	0.16		
<i>Phyllospora comosa</i>	−0.70**			−0.2	
<i>Sargassum decipiens</i>	0.37				
<i>Sargassum fallax</i>	0.43	−0.19	0.17		
<i>Sargassum verruculosum</i>	0.54#	0.18	−0.31		
<i>Undaria pinnatifida</i>	0.43	0.63#			
<i>Zonaria</i> spp.	−0.13				
Algal species richness	0.50	0.29	0.20	−0.72	0.41
Total algal cover	0.32	0.22	0.10	−0.05	−0.45

Spearman rank correlation coefficients (r_s) and related significance values (p) are provided for each test of serial convergence or divergence between mean values for reserve and unprotected locations based on the mean of site means. For the combined reserve analysis mean values used were the mean of individual reserve means. For this test significant results are shown as # for $p < 0.05$, * for $p < 0.02$, ** for $p < 0.01$ and *** for $p < 0.001$. Empty cells indicate where insufficient data were available for tests.

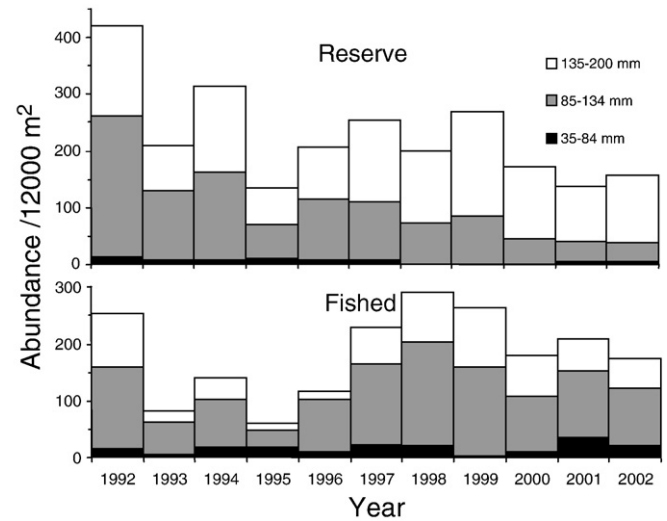


Fig. 6. Abundance per size category (shell length) of *Haliotis rubra* within the Maria I Marine Reserve and at fished reference sites between 1992 and 2002. The minimum legal size for abalone was 132 mm shell length.

Tinderbox (Fig. 3) they included *P. vernicina*, *C. trichoptera*, the urchin *Holopneustes inflatus*, and the sea cucumber *Stichopus mollis*. At Ninepin Point (Fig. 4) they included *N. ocellata*, *P. vernicina*, *G. tubaria* and the urchin *H. erythrogramma*. At Governor I, most species were quite variable through time, with none demonstrating divergence between fished and unfished sites, nor long-term trends (Fig. 5).

At Maria I (Fig. 2), notable exceptions to this pattern were the long-spined urchin (*Centrostephanus rodgersii*), the common urchin (*H. erythrogramma*) and the two species most important to the Tasmanian fishery, blacklip abalone (*H. rubra*) and southern rock lobster (*J. edwardsii*). The large increase in *C. rodgersii* in autumn 2000 was almost entirely due to increases at two fished sites (Isle du Nord and Green Bluff), hence the large standard error. As a similar increase did not occur within the reserve, a statistically significant divergence was evident between fished and reserve sites ($p < 0.02$, Table 2). *H. erythrogramma* showed no protection-related trend in the first 7 years of the study but then underwent a decline of approximately 30% within the reserve over the following 4 years (Fig. 2). A similar decline was not observed at the fished sites where abundances increased slightly over this time, thus resulting in a weakly statistically significant protection-related effect ($p < 0.05$, Table 2).

At Tinderbox (Fig. 3), the pencil urchin *G. tubaria* declined markedly within the reserve while remaining relatively constant at the fished sites ($p < 0.005$, Table 2). A similar pattern was observed with *H. erythrogramma*, with numbers declining within the reserve towards the end of the study, while remaining relatively constant at the fished sites. This resulted in a statistically significant divergence ($p < 0.02$, Table 2). Within the Ninepin Point region, the feather-star *C. trichoptera* was the only species displaying a divergence in abundance between reserve and fished sites, where numbers increased markedly within both reserve and fished sites. This increase was greatest within the fished sites, resulting in a statistically significant divergence ($p < 0.05$, Table 2).

3.2. Focal species

3.2.1. Abalone

At Maria I, the abundance of *H. rubra* varied over the decade of the study with peaks in 1992 and 1998, a pattern evident at both reserve and fished sites (Fig. 2). The most notable component of the abundance-time series was the highly significant decline in abalone numbers within the Maria I reserve with respect to the fished sites ($p < 0.001$, Table 2). The frequency of abundance in three size classes –

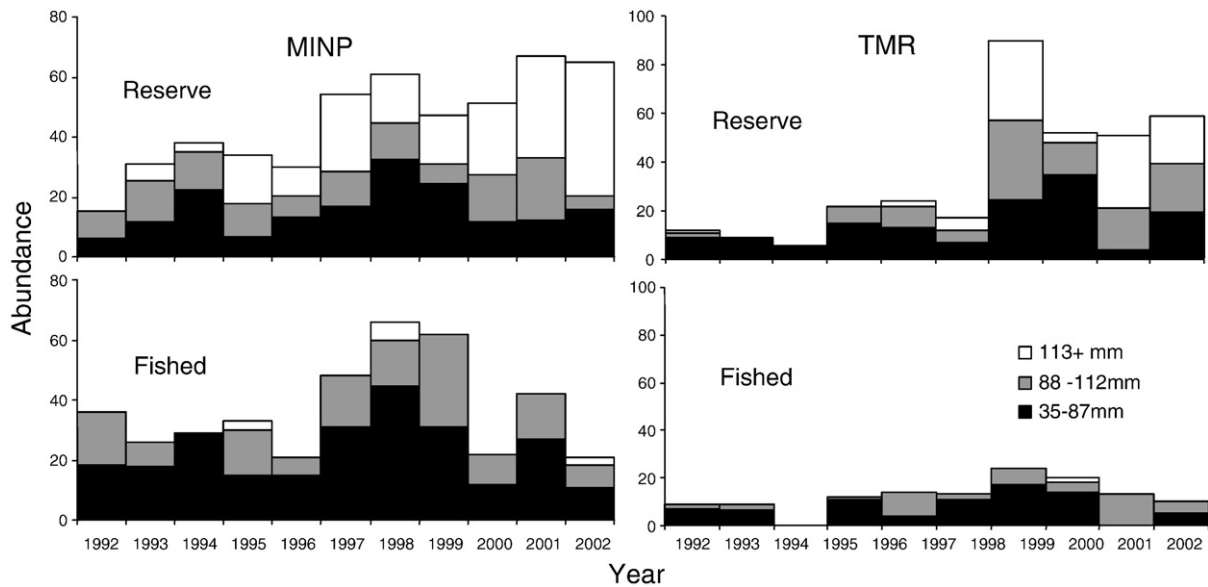


Fig. 7. Abundance of *Jasus edwardsii* by size class for lobsters measured within the Maria I marine reserve (MINP) and Tinderbox Marine Reserve (TMR) and at their respective fished reference sites between 1992 and 2002. Abundance is $N/1200 \text{ m}^2$ for MINP and $N/400 \text{ m}^2$ for TMR, with size classes of carapace length corresponding approximately to immature (35–87 mm), mature sub-legal (88–112 mm) and mature legal (113+ mm) animals.

35–84 mm (a size at which abalone were normally cryptic in this region), 85–134 mm (emergent abalone at or below the legal size limit of 132 mm), and those 135 mm or greater (legal sized animals) – is illustrated in Fig. 6. This revealed that the decline in abundance was primarily due to a significant decline in the small and intermediate size classes in the reserve relative to the fished sites.

While individuals within the smallest size category were rarely sighted due to their cryptic nature and are under-represented in the study, a tenfold decline was evident in the abundance of the intermediate size category (sub-legal) within the reserve between 1992 and 2002 (Fig. 6). This decline was not observed at the fished sites where abundance varied from year to year but was not notably different between 1992 and 2002. Overall, the decline in small abalone within the reserve relative to the fished sites was statistically highly significant ($p < 0.001$, Table 2). In the largest size category (legal sized), the abundance within the reserve remained relatively stable during the study. Although numbers fluctuated markedly at fished sites, no significant divergence was detected between fished and protected sites between 1992 and 2002. Within the largest abalone size class, the mean size of animals increased significantly relative to fished sites by an average of 10 mm between 1992 and 2002 ($p < 0.001$, Table 2).

At Tinderbox, abalone increased in abundance at the fished sites during the study, while within the reserve abundances remained at a low level (Fig. 3). Although statistically significant ($p < 0.01$, Table 2), this difference needs to be treated with caution, as the relative abundance within the reserve was low and variable, possibly masking real trends. As the reserve abundances were low there was insufficient data to assess whether juvenile abalone had undergone a similar decline to that observed at Maria I. At both Ninepin Point and Governor I, no patterns related to protection were detected for abalone (Figs. 4 and 5).

3.3. Rock lobsters

Within the Maria I reserve the abundance of *J. edwardsii* changed markedly over the duration of the study (Fig. 2). The reserve population increased significantly relative to fished sites ($p < 0.01$, Table 2) by approximately 250%. When this change is examined using size categories—immature lobsters (35–87 mm), sub-legal mature lobsters (88–112 mm) and mature legal sized lobsters (113 mm+)—increasing

numbers of “legal” sized lobsters are seen to be largely responsible (Fig. 7). For large animals, divergence between fished and reserve sites is statistically significant ($p < 0.05$, Table 2).

Due to the increasing abundance of large animals, lobsters within the reserve significantly increased in mean length compared with fished sites ($p < 0.001$, Table 2). This increase from 90 mm to 120 mm contrasts with a stable long-term average of 78 mm at the fished sites (Fig. 8). When the size and abundance figures are combined to produce biomass estimates based on the formula $B = 0.000271 * L^{3.135}$ (Punt and Kennedy, 1997) relating lobster biomass (B) in grams with carapace length (L) in mm, the total biomass was estimated to have increased within the reserve by an order of magnitude over the 10-year study period. The biomass at the fished sites remained relatively stable over this period, with no increasing trend between years (Fig. 8).

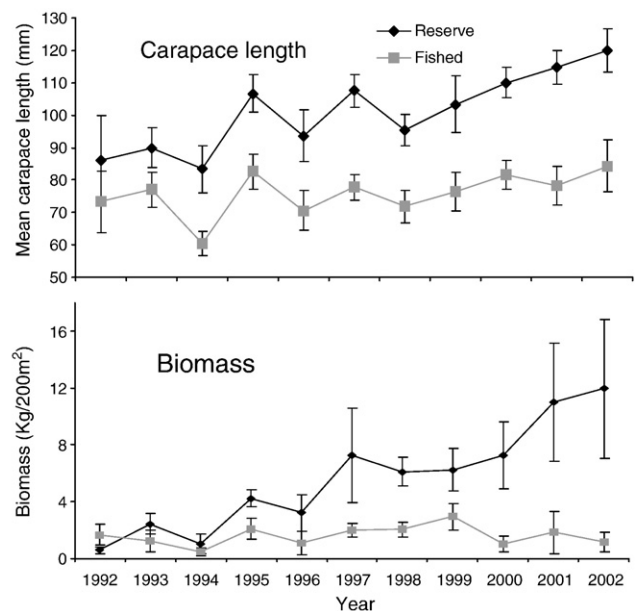


Fig. 8. Mean carapace length (mm) and estimated mean biomass for lobsters measured within the Maria I marine reserve and at fished reference sites between 1992 and 2002.

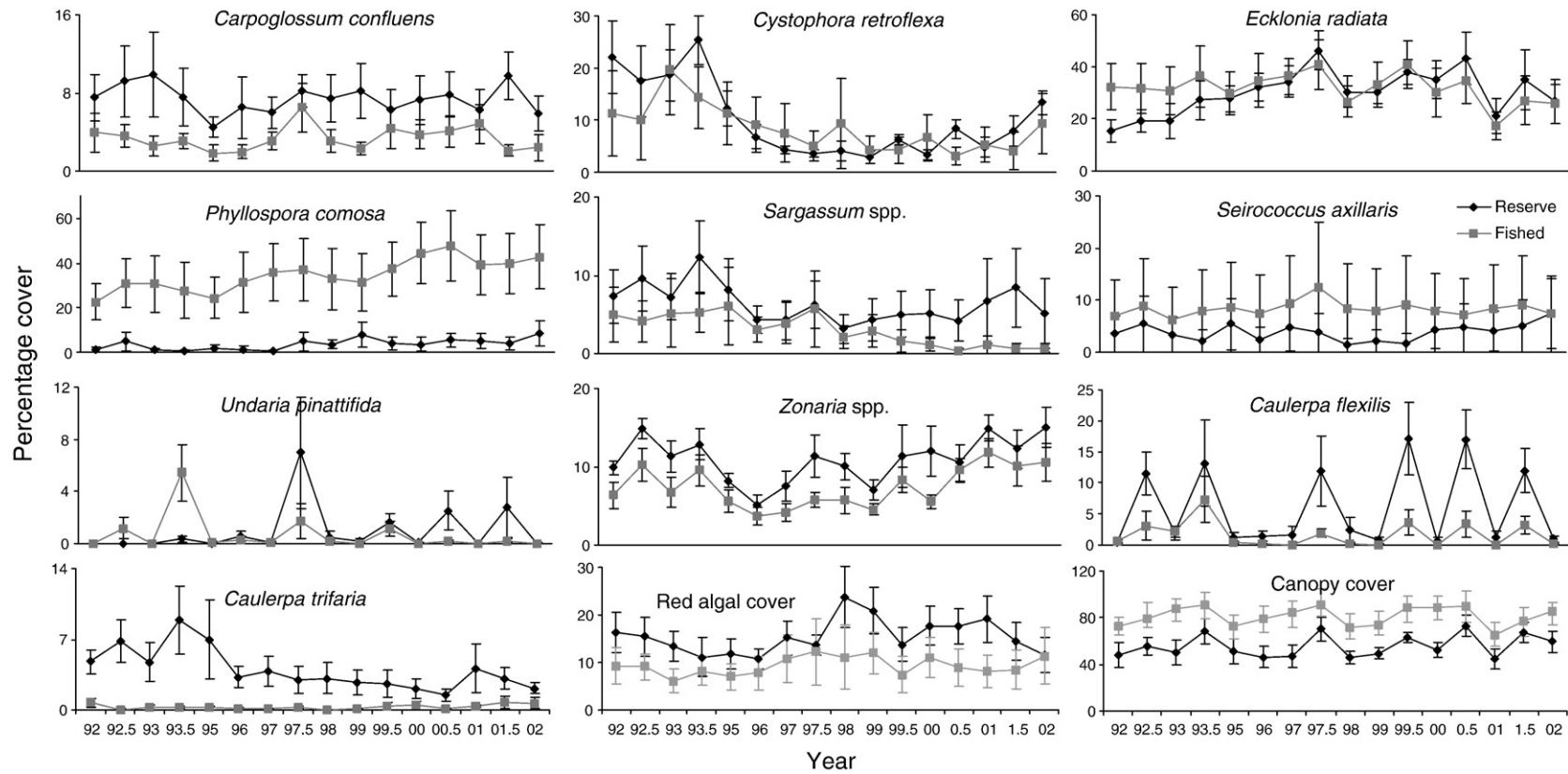


Fig. 9. Percentage cover of common macroalgal species and categories of total cover within the Maria I marine reserve and at fished reference sites between 1992 and 2002. Values shown are the mean of site means (\pm SE).

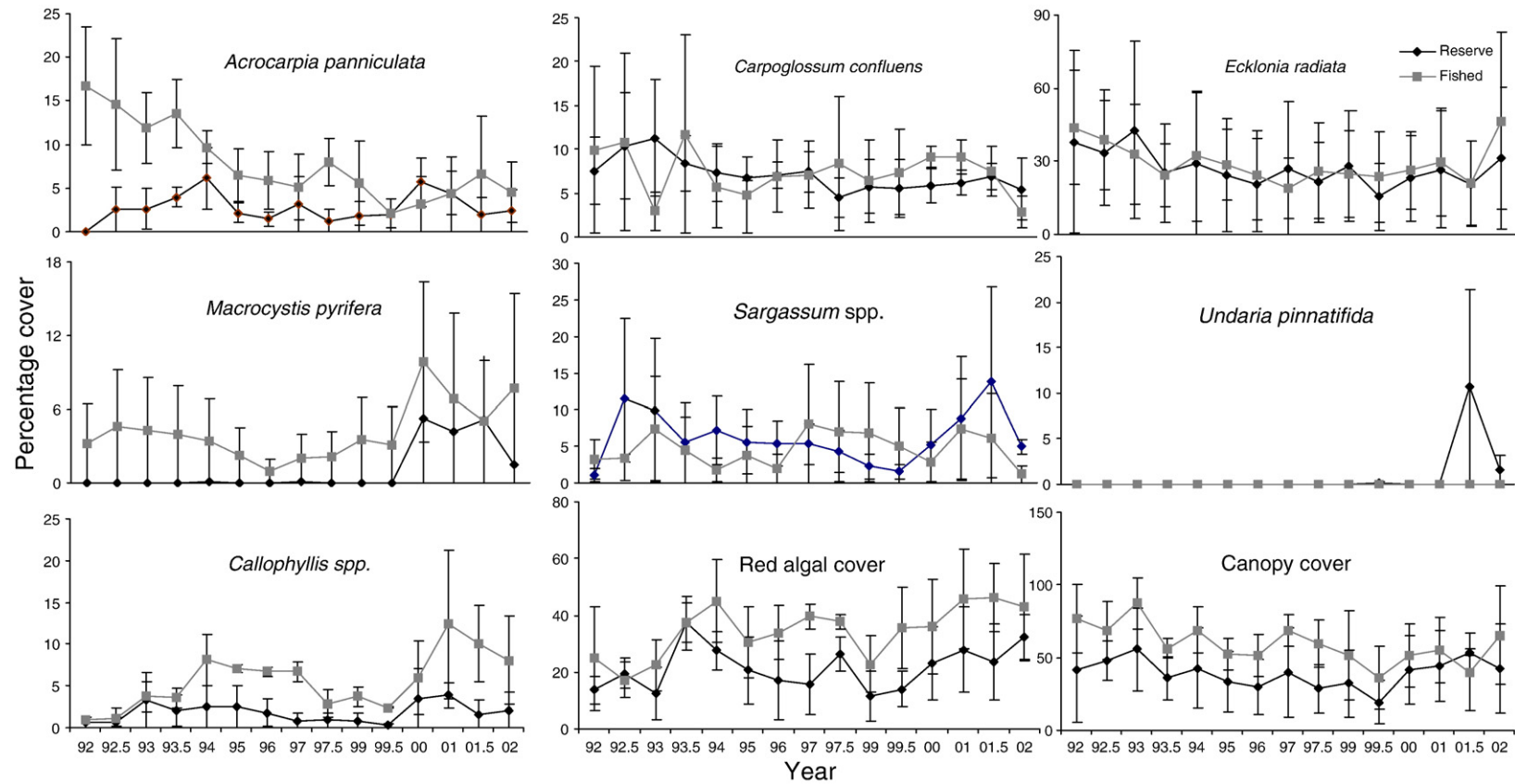


Fig. 10. Comparison between Tinderbox Marine Reserve and external reference sites of the mean percentage cover per site of common macroalgal species, the cover of canopy forming species and red algal species encountered during the years 1992 to 2002. Values are the mean of site means (\pm SE). Spring survey data are included and shown by the 0.5 suffix for years.

At Tinderbox, lobster abundances increased twofold within the reserve during the study, while numbers at fished sites remained relatively constant (Fig. 3), resulting in a statistically significant difference between fished and reserve sites ($p < 0.01$, Table 2). This difference was primarily due to a marked increase in the number of large lobsters within the reserve relative to the fished sites (Fig. 7) ($p < 0.005$, Table 2). Lobster biomass increased 9-fold from 1992 to 2002 within the reserve, while no change was evident at external sites. No protection-related differences in lobster abundances were detected at Ninepin Point or Governor I (Figs. 4 and 5).

3.4. Macroalgal density

A total of 98, 77, 84 and 40 macro-algal taxa were recorded during algal surveys within the Maria I, Tinderbox, Ninepin Point and Governor I regions, respectively. Most species were rarely encountered or formed a minor component of the overall cover and are not considered individually. At Maria I (Fig. 9), densities of most common species were consistent through time, including the brown algae *Carpoglossum confluens*, *Seirococcus axillaris* and *Zonaria* spp., and the groupings red algal cover and total cover. However, a notable trend in abundance of *C. retroflexa* was evident. This species declined

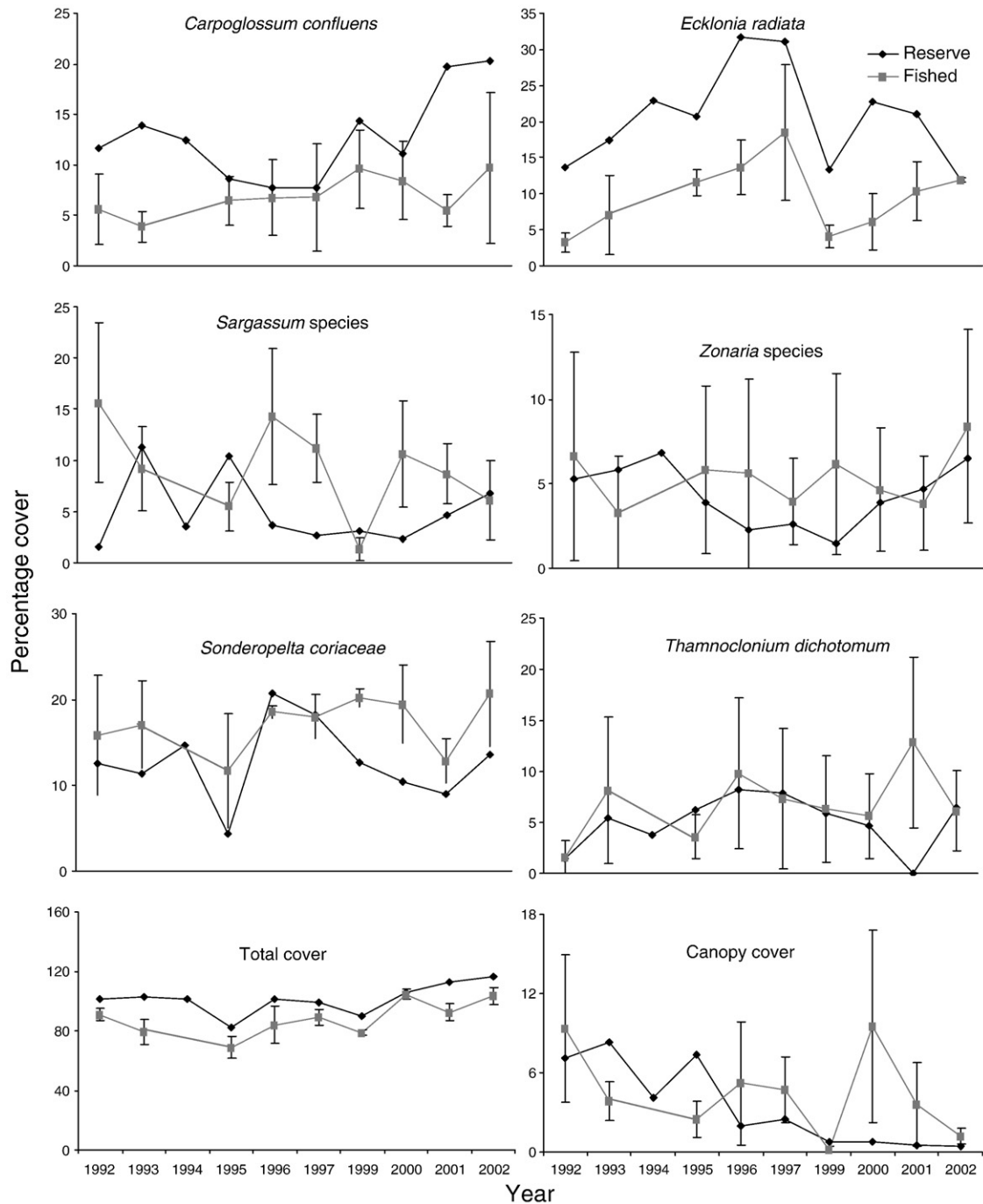


Fig. 11. Comparison between Ninepin Point marine reserve and external reference sites of the mean percentage cover per site of common macroalgal species, canopy forming species, and total species for the years 1992 to 2002. Values represent the mean of site means (\pm SE). The reserve site lacks standard error bars as only one site was surveyed within the reserve due to the lack of suitable habitat.

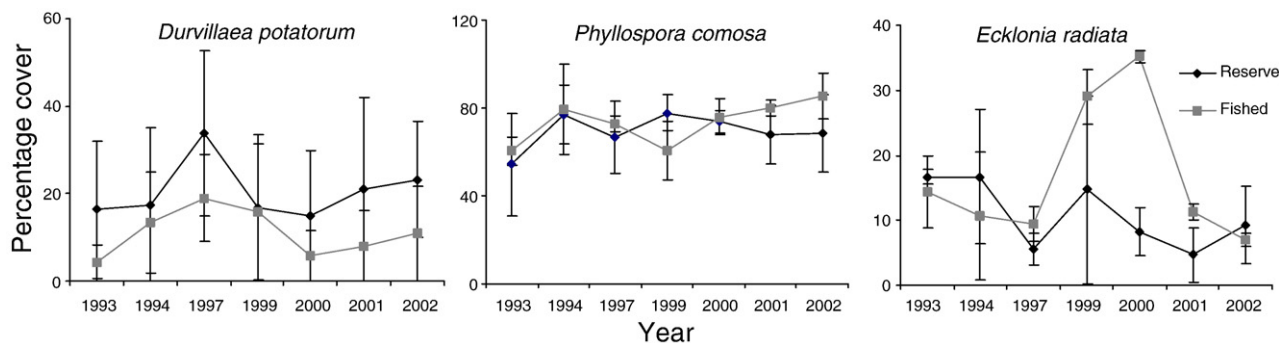


Fig. 12. Comparison between the Governor I marine reserve and fished reference sites of the mean percentage cover per site of common macroalgal species encountered at 5 m depth during the years 1993 to 2002. Values are the mean of site means (\pm SE).

substantially in the first 5 years, particularly within the reserve, then recovered in later years to levels similar to those in 1992.

The cover of *E. radiata* also changed substantially through time, with a significant increase in cover within the reserve relative to fished sites ($p < 0.001$, Table 2). *Ecklonia* steadily increased in density in the first 5 years within the reserve but remained constant at the external sites. After 1997, *Ecklonia* underwent a distinct cycle in abundance. A marked drop between spring 2000 and autumn 2001

coincided with an unusually warm water summer where *Ecklonia* fronds were observed with decayed blades.

Phyllospora comosa also underwent distinct temporal changes in abundance at Maria I (Fig. 9), most notably within the fished sites where it was most abundant. *Phyllospora* cover doubled from 20% in 1992 to 40% in 2002 at fished sites but changed little within the reserve, thereby generating a statistically significant divergence between fished and reserve sites ($p < 0.01$, Table 2). The change in

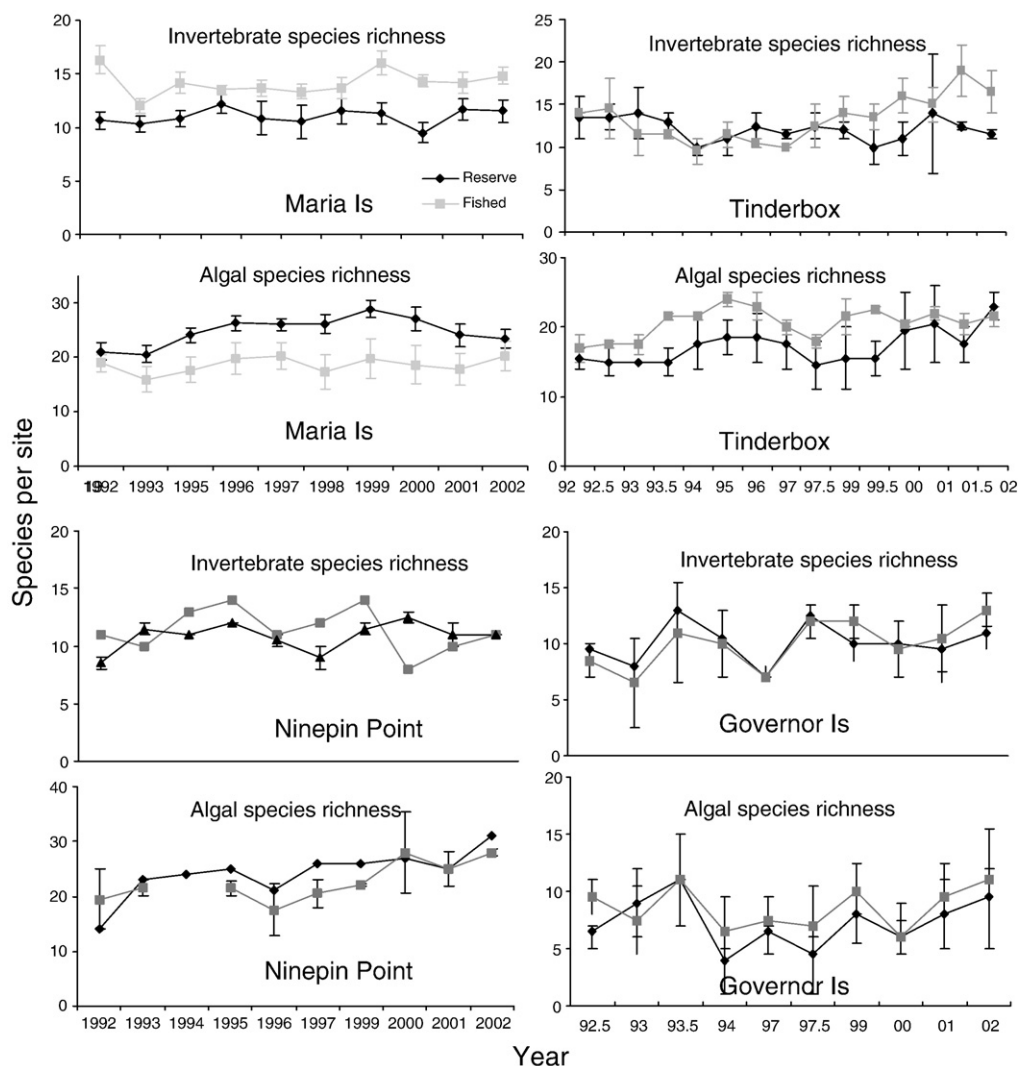


Fig. 13. Mean species richness per site for invertebrates, cryptic fishes and macro-algae counted within all reserves and at their respective fished reference sites between 1992 and 2002. Spring data are included for Tinderbox and Governor I, as shown with the suffix '0.5' on the year axis.

Phyllospora cover was reflected by changing density of *Sargassum* species (primarily *S. verruculosum*, *S. decipiens* and *S. fallax*). *Sargassum* cover declined more rapidly within fished sites than observed within the reserve ($p < 0.05$, Table 2.). The introduced kelp *Undaria pinnatifida*, an annual species, displayed large differences in abundance between spring and autumn. Small mature thalli appeared during the spring surveys but only decaying holdfasts and sporophylls were present in autumn, if present at all. The abundance of *Undaria* varied throughout the decade, but with no evidence of increasing abundance in either the reserve or at the external sites (Fig. 9).

At Tinderbox, cover of the dominant algal species *E. radiata*, fluctuated over the duration of the study with no obvious temporal trend nor divergence between reserve and fished sites (Fig. 10). *Acrocarpia paniculata* was moderately common at fished sites in 1992 but declined by more than 60% over the duration of the study at fished sites (Fig. 10), but with little change at reserve sites ($p < 0.01$, Table 2). No other algal species showed differences between reserve and fished sites through time. One notable feature however, was the conspicuous abundance of *Undaria*, which became established within the reserve in spring 2001 (Fig. 10) on urchin barrens following recent coastwide expansion.

At Ninepin Point (Fig. 11), no divergence between reserve and fished sites was evident for any of the common species, with the flora dominated by the brown algae *E. radiata*, *C. confluens* and *Sargassum* species, and the red alga *Sonderopelta coriacea*. At Governor I, the brown algae *Durvillaea potatorum*, *E. radiata* and *P. comosa* together

usually provided more than 100% cover, with the remaining species rarely contributing more than 1% cover each (Fig. 12). No change relating to protection from fishing was evident.

3.5. Species richness

Other than at Tinderbox, invertebrate species richness remained relatively stable at fished and reserve sites over the duration of the study (Fig. 13). At Tinderbox, a small decrease in invertebrate richness was detected at reserve sites relative to fished sites, resulting in a statistically significant Spearman rank value ($p < 0.02$). The decline within the reserve most likely related to decreasing numbers of *Tosia magnifica*, *G. tubaria* and *H. inflatus* (see Fig. 3), which were rarely encountered on transects towards the end of the survey.

For algae, overall species richness was relatively stable through time across most reserves and associated fished sites (Fig. 13). Species richness displayed a notable peak in 1995 at Tinderbox, which reflected ephemeral red algae dominating species composition in that year.

3.6. Assemblage composition

MDS plots depicting changes in invertebrate assemblages through time (Fig. 14) showed separation between fished and reserve sites that was typically as great as changes through time. While assemblages varied through time, no obvious divergence between reserve and fished sites was evident. At Maria I, the 1992 and 2002 endpoints of the

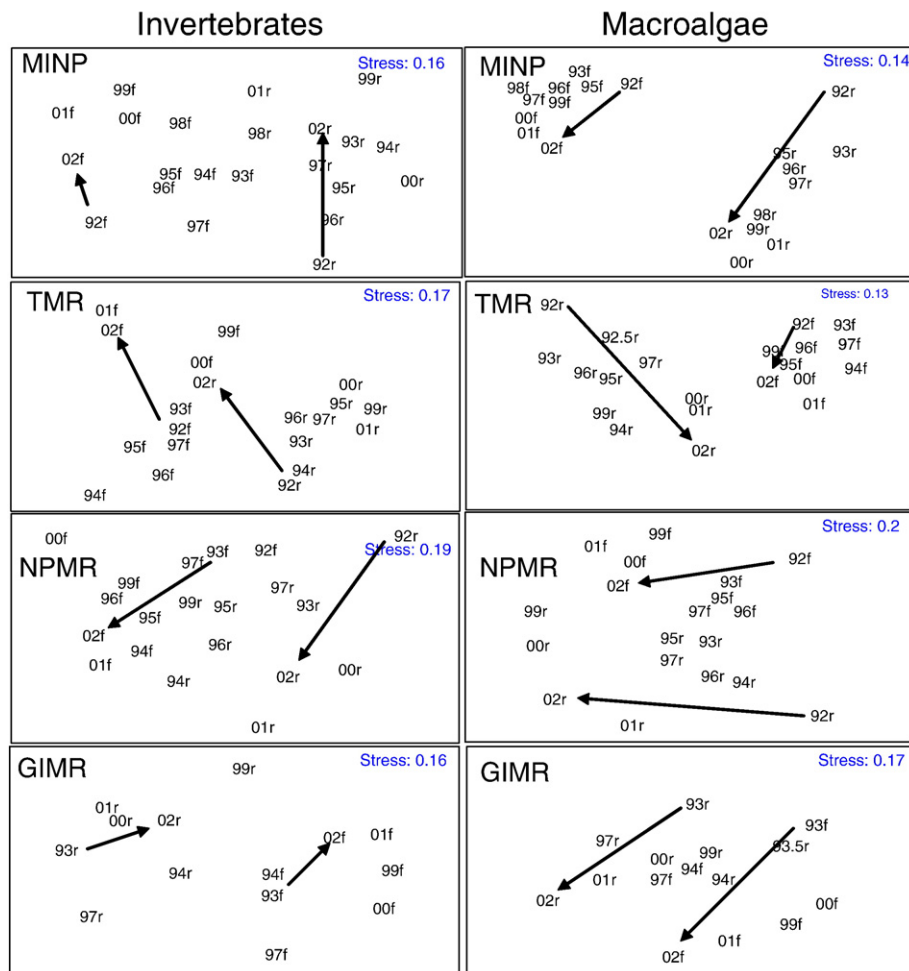


Fig. 14. MDS plots of the similarity between mobile invertebrate and macroalgal assemblages present during autumn within the Maria I (MINP), Tinderbox (TMR), Ninepin Point (NPMR) and Governor I (GIMR) marine reserves and at their respective fished reference sites between 1992 and 2002. Reserve assemblages are denoted by the suffix 'r', fished assemblages by 'f'. Arrows depict overall differences between initial and final assemblages.

reserve assemblage were widely separated compared with the fished assemblage. Regardless, this change was similar in magnitude to the difference between 1992 and 1993 values, suggesting that change over the decade was within the scale of inter-annual variability.

At Tinderbox, the 2002 reserve and fished assemblages both displayed marked temporal change. A SIMPER test of the 2002 reserve assemblage relative to previous years indicated this shift was primarily related to a reduction in the abundance of *H. erythrogramma* within the reserve to levels similar to the reference sites, and to marked decline of *G. tubaria* and *T. magnifica* within the reserve. These latter two species were originally common within the reserve and rare at fished sites, and helped differentiate reserve from fished assemblages prior to 2002.

For macro-algae assemblages, reserve areas generally displayed well-defined parallel trends between the mean annual values for the reserve and fished sites in MDS plots (Fig. 14), indicating consistent change through time. At Maria I, the change within the reserve was substantially greater than at reference sites. A SIMPER analysis of the species contributing mostly to the long-term change within this reserve indicated that in order of importance *E. radiata*, *C. retroflexa*, *Caulerpa flexilis* and *P. comosa* contributed more than 40% of the overall trend, with a wide range of minor species contributing the remaining component of change.

At Tinderbox, the most notable long-term change was also within the reserve assemblage, where a substantial shift occurred between 1992 and 2002 (Fig. 14). While this shift appears large, a SIMPER analysis of the results indicated that most of this was attributable to changes in the abundance of *E. radiata*, *Macrocystis pyrifera* and *Phacelocarpus* species. Of these, only the *M. pyrifera* change was of biological significance, with a *M. pyrifera* stand developing at the eastern reserve site in 2000 and remaining into 2002. At Ninepin Point, no reserve-related pattern was evident, although a directional shift through time was apparent (Fig. 14). A SIMPER analysis of the underlying causes of the shift indicates that it is primarily due to variations in the abundance of annual red algal species that fluctuated between years in response to varying environmental conditions. A similar pattern was evident at Governor I (Fig. 14), with SIMPER analysis indicating that this was related to an overall decline in *E. radiata* and an increase in *Phyllospora*.

3.7. Combined reserves analysis

Trends for species or species groupings common to all reserves were analysed as a Spearman rank correlation of the mean value of individual reserve differences in abundance between reserve and fished sites (Table 2, Fig. 15). *J. edwardsii* abundance ($p < 0.01$) and legal sized *J. edwardsii* abundance ($p < 0.01$) increased within the reserves relative to fished sites, while *H. erythrogramma* ($p < 0.01$) and invertebrate species richness ($p < 0.01$) declined in reserves relative to fished sites.

4. Discussion

Several of the common invertebrate species showed population trends that differed between fished and unfished locations. These responses were species-specific, with different likely causes for observed patterns.

At both Maria I and Tinderbox, and in the combined reserve analysis, abundance of total lobsters and large lobsters increased significantly through the study, but with no consistent change observed at fished sites. Biomass increased an order of magnitude in both reserves with trends not reaching an asymptote after 10 years. Thus, neither food availability nor recruitment appear to be have limited population growth at this stage.

No apparent divergence in population trends associated with protection was evident for sub-legal sized animals, suggesting that the presence of a significantly increased biomass of large lobsters within the reserve had not influenced levels of recruitment and survival of juveniles. Thus, density-dependent processes had little if any effect on recruitment within the first 10 years of protection.

At the Governor I and Ninepin Pt reserves, no significant difference was found between reserve and fished sites. This outcome is most likely related to poaching and boundary effects in these very small reserves. Within the Tinderbox and Maria I reserves, larger animals are concentrated in the central regions away from the boundaries (Edgar et al., 2005).

For lobsters, outcomes were similar to those reported from other regions where lobsters form the basis of local fisheries, including the Florida Keys (Hunt et al., 1991) and north eastern New Zealand

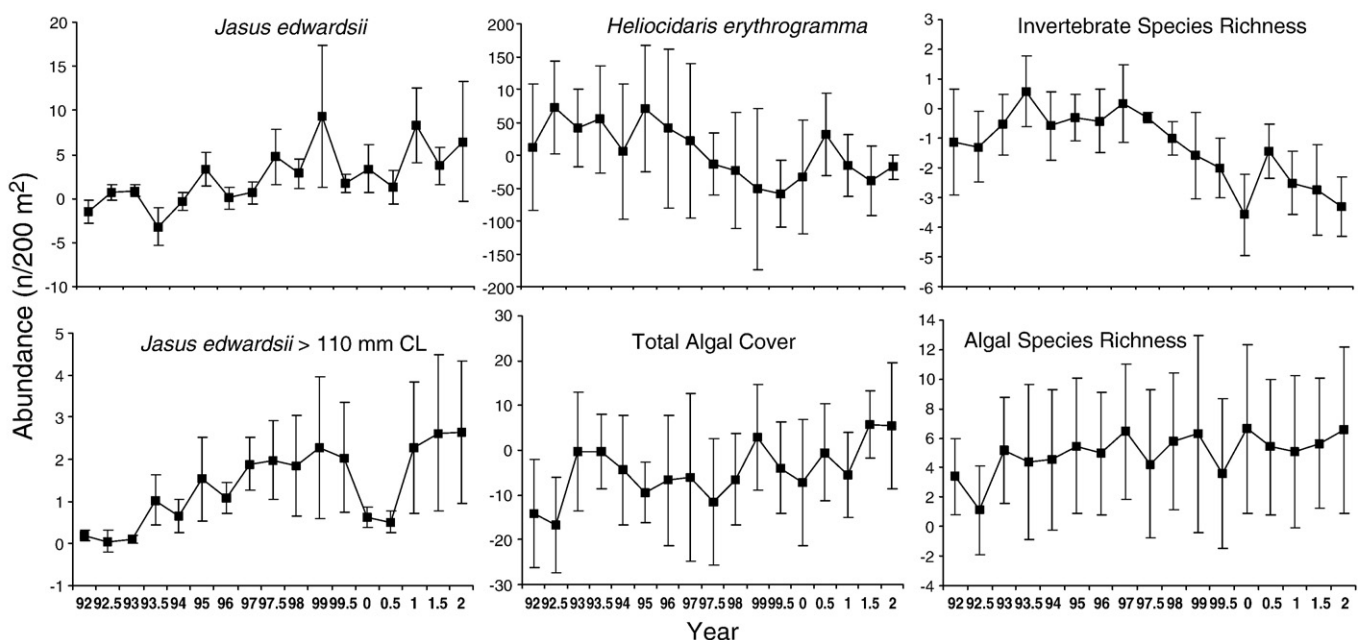


Fig. 15. Difference in mean density (\pm SE) across four MPAs in abundance of common invertebrates, percent cover of alga, and number of species per site.

(MacDiarmid and Breen, 1993; Kelly et al., 2000; Shears et al., 2006), where increases of up to 260% in abundance were reported following closure (Kelly et al., 2000). Shears et al. (2006) reported legal-sized lobsters increasing in abundance by 11 times, and overall lobster biomass increasing by 25 times over 20 years of protection. Such changes are of a similar magnitude to those reported here. While some of the early increases within the Leigh marine reserve in New Zealand have been countered by intense fishing on the outer reserve boundary following the discovery by fishers of offshore feeding migrations of lobsters (Kelly et al., 1999; Kelly et al., 2000), the initial results from Leigh suggest that the changes reported may be typical for exploited lobster stocks that are subject to intense fishing and protected by a minimum legal size.

Like lobsters, blacklip abalone *H. rubra* are heavily exploited along much of the Tasmanian east coast. As a consequence, we expected abalone abundances to increase within reserves following protection. However, within the Maria I reserve, abalone abundances declined over the decade of monitoring to 50% of initial levels. This decline was clearly protection-related, as abundances within the fished reference locations remained relatively constant over this time. The size-partitioned analysis revealed that the decline reflected a seven-fold reduction in the abundance of sub-legal-sized animals, while abundances of abalone above the minimum legal size remained relatively constant.

Several possible hypotheses, either alone or in combination, could account for the observed decline:

1. Increased predation on juvenile abalone following increased predator abundance, particularly from lobsters.
2. Increased cryptic behaviour due to increased predator density or increased conspecific competition for space.
3. Increased mortality due to intra- or inter-specific competition for resources, including food.

While a series of manipulative experiments is needed to determine the exact causes of the abalone decline, recent manipulative studies (Pederson et al., 2008) and circumstantial evidence suggests that lobsters play a pivotal role. Firstly, increased lobster biomass would be expected to have an impact on prey densities. Abalone are known dietary items of lobsters (Edmunds, 1996) and lobsters predominantly forage nocturnally (Frusher et al., 1999) when cryptic abalone emerge to graze (Pederson et al., 2008). Secondly, no other major predator species (such as the wrasse *Notolabrus tetricus*) was observed to increase in abundance within the Maria I reserve during the monitoring period (Barrett et al., 2007), particularly to the numbers that would be needed to impact the abalone population. Elsewhere, we recognise that fish predators can play a major role in structuring abalone populations (Shepherd and Clarkson, 2001), and predators such as predatory crabs can influence the extent of cryptic behaviour (Shepherd, 1973).

In addition, while the mean size of legal-sized abalone within the reserve increased slightly over the study (in response to protection from fishing), the overall number of legal-sized abalone did not change notably and the total abalone biomass declined. This would suggest that intra-specific competition for resources was unlikely. Inter-specific competition would also seem unlikely, as we found no indication of increases in the abundance of potential resource competitors such as urchins over this time.

If the decline in abalone within the Maria I reserve is related to predation by lobsters, it will be the first documented evidence of secondary effects of fishing involving direct lobster–abalone interactions. While lobster–urchin–kelp interactions have been suggested by studies in Nova-Scotia (Breen and Mann, 1976), California (Tegner and Dayton, 1991) and New Zealand (Shears and Babcock, 2002, 2003), and ecosystem cascades have been extensively reviewed in recent years (e.g. Dayton et al., 1998; Pinnegar et al., 2000; Tegner and Dayton, 2000), lobster–abalone interactions have not been reported as important other than during a range expansion of lobsters in South Africa. In that case, an

invasion of lobsters resulted in the loss of urchins, whose spine canopies provided protective shelter and food supply for juvenile abalone (Mayfield and Branch, 2000; Day and Branch, 2002). As this shelter mechanism also has been reported in California, with urchin density correlated with the abundance of juvenile abalone (Rogers-Bennet and Pearse, 2001), there is some generality to this pattern and it may partially explain our result from Maria I.

The decline in juvenile abalone numbers within the Maria I reserve was, however, substantially greater than the observed changes in urchin abundance, hence the most parsimonious explanation involves direct predation on abalone by lobsters rather than urchin interactions, particularly as we have no evidence of the sheltering behaviour operating in Tasmania.

Consequences of a direct lobster–abalone interaction include flow-on effects through the food web. While blacklip abalone feed primarily on drift algae (McShane, 1999), they can also selectively browse attached algae, altering the mix of algal and sessile invertebrate species present near aggregations (Shepherd, 1973). Thus, effects of lobster fishing in optimal abalone habitats may be analogous to the lobster–urchin interaction, which has been identified as a major ecosystem effect of fishing on temperate reefs (e.g. Tegner and Dayton, 2000; Shears and Babcock, 2003). This remains to be tested experimentally, however, as abalone grazing may have a more subtle effect on algal assemblages than the barren formation associated with urchins. The existence of commercial abalone fisheries may limit the natural process of this species interaction, as abalone fishing is likely to be sufficiently intense to regulate abalone numbers in Tasmanian waters (Officer and Tarbath, 2000), mainland Australia (e.g. Andrew et al., 1997), and elsewhere (e.g. Tegner and Dayton, 2000).

A second implication of our results is that in some habitats, abalone populations may not be adequately protected within MPAs when predators are also protected and increasing in abundance. While this would reflect the natural balance following restoration of top-down control, in situations where conservation of abalone is a primary aim of MPA establishment, protection zones may need to be specifically designed to reduce abalone predation, rather than to provide general protection to all organisms (Shepherd and Brown, 1993). Our findings suggest, for example, that targeted conservation measures for conservation of endangered Californian species of abalone (Davis et al., 1998; Rogers-Bennett et al., 2000; Rogers-Bennett et al., 2002) should not rely solely on the concept of fully-protected MPAs or translocation of individuals into areas where predators are also fully protected. These findings also have important implications for the value of no-take areas as reference areas for assessing the condition of adjacent fished stocks, as the abundances in no-take areas that have returned to natural levels may not always reflect the “natural” abundance in the adjacent fishery if targeted abalone fishing were to cease.

The third implication of the rock lobster monitoring data is that there may be a strong interaction between lobster and abalone fisheries in Tasmania and elsewhere. As these are by far the most economically valuable of the wild fisheries in Tasmania, a clear imperative exists to co-manage these species, to understand the broader implication of their interactions with other key components of the ecosystem, including sea urchins, and to incorporate this knowledge into stock assessments.

The purple urchin *H. erythrogramma* was the most abundant urchin recorded during the study, and was usually also the dominant mobile invertebrate species recorded on transects within all reserves. Within both the Maria I and Tinderbox Marine Reserves, and in the combined reserve analysis, this species underwent significant declines (30% and 40% respectively) that were not observed at external fished sites. In both cases this decline did not occur until after 1998, and several years more data were needed to identify the true nature of the response. This pattern is not surprising, however, given the number of studies and reviews (e.g. Mann, 1982; Cowen, 1983; Tegner and Levin, 1983) suggesting that urchin numbers are likely to respond to changing predator density, and that large predators may take many

years to recover to sufficiently high levels of abundance within protected areas to alter prey densities.

As the decline in urchin density was correlated with a large increase in lobster biomass, and lobsters are known urchin predators (e.g. Shears and Babcock, 2002; Pederson, 2003), it is probable that the observed reduction in urchin density was related to increased lobster predation, at least at Maria I. As discussed with regard to the abalone decline, lobsters were the only major known predator to substantially increase in abundance within the Maria I reserve, with fish predator abundance other than bastard trumpeter *Latridopsis forsteri* remaining relatively stable. Recent manipulative experimental work conducted within the Maria I reserve (Pederson and Johnson, 2006) adds support to the observation of urchin decline and the proposed mechanism for that decline, including greater urchin mortality rates in the reserve, size-specific predation by lobsters, and the key role of lobsters as urchin predators.

Other urchin species were also observed to undergo significant declines in abundance following protection of the reserves. The pencil urchin *G. tubaria* underwent a 10-fold reduction within the Tinderbox reserve between 1992 and 2002, presumably related to increased levels of predation. Because both predatory fishes and lobsters have increased in abundance within this reserve it was not possible to partition possible causes without conducting manipulative experiments. The long-spined urchin *C. rodgersii* at Maria I had similar numbers within the reserve and reference sites until 1999, at which time they underwent a significant divergence, with numbers increasing markedly at the external sites and declining within the reserve. This result needs to be interpreted with some caution, however, as it was strongly influenced by one reference site just north of the reserve (Ile du Nord) that showed unusually high recruitment of this urchin.

At least for *H. erythrogramma*, a likely mechanism for the urchin decline within reserves was that in the first few years following protection the lobster biomass was insufficient to substantially alter urchin numbers, and that few lobsters were sufficiently large to consume large urchins. By 1997, after 5 years of protection, lobster biomass had increased at least tenfold and lobsters large enough to consume adult urchins (> 120 mm C.L.; Pederson and Johnson, 2006) comprised a substantial proportion of the population. This increase was then sufficient to initiate a decline in urchin numbers that accelerated with increasing lobster biomass and average size. Such a delayed response in a prey species may be usual following protection of previously fished areas where top predators were substantially reduced by fishing. From observations of the recovery of the reserve at Leigh, New Zealand, Shears and Babcock (2003) suggest that the re-imposition of top-down control through a trophic cascade can be a long-term process. While urchin barrens may be an artefact of fishing at Leigh, the control of urchin numbers and reduction of barrens within that reserve took nearly 25 years of protection.

The decline in urchins within the reserves appears to contribute to the overall decline in invertebrate species richness within the Tinderbox reserve and combined reserve analyses, and suggests that biodiversity will not necessarily respond positively at all trophic levels following protection from fishing. Increasing predator abundance and size can potentially lead to multiple-level interactions and indirect effects, resulting in loss of invertebrate diversity (e.g. Lopez et al., 1999).

In contrast to the invertebrates, algal species richness and total cover varied little throughout the study, suggesting declining grazer numbers had not yet affected algal assemblages. More time may be necessary to determine the overall strength of the algae/grazer relationship in eastern Tasmanian waters, with experiments needed to better understand the potential role of urchins and abalone in this process. Continued long-term monitoring within Tasmanian MPAs should remain a high priority to determine how the reduction in large grazing invertebrates affects cover and species composition of macro-algae.

While many algal species underwent temporal variation in abundance over the duration of the study in response to changing

environmental conditions, for most reserves there was little evidence that such variation was related to protection effects, at either the species or assemblage levels. While assemblage structure did change from year to year, changes were usually of a similar magnitude and direction in reserve and fished locations. The exception to this was the Maria I region where the reserve assemblage underwent a greater rate of change than the reference assemblage over the duration of the study. It was not clear whether this observed pattern was a protection effect or was due to a scale effect of the experimental design. Longer monitoring will be needed for clarification.

At present, the most parsimonious explanation for observed differences in algal changes through time between reserve and reference sites is a scaling effect. Algal assemblages may be responding to localised environmental variables such as incident wave action and water temperature, and because the reserve sites were positioned more closely together than the reference sites, they may have tracked local changes in a more homogeneous way.

In summary, numerous changes in the abundance of invertebrates and cover of algae were observed in reserves in the decade following protection. Many of these, particularly those associated with changes in algal species composition, appear to be due to natural variability within the system rather than fishing-related. The most notable exceptions were increases in the abundance and mean size of rock lobsters, suggesting that this species had been significantly impacted by fisheries within the region. The greatest recovery of lobsters was within the largest reserves, suggesting that boundary effects and possibly poaching associated with the smaller reserves reduced their conservation value.

The study also produced evidence of indirect effects of fishing, with several species of urchin and medium-sized abalone declining in reserves, presumably in response to the increasing abundance of rock lobsters and perhaps also other large predators, although these changes are at an early stage. At present the declining abundance of key grazer species within the Maria I and Tinderbox reserves has not had any identifiable influence on macroalgal assemblages, with overall algal densities currently remaining relatively unchanged. However, this situation may well change through the longer term as a consequence of continued decline in grazer numbers.

Our results highlight the value of marine reserves as reference areas for understanding the effects of fishing on coastal species and systems, and the value of long-term studies for placing the magnitude of observed changes in perspective with natural environmental changes. As the reserves continue to approach their un-impacted state and to provide opportunities to experimentally test the hypotheses developed from observation of change within them, they should significantly contribute to our understanding and management of reef systems and the fisheries that are dependent upon them.

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