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Resilience and elasticity of intertidal communities in response to harvesting of the alien mussel *Mytilus galloprovincialis*

Tamara B. Robinson [a,b,*], George M. Branch [a], Charles L. Griffiths [a,b], Anesh Govender [a]

[a] *Marine Biology Research Centre, Zoology Department, University of Cape Town, Private Bag X03, Rondebosch, 7701, South Africa*
[b] *Centre for Invasion Biology, Zoology Department, University of Cape Town, Private Bag X03, Rondebosch, 7701, South Africa*

Abstract

Besides the direct impacts of exploitation on target species, indirect effects on non-target species are unavoidable and find expression in changes in community structure. We quantified the effects of experimental harvesting of *Mytilus galloprovincialis* on intertidal communities on the South African west coast. In the mid- and low-shore, four months of harvesting at intensities greater than $F=0.3$ and $F=0.6$ respectively, resulted in significant changes in community composition. These changes were driven by progressively greater spatial dominance by the macroalgae *Cladophora flagelliformis*, *Porphyra capensis* and *Ulva* species as harvesting intensity increased. Four months after cessation of harvesting, community structure had not recovered and even areas subjected to as little as $F=0.3$ supported significantly altered communities in both zones. The fact that substantial community changes were induced by even low-intensity exploitation is indicative of low resilience to harvesting. The densities and cover of the dominant taxa returned to a pre-harvest state 16 months after the cessation of harvesting, but multivariate analyses indicated that the overall community composition required 32 months for Cover Letter full recovery. Although these communities displayed elasticity within three years, it is recommended that should a *M. galloprovincialis* fishery be established in the region, harvesting be implemented at a maximum intensity of $F=0.3$. This approach would maximise yields and protect associated intertidal communities.
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1. Introduction

On a global scale shellfish have been exploited by humans for many thousands of years (Walter et al., 2000), and the potential ecological impacts of such utilisation are well recognised (Branch 1975; Castilla and Durán 1985; Keough et al., 1993). The direct consequences of intertidal harvesting typically include reductions of biomass, density, size distribution, reproductive output, demography or geographic distribution of both the target species and associated organisms (Castilla and Durán 1985; Hockey and Bosman 1986; Castilla and Bustamante 1989; Lasiak and Dye 1989; Keough et al., 1993).

Species associated with target species may also inadvertently be removed, altering species diversity and richness within and among communities, with intense exploitation tending to cause convergence of communities in terms of abundance and composition diversity (Hockey and Bosman 1986; Durán and Castilla 1989; Fairweather 1990).

The response of the community can be considered in terms of resilience and elasticity. Resilience, defined as the ability of a system to absorb changes and still persist (Holling, 1973), offers a measure of how resistant communities are to changes induced by harvesting. Elasticity is the speed with which a system returns to its former state following a perturbation (Orians, 1975). The stability of exploited systems reflects interaction between fishing intensity and frequency, and the resilience and elasticity of the community (Keough and Quinn, 1998).

In South Africa, harvesting of intertidal resources is focused in the Eastern Cape (the former Transkei) and northern KwaZulu–

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* Corresponding author. Marine Biology Research Centre, Zoology Department, University of Cape Town, Private Bag X03, Rondebosch, 7701, South Africa. Tel.: +27 21 650 3610; fax: +27 21 650 3301.

E-mail address: trobins@botzoo.uct.ac.za (T.B. Robinson).

Natal (Hockey et al., 1988; Lasiak, 1992; Kyle et al., 1997; Harris et al., 2003) where the brown mussel *Perna perna* forms the major portion of catches (Kyle et al., 1997). As harvesting in this region has occurred over generations and over a wide area, studies considering the effects of exploitation have been limited to comparing utilised areas with those protected by nature reserves. Collectively these studies demonstrated significant changes in target species populations in exploited areas (Branch, 1975; Siegfried et al., 1985; Hockey and Bosman, 1986; Lasiak and Dye, 1989; Lasiak, 1991; Lasiak and Field, 1995). Considering these dramatic changes, it is not surprising that harvesting has also altered the overall intertidal community (Hockey and Bosman, 1986) and resulted in a convergence of exploited communities towards a common state, regardless of the pre-exploitation condition. Typically these changes are manifested in shifts in primary space dominance from mussel beds towards an open algal matrix (Lasiak and Dye, 1989) and are most pronounced in the low-shore zone, where harvesting is concentrated. These communities exhibit extremely low elasticity in response to disturbance, and full recovery has not been observed even after 13 years (Lasiak and Dye, 1989; Dye, 1995).

Despite considerable research on the effects of intertidal harvesting on the east coast of South Africa, this issue has not been considered on the west coast. This is primarily because the shores in this region have been subject to substantially less exploitation, as a result of low human population density and the fact that diamond-mining operations exclude the public from large areas. Nonetheless, large stocks of the alien mussel *Mytilus galloprovincialis* exist along these shores and in an effort to stimulate new fisheries-based industries and address historic imbalances in access to fishing rights in South Africa, a community-based project was initiated in 2002 to determine the potential for exploitation of this mussel in the Northern Cape Province of South Africa (Robinson et al., 2007b). As part of this project, unemployed people from local communities were trained to harvest *M. galloprovincialis*. Although there is a substantial body of knowledge about the effects of harvesting on the east coast, the west and east coast systems differ in a number of ways, so that extrapolation of findings from the east to the west coast is risky. Firstly, on the west coast, intertidal exploitation is focused on *M. galloprovincialis*, which is an aggressive alien invader, whereas indigenous species are harvested elsewhere. Secondly, the west coast itself is inherently different from the east coast, due to the dominance of the cold, nutrient-rich Benguela upwelling system (Hutchings et al., 1995), which generates a highly productive nearshore pelagic environment, and exceptionally productive rocky shores (Bustamante et al., 1995). Thirdly, probably as a consequence of this, mussel biomass on the west coast is about two orders of magnitude greater than on the east coast (Harris et al., 1998). Fourthly, on the east coast, because harvesting is pervasive, it has been difficult to implement controlled fishing at a suite of different fishing intensities to explore the consequences of fishing effort (Harris et al., 2003). In contrast, on the west coast there are large areas where mussels have never been harvested to any significant extent. This situation offered the opportunity to implement harvesting at a range of intensities, including zero

harvest controls, to assess the resilience and elasticity of intertidal communities to mussel harvesting.

Considering the known effects of intertidal harvesting on the east coast and the differences in ecology between the coasts, the following *a priori* hypotheses were constructed: (1) Resilience of intertidal communities will be inversely proportional to the intensity of harvesting; (2) Communities on the west coast will demonstrate greater elasticity than those on the east coast due to their high productivity. Within this framework, our study quantified the effects of harvesting *M. galloprovincialis* on intertidal community structure as a whole, thus explicitly addressing the recognised need to move from single species fisheries management towards a broader ecosystem approach (Cochrane et al., 2004; Shannon et al., 2004).

2. Methods

2.1. Study site

The effects of harvesting on community structure were determined at Flat Rocks (29°48.862′ S; 17°04.472′ E), a rocky platform bordered below by beds of the kelps *Laminaria pallida* and *Ecklonia maxima*. As *M. galloprovincialis* beds along the South African west coast are concentrated in the mid- and low-shore, the study focused on the effects of harvesting in these zones. Prior to harvesting, the mid-shore was covered in a mussel–algal matrix dominated by *M. galloprovincialis* and the algae *Gigartina stiriata* and *Champia lumbricalis*. The low-shore was dominated by dense *M. galloprovincialis* beds.

2.2. Experimental design

Harvesting was done by hand and with screwdrivers and *M. galloprovincialis* individuals with a shell length greater than 50 mm were targeted. To assess the effects of a spectrum of harvesting intensities, five treatments were employed i.e. an unharvested control area (10 m), a once-off total clearance area (3 m) in which all *M. galloprovincialis* were removed, and areas of $F=0.3$ (23 m), $F=0.6$ (11.5 m) and $F=0.9$ (7.5 m), respectively referring to preset harvesting intensities whereby 30%, 60% or 90% of the total mussel biomass present were removed over four months of harvesting. The order of these areas was randomly allocated. Further details of the design of the overall project are given by Robinson et al. (2007b).

Initial data were collected in October 2003, before the commencement of experimental harvesting, in June 2004. Follow-up data were collected in October 2004, after four months of harvesting (Time 1), and in February 2005 (Time 2), April 2006 (Time 3) and finally in August 2007 (Time 4), four 16 and 32 months after the cessation of harvesting respectively.

Within each treatment area the mid-shore (MLWN–MHWN) and low-shore (MLWS–MLWN) were considered separately. In each of these zones, the primary and secondary percentage cover of sessile organisms and algae, and the numbers of mobile organisms were recorded in five randomly-placed replicate 0.25 m^2 quadrats in each zone in each area. Primary cover was defined as the area of primary rock covered by algal attachment

or sessile animals, and secondary cover as the space occupied by organisms living on other plants or animals. Total cover could thus exceed 100%. For each sessile species present, the wet weight supported in areas with 100% primary cover of a given species was multiplied by the actual percentage cover recorded in each quadrat, to convert percentage cover to biomass. Similarly, the mean biomass of at least 10 individuals of each mobile species was multiplied by the number of individuals recorded per quadrat to convert density to biomass. These wet-weight conversions were determined separately for each sampling time.

2.3. Statistical analyses

Due to logistical limitations on access to the coast and funding constraints, impacts on communities could be assessed at one site only and so the design was unavoidably pseudoreplicated. Surveys of community composition prior to harvesting did, however, show there were no significant differences among areas (see Results). To additionally offset the problem of pseudoreplication, treatment areas were divided into two sub-areas and each half analysed separately. This required that one of the five samples be randomly removed from the analyses to obtain a balanced design (i.e. two samples per zone per sub-area in each treatment). As no significant differences emerged between the sub-areas within treatments ($p > 0.25$), these were again combined and the fifth sample returned so as to increase replication. The combined analyses are presented. As a third measure to counter the pseudorepli-cated design, we hypothesised *a priori* that there would be gradients of responses proportional to the intensity of harvesting irrespective of where the plots were positioned.

Community composition (based on non-standardized, square-root transformed wet biomass) was analyzed separately for each intertidal zone using multivariate techniques in the PRIMER (Plymouth Marine Laboratory) and PERMANOVA (FORTRAN) software packages. PERMANOVA was employed to assess differences in community structure among the various treatment areas (a) prior to harvesting, (b) after four months of harvesting, (c) four months, (d) 16 months and (e) 32 months after harvesting had stopped. This approach enables partitioning of multivariate variation among the factors of a multifactorial design (Anderson, 2001; McArdle and Anderson, 2001). PERMANOVA was followed by pair-wise *a posteriori* comparisons and resulting *p*-values corrected for multiple comparisons. SIMPER resolved which species were responsible for any differences among treatments, and a graphic illustration of these differences was gained via non-metric multidimen-tional scaling (MDS). For all multivariate analyses species that occurred only once were excluded.

To compare species richness among treatments at the respective time intervals the incidence-based richness estimate Chao 2 (Chao, 1987) was calculated using the programme EstimateS (Colwell, 2005).

Prior to univariate analyses, data were checked for homo-scedasity using the Kolmogorov–Smirnov one-sample test, and for homogeneity of variances using Levene's test. Separate analyses were performed for each vertical zone. Statistica for Windows (Version 6) was used for all univariate analyses, with $\alpha = 0.05$. A factoral Model 1 ANOVA was employed to test the effects of harvesting intensity and time on (a) the biomass (kg. m^2) supported by the three species contributing the most to community changes (as indicated by SIMPER), (b) grazer densities, and (c) the mean percentage cover of primary rock space by the four dominant space occupiers. Those space occupiers that were present at one time period only were compared between harvesting intensities within that time using a 1-Way ANOVA. Both factoral and 1-Way ANOVAs were followed by *post hoc* Tukey tests.

3. Results

PERMANOVA revealed that time and harvesting intensity interacted significantly in their effect on community composition in both the mid- and low-shore zones (Table 1). In both zones, *post hoc* pair-wise tests demonstrated that before harvesting commenced no differences existed among areas designated for different harvesting intensities, nor were differences recorded between these pre-harvest samples and those collected in the control areas at any other time ($p < 0.05$; Fig. 1a,b).

In the mid-shore, after four months of harvesting (Time 1) a harvesting intensity of $F = 0.3$ resulted in no significant change in community structure when compared with control areas, but harvesting intensities of $F = 0.6$, $F = 0.9$ and total removal of *M. galloprovincialis* resulted in marked changes in community composition ($p < 0.05$; Fig. 1). Four months after cessation of harvesting (Time 2) this pattern persisted, with communities in areas with harvesting intensities above $F = 0.3$ remaining significantly different from those in control areas, but also significantly different from those recorded at Time 1. Sixteen months after harvesting (Time 3) all harvested areas supported communities significantly different to those in the control area. However, 32 months after harvesting stopped (Time 4) communities in all harvested areas had returned to the pre-harvest state.

In the low-shore, four months of harvesting (Time 1) also resulted in significant community changes in areas subjected to harvesting intensities greater than $F = 0.3$ (Fig. 1). As in the mid-shore, this pattern persisted at Time 2. However, unlike the mid-shore, 16 months after harvesting had ended (Time 3)

Table 1
Results of a two-way PERMANOVA on the effects of time and harvesting intensity on community composition in the mid- and low-shore zones

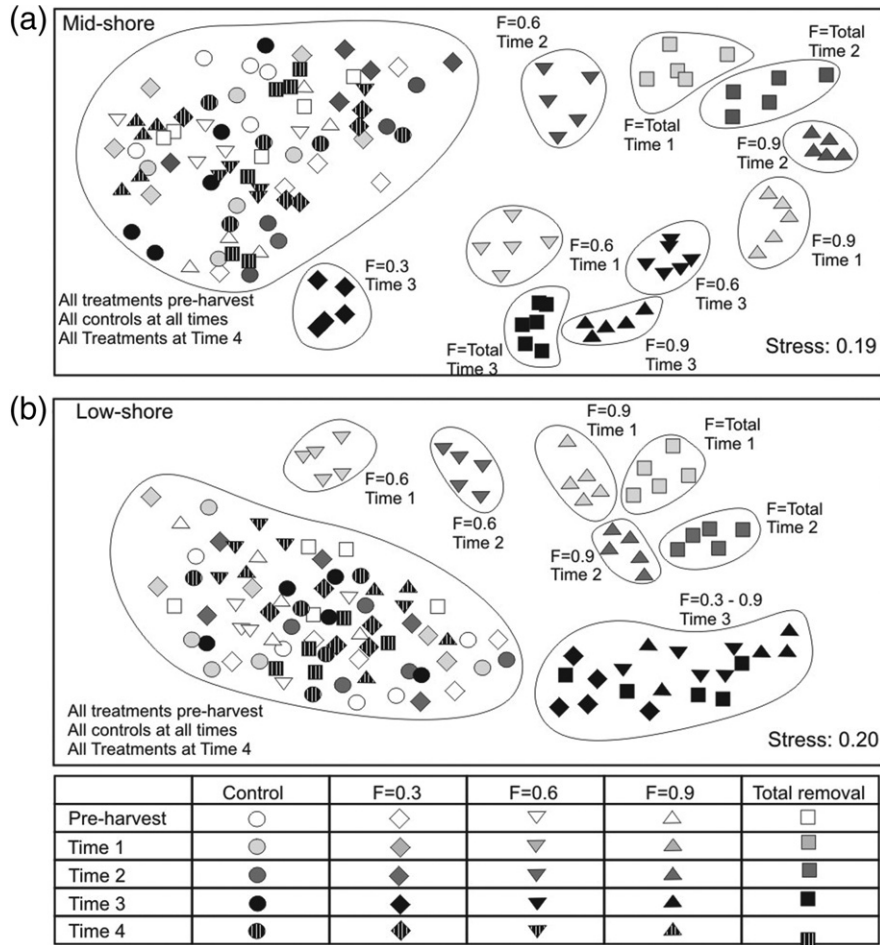| Source	df	MS	F	p
Mid-shore				
Time	4	22,663	33.95	$p < 0.01$
Harvesting intensity	4	13,252	1.72	$p < 0.05$
Time × harvesting intensity	16	7703	11.54	$p < 0.01$
Low-shore				
Time	4	35,365	34.45	$p < 0.01$
Harvesting intensity	4	13,615	1.79	$p < 0.05$
Time × harvesting intensity	16	7605	7.41	$p < 0.01$

Fig. 1. Non-metric multidimentional scaling of species biomass in the (a) mid-(b) low-shore zones under various harvesting intensities. White shapes indicate samples collected prior to harvesting, light grey shapes samples collected after four months of harvesting (Time 1), dark grey shapes, black shapes and hashed shapes samples collected respectively four months (Time 2), 16 months (Time 3) and 32 months (Time 4) respectively after harvested had stopped.

communities in all low-shore harvested areas converged, forming a grouping distinct from the control area and harvested areas at previous time periods ($p < 0.05$). By Time 4, all treatment areas once again supported communities in the pre-harvest state.

The algae *Cladophora flagelliformis*, *Porphyra capensis* and *Ulva* species were the taxa most responsible for the observed changes in both tidal zones. The biomass of *C. flagelliformis* in the mid-shore zone was significantly affected by an interaction between time and harvesting intensity ($F_{4,100} = 4.85$; $p < 0.001$). No significant differences existed between the control area and that of areas $F = 0.3$ and $F = 0.6$ at any time period (Fig. 2). At Time 1, only the area of total removal supported a significantly greater biomass of *C. flagelliformis* than that of the control, while by Time 2 both $F = 0.9$ and total removal showed significantly elevated biomass. However, from Time 3 onwards all harvested areas were indistinguishable from the control. In the low-shore zone, time and harvesting intensity again interacted significantly in their effect on *C. flagelliformis* biomass ($F_{4,100} = 10.99$; $p < 0.001$) with patterns among treatments being almost identical to those in the mid-shore. Overall, *C. flagelliformis*

demonstrated a pattern of increased biomass at high intensities of harvesting, but returned to levels that were not statistically different from the control area 16 months after harvesting had stopped.

The biomass of *P. capensis* in the mid- and low-shore zones was significantly affected by an interaction of time and harvesting intensity ($F_{4,100} = 6.29$ and $F_{4,100} = 4.53$; $p < 0.001$). In the mid-shore, its biomass increased significantly relative to the control in the area exposed to total mussel removal at both Time 1 and Time 2 (Fig. 3). By Time 3 the $F = 0.9$ area also supported significantly elevated biomass. In the low-shore a similar trend was seen at Time 1 and Time 2 but at Time 3, *P. capensis* was only recorded in the control area. By Time 4 the biomass of this algae in all harvested areas resembled that of the control area ($p > 0.05$).

For *Ulva* species (data not shown), biomass in both tidal zones was significantly affected by an interaction of time and harvesting intensity ($F_{4,100} = 8.36$ and $F_{4,100} = 14.89$; $p < 0.001$), with patterns over time and in relation to treatments being identical to those described for *P. capensis*.

Prior to harvesting, densities of grazers (mainly the limpets *Scutallastra granularis*, but also including *Scutallastra*
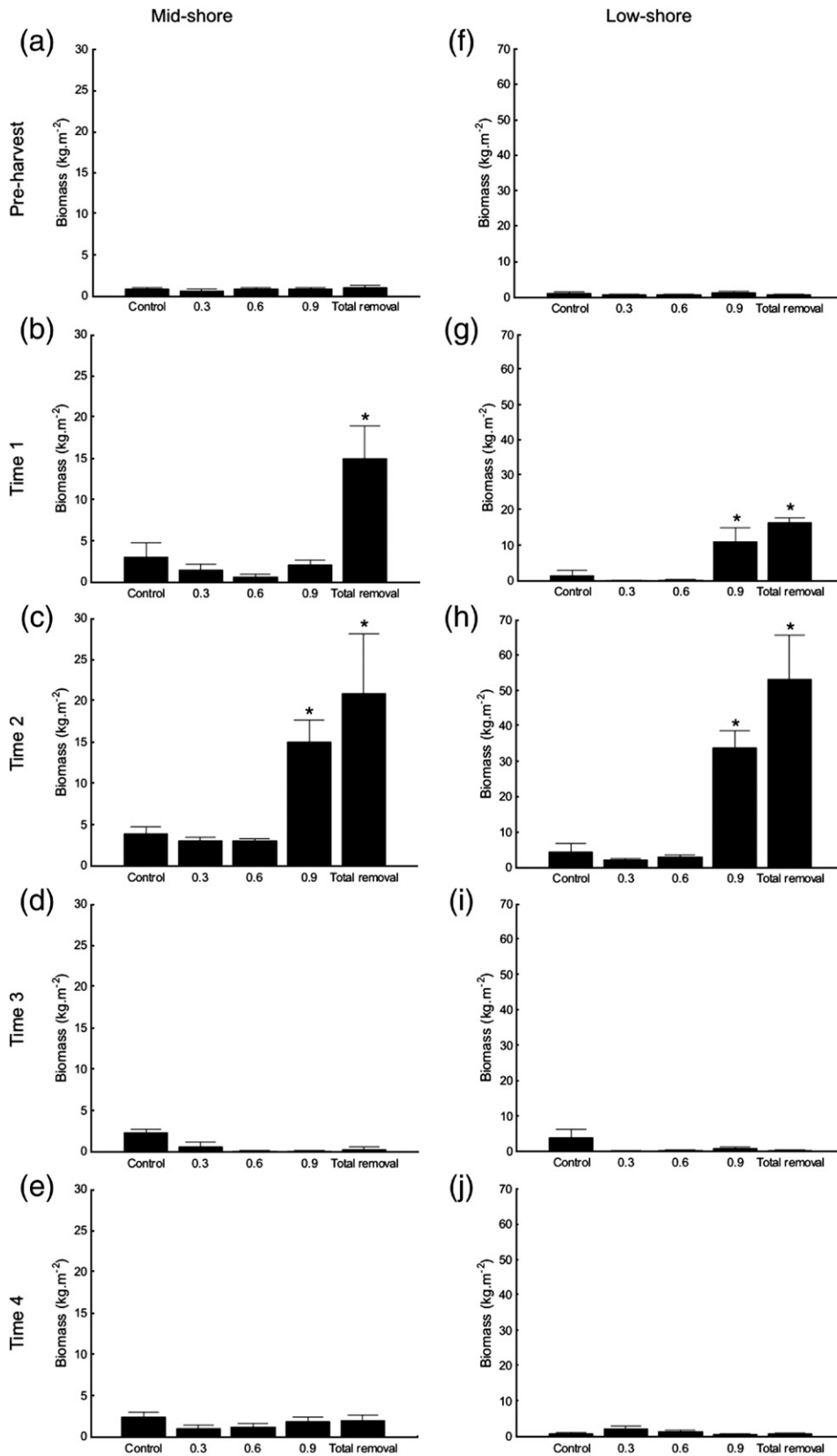
Fig. 2. Mean (+SE) wet biomass (kg m^{-2}) of *Cladophora flagelliformis* (the species contributing most to observed community changes) in the mid- and low-shore prior to harvesting, at Time 1 (after 4 months of harvesting), Time 2, Time 3 and Time 4 (4, 16 and 32 months after harvesting ceased). Harvesting intensities marked by symbols differed significantly from the control area at that particular time (Tukey *post hoc* test, $p < 0.05$).
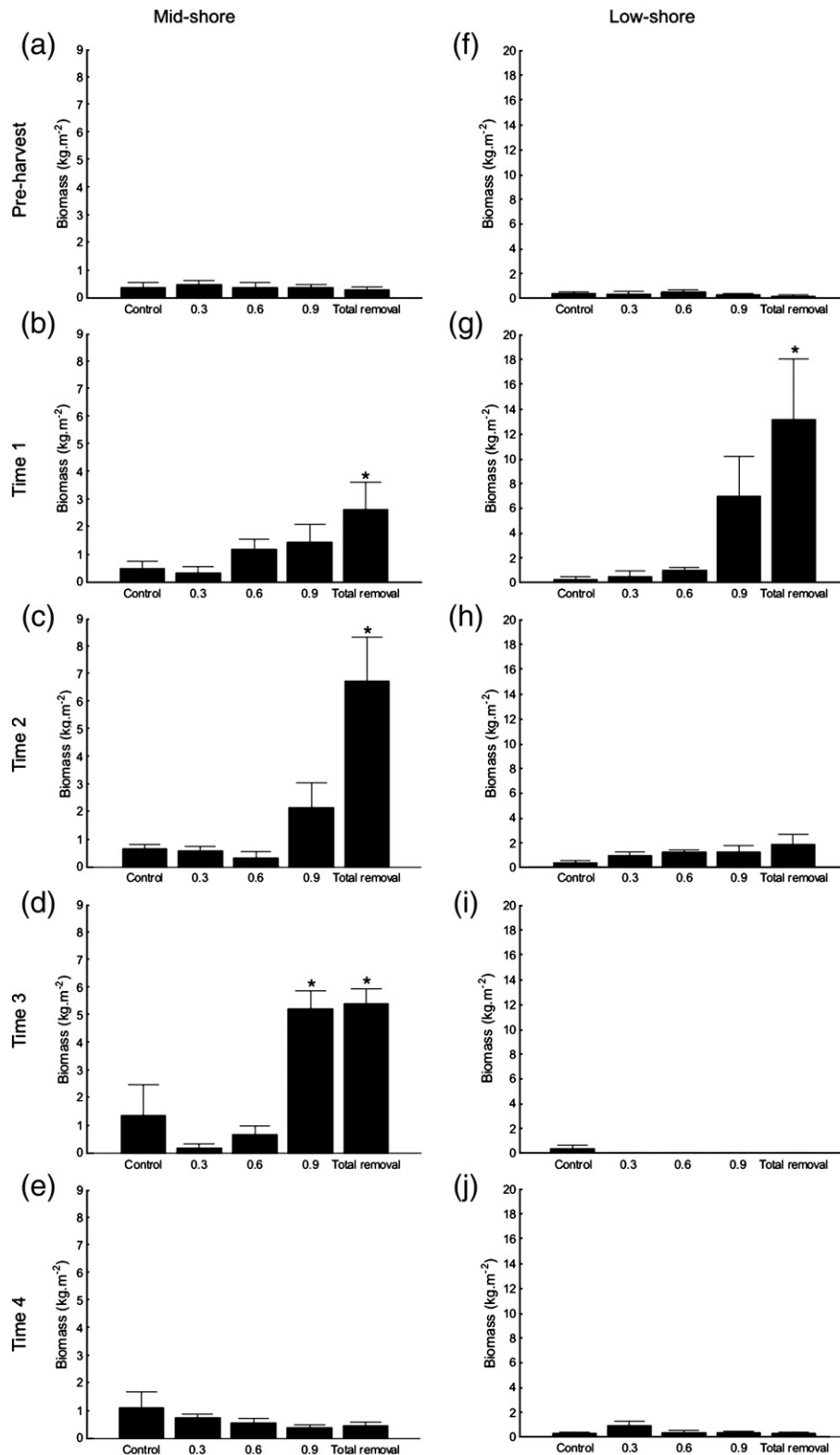
Fig. 3. Mean (+SE) wet biomass (kg m^{-2}) of *Porphyra capensis*, (the second most important species contributing to observed community changes) in the mid- and low-shore prior to harvesting, at Time 1 (after 4 months of harvesting), Time 2, Time 3 and Time 4 (4, 16 and 32 months after harvesting ceased). Harvesting intensities marked by symbols differed significantly from the control area at that particular time (Tukey *post hoc* test, $p < 0.05$).

argenvillei in the low-shore) on primary (rock) and secondary (mainly mussel) substrata showed no differences between the various harvesting areas, but their densities were significantly higher on mussels than on rock (Fig. 4). The primary-substratum densities were significantly affected by an interaction between time and harvesting intensity in both zones
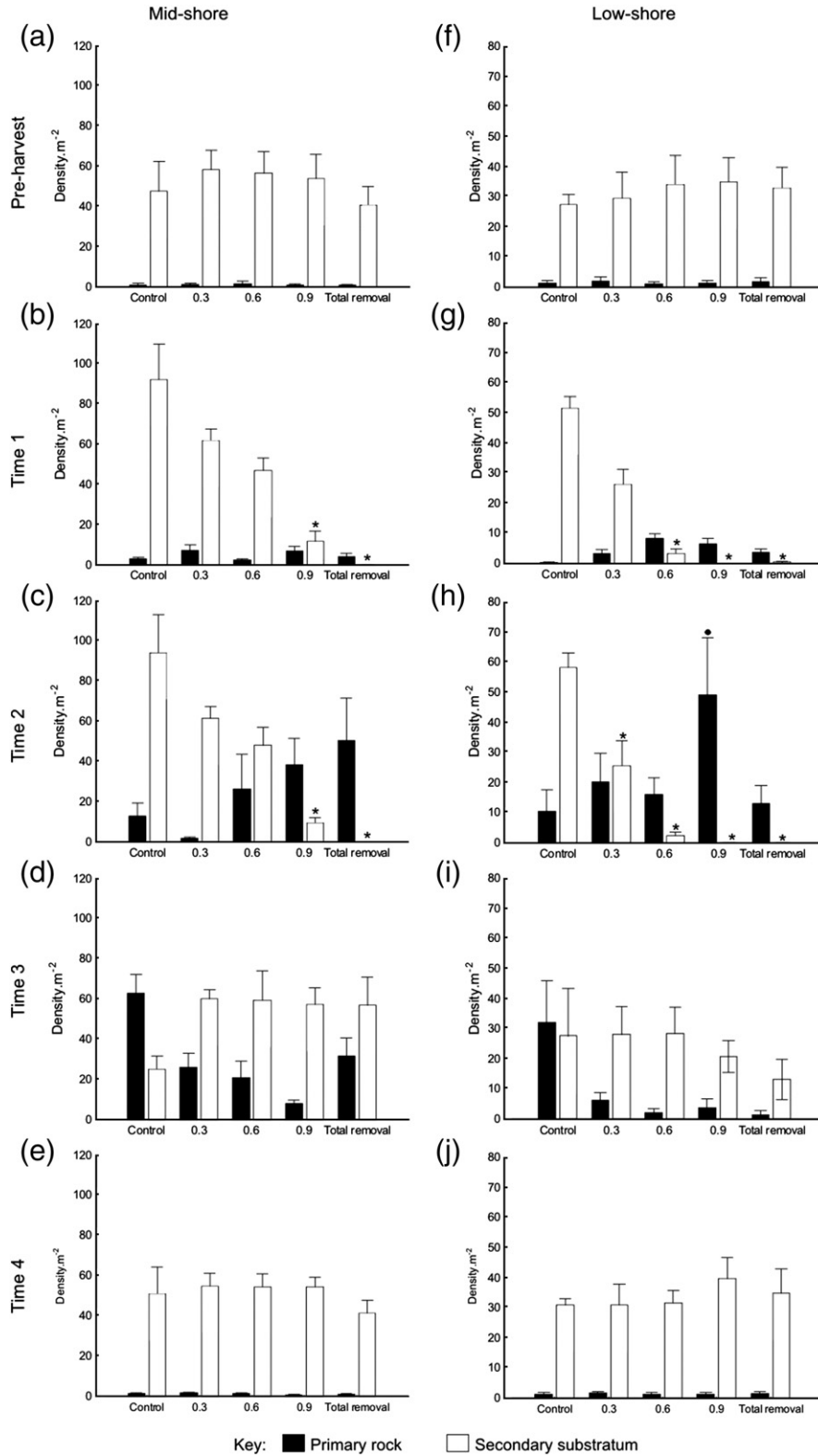
Fig. 4. Mean ($+^2$SE) density m^{-2} of grazers in the mid- and low-shore prior to harvesting, at Time 1 (after 4 months of harvesting), Time 2, Time 3 and Time 4 (4, 16 and 32 months after harvesting ceased). Harvesting intensities marked by symbols (●; primary rock, * secondary substratum) differed significantly from the control area (Tukey *post hoc* test, $p < 0.05$).

($F_{4,100} = 3.13$ and $F_{4,100} = 2.64$; $p < 0.001$). There was a trend of increasing primary-substratum grazer density with increasing harvesting intensity in the mid-shore at Time 2. By Time 3 there

were no significant differences among treatments in either zone and at Time 4 densities had returned to closely resemble those in the pre-harvest condition.
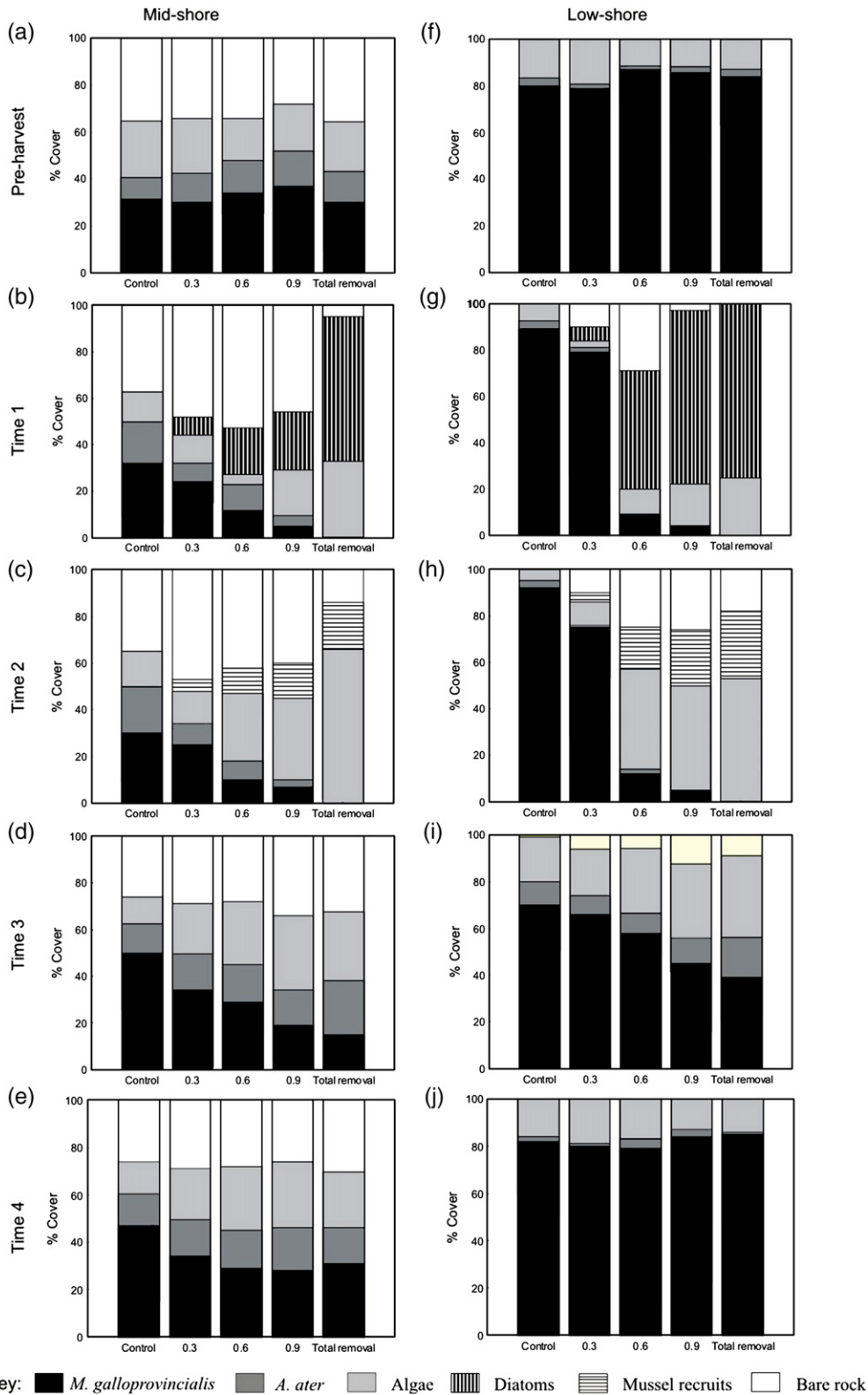
Fig. 5. Mean percentage cover of primary rock space in the mid- and low-shore zones by the four dominant space occupiers prior to harvesting, at Time 1 (after 4 months of harvesting), Time 2, Time 3 and Time 4 (4, 16 and 32 months after harvesting ceased).

Grazer densities on secondary substrata in both zones were also affected by an interaction of time and harvesting intensity ($F_{4,100}=4.93$ and $F_{4,100}=4.03$; $p<0.001$). In the mid-shore, densities decreased with increasing harvesting intensity, becoming significantly different from the control at $F=0.9$ and total removal at Times 1 and 2 (Fig. 4). By Time 3 there were no statistical differences in grazer densities between the control area and any of the harvested areas, and again Time 4
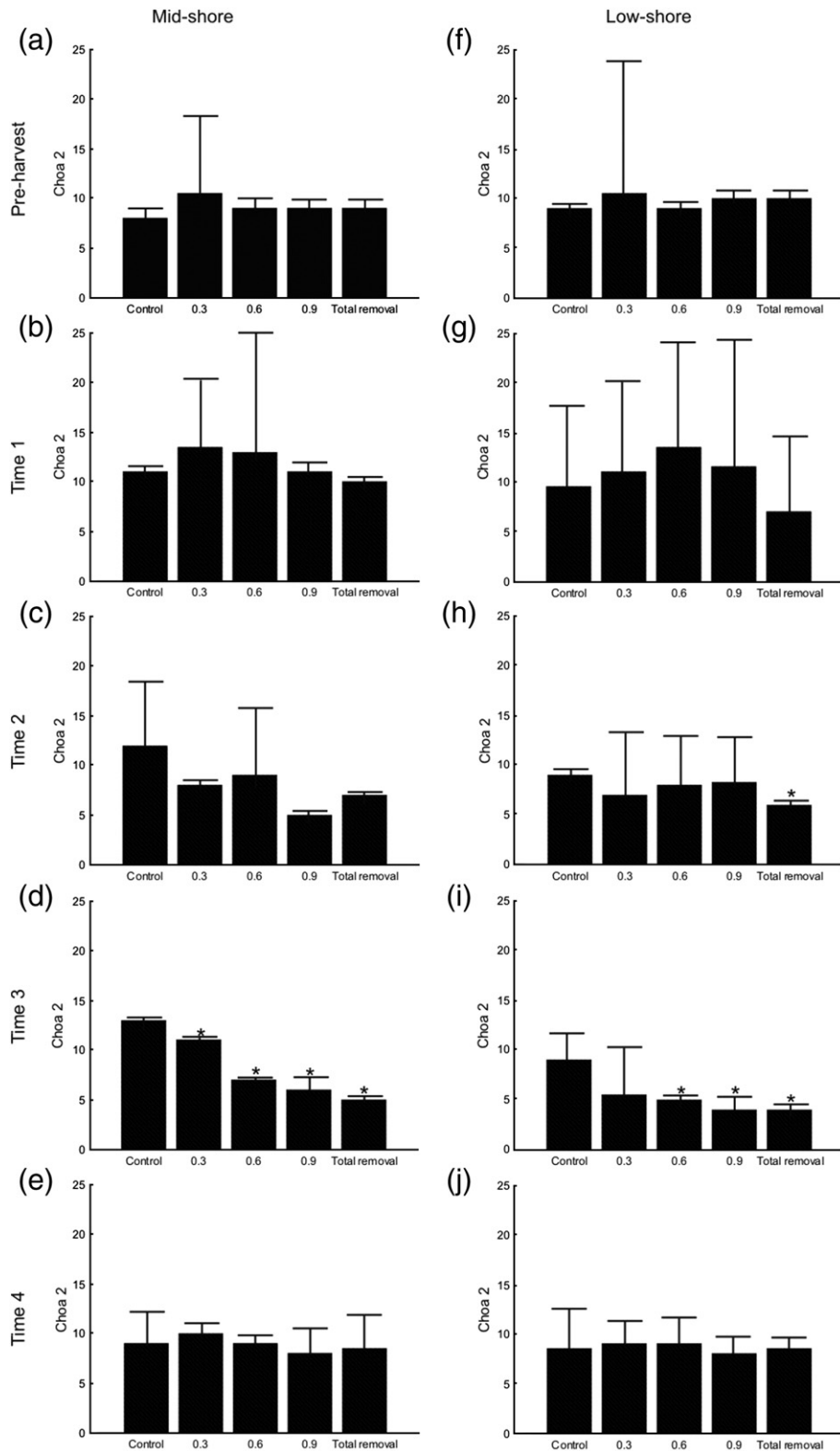
Fig. 6. Chao 2 estimates (+95% confidence intervals) for the control and treatment areas in the mid- and low-shore prior to harvesting, at Time 1 (after 4 months of harvesting), Time 2, Time 3 and Time 4 (4, 16 and 32 months after harvesting ceased). Harvesting intensities marked by symbols differ significantly from the control area at that time period.

had densities closely resembling those of the pre-harvest state. Secondary-substratum grazers in the low-shore showed a similar pattern, but densities were significantly reduced by

harvesting intensities of $F = 0.6$ and above at Time 1 and at $F = 0.3$ and above at Time 2 (Tukey test, $p < 0.05$). Overall, grazers on secondary substrata declined in proportion to

harvesting intensity, while those on primary substrata increased inversely, but these patterns disappeared by Time 3, pre-harvest densities were resumed by Time 4.

Primary cover of the rock face changed strikingly with harvesting (Fig. 5). In both the mid- and low-shore, time and harvesting intensity interacted significantly in their affect on primary cover by the mussels *M. galloprovincialis* and *Aulacomya ater* (Fig. 5; $F_{4,100} = 3.59$ and $F_{4,100} = 13.27$ $p < 0.001$ in the mid-shore; $F_{16,100} = 4.47$ and $F_{16,100} = 1.78$ $p < 0.001$ in the low-shore). Primary cover of both species decreased significantly with increasing harvesting intensity at Time 1 and Time 2 (Tukey test, $p < 0.05$) but returned to levels comparable with that of the control area by Times 3 and 4 (Tukey test, $p > 0.05$). Time and harvesting intensity also interacted significantly in their affects on algal cover and bare rock ($F_{4,100} = 8.44$ and $F_{4,100} = 3.52$ $p < 0.001$ in the mid-shore; $F_{4,100} = 3.67$ and $F_{4,100} = 5.23$ $p < 0.001$ in the low-shore). At Time 1 diatoms covered a significantly greater percentage of primary rock with increasing harvesting intensity in both zones ($F_{4,20} = 36.22$ and $F_{4,20} = 96.34$; $p < 0.001$), but were not recorded thereafter (Fig. 5). Primary cover by mussel recruits increased significantly and proportionally to harvesting intensity in both zones at Time 2 ($F_{4,20} = 39.73$ and $F_{4,20} = 22.74$; $p < 0.001$), but no recruits were recorded at any other time. In summary there were significant decreases in mussel cover that spanned Time 1 and Time 2, but disappeared by Time 3, and transient appearances by diatoms (Time 1) and algae and mussel recruits (Time 2), all of which were proportional to harvesting intensity but disappeared by Time 3. By Time 4 the percentage cover of primary rock in both the mid- and low-shore zones had returned to the pre-harvest state.

Prior to harvesting, no significant differences existed in Chao 2 estimates of total species richness among treatments in either the mid- or low-shore (based on overlapping confidence intervals; Fig. 6). In the mid-shore the same pattern was observed at both Time 1 and Time 2. At Time 3, however, all harvested areas supported significantly lower species richness when compared to the control and the magnitude of the decline was proportional to harvesting intensity. In the low-shore a similar pattern was observed at Time 1, but by Time 2 total species richness was significantly lower in the total removal treatment. Time 3 saw this reduced diversity reflected in areas of $F = 0.6$, $F = 0.9$ and total removal and again the declines were proportional to harvesting intensity. By Time 4 diversity in all previously harvested areas in both shore zones was comparable that in controls and indistinguishable from that in the pre-harvest condition.

4. Discussion

Changes in the structure of intertidal communities subjected to mussel harvesting pressure have been recorded by a number of authors (Hockey and Bosman, 1986; Lasiak and Dye, 1989), but demonstration of cause and effect through experimental controls and manipulation of harvesting pressure has been less frequent. This study offered a unique opportunity to address this aspect of applied intertidal ecology, and clearly demonstrated

significant changes in community structure under a spectrum of harvesting intensities through time.

Despite the fact that harvesting was limited to a single site, we are confident in the trends that emerged because (a) no significant differences existed among treatment areas prior to harvesting, (b) control areas remained unchanged through time, (c) no significant intra-treatment differences were detectable at any time, (d) both multivariate community responses and univariate species responses displayed consistent gradients that were proportional to harvesting intensity and (e) treatment areas were randomly interspersed on the shore.

Changes in community structure recorded in the mid- and low-shore were driven by an interaction between time and harvesting intensity (PERMANOVA $p < 0.01$). Statistically discernable changes in community structure were induced by harvesting intensities $F > 0.3$ and $F > 0.6$ in the mid- and low-shore respectively. Thus, as hypothesised, intertidal communities were resilient only to low-intensity harvesting. However, in both intertidal zones, even 16 months after harvesting ceased, all harvested areas supported significantly altered communities. This may indicate that a lag period exists before the effects of low-intensity harvesting are manifested. It is interesting that all low-shore harvested communities converged over time, whereas this was not observed in the mid-shore. Overall, the associated intertidal communities appear to have very low resilience to exploitation of *M. galloprovincialis*, even at low harvesting intensity.

In terms of elasticity, intertidal communities along the east coast of South African exhibit extremely low elasticity in response to disturbance. In fact, no study has demonstrated full recovery, even after 13 years (Lasiak and Dye, 1989; Dye, 1995). Due to the highly productive nature of the Benguela upwelling system we hypothesised that elasticity would be greater on the west coast than on the east coast. Sixteen months after the cessation of harvesting at our west coast site, virtually all univariate measures indicated a return to the pre-harvest state and 32 months after harvesting ceased this was also reflected in multivariate measures in both the mid- and low-shore zones. Thus, as hypothesised, west coast intertidal communities are substantially more elastic than those of the east coast.

In both the mid- and low-shore the observed changes in community structure were driven by three algae: *C. flagelliformis*, *P. capensis* and *Ulva* species. After four months of harvesting, biomass of these algae increased significantly in areas subjected to intense harvesting in the mid- and low-shore (Figs. 2 and 3). This trend was still apparent four months after harvesting stopped. However, after 16 months of no harvesting, *C. flagelliformis* biomass showed no difference between control and harvested areas, and only in areas of $F = 0.9$ and total removal in the mid-shore did *P. capensis* still show elevated biomass. Total recovery was evident 32 months after harvesting stopped.

M. galloprovincialis presently dominates primary rock surfaces on exposed shores along the South African west coast, at the expense of various competitively inferior indigenous limpet species (Branch and Steffani, 2004). By excluding *Scutellastra granularis* from open rock, *M. galloprovincialis* has reduced the

density of this species on rock, but at the same time has increased its overall density by providing a favourable settlement and recruitment substratum for juveniles (Hockey and Van Erkom Schurink, 1992). A competitive interaction between *M. galloprovincialis* and *Scutellastra argenvillei* has also been demonstrated (Steffani and Branch, 2003a,b, 2005; Branch and Steffani, 2004), whereby *S. argenvillei* is present at high densities at semi-exposed sites, but is largely excluded from primary rock by *M. galloprovincialis* at stronger (but not extreme) wave exposures. Considering the above, it was expected that pre-harvest grazer density would be low on primary rock, but considerably higher on secondary substratum. This proved to be the case (Fig. 4). As most secondary substratum constituted mussel bed, it was anticipated that the density of secondary-substrate grazers would decrease with increasing harvesting intensity, and that the density of primary-substrate grazers would concurrently increase, as primary space was released from dominance by *M. galloprovincialis*. Although the density of secondary-substrate grazers clearly demonstrated the predicted pattern at Time 1 and Time 2, the trend shown by primary-substrate grazers was less clear and only evident at Time 2 (Fig. 4), despite the presence of elevated food levels for *S. granularis* in the form of diatoms at Time 1. The slow occupation of primary space may have been because of trampling by harvesters, who selectively walked on areas not supporting *M. galloprovincialis* to avoid damaging the target species. This reasoning is supported by the fact that the density of primary-substrate grazers increased at Time 2, four months after harvesting (and therefore trampling) ceased. Reductions in abundance of intertidal organisms as a result of human trampling have been well documented elsewhere (Povey and Keough, 1991, Schiel and Taylor, 1999). A year later (Time 3), the densities of primary- and secondary-substrate grazers in harvested areas had recovered to levels that were statistically indistinguishable from those of the control in both the mid- and low-shore, and by Time 4 pre-harvest densities had been restored.

The most obvious changes induced by harvesting were seen in changes in the cover of primary rock space (Fig. 5). The decline in primary cover by *M. galloprovincialis* with increasing harvesting intensity simply reflected the removal of this target species. This effect was observed in both the mid- and low-shore, whereas Harris et al. (2003) reported a 'mowing' effect whereby mussel beds were mowed back by harvesters starting in the mid-shore and only later moving to the low-shore. The concurrent decline in rock cover by *A. ater* was most likely due to (a) incidental removal during harvesting and (b) the fact that harvesters selectively trampled on areas covered by *A. ater*, because it offered a firm foothold. The increase in primary space dominance by algae with increasing harvesting intensity in both the mid- and low-shore is in line with results of other studies conducted both along the South African east coast (Lasiak and Dye, 1989) and internationally (Dayton, 1971) and would have been enhanced by reductions in the densities of grazers in harvested areas (Dye, 1995). Diatoms became dominant space occupiers at Time 1, reflecting their role as early colonisers of disturbed intertidal areas. As is typical of such early successional species, diatoms were quickly out-competed and were replaced at Time 2 by larger algal species (predominantly *C. flagelli-*

formis and *P. capensis*) and mussel recruits. The succession of diatoms by *Porphyra* species has also been noted by other authors (Dayton, 1971). The dominance of mussel recruits at Time 2 reflects the high recruitment recorded along the west coast in 2004 (Robinson et al., 2007a). *M. galloprovincialis* is known to have two spawning seasons along this section of the South African coast: March–April and September–October (Van Erkom Schurink and Griffiths, 1991, G.M. Branch unpubl. data). The second spawning season would have occurred just after harvesting stopped. As *M. galloprovincialis* recruits are known to smother even bare rock at times of exceptional settlement (G.M. Branch unpubl. data), the recruitment recorded in Fig. 5 may merely reflect the coincidence of prolific recruitment with the availability of open rock in areas that had been intensely harvested. As harvesting had taken place recently, the byssus threads of harvested mussels were most likely still attached to the rocks and *M. galloprovincialis* is known to preferentially settle onto them (Ceccherelli and Rossi, 1984), so this may have facilitated the settlement of recruits into harvested areas. These changes in percentage cover of diatoms and mussel recruits were not important in defining changes in community structure because they were too small to influence biomass. The return of *M. galloprovincialis* and *A. ater* as dominant space occupiers in harvested areas at Time 3 is a likely reflection of the growth of the mussel recruits recorded at Time 2. Nonetheless, a trend of decreasing mussel cover with increasing harvesting intensity was still apparent at Time 3, and *M. galloprovincialis* had not regained the spatial dominance it demonstrated prior to harvesting, and its cover was still inversely proportional to harvesting intensity (Fig. 5). By Time 4 no effect of harvesting was visible on patterns of primary space coverage in either zone.

Decreased diversity under conditions of disturbance has been demonstrated by a number of authors in a variety of habitats (Addessi, 1994; Clarke and Warwick, 1994). As harvesting constitutes a disturbance, a decrease in species richness was expected with increasing harvesting intensity. This trend was, however, not observed until Time 3 when harvested areas in both the mid- and low-shore supported significantly reduced richness (Fig. 6). Although the delay was unexpected, it may reflect a lag between harvesting and the manifestation of changes in diversity. Nonetheless, by Time 4 diversity in harvested areas resembled not only that of the control areas, but also that in all treatment areas prior to harvesting.

5. Conclusion

Intertidal communities along the South African west coast exhibited low resilience in response to harvesting of *M. galloprovincialis*, although relatively high elasticity enabled the return of these communities to the pre-harvest state within 32 months of the cessation of harvesting. This demonstrates the substantial greater elasticity of west coast communities compared to those of the less productive east coast of South Africa. Despite this elasticity, studies of the ability of west coast *M. galloprovincialis* populations to support a mussel fishery have indicated that harvesting intensities above $F = 0.3$ are unlikely to be sustainable (Robinson et al., 2007b). Thus, should a fishery be

established with $F = 0.3$ as a maximum intensity and adherence to a recommendation that harvesting be limited to seasons when yields are high (Robinson et al., 2007b), the integrity of associated communities is unlikely to be disrupted.

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