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Temporal changes in kelp forest benthic communities following an invasion by the rock lobster Jasus lalandii

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The rock lobster *Jasus lalandii* expanded its centre of distribution south-eastwards into an area known as 'East of Cape Hangklip' on the south-west coast of South Africa in the early 1990s. Using historical and present data, we analysed differences in the abundance of key species and functional groups between the pre- and post-rock lobster invasion periods at two sites along that coast: Cape Hangklip and Betty's Bay. Pre-1989, lobsters were absent, but after 1995 they reached densities approximating 0.4–0.8 m^{-2}. Benthic community composition also changed significantly with herbivores being abundant whereas macroalgae and sessile invertebrates were scarce pre-invasion. We attribute the decline of herbivores to the direct effects of lobster predation, in turn indirectly promoting macroalgae. Post-invasion sessile invertebrates and macroalgae increased by 2 600% and 453% respectively, whereas herbivores declined by 99.3%. The virtual elimination of the sea urchin *Parechinus angulosus* by rock lobsters has substantial implications for the commercial harvesting of the abalone *Haliotis midae*, because its juveniles are intimately associated with this urchin. The lobster invasion has thus not only led to a regime shift of the ecosystem but has also substantial economic consequences, which calls for an ecosystem approach to the management of the pool of commercially exploited resources in this region.

Keywords: abalone, ecosystem effects of fishing, kelp, predation, range shift, regime shift, urchins

Introduction

The strong top-down effects of predators were first demonstrated on intertidal rocky shores (Paine 1969, 1974) but are now known to exist in all coastal ecosystems, including kelp forests (Estes et al. 1998, Steneck et al. 2002, Halpern et al. 2006) and subtidal temperate reefs (Shears and Babcock 2002, 2003, Barrett et al. 2009, Götz et al. 2009a, 2009b), and even farther offshore in exploited ecosystems (Worm and Myers 2003, Frank et al. 2005). Along the South African west coast, the predatory effects of the West Coast rock lobster *Jasus lalandii* can be responsible for regime shifts in subtidal benthic community structure, and the maintenance of alternative stable states (Barkai and Branch 1988a, 1988b, Barkai and McQuaid 1988).

Although *J. lalandii* has historically been concentrated on the West Coast, a south-eastward shift in the early 1990s resulted in a massive 'invasion' of rock lobsters along the south-west coast (Tarr et al. 1996, Mayfield and Branch 2000, Cockcroft et al. 2008). This essentially divided the south-west coast into 'invaded' and 'non-invaded' regions, based on fisheries surveys (Cockcroft et al. 2008) showing a west to east decline in rock lobster abundance and an abrupt reduction in catches and catch rates east of Hermanus (Figure 1). Similar geographic shifts have also been reported for other coastal species including kelps *Ecklonia maxima* and *Laminaria pallida* (GMB pers. obs.), sardine *Sardinops sagax* (van der Lingen et al. 2001, Fairweather et al. 2006a) and anchovy *Engraulis encrasicolus* (van der Lingen et al. 2002). The shifts in pelagic fish, possibly as a result of environmental change, altered abundance levels and range distributions of pelagic-feeding coastal birds (Crawford et al. 2008). Rouault et al. (2009) reported changes in the Agulhas Current system since the 1980s, in which offshore waters have warmed along the South Coast whereas inshore waters have cooled. Roy et al. (2007) specifically recorded inshore cooling east of Cape Agulhas. This inshore cooling may explain the eastward shift in the abovementioned cold-water species (Roy et al. 2007), but data are insufficient to rigorously evaluate this proposition (Cockcroft et al. 2008). Nevertheless, environmental changes and geographic shifts in commercially important species can have serious consequences for associated fisheries. For example, the pelagic fishery incurred large increases in expenses in transporting fish from the South Coast to the West Coast — where fish-processing factories are located (Fairweather et al. 2006b).

The commercial fishery for *J. lalandii* was expanded east of False Bay in 2003 following the 'lobster invasion' into the area known as 'East of Cape Hangklip' (EOCH). This area was once the centre of a lucrative wild-caught abalone fishery targeting *Haliotis midae* (Hauck and Sweijd 1999, Hauck 2009), but illegal fishing in the mid-1990s escalated to such levels that the recreational abalone fishery was closed in 2003, followed by a temporary closure of the commercial fishery in 2008. The decline in abalone due to poaching was intensified by the invasion of rock lobsters. *Jasus lalandii* is a major predator of the urchin *Parechinus angulosus*, and the increased rock lobster densities EOCH coincided with a significant decrease in urchins (Tarr et al. 1996, Mayfield and Branch 2000). At least in the Western Cape, *P. angulosus* feeds largely by trapping drift kelp rather than actively grazing, and provides both protection and nourishment to juvenile abalone (Day and Branch 2000a, 2000b), so the collapse of the urchin population EOCH has important repercussions for the survival of juvenile abalone, and hence the abalone fishery, in this region.

Given the complex relationships among rock lobsters, urchins, abalone and kelp (Tarr et al. 1996), changes in benthic communities could have severe implications for a range of commercial fisheries. Against this background, we provide evidence of temporal changes in the abundance of rock lobsters and the composition of benthic communities at two sites EOCH, based on comparisons between our surveys and historical data drawn from three main sources:

Field et al. (1980) for Betty's Bay, Jackleman (1996) for the Cape Hangklip area, and unpublished data collected in 2001 for both Cape Hangklip and Betty's Bay.

The aim of this study is to compare recent benthic community data (lobsters present) with past data (lobsters absent), obtained from two sites on the South-West Cape coast, Cape Hangklip and Betty's Bay, both of which experienced large increases in *J. lalandii* during the early 1990s. We explore three questions: (1) To what extent did the densities of *J. lalandii* increase EOCH post-1990?; (2) Is the 'post-invasion' benthic community different from the 'pre-invasion' community?; and (3) If so, how is it different and what groups of organisms are responsible for these differences? Whereas data limitations require this study to be principally comparative, these questions provide a framework for examining the causes and consequences of ecosystem changes arising from the range shift of *J. lalandii*.

Material and methods

Study sites

Between 2005 and 2006, we surveyed two kelp beds (sites) along the south-west coast of South Africa (Figure 1), for which historical data were available: Cape Hangklip (34°23′09″ S, 18°51′12″ E) and Betty's Bay (34°22′08″ S, 18°54′20″ E). Both sites were regarded as falling within the 'lobster-invaded' region.
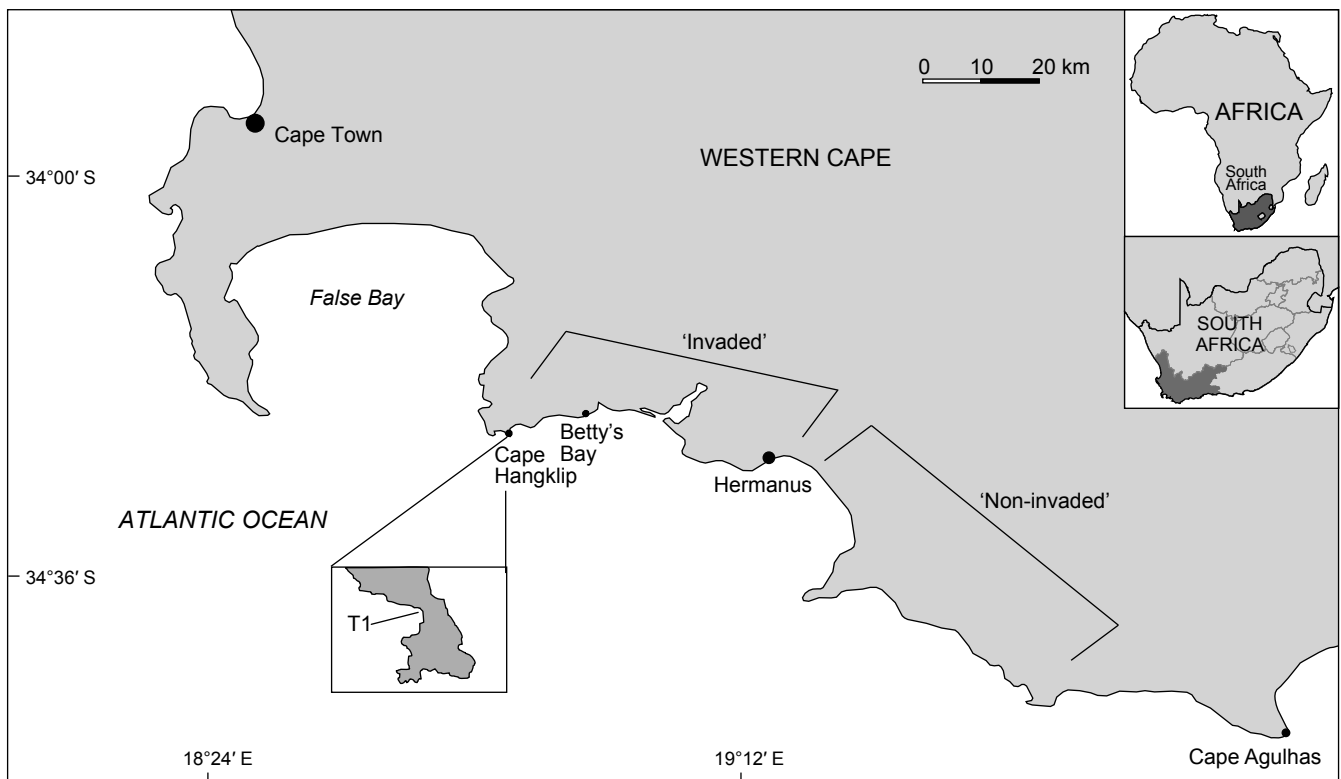

Figure 1: Map showing the two study sites along the south-west coast of South Africa and locations mentioned in the text. T1 indicates the transect surveyed by Jackleman (1996) in 1988/1989 with which we made comparisons in 2005/2006

Data collection

Data collected prior to 1990 (two sets) were *a priori* considered pre-lobster invasion and those collected after 1990 (four sets) as post-lobster invasion. Some of these data are published and some not but, wherever possible, we used the raw data for comparisons. All the data were collected using scuba and were quantitative, but the level of replication and the taxonomic resolution of identifications varied, imposing limits on statistical comparisons and necessitating pooling of data in some instances. Table 1 summarises these data, including sampling dates, taxa sampled, sampling methods, replication and data units.

Three different depth zones (<5 m, 6–12 m and 13–20 m) were sampled per region. However, Jackleman (1996) sampled only in the 0–5 m zone, so from the sources listed in Table 1, we only extracted data for the 0–5 m depth interval, from which we could make valid temporal comparisons. Because data were recorded in different units, they were all converted to g m^{-2} wet weight, using conversion tables provided in Field et al. (1980) or in Blamey (2010, Appendix A1.01).

Taxonomic/functional groups

Data were variously recorded to the level of species or to functional or higher taxonomic groups (Table 1). Consequently, for the temporal comparisons, we employed taxonomic or functional groups, with the exception of 'major species', which were examined at species level: *J. lalandii*, *P. angulosus*, *H. midae*, *E. maxima* and *L. pallida*. All other invertebrates were grouped into taxonomic groups (e.g. asteroids, holothuroids, cnidarians, etc.) and all other algae were grouped into functional groups (turf, foliar or encrusting). In cases where turf and foliar algae were not separated in the historical data, they were grouped as 'understorey algae'.

Statistical analyses

Data for different periods of sampling at Cape Hangklip and Betty's Bay were analysed using PRIMER (Plymouth Routines in Multivariate Ecological Research version 6.1.5; Clarke and Gorley 2006) and PERMANOVA+ for PRIMER (Anderson et al. 2008). The data were fourth-root transformed to downweight the dominance of abundant species, and then used to generate a Bray-Curtis similarity matrix. From the similarity matrix, an analysis of similarity (ANOSIM) and a semi-parametric PERMANOVA (permutational analysis of variance) were performed *a priori* to test for differences between pre-invasion and post-invasion groups. The PERMANOVA was an unrestricted permutation of raw data using a Type III sum of squares.

Following this, hierarchical clustering (using Bray-Curtis coefficients) and multidimensional scaling (MDS) were carried out to compare community structure before and after the lobster invasion. The cluster analyses were used to

Table 1: Summary of sources, data and sampling methods used for analyses. 'Major species' = *J. lalandii*, *P. angulosus*, *H. midae*, *E. maxima* and *L. pallida*. Spp = species level, FG = functional- or taxonomic-group level, T = transect, Q = quadrats per transect. When sampling methods involved 0.25 m^2 quadrats, kelps were recorded in 1 m^2 quadrats due to their size

Site	Dates sampled	Source of data	Taxa sampled	Resolution	Sampling methods	Replication	Data units
				Pre-invasion			
Betty's Bay	1978/1979	Field et al. (1980)	All benthic taxa	Spp	1 300 m transect, 50 m intervals, 1 m^2 quadrats	T: $n = 1$ Q: $n = 3$	kJ m^{-2}
				Post-invasion			
	1996/1997	Mayfield (1998)	Rock lobsters, urchins	Spp	26 m transect, 0.25 m^2 quadrats	T: $n = 1$ Q: $n = 45$	Density
	1998	Marine and Coastal Management unpublished data	Major species and benthic algae	Spp FG	100 m transect, 10 m intervals, 0.25 m^2 quadrats	T: $n = 1$ Q: $n = 10$	Density or % cover
	2001	GM Branch unpublished data	Major species and other benthos	Spp FG	One transect, 0.25 m^2 quadrats	T: $n = 1$ Q: $n = 10$	Density or % cover
	2005/2006	Present surveys	All benthic taxa	Spp	10 m transects, 0.25 m^2 quadrats	T: $n = 3$ Q: $n = 6$	g m^{-2} wet weight
				Pre-invasion			
Cape Hangklip	1988/1989	Jackleman (1996)	Major species, understorey algae and other invertebrates	Spp Spp FG	One transect, 0.25 m^2 quadrats	T: $n = 1$ Q: $n = 10$	g m^{-2} wet weight
				Post-invasion			
	1996/1997	Mayfield (1998)	Rock lobsters, urchins	Spp	26 m transect, 0.25 m^2 quadrats	T: $n = 1$ Q: $n = 40$	Density
	2001	GM Branch unpublished data	Major species and other benthos	Spp FG	One transect, 0.25 m^2 quadrats	T: $n = 1$ Q: $n = 10$	Density or % cover
	2005/2006	Present surveys	All benthic taxa	Spp	10 m transects, 0.25 m^2 quadrats	T: $n = 3$ Q: $n = 6$	g m^{-2} wet weight

validate interpretation of the MDS plots, but are not presented here. A SIMPER (similarity percentage) analysis (with a cut-off of 90%) was then performed on the transformed data to determine which taxa were responsible for any emergent dissimilarities between the pre-invasion and post-invasion groups. Due to small sample sizes or lack of replication in some of the historical datasets, univariate statistical analyses could not be validly performed, and these data were treated descriptively.

Results

Temporal changes in J. lalandii

Jasus lalandii was absent from Betty's Bay in 1978/1979 (Table 2). By 1996/1997, it was present at 125 g m^{-2}, equating to about 0.4 lobsters m^{-2}. The highest abundance was observed in 1998 at 257 g m^{-2} (0.8 m^{-2}). A similar pattern occurred at Cape Hangklip — prior to 1990, lobsters were absent (Table 2), but became abundant by the mid-1990s, and have remained so since, although their biomass was consistently less there than at Betty's Bay.

These data clearly demonstrate that rock lobsters were absent from Betty's Bay and Cape Hangklip in 1980 but present at high densities (0.4–0.8 m^{-2}) from 1996 onwards. No valid statistical test of this change is possible because of the zero variance in 1980, but the change is evident.

Changes in community composition

Analysing the entire dataset at a functional-group level, significant differences in community structure pre- and post-rock lobster invasion were revealed for Betty's Bay (BB) and Cape Hangklip (CH) using both an *a priori* ANOSIM (BB: r = 0.85, p < 0.001; CH: r = 0.763, p < 0.001) and a semi-parametric PERMANOVA (BB: pseudo-F = 10.84, p(perm) < 0.0004, SS = 13 707; CH: pseudo-F = 22.98, p(perm) < 0.0001, SS = 18 115). These results were supported by MDS analyses (Figure 2a, b), which separated the BB and CH pre-invasion communities (Group 1) from post-invasion communities (Group 2) at 91.6% and 83.6% dissimilarity respectively. The Betty's Bay post-invasion group was further divided into two subgroups — a 2001 benthic community (Figure 2a, Group 2a) and a 2005/2006 benthic community (Figure 2a, Group 2b).

The Cape Hangklip analyses were also run using only data from Jackleman (1996) and our current surveys, because these two datasets allowed analyses of algae at

species level. The resultant ANOSIM again revealed a significant difference between pre-invasion and post-invasion communities (r = 0.897, p < 0.001) as did a PERMANOVA (pseudo-F = 20.80, p(perm) < 0.0001, SS = 35 957), and an
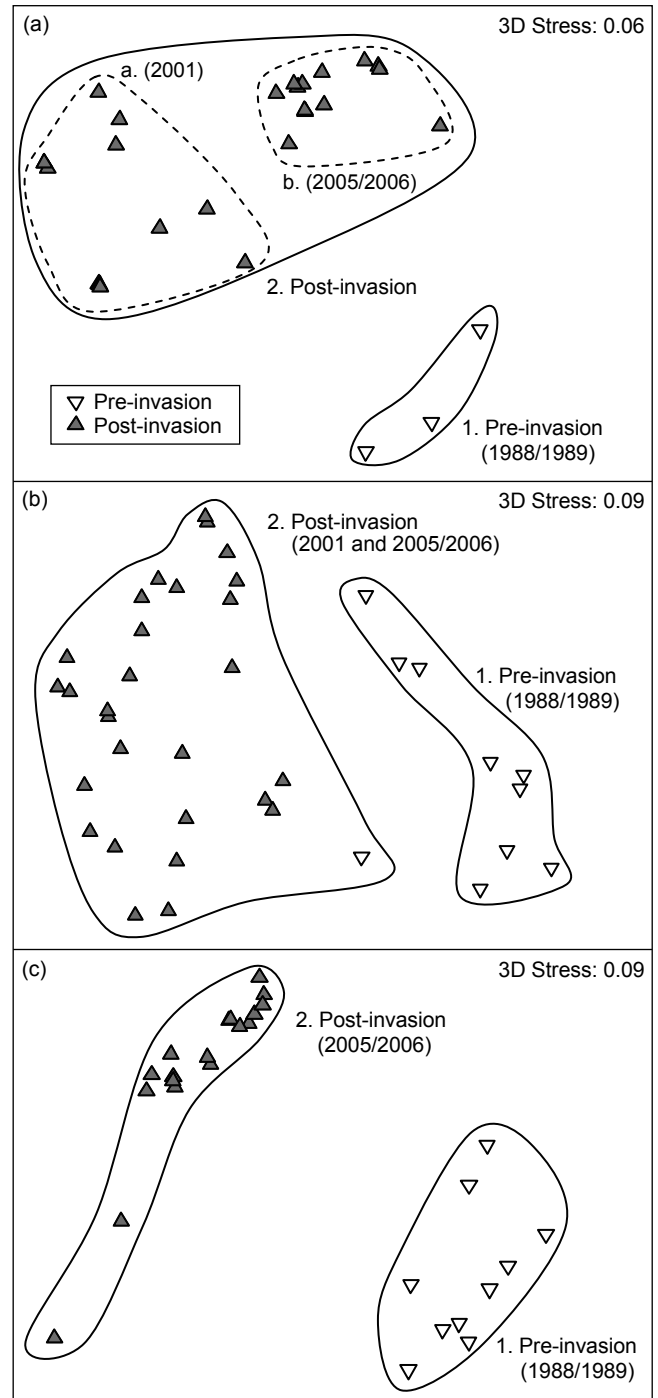

Figure 2: MDS plots based on standardised fourth-root transformed biomass data for (a) Betty's Bay (based on functional groups), (b) Cape Hangklip (based on functional groups) and (c) Cape Hangklip (based on floral species and faunal functional groups), comparing communities before and after the rock lobster invasion

Table 2: Temporal changes in *J. lalandii* mean abundance at Betty's Bay and Cape Hangklip pre- and post-rock lobster invasion

Site	Mean abundance (log g m^{-2}, +SE)				
	Pre-invasion	Post-invasion			
	1978/1979	1996/1997	1998	2001	2005/2006
Betty's Bay	0 (0.00)	2.1 (0.31)	2.41 (0.21)	2.11 (0.19)	2.06 (0.04)
	1988/1989	1996/1997	1998	2001	2005/2006
Cape Hangklip	0 (0.00)	1.98 (0.12)	No data	0.98 (0.15)	1.93 (0.05)

even more clear-cut division between communities (Figure 2c), which were 97.27% dissimilar.

The pre-invasion benthic community at Betty's Bay was dominated by herbivores (Figure 3), including *P. angulosus* and *H. midae*, and by scavengers (decapods, excluding *J. lalandii*). There was a notable absence of *J. lalandii*, understorey algae and Porifera. The post-invasion benthic community was dominated by *J. lalandii*, kelps, understorey algae and Porifera. *Haliotis midae* and other gastropods were greatly reduced, and *P. angulosus* and other echinoderms were absent. Understorey algae, which were virtually absent prior to the lobster invasion, reached substantial levels, and *E. maxima* (but not *L. pallida*) and Porifera increased by almost an order of magnitude subsequent to the rock lobster invasion.

A similar pattern was observed at Cape Hangklip, where the pre-invasion benthic community was also dominated by herbivores (Figure 4), with high densities of *P. angulosus*, *H. midae* and other gastropods and echinoderms. Understorey algae were also present. There was a notable absence of *J. lalandii* and scavengers, as well as a range of sessile taxa such as Porifera, Bryozoa and Acidiacea. Following the rock lobster invasion, surveys in 2001 and 2005/2006 showed that *J. lalandii* had become established, although its mean abundance was relatively low. The dominant organisms comprising the post-invasion benthic community were kelps and understorey algae, as well as sessile species. *Ecklonia maxima* increased 15-fold and *L. pallida* increased from being absent to a mean of 821 g m^{-2}. Although understorey
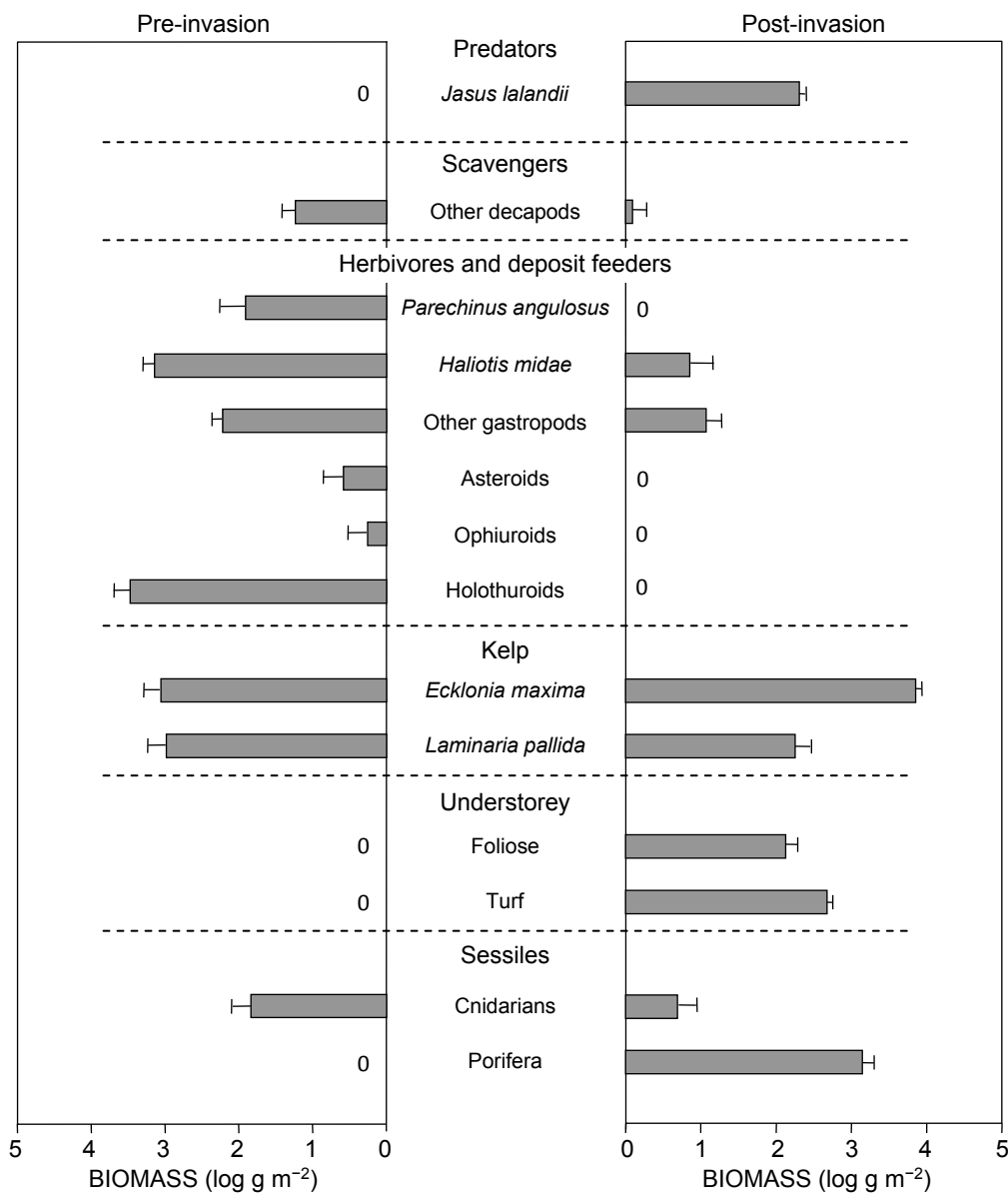

Figure 3: Average biomass (+SE) of taxa contributing most to the dissimilarity between pre-invasion (1978/1979) and post-invasion communities (2001 and 2005/2006) at Betty's Bay; 0 = absent

algae were present prior to the rock lobster invasion, they doubled in biomass following the invasion. Sessile species, which were absent pre-invasion, became abundant post-invasion at both sites. In contrast, *P. angulosus* and *H. midae*, which were abundant pre-invasion, were absent post-invasion. Other grazing gastropods were present but at a reduced abundance, and neither asteroids nor holothuroids were present.

Key role players influential in structuring the kelp forest benthic ecosystem differed radically in abundance pre- and post-invasion. As already noted, *J. lalandii* was entirely absent during the late 1970s and 1980s, but was present at a mean of 257 g m^{-2} (about 0.8 m^{-2}) in the 1990s/2000s (Table 2).

The opposite was the case for *P. angulosus*. At Betty's Bay, its mean abundance was 82 g m^{-2} in the late 1970s, but was at undetectable levels in surveys carried out in 1996, 1998, 2001 and 2005/2006 (Figure 5a). *Haliotis midae* followed a similar trend (Figure 5b), with a high mean abundance in the late 1970s (1 400 g m^{-2}), declining rapidly

in the late 1990s/early 2000s, to the extent that it was not observed in the 2005/2006 survey. *Ecklonia maxima* (Figure 5c) showed no long-term trend, but *L. pallida* (Figure 5d) remained stable until the 2005/2006 survey, when it's density had reduced to undetectable levels. Understorey algae increased from the late 1970s, when they were virtually absent, to a peak of 338 g m^{-2} in 2001, and remained fairly constant thereafter (Figure 5e).

At Cape Hangklip, both *P. angulosus* (Figure 5f) and *H. midae* (Figure 5g) were present in 1988/1989 with mean abundances of 604 g m^{-2} and 288 g m^{-2} respectively, but absent thereafter. *Ecklonia maxima* and *L. pallida* were both more abundant in the post-invasion period than in 1988/1989. The former species (Figure 5h) increased from a mean of 185 g m^{-2} in 1988/1989 to 4 133 g m^{-2} in 2005/2006 and *L. pallida* (Figure 5i) increased from being absent in 1988/1989 to 968 g m^{-2} in 2005/2006. Understorey algae (Figure 5j) were relatively unchanged between 1988/1989 and 2001, but doubled in 2005/2006 to 1 867 g m^{-2}.
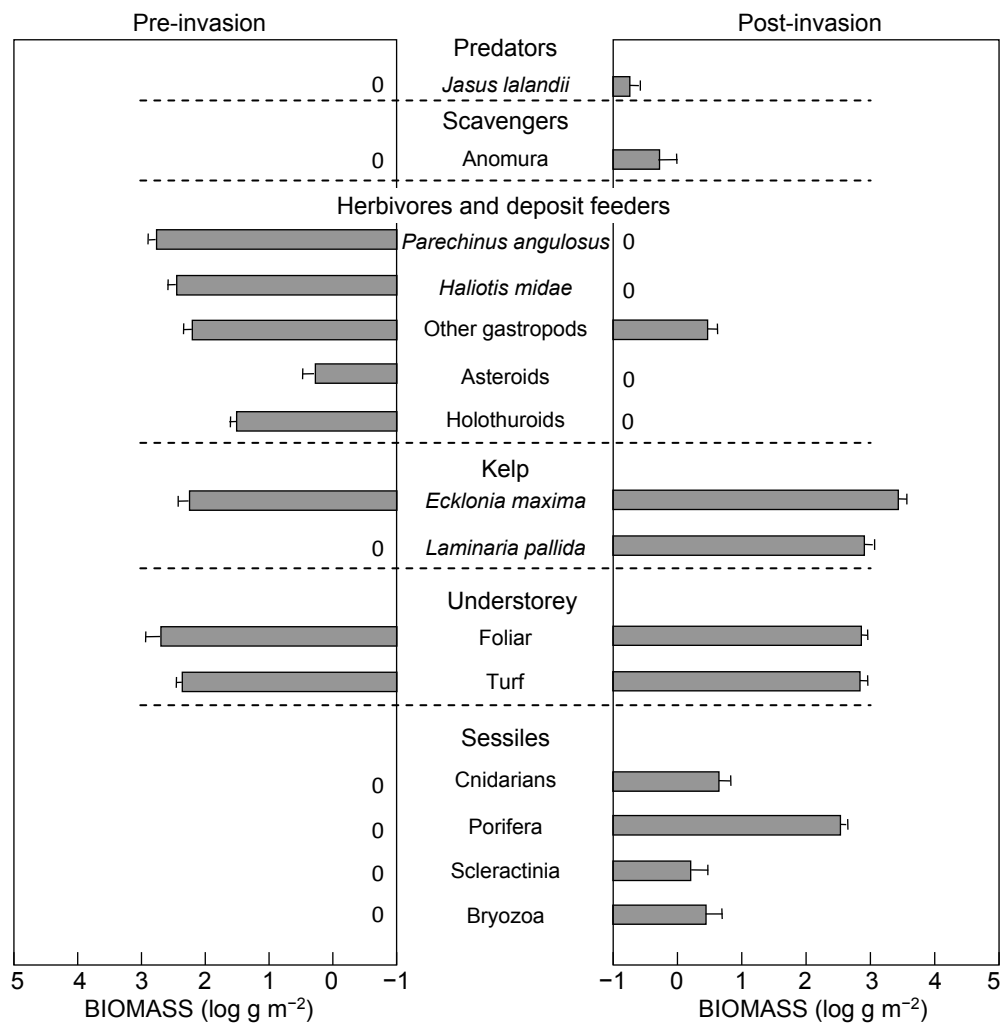

Figure 4: Average biomass (+SE) of taxa contributing most to the dissimilarity between pre-invasion (1988/1989) and post-invasion communities (2001 and 2005/2006) at Cape Hangklip; 0 = absent
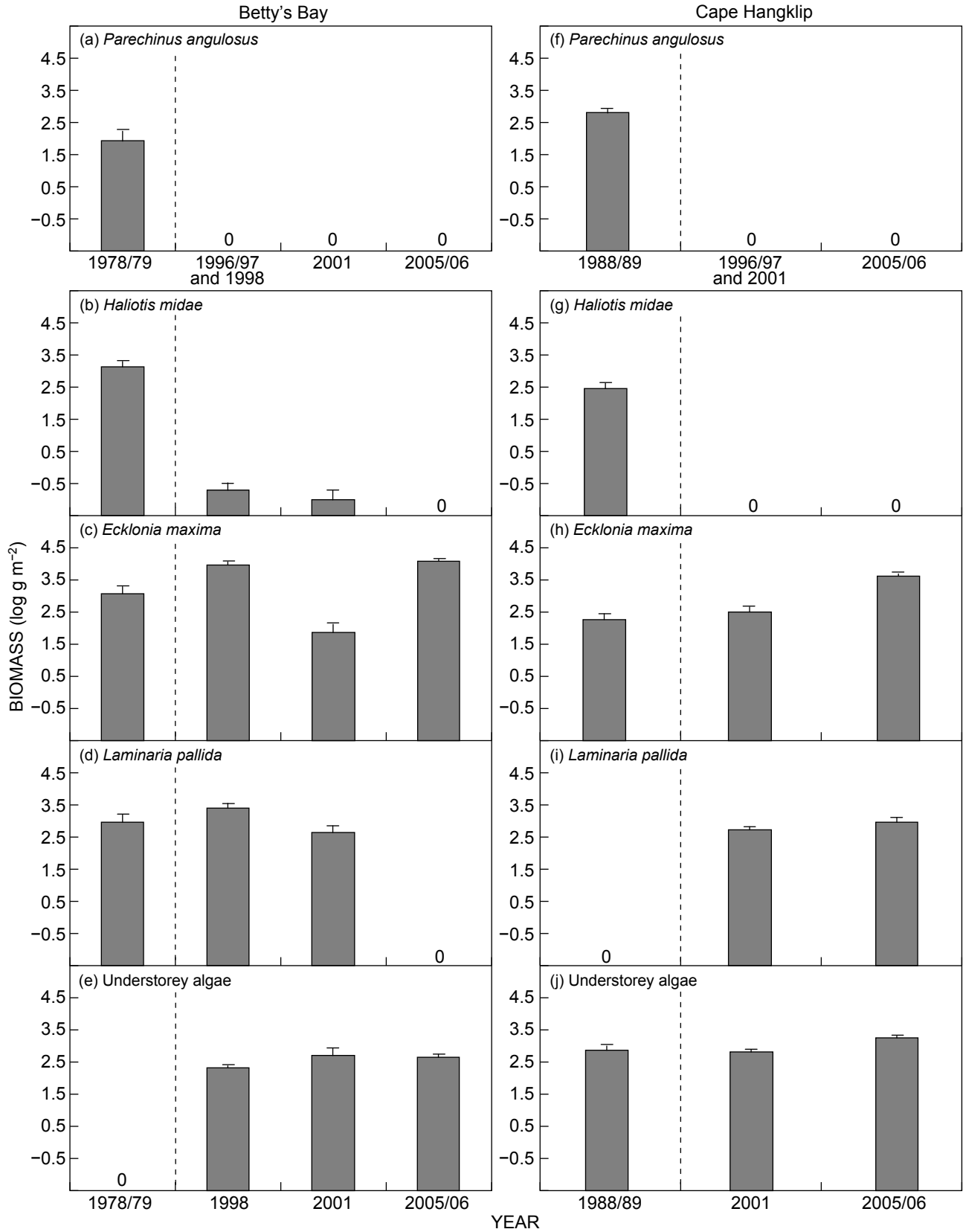
Figure 5: Temporal changes in abundance (+SE) of major species at Betty's Bay (a–e) and Cape Hangklip (f–j). Broken lines separate pre-invasion from post-invasion periods; 0 = absent

Discussion

We report on changes to benthic assemblages following an invasion of *J. lalandii* EOCH, along the south-west coast of South Africa. Our study found that the species had increased significantly post-1990 and within approximately 20 years of the invasion, the effects on the community were far reaching. Herbivores (particularly urchins) disappeared or decreased significantly, kelps increased, and understorey algae and sessile animals proliferated dramatically. These conclusions remained unchanged irrespective of whether the analyses were based on algae being divided into functional groups or treated as individual species, although the differences were more pronounced when the latter approach was employed.

The time-series data and our current analyses suggest that four main changes took place in the EOCH ecosystem. First, *J. lalandii* increased significantly post-1990, supporting similar observations made by Tarr et al. (1996), Mayfield and Branch (2000) and Cockcroft et al. (2008). Both Tarr et al. (1996) and Mayfield and Branch (2000) outline the implications of this increase in rock lobsters for the rest of the ecosystem, given the broad diet of *J. lalandii* (Pollock 1979, Mayfield et al. 2000a, 2000b, 2001, van Zyl et al. 2003) and its well-known ecosystem-altering predatory capabilities (Barkai and Branch 1988a, 1988b, Barkai and McQuaid 1988).

Second, herbivores declined significantly, with some species even disappearing. This was almost certainly on account of increased top-down predation by rock lobsters, and similar effects have been documented in many other predator-controlled systems (Paine 1974, 1980, Estes et al. 1998, Castilla 1999, Menge 2000, Steneck et al. 2002, Shears and Babcock 2002, 2003, Halpern et al. 2006, Barrett et al. 2009). Lobster predation has often been linked to changes in kelp forest communities (Breen and Mann 1976, Tegner and Dayton 1991, Shears and Babcock 2002, 2003, Barrett et al. 2009). In north-eastern New Zealand, the establishment of 'no take' marine protected areas (MPAs) led to an increased abundance and mean size of two important predators: the demersal predatory fish *Pagrus auratus* and the rock lobster *Jasus edwardsii* (Babcock et al. 1999). Shears and Babcock (2002, 2003) demonstrated top-down control on community structure in these MPAs, where intensified predation has diminished destructive grazing by the urchin *Evechinus chloroticus*. As a result, encrusting-coralline habitat has become transformed into a macroalgal-dominated habitat. A similar situation has been observed in Tasmania where protection of *J. edwardsii* inside MPAs has increased its abundance and mean size (Barrett et al. 2009). Following this, significant declines in the urchins *Centrostephanus rodgersii* and *Heliocidaris erythrogramma* and the black-lip abalone *Haliotis rubra* occurred in MPAs relative to adjacent areas that remained open to fishing. However, the decline or disappearance of the South African abalone *H. midae* would have been partly human-induced as the period of decline coincided with the intensification of poaching directed at this species (Hauck and Sweijd 1999, Tarr 2000, Plagányi and Butterworth 2010).

The third change was the proliferation of macroalgae, particularly understorey foliar and turf forms, although kelps also increased. Whereas this is likely an indirect ripple effect of lobster predation following from their depletion of herbivores, our assertion could be challenged on the grounds that the most dramatic decline among the herbivores was that of the urchin *P. angulosus*. Although many urchins are well known for their ecological role in structuring temperate kelp forests through intense grazing, often transforming these forests into bare coralline-covered barrens (Breen and Mann 1976, Mann 1977, Tegner and Dayton 1991, Estes and Duggins 1995, Steneck 1997, Dayton et al. 1998, Steneck et al. 2002), *P. angulosus* fulfils a different role. First, because the species is much smaller than many other urchins, it is not able to ascend adult kelp plants in the turbulent coastal waters that are prevalent in the region (Fricke 1979, Anderson et al. 1997). It is therefore prevented from removing whole adult kelp plants. Second, *P. angulosus* traps drift kelp rather than actively grazing on attached algae (Velimirov et al. 1977, Velimirov and Griffiths 1979). It is thus unlikely to control macroalgae, which has been confirmed through experimental removals (Day and Branch 2002a). Day (1998) has, nevertheless, shown that exclusion of all benthic herbivores (including *P. angulosus*) does enhance macroalgal growth.

Finally, a range of sessile taxa increased in the post-invasion period, including hydroids, sponges, solitary hard corals and bryozoans. Causes of their increases are obscure, but increased food supply could be considered an important factor in determining growth (Shepherd and Thomas 1982) and, in turn, abundance. Alternatively, the increase of sessile invertebrates at both locations post-invasion may also be due to recruitment success in the absence of herbivores.

Datasets from the region EOCH do not extend back far enough in time to ascertain if similar changes have occurred in the past. It is possible that shifts in *J. lalandii* abundance have happened before, periodically changing the benthic community between a herbivore-dominated system and one dominated by sessile species and algae. However, given that the current changes in the ecosystem are additional to pressures being exerted by ever-increasing human influences, they are likely to be prolonged and intensified. This is because historical changes also influence the present functioning of kelp beds (Dayton et al. 1998). For example, during the 20th century, commercial catch rates for the majority of linefish species along the South and West coasts (including temperate-reef sparids that can feed on *J. lalandii*) have declined by 75–99%, and many of these stocks are now considered overexploited (Griffiths 2000). With depressed densities of predatory fish, rock lobsters are likely to remain abundant, and herbivores rare, unless environmental conditions change and force a retraction of lobsters (Blamey 2010). Similarly, illegal fishing of the abalone resource has intensified in the 1990s, about the same time at which the *J. lalandii* invasion and *P. angulosus* decline are believed to have occurred (Tarr et al. 1996). Perpetuation of the current near-absence of urchins, in combination with (1) depletion of abalone parent stock due to overexploitation caused by poaching and (2) the reliance of juvenile abalone on *P. angulosus* for protection

and nourishment (Tarr et al. 1996, Day and Branch 2000a, 2000b, 2002a, 2002b), constitutes a severe threat to the abalone stocks, and it is not surprising that abalone recruitment is at an all-time low with prognosis for stock recovery poor (Tarr et al. 1996, Tarr 2000).

Whereas our study was necessarily comparative given the nature of the historical data available with its inherent limitations (e.g. two study sites, periodic sampling, small sample sizes), it is evident that *J. lalandii* densities have increased significantly post-1990 and that, following this increase, the benthic communities at both Betty's Bay and Cape Hangklip have been substantially altered. The magnitude of the changes in the community associated with the arrival of high densities of rock lobsters emphasise the regime shift that has taken place: averaged over the two sites, herbivores declined by 99.3%, macroalgae increased 453% and sessile animals increased 2 600%. Importantly, depletions of urchins have enormous repercussions for juvenile abalone, which normally shelter beneath them. The invasion by rock lobsters thus has profound ecological and economic implications, which calls for an ecosystem approach to the management of the pool of commercially exploited resources in this region.

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