

Changes in South African rocky intertidal invertebrate community structure associated with the invasion of the mussel *Mytilus galloprovincialis*

Tamara B. Robinson^{1,2,*}, George M. Branch¹, Charles L. Griffiths^{1,2},
Anesh Govender¹, Philip A. R. Hockey³

¹Marine Biology Research Institute, Zoology Department, University of Cape Town, Private Bag X 03, Rondebosch 7701, South Africa

²Centre of Invasion Biology, Zoology Department, University of Cape Town, Private Bag X 03, Rondebosch 7701, South Africa

³DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town, Private Bag X 03, Rondebosch 7701, South Africa

ABSTRACT: Since the establishment of the alien mussel *Mytilus galloprovincialis* in South Africa, several authors have studied its interactions with individual indigenous species. However, the broader implications of this invasion on the intertidal zone remain undocumented. This paper analyses the impacts of this mussel on the rocky-shore invertebrate community structure at Marcus Island on the west coast of South Africa. The effects of the invasion were linked to 3 key elements and were not consistently spread across the intertidal zone, but were focused within the mid-to-low shore. Firstly, physical stress in the mid-intertidal zones was ameliorated by the presence of *M. galloprovincialis* beds. Secondly, habitat complexity was increased where *M. galloprovincialis* replaced bare rock or less complex secondary habitat. Thirdly, habitat became less patchy as mussel beds blanketed the shore. Consequently, invertebrate density and species richness increased substantially, and community composition changed significantly in the mid-shore. Lower on the shore, significant changes in invertebrate community structure were driven by a switch from mono-layered beds of the small indigenous mussel *Aulacomya ater* to multilayered beds of *M. galloprovincialis*, despite no change in total species richness.

KEY WORDS: Alien mussel · Community structure · Marine invasions · *Mytilus galloprovincialis* · Rocky shores

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

The spread of alien species is altering the composition of marine communities on a global scale (Ruiz et al. 1999, Mack et al. 2000, Grosholz 2002) and has been identified as a major threat to biodiversity (Occhipinti-Ambrogi & Savini 2003). Many studies have considered direct interactions between alien and indigenous species (Berman & Carlton 1991, Byers 2000, Byrnes & Witman 2003, Bachelet et al. 2004, Le Pape et al. 2004), but relatively little attention has been paid to

the impacts of alien species on the biological structure of the communities they invade.

One alien species that has received substantial attention at the level of species-specific effects is the mytilid mussel *Mytilus galloprovincialis* along the South African coast. As the most abundant and widespread invasive marine species in this region (Robinson et al. 2005), *M. galloprovincialis* has partially displaced the local mussels *Choromytilus meridionalis* and *Aulacomya ater* along the west coast (Hockey & Van Erkom Schurink 1992), while exhibiting spatial segregation

with the indigenous mussel *Perna perna* on the south coast (Robinson et al. 2005). As a consequence of the rapid growth rate, high fecundity and desiccation tolerance of this invasive mussel (Van Erkom Schurink & Griffiths 1990, Hockey & Van Erkom Schurink 1992), its arrival resulted in a net upshore shift in the zonation of intertidal mussel beds. Due to extremely high recruitment rates (up to 20 000 recruits m^{-2} ; Harris et al. 1998), *M. galloprovincialis* presently dominates primary rock surfaces at the expense of various competitively inferior limpet species (Branch & Steffani 2004). By excluding the limpet *Scutellastra granularis* from open rock, *M. galloprovincialis* has reduced the number of individuals that occur directly on rock, although at the same time it offers the potential of increasing overall *S. granularis* density by providing a favourable settlement and recruitment substratum for juveniles (Griffiths et al. 1992, Hockey & Van Erkom Schurink 1992). A second limpet species, *Scutellastra argenvillei*, has also been significantly affected by this invasion, although the strength of the interaction between these 2 species is mediated by wave action (Steffani & Branch 2003a,b). On exposed shores, *M. galloprovincialis* outcompetes *S. argenvillei* and dominates the primary substratum, while, on semi-exposed shores, the mussel is relatively scarce and *S. argenvillei* maintains dominance in open rock space (Steffani & Branch 2003a,b).

Besides the biological role of mussels on rocky shores, they also form an important biotic substratum (Seed & Suchanek 1992). Mussel beds impact surrounding community structure as the highly complex configuration of mussel matrices offers a multitude of microhabitats, which ameliorate fluctuating environmental conditions and provide protection from predation (Gosselin & Chia 1995). The physical presence of the mussel shells also constitutes a suitable hard substratum for settlement and development of co-occurring species.

Despite substantial work on the ecological impacts of *Mytilus galloprovincialis* and the known role of mussels as biotic substratum, the impact of this invasion on the intertidal community has not been considered. In an effort to elucidate community impacts of such invasions, this study characterises changes in intertidal invertebrate community composition following invasion of South African rocky shores by *M. galloprovincialis*.

MATERIALS AND METHODS

This study took place on the southern shores of Marcus Island in Saldanha Bay (33° 02.59' S, 17° 58.26' E) on the west coast of South Africa. The distribution and abundance of intertidal invertebrates was recorded in 1980, before the invasion of *Mytilus galloprovincialis* was recognised (although this species may have been

present in low numbers) and again in 2001, by which time *M. galloprovincialis* was well established and had invaded much of the South African coast (Robinson et al. 2005). In 1980, 7 intertidal zones were identified and sampled. They were (in descending order of tidal height):

(1) The *Porphyra* zone, consisting of patchy beds of the alga *Porphyra capensis*.

(2) The *Ulva* zone, characterised by mixed beds of the algae *Ulva capensis* and *Ulva* (= *Enteromorpha*) *linza*.

(3) The *Granularis* zone, dominated by the limpet *Scutellastra granularis*.

(4) The algal turf zone, covered by a moss-like red algal community dominated by *Caulacanthus ustulatus*.

(5) The *Gigartina* zone, characterised by the algae *Gigartina radula* and *Pterosiphonia cloiophylla*.

(6) The *Aulacomya* zone, dominated by the ribbed mussel *Aulacomya ater*.

(7) The *Choromytilus* zone, comprising beds of the black mussel *Choromytilus meridionalis*.

In 1980, 10 to 16 quadrats, each of 0.01 m^2 , were selected randomly in each zone from within areas of 100% algal or mussel cover. These quadrats were cleared, and all mobile and sessile invertebrates >1 mm in size were counted and identified to species level. In the *Granularis* zone, where invertebrates tend to be large and sparsely distributed, animals were counted *in situ* in 27 quadrats of 0.5 m^2 .

In 2001, the same survey protocol was used, with 2 exceptions. Firstly, *Mytilus galloprovincialis* had overrun most of the *Granularis* zone, making it inappropriate to employ the 0.5 m^2 quadrats previously used to sample this zone, and 0.01 m^2 quadrats were cleared. Secondly, 7 samples were taken per zone. These were randomly, horizontally interspersed between the 1980 samples. To ensure equivalent areas were analysed in 1980 and 2001, in each zone a randomly selected subset of 7 samples from 1980 was compared with the 7 samples taken in 2001. All calculations, except those of rarefaction curves, were conducted using the random sub-sample.

Prior to univariate analyses, data were tested for normality using the Kolmogorov-Smirnov 1-sample test and for homogeneity of variances using Levene's test. All univariate analyses were conducted using STATISTICA for Windows (Version 6), StatSoft Inc. (2004), with α set at 0.05.

Densities per square metre of mussels and other invertebrates were compared before and after the *Mytilus galloprovincialis* invasion (1980 versus 2001) using the Mann-Whitney *U*-test. Each intertidal zone was considered separately.

To estimate the sufficiency of our sample size and compare species richness between times in the respective zones, sample-based rarefaction curves (Gotelli &

Colwell 2001) and the incidence-based richness estimate Chao 2 (Chao 1987) were calculated using the programme EstimateS (Colwell 2005).

Community composition (based on numerical abundance) was analysed separately for each intertidal zone using multivariate techniques in the PRIMER software package (Plymouth Marine Laboratory) and non-standardised, fourth-root transformed data. ANOSIM was employed to detect significant changes in community structure between 1980 and 2001. SIMPER resolved which species were responsible for these changes. Non-metric multidimensional scaling was used to generate graphic illustrations of the differences between the 1980 and 2001 communities in each zone.

RESULTS

In 2001, only 6 of the original 7 intertidal zones could be detected. The algal turf zone could no longer be distinguished and thus could not be resampled. Despite the exclusion of this zone from the following analyses, it should be noted that the disappearance of a zone in itself represents a major change in community structure. As the vertical heights of the respective zones were not recorded in 1980, it was not possible to determine if this zone had become dominated by *Mytilus galloprovincialis*, or if it had been incorporated into the zones previously occurring above or below it.

The densities of the various mussel species in each zone in 1980 and 2001 are shown in Fig. 1. In 1980, *Choromytilus meridionalis* occurred at relatively low densities of 2000 to 5000 m⁻² across most of the shore, except in the *Granularis* zone and in the algal-dominated zones higher on the shore. The smaller *Aulacomya ater* attained much higher densities, but was confined to the lower intertidal zone. In 2001, *Mytilus galloprovincialis* was recorded in all sampling zones, with the exception of the *Porphyra* zone, and dominated 4 out of 5 of these zones, reaching densities of 2000 to 10 000 m⁻². In the mid-shore *Ulva* and *Granularis* zones, the *M. galloprovincialis* invasion increased the total number of mussels present, but did not replace those present prior to its invasion. This was, however, not the case in the *Aulacomya* and *Choromytilus* zones, where the invasion markedly decreased the densities of indigenous mussel species, particularly *A. ater*. By 2001, there had been a shift in the distribution and abundance of mussels from the *Aulacomya* zone to higher up the shore, with all zones except the *Aulacomya* zone showing an increase in overall mussel density (Fig. 1).

In the *Porphyra* and *Choromytilus* zones there were no significant differences in the overall densities of invertebrates between 1980 and 2001 (Mann-Whitney *U*-tests, $p < 0.05$; Fig. 2). In the *Ulva* and *Granularis* zones there

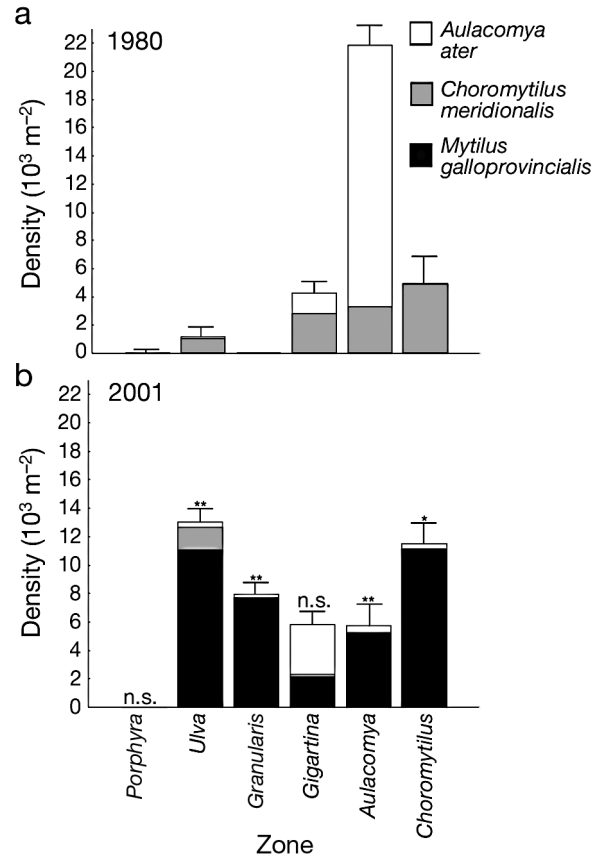


Fig. 1. Mean densities (+SD) of the various mussel species recorded per square metre in each intertidal zone on Marcus Island in 1980 and 2001. *Mytilus galloprovincialis* may have been present in low numbers in the 1980 survey, but undetected due to misidentification (n.s.: no significant difference in overall mussel densities between years; * $p < 0.05$; ** $p < 0.01$)

were substantial and significant increases in invertebrate density ($p < 0.01$), whereas decreases occurred in the *Gigartina* and *Aulacomya* zones (respectively, $p < 0.05$ and $p < 0.01$). The increases reflected invasion by *Mytilus galloprovincialis* of zones that previously supported few mussels. The reduction in invertebrate density in the *Gigartina* zone was a result of the disappearance of a single gastropod species (*Aetoniella nigra*), which was common in 1980. The decline in the *Aulacomya* zone reflected a shift from the typically smaller but abundant *Aulacomya ater* to larger but less dense *M. galloprovincialis* and a reduction in crustacean numbers. Except in the *Porphyra* and *Aulacomya* zones, there was a dramatic increase in the density of mussels between 1980 and 2001. The most striking increase occurred in the *Granularis* zone, where mussels were absent in 1980, but, in 2001, occurred at a density of 2660 individuals m⁻² (4012 SD). In contrast, there was a marked decrease in density of mussels in the *Aulacomya*

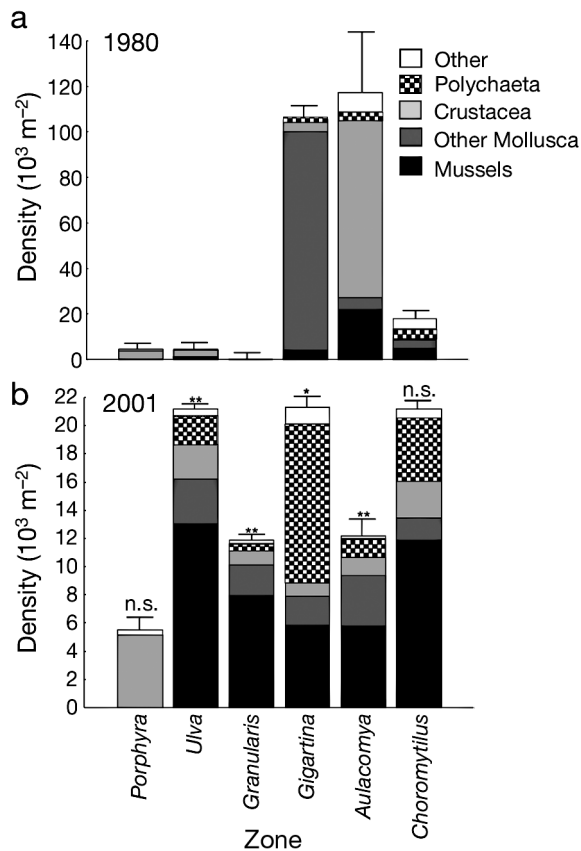


Fig. 2. Mean densities (+SD) of invertebrates recorded per square metre in each zone on Marcus Island in 1980 and 2001, coded by major taxonomic groups. Note the difference in the scales of the y-axes in the 2 data sets (n.s.: no significant difference in invertebrate density between years; * $p < 0.05$; ** $p < 0.01$)

zone. In particular, *A. ater* decreased from 18 529 (5905 SD) to 514 (367 SD) individuals m^{-2} .

Sample-based rarefaction curves reached a plateau only in the *Porphyra* zone in 2001 (Fig. 3). Chao 2 estimates of total species richness showed a significant decline in the *Porphyra* zone in 2001, with increases in the *Ulva* and *Granularis* zones (based on the lack of overlapping confidence intervals; Fig. 4). No significant changes in total species richness were detected in the 3 zones lowest on the shore.

The communities in all 6 zones changed significantly between 1980 and 2001, even when the contribution made by *Mytilus galloprovincialis* was excluded (ANOSIM, $p < 0.01$; Fig. 5). In the *Porphyra* zone, 90% of the average difference between these 2 groups was accounted for by a decrease in the abundance of 1 species, the isopod *Exosphaeroma varicolor*. Over the same period, the *Ulva* and *Granularis* zones, respectively, had average community dissimilarities of 86.4 and 99.8%. In both zones, this difference was explained primarily by increased densities of the nudibranch *Onchidella*

capensis. In the *Gigartina* zone, the small gastropods *Aetoniella nigra* and *Tricolia neritina* contributed the most to the 93.7% dissimilarity between years. Both species were abundant in 1980 (mean densities of 14 771 m^{-2} [6107 SD] and 5729 m^{-2} [2758 SD], respectively), but were absent in 2001. Within the *Aulacomya* zone, *Aulacomya ater*, which decreased dramatically between 1980 and 2001, contributed most to the 96.8% dissimilarity between the pre- and post-invasion communities. Similarly, community differences in the *Choromytilus* zone were explained primarily by the replacement of *Choromytilus meridionalis* by *M. galloprovincialis*.

DISCUSSION

The role of mussels as dominant species affecting community structure of benthic intertidal habitats is well established (Petraitis 1995, Tokeshi & Romero 1995, Enderlein & Wahl 2004, Miyamoto & Noda 2004). Mussels play a regulating role in community structure in 3 ways. Firstly, through their monopolisation of primary rock space (Ruiz Sebastián et al. 2002, Steffani & Branch 2003b), secondly, by providing secondary habitat in the form of a 3-dimensional matrix (which provides habitat for other species and may enhance their recruitment; Crooks & Khim 1999, Miyamoto & Noda 2004), and thirdly, through their biological activities (e.g. by filter-feeding they remove large quantities of particulate matter and plankton from near-shore waters, reducing larval settlement of some associated species; Tsuchiya & Nishihira 1986, Asmus & Asmus 1991). The structural complexity of mussel beds provides a multitude of microhabitats that ameliorate fluctuating environmental conditions and offer protection from predation (Dumas & Witman 1993). Thus, it is not surprising that the intertidal fauna on Marcus Island changed considerably following the arrival of the invasive mussel *Mytilus galloprovincialis*.

As invasions by marine alien species are to a large extent unpredictable, it is exceptionally difficult to assess the impact of these species through replicated experimental manipulations. As such, this study makes use of data collected at a single point in time in 1980 (prior to the invasion of *Mytilus galloprovincialis*) in order to make comparisons with post-invasion communities. This pre-invasion data, however, has limitations that govern the extent of the current comparison. Firstly, no data on the algal component of the intertidal community were collected. Secondly, no measure of biomass was made for any species. Thirdly, no assessment was made of open rock space, and, lastly, a small number of samples were collected. In order to assess the adequacy of our sample size, rarefied species accumulation curves were constructed. Only in the *Por-*

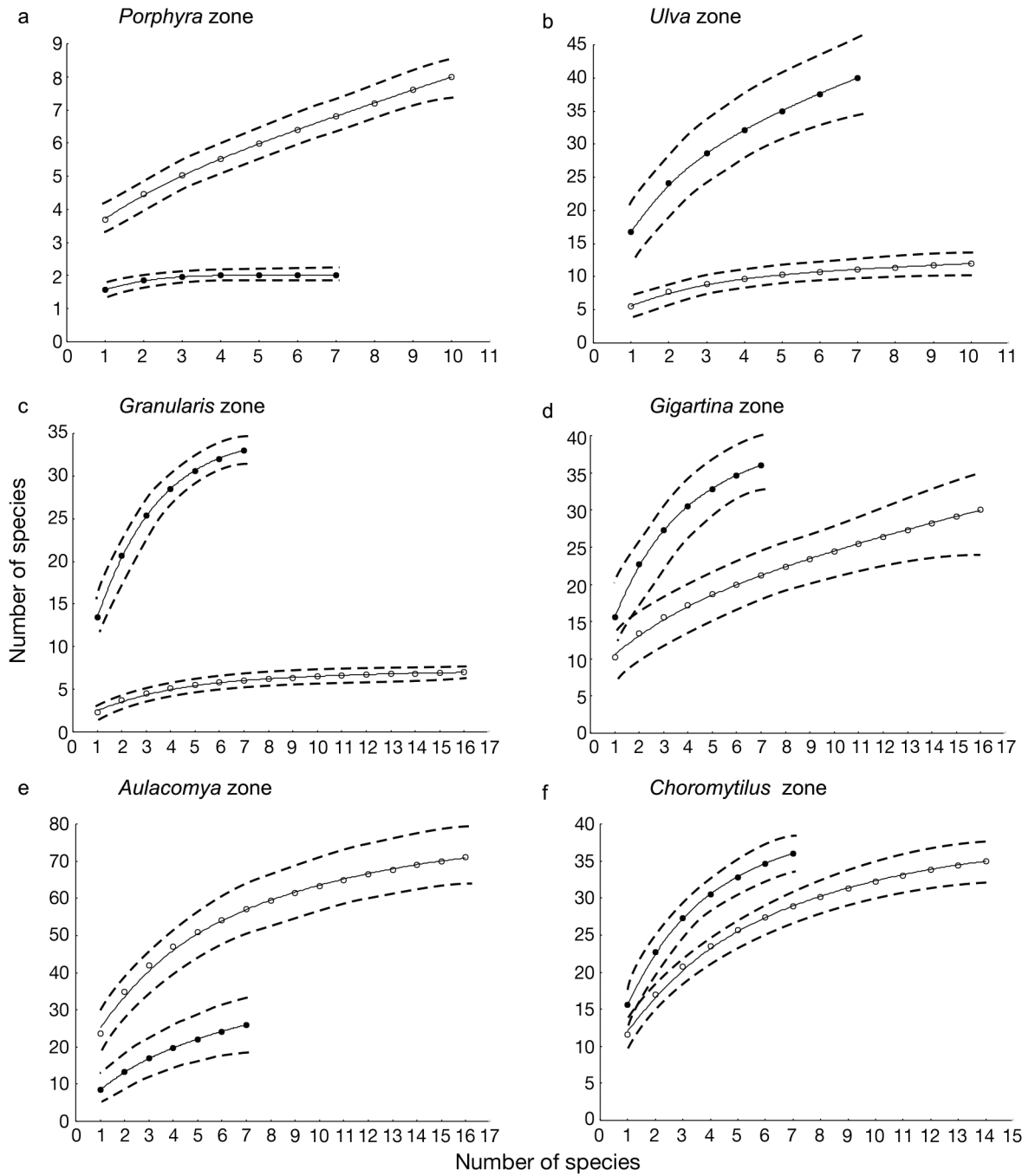


Fig. 3. Sample-based rarefaction species curves with 95% confidence intervals for all sampling zones in 1980 (○) and 2001 (●)

phyra zone in 2001 was an asymptote reached, indicating that the sampling effort was too low to fully characterise species composition. However, the Chao 2 incidence-based richness estimate is still considered an appropriate measure of total diversity as it usually requires ca. 50% of species to be sampled (Colwell & Coddington 1994). As no long-term continuous monitoring has taken place on Marcus Island, it is not possible to unequivocally ascribe the observed community

changes solely to the invasion of *M. galloprovincialis*. Nonetheless, inter-annual changes of species richness and abundance within the benthic communities of Saldanha Bay (in which Marcus Island is located) are known to be minimal (Jackson & McGibbon 1991), and it is likely that a similar pattern applies to intertidal communities.

The *Mytilus galloprovincialis* invasion affected the indigenous mussels *Aulacomya ater* and *Choromytilus*

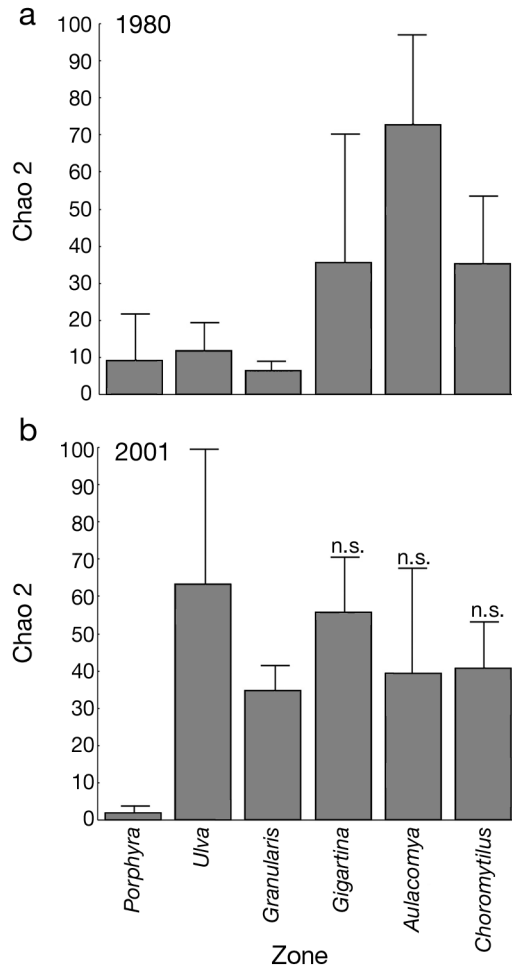


Fig. 4. Chao 2 estimates (+95% confidence intervals) for all sampling zones on Marcus Island in 1980 and 2001 (n.s.: no significant difference based on overlapping confidence intervals)

meridionalis in several ways. In the low-shore (*Aulacomya* zone), the density of *A. ater* decreased by almost 2 orders of magnitude as this slow-growing species was outcompeted by *M. galloprovincialis*. There was also a decrease in the overall density of mussels in this zone, as the small *A. ater* has been largely replaced by the larger *M. galloprovincialis*. In the high- to mid-shore, densities of *A. ater* increased dramatically as protection provided by *M. galloprovincialis* beds enabled this species to survive high on the shore, from where it was precluded previously by virtue of its intolerance to desiccation (Van Erkom Schurink & Griffiths 1990), although it was still numerically far subordinate. The most striking impact of the *M. galloprovincialis* invasion was the total replacement of *C. meridionalis* in both the *Aulacomya* and *Choromytilus* zones and, to a lesser extent in the *Gigartina* zone (Fig. 1). It should, however, be noted that *C. meridionalis* still thrives in substantial subtidal

stocks and often occupies heavily silted and sandy areas among rocks (T. B. Robinson pers. obs.), both habitats rarely occupied by *M. galloprovincialis* along the South African coast. Due to the presence of these refuges, it is highly unlikely that *C. meridionalis* will be driven to local extinction by the appearance of *M. galloprovincialis*.

The change in community structure in the *Porphyra* zone is unlikely to be a consequence of the mussel invasion, as *Mytilus galloprovincialis* does not occur this high on the shore. Crustacea and insect larvae dominated in both 1980 and 2001, and minor changes in abundance of these taxa probably result from seasonal variation in abundance of the dominant alga *Porphyra capensis* (Griffin et al. 1999).

Prior to the arrival of *Mytilus galloprovincialis*, both the *Ulva* and *Granularis* zones were patchy environments, comprising mainly bare rock interspersed with patches of algae and large limpets. These zones were therefore spatially simple habitats in which physical stress would have played an important role in determining biological assemblages. However, following the mussel invasion, the patchy mosaic of bare rock, algae and limpets was transformed to a less patchy but structurally more complex mussel matrix. Reduced patchiness in the *Granularis* zone is reflected in the reduction in sample variability from 1980 to 2001 (Fig. 5). Thus, the physical stresses previously typical of these zones were ameliorated, and the nature of the habitat in these zones was dramatically altered. This accounts for the massive increase in invertebrate density, total species richness, as well as the changes in community composition recorded in these zones.

In the *Gigartina* zone, the density of mussels remained unaltered, despite changes in the species composition (Fig. 1). However, unlike the indigenous mussels, *Mytilus galloprovincialis* develops multi-layered beds (Hockey & Van Erkom Schurink 1992, McQuaid & Phillips 2000). Consequently, the invasion has resulted in an increase in structural complexity in this zone. Despite this change, total species richness remained unaltered. This is in line with findings by Hammond (2001) who recorded no difference in infaunal species diversity between indigenous mussels and *M. galloprovincialis*. The substantial decrease in the invertebrate density was due to extreme reductions in the number of gastropods *Aetoniella nigra* and *Tricolia neritina*, although it remains unclear whether these decreases are a consequence of natural variation, or reflect changes induced by the arrival of *M. galloprovincialis*.

Because the *Aulacomya* zone was previously characterised by the presence of mussel beds, the invasion of *Mytilus galloprovincialis* is unlikely to have altered the uniformity of the habitat in this zone to any great

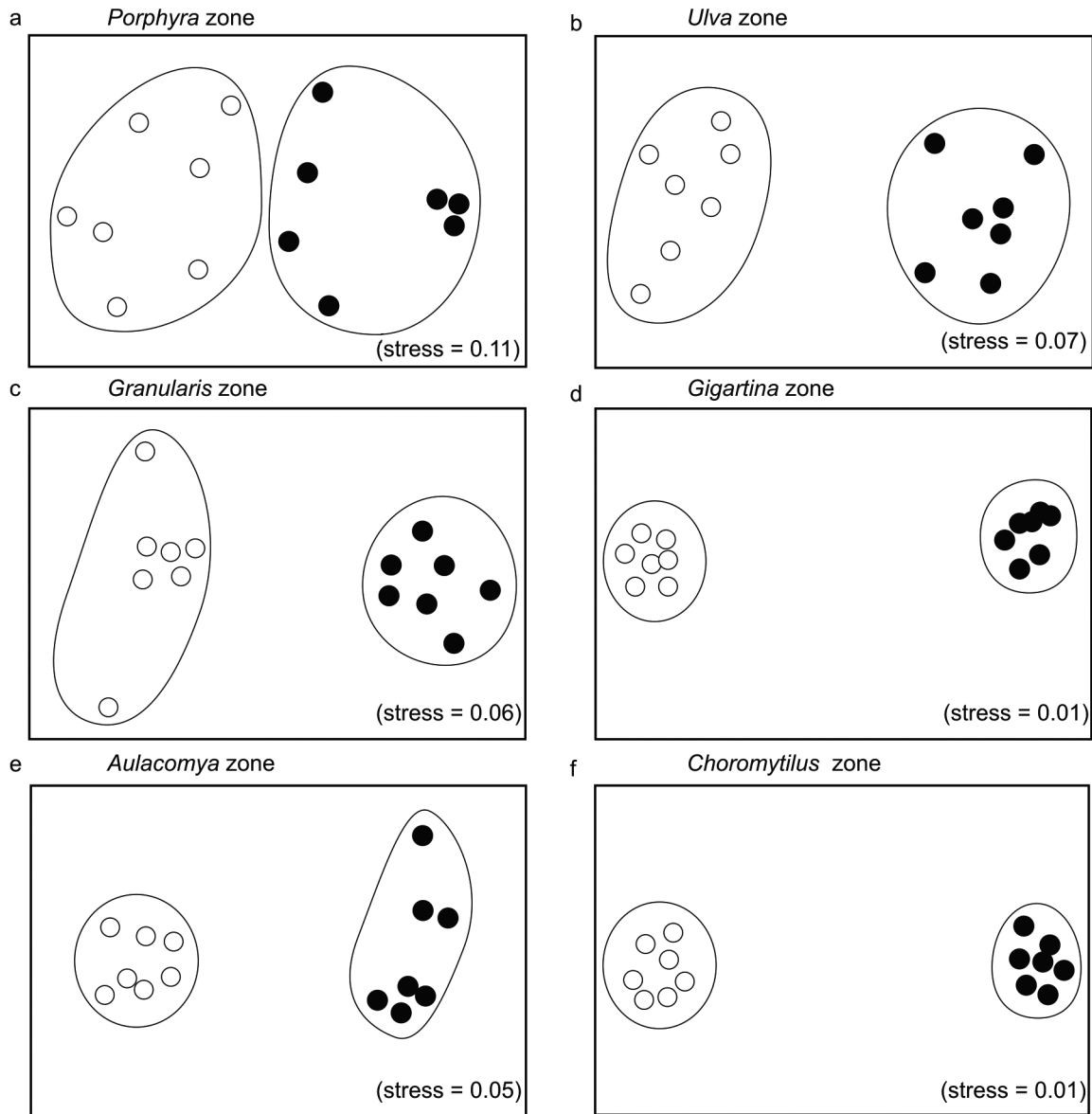


Fig. 5. Non-metric multidimensional scaling of species abundance (fourth-root transformed) for all 6 sampling zones (a) to (f) in 1980 (O) and 2001 (●), excluding the contribution made by *Mytilus galloprovincialis*

extent. However, *Aulacomya ater* decreased considerably in density between 1980 and 2001 (from 18 529 to 514 individuals m^{-2}), while *M. galloprovincialis* conversely increased. The switch from mono-layered beds of small mussels to multilayered beds of large mussels resulted in a significant reduction in the overall density of mussels present in this zone. Van Erkom Schurink & Griffiths (1990) reported a density of 10 000 *A. ater* m^{-2} in this zone at Marcus Island. Thus, it would appear that *A. ater* has decreased progressively in abundance at Marcus Island since the arrival of *M. galloprovincialis*. The poor competitive ability of *A. ater* (relative to *M. galloprovincialis*) is thought to

be a consequence of its relatively slow growth rate (Hockey & Van Erkom Schurink 1992, Van Erkom Schurink & Griffiths 1993).

The *Choromytilus* zone was originally characterised by substantial beds of this indigenous mussel. The arrival of *Mytilus galloprovincialis*, thus, did not replace the type of habitat present, but altered it from a single-layered mussel bed, typical of *Choromytilus meridionalis*, to a multi-layered mussel matrix associated with *M. galloprovincialis* (Griffiths et al. 1992). As a result, no change was recorded in total species richness. The fact that *M. galloprovincialis* reached its highest densities in this lower-most zone is unexpected, as the den-

sity of this species on South African shores is generally accepted to be maximal in the mid-intertidal zone (Van Erkom Schurink & Griffiths 1990).

In conclusion, the biological impacts of the *Mytilus galloprovincialis* invasion on intertidal invertebrate communities were linked to 3 key elements and were not evenly spread across the shore. Firstly, physical stress in the mid- to high-shore zones was ameliorated by the presence of *M. galloprovincialis*. Secondly, habitat complexity was increased in zones where *M. galloprovincialis* replaced bare rock or biota that provided a physically less complex secondary habitat. Thirdly, patchiness was reduced, at least in the *Granularis* zone.

Mytilus galloprovincialis is an aggressive invader, and, apart from exhibiting strong competitive interactions with other species along the South African coast (Branch & Steffani 2004, Robinson et al. 2005), it has also resulted in striking direct and indirect changes to the invertebrate community structure of rocky-shores.

Acknowledgements. We thank the National Research Foundation, Marine and Coastal Management, the Mellon Foundation, the Marine Biology Research Institute (University of Cape Town) and the Centre for Invasion Biology (University of Cape Town) for funding this project.

LITERATURE CITED

- Asmus RM, Asmus H (1991) Mussel beds: Limiting or promoting phytoplankton? *J Exp Mar Biol Ecol* 148:215–232
- Bachelet G, Simon-Bouhet B, Desclaux C, Gracia-Meunier P and 6 others (2004) Invasion of the eastern Bay of Biscay by the nassariid gastropod *Cyclope neritea*: origin and effects on resident fauna. *Mar Ecol Prog Ser* 276:147–159
- Berman J, Carlton JT (1991) Marine invasion processes: interactions between native and introduced marsh snails. *J Exp Mar Biol Ecol* 150:267–281
- Branch GM, Steffani CN (2004) Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *J Exp Mar Biol Ecol* 300:189–215
- Byers JE (2000) Competition between two estuarine snails: implications for invasions of exotic species. *Ecology* 81:1225–1239
- Byrnes J, Witman JD (2003) Impact assessment of an invasive flatworm, *Convoluta convoluta*, in the southern Gulf of Maine. *J Exp Mar Biol Ecol* 293:173–191
- Chao A (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43: 783–791
- Colwell RK (2005) EstimateS: statistical estimation of species richness and shared species from samples, Version 7.5. User's guide and application. Available at <http://purl.oclc.org/estimates>
- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Philos Trans R Soc Lond Ser B* 345:101–118
- Crooks JA, Khim HS (1999) Architectural vs biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *J Exp Mar Biol Ecol* 240:53–75
- Dumas JV, Witman JD (1993) Predation by herring gulls (*Larus argentatus* Coues) on two rocky intertidal crab species (*Carcinus maenas* (L.) & *Cancer irroratus* Say). *J Exp Mar Biol Ecol* 169:89–101
- Enderlein P, Wahl M (2004) Dominance of blue mussels versus consumer-mediated enhancement of benthic diversity. *J Sea Res* 51:145–155
- Gosselin LA, Chia F (1995) Distribution and dispersal of early juvenile snails: effectiveness of intertidal microhabitats as refuges and food sources. *Mar Ecol Prog Ser* 128: 213–223
- Gotelli N, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391
- Griffin NJ, Bolton JJ, Anderson RJ (1999) Distribution and population dynamics of *Porphyra* (Bangiales, Rhodophyta) in the southern Western Cape, South Africa. *J Appl Phycol* 11: 429–436
- Griffiths CL, Hockey PAR, Van Erkom Schurink C, Le Roux PJ (1992) Marine invasive aliens on South African shores: implications for community structure and trophic functioning. *S Afr J Mar Sci* 12:713–722
- Grosholz ED (2002) Ecological and evolutionary consequences of coastal invasions. *Trends Ecol Evol* 17:22–27
- Hammond W (2001) Factors affecting the infauna associated with mussel beds. MSc thesis, University of Cape Town
- Harris JM, Branch GM, Elliott BL, Currie B, Dye AH, McQuaid CD, Tomalin BJ, Velasquez C (1998) Spatial and temporal variability in recruitment of intertidal mussels around the coast of southern Africa. *S Afr J Zool* 33:1–11
- Hockey PAR, Van Erkom Schurink C (1992) The invasive biology of the mussel *Mytilus galloprovincialis* on the southern African coast. *Trans R Soc S Afr* 48:123–139
- Jackson LF, McGibbon S (1991) Human activities and factors affecting the distribution of macrobenthic fauna in Saldanha Bay. *S Afr J Aquat Sci* 17:89–102
- Le Pape O, Gueraud D, Desaunay Y (2004) Effect of an invasive mollusk, American slipper limpet *Crepidula fornicata*, on habitat suitability for juvenile common sole *Solea solea* in the Bay of Biscay. *Mar Ecol Prog Ser* 277:107–115
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- McQuaid CD, Phillips TE (2000) Limited wind-driven dispersal of intertidal mussel larvae: *in situ* evidence from the plankton and the spread of the invasive species *Mytilus galloprovincialis* in South Africa. *Mar Ecol Prog Ser* 201: 211–220
- Miyamoto Y, Noda T (2004) Effects of mussels on competitively inferior species: competitive exclusion to facilitation. *Mar Ecol Prog Ser* 276:293–298
- Occhipinti-Ambrogi A, Savini D (2003) Biological invasions as a component of global change in stressed marine ecosystems. *Mar Pollut Bull* 46:542–551
- Petraitis PS (1995) The role of growth in maintaining spatial dominance by mussels (*Mytilus edulis*). *Ecology* 76: 1337–1346
- Robinson TB, Griffiths CL, McQuaid CD, Rius M (2005) Marine alien species of South Africa — status and impacts. *Afr J Mar Sci* 27:297–306
- Ruiz GM, Fofonoff P, Hines AH, Grosholz ED (1999) Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnol Oceanogr* 44:950–972
- Ruiz Sebastián C, Steffani CN, Branch GM (2002) Homing and movement patterns of a South African limpet *Scutellastra argenvillei* in an area invaded by an alien mussel *Mytilus galloprovincialis*. *Mar Ecol Prog Ser* 243:111–122
- Seed R, Suchanek TH (1992) Population and community ecol-

- ogy of *Mytilus*. In: Gosling E (ed) *The mussel Mytilus: ecology, physiology, genetics and culture*. Elsevier, New York
- Steffani CN, Branch GM (2003a) Spatial comparisons of populations of an indigenous limpet *Scutellastra argenvillei* and an alien mussel *Mytilus galloprovincialis* along a gradient of wave energy. *Afr J Mar Sci* 25:195–212
- Steffani CN, Branch GM (2003b) Temporal changes in an interaction between an indigenous limpet *Scutellastra argenvillei* and an alien mussel *Mytilus galloprovincialis*: effects of wave exposure. *Afr J Mar Sci* 25:213–229
- Tokeshi M, Romero L (1995) Filling a gap: dynamics of space occupancy on a mussel dominated subtropical rocky shore. *Mar Ecol Prog Ser* 119:167–176
- Tsuchiya M, Nishihira M (1986) Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. *Mar Ecol Prog Ser* 31: 171–178
- Van Erkom Schurink C, Griffiths CL (1990) Marine mussels of southern Africa—their distribution patterns, standing stocks, exploitation and culture. *J Shellfish Res* 9:75–85
- Van Erkom Schurink C, Griffiths CL (1993) Factors affecting relative rates of growth in four South African mussel species. *Aquaculture* 109:257–273

Editorial responsibility: Steven Morgan (Contributing Editor), Bodega Bay, California, USA

*Submitted: May 3, 2006; Accepted: December 1, 2006
Proofs received from author(s): May 28, 2007*