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Tamara B. Robinson, Charles L. Griffiths, Christopher D. McQuaid, Marc Rius

Institutions: University of Cape Town, Rhodes University

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Marine alien species of South Africa — status and impacts

TB Robinson[1]*, CL Griffiths[1], CD McQuaid[2] and M Rius[2]

[1] Centre for Invasion Biology, Zoology Department and Marine Biology Research Institute, University of Cape Town, Private Bag, Rondebosch 7701, South Africa
[2] Department of Zoology and Entomology, Rhodes University, PO Box 94, Grahamstown 6140, South Africa
* Corresponding author, e-mail: trobins@botzoo.uct.ac.za

The current status of marine alien species along the South African coast is reviewed and the ecological and economic impacts of these invasions are discussed. In all, 10 confirmed extant alien and 22 cryptogenic species are recorded from the region. All 10 alien species support well-established populations and the majority of these remain restricted in distribution to sheltered bays, estuaries and harbours. Only one species, the Mediterranean mussel *Mytilus galloprovincialis*, has spread extensively along the coast and caused significant ecological impacts. These include the competitive displacement of indigenous species and a dramatic increase in intertidal mussel biomass. These changes have also increased available habitat for many infaunal species and resulted in enhanced food supply for intertidal predators. Considerable economic benefits have also resulted from this invasion because *M. galloprovincialis* forms the basis of the South African mussel culture industry.

Keywords: *Carcinus maenas*, *Crassostrea gigas*, marine alien species, *Mytilus galloprovincialis*

Introduction

Marine organisms have been accidentally and/or intentionally moved around the world's oceans since people first began navigating the seas (Carlton 1987, 1999), and the increase in volume and speed of transoceanic travel during the previous century (as well as the increased use of ballast water) has seen a concurrent rise in the rate of introductions (Carlton and Geller 1993, Carlton 1996, Ruiz *et al.* 1997, 2000, Cohen and Carlton 1998, Mack *et al.* 2000). This increase in prevalence of invasions of the nearshore environment in recent years has stimulated considerable research into both the mechanisms of anthropogenic dispersal of marine organisms, and the ecological and economic impacts of such invasions (Carlton 1987, Fraser and Gilliam 1992, Minchin 1996, Crooks and Khim 1999, Ruiz *et al.* 2000, Lewis *et al.* 2003). Most of this research has, however, focused on Australia, the United States of America and Europe (Orensanz *et al.* 2002), with comparatively little published data regarding marine invasions in other areas, particularly Africa.

Whereas several papers note the presence of, or examine aspects of the biology of, individual marine alien species in South Africa, we are aware of only three sources that attempt to list marine alien species from the region. Griffiths *et al.* (1992) list marine alien species known at that time, but several of these species no longer support extant populations, and several new invasions of other species have since occurred. Griffiths (2000) and Awad (2002) also provide lists of species, but these reports are not widely available and were merely based on the earlier list. Therefore, despite their recent date of publication, these reports contain dated information. None of the above sources deal with cryptogenic species in the region.

In this paper, the current status of marine alien species along the South African coast is reviewed, and for the first time cryptogenic species are considered in the region. The current distributions and known ecological and economic impacts of these invasions are discussed in an attempt to set a baseline against which future expansions and population changes can be measured.

Material and Methods

Existing records of marine alien species in South Africa were extracted from the literature (see below). In cases where the distribution and status of a species were last assessed over 10 years ago, a directed survey was undertaken to establish its present status. Three species fell within this category — the European shore-crab *Carcinus maenas*, the Mediterranean mussel *Mytilus galloprovincialis* and the Australian whelk *Bedeva paivae*. The methods employed during these surveys are described below. For detailed methods used in the assessment of the other species considered in this paper see the primary works listed in Tables 1, 2 and 3.

C. maenas

Both intertidal and subtidal habitats were sampled for *C. maenas*. All intertidal sites where *C. maenas* was recorded by le Roux *et al.* (1990) were searched by four researchers for 30 minutes each. Searches were also undertaken at several sites beyond the known range of *C. maenas* that offered an appropriate habitat for this species. Subtidal areas along the open coast were surveyed by divers, whereas baited traps (18.8l volume) made of 1.5-cm mesh were used to detect crabs within harbours. Because the sibling species *C. aestuarii* was recorded in Table Bay Harbour by Geller *et al.* (1997), three defining morphometric characteristics — carapace width-to-length ratio, male pleo-pod orientation and the shape of the frontal margin between the eyes (Behrens Yamada and Hauck 2001) — were used in combination to distinguish between the two species in the field. Where *C. maenas* was found within a harbour area, the size of the population was estimated using the mark-recapture method. Marking was continued until the percentage of crabs recaptured was >10%.

M. galloprovincialis

To investigate the current status of this mussel, the South African coast was divided into 100-km sampling areas extending east and west of Cape Point (Figure 1). Within each of the areas, three rocky-shore sites were randomly selected and sampled. At each site, the mussel bed was divided into three vertical zones: low-mussel zone (i.e. approx. Mean Low Water Spring – Mean Low Water Neap); mid-mussel zone (i.e. approx. Mean Low Water Neap – Mean High Water Neap); high-mussel zone (i.e. approx. Mean High Water Neap – lower balanoid zone). The width of each of these zones was recorded and six replicate measures of mussel percentage cover were taken in each zone, using randomly placed 0.5-m^2 quadrat. In addition, all mussels were removed from six 0.01-m^2 quadrats (two in each mussel zone), from areas with 100% mussel cover. All *M. galloprovincialis* in the latter samples were separated out and weighed. The mean percentage cover of *M. galloprovincialis* was combined with measures of the mean biomass per 0.01m^2 to obtain a measure of biomass m^{-2} of shore in each of the mussel zones. The Coastal Sensitivity Atlas of southern Africa (Jackson and Lipschitz 1984) was then used to measure the total length of rocky shore in each 100-km sampling area. The mean biomass per m^2 of shore in each mussel zone was multiplied by the area covered by that zone, thus allowing the calculation of total biomass supported in each mussel zone in each sampling area. These area totals were summed, giving an estimate of total *M. galloprovincialis* biomass supported on the West and South coasts respectively.

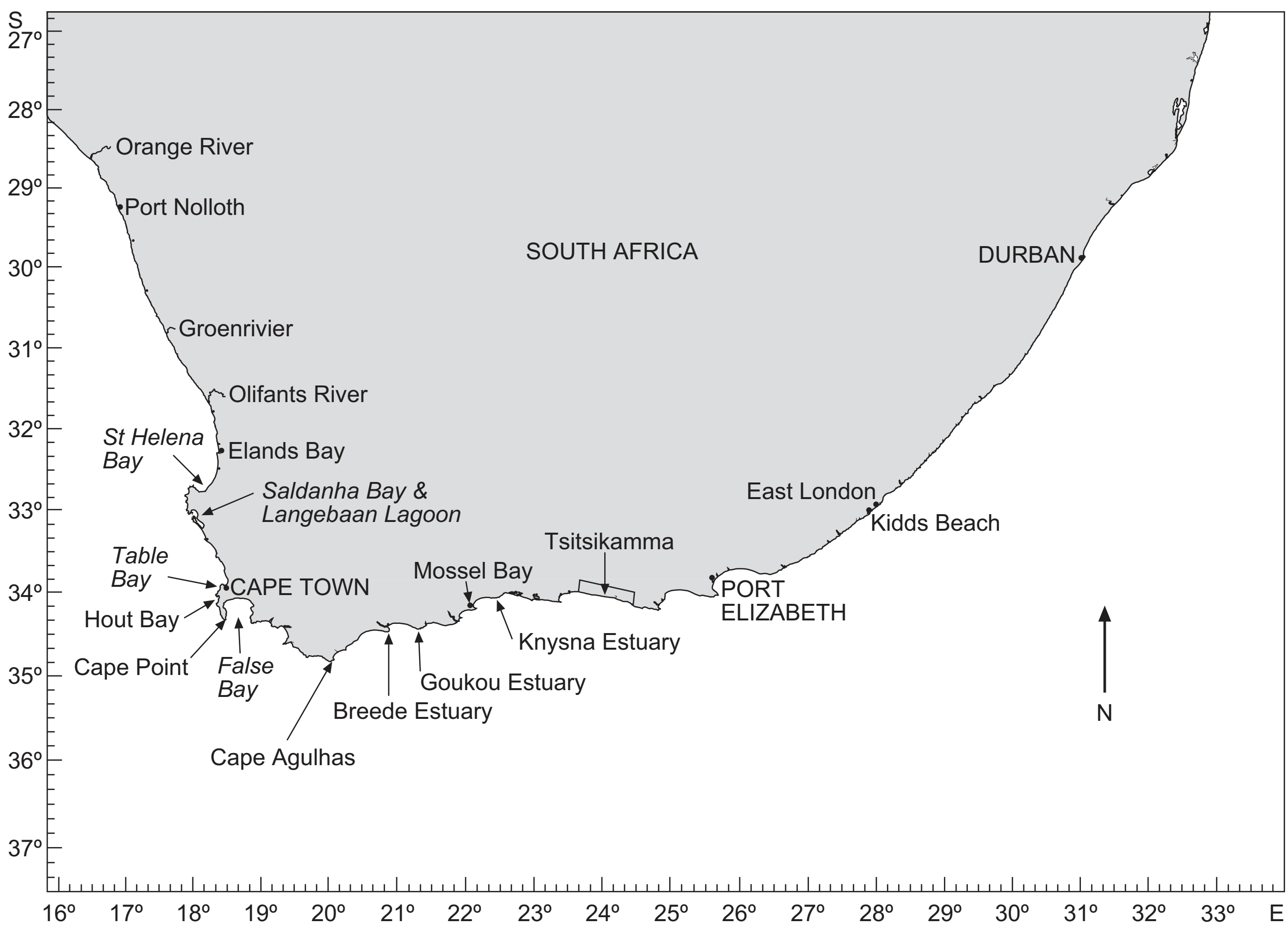

Figure 1: Map of the South African coast showing place names mentioned in the text

B. paivae

This whelk was first recorded in South Africa in 1968, when a thriving colony in the Buffalo River mouth (the location of East London Harbour) was first observed (Kilburn and Rippey 1982). In order to assess the current status of *B. paivae*, the coast surrounding the river mouth was divided into 2-km areas (spanning a total of 10km either side of the Buffalo River), in which three sampling sites were randomly chosen. At each site, a 0.5-m^2 quadrat was used to run three transects from MLWS to MHWS. The number of individuals in each quadrat was recorded.

Cryptogenic species

Previous considerations of marine alien species in South Africa have paid little attention to the conceptual category of cryptogenic species. In this study, species have been allocated to this grouping if all of the following criteria were met:

i the species has a substantiated presence in South African waters;
ii the species has a well-established global range or a range crossing known biogeographic boundaries;
iii the species exhibits life-history characteristics that facilitate dispersal via human mediated vectors; and
iv there are, or were, such vectors in South African waters.

Results

Known introductions

A list of species known to be introduced to the region and which presently support extant populations is given in Table 1. Further information about each species is provided below.

Ascidians

Ciona intestinalis is the earliest known accidental introduction to South African shores (Millar 1955). At present, it occurs in harbours along the entire coast (Monniot *et al.* 2001), where it is a dominant fouling organism. This distribution pattern suggests that shipping has been the dispersal vector for this species. Despite *C. intestinalis* being well documented and common, the ecological impacts of this invasion have not been quantified. Economic impacts have, however, been reported by mussel farmers who spend up to R100 000 per annum in Saldanha Bay in an effort to maintain their mussel ropes free of this ascidian, which grows mainly towards the lower sections of mussel ropes, smothering mussels and reducing growth and survival (Heasman 1996, T Tonin, Mariculture Development Services, pers. comm.).

A review of South African ascidians by Monniot *et al.* (2001) documented two introduced species, *Clavelina lapadiformis* and *Diplosoma listerianum*. *C. lapadiformis* appears to be limited to Knysna Estuary and Port Elizabeth Harbour, and it seems likely that the two populations represent a spread of the species rather than two separate invasions. Such dispersal may have been aided by mariculture operations that translocate oysters between these localities. In contrast, *D. listerianum* is widely distributed in all harbours between Saldanha Bay and Port Elizabeth. This may indicate numerous invasions or intraregional transport between harbours. The ecological

Table 1: Invasive species along the South African coast

Species name	Common name	First record	Present distribution	Known impacts	Source
Ciona intestinalis	Ascidian	1955	Harbours along the whole South African coast	Significant economic impact — negatively affects mussel culture industry	Millar (1955), Monniot *et al*. (2001)
Clavelina lapadiformis	Ascidian	2001	Knysna Estuary and Port Elizabeth Harbour		Monniot *et al.* (2001)
Diplosoma listerianum	Ascidian	2001	All harbours from Saldanha Bay to Port Elizabeth		Monniot *et al.* (2001)
Metridium senile	Anemone	1995	Cape Town Harbour		Griffiths *et al.* (1996)
Sagartia ornata	Anemone	2002	Langebaan Lagoon		Acuna *et al.* (2004), Robinson *et al.* (2004)
Carcinus maenas	Crab	1983	West Coast between Table Bay Harbour and Hout Bay Harbour	Potential ecological and economic impacts	le Roux *et al*. (1990), Griffiths *et al*. (1992)
Littorina saxatilis	Periwinkle	1974	Langebaan Lagoon and Knysna Lagoon		Day (1974), Hughes (1979)
Mytilus galloprovincialis	Mussel	1979	Entire West Coast, South Coast up to 20km west of East London	Significant ecological and economic impacts	Hockey and van Erkom Schurink (1992), Griffiths *et al*. (1992), Branch and Steffani (2004)
Crassostrea gigas	Oyster	2001	Breede, Goukou and Knysna estuaries		Robinson *et al.* (in press)
Schimmelmannia elegans	Red algae	2002	Cape Town Harbour		de Clerck *et al.* (2002)

and economic impacts of the presence of these ascidians in South African waters are presently unknown, but because both are relatively small encrusting species and appear to occur at relatively low densities, it is unlikely that they have significant ecological effects.

In 1995, the anemone *Metridium senile* was reported from Table Bay Harbour, where it occurred in densities of up to about 10 individuals m^{-2} (Griffiths *et al.* 1996). The ecological impacts of the invasion are at present unmeasured, but are unlikely to be significant because this anemone remains confined to the harbour.

Sagartia ornata is widely distributed throughout western Europe, the United Kingdom and the Mediterranean (Manuel 1981), and was first recorded in South Africa in 2002 (Acuna *et al*. 2004). At present, this species is reported only from the intertidal zone within Langebaan Lagoon, where it occurs in densities of up to 426 ± 81 (SD) individuals m^{-2} in *Spartina. maritima* beds and on rocks covered by sand (Robinson *et al.* 2004). This is in contrast to its habitat along British coasts, where it occurs in crevices on rocky shores and on kelp holdfasts (Gibson *et al.* 2001). There is therefore the potential for this species to spread extensively along the South African coast, which offers cold water and vast kelp beds typical of its home range. The ecological influences of this invasion are likely to be restricted to local effects on small invertebrate prey.

Decapods

South African populations of the European shore-crab *Carcinus maenas* were first detected in Table Bay Harbour in 1983 (Joska and Branch 1986). It has been proposed that these crabs reached the port via fouling of international oil exploration vessels, which have docked within the harbour since 1969 (le Roux *et al.* 1990). By 1990, this species had been recorded at seven intertidal sites along the west coast of South Africa, six in the vicinity of Cape Town and the other in Saldanha Bay (le Roux *et al.* 1990, Figure 1). The present study recorded no intertidal range extension, but the species was recorded in Hout Bay Harbour for the first time. This lack of intertidal range expansion by *C. maenas* is probably a reflection of the wave-exposed nature of South African shores, and the crab's apparent inability to inhabit wave-exposed habitats (Crothers 1968). Mark-recapture experiments suggested substantial subtidal populations of 133 568 individuals (95% confidence limits = 97 694–166 862) and 9 180 individuals (95% confidence limits = 5 870– 12 003) in Table Bay Harbour and Hout Bay Harbour respectively. Because small rock lobster vessels often move between these harbours, it is highly likely that adult crabs from Table Bay Harbour were inadvertently transported to Hout Bay by these boats. Despite extensive subtidal sampling within Saldanha Bay (baited traps, grabs and dredges), no subtidal specimens of this species have ever been recorded (Robinson *et al.* 2004). Given the reputation of *C. maenas* as a highly successful invasive species, the lack of a well-established population within Saldanha Bay 12 years after its initial discovery there (le Roux *et al.* 1990) is curious. An extensive invasion of this area would be potentially disastrous for the local biota, which is likely to be highly vulnerable to predation by *C. maenas* (le Roux *et al.* 1990).

Gastropods

Littorina saxatilis, a small intertidal periwinkle, was first recorded in South Africa in 1974 (Day 1974). The only known populations occur in two discrete locations: Langebaan Lagoon and Knysna Estuary (Hughes 1979, Figure 1), and it has been proposed that these introductions may have resulted from early European shipping (Knight *et al.* 1987, McQuaid 1996). Despite occurring in crevices on rocky shores within its home range (Gibson *et al.* 2001), along the South African coast *L. saxatilis* is restricted to sheltered salt marshes and lagoons, where it is found on the stems of the cord grass *S. marimitma*. In 2002, densities of up to 433 ± 123 (SD) individuals m^{-2} were recorded in Langebaan Lagoon (Robinson *et al.* 2004). The present status of the Knysna population is unknown. Despite its 20-year presence along the South African coast, this species has remained geographically restricted. No ecological effects of the invasion are known, although these small gastropods could form an abundant food source for wading birds and crabs (Robinson *et al.* 2004).

Bivalves

The most significant invasion along the South African coast is that of the Mediterranean mussel *M. galloprovincialis*. Although first noted in Saldanha Bay in 1979 (Branch and Steffani 2004), genetic confirmation of this species identification was only published in 1984 (Grant *et al.* 1984), by which time the species was already the dominant intertidal mussel along sections of the west coast. *M. galloprovincialis* first appeared on the south coast of the country in 1989 (McQuaid and Phillips 2000) as an isolated population in Port Elizabeth Harbour, where it was introduced for mariculture. Subsequently, this population was removed and the small populations it had spawned died out. Natural spread from the West Coast began about the same time (Phillips 1994), and during the present survey it was recorded along the entire west coast of South Africa, with populations extending eastwards around Cape Point and intermittently as far as Kidds Beach, i.e. 20km west of East London, (Figure 1). This species presently occupies a total of 2 050km of the South African coast (Figure 2), with a total standing stock of 35 403.7 tons (± 9 099.6 tons SD), 88% of which is on the West Coast (31 054.5 tons ± 6 730.0 tons SD).

The ecological effects of the *M. galloprovincialis* invasion are wide-ranging and have been most profound on the West Coast. In comparison with the indigenous mussels *Choromytilus meridionalis* and *Aulacomya ater*, *M. galloprovincialis* exhibits a heightened growth rate, fecundity and tolerance to desiccation (van Erkom Schurink and Griffiths 1990, 1991, 1992, Hockey and van Erkom Schurink 1992). Consequently, there has been an upshore movement in the centre of distribution of intertidal mussel beds, because this species has dominated local mussels along the West Coast (Hockey and van Erkom Schurink 1992). It is only in sand-inundated areas that *C. meridionalis* remains dominant. Coupled with the fact that *M. galloprovincialis* beds consist of multiple layers and support a higher biomass per m^2 than the single-layered beds of indigenous mussels, the increased vertical range of *M. galloprovincialis* beds has led

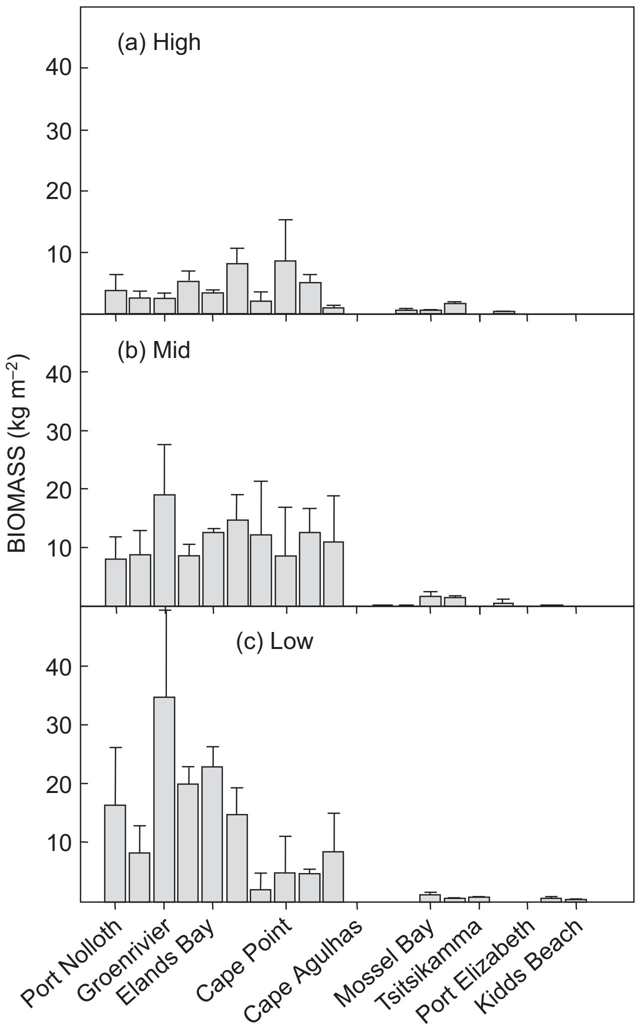

Figure 2: Mean (± SD) biomass (kg m^{-2}) supported by *M. galloprovincialis* in the (a) high, (b) mid and (c) low mussel zones in each 100-km area around the South African coast

to a massive increase in mussel biomass along the South African west coast (Griffiths *et al.* 1992), and a simultaneous rise in density of associated infauna (Hammond and Griffiths 2004). This effect may be related not only to species, but also to inshore productivity: in contrast to the situation on the West Coast, *M. galloprovincialis* on the more oligotrophic South Coast forms mono-layered beds (Phillips 1994). *M. galloprovincialis* is immune to the trematode parasites that are common in indigenous mussels and that reduce both individual growth rates and population reproductive output by castrating females (Calvo-Ugarteburu and McQuaid 1998a, 1998b). On the South Coast, this mussel has not yet completely replaced the indigenous mussel *Perna perna*. Instead, the two exhibit spatial segregation, with *P. perna* dominating the low shore, *M. galloprovincialis* the high shore and an overlap zone between the two (CDM unpublished data).

The most important predator of *M. galloprovincialis* along the West Coast is the whelk *Nucella cingulata* (Branch and Steffani 2004). However, owing to the extremely high rate of recruitment of this mussel (up to 20 000 recruits m^{-2}, Harris *et al.* 1998) and the relatively low numbers of *N. cingulata*, whelk predation is unable to control South African *M. galloprovincialis* populations (Branch and Steffani 2004). These high rates of recruitment have also allowed *M. galloprovincialis* to dominate primary rock surfaces at the expense of various competitively inferior limpet species. By excluding *Scutellastra granularis* from open rock, *M. galloprovincialis* has reduced the number of individuals occurring directly on rock, but at the same time has increased the overall density of this species by providing a favourable settlement and recruitment substratum for juveniles (Hockey and van Erkom Schurink 1992). Associated with this increase in density, *S. granularis* has shown a decrease in mean size, as the maximum size of limpets within the mussel beds is limited by the size of the host mussels (Griffiths *et al.* 1992). A second limpet species, *Scutellastra argenvillei*, has also been significantly affected by the invasion of *M. galloprovincialis*, although the strength of the interaction between these two species is mediated by wave action (Steffani and Branch 2003a, 2003b). On exposed shores, *M. galloprovincialis* displaces *S. argenvillei* and dominates the primary substratum, whereas on semi-exposed shores the mussel becomes relatively scarce and *S. argenvillei* maintains dominance of open rock space (Steffani and Branch 2003a, 2003b). Additional impacts on *S. argenvillei* include reductions in reproductive output and mean size of those individuals which now occur on mussels (Griffiths *et al.* 1992, Branch and Steffani 2004).

M. galloprovincialis has also affected some sandy shores, though to a lesser degree. In 1992, *M. galloprovincialis* invaded the centre banks of Langebaan Lagoon, an important marine conservation area along the West Coast. There it considerably altered the natural community composition by inducing a replacement of sandbank communities by those more typical of rocky shores (Robinson and Griffiths 2002). Interestingly, after supporting a biomass of 7.7 tons in 1998 (Robinson *et al.* 2004), the beds present on the centre banks decreased in size by 88% by 2001 (Hanekom and Nel 2002), and by 2003 only empty shells remained (TBR and CLG, unpublished data). The reason for this decline remains unclear.

Despite the many negative ecological impacts resulting from this invasion, one species, the near-threatened African black oystercatcher *Haematopus moquini*, has benefited from the presence of the mussel. This endemic intertidal forager has shown a shift in diet since the arrival of *M. galloprovincialis*, and now feeds predominantly on the foreign mussel (Hockey and van Erkom Schurink 1992). Concurrent with this change in diet has come a dramatic increase in breeding success of *H. moquini* as a result of increased food supply (Hockey and van Erkom Schurink 1992). From an economic perspective, the invasion of *M. galloprovincialis* has had considerably positive impacts, because the entire mussel culture industry in South Africa is based on this alien species.

In line with global trends, the South African oyster industry is based on the Japanese oyster *Crassostrea gigas*, which was first introduced into Knysna Estuary in the early 1950s (de Moor and Bruton 1988). On account of the difficulties in inducing predictable spawning and subsequent settlement under South African conditions, the industry is fuelled by spat imported from Chile, the United Kingdom and France. Because *C. gigas* has appeared unable to complete its life cycle under local environmental conditions, this species was not previously considered likely to become invasive along South African shores (Griffiths *et al*. 1992). However, in 2001, oysters — unlike any indigenous species — were recorded in estuaries along the South Coast. Robinson *et al.* (in press) subsequently confirmed the identification of these oysters as *C. gigas*, and documented populations of 184 206 ± 21 058.9 (SE), 876 ± 604.2 (SE) and 1 228 ± 841.8 (SE) individuals in the Breede, Goukou and Knysna estuaries respectively. To date, however, this species has not been recorded on the open coast, and the invasion appears to be restricted to estuarine environments. At present, the rate of spread and ecological impacts of this invasion are undocumented. Similar invasions elsewhere have resulted in a variety of serious impacts, including the simultaneous introduction of associated fauna (Kaiser *et al.* 1998), the introduction of disease organisms (Ford 1992), genetic pollution of local oyster species (Gaffney and Allen 1992, 1993) and the reduction of indigenous oyster populations to threatened levels (Mann *et al.* 1991).

Algae

Only a single alien algal species, *Schimmelmannia elegans*, is known from South Africa. First recorded in the 'Kelp Tank' of the Two Oceans Aquarium in Cape Twn in 2002 (de Clerck *et al*. 2002), this species was also found growing below a water outlet where aquarium water enters Cape Town Harbour. Previously only known from the islands of Tristan da Cunha and Nightingale (de Clerck *et al.* 2002), this alga has no history as an invasive species. Its status as alien in South Africa is, however, well established, because it has not been detected in extensive surveys of the West Coast conducted by Stegenga *et al.* (1997) and Bolton (1999). Owing to its very limited distribution, it is unlikely that *S. elegans* presently exerts any significant ecological or economic impacts.

Phytoplankton entering Saldanha Bay via shipping ballast water was considered by Marangoni *et al.* (2001). However, despite listing 173 taxa, this paper offers no classification of species as alien or indigenous.

Cryptogenic species

Applying the selected criteria to South African marine fauna and flora lists resulted in 22 species from the region being classified as cryptogenic (Table 2). It should be stated, however, that such lists are dependant on the current taxonomic knowledge of the different groups. This is strongly reflected in the dominance of Table 2 by amphipods, one of the better studied marine taxa in South Africa. It is therefore predicted that, as the taxonomic knowledge base of South African marine organisms improves, many more species will be added to this list.

The ascidian *B. leachi* has previously been categorised as a South African cryptogenic (Griffiths *et al.* 2004), but has been excluded from the present list. This is owing to its absence from collections made by Monniot *et al.* (2001), who concluded that the original identification of this species in South Africa was in fact a misidentification of the congeneric species *Botrylloides gregalis*.

The amphipod *Maera grossimana* is a common fouling species and is listed as cryptogenic in many regions of the world (Orensanz *et al.* 2002), but the species has not been added to the South African list despite species records for the region. Again, this relates to the probably incorrect identification of this species in southern Africa (Karaman and Ruffo 1971). Should the identification of this species be confirmed it would most certainly be added to future lists of cryptogenics in the region.

Species to be removed from lists of alien species

Previous papers dealing with alien species in southern Africa have listed various dubious records of non-indigenous species (Griffiths *et al.* 1992, Griffiths 2000, de Clerck *et al.* 2002, Awad 2002). These unsubstantiated and one-off records are listed in Table 3. These species no longer support extant populations, or were originally incorrectly listed as alien. In order to keep the records of South African marine alien species current, such species need to be removed from all future lists.

Decapods

The cryptic green crab *Carcinus aestuarii* was first detected in Table Bay Harbour by Geller *et al.* (1997). Despite this species constituting 7.7% of a random sample of 52 *Carcinus* individuals considered in that study, no *C. aestuarii* were recorded among 4 600 individuals captured in the harbour during the present survey for *C. maenas*. This species was also absent from the collection of 500 crabs made in Hout Bay Harbour, and was not recorded during intertidal searches along the Cape Peninsula.

The bristle crab *Pilumnus hirsutus* was first noted by Branch and Branch (1981) as a species of probable alien origin. The indigenous status of this species appeared suspect owing to its restricted distribution within Langebaan Lagoon on the temperate West Coast, which contrasts with the species native Indo-West Pacific range. However, Compton (2001) confirmed the native status of this species when its fossils were recorded in Holocene deposits in the Lagoon.

Gastropods

The present survey for the whelk *B. paivae* revealed no individuals within 10km of the river mouth. This species is therefore taken to be extinct along the South African coast.

The red abalone *Haliotis rufescenens* was introduced into Saldanha Bay in 1988 by local mariculture operations (Griffiths 2000). All individuals died, however, before being released into the open-water culture system (Griffiths 2000).

Bivalves

The commercially cultured European flat oyster *Ostrea edulis* and the Portuguese oyster *Crassostrea angulata* were introduced into Knysna Estuary in the late 1940s (Korringa 1956), but shortly thereafter both populations became extinct, and neither species has been recorded subsequently.

In 1988 the Manila clam *Tapes philippinarum* was imported into Saldanha Bay as a mariculture species. However, the

Table 2: Cryptogenic species along the South African coast

Species name	Common grouping	South African distribution	Global distribution	Source
Bugula neritina	Bryozoa	Entire coast	Cosmopolitan	Day (1974), Branch *et al.* (1994), Ruiz *et al.* (2000)
Membranipora membranacea	Bryozoa	Saldanha Bay to Durban	Cosmopolitan	Branch *et al.* (1994), Ruiz *et al.* (2000), Gibson *et al.* (2001)
Cliona spp	Sponge	Entire coast	Cosmopolitan	Day (1974)
Obelia dichotoma	Hydroid	Entire coast	Cosmopolitan	Branch *et al.* (1994)
Obelia geniculata	Hydroid	Entire coast	Cosmopolitan	Branch *et al.* (1994)
Balanus amphitrite	Barnacle	Entire coast except north of St Helena Bay	Cosmopolitan	Branch *et al.* (1994), Eno *et al.* (1997), Orensanz *et al.* (2002)
Caprella equilibra	Amphipod	Entire coast	Cosmopolitan	Griffiths (1976)
Caprella penantis	Amphipod	Entire coast	Circumtropical	Griffiths (1976)
Cerapus tubularis	Amphipod	Entire coast, except north of Saldanha Bay	Circumtropical	Griffiths (1976)
Chelura terebrans	Amphipod	Saldanha Bay to Port Elizabeth	Cosmopolitan	Bousfield (1973), Griffiths (1976)
Corophium acherusicum	Amphipod	Entire coast, except north of Durban	Circumtropical	Bousfield (1973), Griffiths (1976)
Cymadusa filosa	Amphipod	Entire coast	Circumtropical	Griffiths (1976)
Ericthonius brasiliensis	Amphipod	Entire coast, except north of the Olifants River Mouth	Circumtropical	Bousfield (1973), Griffiths (1976)
Ischyrocerus anguipes	Amphipod	Entire coast	Circumtropical	Bousfield (1973), Griffiths (1976)
Jassa marmorata	Amphipod	KwaZulu-Natal coast, Table Bay Harbour	Cosmopolitan	Griffiths (1976), Conlan (1990)
Jassa morinoi	Amphipod	KwaZulu-Natal coast, Port Elizabeth, False Bay	Cosmopolitan	Conlan (1990)
Jassa slatteryi	Amphipod	Langebaan Lagoon, False Bay, Knysna Estuary	Cosmopolitan	Conlan (1990)
Limnoria quadripunctata	Isopod	Table Bay to Port Elizabeth	Britain, Holland, California, Chile, St Paul and Amsterdam islands	Kensley (1978)
Sphaeroma terebrans	Isopod	Knysna Estuary eastwards	Cosmopolitan	Kensley (1978)
Bankia carinata	Shipworm	East of Goukou Estuary	Indo-Pacific, Europe, western Atlantic	Kilburn and Rippey (1982)
Marthasterias glacialis	Starfish	St Helena Bay to Port Elizabeth	Britain, Mediterranean, Cape Verde Islands	Branch *et al.* (1994), Gibson *et al.* (2001)
Antithamnionella spirographidis	Algae	Langebaan Lagoon	Warm, temperate European coasts, Mediterranean, northern Pacific, southern Australia	Stegenga *et al*. (1997), de Clerck *et al.* (2002)
Antithamnionella ternifolia	Algae	West Coast	Warm, temperate European coasts, Mediterranean, northern Pacific, southern Australia	de Clerck *et al.* (2002)

indigenous eagleray *Myliobatis aquilla* consumed all individuals shortly after they were released from quarantine. This species has not been reintroduced, and no naturalised population was ever established.

Discussion

In all, 10 alien marine species are well established along the South African coast (Table 1). Whereas the majority of these remain restricted to harbours (e.g. *C. intestinalis*, *C. maenas, M. senile*) and sheltered lagoons or estuaries (e.g. *C. gigas, L. saxatilis, S. ornata*), a single species, *M. galloprovincialis,* has spread extensively and now covers 2 050km of South African shores.

The small number of alien species recorded along the South African coast represents a considerably lower prevalence of non-indigenous marine species than has been reported for other regions of the world. For example, in an analysis of exotic marine organisms off North America, Ruiz *et al.* (2000) recorded 298 species. On a smaller scale, 30, 51, 99, 150 and 180 marine alien species have been reported from Hawaii, Great Britain, San Francisco Bay (USA), Chesapeake Bay (USA) and Port Phillip Bay (Australia) respectively (Eno *et al.* 1997, Cohen and Carlton 1998, Ruiz *et al.* 1999, Defelice *et al.* 2001, Hewitt *et al.* 2004). The relatively low number of alien species in southern Africa should, however, be treated with reserve, because the true pervasiveness of invasions in the region may be obscured by several external factors. First, large areas of the South African coast remain unexplored with regards to non-indigenous species, with the Indian Ocean coast in particular having received little consideration. Second, the taxonomy

Table 3: Species to be removed from lists of South African marine alien species

Species name	Common name	First record	Reason for removal	Source
Polydora spp.	Polychaete	1988	Unsubstantiated record	de Moor and Bruton (1988)
Carcinus aestuarii	Crab	1997	Population extinct	Geller *et al*. (1997)
Pilumnus hirsutus	Crab	1981	Confirmation of native status	Compton (2001)
Bedeva paivae	Whelk	1968	Population extinct	Kilburn and Rippey (1982), Griffiths *et al*. (1992)
Thais haemastoma	Whelk	1975	Single record	Kilburn and Rippey (1982)
Latiaxis mawae	Whelk	1985	Only shell found	Griffiths (2000)
Harpa ventricosa	Whelk	1985	Only shell found	Griffiths (2000)
Urosalpinx spp.	Whelk	1988	Unsubstantiated record	de Moor and Bruton (1988)
Haliotis rufescenens	Abalone	1988	No naturalised populations and no longer cultured	Griffiths (2000)
Ostrea edulis	Oyster	Late 1940s	Population extinct	Korringa (1956)
Crassostrea angulata	Oyster	Late 1940s	Population extinct	Korringa (1956)
Tapes philippinarum	Clam	1988	No naturalised populations and no longer cultured	Griffiths (2000)
Bonnemaisonia hamifera	Algae	1938	Single record	de Clerck *et al.* (2001)

of marine groups is poorly developed within South Africa (Griffiths 1999, Linder and Griffiths 1999). At present, only four full-time professional marine invertebrate taxonomists are working within South Africa, and research is restricted to seaweeds and the phyla Porifera and Mollusca. It is highly likely that the number of alien species recorded along the South African coast will increase as more surveys are undertaken and additional taxa are investigated.

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