Biol Invasions
DOI 10.1007/s10530-011-0016-9

ORIGINAL PAPER

Revealing the scale of marine bioinvasions in developing regions: a South African re-assessment

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Received: 16 August 2010 / Accepted: 30 April 2011

Abstract As recently as 2009 the number of introductions recorded for South Africa comprised 22 marine and estuarine species. This review aims to reassess the diversity and scale of introduced marine and estuarine species in the region. Accurate taxonomic and systematic work, broad review of historical records and new sampling surveys across selected marine habitats conducted by a team of local and international experts has effectively revealed the presence of previously misidentified, overlooked, or new introductions. A total of 86 introduced and 39 cryptogenic species are recognized, increasing known numbers four and twofold respectively within 1 year, although the current assessment is far from fully comprehensive. Additional species were revealed within the historic literature (76%), from surveys conducted post-2005 (11%) and following taxonomic resolution (13%). Temporal analyses confirmed discovery rates were increasing over time. Ship fouling and ballast water were the dominant vector pathways, accounting for 48 and 38% respectively. Spatial analyses revealed patterns of bioinvasion to be significantly higher on the west coast compared to the other coastal regions. Overall, 53% of introductions were concentrated within harbour areas with only 4 open-coast invaders detected at present. Introduced species found in the cool and warm-temperate provinces of the west and south coast mainly originated from the northern hemisphere (65%). In contrast, introductions located in the sub-tropical and tropical provinces of the east coast mainly originated from the southern hemisphere (18%), with the remaining 17% of introduced species being of unknown origin. The research approach described has proven pivotal, contributing massively toward revealing the true scale and patterns of bioinvasion for a developing region within a relatively short period of time.

Keywords Ballast · Bioinvasions · Cryptogenic · Fouling · Vectors · South Africa

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Introduction

The frequency of human-mediated marine introductions is increasing globally and their role and

Published online: 15 May 2011

importance as agents of global change is becoming ever more apparent (Ruiz et al. 1997; Sala et al. 2000; Wonham and Carlton 2005). As a result, considerable resources have been directed into research on this topic. However, a few regions, such as Europe, North America, New Zealand, and Australia dominate the literature in terms of reporting the presence and impacts of marine introduced species at a variety of spatial scales (Byers 2009; Carlton 1996; Cranfield et al. 1998; Leppakoski and Olenin 2000; Levings et al. 2002; Hewitt et al. 2004; Ruiz et al. 1997, 1999, 2000; Sala et al. 2000). In part this domination is due to the greater availability of financial, scientific and in particular taxonomic resources in these regions.

Obtaining a realistic 'fix' on the number of marine introductions within a region can be a challenging task (Carlton 2009). However, it has been attempted across a number of regions (Carlton 1987; Castilla and Neill 2009; Cohen and Carlton 1998; DeFelice et al. 2001; Ferreira et al. 2009; Galil and Zenetos 2002; Gollasch and Nehring 2006; Hewitt et al. 2004; Leppakoski et al. 2009; Orensanz et al. 2002; Ruiz et al. 2000; Seo and Lee 2009). Ruiz et al. (2000) recorded 298 marine and estuarine introduced species in North America, a comparatively well-known region. However, the authors suggest that the real number of introductions could easily be 600–900 species and thus the reported figure should not be interpreted as accurate and final. Coles et al. (1999) reported 101 introduced species from Pearl Harbour on Oahu Island, Hawaii. Ten years later, Carlton and Eldredge (2009) report nearly twice that number for the same region, based almost entirely on retrospective historical analysis and greater taxonomic resolution, rather than on new introductions that had occurred post 1999. Thus even in well-studied areas, the diversity of introduced species is rarely adequately resolved.

The situation is of even greater concern in regions of the world where the state of knowledge of the marine biota remains relatively poor, or where there has been less historical interest in invasions (Nuñez and Pauchard 2010), as a result of several confounding reasons. These include (i) systematic and taxonomic challenges, (ii) access issues in order to undertake new sampling surveys across a variety of marine habitats and (iii) availability of historic records (Carlton 1996, 2003, 2009; Wonham and Carlton 2005). Denmark, Japan, Uruguay/Argentina, the Azores and Chile have recently reported totals of 18, 25, 31, 33 and 51 marine introductions respectively (Castilla and Neill 2009; Hewitt et al. 2004; Jensen and Knudsen 2005; Orensanz et al. 2002; Otani 2004). Based on the aforementioned reasons, Carlton (2009) suggests that the actual number of introductions in these regions is probably 5–10 times the number reported. In addition, many regions fail to report cryptogenic species (Carlton 1996, 2009). Cryptogenics represent 'red lights' as they emphasize the *potential* depth and breadth of a region's cryptic introduction history. It is critical to call attention to the many species that have been assumed to be native without compelling evidence otherwise substantial underestimates will be made when determining the potential scale of regional and global invasions (Carlton 1996, 2009).

There are regions where the number of reported bioinvasions is sufficiently high to facilitate a spatio-temporal bioinvasive patterns analysis. To date, these have been conducted at both local and pan-regional scales for marine species (Carlton 2003; Castilla and Neill 2009; Fofonoff et al. 2009; Hayden et al. 2009; Rilov and Galil 2009; Sliwa et al. 2009; Wonham and Carlton 2005). Vector types, dispersal pathways, source regions, taxonomic composition, spatial distribution, receiving habitat types, measured impacts and rates of successful introduction have all been investigated (Carlton 2003, 2009; Hewitt et al. 2009; Miller and Ruiz 2009; Minchin et al. 2009; Ruiz and Hewitt 2002; Wilson et al. 2009; Wonham and Carlton 2005). These analyses are an important step toward understanding the patterns and processes behind successful introductions (Byers 2009; Carlton 1996; Lonhart 2009; Occhipinti-Ambrogi 2007; Olyarnik et al. 2009; Ruiz and Hewitt 2002). Moreover, cross-regional comparisons will facilitate bioinvasion predictions on a global scale and the formulation of effective management policies (Bax et al. 2004; Carlton 1996, 2009; Kolar and Lodge 2001). However, it is recognized that sound interpretation is dependent on the quality of baseline knowledge available and that, in the interim, assessing spatio-temporal patterns using the uneven data available needs to be undertaken with caution (Ruiz and Hewitt 2002).

In South Africa, there has been limited long-term historical focus on bioinvasions within the marine environment. Although there have been several ecological studies on conspicuous invasions, such as

the western European crab *Carcinus maenas* (Hampton and Griffiths 2007; Le Roux et al. 1990) and the Mediterranean mussel *Mytilus galloprovincialis* (Bownes and McQuaid 2009; Branch and Steffani 2004; Branch et al. 2010; Rius and McQuaid 2009), far less work has been invested in resolving the potential scale of invasions that may have occurred over the past several centuries. Several progressive publications over the past two decades have offered estimates of numbers for both introduced and cryptogenic species (Griffiths 2000; Griffiths et al. 1992; Robinson et al. 2005) the most recent giving estimated numbers of 22 and 18 species respectively (Griffiths et al. 2009). However, it is suspected, a priori, that these numbers are substantial underestimates and that a more thorough investigation would reveal a far greater scale of bioinvasions within the region, which would in turn facilitate an assessment of bioinvasion patterns.

South Africa provides a clear example of a region where confounding factors have hindered progress when assessing the diversity of marine bioinvaders. One major hurdle is a lack of pre-invasion information. Given that the region lies along major shipping routes, a well documented vector of marine bioinvasions (Carlton and Hodder 1995; Carlton 2003; Carlton and Cohen 2003; Occhipinti-Ambrogi and Savini 2003; Wonham et al. 2000; Wonham and Carlton 2005) it is virtually certain that marine introductions consistently took place over the first 400 years of European colonial history. Whereas by 1699 there were 46 exotic plants already established in South Africa (Wells et al. 1986), no formal research endeavours on the introduced marine fauna and flora extend to these early periods.

Besides historical data gaps, Robinson et al. (2005) note that large areas of the South African coastline remain unexplored in terms of marine introductions. Similarly, not all coastal habitats have been investigated equally, if at all. In addition, there are few marine taxonomists available in South Africa to make authoritative identifications, even of native species. Additional taxonomic complications further confound interpretation of faunal and floral history. For example, species carried around the world by ships were frequently described over and over again as regional endemics in their areas of introduction, leading to individual introduced species "hiding" around the world under many different names (Carlton 2009).

This body of research aims to rectify the situation by, firstly applying a wider range of investigatory approaches in order to reveal a far greater diversity of introduced species than previously recognized within the region. Secondly, a preliminary spatio-temporal assessment of the extent of South African patterns of bioinvasion will be presented.

Materials and methods

Re-assessment of the South African bioinvasion inventory

A combination of approaches were employed to examine in detail the potential biogeographic histories and affinities of marine and estuarine taxa. The previous work of Griffiths et al. (2009) was expanded to capture additional nineteenth century literature (peer reviewed publications and monographs) and grey literature (government reports and maritime records) previously overlooked. Grey literature sources were used judiciously and only when the levels of expertise and scholarship could be adequately assessed. Voucher specimens and unpublished species records stored within the Iziko South African Museum Marine Collection, Cape Town, were examined.

Comparative invasion biogeography

Firstly, we identified marine and estuarine species that were recognized as bioinvasions elsewhere, but had not yet been recognized as introduced to South Africa using the aforementioned historic literature and through cross-checking lists of South African marine species with lists of species considered to be introduced in other climatically comparable regions. This included regions at similar latitudes in the southern hemisphere, for example Australia, New Zealand and South America, but also in northern latitudes, such as North America and Europe. The question was posed as to whether selected taxa recognized in South Africa, whose systematic status appeared to be reasonably resolved, had highly disjunct global distributions. It should be noted that large suites of microscopic species (protozoans, nematodes, rotifers, diatoms, dinoflagellates) do not lend themselves to this approach, as their global

status has largely been defined based upon the morphospecies concept, rather than genetic verification. Secondly, South African species with questionable systematic status were investigated and evidence as to their modern systematic status derived from re-examination of voucher specimens as well as paleontological, archeological, historic, biogeographic, genetic and systematic studies (taxonomic resolution). The criteria of Carlton (1996), Chapman (1988) and Chapman and Carlton (1991) were applied to determine if species identified should be allocated introduced or cryptogenic status.

Under-considered habitats and rapid assessment surveys

Numerous introductions are found in habitats that are rarely or insufficiently explored (Carlton 2009). Through rapid assessment surveys (field surveys), the aim was to reveal species that were recognizable as bioinvasions in under-considered habitats. Sampling was conducted in September 2008 at locations on the southern and western coasts of South Africa. These were (i) Table Bay Harbour, Cape Town, (ii) Milnerton Lagoon, Table Bay, (iii) Langebaan Lagoon, Saldanha Bay and (iv) Zandvlei Lagoon, False Bay, Cape Town. For new species records, the date of first collection (DOC) was recorded as the sampling date.

Fouling and wood-boring communities were sampled in Table Bay Harbour (Cape Town). The emphasis was placed on fauna associated with gribble (*Limnoria*)-infested wood. Peices of wood were removed from wooden structures within the harbour and taken to the laboratory. At Milnerton Lagoon, Table Bay, quadrats were placed randomly along the strandline habitat located in the supralittoral zone. All debris (inclusive of decomposing kelp) and samples of sand from within the quadrats were removed and returned to the laboratory. At Langebaan Lagoon, Saldanha Bay, quadrats were placed randomly along sandy beach and marsh habitats. Organic material and samples of sand/mud from within the quadrats were removed and returned to the laboratory. At Zandvlei Lagoon, False Bay, Cape Town, the emphasis was on the tubeworm *Ficopomatus enigmaticus* and the associated biota found within the reefs formed by the tubeworm. Several sections of reef were removed from within the water and returned to the laboratory. Organisms across all size ranges were extracted from all samples and identified through examination under microscopes. Voucher specimens were preserved in 70% ethanol for long-term archival purposes and where necessary, for distribution to systematists.

Species categorization

The date of first collection (DOC) or date of publication (DOP) when DOC was not available was derived from several sources, inclusive of peer reviewed literature, museum collections, and field sampling post-2008. Native regions (regions of origin) were determined from highly specialized taxonomic literature and the biogeographic patterns of sister taxa. For cosmopolitan species, the origin was classified as 'unknown'. Transport vector (vector pathway) assignment was based on both life history knowledge and the date/site of introduction as extracted from peer reviewed literature records. Analyses were based on subsets of species with the exclusion of cryptogenic species, depending on available data for each parameter. Introduced species counts were analyzed for temporal trends and distributional patterns for regions of origin, taxonomic groups, invasion pathways, vector and habitat type.

Temporal patterns analyses

Temporal analyses are currently confounded by a lack of ability to accurately assess rate of introduction. At this stage, the majority of South African bioinvasions are linked to the DOC rather than date of actual introduction, which may in fact be decades or centuries before. Therefore, using DOC's, species counts were regressed against collection year since 1840 (this being the earliest collection decade known) in order to establish the rate of discovery. Discovery rate was tested using a least squares linear fit regression ($y = \alpha + \beta x$) where β is the rate of change of the rate of discovery. The null hypothesis, which assumes a constant rate of discovery over the 170 year period, will be rejected if $P < 0.05$. If $\beta < 0$, this indicates the rate is increasing over the 170 year period. In addition, the mean number of introduced species collected per decade was calculated across 30 year periods, in order to compare discovery rates during periods where introductions were collected as a bi-product of maritime surveys or

indigenous biodiversity surveys (1840–1990) relative to where introductions were collected as a product of focused bioinvasive research (1990–2010).

Spatial patterns analysis

Distribution ranges were not inferred from single point location records, in order not to assume that a species occurs between two known points, such as two ports (Mead et al. 2011). The coastline of South Africa can be divided into separate biogeographical regions with transition zones in-between (Fig. 1). The bioregions are defined based on climatic and oceanographic regimes combined with known species assemblages present, summaries of which are found in several sources but in this case are adapted from Lombard (2004). To test if regional distribution of introduced species was dependent on region of origin, vector pathway, habitat or species number (and an $\propto$ value of 0.05) species count data were arranged into contingency tables and the Chi-squared statistic applied (Zar 2004).

Species uniqueness per biogeographic region or transition zone was determined. The number of species shared between bioregions and those that were unique to a specific bioregion were identified and tallied. The Jaccard Similarity Index was used to identify similarity between regions (%) based on the numbers of shared and unique species present within a bioregion. The following formula was applied: $S_{AB} = A_nB/A_uB$, where S = Similarity, A and B represent bioregions or transition zones being compared, A_nB represents the total number of unique species found across both region A and B and A_uB represents the total number of shared species found in both region A and B.

Results

Bioinvasion inventory

In total, 86 introduced and 39 cryptogenic marine and estuarine species were resolved for South Africa (Table 1). This is a major re-assessment of the previous inventory and expands substantially on the 22 and 18 species reported previously (Griffiths et al. 2009). Of the 64 species added as introductions, 76% were sourced from within the historic literature, 11% were identified following field surveys conducted post-2008 and 13% were revealed following taxonomic resolution. Of the 21 cryptogenic species newly resolved, 64% were sourced from within the historic literature, 14% were identified following field surveys conducted post-2008 and 22% were revealed following taxonomic resolution (Fig. 2). All taxa were identified to species level and Mead et al. (2011) provides the species-by-species treatment of the introduced and cryptogenic biota in a monographic format.

No fewer than 14 of the species in Table 1 were originally mistakenly re-described as new endemic species after they had arrived in South Africa (Table 2). Five species in the South African marine fauna were retained as introduced, although they were last collected over 50 years ago (Table 3) because they are either in locations or in habitats that have not been thoroughly re-explored for that specific species since the original record. Two additional species are recognized as introductions, but to date are only present within closed aquaculture facilities (Table 1). One bryozoan species, *Membranipora membranacea*, was removed from previous lists of introduced species (Griffiths et al. 2009; Robinson et al. 2005), as it is now recognized as a previously undescribed inidigenous species, *M. rustica* (Florence et al. 2008).

Rate of discovery

This analysis was based on 71 of the possible 86 species records as date of first collection was not determined for 15 species. As the number of species records accumulated over the past 170 years (Fig. 3a), the rate of discovery has increased over time ($P = 0.25$; confidence range of $\beta = 0.007$–0.1; $R^2 = 0.27$; Fig. 3b). Species collection rates were lower in periods where introductions were collected as bi-products of maritime or indigenous biodiversity surveys (1840–1990), compared to focused bioinvasive research (1990–2010). During the maritime and biodiversity surveys, the average species addition rate between 1840 and 1940 was 1.9 species per decade, rising to 3.2 species per decade between 1940 and 1990 (Fig. 3). During the period of focused invasive research, between 1990 and 2010, the average species addition rate was 17 species per decade (Fig. 3). Of the total known number of marine introductions to date (86 species), Robinson et al. (2005) revealed

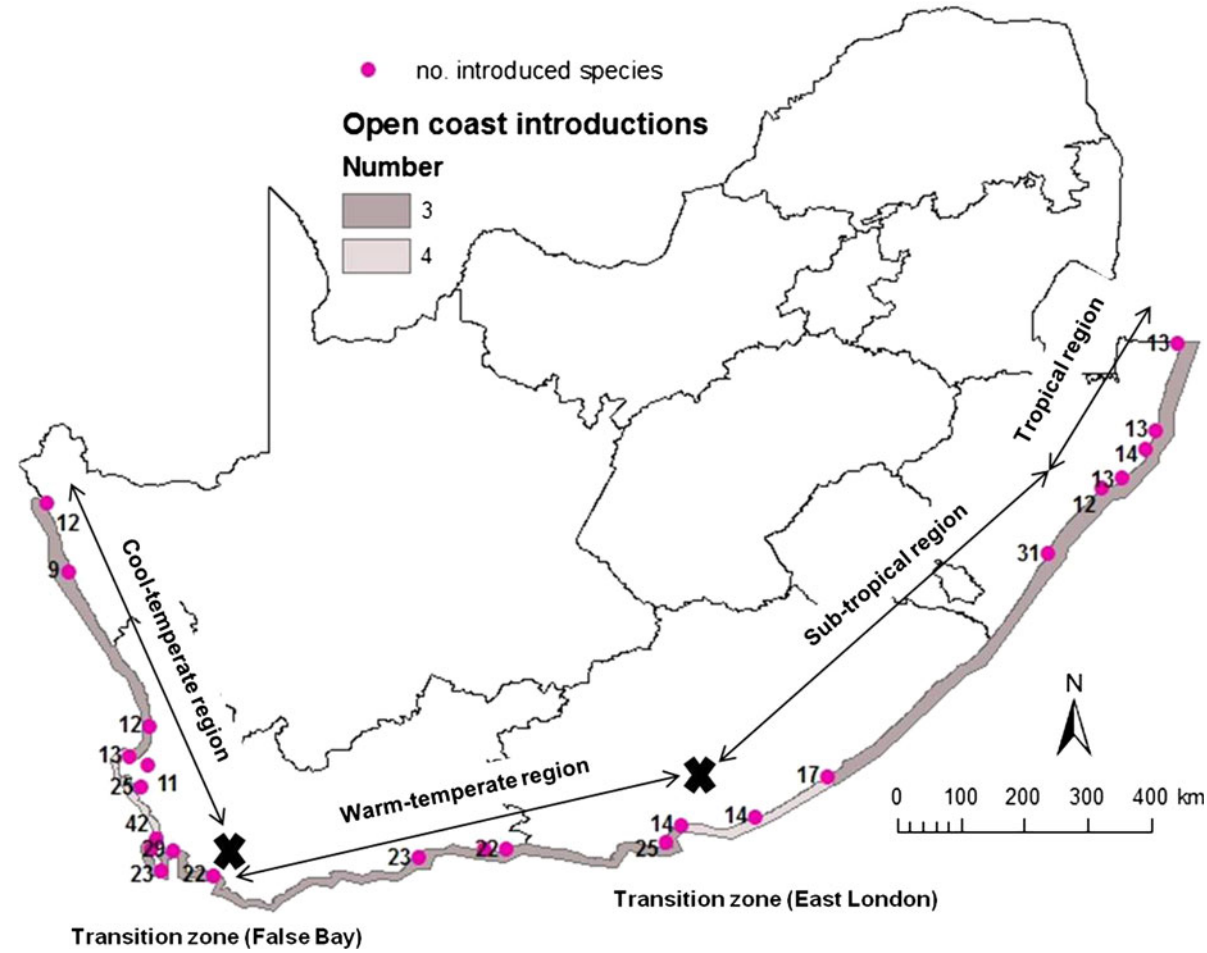

Fig. 1 Number of marine introduced species within major towns, harbours, estuaries and along the open coast of South Africa

11.7%, Griffiths et al. (2009) revealed 14.1% and the current re-assessment revealed 74.2%.

Biogeography

This analysis was based on 80 of the possible 86 introductions, as distributional records were not determined for 4 species and 2 species were located within aquaculture facilities. The highest numbers of introductions (55 species) were reported from the cool-temperate region (Fig. 1), hereafter refered to as the west coast. The lowest numbers of introductions (15 species) were reported from the tropical region (Fig. 1), hereafter refered to as the north-east coast. According to *Chi-square* analysis, indigenous regions, invasion pathways, habitat type, taxonomic groupings and shared or unique species differed significantly among regions ($P < 0.001$; Table 4). The west coast has the highest proportion of introductions that are unique to the region (42%; 55 species), followed by the sub-tropical region (Fig. 1), hereafter refered to as the east coast (26%; 31 species). The transition zones (Fig. 1) located in between bioregions (False Bay and East London) have the highest proportion of species shared across regions, with 94% (35 species) and 100% (21 species) respectively (Fig. 4). The Jaccard Similarity Index revealed that there were dissimilarities between regions based on respective shared and unique species compositions. The west coast shared the highest similarities (40–60%) with all other biogeographic regions and transition zones. The transition zones were most dissimilar to each other (96%).

Table 1 Marine and estuarine introductions of South Africa

Vectors				Status		Date	
SB	Ship boring	M	Mariculture (aquaculture)	I	Introduced	NDD	No date determined
SF	Ship fouling	I	Intentional release (other)	C	Cryptogenic	DOC	Date of collection
BW	Ballast water					DOP	Date of publication
BS	Solid ballast			Origin:			
OR	Oil rigs			NA	North Atlantic	NP	North Pacific
				WA	Western North Atlantic	EA	Eastern North Atlantic
				WP	Western North Pacific	EP	Eastern North Pacific
				PC	Ponto-Caspian	IO	Indian Ocean
				SH	Southern Hemisphere	IP	Indo-Pacific

Taxon	Status	Date	DOC/DOP	Origin	Vector
PROTOCTISTA					
Mirofolliculina limnoriae	I	2008	DOC	Unknown	SB
Zoothamnium sp.	C	<1947	DOP	Unknown	SF/BW
DINOFLAGELLATA					
Alexandrium tamarense-complex:	I	1948	DOC	NA/NP	BW
Alexandrium minutum	I	2003	DOC	EA	BW
Dinophysis acuminata	I	1991	DOC	EA	BW
PORIFERA					
Suberites ficus	I	1998	DOC	EA	SF
CNIDARIA					
Anthozoa					
Sagartia ornata	I	1963	DOC	EA	SF/BW
Metridium senile	I	1995	DOC	NA/NP	SF
Hydrozoa					
Eudendrium carneum	C	<1975	DOP	Unknown	SF/BW
Pachycordyle navis	I	1958	DOC	EA	SF/BW
Coryne eximia	I	1946	DOC	NA/NP	SF/BW
Coryne pusilla	C	<1975	DOP	Unknown	SF/BW
Moerisia maeotica	I	1965	DOC	PC	SF/BW
Pennaria disticha	I	1901	DOC	Unknown	SF/BW
Pinauay larynx	I	1947	DOC	NA	SF/BW
Pinauay ralphi	I	1947	DOC	NA	SF/BW
Laomedea calceolifera	I	1948	DOC	NA	SF/BW
Gonothyraea loveni	I	1946	DOC	NA	SF/BW
Obelia bidentata	I	1948	DOC	Unknown	SF/BW
Obelia dichotoma	I	1938	DOC	Unknown	SF/BW
Obelia geniculata	I	1934	DOC	Unknown	SF/BW
ANNELIDA					
Polychaeta					
Boccardia proboscidea[a]	I	2004	DOC	EP	M
Neanthes succinea	I	1947	DOC	NA	SF/BW
Capitella sp./spp. *complex*	C	<1952	DOP	Unknown	SF/BW
Polydora hoplura	I	1947	DOC	EA	SF/BW/M

Table 1 continued

Taxon	Status	Date	DOC/DOP	Origin	Vector
Dodecaceria fewkesi	I	2007	DOC	EP	SF/BW
Ficopomatus enigmaticus	I	1951	DOC	SH	SF/BW
Hydroides elegans	I	1970	DOC	SH	SF/BW
Neodexiospira brasiliensis	I	1953	DOC	SH	SF/BW
Janua pagenstecheri	I	1971	DOC	EA	SF/BW
Simplicaria pseudomilitaris	C	1971	DOC	Unknown	SF/BW
CRUSTACEA					
Cirripedia					
Balanus glandula	I	1992	DOC	EP	SF/BW
Amphibalanus venustus	I	1938	DOC	WA	SF
Copepoda					
Acartia spinicauda	I	2003	DOC	WP	BW
Isopoda					
Dynamene bidentata	I	2006	DOC	EA	SF/BW
Sphaeroma serratum	I	1950	DOC	EA	SF/BW
Sphaeroma annandalei	C	1926	DOC	Unknown	SF/BW
Sphaeroma terebrans	C	1926	DOC	IO	SF/BW
Sphaeroma walkeri	I	1915	DOC	IO	SF/BW
Paracerceis sculpta	I	2006	DOC	EP	SF/BW
Synidotea hirtipes	C	<1897	DOP	IO	SF/BW
Synidotea variegata	C	<1991	DOP	SH	SF/BW
Ligia exotica	C	<1932	DOP	Unknown	BS
Limnoria quadripunctata	I	<1978	DOP	Unknown	SB
Limnoria tripunctata	I	<1978	DOP	Unknown	SB
Amphipoda					
Chelura terebrans	I	1888	DOC	SH	SF/SB
Ischyrocerus anguipes	I	1913	DOC	NA	SF/BW
Erichthonius brasiliensis	I	1910	DOC	NA	SF/BW
Cymadusa filosa	C	1913	DOC	Unknown	SF
Caprella equilibra	C	1889	DOC	Unknown	SF/BW
Caprella penantis	C	1889	DOC	Unknown	SF/BW
Paracaprella pusilla	C	<1955	DOP	Unknown	SF/BW
Corophium triaenonyx	C	1931	DOC	WP	SF/BW
Apocorophium acutum	I	1915	DOC	NA	SF/BW
Monocorophium acherusicum	I	1915	DOC	NA	SF/BW
Melita zeylanica	C	<1916	DOP	Unknown	SF/BW
Jassa marmorata	I	<1990	DOP	EA	SF/BW
Jassa morinoi	I	<1990	DOP	EP	SF/BW
Jassa slatteryi	I	<1990	DOP	EP	SF/BW
Orchestia gammarella	I	1949	DOC	EA	BS
Platorchestia platensis	I	1904	DOC	Unknown	BS
Cerapus tubularis	I	1901	DOC	WA	SF/BW

Table 1 continued

Taxon	Status	Date	DOC/DOP	Origin	Vector
Decapoda					
Xantho incisus	I	2008	DOC	EA	M
Carcinus maenas	I	1983	DOC	EA	SF/BW/OR
PYCNOGONIDA					
Ammothella appendiculata	I	1951	DOC	WP	SF/BW
INSECTA					
Coleoptera					
Cafius xantholoma	I	1936	DOC	EA	BS
MOLLUSCA					
Gastropoda					
Littorina saxatilis	I	<1972	DOP	EA	BS
Thais blanfordi	I	1950	DOC	IO	SF/BW
Thais tissoti	I	1950	DOC	IO	SF/BW
Tarebia granifera	I	2005	DOC	SH	SF/BW
Catriona columbiana	I	1972	DOC	NP	SF/BW
Polycera hedgpethi	C	1980	DOC	NP	SF/BW
Thecacera pennigera	C	<1987	DOP	Unknown	SF/BW
Anteaeolidiella indica	C	<1927	DOP	Unknown	SF/BW
Bivalvia					
Mytilus galloprovincialis	I	1979	DOC	EA	SF/BW
Ostrea edulis	I	2007	DOC	EA	M
Perna viridis	I	2009	DOC	IO	SF/BW
Semimytilus algosus	I	2009	DOC	EA	SF/BW
Crassostrea gigas	I	2001	DOC	WP	M
Hiatella arctica	C	<1969	DOP	Unknown	SF
Teredo navalis	I	<1886	DOP	EA	SB
Lyrodus pedicellatus		<1931	DOC	Unknown	SB
Bankia carinata	C	<1982	DOP	Unknown	SB
Bankia martensi	C	<1920	DOP	Unknown	SB
Dicyathifer manni	C	<1964	DOP	Unknown	SB
Teredo somersi	C	<1937	DOP	Unknown	SB
Martesia striata	C	<1910	DOP	Unknown	SB
BRACHIOPODA					
Discinisca tenuis[a]	I	2008	DOC	SH	M
BRYOZOA					
Watersipora subtorquata	I	1937	DOC	WA	SF
Bugula neritina	I	1944	DOC	Unknown	SF
Bugula flabellata	I	1880	DOC	Unknown	SF
Bugula dentata	I	1852	DOC	SH	SF
Conopeum seurati	I	2001	DOC	EA	SF
Cryptosula pallasiana	I	1947	DOC	EA	SF
ECHINODERMATA					
Tetrapygus niger	I	2007	DOC	SH	M
Ophiactis savignyi	I	1950	DOC	SH	SF

Table 1 continued

Taxon	Status	Date	DOC/DOP	Origin	Vector
CHORDATA					
Ascidiacea					
Cystodytes dellechiajei	C	1962	DOP	Unknown	SF
Clavelina lepadiformis	I	2001	DOP	EA	SF
Didemnun granulatum	C	2001	DOP	Unknown	SF
Didemnun psammathodes	C	2001	DOP	Unknown	SF
Didemnun rodriguesi	C	2001	DOP	Unknown	SF
Tridemnun cerebriforme	C	1913	DOC	Unknown	SF
Diplosoma listerianum	I	1949	DOC	EA	SF
Ciona intestinalis	I	1955	DOC	NA	SF
Corella eumyota	C	1898	DOP	Unknown	SF
Ascidia sydneiensis	I	1932	DOC	SH	SF
Ascidiella aspersa	I	2001	DOP	EA	SF
Botryllus schlosseri	I	1946	DOC	Unknown	SF
Symplegma brakenhielmi	C	1952	DOC	Unknown	SF
Polycarpa insulsa	C	2001	DOP	Unknown	SF
Cnemidocarpa humilis	I	2001	DOP	Unknown	SF
Styela canopus	C	1934	DOP	SH	SF
Styela plicata	I	1951	DOC	WP	SF
Microcosmus squamiger	I	1950	DOC	SH	SF
PISCES					
Cyprinus carpio	I	1860	DOC	EA	M
RHODOPHYTA					
Schimmelmannia elegans	I	2002	DOC	WA	BW
Schottera nicaeensis	C	<1985	DOP	WA	SF/BW
Antithamnionella ternifolia	C	<1997	DOP	SH	SF/BW
Antithamnionella spirographidis	I	1989	DOC	NP	SF/BW
CHLOROPHYTA					
Cladophora prolifera	I	1999	DOC	EA	SF
Ulva fasciata	C	<1997	DOP	Unknown	SF
Codium fragile fragile (*tomentosoides* strain)	I	1937	DOC	WP	SF
VASCULAR PLANTS					
Ammophila arenaria	I	1876	DOC	EA	I
Spartina maritima	C	1829	DOC	EA	BS
Stuckenia pectinata	C	1896	DOC	Unknown	BS/BW

[a] These species are only found within closed aquaculture facilities to date

Regions of origin and vector pathways

The region of origin analysis was based on 70 of the possible 86 introductions, as origins were not determined for 16 species and therefore classed as 'unknown'. The majority of introduced species were native to the northern hemisphere (65%) although 18% originated from the southern hemisphere (Fig. 5). Northern hemisphere species have established themselves on the cool-temperate west coast and warm-temperate south-east coast (Fig. 1), plus the transition zones either side. Conversely, the majority of southern hemisphere species have established all along the warmer east coast.

The vector pathway analysis was based on all of the possible 86 introductions. An overwhelming proportion of species (94%) were introduced unintentionally with a

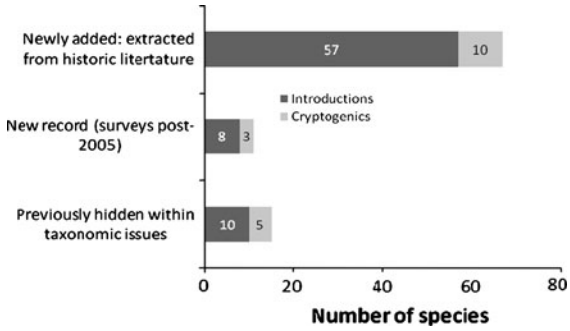

Fig. 2 Summary of sources for new additions to the updated South African inventory of marine introduced and cryptogenic species

very small percentage (6%) being imported intentionally or through mariculture practice (Fig. 6). Ship fouling (48%) and ballast water (38%) are the commonest vectors of marine introduced species to the South African coast (86%) with 51% of species potentially arriving at the South African coastline through multiple vectors. The west coast and adjacent transitional zone (False Bay) had introduced species vectored by all the pathways listed, inclusive of introduction through oil rigs. Ship boring species had arrived predominantly on the north-east coast, as well as the west coast and False Bay, although in relatively low numbers compared to the other listed vectors. This is probably attributable to the fact the materials used to build ships have changed historically, limiting the temporal window of opportunity for boring species. The south-east coast has the highest number of species arriving through the mariculture industry, reflective of the number of mariculture facilities present within this province.

Table 2 Introduced or cryptogenic species in South Africa mistakenly redescribed as new endemic species

Species	Origin	Redescribed from South Africa as	Synonymy
CNIDARIA			
Hydrozoa			
Pinauay ralphi	North Atlantic	*Tubularia ralphi* Ewer 1953	Peterson 1990
Pennaria disticha	Unknown	*Halocordyle cooperi* Warren 1906	Millard 1975
CRUSTACEA			
Amphipoda			
Cymadusa filosa	Unknown	*Grubia australis* Barnard 1916	Barnard 1955
Orchestia gammarella	North Atlantic	*Talorchestia inaequalipes* Barnard, 1951	Griffiths 1975
MOLLUSCA			
Bivalvia			
Lyrodus pedicellatus	Unknown	*Teredo robsoni* Roch 1931	Turner 1966
Bankia martensi	Unknown	*Bankia capensis* Calman 1920	Turner 1966
Dicyathifer manni	Unknown	*Teredo ancila* Barnard 1964	Turner 1966
Teredo somersi	Unknown	*Teredo radicis* Moll 1937	Turner 1966
Gastropoda			
Thecacera pennigera	Unknown	*Thecacera lamellata* Barnard 1933	Gosliner 1987
Anteaeolidiella indica	Unknown	*Aeolidiella saldanhensis* Barnard 1927 *Aeolidiella multicolor* Macnae 1954	Gosliner and Griffiths 1981
CHORDATA			
Ascidiacea			
Styela canopus	Unknown	*Styela stephensoni* Michaelsen 1934	Monniot et al. 2001
ECHINODERMATA			
Marthasterias glacialis	Europe	*Asteracanthion africanus* Muller & Troschel 1842	Clark & Courtman-Stock 1976
VASCULAR PLANTS			
Spartina maritima	North Atlantic	*Spartina capensis* Nees 1841	Pierce 1982
Stuckenia pectinata	Unknown	*Potamogeton pectinata ungulatus* Hagstrom 1916	Kaplan 2008

Table 3 Introduced species retained here as members of the South African marine fauna, although collected more than 50 years ago (see text discussion)

Species	Location	Last known collection
Amphipoda (amphipods)		
Platorchestia platensis	Danger Point, Gansbaai	1904
Apocorophium acutum	Durban Bay	1915
Chlorophyta (green algae)	Melkbosstrand	1937
Codium fragile fragile strain*tomentosoides*		
Pycnogonida (sea spiders)		
Ammothella appendiculata	Durban Bay	1951
Hydrozoa (hydroids)		
Pachycordyle navis	Table Bay	1958

Habitat and taxonomic distribution

The habitat and taxonomic analysis was based on all of the possible 86 introductions. The marine introduced species of South Africa are currently known from 11 habitats (Fig. 7). A large proportion of introductions (53%) were found within harbours (most South African harbours are not located within estuaries), with a further 30% found equally between rocky shores and estuaries and a small percentage found offshore (Fig. 7). Whereas introduced species found on rocky shores were evident consistently across all regions, estuarine species were mainly concentrated on the east and north-east coasts.

Marine introduced species were distributed over 17 taxonomic groups (Table 1). The cnidarians, annelids, crustaceans, molluscs and chordates made up over three quarters of the species (Fig. 8). The cnidarians (13 species) consisted of anthozoans (2 species) and hydrozoans (11 species) and the molluscs (12 species) comprised of gastropods (7 species) and bivalves (5 species). The crustaceans (22 species) primarily consisted of isopods (6 species) and 11 species of amphipod (Table 1). There was one fish, an estuarine species, *Cyprinus carpio* and the echinoderms included one echinoid and one ophiuroid. Algal records consisted of two green algae plus three red algae and there was one flowering plant reported, a dune dwelling species, *Ammophila arenaria* (Table 1). The earliest collection records of introduced species in South Africa are of the alga, *Chlorophyta prolifera,* the bryozoans, *Bugula flabellata* and *B. dentata*, the estuarine fish, *Cyprinus carpio*, the dune plant, *Ammophila arenaria* and the crustacean, *Chelura terebrans*. All these species were reported between 1846 and 1888 (Table 1). Impacts are only known for 5% of all the bioinvaders listed within the current inventory, with the majority of studies concentrating on one or two of the more conspicuous species. The total number of marine introduced species within the current inventory represents 0.7% of the total known marine biodiversity for South Africa, based on an updated version of the marine species list compiled by Gibbons et al. (1999).

Discussion

The present study primarily showed that expanding the approaches used within the methods resulted in a

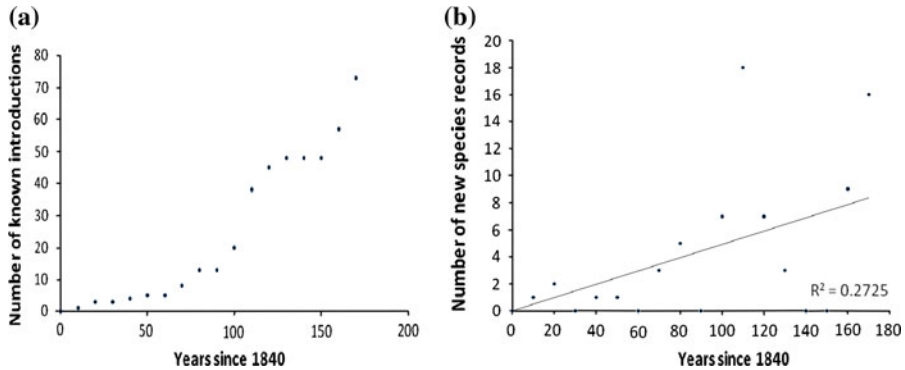

Fig. 3 **a** Cumulative number of marine introduced species recorded since 1840. **b** Linear regression indicating rate of discovery of marine introduced species since 1840

Table 4 Summary of *Chi-squared* statistic testing dependence of established marine introduction distribution on the indigenous region of origin, invasion pathway, habitat and species uniqueness

Factor	*df* (*v*)	Chi crit	Chi obs	*P*
Indigenous region	50	86.66	90	<0.001
Invasive pathway	35	66.61	135.88	<0.001
Habitat	50	86.66	117.2	<0.001
Taxonomic group	35	66.61	93.5	<0.001
Species Uniqueness	5	20.51	97	<0.001

Key: *df* (*v*) = degrees of freedom; Chi crit = critical *Chi-squared* value; Chi obs = observed *Chi-squared* value; *P* = significance level. Bioregions tested were those in Fig. 1

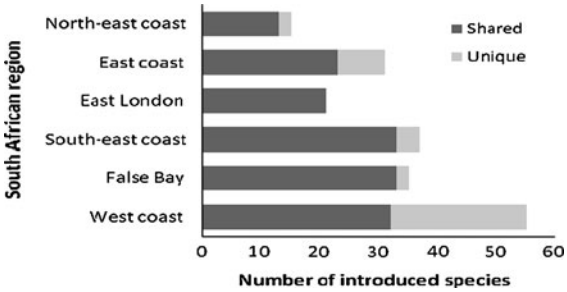

Fig. 4 Number of species with a unique or shared distribution for known South African marine introductions. *Note*: East London and False Bay are transitional zones between bioregions (refer to Fig. 1)

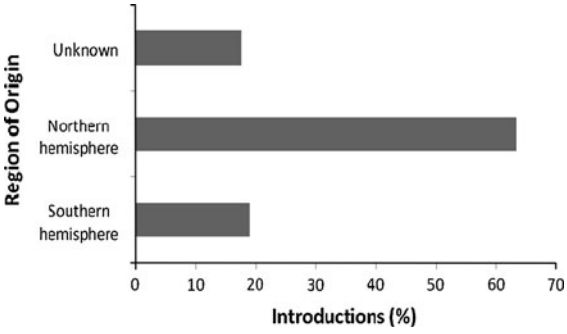

Fig. 5 Summary of bioregions of origin for South African marine introductions

large increase in the number of introduced and cryptogenic species recognized within the South African region. More specifically, the advances of the present re-assessment can be divided into: (i) A temporal approach that further contributes to our understanding of the colonization history of introduction in the studied region and (ii) spatial

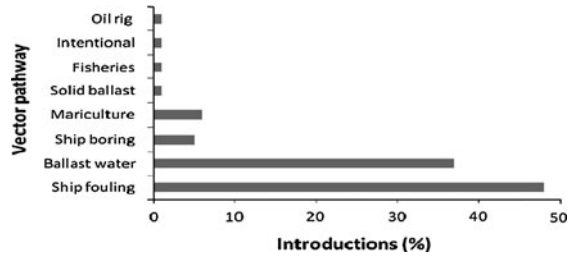

Fig. 6 Summary of vector pathways for South African marine introductions

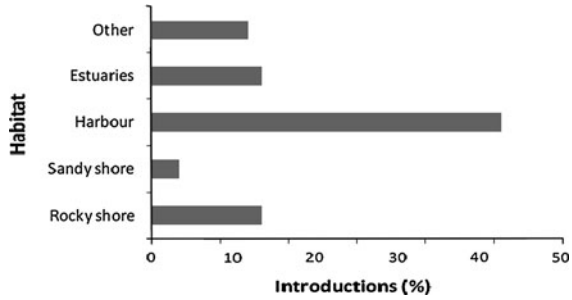

Fig. 7 Summary of habitat distribution for South African marine introductions

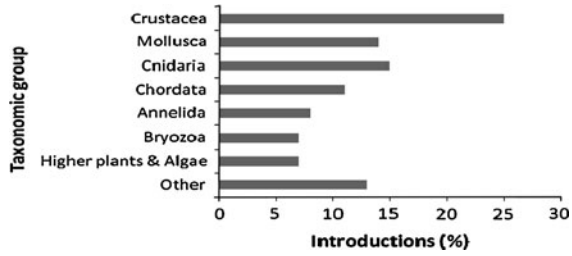

Fig. 8 Distribution of South African marine introduced species across taxonomic groups

assessments that revealed differences within the patterns of regional bioinvasions.

The bioinvasion inventory: a temporal perspective

The current re-assessment resulted in the 'earliest collection date' for an introduced species being pushed back over a century to 1846 (the alga, *Cladophora prolifera*) rather than 1955 as previously recorded (Robinson et al. 2005). This clearly indicates that marine introductions started establishing in the South African marine environment a long time ago and is comparable to the earliest records of

Denmark (1895), the Azores (1887) and Chile (1864) (Carlton 2009).

Based on a model developed by Wonham and Pachepsky (2006), an exponential increase in detection rates would be the expected (null) trend for the region. However, the authors recognize that data sets spanning short temporal periods may not reveal a 'true' best fit model, due to record limitation. In addition, their model assumes regular (non-random), standardized surveys have been sustained within the region in question over a period of decades, which is not the case for South Africa. Therefore, at this stage, it is only possible to identify that rate of discovery is increasing. Under similar assumptions, Solow and Costello (2004) clearly demonstrate that it is possible to have an accelerating rate of detection without an increasing rate of invasion and that the former does not necessarily prove or indicate the latter. Therefore, although the South African discovery rate is increasing over time, it cannot be implied from these results that introduction rate is also increasing. The records that will facilitate accurate assessment of bioinvasion rates start with and will continue from the 2000s, where prior absence can be demonstrated. What is clear is that an increase in effort per unit time has been highly effective in revealing marine introductions. The peak in the number of species revealed per decade coincides with the period of focused bioinvasive research within marine habitats spanning 1990 to the present day (Griffiths 2000; Griffiths et al. 1992, 2009; Robinson et al. 2005), the largest contributor being this re-assessment.

Although a collection date has been identified for the majority of introductions in the inventory, many of these species could have arrived decades and even centuries earlier. The date of collection is primarily tied to the expertise of the early taxonomists working within the region and thus an unquantifiable effort bias exists within the data. Cohen and Carlton (1998) removed over one-third of known introductions from their temporal analyses because they were artifacts of effort bias. Despite the fact that South Africa is a region that has sustained approximately 400 years of shipping history, little baseline data pertaining to the status of marine introductions is available.

The design and implementation of a well-planned investigative programme has paid dividends in terms of making dramatic progress within a very short space of time. In 1 year, the current re-assessment revealed three quarters of the introduced and cryptogenic species within South Africa. This substantially increased the known resolution by over four and twofold respectively from the last publication (Griffiths et al. 2009). According to Carlton (2009), the number of introductions within the South African region could easily be as high as 220 species. Through continued use of the methods applied within this re-assessment, it may be possible to reveal these introductions within a decade, based on the fact 64 introduced species were added over a 12-month period spanning 2009 and 2010.

In comparison, New Zealand added 40 introduced and 27 cryptogenic species over a period of 9 years between 1998 and 2007 (Hayden et al. 2009). This coincided with the commencement of targeted surveillance aimed at identifying marine introduced species (Hewitt et al. 2004) and represents an average rate of 4.4 introduced species and 1.8 cryptogens added per year. Australia increased the number of introductions two-fold over a period of 14 years following the establishment of the CSIRO Centre for Research on Introduced Marine Pests in 1994 (Sliwa et al. 2009) which represents an average rate of 4.3 introduced species added per year. Although South Africa has added 1.7 introductions and 0.9 cryptogens on average, per year from 1990 to 2010, the reality is that the additions were not temporally equal, with the majority of species added as a result of the current re-assessment. Thus, this provides strong motivation for other regions to initiate similar programs aimed at effectively and efficiently detecting marine introductions and cryptogenic species.

While we report a far wider diversity of marine and estuarine introductions than previously recorded, we emphasize that even this work remains a preliminary assessment in which we have identified only part of the real number of introductions. For example, a great many more species of sponges, hydroids, flatworms, polychaetes, bryozoans and other taxonomically-challenging groups (Gibbons et al. 1999) are neither clearly recognized as indigenous nor introduced at this stage. Through continued application of the methodologies utilized within this re-assessment, combined with finer-scale morphological and genetic work aimed at resolving taxonomic issues, it is predicted that many more species will be discovered within the region, in line with the predictions of Carlton (2009). Thus, we caution those making global assessments to avoid

assuming that the number of non-native marine species in South Africa is sufficiently well-known to invite conclusive comparisons with other regions at this stage (such as attempted by Molnar et al. 2008).

A recent study by Nuñez and Pauchard (2010) revealed that the challenge in forming global strategies to deal with biological invasions is the fact that there are differences in data quality and availability between developed and developing regions, hindering comparative analyses. In order for scientists to fully understand the potential depth and breadth of this striking global phenomenon, it is imperative that the key issues of commitment to monitoring and vigilance and implementation of standardized assessments across areas (e.g., Hewitt et al. 2009; Sliwa et al. 2009) are addressed.

Spatial patterns of bioinvasion

Based on the current inventory, the northern hemisphere appears to be the main source of introduced species into the region with temperate species located from the west coast to the south-east coast. In contrast, those species originating from southern hemisphere regions appear to have more success establishing on the east and north-east coast. This is despite the fact there are major ports located all along the coastline that would have been exposed to centuries of shipping history from all global regions. Thus, it would initially appear that the combined climatic and oceanographic regimes that form the environmental backdrop within the different biogeographic regions (Bustamante and Branch 1996; Emanuel et al. 1992; Lombard 2004; Sink and Branch 2005) are influential in bioinvasion success and spread along the South African coastline. Interestingly, a high number of introduced species are shared across bioregions, the majority of these being found on the west coast and within the transitional zone between the west and south-east coast, where there is a well-documented overlap of indigenous species (Griffiths and Branch 1991). This suggests that there are introduced species which can exhibit high levels of plasticity, adapting to a range of temperate conditions, thus increasing establishment success (Occhipinti-Ambrogi 2007).

As with other regions, the chances of an introduction being initially introduced by certain vector pathways is likely to have peaked in the past, whereas others will have increased over time (Wonham and Carlton 2005). Wilson et al. (2009) attempted to represent the temporal windows and peaks of vectors within South Africa. However, these windows were broad estimations of vector pulses over time with an assessment of their potential role in successful establishment of introduced species. Thus, while Wilson et al. (2009) show dry ballast persisting as a vector well past the 1950s, this vector ceased in the mid-twentieth century; they show ballast water as commencing in 1900, when it was in regular use by the 1880s in ships arriving in South Africa, and they show mariculture as beginning in the mid-1700s, whereas this vector is a relatively new phenomena (last two or three decades) on South African shores.

One also needs to be aware of the adaptive nature of introduced species with regards to vector pathways. For example, the boring bivalve, *Martesia striata*, is able to bore into ABS (Acrylonitrile butadiene styrene) pipes (Jenner et al. 2003). In addition, pelagic plastics are becoming an increasing concern as the latest modern vector for bryozoans (Winston 1982; Barnes and Milner 2005). In South Africa, it appears both ballast water (since 1880s) and ship fouling (since 1600s) are the dominant invasive pathways with mariculture becoming more prominent. If linked to information related to the evolution of the shipping and mariculture through time and space, these vectors are highly likely to be on the increase in line with these industries.

The majority of the introduced species recorded are invertebrates which is consistent with other studies (Cohen and Carlton 1998; Ruiz et al. 2000; Wonham and Carlton 2005). The low number of macroalgal species identified is most probably due to sampling biases, especially given the high algal diversity and historically limited access in the sub-tropical and tropical provinces of the east coast (Stegenga et al. 1997). Many taxa that are not represented within the current inventory are likely to be the result of sampling and taxonomic bias. Many taxa, such as Nematoda, are undersurveyed or have not been surveyed at all due to the lack of taxonomic expertise (Gibbons et al. 1999) and introduced species certainly lie undetected within such groups (Carlton 2009).

Although we recognize that more work is needed to fully reveal all South African bioinvasions in order to facilitate conclusive comparisions with other regions, a preliminary comparison with similar assessments reveals some interesting concurrences and contrasts

between regional bioinvasion patterns. Rilov and Galil (2009) report that up to 95% of Mediterranean bioinvaders have tropical (Indo-Pacific) origins which is in line with that region's shipping history. South African bioinvasions also appear to originate from historical shipping regions such as Europe. Hayden et al. (2009) reported that the discovery rate of marine introductions was on the increase within New Zealand with ballast water and ship fouling as major invasive pathways, which is in agreement with our South African findings. Mariculture is recognized as an emerging vector pathway in both Korea and South Africa (Seo and Lee 2009) and as with South Africa, the majority of Australian and South East Pacific bioinvaders are dominated by the annelids, molluscs, crustacea and chordates (Castilla and Neill 2009; Sliwa et al. 2009).

At the present time, we recognize that the patterns of biological invasions described here represent a coarse measure, limited by the information available on known introductions in the region. However, the current research can be used to effectively re-direct and focus regional research, ensuring a comprehensive coverage that parallels studies undertaken in well-studied regions globally, as well as act as a role model approach for developing regions with similar constraints.

Acknowledgments We are grateful to a large number of colleagues (cited in Mead et al. 2011) who generously provided unpublished records, museum data, systematic expertise, identified specimens or gave valuable advice. This research was conducted with support from History of the Near-shore (HNS) and the South African Environmental Observation Node (SAEON) to AM, and a grant from the Department of Science and Technology/National Research Foundation Centre of Excellence for Invasion Biology to CLG, MR and JTC. MR was supported by the 'Agencia Española de Cooperación Internacional para el Desarrolló from the Spanish 'Ministerio de Asuntos Exteriores y de Cooperación'.

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