

Introduced and cryptogenic marine and estuarine species of South Africa

A. Mead^{a*}, J.T. Carlton^b, C.L. Griffiths^a and M. Rius^{a†}

^aCentre for Invasion Biology, Department of Zoology, University of Cape Town, Private Bag X3, Rondebosch 7701, Cape Town, South Africa; ^bMaritime Studies Program, Williams College-Mystic Seaport, P.O. Box 6000, Mystic, CT 06355, USA

(Received 17 October 2010; final version received 7 June 2011; printed 3 August 2011)

The introduction history, systematics, transport vectors and distribution patterns of 85 introduced and 39 cryptogenic marine or estuarine animals and plants of South Africa are presented. This represents an addition of 93 species compared with previous lists. Taxa covered include protists, dinoflagellates, sponges, cnidarians, annelids, crustaceans, pycnogonids, insects, molluscs, brachiopods, bryozoans, echinoderms, ascidians, fish, algae and higher plants. For each species a justification motivating its inclusion as an introduction into South African shores or its cryptogenic status, is provided. Challenges associated with this type of inventory work are explored and major patterns of bioinvasion within the region are summarized briefly.

Keywords: bioinvasions; cryptogenic; estuarine; introduced; marine; South Africa

Introduction

The identification and documentation of introduced and cryptogenic species in South Africa remains a relatively recent area of research within this developing region. Griffiths et al. (1992) first recognized and documented 15 introduced species within South African marine and estuarine environments, followed by Griffiths (2000) and Awad et al. (2002) who produced similar inventories, listing 17 introductions. Robinson, Griffiths, McQuaid et al. (2005) were the first to distinguish between introduced and cryptogenic (*sensu* Carlton 1996) species, presenting 10 and 22 confirmed introduced and cryptogenic species respectively.

Given the rich South African shipping history that extends over at least 400 years, since the arrival of the first European settlers, it was recognized that the number of marine introduced and cryptogenic species was more than likely being underestimated (Robinson, Griffiths, McQuaid et al. 2005; Griffiths et al. 2010; Mead et al. 2011). Shipping is recognized as a major vector distributing species across the globe (Hewitt et al. 2009; Minchin et al. 2009) and northern hemisphere regions with similar shipping histories report much higher numbers of introductions (for example, Cohen and Carlton 1998; DeFelice et al. 2001; Ruiz et al. 2000; Galil and Zenetos 2002; Hewitt et al. 2004; Gollasch and Nehring 2006; Leppakoski et al. 2009). Reasons for the shortfall in knowledge of invasions in South Africa include a lack of local taxonomic

*Corresponding author. Email: angela.mead@uct.ac.za

†Present address: Department of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA

expertise, challenges with taxonomic resolution globally of a number of species and a lack of surveys across a number of marine environments and regions in South Africa (Robinson et al. 2005; Griffiths et al. 2010; Mead et al. 2011).

In response to these shortfalls, a protocol was developed with the aim of resolving a more realistic number of regional marine introduced and cryptogenic species. It combined international expertise with accurate taxonomic and systematic work and new sampling surveys as well as a review of historical records and museum specimens held within the Iziko South African Museum collections, Cape Town. Mead et al. (2011) review the advance in knowledge of the marine invasive biota of South Africa, which has grown considerably in a short space of time as a result of applying this protocol. Mead et al. (2011) also present initial assessments of vector history and spatial and temporal patterns of bioinvasion, a brief synopsis of which will be discussed within this paper.

The purpose of the monographic treatment detailed here is to present the motivations and background references that support the inclusion of each of these species in the revised list of introductions and cryptogenics and hence to act as a preliminary guide and reference source for continuation of similar research within South Africa and indeed other developing regions that experience similar resource constraints (Nuñez and Pauchard 2009). This gives a clear insight into the mechanics, range of information sources and research techniques involved in the decision-making process. Details of the history, systematics, vectors and biogeography of the introduced and cryptogenic marine and estuarine protists, invertebrates, fish, birds, algae and higher plants of the South African coast are presented.

Materials and methods

Mead et al. (2011) set forth the basic methods by which an expanded understanding of invasion diversity was achieved; an abridged version is given here. Criteria identified by Carlton (1996), Chapman (1988) and Chapman and Carlton (1991) were used to distinguish introduced, cryptogenic and native species. The evidence used to assign either “introduced” or “cryptogenic” status is detailed in each species treatment below (hereafter referred to as a “vignette”). The cryptogenic species treated here are only of this biogeographic category: a great many more species, with additional investigation, would doubtless qualify for cryptogenic status.

In some cases we have chosen examples of taxa from known species complexes (such as within the polychaete worm genus *Capitella*, the hydroid *Eudendrium* and the amphipod *Caprella*), emphasizing that harbour and port clades of these lineages are not biogeographically resolved. An attempt has been made to strengthen knowledge of dates of first collection, origins, vectors and biogeography, as well as to summarize what is known of the impacts of these species.

Date of first known collection

These dates were derived from several sources. Primary, peer-reviewed literature, archives and museum websites were searched to determine whether an actual collection date had been published or recorded for a given species. In addition, specimens deposited at the Iziko South African Museum, Cape Town were studied for earliest records. A great many early collections of South African animals and plants made

their way to northern hemisphere institutions, such as the British Museum (Natural History) (London, UK), the Museum National d'Histoire Naturelle (Paris, France) and the Smithsonian Institution (Washington, DC, USA). Such collections warrant future investigation, as they may provide a rich resource for further resolving the history of many of the species discussed here. On occasion, the first date of collection derives directly from the first specimens in hand obtained during sampling work conducted by the authors or colleagues.

It is important to note that the date of first collection may be many years after a species in fact entered South Africa and became well-established and spread. This is particularly the case for earlier invasions because very few baseline biological collections were made in the first few centuries of foreign vessel contact with South African shores. For bioinvasions first detected in the late twentieth or early twenty-first centuries, the collection date is more likely to be closer to the actual date of introduction, particularly for relatively large-bodied organisms (such as the mussel *Mytilus galloprovincialis*) that appear in communities that have received careful attention over the past few decades. On the other hand, newly detected smaller-bodied organisms (such as the wood-boring isopod *Limnoria tripunctata*) found within relatively undersurveyed habitats may have simply been overlooked for many decades, if not centuries.

Region of origin

Native regions were determined from a combination of published literature and deductions based upon multiple sources of evidence, such as the distribution of ostensibly “sister” taxa, usually at the species level. By definition “cosmopolitan” species have no region of origin and it should be noted that many such taxa are in fact probably composed of species complexes.

Distribution in South Africa

Distribution was based upon primary literature records, museum and field records, combined with personal communications from colleagues. Continuous distributions along the coast were distinguished from species that are known from only one or two locations. It was important not to imply that certain taxa range continuously between two or more points at which they have been recorded, particularly when these are disturbed sites, such as harbours.

Probable vectors

Probable human-mediated transport vectors were assigned based upon peer-reviewed literature imparting knowledge of the history and biology of a given species.

Known ecological and environmental impacts

Where possible, discussions of environmental and ecological impacts were based upon experimental evidence (either within South Africa or in other regions where available). Observational studies have also been noted. For many of the introduced species recorded here, it should be emphasized that there are no data (experimental or observational) on their impact and so no conclusions can be reached as to whether or not they have led to alterations in the communities they now occupy.

Results

In total, 86 introduced and 39 cryptogenic species, distributed over 17 major taxonomic groups, are recognized in the South African inventory of marine and estuarine bioinvasions to date. Recent additions to the inventory have increased the total number of known introductions and cryptogenics threefold in comparison with previous lists (Mead et al. 2011). Specimens of these species have been deposited in the Iziko South African Museum, Cape Town. The distribution of each introduced species in South Africa is summarized in Table 1 according to biogeographic region or the transitional zones in between (Figure 1), modified after the definitions provided by Lombard (2004).

Table 1. Known South African distribution of marine and estuarine introductions

Taxon	South African Biogeographic Distribution					
	WC	TZ1	SEC	TZ2	EC	NEC
PROTOCTISTA						
<i>Mirofolliculina limnoriae</i>	X					
DINOFLAGELLATA						
<i>Alexandrium minutum</i>	X					
<i>Alexandrium tamarense</i> -complex	unknown					
<i>Dinophysis acuminata</i>	X					
PORIFERA						
<i>Suberites ficus</i>	X					
CNIDARIA						
Anthozoa						
<i>Metridium senile</i>	X					
<i>Sagartia ornata</i>		X				
Hydrozoa						
<i>Coryne eximia</i>		X				
<i>Gonothyrea loveni</i>	X					
<i>Laomedea calceolifera</i>		X				
<i>Moerisia maeotica</i>		X				
<i>Obelia bidentata</i>	X					
<i>Obelia dichotoma</i>	X	X	X			
<i>Obelia geniculata</i>	X					
<i>Pachycordyle navis</i> *	X					
<i>Pennaria disticha</i>					X	X
<i>Pinna larynx</i>		X	X			
<i>Pinna ralphii</i>		X				X
ANNELIDA						
Polychaeta						
<i>Boccardia proboscidea</i> †			X			
<i>Dodecaceria fewkesi</i>	X					
<i>Ficopomatus enigmaticus</i>	X	X	X	X	X	X
<i>Hydroides elegans</i>		X				
<i>Janua pagenstecheri</i>	X	X	X	X	X	
<i>Neanthes succinea</i>			X		X	

(Continued)

Table 1. (Continued).

Taxon	South African Biogeographic Distribution					
	WC	TZ1	SEC	TZ2	EC	NEC
<i>Neodexiospira brasiliensis</i>	X	X	X			
<i>Polydora hoplura</i>			X		X	
CRUSTACEA						
Cirripedia						
<i>Amphibalanus venustus</i>			X	X	X	X
<i>Balanus glandula</i>	X					
Copepoda						
<i>Acartia spinicauda</i>				X		
Isopoda						
<i>Dynamene bidentata</i>			X			
<i>Limnoria quadripunctata</i>	X	X	X			
<i>Limnoria tripunctata</i>	X					
<i>Paracerceis sculpta</i>			X			
<i>Sphaeroma serratum</i>					X	
<i>Sphaeroma walkeri</i>					X	
Amphipoda						
<i>Apocorophium acutum*</i>	unknown					
<i>Chelura terebrans</i>	X	X	X			
<i>Cerapus tubularis</i>	X	X	X	X	X	X
<i>Erichthonius brasiliensis</i>	X	X	X	X	X	X
<i>Ischyrocerus anguipes</i>	X	X	X	X	X	X
<i>Jassa marmorata</i>	X				X	X
<i>Jassa morinoi</i>		X	X	X	X	X
<i>Jassa slatteryi</i>	X	X	X			
<i>Monocorophium ascherusicum</i>						X
<i>Orchestia gammarella</i>		X	X	X		
<i>Platorchestia platensis*</i>				X		
Decapoda						
<i>Carcinus maenas</i>	X					
<i>Xantho incicus</i>	X					
PYCNOGONIDA						
<i>Ammothella appendiculata*</i>					X	
INSECTA						
Coleoptera						
<i>Cafius xantholoma</i>	X	X	X	X	X	X
MOLLUSCA						
Gastropoda						
<i>Catriona columbiana</i>	X					
<i>Littorina saxatilis</i>	X		X			
<i>Tarebia granifera</i>						X
<i>Thais blanfordi</i>						X
<i>Thais tissoti</i>					X	
Bivalvia						
<i>Crassostrea gigas</i>	X		X			

(Continued)

Table 1. (Continued).

Taxon	South African Biogeographic Distribution					
	WC	TZ1	SEC	TZ2	EC	NEC
<i>Lyrodus pedicellatus</i>		X				
<i>Mytilus galloprovincialis</i>	X	X	X	X		
<i>Ostrea edulis</i>	X					
<i>Perna viridis</i>				X		
<i>Semimytilus algosus</i>	X					
<i>Teredo navalis</i>			X			
BRACHIOPODA						
<i>Discinisca tenuis</i> [†]		X				
BRYOZOA						
<i>Bugula dentata</i>			X	X	X	X
<i>Bugula flabellata</i>	X	X	X			
<i>Bugula neritina</i>		X	X	X	X	X
<i>Conopeum seurati</i>	X	X				
<i>Cryptosula pallasiana</i>	X	X				
<i>Watersipora subtorquata</i>	X	X				
ECHINODERMATA						
<i>Tetrapyrgus niger</i>	X					
<i>Ophiactis savignyi</i>						X
CHORDATA						
Ascidacea						
<i>Ascidia sydneyensis</i>		X	X			
<i>Ascidella aspersa</i>	X					
<i>Botryllus schlosseri</i>	X	X	X	X	X	
<i>Ciona intestinalis</i>	X	X	X	X	X	
<i>Clavellina lepadiformis</i>	X	X	X	X	X	
<i>Cnemidocarpa humilis</i>	X	X				
<i>Diplosoma listerianum</i>	X	X	X	X	X	
<i>Microcosmus squamiger</i>			X	X	X	X
<i>Styela plicata</i>	X		X	X	X	X
PISCES						
<i>Cyprinus carpio</i>	X	X	X	X	X	X
RHODOPHYTA						
<i>Anthithamnionella spirographidis</i>	Unknown					
<i>Schimmelmania elegans</i>	X					
<i>Schottera nicaeensis</i>					X	X
CHLOROPHYTA						
<i>Cladophora prolifera</i>					X	
<i>Codium fragile fragile</i> *	X	X	X			
HIGHER PLANTS						
<i>Ammophila arenaria</i>	X	X	X	X	X	

Notes: Regional key: WC (west coast: cool-temperate); TZ1 (False Bay transition zone); SEC (southeast coast: warm-temperate); TZ2 (East London transition zone); EC (east coast: subtropical); NEC (northeast coast: tropical) modified after Lombard (2004). Refer to Figure 1.

*Not collected for over 50 years but retained within inventory (see text discussion).

[†]Found only within marine aquaculture facilities.

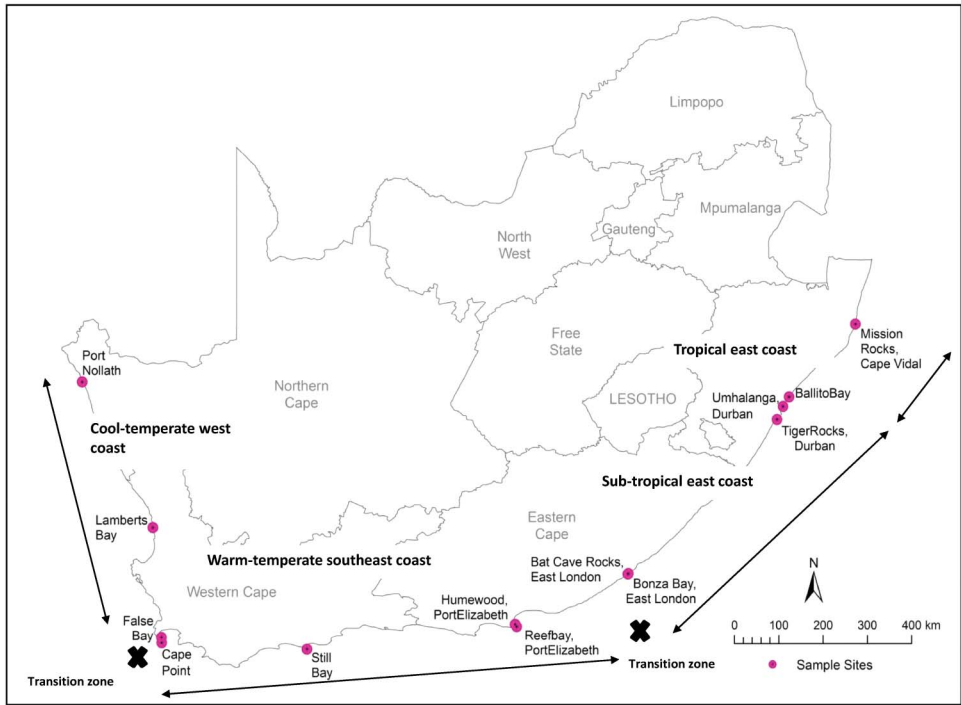


Figure 1. Biogeographic regions and transition zones of South Africa. Modified after Lombard (2004).

Systematic accounts of introduced and cryptogenic species

Kingdom CHROMALVEOLATA

Numerous species of protists, ranging from free-living hypotrichous ciliates to ecto-commensal and endosymbiotic taxa, have probably been introduced to South Africa over the past several centuries. However, no biogeographic review of the marine and estuarine protozoans for southern Africa has been conducted and the regional fauna remains almost completely undescribed, which is very much reflective of the global situation. We therefore note only two (of what may be scores) of potentially introduced and cryptogenic species here.

Phylum CILIOPHORA Order HETEROTRICHIDA Family FOLLICULINIDAE

Mirofolliculina limnoriae (Giard, 1883)

Introduced

This tiny green folliculinid protist is host-specific and lives on the dorsal surface of the pleotelson of the wood boring isopod (gribble) *Limnoria* (Delgery et al. 2006).

We found this species in September 2008 on *Limnoria tripunctata* collected from wooden pilings in Table Bay Harbour, Cape Town. It has doubtless been present in South Africa for a very long time. We regard it as a co-introduction with *Limnoria tripunctata*. However, the biogeographic origins of both host and commensal remain unknown.

Order **PERITRICHA**
Family **ZOOTHAMNIIDAE**

Zoothamnium sp.

Cryptogenic

This abundant colonial protist is often a dominant member of marine and estuarine microfouling communities. Millard (1952) may have been among the first to note its presence (as “*Zoothamnion*”) in South Africa, reporting it within fouling records from Table Bay Harbour, Cape Town. The collections were made in 1947–1949. Assuming the one or more species present in South African harbours are not native, they were probably introduced centuries ago with ship fouling. Modern era introductions have no doubt supplemented the populations by means of ballast water.

Phylum **DINOFLAGELLATA**
Class **DINOPHYCEAE**

A thorough review of the biogeographic and evolutionary history of dinoflagellates in South Africa still remains to be done. We identify three taxa that we regard as introductions. Many more species of South African dinoflagellates, as well as estuarine and marine diatoms, bear strong consideration as possible introduced and cryptogenic taxa. Marangoni et al. (2001) consider the potential for the introduction of exotic phytoplankters by ballast water in South Africa. Hallegraeff (1998) and Bolch and de Salas (2007) further demonstrate the efficacy and probabilities of the transport of dinoflagellates by ships’ seawater ballast.

Order **PERIDINIALES**
Family **GONYAULACACEAE**

Alexandrium tamarense-complex
(Group I *sensu* Lily et al. 2007)

Introduced

Saxitoxin-producing *Alexandrium* dinoflagellates are responsible for paralytic shellfish poisoning, which was unambiguously first reported from South Africa in 1948 (Sapeika 1948). South African populations are genetically members of Group I of a monophyletic clade with origins in the northern hemisphere (Lily et al. 2007). Reports of possibly historical paralytic shellfish poisoning incidents in South Africa, as early as 1888 (Sebastian et al. 2005; Lily et al. 2007), do not preclude introduction by ballast water, which was already in international use by that time (Carlton 1985). This complex includes several other species, including *Alexandrium catenella*. It seems probable that

the modern-day (twentieth century) occurrences of *Alexandrium tamarense* in South Africa may be linked to increased shipping traffic during and after World War II.

Alexandrium minutum Halim, 1960
(Global clade *sensu* Lily et al. 2005)

Introduced

Alexandrium minutum was first recorded in South Africa in 2003 when it formed a bloom in Cape Town Harbour (Pitcher et al. 2007). Molecular analysis indicates that it groups with a monophyletic “global clade” found in Europe and in Western Australia, which Lily et al. (2005) suggested was native to Europe. Pitcher et al. (2007) suggest that “the same consideration can be made of the South African population present at Cape Town Harbour, moreover because this species has not been previously reported in the region.” Despite this comment, Pitcher et al. (2007) concluded their paper by noting that the phytoplankton flora of southern Africa is poorly known, and that “it is difficult to assess whether this first record of *Alexandrium minutum* in South African waters represents a new introduction to the region.” Nevertheless, we are compelled by the global genetic picture that paints a path back to the European-Mediterranean theatre as the biogeographic roots of this clade, which was probably dispersed through ballast water.

Family **DINOPHYSACEAE**

Dinophysis acuminata Claparède and Lachmann, 1859

Introduced

Dinophysis acuminata, the cause of diarrhoetic shellfish poisoning, was long known from Europe, where it was first described from Norway in the mid-nineteenth century. Reported worldwide since then, it was first detected in South Africa in 1991 (Pitcher et al. 1993). In March 1994 it appeared as part of a multi-species harmful algal bloom in St Helena Bay (Matthews and Pitcher 1996). We regard it as transported by ballast water, in which it has been found (Okamoto et al. 2007).

Kingdom **ANIMALIA**
Phylum **PORIFERA**
Class **DEMOSPONGIAE**
Family **SUBERITIDAE**

Suberites tylobtusus Lévi, 1958

Not introduced

Uriz (1990) proposed that this Red Sea sponge, found at depths of 100–500 m, was translocated by fisheries activities to the continental shelf off southern Africa, between Namibia and South Africa, where earlier thorough surveys over many decades had failed to detect it. Uriz proposed that this introduction may have occurred between 1960 (when the fisheries activity in question commenced) and 1984, the date of the first collections. However, it is now recognized as a mis-identification and is therefore not introduced (Uriz personal communication 2009). We follow the World Porifera Database in the spelling of the species name.

Suberites ficus (Johnston, 1842)**Introduced**

This European irregularly rounded, yellow sponge is lobed and has large oscula that are flush with the sponge surface. It was first reported within South Africa from specimens collected in 1998 (Samaai and Gibbons 2005). It can form significant fouling growths, which provide habitat to other smaller animals, and is found within docks on hard substrata. It is recorded from Luderitz to Table Bay docks and the most probable vector is ship fouling.

Phylum **CNIDARIA**
 Class **ANTHOZOA**
 Family **SAGARTIIDAE**

Sagartia ornata (Holdsworth, 1855)**Introduced**

Acuna et al. (2004) report the discovery of this well-known European sea anemone in 2002 in Langebaan Lagoon on the west coast, where it is found in the intertidal zone among the cryptogenic salt marsh plant *Spartina maritima* and attached to stones shallowly buried in sand. Robinson et al. (2004) provide quantitative data on its abundance at Langebaan, where its populations can reach hundreds of individuals per m². However, we take the first record to be 1955, when Day (1955) reported a *Sagartia*-like species from the same location. No other native South African sea anemone could be confused with this distinctive species. The first museum records are from Langebaan in 1963 (SAM collections: catalogue numbers H1579 and H1594). Ship fouling and ballast water are the most probable vectors.

Metridium senile (Linnaeus, 1761)**Introduced**

This large, white Northern Hemisphere sea anemone with distinctive frilly tentacles was first detected in September 1995 in Table Bay Harbour, Cape Town (Griffiths et al. 1996), where it occurs on a wide variety of substrata from 6 to 12 m depth. In 2006 photographic evidence was presented to the authors of a deep-water population of *Metridium senile* at depths up to 126 m. These populations were associated with oil-rigs on the Agulhas Bank off the south coast. Ship fouling from the North Atlantic or the North Pacific is a probable vector for the harbour population.

Class **HYDROZOA**

As with other challenging groups, we can only make a first approximation of the numbers of introduced hydroids, especially as these invasions may have commenced in the 1600s. We select, as examples only, 11 species of hydroids as introduced and three species as cryptogenic. There are dozens, if not scores, of species of hydroids that could be considered for candidacy as introduced or cryptogenic in the South African fauna. For example, of the eight hydroid taxa identified to species found by Henschel et al. (1990) on fouling panels in Simon's Bay (False Bay), we consider two

species (*Obelia dichotoma* and *Tubularia warreni*, the latter now known as *Pinauay ralphi*). The remaining species, *Campanularia integra*, *Sertularella arbuscula*, *Plumularia setacea*, *Plumularia lagenifera*, *Nemertesia cymodocea* and *Amphisbetia operculata*, are but six examples (all of which are found elsewhere in the world) of a very large guild of species that bear careful global biogeographic, systematic and genetic study. The 11 introduced species treated here originate either from the North Atlantic, Europe, Eurasia (Ponto-Caspian) or are of unknown provenance. As a consequence, the Pacific taxa (for example, those from Japan or the western Americas) are missing from our assessment. Rather than Pacific hydroids not being represented as introductions in the South African biota, it is probable that species from these regions are buried in the very large “cosmopolitan” (and so cryptogenic) hydrozoan element present in South Africa. For all the examples presented, we consider ship fouling and ballast water the most probable vectors.

Order ANTHOATHECATA (ATHECATA)
Family EUDENDRIIDAE

Eudendrium carneum Clarke, 1882

Cryptogenic

Marques et al. (2000) have reviewed the Mediterranean species of *Eudendrium*, including this species, which is said to be cosmopolitan. Millard (1975) notes its presence as “on ships’ hulls and in littoral and shallow waters” and records it from Durban on the east coast. It may represent a species complex.

Family OCEANIDAE

Pachycordyle navis (Millard, 1959)
(= *Clavopsella navis*)

Introduced

Pachycordyle navis is an example of an exotic species first described from the region to which it was introduced. Schuchert (2004) placed Millard’s *Rhizorhagium navis* (as *Clavopsella navis* in her 1975 monograph) in the genus *Pachycordyle* and recorded a wide European (including Mediterranean and Black Sea) distribution. It was found in 1958 in South Africa on the hull of a ship which had never left Table Bay (Millard 1975). Although not recorded since 1958, it has also not been searched for since then, hence there is no reason to presume that it is not still present.

Family CORYNIDAE

Coryne eximia Allman, 1859
(= *Sarsia exima*)

Introduced

Millard (1975) notes this species as “common in the environs of Cape Town, on ships’ hulls, pylons and floating objects, and also on rocky shores.” The species is of either North Atlantic or North Pacific origin. The first South African specimens were

collected in 1946. In addition to Cape Town docks, Millard (1975) gives the South African distribution as along the west coast as far as Llandudno, with Schuchert (2005) including material from Langebaan on the west coast in his genetic studies.

Coryne pusilla (Gaertner, 1774)

Cryptogenic

Millard (1975) reports this species from KwaZulu-Natal with the original SAM record reflecting distribution from Durban to Mozambique. As this taxon represents multiple species (Schuchert 2005) no origin can be assigned. Introduced port and harbour populations may be embedded within one or more clades, therefore the South African material requires molecular and morphological re-examination.

Family **MOERISIIDAE**

Moerisia maeotica (Ostroumov, 1896)
(= *Ostroumovia inkermanica*)

Introduced

Millard (1970) reported this distinctive Ponto-Caspian species (as *Ostroumovia inkermanica*) from the brackish waters of Nhlange Lake (Kosi Bay), Lake St Lucia, and Lagoa Poelela, all on the east coast. She noted that hydranths occurred at 2–16 m, and that medusae were found in the plankton. Millard (1975) noted that previous suggestions that *Moerisia maeotica* was distributed by ships did not apply to these South African lakes. Other dispersal vectors are therefore involved that would bring this European species to African shores. Further knowledge of the biota of these brackish lakes would clarify these vectors. *Moerisia maeotica* was first collected in 1965.

Family **PENNARIIDAE**

Pennaria disticha (Goldfuss, 1820)
(= *Halocordyle disticha*; = *Halocordyle cooperi* Warren, 1906).

Introduced

This hydroid is now too widespread to determine its biogeographic origins without extensive molecular genetic analysis. The first South African specimens were collected in Natal (now KwaZulu-Natal) in 1906 (Warren 1906, 1907) and were mistakenly re-described as a native species, *Halocordyle cooperi*. Millard (1975) gives the South African distribution as Durban to the Mozambique border on the east coast. The habitat is described as “lower littoral to 3 m and on ships’ hulls” (Millard 1975).

Family **TUBULARIIDAE**

Pinauay larynx (Ellis and Solander, 1786)
(= *Tubularia larynx*)

Introduced

This North Atlantic hydroid was first collected in South Africa in 1947 from the south coast “on a ship’s hull in Table Bay” (Millard 1959, 1975); Peterson (1990) reviews

some of the world records. Millard (1959) notes that “This species has only once before been reported from South Africa, from the Agulhas Bank by Stechow (in) 1925.” Stechow’s material should be re-examined because the recorded depth of 126 m is not probable for this species (Millard 1975; Peterson 1990). We therefore take 1947 as the first verified date of record. Henschel et al. (1990) recorded it within False Bay (also on the south coast) in fouling.

Pinauay ralphi (Bale, 1884)

Introduced

(= *Ectopleura ralphi*; = *Tubularia warreni*)

This North Atlantic species was inadvertently re-described as a new species, *Tubularia warreni*, by Ewer (1953), leading Millard (1975) to list it as a species endemic to South Africa. Ewer’s material was collected in 1947 from Durban Harbour. It is “common in dock areas on pylons and on ships’ hulls” (Millard 1975). She also notes that Broch’s record in 1914 of “*Tubularia crocea*” (now known as *Pinauay crocea*) from Luderitz Bay is “probably referable to *T. warreni*”. However, as Millard notes, “the specimens were young and no description was given,” and we do not further consider the record here. Peterson (1990) synonymized Ewer’s *Tubularia warreni* with *Pinauay ralphi* (as *Ectopleura ralphi*), known only from harbours in Australia and South Africa. As Peterson noted, *Pinauay ralphi* “is practically identical to *E. crocea*” and, indeed, it may be an ecophenotype of that species, or reflect hundreds of years of isolation from the stem species. The molecular genetics of this clade have not been studied. *Pinauay ralphi* is a member of the Northern Hemisphere ectopleuras (Peterson 1990) and is clearly native specifically to the North Atlantic, as is its sister (or identical) species *Pinauay crocea*. Presciently, Millard (1959) recognized that *Tubularia warreni*, albeit ostensibly endemic to South Africa, might not be specifically distinct from *Tubularia crocea* and speculated that it might be introduced from Europe. We retain *Pinauay ralphi* as a distinct species here and presume that Millard’s (1952) record of *Tubularia crocea*, collected in 1947–1949, from Table Bay Harbour, is this species. As a consequence, we take the date of 1947 as the first record of this species from South Africa.

Subclass LEPTOTHECATA (THECATA)

Family CAMPANULARIIDAE

Laomedea calceolifera (Hincks, 1871)

Introduced

(= *Eulaomedea calceolifera*; = *Campanularia calceolifera*; = *Laomedea angulata*).

This well-known North Atlantic fouling hydroid was recorded from Cape Town docks by Millard (1959) as *Laomedea angulata* and Millard (1975) as *Eulaomedea calceolifera*. Millard (1959) and Millard (1978) (recorded as *Campanularia calceolifera*) regard it as introduced by ships to South Africa. Zvyagintsev (2003) discusses its anthropogenic dispersal out of the North Atlantic Ocean since the nineteenth century. Stechow’s (1925) record of this species from 70 m in Simon’s Bay (False Bay) is in doubt (Millard 1978) and we do not include it here. Hence, the first South African collections of *Laomedea calceolifera* were made in 1948 (Millard 1959).

Gonothyrea loveni (Allman, 1859)**Introduced**

Millard (1975, 1978) suggested that this well-known North Atlantic hydroid was introduced to the southern hemisphere by ships, with which conclusion we agree. Millard (1975) noted that it was restricted to Cape Town docks “on ships’ hulls, experimental submerged plates, pylons and cables.” The first South African collections were made in 1946 (Millard 1959).

Obelia bidentata Clark, 1875
(= *Obelia bicuspidata*)**Introduced**

We recognize the harbour, port and lagoon populations of this and the other two species of *Obelia* treated here as introduced. Although invasions (such as *Mytilus galloprovincialis* and *Balanus glandula*) occur on open rocky shores and in offshore waters (such as *Metridium senile*) of South Africa, we reserve judgement on the biogeographic status of the populations of *Obelia* from other than harbours until genetic data are in hand. The first collections of which we are aware were made in 1948 on the hull of a ship in Table Bay. Millard (1975) notes the habitat as “on ships’ hulls, hermit shells and weed” and gives an additional South African distribution as Durban to the Mozambique border on the east coast. In the absence of global population molecular genetics, the biogeographic origin of this and the following two *Obelia* spp. remains unknown.

Obelia dichotoma (Linnaeus, 1758)**Introduced**

As noted above, we regard inshore populations as the probable non-native genotypes of these *Obelia* clades. Millard (1975) notes, “Colonies are commonly epizootic on other hydroids and algae, and have also been found on *Squalus acutipinnis*, *Aulacomya magellanica* (now *Aulacomya ater*), *Lepas* sp. and *Caretta caretta*. It is very common in dock areas on pylons and ships’ hulls.” We suggest that these non-harbour habitats may represent native *dichotoma*-like clades. The first collections appear to be those from 1938. Millard (1975) gives the South African distribution as Lambert’s Bay on the west coast to Algoa Bay on the south coast.

Obelia geniculata (Linnaeus, 1758)**Introduced**

Millard (1975) described the habitat of this species as, “littoral to 80 m . . . and on ships’ hulls, especially common on laminarians, also on *Jasus lalandii*.” We suggest that the deep-water populations, including those on the rock-lobster *Jasus*, may not be genetically identical to global harbour populations of this species. The first collections that have come to our attention are those from 1934 in Oudekraal, on the Cape Peninsula. Millard (1975) gives the South African distribution as Lambert’s Bay on the west coast to Cape Town Docks.

Phylum ANNELIDA
Class POLYCHAETA

We consider ship fouling and ballast water to be the most probable vectors for all of the examples of polychaetes given here.

Family NEREIDAE

Neanthes succinea (Leuckart, 1847)

Introduced

This estuarine polychaete was first recorded in South Africa by Day and Morgans in 1956, based on specimens from Durban Bay (east coast) and has been described as “fairly common in muddy estuaries” (Day 1967). Originating from the North Atlantic, its South African distribution is recorded as Mossel Bay, Plettenberg Bay and Port Elizabeth on the southeast coast, as well as Durban (Day 1967).

Family CAPITELLIDAE

Capitella sp. / spp. complex

Cryptogenic

One or more species of *Capitella* occur in fouling communities in South African harbours. Almost certainly some of these taxa are non-native. South African material requires molecular and morphological re-examination. Millard (1952) reported *Capitella capitata* in fouling, in Table Bay Harbour, a name long abandoned and known to encompass many species. It continues to be reported under this name in South African estuaries (Schlacher and Wooldridge 1996; Teske and Wooldridge 2003, 2004).

Family CIRRATULIDAE

Dodecaceria fewkesi Berkeley and Berkeley, 1954

Introduced

This polychaete constructs large, greyish, rock-like structures composed of individual tubes of hundreds of jet black worms, each of which has a long pair of feeding tentacles (prostomial palps). Behind these lie four or five pairs of prominent elongate branchiae. It is thought that colonies are derived asexually from a single individual and hence retain the sex of the founder. The species (identification by James A. Blake, January 2008) was first observed in Table Bay Docks in 2007, where it formed regularly spaced, fist-sized colonies on a vertical concrete wharf. A strong black pigment was released when the colonies were handled and preserved. *Dodecaceria fewkesi* is native to the Pacific coast of North America, ranging from British Columbia to southern California, where it can form massive sheets of rock-like colonies more than one metre in length (Abbott and Reish 1980). It occurs in the “middle intertidal zone on protected rocky shores and dock pilings” (Abbott and Reish 1980), typically in fully

marine situations (J. T. Carlton, personal observations) on open coasts, not in estuaries or bays. Its presence on harbour pilings (Abbott and Reish 1980), presumably in such sites as the marine pilings of Monterey Bay wharves in central California, however, suggests possible interfaces with ship-mediated transport. Reminiscent of *Balanus glandula*, *Dodecaceria* is a species capable of living on outer coasts as well, and we therefore predict that it will make its way out of Table Bay in due course.

Family SPIONIDAE

Polydora hoplura Claparede, 1870

Introduced

This well-known European mudworm was first reported from the southern hemisphere by Millard (1952) as “*Polydora hoplura?* (common)” in fouling in Table Bay Docks on the south coast. This was based upon specimens collected as early as 1947. Day (1967) noted intertidal and shallow water stations in South Africa from Saldahna Bay (west coast) to Plettenberg Bay on the south coast. It was next found in New Zealand by Read (1975), based upon specimens collected in 1972. Read’s independent determination of this species from New Zealand lends support to Day’s identification of this species from South Africa. We accept this species as an introduction, pending genetic confirmation that these populations are derived from Europe. Nel et al. (1996) reported upon the forming of mud blisters and infestations by *Polydora hoplura* in commercially reared oysters in South Africa. In 2006, Simon et al. found this species to be one of several spionids infesting cultured South African abalone farms, where it was subsequently reported from farms in Saldahna Bay and Hermanus on the same species (Simon et al. 2006; Simon and Booth 2007).

Boccardia proboscidea Hartman, 1940

Within aquaculture facilities

Boccardia proboscidea is a tube-dwelling polychaete often found on the surfaces of oysters, abalones and other molluscs. It originates from the North Pacific Ocean and is considered to be an introduction to Australia (Blake and Ruff 2007). Simon et al. (2006) first reported this species in South Africa, based on specimens collected in 2004. It is one of several spionids embedded within the shells of *Haliotis midae* cultured in abalone farms. In addition, *Boccardia proboscidea* has been collected from abalone farms in Jakobsbaai (near Saldahna Bay) and Hermanus. Subsequently, *Boccardia proboscidea* has been found embedded within oyster shells from farms in Knysna and Alexander Bay (T. Haupt, personal communication 2009). To date, wild populations have not been identified (Simon and Booth 2007; Simon et al. 2009), so this species will not be counted within the overall number of wild introductions. However, it should be noted that this species has not been looked for within open environments outside aquaculture facilities.

Family SERPULIDAE

Ficopomatus enigmaticus (Fauvel, 1923)
(= *Mercierella enigmatica*)

Introduced

This well-known tubeworm constructs large reefs of entwined calcareous tubes; the animal's opercula are cone-shaped and edged by about 25 tiny chitinous spines. Colonies have been observed up to 50 cm across and are found attached to hard substrata in estuaries. It is thought to originate in southern or western Australia (Carlton unpublished). Its presence in South Africa was first recorded in 1955, based on specimens collected in 1951 (by Day, as *Mercierella enigmatica*) and by 1967 its South African distribution was described by Day as 'widespread.' Blaber et al. (1974) reported it from the deep, fjord-like Maikaba Estuary, 30 km north of Port St Johns on the Pondoland (east) coast, where it occurs down to 33 m and was the 'only species found below' 10 m. *Ficopomatus enigmaticus* ranges from Milnerton Lagoon (Table Bay) on the west coast to Kosi Bay on the east coast and was introduced by ship fouling. The reefs *Ficopomatus enigmaticus* forms are perceived as a problem in areas such as Zandvlei on the Cape Peninsula, where dense encrustations on the walls of canals can be hazardous to residents, who make intense recreational use of these waterways (Davies et al. 1989). In addition, Davies et al. (1989) highlight the role that the filter-feeding activity of the worm may play within estuaries in terms of reducing particle loads. For example, in the Zandvlei system *Ficopomatus enigmaticus* are estimated to remove up to 130 kg wet mass of suspended material per hour, effectively filtering the entire water volume every 26 h. Although this could be described as a "positive" effect relative to apparent water quality, we note that water clarity and water cleanliness are not necessarily the same (i.e. the load of free, non-adsorbed toxic compounds in the water may not be reduced). In addition, filter-feeders enhance pelagic-benthic coupling, depositing large amounts of pseudofaeces into the benthos, leading to enhanced bio-concentration of pesticides, heavy metals and other pollutants that were adsorbed onto particulate material. Finally, *Ficopomatus enigmaticus* may be competing with native filter-feeders in South African estuaries, reducing the population sizes of such species.

Hydroides elegans (Haswell, 1883)

Introduced

Henschel et al. (1990) reported this slender, Indo-Pacific tube-dwelling polychaete in False Bay in 1979 within fouling communities. This was based on specimens collected in 1970 (Iziko South African Museum collection).

Neodexiospira brasiliensis (Grube, 1872)

Introduced

(= *Janua brasiliensis*; = *Spirorbis foraminosus*)

This Indo-Pacific polychaete was originally misidentified and recorded as present in South Africa as *Spirorbis foraminosus* by Day in 1961, based on specimens collected in 1953 (SAM collection). In 1967, Day noted the presence of *Neodexiospora brasiliensis*, again as *Spirorbis foraminosus*, from Table Bay. Knight-Jones and Knight-Jones (1974) give its South African distribution as Cape Town to Port Elizabeth, where it has since been found on the algae, *Ceramium planum*, in shore pools (Knight-Jones et al. 1975).

Janua pagenstecheri (de Quatrefages, 1865)

Introduced

This European estuarine polychaete was first collected in South Africa in 1971 and is found from Cape Town Docks to Durban on the east coast (Knight-Jones et al. 1975). Day's 1967 monograph does not include *Janua pagenstecheri*.

Simplicaria pseudomilitaris Thiriot-Quiévreux, 1965
(= *Pileolaria pseudomilitaris*)

Cryptogenic

As with *Janua pagenstecheri*, this estuarine polychaete was first collected in South Africa in 1971 (Knight-Jones et al. 1975) and is absent from Day's 1967 monograph. While first described from the Mediterranean, it has now been widely reported from the Atlantic and Pacific Oceans and its origin remains unknown.

Subphylum **CRUSTACEA**
Order **CIRRIPEDIA**
Family **BALANIDAE**

Balanus glandula Darwin, 1854

Introduced

Balanus glandula is a common mid-intertidal barnacle, occupying exposed rocky shores on the west coast of North America. Introduced populations are now known from Argentina, Japan and South Africa. Its presence in South Africa was first reported by Simon-Blecher et al. (2008), based upon specimens first collected in Cape Town in 2007. However, photographic evidence indicates that populations were already well established by 1992 on the Cape Peninsula (Laird and Griffiths 2008). It now ranges from Cape Point to Eland's Bay on the west coast (Laird and Griffiths 2008). It is the most abundant barnacle within the invaded area and major impacts on the distribution and abundance of other organisms in its range are predicted. We consider ship fouling to be the most likely vector of this species.

Amphibalanus venustus (Darwin, 1854)

Introduced

(= *Balanus venustus*; = *A. amphitrite* of authors, not of Darwin)

This pink-striped barnacle was first recorded from Salisbury Island, in Durban Harbour, KwaZulu-Natal in 1938 as *Balanus amphitrite* (Henry and McLaughlin 1975). It was not recorded by Barnard (1924) in his monograph on South African barnacles. Found on the low-shore under boulders, the origins of this species lie in the tropical and subtropical western North Atlantic (Carlton unpublished results). Its South African distribution ranges from Hermanus on the south coast to Mozambique (east coast) and we considered ship fouling to be the vector.

Subclass **COPEPODA**
 Order **CALANOIDA**
 Family **ACARTIIDAE**

Acartia spinicauda Giesbrecht, 1889

Introduced

Acartia spinicauda is a planktonic copepod that originates from the coastal regions and estuaries of the western Pacific (Japan, China, Indonesia and India). The first South African record is from 2003 in Richard's Bay Harbour on the east coast (Jerling 2008). It is thought to have been present both in Richard's Bay and Durban Harbour (also on the east coast) 15 years earlier, since at least 1993 (A. Connell CSIR Durban, personal communication). We consider this species to be a ballast water introduction.

Order **ISOPODA**
 Family **SPHAEROMATIDAE**

Dynamene bidentata (Adams, 1800)

Introduced

Dynamene bidentata is easily recognized by the large paired horn-like projections extending backwards from the posterior margin of pereon segment six and the enlarged, outward-pointing uropods. The first South African record of this rocky infaunal isopod is from 2006 by the authors in Port Elizabeth harbour on the south-east coast. Maggiore and Fresi (2008) record it as native to the Atlantic coast of Europe and as possibly introduced in the Mediterranean. We consider ship fouling and ballast water as the vectors.

Sphaeroma serratum (Fabricius, 1787)

Introduced

This intertidal isopod is especially common on mangroves and is native to Europe. It was subsequently introduced to Australia, the southeast coast of Africa and Argentina (Kittlein 1991) and first recorded from Durban Bay on the east coast of South Africa in 1950 (Barnard 1951; Day and Morgans 1956). We consider ship fouling and ballast water to be the vectors.

Sphaeroma annandalei Stebbing, 1911

Cryptogenic

This intertidal isopod is found in estuarine systems where it bores into waterlogged mangrove wood. It was first described from and appears to be at least native to the Indian subcontinent (Pillai 1961); it also occurs in the Persian Gulf, where it was redescribed as *S. irakiensis* Ahmed, 1971 (Harrison and Holdich 1984), and it has been introduced to Brazil (Loyola and Silva 1960). We consider *Sphaeroma annandalei* as a possible introduction to KwaZulu-Natal on the east coast of South Africa. It was first recorded in 1926 at the mouth of the Mtunzini River. The most likely mode of introduction is ship fouling and ballast water; it remains cryptogenic, however, as infested floating mangrove wood may also be a vector.

Sphaeroma terebrans Bate, 1866**Cryptogenic**

Sphaeroma terebrans is an estuarine wood-borer associated mainly with aerial roots of mangroves. It is thought to originate from the northern Indian Ocean, but is now widely distributed in warm and tropical waters including Australia, Sri Lanka, East Africa, Costa Rica, Brazil and the eastern and Gulf regions of the United States. The first South African record is from Barnard (1940). Its South African distribution ranges from Knysna Estuary on the southeast coast to Mtunzini River on the east coast. Ship fouling and ballast water are the likely vectors, although infected mangrove wood may also be a possible vector.

Sphaeroma walkeri Stebbing, 1905**Introduced**

This fully marine species is found in estuaries to 5 m depths and is associated with fouling communities, as a result it is now one of the most widely distributed ship-transported isopods in the world. Its origins lie in the northern Indian Ocean (Carlton and Iverson 1981), from where it was subsequently introduced to California, Florida, East Africa, Hong Kong and Spain, to name but a few regions. It was first collected in South Africa in 1915 and in 1917 in 9 m of water in Durban (Barnard 1920), and by Stebbing (1917), without specified collection date, from Durban Bay on posts with ascidians. Ship fouling and ballast water are, without a doubt, the most likely vectors.

Paracerceis sculpta (Holmes, 1904)**Introduced**

This is an intertidal sphaeromatid isopod easily identified by its granular pleon, three prominent longitudinal ridges on the pleotelson and greatly extended, pointed exopod (of the uropod). It is found in shallow water on rocky shores. The first South African record is from Port Elizabeth harbour on the southeast coast in Barnard (1940). It originates from the Pacific coast of North America, but has also been recorded from Hawaii, Hong Kong, Australia, Brazil and the Mediterranean (Espinosa-Perez and Hendrickx 2002). We consider it a ship fouling and ballast water introduction.

Family **IDOTEIDAE**

Synidotea hirtipes (Milne-Edwards, 1840)**Cryptogenic***Synidotea variegata* Collinge, 1917**Cryptogenic**

Chapman and Carlton (1991) proposed that these two isopods were cryptogenic in the South African fauna. We note them here because they represent a broad guild of peracarid crustaceans (including amphipods, isopods and tanaids) that occur in fouling communities from the West African coast to the Indo-Pacific, almost all of which distributions are now regarded as “natural” but whose aboriginal ranges, before the advent of interoceanic shipping, we in fact do not know. To list all of these here

would almost comprise another monograph. *Synidotea variegata*, for example, occurs both in fouling communities and in littoral algal communities from the Indo-Pacific to the west coast of Africa (Chapman and Carlton 1991). It occurs as far north as Cameroon and Namibia on the Atlantic, in Port Elizabeth and KwaZulu-Natal in South Africa, and with further records throughout the greater Red Sea and Indian Ocean region (Mozambique, Madagascar, Suez Canal, India, Sri Lanka). *Synidotea hirtipes* occurs, often in fouling, from the west coast of Africa (Namibia) around South Africa and north to the Suez Canal. Indeed, its type locality is the “Cape of Good Hope” and records include Saldanha, Table Bay, Simon’s Bay, Cape St Blaize (Mossel Bay) and Port Elizabeth (Benedict 1897; Chapman and Carlton 1991). As Chapman and Carlton note (and as is applicable to a great many potential candidate taxa), these distributions also mirror the great shipping routes from China and India to around Africa and Europe, commencing centuries ago.

Family **LIGIIDAE**

Ligia exotica Roux, 1828

Cryptogenic

This semi-terrestrial isopod, now widely reported from harbours around the world, was first recorded in South Africa by Barnard (1932). It was also reported only several years earlier from Namibia (Panning 1924, as Deutsch-Sudwestafrika, or German Southwest Africa). It is now found along the east coast of South Africa (KwaZulu-Natal). Although originally described from the Mediterranean coast of France, and although Van Name (1936) stated that it was “undoubtedly of Old World origin”, its native range is not yet known, pending global genetic analyses. Given its semi-terrestrial nature, we consider dry ballast or dunnage to be the most likely vectors since the earliest days of wooden sailing vessels.

Family **LIMNORIIDAE**

Limnoria quadripunctata Holthius, 1949

Introduced

The first record of wood-boring *Limnoria* in South Africa that has come to our attention is that of Hammersley-Heenan (1897), who reported that in Algoa Bay, “The greenheart piles, fenders, and walings which had been in use for only 8 years, were found to have been attacked in several instances . . . at almost every scarf, and where the vertical fenders were cleated to the walings, the limnoria had completely destroyed the timber under the surface, and in some cases, the fenders could readily be removed by the hand.” Until the mid-nineteenth century, most wood-boring gribbles around the world were referred to as the “cosmopolitan” *Limnoria lignorum*, a clade now recognized as composing many different species. At least two species of introduced limnoriids now occur in South Africa, so re-examination of museum material held in both Europe and South Africa is required to establish distribution and temporal records. Kensley (1978) reported *Limnoria quadripunctata* as occurring from Table

Bay to Port Elizabeth (on the southeast coast). The origins of *Limnoria quadripunctata* and *Limnoria tripunctata* remain unknown, although both may be rooted in the Indo-Pacific. The most likely vector of limnoriid isopods is infested wooden hulls, since the earliest days of wooden sailing vessels, and in more modern times, ballast water.

Limnoria tripunctata Menzies, 1951

Introduced

We found this species infesting wooden pilings at Table Bay docks in 2008, apparently the first report of this species in South Africa. As with *Limnoria quadripunctata*, retrospective examination of museum material is required to establish earlier dates and the distribution of wood-boring limnoriids in South African waters.

Order **AMPHIPODA**
Family **CHELURIDAE**

Chelura terebrans Philippi, 1839

Introduced

Chelura terebrans is a cosmopolitan reddish wood-boring amphipod that is easily recognizable due to its fused urosomites and enormously enlarged third uropods. It is found in temperate waters of both northern and southern hemispheres burrowing into waterlogged wood that has previously been excavated by isopods of the genus *Limnoria*. Stebbing (1910) first reported its presence in South Africa, based on specimens from 1888. It is found in all harbours between Langebaan on the west coast and Port Elizabeth on the east coast and is likely to have been distributed in ship fouling and boring communities in the era of wooden vessels.

Family **AMPITHOIDAE**

Cymadusa filosa Savigny, 1818
(= *Grubia australis* Barnard, 1916)

Cryptogenic

Weaving a nest out of algal fronds, this amphipod inhabits estuarine areas. It was first recorded from South Africa by Barnard (1916) based on specimens collected in 1913. He described it as a new species, *Grubia australis*, and later transferred it to the genus *Cymadusa* (Barnard, 1940); in turn, it was later synonymized with the older name *Cymadusa filosa* by J.L. Barnard (1955). Transport in algae on ships' hulls appears to be the most probable vector. Once thought to be globally distributed, *Cymadusa filosa*, originally described from the Mediterranean (Egypt), has been shown to be a species complex (Peart 2004). South African material now bears re-examination to determine whether the stem species, the Mediterranean *Cymadusa filosa*, is in South Africa, or whether another species is involved.

Family COROPHIIDAE

Corophium triaenonyx Stebbing, 1904**Cryptogenic**

This is one of a series of cylindrical tube-building amphipods commonly associated with fouling communities and it probably originates from Asia. Within South Africa, it is common in brackish-water habitats, ranging from False Bay on the southeast coast to Mozambique (east coast). *Corophium triaenonyx* has been recorded as a dominant peracarid in benthic communities, such as in the Gamtoos Estuary, Eastern Cape Province (Schlacher and Wooldridge 1996) and the Nhlabane coastal lake system, KwaZulu-Natal (Vivier and Cyrus 1999). It was first reported by Barnard (1940), based on material collected in southern Cape estuaries as early as 1931. We regard ship fouling and ballast water as the most probable vectors.

Apocorophium acutum (Chevreux, 1908)
(= *Corophium acutum*)

Introduced

This species builds tubes on algae as well as on hard substrata such as pilings. It appears to originate from the North Atlantic, where it is widespread along the east coast of North America, Europe and the Mediterranean (with a type locality in Algeria). It is now widely distributed in warm-temperate and tropical regions worldwide, with ship fouling and ballast water as the most likely vectors. *Apocorophium acutum* was first collected in South Africa in Durban in 1915 (Barnard 1916, as *Corophium ascherusicum, partim.*). Crawford (1937) noted that Barnard's material contained mixed *Apocorophium acutum* and *Monocorophium ascherusicum*, with the smaller specimens being *Apocorophium acutum*. Although there are no post-1915 records, we retain it in the fauna, presuming that it remains present, mixed with *Monocorophium ascherusicum* populations. The South African distribution is thus unknown.

Monocorophium ascherusicum (Costa, 1857)
(= *Corophium ascherusicum*)

Introduced

This amphipod has a similar habitat to *Corophium triaenonyx*, but is recognized by the coalesced pleon segments 4–6. It builds fragile tubes among fouling communities, especially on man-made structures, and can tolerate a range of salinities. It is considered native to the North Atlantic (but on which side is not yet known) and is now probably one of the most widely distributed amphipods in warm-temperate coastal waters, including the American Atlantic and Pacific coasts, Japan and Australia. It was first recorded in South Africa by Barnard (1916) based on material collected in 1915, in Durban Bay on the east coast and is most likely to have been distributed by ship fouling and ballast water.

Erichthonius brasiliensis Dana, 1853

Introduced

This amphipod constructs muddy tubes on the stems and branches of hydroids and other fouling species. Although originally described from the North Atlantic, it is now

widely distributed in warm seas and may further represent a species complex. It was first collected and reported in South Africa by Stebbing in 1910 and can now be found from Olifants River (west coast) to Mozambique (east coast). It has probably been distributed on ships as a fouling organism.

Family MELITIDAE

Melita zeylanica Stebbing, 1904

Cryptogenic

(= *Melita inaequistylis* of Barnard 1916, not Dana 1852)

This widespread brackish-water amphipod has been recorded from Australia and throughout the Indian Ocean. It occurs in South African estuaries, at times in vast numbers, for example among the tubes of the introduced tubeworm *Ficopomatus enigmaticus* in Zandvlei Lagoon (False Bay). Of interest is that early brackish-water collections of gammarids in locations where *Melita zeylanica* is now abundant did not find this species. Barnard (1916) therefore reported *Austrochiltonia capensis* (as *Chiltonia capensis*) from Milnerton in 1898 and 1913, in “brack[ish]-waters among green weeds,” whereas the first specimens of *Melita zeylanica* were not reported until 1940, by Barnard, based upon specimens collected in 1931 and 1938 from several South African estuaries. However, Barnard (1916) reported collections of *Melita* as *Melita inaequistylis* in 1897 and 1914, but by 1940 he judged South African *Melita* to belong to either a new species (*Melita orgasmos*) or to *Melita zeylanica* (which in 1916 he had treated as a junior synonym of *inaequistylis*). While Barnard (1940) referred to his *Melita inaequistylis* of 1916 as being in part referable to *Melita zeylanica*, he did not indicate which locations of the 1898 or 1914 material might be *zeylanica*. Although compelled by the apparent absence of *Melita zeylanica* from the locations that produced *Austrochiltonia*, we treat *Melita* as cryptogenic, in part pending re-examination of this earlier material. Ship fouling and ballast water are the likely vectors.

Family ISCHYROCERIDAE

Ischyrocerus anguipes Krøyer, 1838

Introduced

This is a common tube-dwelling North Atlantic amphipod found on buoys and pilings. It has been introduced to the Pacific coast of North America and was first recorded in South Africa by Barnard (1916) based on specimens from 1913 onward. Its South African distribution ranges from Namibia (west coast) to Mozambique (east coast) and it is most likely a ship fouling and ballast water introduction.

Jassa species-group

Until 1990 all *Jassa* collected in South Africa were allocated to *Jassa falcata*, but in a major review of the genus, Conlan (1990) described several new species and reallocated South African material among a number of *Jassa* species. Three of those species are treated here, as they have been introduced to the southern hemisphere (Conlan 1988). Barnard (1916) reported *Jassa falcata* from False Bay, Sea Point (near Cape

Town), and Swakopmund, collected between 1908 and 1914. These specimens, and other museum material, require re-examination and assignment to the species below (or conceivably to other species as well). For this reason, only the locations given by Conlan (1990) are cited below. Stebbing (1888) reported “*Podocerus falcatus*” (= *Jassa falcata*) collected in fouling on the screw of the HMS *Challenger* as the vessel sailed off the Cape of Good Hope in December 1873, evidence that these fouling amphipods have long been in motion on sailing ships around the world (and suggesting that the *Challenger* itself may have been a vector of transportation and introduction!).

Jassa marmorata Holmes, 1903

Introduced

(= *Jassa falcata partim*)

This is a North Atlantic species, transported by shipping (ship fouling and ballast water) to the Pacific Ocean and various stations in the southern hemisphere, including South Africa. Conlan (1990) reports specimens from Table Bay (collected in 1948, K. Conlan, personal communication, February 2009), Durban and KwaZulu-Natal (east coast). As noted above, we do not take 1948 as the first date of record, pending re-examination of K. Barnard’s early twentieth century *Jassa* material.

Jassa morinoi Conlan, 1990

Introduced

(= *Jassa falcata partim*)

This North Pacific species has introduced populations in the eastern Atlantic and Mediterranean (Europe, Senegal, Algiers). Japanese specimens were collected on the brown alga *Sargassum* “at low intertidal level” Conlan (1990) and reported locations on the American Pacific coast suggest both rocky intertidal environments, as well as bays. These are all habitats where this species could have interfaced with shipping, so we consider ship fouling and ballast water to be probable vectors. It was reported in South Africa from False Bay (southwest coast; collected in 1952, K. Conlan, personal communication, February 2009), Port Elizabeth (southeast coast) and on the east coast in KwaZulu-Natal (Conlan 1990).

Jassa slatteryi Conlan, 1990

Introduced

(= *Jassa falcata partim*)

This is another North Pacific species with outlier populations in the Atlantic Ocean (Europe and Brazil) and in the South Pacific (Chile, Australia and New Zealand). Its South African distribution is recorded by Conlan (1990) as Langebaan (west coast), False Bay (southwest coast), Mossel Bay and Knysna (both on the southeast coast). The Langebaan, False Bay and Knysna specimens were collected in 1950–1952, and the Mossel Bay material was collected in 1956 (K. Conlan, personal communication, February 2009). North Pacific habitats include fouling communities (Conlan 1990) and estuaries (Jeong et al. 2007), from where this species may have been transported by ships (fouling and ballast water).

Cerapus tubularis Say, 1817
(= *Cerapus abditus* Barnard, 1916)

Introduced

This species was first recorded from South Africa as *Cerapus abditus* by Barnard in 1916, based on specimens collected off KwaZulu-Natal in 1901. *Cerapus abditus* was subsequently synonymized with *Cerapus tubularis* by J.L. Barnard (1962). The species originates from North America, but is now widely distributed in tropical and temperate seas. It ranges from Saldahna Bay (west coast) to the South African border on the east coast, with ship fouling and ballast water as the most probable vectors.

Family TALITRIDAE

Orchestia gammarella Pallas, 1776
(= *Orchestia gammarellus*; = *Talorchestia inaequalipes* Barnard, 1951)

Introduced

This well-known, globally distributed, European shore hopper (Henzler and Ingolfsson 2008) was collected by the University of Cape Town Ecological Survey from Langebaan on the west coast of South Africa. This led Barnard (1951) to describe it as a new species, *Talorchestia inaequalipes*. Long regarded as an endemic species, this was recognized as synonymous with *Orchestia gammarella* by Griffiths (1975). It is locally common along the drift-line (under rocks and on debris) and among dune vegetation. It is known in South Africa from Langebaan (Barnard 1951), Table Bay (from our own 2008 collections at Milnerton Lagoon) and from 1949, in Knysna Estuary on the southeast coast (Griffiths 1974). We regard it as an early introduction with solid (dry) ballast.

Platorchestia platensis (Krøyer, 1845)
(= *Orchestia platensis*)

Introduced

This “tramp” amphipod was reported as *Orchestia platensis* from a single coastal location at Danger Point, Gansbaai, on the Cape South coast in 1904 (Griffiths 1975). Surveys have not been conducted at Danger Point since 1904 so there is no evidence that populations of *Platorchestia platensis* are no longer present at this location. It has been recorded from many warm shores of the world and may be a species complex. Although of unknown geographic origin, we regard it as introduced to South Africa because of its highly restricted distribution and its known “weed” status. As with *Orchestia gammarella*, we consider it to be an early introduction with solid ballast.

Family CAPRELLIDAE

Caprella equilibra Say, 1818

Cryptogenic

This amphipod clings tightly to hydroids, algae and other typical fouling species, leading to easy transportation by shipping. We therefore consider ship fouling and ballast

water as the most probable vectors. The origin of *Caprella equilibra* is unknown. It is now globally distributed (McCain 1968) and common in South Africa from Namibia (west coast) to Mozambique (east coast), where it frequently forms part of the diet of reef fish. It was first recorded in South Africa “from screw of HMS *Challenger*, off Cape of Good Hope” by Stebbing (1888) and was established on the shore in False Bay by 1889 (Stebbing 1910).

Caprella penantis Leach, 1814

Cryptogenic

Caprella penantis can be distinguished from *Caprella equilibra* by a distinct rostral tooth on the head. It also clings to various algae, sponges, hydroids, alcyonarians, zoantharians and bryozoans (McCain 1968). The origin remains unknown: as with *Caprella equilibra* it is now widely distributed and is found in Hawaii, Japan, Australia, New Zealand and on both coasts of the United States, where it was one of the most common caprellids (McCain 1968) before the arrival of *Caprella muticum* (Carlton unpublished findings), a species we expect to arrive soon in South Africa (if it is not already here). It was first reported in South Africa by Mayer (1903) from material collected in 1888 and is most likely transported through ship fouling and ballast water. In South Africa, it is distributed from Namibia (west coast) to KwaZulu-Natal (east coast).

Paracaprella pusilla Mayer, 1890

Cryptogenic

The male of this species is easily identified by the large triangular projection on the front of pereonite 2. The origin of *Paracaprella pusilla* is unknown. Its global distribution includes the Caribbean, the Atlantic coast of the United States, Tropical West Africa, East Africa, China and Hawaii. It has the same habitat as the other caprellids. As the first South African record is by Barnard (1955), who recorded it from Durban Harbour on the east coast, scraped from a ship’s hull, we regard ship fouling and ballast water are the most probable vectors.

Order **DECAPODA**
Family **XANTHIDAE**

Xantho incisus Leach, 1814

Introduced

This European crab has distinctive chelipeds, which are large and heavy with black tips. It is found among boulders on shallow stony substrata. In South Africa it is recorded only from the Kleinsee Oyster Farm (west coast) with the first collection made in 2008 (Haupt et al. 2010a). We consider this an introduction with oyster spat imported from France.

Family **PORTUNIDAE***Carcinus maenas* (Linnaeus, 1758)**Introduced**

This crab is a well-known European introduction on both the Atlantic and Pacific coasts of North America, in Australia, Argentina, Japan and South Africa (Carlton and Cohen 2003). Interestingly, *Carcinus maenas* is restricted to sheltered, coastal sites and appears to be unable to establish on the open wave-swept coastline in South Africa (Hampton and Griffiths 2007) as on the west coast of North America, but not on the east coast. In South Africa it is restricted to the Atlantic coast of the Cape Peninsula (southwest coast). It was first collected from Table Bay Docks in 1983, where it has established dense populations and has decimated shellfish populations (Robinson, Griffiths, McQuaid et al. 2005). We consider that it was probably introduced by ship fouling, ballast water or oil rigs.

Subphylum **CHELICERATA**Class **PYCNOGONIDA**Family **AMMOTHEIDAE***Ammothella appendiculata* (Dohrn, 1881)
(= *Ammothella indica* Stock, 1954)**Introduced**

This sea spider was collected in the fouling of a ship's hull in Durban Bay in 1951 where the vessel had been solely resident. It was first recorded by Stock (1954, 1959) as *Ammothella indica*, a species described from Singapore, and was synonymized with *Ammothella appendiculata* by Bamber (2000). The port-dwelling sea spiders of South Africa have not been resurveyed in recent decades, but we have no reason to suspect that *Ammothella appendiculata* no longer occurs in Durban Bay, and we retain it on the South African faunal list. *Ammothella appendiculata* was described from the Mediterranean, where it still occurs, but is otherwise patchily distributed around the Atlantic rim, being recorded, for example, outside the Mediterranean from the West Indies and Florida (Child 1974) and Brazil (Ribeiro et al. 1982). In contrast, largely under the name *Ammothella indica*, it is reported as widely distributed throughout the western Pacific Ocean (Bamber 2000), where it occurs in natural habitats (such as coral rubble) and where closely related endemic species occur (Child 1988). It also occurs in the Red Sea (Stock 1957), to where it may have been carried from the Mediterranean, or from the Pacific. We tentatively suggest that it may be native to the Pacific Ocean and is a nineteenth-century (or earlier) introduction to the Mediterranean and the Atlantic Ocean, with ship-fouling. Alternatively, Mediterranean–Atlantic stocks may represent distinct species, a question that is best approached genetically (R. Bamber, personal communication, 2009). It may have been introduced to South Africa in ship fouling or in ballast water.

Subphylum **HEXAPODA**Class **INSECTA**

The historical biogeography of the beach and maritime shore insects of South Africa remains to be explored. We suspect that a number of shore insects were introduced

from the 1600s to 1800s with beach ballast from around the world. We identify one common European strand beetle as an example of such an introduction.

Order **COLEOPTERA**
Family **STAPHYLINIDAE**

Cafius xantholoma (Gravenhorst, 1806)

Introduced

This common European rove beetle (Haghebaert 1989) occurs on South African beaches (Prins 1984; Stenton-Dozey and Griffiths 1983), where it is found in decaying kelp and other microhabitats. We have not yet determined the first record of this species in South Africa, although we assume it to be an early introduction, perhaps centuries ago, given that solid ballast is the most likely vector.

Phylum **MOLLUSCA**
Class **GASTROPODA**
Order **CAENOGASTROPODA**
Family **LITTORINIDAE**

Littorina saxatilis (Olivi, 1792)

Introduced

(= *Littorina punctata* of authors; = *Littorina rudis* Maton, 1797)

The history of this well-studied, North Atlantic, intertidal snail in South Africa remains to be fully explored. Kilburn (1972) was the first to properly recognize this species in the modern-day marine fauna of South Africa. He noted that it had previously been identified as *Littorina punctata* in Langebaan (west coast) by Barnard (1963) and from the Berg River Estuary (west coast) and Knysna Lagoon (south-east coast) by Day (1969). In addition, a fourth African population is known from Luderitz, in Namibia (Reid 1996). Kilburn (1972) described the morphology and colour of the Langebaan Lagoon snails and noted that the population “was found to be a very large and well-established one. In habitat it occurred chiefly on firm, slightly muddy sandflats in the upper midtidal region, especially on *Zostera* beds.” Kilburn remarked that as it had been previously known only from the North Atlantic “it at first appeared probable that it had been introduced.” However, he then noted that “Subsequently I have material collected from Pleistocene beds on the Cape Flats and adjacent areas, which indicates that the population is an indigenous one.” Reid (1996) noted that *Littorina saxatilis* has not been found alive in the immediate Cape Town area. Reid (personal communication, 2008) reported that he had examined “possibly subfossil samples from raised beaches” in the Cape Town area; this may be the same material to which Kilburn refers (Kilburn notes that he was in communication with a “Mr S. Fenwick,” and the samples examined by Reid were collected by S. Fenwick). The shells are at the Natal Museum and are described as being from the “bed of the Diep River, Table Bay,” and from the “shores of Zandvlei, Muizenberg.” The shells have not been radiocarbon dated, nor are there any further data on the actual age of the strata from which the shells were recovered.

One year later, Schalke (1973) reported that *Littorina saxatilis* (the number of specimens is not mentioned) were found in boreholes at Rietvlei, immediately north of Table Bay. The snails were said to be found in two horizons in a borehole, with one level antedating 45,000 years before present, and the other with an age range of 40,500 to 36,500 years before present. Strata level ages were determined from radiocarbon datings and pollen analyses, but the *Littorina saxatilis* shells themselves were not aged.

Hughes (1979; as *Littorina rudis*) then reported on further details of morphology, colour and reproduction of the Langebaan and Knysna populations, and on searches for *Littorina saxatilis* at other sites (none was found). Knight *et al.* (1987) undertook genetic analyses of the South African populations, comparing them with both North American and European material; South African *Littorina saxatilis* “showed a severely reduced heterozygosity compared with Atlantic populations.” Both Hughes (1979) and Knight *et al.* (1987) suggested ship-mediated introduction.

Reid (1996) provided a detailed review of the history of the occurrence of *Littorina saxatilis* in South Africa, noting the reported fossil material, the known living populations, and previous hypotheses (relictual but natural distribution, or human-mediated introduction) that had sought to explain the presence of this species in the South Atlantic Ocean. Reid offered a third hypothesis, that migrating birds may have carried *Littorina saxatilis* from Europe to Africa. Reid also noted the existence of a fourth southern Africa population, in Luderitz, in Namibia, based upon Natal Museum material.

We consider that the most probable origin of the modern-day populations of *Littorina saxatilis* in Namibia and in South Africa is human-mediated introduction, possibly in the days of wooden sailing ships transporting shore ballast from Europe. Genetic analyses are required to match the South African populations with North Atlantic populations, not only to determine possible origin, but also to determine whether unique haplotypes exist in the former, and if so how many, to determine (by molecular clock estimations) how long this snail has been in the southern hemisphere. Although it is not likely that snails would survive on birds on the wing from Europe, its presence in locations such as the Berg River Estuary could well be accounted for by post-introduction dispersal by birds within South Africa (Kalejta and Hockey 2008).

The ostensible fossil material from the Cape Town area is not dated, and could represent Holocene occurrences; if so, these could represent specimens transported out of a region such as Saldanha Bay (Langebaan Lagoon), or introduced populations from Europe that failed to survive. Of more interest certainly are the Pleistocene Rietvlei specimens: these would bear re-examination and verification as *Littorina saxatilis*, and it would be of no small interest to perform radiocarbon testing on the shells. Even if these prove to be *Littorina saxatilis* with good stratigraphic control, we suspect that there is no link between these fossils and modern-day populations in South Africa. Had *Littorina saxatilis* become established tens of thousands of years ago in South Africa, it would have long since become very widespread, despite its lack of planktonic larvae (given time, *Littorina saxatilis* are transported by floating materials, for example, or simply expand their range by moving along coastlines for aeons); instead, it remains highly restricted to a few locations, suggestive of relatively recently established populations.

We have as yet no first date of record of living *Littorina saxatilis* populations in South Africa. The dates of collection of Barnard’s (1963) specimens (identified as

Littorina punctata) from Langebaan, of other material, and of the Namibia population, remain to be determined (we note that Museum material should be searched for under both the name *Littorina punctata* and other names as well).

Family MURICIDAE

Thais species

The recent history, occurrence, and distribution of a number of species of muricids along the South African coast remain to be investigated. On the one hand, we are compelled by the evidence that a number of Indo-Pacific *Thais* have been and are being transported by human means. Both *Thais sacellum* and *Thais lacera* have been introduced to the Mediterranean (Gofas and Zenetos 2003; Singer 2005) and *Thais blanfordi* has been found being transported long distances in ships' sea chests (Richards 1990). On the other hand, it is not clear if some western Indian Ocean muricids naturally find their southernmost distributions extending to Mozambique, South Africa or Madagascar. Another layer of complexity is that we further expect that more northern species may now be extending their ranges south with coastal warming.

We treat two species, *Thais blanfordi* and *Thais tissoti* as introductions. In addition, *Thais lacera* (Kilburn and Rippey 1982), *Stramonita haemastoma* (Kilburn and Rippey 1982 as *Thais haemastoma*), *Thais aculeata* (Steyn and Lussi 1998) and *Thais sacellum* (G. Branch, personal communication, 2009), have all been reported from South African coasts, but their distribution and current status require further study.

Thais blanfordi (Melvill, 1893)

Introduced

We tentatively admit this well-known muricid as a non-native species because of its apparent historical absence from South Africa, combined with its known association with shipping. Kilburn and Rippey (1982) noted its presence on the east coast in Durban Bay with the compelling observation that it had not been reported in Natal "until a few decades ago," speculating that it "may originally have been introduced into Durban Bay on the hulls of ships." Tan and Sigurdsson (1996), in a review of several *Thais* species from the Indian Ocean, noted that *Thais blanfordi* was restricted to the western half of the Indian Ocean, and cited material from India, Kenya, Madagascar, Mozambique and Pakistan. Within the same review, South African specimens were cited from Delagoa and Durban Bay. This snail was first collected in South Africa in 1950 and we consider ship fouling and ballast water to be the likely vectors.

Thais tissoti (Petit, 1852)

Introduced

As with *Thais blanfordi*, Kilburn and Rippey (1982) remarked on the historical absence of this species in Durban Bay, and suggested ship-mediated introduction. Tan and Sigurdsson (1996) note that it appears to be restricted to the Indian west coast, Sri Lanka and the African east coast, specifically reporting material from India, Mozambique, Oman, Pakistan, Sri Lanka and Thailand. Within this review South

African specimens were cited from Durban and Thompson's Bay on the east coast. The first collection date was 1950 and we also consider ship fouling and ballast water to be the likely vectors for this species.

Family **THIARIDAE**

Tarebia granifera (Lamarck, 1822)

Introduced

A freshwater prosobranch originating from South-East Asia, *Tarebia granifera* can tolerate high salinities for relatively long periods of time and is therefore found within estuaries. It has spread rapidly across a number of countries in recent years, displacing other invertebrates. It was first recorded in St Lucia Estuary on the east coast in 2005 and by 2007 had spread along the eastern shores, as far as Kosi Bay (Miranda 2009).

Order **OPISTHOBRANCHIA**

Order **NUDIBRANCHIA**

Family **TERGIPEDIDAE**

Catriona columbiana O'Donoghue, 1922

Introduced

This North Pacific nudibranch, identified by its pink to creamy cerata, feeds on hydroids of the genus *Tubularia* (*sensu lato*) (Gosliner 1987). It was first collected on pilings in Cape Town Docks in 1972, where it was found on the introduced ascidian *Ciona intestinalis* (Gosliner and Griffiths 1981). We recognize that this is a variable species with many synonyms (McDonald 2007). In South Africa it has only been recorded in Cape Town Docks so we concur with Gosliner (1987) that it represents an introduction, likely to have arrived in South Africa through ship fouling and ballast water.

Family **POLYCERIDAE**

Polycera hedgpethi Marcus, 1964

Cryptogenic

Gosliner (1982) extended the range of this nudibranch, which eats the bryozoan *Bugula*, from the North American Pacific coast to South Africa, where it was found in 1980 in the Keurbooms River Estuary, near Plettenberg Bay (on the southeast coast). Willan (1984) suggested that this species was introduced to South Africa (also repeated by Wilson 2006), whereas Gosliner (1987) suggested that "it is unlikely that this species has been introduced to southern Africa," arguing that the Keurbooms Estuary "is shallow and certainly is not subject to international shipping." However, *Polycera* may have arrived in the Plettenberg Bay area by secondary coastal dispersal from larger bays in South Africa supporting international shipping, suggesting ship fouling and ballast water as the most likely vectors.

Thecacera pennigera (Montagu, 1815)
 (= *Thecacera lamellata* Barnard, 1933)

Cryptogenic

Now occurring in the Pacific, Atlantic and Indian Oceans, this nudibranch has been dispersed globally along with its bryozoan prey, *Bugula*, in ship fouling communities and, in more modern times, probably with ballast water. This species was first collected and inadvertently re-described as a new species, *Thecacera lamellata* by Barnard (1933). Gosliner (1987) noted that this species is “commonly found along the coast of southern Africa from Cape Town to Umgazana in the Transkei (east coast). As several localities, including Umgazana, are over 250 km from the nearest harbour, it is difficult to attribute the distribution of this species in southern Africa solely to introduction by shipping.” However, introduced species can spread long distances along coastlines after their introduction, far from their initial point of entry. Hence the occurrence of this species at distant points does not argue against its being non-native.

Family AEOLIDIIDAE

Anteaeolidiella indica (Bergh, 1888)
 (= *Aeolidiella indica*; = *Aeolidiella multicolor* Macnae, 1954; = *Aeolidiella saldanhensis* Barnard, 1927)

Cryptogenic

Another species probably transported by shipping globally, it now occurs in the Pacific (most records), Atlantic (apparently isolated occurrences in the Mediterranean, Brazil and Florida), and the Indian Ocean (Mauritius, Tanzania and the Red Sea). Perhaps rooted in the Pacific, it may have been transported through the Indian Ocean to the Atlantic theatre. The first South African collections are those from Saldanha Bay, from where Barnard (1927) described this nudibranch as a new species, *Aeolidiella saldanhensis*. It was described again from South Africa, as another new species, *Aeolidiella multicolor*, by Macnae (1954). Gosliner and Griffiths (1981) established these and other synonymies and added additional South African records. The full South African range now extends from Saldanha Bay (west coast) to KwaZulu-Natal on the east coast. In South Africa, *Anteaeolidiella indica* feeds on the presumably native sea anemone *Anthothoe chilensis* (a species which itself may represent a complex or two or more taxa).

Class BIVALVIA Family MYTILIDAE

Mytilus galloprovincialis Lamarck, 1819

Introduced

The Mediterranean mussel forms dense beds in the high to mid intertidal zones (Rius and McQuaid 2009). It is easily confused with the indigenous mussel, *Choromytilus meridionalis*, but is fatter, has a pitted resilial ridge and differs in habitat (occurring higher on the shore and away from sand-inundated sites). It is now globally distributed as a result of ship fouling and ballast water (Branch and Steffani 2004).

It was first collected in Saldahna Bay, South Africa in 1979 with genetic confirmation of the identification published 5 years later (Grant et al. 1984). It is now the most significant marine introduction on rocky intertidal shores in this region, ranging from central Namibia (west coast) to East London on the east coast (Robinson, Griffiths, McQuaid et al. 2005). There have been several studies into a variety of ecological impacts (Branch and Steffani 2004; Rius and McQuaid 2009) and it is commercially cultured and exploited by recreational and subsistence fishers (Robinson, Griffiths, McQuaid et al. 2005, 2007).

Perna viridis (Linnaeus, 1758)

Introduced

We identified large green mussels collected from East London Harbour in 2010 as *Perna viridis*, based on shell colour and shape, shape of the posterior adductor muscle and shape of the pallial line (Siddall 1980). However, we await confirmation via genetic studies, as this species is closely related to the endemic and highly variable *Perna perna*. To date there is no evidence of spread onto the open coast but if this occurs there is potential for hybridization with native *Perna perna*. *Perna viridis* is native to India and Southeastern Asia, but it has been widely introduced to Australia, Japan, the Caribbean, Gulf of Mexico and southeast United States. Hull fouling and ballast water are the most likely vectors.

Semimytilus algosus (Gould, 1850)

Introduced

This small reef-forming mussel was first reported from South Africa only in 2010 and an initial survey has shown that it already forms dense and extensive beds in the lower intertidal and shallow subtidal on exposed rocky shores between Cape Town and the Namibian border. The species has long been known from Namibia, from where it was first reported in a somewhat obscure publication by Lamy (1931), under the name *Modiola pseudocapensis*. We have been unable to detect any later use or formal synonymy of that name. For example, it is not mentioned in the extensive taxonomic monograph of Soot-Ryan (1955). However, only *Semimytilus algosus* is currently recognized within the genus and this name has been the only one used by all local researchers (for example, Branch et al. 1994) subsequent to Lamy (1931). The species originates from the Pacific coast of South America and it is not clear whether its sudden appearance in South Africa represents a dramatic southerly range extension of a newly introduced population.

Family OSTREIDAE

Ostrea edulis Linnaeus, 1758

Introduced

This well-known European flat oyster is identified by a cup-shaped lower valve and flat upper one. It has been widely distributed around the world by the aquaculture industry. For example, populations are now common in areas along the Nova Scotia, Maine and Massachusetts coasts, following its introduction to the Gulf of Maine in the 1940s (Robinson, Griffiths, McQuaid et al. 2005). It was intentionally introduced to Knysna in 1946 without success (Korringa 1956). Surveys by us in 2008 found a

reproducing population in the Alexander Bay oyster dams on the west coast of South Africa (Haupt et al. 2010a).

Crassostrea gigas (Thunberg, 1795)

Introduced

A deep lower valve, flat upper valve and undulating margins are the identifying features of this oyster, which is widely cultured around the world in both marine and estuarine habitats. Originally from Japan, populations are now widespread, notably in Europe, Australia and New Zealand. It was introduced to South Africa for culture purposes in 1955, but it was not until 2001 that wild populations were first detected (Robinson, Griffiths, Tonin et al. 2005). Naturalized populations are currently known from the Breede, Goukou and Knysna Estuaries, all along the southern coast (Haupt et al. 2010b).

Family HIATELLIDAE

Hiatella arctica (Linnaeus, 1767)
(= *Saxicava arctica*)

Cryptogenic

This small clam is recorded from fouling communities around the world, and probably consists of multiple species (Coan et al. 2000; Mikkelsen and Bieler 2008). We have not yet been able to establish when this species was first collected in South Africa, but if it was introduced it may have been one of the earliest invasions arriving from the 1600s onwards. It is recorded in Day (1969) as *Saxicava arctica*, occurring from False Bay (southwest coast) to East London (east coast) “in rock crevices and burrows in sandy limestone.” In addition, it was reported by Henschel et al. (1990), also as *Saxicava arctica*, from False Bay. Originally described from the North Atlantic Ocean, it is widely acknowledged as having been dispersed globally in ship-fouling, but which species are involved and their genetic identity remain to be determined. Only genetic studies will reveal the origin of South African populations and if the origin proves to be Europe, we would regard *Hiatella arctica* as introduced.

Family TEREDINIDAE

The biogeographic origins of many species of shipworms are now obfuscated by centuries of global shipping. We identify two teredinids here as introduced, but note that there are several additional cryptogenic species. We consider all shipworms noted here to have been transported historically in the wooden hulls of sailing vessels, although modern day transport for those species with planktotrophic larvae in ballast water is also possible.

Teredo navalis Linnaeus, 1758

Introduced

It seems likely that this possibly European (Hoppe 2002) shipworm was one of the earliest introductions to South Africa. Noble (1886) and Hammersley-Heenan (1893) appear to be among the first to collect and record *Teredo navalis* from South Africa, but these dates cannot be taken as evidence of the timing of their introduction, as

the species may of course have been present for centuries. Noble (1886) noted that attacks of *Teredo navalis* were “exceptionally virulent” on the Port Elizabeth break-water (southeast coast). Waldron (1904a,b) noted that at the turn of the previous century, it was most prolific and destructive on the warmer parts of the South African coast, such as in Mossel Bay (southeast coast) in the Indian Ocean. Douglas (1981) reported on control measures for *Teredo navalis* on a jetty at Knysna, based on a 10-year study. The distribution of *Teredo navalis* and all other South African shipworms is not known.

Lyrodus pedicellatus (Quatrefages, 1849)
(= *Teredo robsoni* Moll and Roch, 1931)

Introduced

Lyrodus pedicellatus is another globally occurring shipworm whose origins have not yet been determined (Coan et al. 2000; Mikkelsen and Bieler 2008). As with *Teredo navalis*, it may have been introduced to South Africa centuries ago. It was first collected and re-described from South Africa as a new species (*Teredo robsoni*) by Moll and Roch (1931) from Simon’s Town on the southwest coast, but this cannot be taken as the first date of occurrence of *Lyrodus pedicellatus* in South Africa.

Bankia carinata (Gray, 1827)
Bankia martensi (Stempell, 1899)
(= *Bankia capensis* Calman, 1920)
Dicyathifer manni (Wright, 1866)
(= *Teredo ancila* Barnard, 1964)
Teredo somersi Clapp, 1924
(= *Teredo radialis* Moll, 1937)

Cryptogenic

Cryptogenic

Cryptogenic

Cryptogenic

All four of these shipworm species are said to occur widely in ports and harbours around the world (Turner 1966), and are striking candidates for ship-borne introduction centuries ago. No fewer than three out of four were inadvertently re-described as native South African species, despite the existence of older available names. For all four of these species, local dispersal along coastlines may occur in floating wood, but none of these species are known from floating wood taken at sea, whereas they have been reported infesting harbour pilings or in ships’ hulls.

Family PHOLADIDAE

Martesia striata (Linnaeus, 1758)

Cryptogenic

Smith (1910) may have been the first to collect and record this well-known and now cosmopolitan boring piddock from South Africa, from floating seeds of the poison tree *Barringtonia asiatica* (as *Barringtonia speciosa* in Smith 1910). It was collected in Tongaat, KwaZulu-Natal, on the east coast. Day (1969) recorded it from Durban Bay to Delagoa Bay, “found boring in old mangrove roots”. The role of floating seeds in distributing this species is obfuscated by its presence in ships’ hulls in all tropical and

subtropical waters. Global genetic studies are now required to sort out possible origins and biogeographic tracks.

Phylum **BRACHIOPODA**
Family **DISCINIDAE**

Discinisca tenuis (Sowerby, 1847)

Within aquaculture facilities

This brachiopod has flat, transparent, horny discs that attach to each other, or to other shells, as well as a distinctive transparent hairy fringe at the shell edges. Until recently, it was only known from Namibia, where it is endemic; however, in 2008 it was recorded for the first time on shells of the introduced oyster, *Crassostrea gigas*, in Saldanha Bay on the west coast of South Africa (Haupt et al. 2010a). These oysters were translocated from Namibia. We also have unsubstantiated reports that *Discinisca tenuis* has been seen on the shells of oysters reared in Algoa Bay (southeast coast). Species coming from the immediate north (on west or east coasts) are now by default on our radar as moving south with climate change; this said, *Discinisca tenuis* has not yet been found outside oyster farms, so will not be included in the total number of wild introductions. It should be noted it has not been looked for in other areas. This is the first example to date of an introduction in South Africa originating from a neighbouring country. We consider mariculture to be the most probable vector.

Phylum **BRYOZOA**
Family **MEMBRANIPORIDAE**

Membranipora membranacea (Linnaeus, 1767)

Removed

Griffiths et al. (2009) treated this European bryozoan as an introduced species in the South African fauna. However, Florence et al. (2007) have shown that the South African populations were in fact an endemic, undescribed species (newly named as *Membranipora rustica*).

Conopeum seurati (Canu, 1928)

Introduced

This well-known European bryozoan (Ryland and Hayward 1977; Poluzzi and Sabelli 1985) is a classic fouling species of brackish lagoons and estuaries. Outside the European theatre, *Conopeum seurati* has been introduced by ship fouling to New Zealand (Gordon and Mawatari 1992), Australia (Wyatt et al. 2005) and the eastern United States (Winston 1982, 1995), who speculated that the largest American populations “are located in the James River, adjacent to Jamestown, making a scenario of an early introduction from the southeastern coast of England intriguing.” [Jamestown, Virginia is an early (1607) British settlement in North America.] It has probably been introduced to, and overlooked in, many estuaries around the world so it is not surprising that it occurs in South Africa (Awad et al. 2005), where it was collected in Saldanha (west coast) in 2001 (identification by Wayne Florence, SAM). A *Conopeum* species is

also abundant coating the tubes of the serpulid polychaete (tubeworm) *Ficopomatus enigmaticus* in the brackish Zandvlei Lagoon, False Bay (southwest coast). These populations appear similar if not identical to *Conopeum seurati*, but this identification requires confirmation. We regard it as a ship-fouling invasion from Europe. It may have been present in South Africa for decades or centuries.

Family WATERSIPORIDAE

Watersipora subtorquata (d'Orbigny, 1852)
(= *Watersipora cucullata*)

Introduced

This common, shallow-water bryozoan originates from the Caribbean and has been dispersed worldwide through shipping (fouling and ballast water). Although possibly a very early introduction, it was first collected and reported in South Africa by O'Donoghue and de Watteville (1935) as *Watersipora cucullata* and later synonymized by Florence et al. (2007) with *Watersipora subtorquata*, based on identical morphological characteristics described by Gordon (1989). Florence et al. (2007) report its South African distribution as Saldahna Bay (west coast) to False Bay (southwest coast). There is some question as to whether *Watersipora subovoidea* and *Watersipora subtorquata* are separate species because of the weak characterization of the former so to establish the species boundaries within the genus, molecular techniques need to be applied (Florence et al. 2007).

Family BUGULIDAE

Bugula neritina (Linnaeus, 1758)

Introduced

This common bryozoan with anticarcinogenic biochemical properties is often found attached to the hulls of ships. It has a global distribution, although it is not present in the cold polar or sub-Arctic/Antarctic regions (Gordon and Mawatari 1992). As a result, its origin is as yet unknown; however, it is assumed to be introduced via shipping (fouling and ballast water) to most areas (Ryland and Hayward 1977). It was first collected and reported by O'Donoghue and de Waterville in 1944, but was probably a very early introduction in South Africa. Florence et al. (2007) describe its distribution in South Africa as "prevalent in all areas with a harbor." It ranges from Port Nolloth (west coast) to Durban (east coast).

Bugula flabellata (Thompson in Gray, 1848)

Introduced

Gordon and Mawatari (1992) report this bryozoan as globally distributed in both warm and cold temperate waters of both hemispheres. It is, therefore, not surprising to find its distribution in South Africa spanning the cold and warm temperate provinces, from Port Nolloth (west coast) to the southeast coast as far as Plettenberg Bay (Florence et al. 2007). Although its origin is unknown, this is a well-known fouling organism found on the hulls of ships. It was first collected and reported in South

Africa by Hincks (1880), although its actual date of introduction is likely to have been much earlier.

Bugula dentata (Lamouroux, 1816)

Introduced

With its origin in the Indo-Pacific and a pan-warm temperate-tropical distribution, *Bugula dentata* has been reported from Australia-New Guinea, the Celebes Sea, New Zealand, Japan, Madeira, Brazil and South Africa (Florence et al. 2007). Although there are some morphological differences in the avicularia between specimens described from these regions, the populations appear to be conspecific (Harmer 1926; Ryland 1974; Mackie et al. 2001; Florence et al. 2007). It was first collected and reported from South Africa by Busk (1852). It ranges from Cape Point to Durban. As with *Bugula neritina*, it is likely to have been a very early introduction in ship fouling.

Family CRYPTOSULIDAE

Cryptosula pallasiana (Moll, 1803)
(= *Lepralia pallasiana*)

Introduced

We tentatively admit this European fouling bryozoan (Ryland and Hayward 1977) to the list of non-native species in South Africa, although there is little doubt that this morphotaxon is a global species complex, possibly involving a combination of regional endemic species, upon which ship-fouling introductions have been added. Millard (1952) appears to be the first to report it from South Africa (as *Lepralia pallasiana*), based upon collections from 1947 to 1949 in Table Bay Harbour. Henschel et al. (1990) report it as a fouling organism in Simon's Town, on the west side of False Bay (south-west coast), in 1979. It is doubtless widespread in harbours and estuaries around South Africa and has also been reported from the west coast at Saldanha Bay (identification by Wayne Florence, SAM: see Awad et al. 2005). Since its description in the early nineteenth century, it has been reported from ports around the world (Gordon and Mawatari 1992). Winston (1982) noted that the late Ernst Marcus had speculated as early as the 1940s that its "distribution may be related to proximity to shipping lanes." As with *Conopeum seurati*, the *Bugula* species and *Watersipora subtorquata*, it would be instructive to examine bryozoan-covered hard substrata (molluscs, tubeworms, barnacles, oysters and so forth) in museum collections for earlier records to establish the earliest specimens collected.

Phylum ECHINODERMATA Class ECHINOIDEA Family ARBACIIDAE

Tetrapygus niger (Molina, 1782)

Introduced

This "black sea urchin" actually has a distinctive purple test, unlike any other species of urchin found in South Africa. Native to the west coast of South America from Peru

to Chile, its presence in South Africa represents the first record of introduction for this species, globally. It was first collected by us during a survey of the Alexander Bay oyster dams in 2007 (Haupt et al. 2010a). During the survey, a breeding population, composed of both adults and juveniles, was recorded. *Tetrapyrgus niger* is the most abundant urchin along the Chilean coast (Rodriguez and Ojeda 1993). It is a well-known ecosystem engineer that is both an economic and ecological pest in its areas of origin, because of its grazing impact upon species of kelp (Vasquez and Santelices 1990; Vasquez and Buschmann 1997; Rodriguez 2003; Vega et al. 2005). We consider the most probable vector to have been import with the *Crassostrea gigas* spat, for mariculture purposes.

Class **OPHIUROIDEA**
Family **OPHIACTIDAE**

Ophiactis savignyi (Müller and Troschel, 1842)

Introduced

This small six-armed brittlestar is common in fouling communities and we therefore consider ship fouling to be the most probable vector. It is originally from the Indo-west Pacific but is now cosmopolitan. It was reported in Durban Bay on the east coast of South Africa by Day and Morgans (1956) based on samples collected between 1950 and 1952.

Phylum **CHORDATA**
Subphylum **TUNICATA**
Class **ASCIDIACEA**

Several species of colonial and solitary ascidian have been recognized as introduced along South African shores. Given the fouling nature of ascidians and the fact that the majority of the species identified here as introduced have their origins in Europe, we propose that the most probable vector of all these species is ship fouling. The ascidians listed are capable of forming large monospecific aggregates and often occur in high densities in artificial hard substrata (Rius et al. 2009a; Rius et al. 2010) and mussel farms (Carver et al. 2003) along the South African coast. Although research is needed to investigate the ecological impacts of these species in South Africa, it is highly likely that these species are producing the same or other significant effects as seen in other parts of the world.

Family **POLYCITORIDAE**

Cystodytes dellechiaiei (Della Valle, 1877)

Cryptogenic

An ascidian of unknown origin, first reported in South Africa by Millar (1962) from the Mozambique border. Monniot et al. (2001) found it in False Bay on the south-west coast and in KwaZulu-Natal (Isipingo and Sodwana Bay) on the east coast. This widespread species can be found in warm waters of other world regions, such

as the eastern Atlantic Ocean and the Mediterranean Sea (Monniot et al. 2001). Interestingly, as with the bryozoan *Bugula dentata*, there is an important degree of morphological variability among specimens found in different regions, although they are still considered to be conspecific (Monniot et al. 2001).

Family CLAVELINIDAE

Clavelina lepadiformis (Müller, 1776)

Introduced

This European ascidian has a characteristic transparent tunic that embeds the zooids. This species can be found in both Atlantic and Mediterranean waters (Tarjuelo et al. 2001). The first record from South Africa was by Monniot et al. (2001) based on specimens from Port Elizabeth and Knysna on the southeast coast. Subsequently, this species has also been found in other locations along the South African coast (M. Rius, unpublished results). Colonies are often found attached to the undersides and sides of boats and jetties.

Family DIDEMNIDAE

Didemnum granulatum Tokioka, 1954

Cryptogenic

This species was first found in South Africa by Monniot et al. (2001) from samples collected off Port Elizabeth on the southeast coast and KwaZulu-Natal on the east coast. Although the origin of this species is unclear, it is present in the Atlantic, Pacific and Indian oceans, as well as the Red Sea. This widespread global distribution leads us to suspect it as cryptogenic.

Didemnum psammathodes (Sluiter, 1895)

Cryptogenic

Monniot et al. (2001) first reported this species based on specimens collected from Thompson's Pool in KwaZulu-Natal (east coast). As with *Didemnum granulatum*, the origin of this species is unknown; however it is widely distributed around the world, and so thought to be cryptogenic.

Didemnum rodriguesi Rocha and Monniot, 1993

Cryptogenic

This species represents another ascidian of unknown origin, but because of a global distribution throughout tropical seas and it is thought to be cryptogenic. This species was first detected in South Africa by Monniot et al. (2001), based on specimens collected from Sodwana Bay on the east coast.

Trididemnum cerebriforme Hartmeyer, 1913

Cryptogenic

This species was first described by Hartmeyer (1913) from South African samples. Subsequently, it has been recorded in several regions around the world, including

the western Indian Ocean, Australia, Japan and the western tropical Pacific Ocean (Monniot et al. 2001); we therefore suspect it to be cryptogenic. It is widespread along South African coasts, ranging from Saldahna Bay (west coast) to Sodwana (east coast). Both Millar (1955) and Monniot et al. (2001) noticed a large morphological variability between the South African specimens, although no distinct characteristic exists that would justify splitting them in different species.

Diplosoma listerianum (Milne-Edwards, 1841)

Introduced

This species forms transparent colonies (although they can also appear grey and opaque yellow) that, despite the small size of its zooids, can colonize very large areas. *Diplosoma listerianum* is common in harbours, where it overgrows other sessile organisms such as mussels, algae and other ascidians. The origin is Europe (Monniot et al. 2001), but this species now occurs globally (Lambert and Lambert 1998). The first South African record is by Millar (1955) based on specimens collected from Langebaan on the west coast in 1949. It is found from Alexander Bay on the west coast to Durban on the east coast (M. Rius unpublished results).

Family CIONIDAE

Ciona intestinalis (Linnaeus, 1767)

Introduced

This North Atlantic solitary ascidian has a yellow semi-transparent tunic and can reach a body size greater than 100 mm. It attaches to harbour ropes, kelp or mussel farm rafts in sheltered and shadowed areas (Carver et al. 2003; Rius et al. 2010). It now occurs in temperate waters worldwide (Lambert and Lambert 1998; Clarke and Castilla 2000; Marshall and Keough 2003; Howes et al. 2007). It was first collected in Durban (Millar 1955) but it can be found all along the South African coast (M. Rius unpublished results). *Ciona intestinalis* can cause severe damage to mussel farms which results in important economic losses (Robinson, Griffiths, McQuaid et al. 2005; Howes et al. 2007).

Family CORELLIDAE

Corella eumyota Traustedt, 1882

Cryptogenic

This species is found among other ascidians species in harbour communities as a fouling organism. *Corella eumyota* is considered a cosmopolitan (Primo and Vázquez 2004) or circumpolar (Turon 1988) species with unknown origin. It is widespread throughout the southern hemisphere and is known to be introduced in the northern hemisphere (Dupont et al. 2007), hence we consider it as cryptogenic. *Corella eumyota* was first identified in South Africa by Sluiter (1898) and it has been consistently identified during subsequent ascidian studies (Michaelsen 1934; Millar 1955, 1962; Monniot et al. 2001). Its distribution within South Africa is from the west coast (Saldahna Bay), to the east coast (East London) (M. Rius unpublished results).

Family ASCIDIIDAE

Ascidia sydneiensis Stimpson, 1855**Introduced**

This solitary ascidian can reach up to 100 mm and has a tunic that is often covered by mud and epibionts. It is commonly found on pontoons and jetties, where it lives within a matrix of fouling organisms (M. Rius personal observation). Primo and Vasquez (2004) considered *Ascidia sydneiensis* as a cosmopolitan species, because of lack of evidence for its origin, however Monniot et al. (2001) consider it a Pacific Ocean species. In South Africa, it was first recorded by Michaelsen (1934) from samples collected in False Bay (southwest coast) in 1932. Since then, it has been found in Port Elizabeth on the southeast coast (M. Rius, unpublished results). It is usually a dominant fouling organism in harbour communities.

Asciella aspersa (Müller, 1776)**Introduced**

The tunic of this abundant European ascidian is semi-transparent and the mantle is normally white with pale red siphons, which make it easy to identify on ropes, tyres and pontoons within harbours (M. Rius, unpublished results). It is now found worldwide (Monniot et al. 2001). The first South African record was by Monniot et al. (2001) from Table Bay Harbour on the southwest coast.

Family STYELIDAE

Botryllus schlosseri (Pallas, 1766)**Introduced**

This colonial ascidian forms characteristic star-shaped zooid systems and although it has been considered to be native from Europe (López-Legentil et al. 2006), a confirmation of the native range remains. Therefore we have considered this species for now as being of unknown origin. It was first recorded by Millar (1955) based on specimens collected in 1946 from Durban harbour on the east coast. It is now found in many South African harbours as a fouling organism, from Alexander Bay (west coast) to Port Elizabeth on the southeast coast (M. Rius, unpublished results). As *Botryllus schlosseri* often colonizes other species when they are present in harbours, there is some concern as to possible impacts on indigenous kelp species; Griffiths et al. (2009) also recognize the potentially negative impact of *Botryllus schlosseri* on the eelgrass *Zostera capensis* (mistakenly referred to as *Spartina maritima* therein).

Symplegma brakenhielmi (Michaelsen, 1904)
(= *Symplegma viride* of authors, not of Herdman 1886)

Cryptogenic

This species is common in many harbours of the Atlantic and Pacific Oceans, as well as in Australia (Monniot et al. 2001). First recorded by Millar (1955) as *Symplegma viride*, Monniot et al. (2001) recognized that the specimens collected from Durban Harbour (east coast) in 1952 were *Symplegma brakenhielmi*. Its distribution remains

on the east coast (M. Rius, unpublished results), concurring with Millar (1962) who attributed it as a warm-water component of the South African ascidian fauna.

Polycarpa insulsa (Sluiter, 1898)

Cryptogenic

One specimen of this species was collected and reported by Monniot et al. (2001) from KwaZulu-Natal (Isipingo) on the east coast. Of unknown origin, it is widespread throughout the western tropical Atlantic Ocean and New Caledonia (Monniot et al. 2001).

Cnemidocarpa humilis (Heller, 1878)

Introduced

This solitary ascidian has a leathery tunic and adults can be found attached to floating pontoons and harbour ropes (Monniot et al. 2001; M. Rius, unpublished results). Its origin remains unknown. It is a common species in New Zealand, Australia and the southern part of South America (Primo and Vázquez 2004). The fact that it is such a large, conspicuous species that had not been reported previously led Monniot et al. (2001) to regard it as an introduction into South Africa. *Cnemidocarpa humilis* is found along the west coast all the way down to False Bay on the southwest coast (M. Rius, unpublished results).

Styela canopus (Savigny, 1816)

Cryptogenic

(= *Styela stephensoni* Michaelsen 1934; = *Styela marquesana* Michaelsen, 1918)

This small and inconspicuous solitary ascidian originally from the Western Indo-Pacific can be found in sheltered areas (mainly harbours) as a fouling organism, although it can occur in natural habitats such as mangrove swamps (Monniot et al. 2001). According to Monniot et al. (2001), Michaelsen (1934) first recorded *Styela canopus* as *Styela stephensoni* (a South African endemic) and Millar (1955) subsequently recorded it as *Styela marquesana*. This species is found on the east coast (M. Rius, unpublished results).

Styela plicata (Lesueur, 1823)

Introduced

This solitary western Pacific ascidian has a characteristic thick, tough tunic and it is commonly found attached to floating pontoons and harbour ropes. It can compete and displace native species (Rius et al. 2009b). It is one of the most common harbour ascidian species worldwide (Lambert and Lambert 2003; Rocha and Kremer 2005; Wyatt et al. 2005). *Styela plicata* was first detected in South Africa by Millar (1955) based on specimens from Durban collected in 1951 and 1952. It is surprising that a species of such large size was not identified by Monniot et al. (2001), as later samplings by M. Rius (unpublished results) found this species to be very abundant in several

locations along the South African coast. It ranges from Mossel Bay (southeast coast) to Durban on the east coast (M. Rius, unpublished results).

Family PYURIDAE

Microcosmus squamiger Michaelsen, 1927

Introduced

A highly successful fouling solitary ascidian that forms dense monospecific clumps within its introduced range (Rius et al. 2009a). The tunic is generally covered by mud and epibionts, which makes its identification in the field difficult. As many studies have wrongly identified *Microcosmus squamiger* as *Microcosmus exasperatus* (Turon et al. 2007) a careful observation of the shape of the siphonal spines is required to differentiate these closely related species (Monniot et al. 2001). Both taxonomic (Michaelsen 1927; Kott 1985; Monniot et al. 2001) and genetic (Rius et al. 2008) studies indicate that the origin of *Microcosmus squamiger* is Australia. This species has a worldwide distribution, including Australia, Europe, California, India and South Africa (Rius et al. 2008). Millar (1955, 1962) reported *Microcosmus exasperatus* from Durban samples collected in 1950 and 1952 (east coast). However, the description was so poor that the specimens described could be attributed to either *Microcosmus exasperatus* or *Microcosmus squamiger*. As no *Microcosmus exasperatus* have been found in recent surveys (Monniot et al. 2001; M. Rius, unpublished results), we assume that the specimens collected by Millar were *Microcosmus squamiger* so we take the first collection of this species in South Africa as 1950. The reports of *Microcosmus squamiger* in Alexander Bay and Table Bay by Griffiths et al. (2009) and again by Haupt et al. (2010a) were misidentifications of another introduced ascidian, *Cnemidocarpa humilis*. Besides the fact of being a harbour species, *Microcosmus squamiger* has been found in open coast locations within its introduced range. In the Mediterranean Sea, it can cover all available substrata, achieving densities of up to 2300 individuals/m² and displacing native communities (Rius et al. 2009a).

Subphylum VERTEBRATA Class PISCES OSTEICHTHYES Family CYPRINIDAE

Cyprinus carpio Linnaeus, 1758

Introduced

An intentional introduction, the common carp is a large and mainly freshwater species, but extends well into the upper or even middle reaches of estuaries, so is included here. It has a natural distribution from Central Asia to Europe, but has been widely distributed around the world as a food or sport fish. It was introduced to South Africa perhaps as early the 1700s and certainly in the 1800s (Skelton 2001) and is found in all major estuaries from the Berg River Estuary (west coast) to St Lucia on the east coast. Although potential impacts have not been studied, this fish is known to increase turbidity by grubbing in sediments for food, and is considered a pest by conservation authorities.

Kingdom **PLANTAE**
 Phylum **RHODOPHYTA**
 Family **GLOIOSIPHONIACEAE**

Schimmelmannia elegans Baardseth, 1941

Introduced

This alga, originating from Tristan da Cunha, was first collected in Table Bay Harbour, Cape Town on the south-west coast by De-Clerck et al. (2002). Two populations were found, one on the wall of a kelp tank at the Two Oceans Aquarium, Cape Town and the other within the harbour itself, growing close to an outlet pipe connected to the kelp tank and discharging into the harbour. Although this second patch was not fertile, those within the tank were. Ballast water is considered to be the most likely vector.

Family **PHYLLOPHORACEAE**

Schottera nicaeensis Guiry and Hollenberg, 1975

Cryptogenic

The history, biogeography, and systematics of this European alga in the southern hemisphere remain to be worked out. We are compelled by Lewis and Kraft's (1979) report that while previously known only from Europe, it has been introduced to Port Philip Bay, Australia. That noted, Silva et al. (1996) report that it was known earlier both from Réunion in the Indian Ocean (in the 1930s) and from Mauritius (where it was described as a new species, *Phyllophora morinii* Borgesen in 1954). Norris and Aken (1985) then reported it from South Africa. De Clerk et al. (2005) note that it is a "common component of algal turf in intertidal pools", in several locations in southern KwaZulu-Natal.

Family **CERAMIACEAE**

Antithamnionella ternifolia (Hooker and Harvey, 1845)
 (= *A. tasmanica* Wollaston, 1968)

Cryptogenic

This southern hemisphere (Eno et al. 1997) alga was first described from the tip of South America, much later recorded from Australia (Silva et al. 1996, as *Antithamnionella tasmanica*), later still from New Zealand (Nelson and Maggs 1996) and then recorded from South Africa (Stegenga et al. 1997). It was introduced to Europe in the early 1900s (Eno et al. 1997), where it is a well-known invader. It is also considered to be a ship-borne introduction to New Zealand (Nelson and Maggs 1996). Given its propensity to be distributed by ship fouling, but pending genetic resolution of the relationship between Australian, South African and Chilean populations, we consider it cryptogenic. Stegenga et al. (1997, as *Antithamnionella tasmanica*) recorded it "growing on animal substrates (*Pyura*, *Lepas*, soft coral) and on other algae . . . washed ashore between Kalk Bay and the Kowie."

Antithamnionella spirographidis (Schiffner, 1916)**Introduction**

This North Pacific alga (Lindstrom and Gabrielson 1989) has been introduced to Europe (Eno et al. 1997), Australia (Wollaston 1968), and elsewhere. In South Africa it was recorded by Stegenga et al. (1997) only “in the very sheltered sublittoral of Kraalbaai, growing on wooden jetty posts.” The date of collection of this material is 1989 (R. Anderson, personal communication, August 2009). It is now also known from Kowie Estuary, based upon specimens collected in 2003 (R. Anderson, personal communication). We regard it as a ship-fouling introduction, probably via Australasia rather than directly from the North Pacific.

Phylum **CHLOROPHYTA**
Family **CLADOPHORACEA**

Cladophora prolifera (Roth, 1797)**Introduced**

Leliaert and Coppejans (2003) record this now widespread filamentous green alga from Rabbit Rock, Kosi Bay, based upon 1999 collections. They reverse a previous synonymy with *Cladophora rugulosa* Martens, 1868 (reviewed in Silva et al. 1996), concluding that *Cladophora rugulosa* may be a South African endemic. Although noting that records of *Cladophora prolifera* in South Africa date back to the 1840s, they suggest that such early records may also have been confused with *Cladophora rugulosa* (so the earliest available herbarium material requires re-examination). Widespread through southern Europe, and recorded from other areas of the world, this may have been an early ship fouling introduction. We tentatively accept the designation of Hewitt et al. (2004) that this alga has been introduced from the Mediterranean to the southern hemisphere.

Family **ULVACEAE**

Ulva fasciata Delile, 1813**Cryptogenic**

While Hewitt et al. (2004) treated this species – perhaps in reality a species complex – as introduced to Australia from the Mediterranean, it (unlike *Cladophora prolifera* perhaps) is now too widespread to determine its origins [for example, *Ulva fasciata* is said to be the commonest species of *Ulva* in the Hawaiian Islands, where *Cladophora prolifera* is not recorded (Abbott and Huisman 2004)]. Aguilar-Rosas et al. (2005) consider it introduced to Mexico; Carlton and Eldredge (2009) consider it cryptogenic in Hawaii. Stegenga et al. (1997) report it as occurring from False Bay to tropical East Africa, noting that it is considered a pantropical species.

Family **CODIACEAE**

Codium fragile fragile (Suringar, 1867)
(= invasive strain *tomentosoides* (van Goor) P. C. Silva 1955)

Introduced

Under the name *Codium fragile* ssp. *tomentosoides*, this green alga has been dispersed out of Asia to numerous coasts around the world in the 1800s and 1900s (Provan et al. 2005), resulting in an extensive literature on its distribution, dispersal vectors, and ecological impacts. Recent molecular work (Provan et al. 2008) combined with attendance to botanical nomenclatural rules have led to the necessary but cumbersome new name *Codium fragile fragile* invasive *tomentosoides* strain. Provan et al. (2005) reported that this non-native *Codium* was “reported recently” in South Africa, citing Dromgoole (1982) and Chapman (1999), neither of which paper reports South Africa as a location for this taxon. Provan et al. (2008) stated that this alga had recently been reported from South Africa “in 1999”, citing Begin and Scheibling (2003). However, Begin and Scheibling (2003) cite Trowbridge (1998) as the source of that record, but such a record does not appear in Trowbridge’s paper, and the citation was based on a mis-reading of that paper (R. Scheibling, personal communication, 2007).

However, Provan et al. (2008) discovered that material of *Codium* collected in 1937 at “Melkbosch” (Melkbos, or Melkbosstrand, just north of Cape Town) in South Africa by the well-known phycologist G. F. Pappenfuss was the invasive strain *tomentosoides*. Ironically, this material consisted of the type specimens of *Codium fragile* ssp. *capense* Silva, 1959, a taxon which is still recognized, based upon other material from South Africa that is not *tomentosoides* (Provan et al. 2008).

Stegenga et al. (1997) note that *Codium fragile* ssp. *capense* is “a species of the sublittoral fringe and intertidal rockpools” occurring “along the whole of the Cape west coast and most of Namibia, eastward as far as Robberg (Plettenberg Bay).” It seems probable that within these populations the *tomentosoides* strain has gone unrecognized so we retain it in the South African invasive algal flora pending further collections from the Melkbosstrand and other regions.

Subkingdom **TRACHEOBIONTA**
Family **POACEAE**

Ammophila arenaria (Linnaeus, 1756)

Introduced

This well-known European pioneer dune plant, known as marram grass, was intentionally imported to South Africa in 1876, via imported seed from Lincolnshire, UK, to stabilize sand dunes and to control drift sand (Hertling and Lubke 1999a, 1999b, 2000). Much larger amounts of seed were then imported from France in 1892, with seedlings grown in Cape Town area nurseries. Extensive regions of coastal dunes were then planted between 1920 and 1996 between Saldanha (west coast) and Gonubie near East London (east coast); today, *Ammophila* is one of the predominant coastal dune plants in South Africa. Hertling and Lubke (2000) attributed its success to a combination of its ecological plasticity (ranging from its establishment from the semi-arid west coast to the subtropical Eastern Cape) and its “vigorous rhizomatous reproduction.” Hertling and Lubke (1999b) examined, using quantitative but not experimental approaches, the species richness, species diversity, relative abundance and species associations in dunes dominated by *Ammophila* and by indigenous vegetation; they found that while diversity indices are significantly lower in *Ammophila*-dominated systems, *Ammophila arenaria* “does not show extreme dominance to the exclusion of other species,” as it does in other regions of the world where it has been introduced (such

as on the American Pacific coast). Knevel et al. (2004) found that both release from native (European) root herbivores and biotic resistance by soil pathogens affect the invasiveness of *Ammophila* in South Africa.

Spartina maritima (Curtis, 1787)
(= *Spartina capensis* Nees, 1841)

Cryptogenic

Spartina maritima is widely distributed through western and southern Europe, north-west Africa, and also occurs on the west coast of South Africa (Chevalier, 1923, who suggested that this species is native to South Africa). Pierce (1982) argued that *Spartina maritima* is a European introduction. Adams et al. (1999) noted that the status of *Spartina maritima* as introduced has “not been fully resolved as the taxonomic history and ecology of the species does not seem to support this postulate;” their statement is, however, not supported by citations. Yannic et al. (2004) conducted genetic work on European *Spartina maritima*, although not on populations from South Africa. *Spartina maritima* was first described from South Africa as *Spartina capensis* on the basis of material collected in 1829 in the Swartkop River and now held in both the Museum National d’Histoire Naturelle in Paris and in the Botanic Garden and Botanical Museum, Berlin-Dahlem (www.aluka.org; accessed August 2009). Pending further genetic evidence, we consider *Spartina maritima* as cryptogenic, and possibly introduced by solid ballast. If so, it would be one of South Africa’s first recorded marine invasions.

Family POTAMOGETONACEAE

Stuckenia pectinata (Linnaeus, 1753)

Cryptogenic

(= *Potamogeton pectinatus*; = *P. pectinatus unguulatus* Hagstrom, 1916)

This macrophyte, known as pondweed, is the most widely distributed species of *Stuckenia* (long known in almost all South African literature as *Potamogeton*) in the world (Kaplan 2008). Despite its well-known weedy proclivities, there appears to have been little global analysis, based either on historical or genetic data that might elucidate its biogeographic tracks (Mader et al. 1998, were able to examine the genetic variation of northern, but not southern, African stocks of *Stuckenia pectinata*). Nevertheless, the ancestral distribution of the genus is rooted, as it were, in the northern hemisphere (Lindqvist et al. 2006), and *Stuckenia pectinata*, although widespread in northern waters, is highly patchy and isolated in the southern hemisphere (Santamaria 2002), which is strongly suggestive of recent colonization potentially mediated by human-related vectors. While long-distance bird (in particular swan) dispersal appears to have played a role across Eurasia (Mader et al. 1998), human-mediated mechanisms may be more at play in interhemisphere dispersal.

The extensive South African biological and ecological literature is summarized in part in Byren and Davies (1986), Thornton et al. (1995), Adams et al. (1999), and Riddin and Adams (2008). Although *Stuckenia* has been said to have so-called “positive” impacts in South African estuaries related to refugial habitat for juvenile fishes

(Thornton et al. 1995), it can become sufficiently dense to be a nuisance to recreational users, and biological control has been attempted in South Africa (Schoonbee 1991). If *Stuckenia* proves to be introduced (by genetic analysis that might suggest, for example, both European linkages and reduced haplotype diversity), it would be of no small interest to experimentally determine how the extensive beds of this pondweed (such as those in the Zandvlei) have acted to displace or replace native aquatic flora or infauna, impacted sediment dynamics or nutrient turnover. Relative to the latter, *Stuckenia pectinata* appears to be important in estuarine phosphorus cycles (Thornton et al. 1995; Adams et al. 1999). The earliest record we have found to date is that of Hagstrom (1916), who described *Potamogeton pectinatus* var. *ungulatus* (now regarded as a synonym of *Stuckenia pectinata*; Kaplan 2008), from the Koude River, Cape Province (www.aluka.org, accessed August 2009; specimens collected in 1896 by F. R. R. Schlecter and deposited in the South African National Herbarium in Pretoria). However, we have no doubt that earlier records will surface.

Discussion

Whereas application of the expanded protocol has substantially improved the reported diversity of marine and estuarine introduced and cryptogenic species within the South African region, conducting research of this nature is not without its challenges, discussed at length in Mead et al. (2011). We emphasize that this work remains a preliminary assessment and research must continue to reveal the full scale of bioinvasions that are likely within the region (Carlton 2009; Mead et al. 2011).

Mead et al. (2011) present a detailed analysis and discussion of both temporal and spatial patterns of bioinvasion for the South African region. This paper and Mead et al. (2011) represent the first detailed study of its kind for this region and indeed for all of Africa. Mead et al. (2011) found that the majority of introductions arrived from the northern hemisphere (mainly Europe), that ship fouling and ballast water were the dominant vectors, and that most introductions were confined to harbour areas. Marine introduced species have been found in all marine and estuarine habitats surveyed to date inclusive of the open coast. The west coast, inclusive of the False Bay transition zone, appears to contain the highest number of introduced species (Mead et al. 2011).

Acknowledgements

We are grateful to the following colleagues who generously provided unpublished records, museum data, or systematic expertise, or who identified specimens or gave valuable advice: R. Anderson (algae), R. Bamber (pyncogonids), G. Branch (gastropods), J. Chapman (gammarid amphipods), R. Collin (gastropods), K. Conlan (*Jassa* amphipods), A. Connell (copepods), J.A. Blake (*Dodecaceria* polychaetes), D. Herbert (gastropods), C. Maggs and R. Scheibling (*Codium*), G. Read (*Polydora*), D. Reid (*Littorina*), and M. Roy (ophiuroids). Our thanks to E. Hoensen, Curator of the Iziko South African Museum marine collections in Cape Town for providing access to the collections and helping us to determine dates of first collection. This research was conducted with support from History of the Near-shore (HNS) and the South African Environmental Observation Node (SAEON) to A.M., and a grant from the Department of Science and Technology/National Research Foundation Centre of Excellence for Invasion Biology to C.L.G., M.R. and J.T.C. M.R. was supported by the 'Agencia Española

de Cooperación Internacional para el Desarrollo' from the Spanish 'Ministerio de Asuntos Exteriores y de Cooperación'.

References

- Abbott DP, Reish DJ. 1980. Intertidal invertebrates of California. In: Morris RH, Abbott DP, Haderlie DC. editors. Polychaeta: the marine annelid worms. Stanford (CA): Stanford University Press. p. 448–489.
- Abbott IA, Huisman JM. 2004. Marine green and brown algae of the Hawaiian Islands. Honolulu: Bishop Museum Press. 260 pp.
- Acuna FH, Excoffon AC, Griffiths CL. 2004. First record and redescription of the introduced sea anemone *Sagartia ornata* (Holdsworth, 1855) (Cnidaria: Actinaria: Sagartiidae) from South Africa. *Afr J Zool.* 39:314–318.
- Adams J, Bate G, O'Callaghan M. 1999. Primary producers. In: Allanson D, Baird D. editors. Estuaries of South Africa. Cambridge, UK: Cambridge University Press. p. 100–118.
- Aguilar-Rosas RLE, Aguilar-Rosas LE, Pedroche FF. 2005. *Ulva fasciata* Delile (Ulveaceae, Chlorophyta): a species newly introduced into Pacific Mexico. *Bot Mar.* 48:46–51.
- Awad A, Greyling L, Kirkman S, Botes L, Clark B, Prochazka K, Robinson T, Kruger L, Joyce L. 2005. Port Biological Baseline Survey. Draft Report. Port of Saldanha, South Africa. 41 pp.
- Awad AA, Griffiths CL, Turpie JK. 2002. Distribution of South African marine benthic invertebrates applied to the selection of priority conservation areas. *Div. Dist.* 8:129–145.
- Barnard JL. 1955. Gammaridean Amphipoda (Crustacea) in the collections of the Bishop Museum. *Bernice P. Bishop Mus Bull.* 215:1–46.
- Barnard JL. 1962. Benthic marine Amphipoda of Southern California: families Aoridae, Photidae, Ischyroceridae, Corophiidae, Podoceridae. *Pac Nat.* 3:1–72.
- Bamber RN. 2000. Pycnogonids (Arthropoda, Pycnogonida) from French cruises to New Caledonia, Fiji, Tahiti, and the Marquesas. New records and new species. *Resultats des Campagnes Musorstom. Mem Mus Natl Hist Nat.* 21:199–205.
- Barnard KH. 1916. Contributions to the Crustacean Fauna of South Africa. *Ann S Afr Mus.* 15(3):1–302.
- Barnard KH. 1920. Contributions to the Crustacean Fauna of South Africa 6. Further additions to the list of marine Isopoda. *Ann S Afr Mus.* 17(5):319–438.
- Barnard KH. 1924. Contributions to the Crustacean Fauna of South Africa 7. Cirripedia. *Ann S Afr Mus.* 20(1):1–103.
- Barnard KH. 1927. South African nudibranch Mollusca, with descriptions of new species and a note on some species from Tristan d'Acunha. *Ann S Afr Mus.* 25:171–215.
- Barnard KH. 1932. Contributions to the crustacean fauna of South Africa. No. 11. Terrestrial Isopoda. *Ann S Afr Mus.* 30:179–388.
- Barnard KH. 1933. Description of a new species of *Thecacera*. *J Conch.* 19:294–295.
- Barnard KH. 1940. Contributions to the crustacean fauna of South Africa 12 Further additions to the Tanaidacea, Isopoda and Amphipoda with keys for the identification of hitherto recorded marine and fresh-water species. *Ann S Afr Mus.* 32:381–543.
- Barnard KH. 1951. New records and descriptions of new species of isopods and amphipods from South Africa. *Ann Mag Nat Hist.* 12(5):698–709.
- Barnard KH. 1955. Additions to the fauna list of South African Crustacea and Pycnogonida. *Ann S Afr Mus.* 43(1):1–107.
- Barnard KH. 1963. Contributions to the knowledge of the South African marine Mollusca. Part III. Gastropoda: Prosobranchiata: Taenioglossa. *Ann S Afr Mus.* 47:1–199.
- Begin C, Scheibling R. 2003. Growth and survival of the invasive green alga *Codium fragile* subsp. *tomentosoides* in tide pools on a rocky shore in Nova Scotia. *Bot Mar.* 46:404–412.

- Benedict JC. 1897. A revision of the genus *Synidotea*. Proc Acad Nat Sci Phil. 49:389–404.
- Blaber SJM, Hill BJ, Forbes AT. 1974. Infratidal zonation in a deep South African estuary. Mar Biol. 28:333–337.
- Blake JA, Ruff RE. 2007. The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon. 4th edition. Berkeley, Los Angeles: University of California Press. J. T. Carlton. Polychaeta. p. 309–410.
- Bolch CJS, de Salas MF. 2007. A review of the molecular evidence for ballast water introduction of the toxic dinoflagellates *Gymnodinium catenatum* and the *Alexandrium tamarensis* complex to Australasia. Harmful Algae. 6:465–485.
- Branch GM, Griffiths CL, Branch MI, Beckley LE. 1994. Two Oceans. A Guide to the Marine Life of Southern Africa. Cape Town: David Philip Publishers. 360 pp.
- 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.
- Busk G. 1852. Catalogue of marine Polyzoa in the collection of the British Museum. London: Department of Zoology, Natural History Museum.
- Byren BA, Davies BR. 1986. The influence of invertebrates in the breakdown of *Potamogeton pectinatus* L. in a coastal marina (Zandvlei, South Africa). Hydrobiologia 137:141–151.
- Carlton JT. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanog Mar Biol Annu Rev. 23:313–371.
- Carlton JT. 1996. Pattern, process and prediction in marine invasion ecology. Biol Conserv. 78:96–106.
- Carlton JT. 2009. Deep invasion ecology and the assembly of communities in historical time. In: Rilov G, Crooks JA, editors. Biological invasions in marine ecosystems. Berlin, Heidelberg: Springer-Verlag. p. 13–56.
- Carlton JT, Cohen AN. 2003. Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *Carcinus aestuarii*. J Biogeog. 30:1809–1820.
- Carlton JT, Eldredge LG. 2009. Marine bioinvasions of Hawai'i. The introduced and cryptogenic marine and estuarine animals and plants of the Hawaiian Archipelago. Bishop Museum Bulletins in Cultural and Environmental Studies 4. Honolulu: Bishop Museum Press. 202 pp.
- Carlton JT, Iverson, EW. 1981. Biogeography and natural history of *Sphaeroma walkeri* Stebbing (Crustacea: Isopoda) and its introduction to San Diego Bay, California. J Nat Hist. 15:31–48.
- Carver CE, Chisholm A, Mallet AL. 2003. Strategies to mitigate the impact of *Ciona intestinalis* (L.) biofouling on shellfish production. J Shellfish Res. 22:621–631.
- Chapman AS. 1999. From introduced species to invader: what determines variation in the success of *Codium fragile* ssp. *tomentosoides* (Chlorophyta) on the Atlantic coast of North America. Bot Mar 28:155–165.
- Chapman JW. 1988. Invasions of the northeast Pacific by Asian and Atlantic gammaridean amphipod crustaceans, including a new species of *Corophium*. J Crust Biol. 8:364–382.
- Chapman JW, Carlton JT. 1991. A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). J Crust Biol. 11: 386–400.
- Chevalier A. 1923. Note sur les *Spartina* de la flore française. Bull Soc Bot Fr.70:54–63.
- Child CA. 1974. *Hedgpeithius tridentatus*, a new genus and new species, and other Pycnogonida from Key West, Florida, U.S.A. Proc Biol Soc Wash. 87:493–500.
- Child AC. 1988. Pycnogonida from Aldabra Atoll. Biol. Soc. Wash. Bull. 8:45–78.
- Clarke M, Castilla JC. 2000. Dos nuevos registros de ascidias (Tunicata: Ascidiacea) para la costa continental de Chile. Revista Chilena de Historia Natural 73:503–510.

- Coan EV, Scott PV, Bernard FR. 2000. Bivalve seashells of western North America. Marine bivalve mollusks from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History, Natural History Monographs 2, 764 pp.
- Cohen AN, Carlton JT. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–558.
- Conlan KE. 1988. Systematics and sexual dimorphism: reclassification of the crustacean amphipod genus *Jassa* Leach (Corophioidea: Ischyroceridae). Doctoral dissertation, Department of Biology, Carleton University, Ottawa, Ontario.
- Conlan KE. 1990. Revision of the crustacean amphipod genus *Jassa* Leach (Corophioidea: Ischyroceridae). *Can J Zool.* 68:2031–2075.
- Crawford GI. 1937. A review of the amphipod genus *Corophium*, with notes on the British species. *J. Mar. Biol. Assoc. UK.* 21:589–630.
- Davies BR, Stuart V, de Villiers M. 1989. The filtration activity of a serpulid polychaete population *Ficopomatus enigmaticus* (Fauvel) and its effects on water quality in a coastal marina. *Est Coast Shelf Sci.* 29:613–620.
- Day JH. 1955. Keys to the Common Shore Animals of Langebaan. Unpublished handbook printed by Zoology Department, University of Cape Town.
- Day JH. 1961. The polychaete fauna of South Africa. Part 6. Sedentary species dredged off Cape coasts, with a few new records from the shore. *J Linn Soc Lon (Zool.)* 44:463–560.
- Day JH. 1967. A Monograph of the Polychaeta of South Africa. Part 2. Sedentaria. London: British Museum. p. 459–878.
- Day JH. 1969. A Guide to Marine Life on South African Shores. Cape Town: A. A. Balkema. 300 pp.
- Day JH, Morgans JFC. 1956. The ecology of South African estuaries. Part 7. The biology of Durban Bay. *Ann Natal Mus.* 13:259–312.
- De Clerk O, Anderson RJ, Bolton JJ, Robertson-Anderson D. 2002. *Schimmelmannia elegans* (Gloiosiphoniaceae, Rhodophyta): South Africa's first introduced seaweed? *Phycologia* 41:184–190.
- De Clerk O, Tronchin E, Schils T. 2005. Red Algae (Rhodophyceae). In: De Clerck O, Bolton JJ, Anderson RJ, Coppejans E, editors. Guide to the seaweeds of KwaZulu-Natal. *Scripta Botanica Belgica.* 33:133–267.
- DeFelice RC, Eldredge LG, Carlton JT. 2001. Non-indigenous marine invertebrates. In: Eldredge LG, Smith CM, editors. A Guidebook of Introduced Marine Species in Hawaii, Bishop Museum Technical Report 21: 70 pp.
- Delgery CC, Cragg SM, Busch S, Morgan EA. 2006. Effects of the epibiont heterotrich ciliate *Mirofolliculina limnoriae* and of moulting on faecal pellet production by the wood-boring isopods, *Limnoria tripunctata* and *Limnoria quadripunctata*. *J Exp Mar Biol Ecol.* 334: 165–173.
- Douglas WS. 1981. The preservative treatment of pine poles for use in the intertidal zone of warm waters. *S Afr For.* 116:64–68.
- Dromgoole FI. 1982. The buoyant properties of *Codium*. *Bot Mar.* 25:391–397.
- Dupont L, Viard F, David P, Bishop JDD. 2007. Combined effects of bottlenecks and selfing in populations of *Corella eumyota*, recently introduced sea squirt in the English Channel. *Div Dist.* 13:808–817.
- Eno NC, Clark RA, Sanderson WG. 1997. Non-native species in British waters: a review and directory. Peterborough: Joint Nature Conservation Committee. 136 pp.
- Espinosa-Perez MA, Hendrickx ME. 2002. The genus *Paracerceis* Hansen, 1905 (Isopoda, Sphaeromatidae) in the eastern tropical Pacific, with the description of a new species. *Crustaceana:* 74(11):1169–1187.
- Ewer DW. 1953. On a new tubularian hydroid from Natal. *Ann Natal Mus.* 12:351–357.
- Florence WK., Hayward PJ, Gibbons MJ. 2007. Taxonomy of shallow-water Bryozoa from the west coast of South Africa. *Afr Nat Hist* 3:1–58.

- Galil BS, Zenetos, A. 2002. A sea change – exotics in the eastern Mediterranean. In: Leppakoski E, Gollasch S, Olenin S, editors. *Invasive Aquatic Species of Europe: Distributions, Impacts and Management*. Dordrecht, the Netherlands: Kluwer Academic Publishers. p. 325–336.
- Gofas S, Zenetos A. 2003. Exotic molluscs in the Mediterranean basin: current status and perspectives. *Oceanog Mar Biol Annu Rev.* 41:237–277.
- Gollasch S, Nehring S. 2006. National checklist for aquatic alien species in Germany. *Aquat Inv.* 1:245–269.
- Gordon DP. 1989. The marine fauna of New Zealand: Bryozoa: Gymnolaemata (Cheilostomida Ascophorina) from the western south Island continental shelf and slope. *NZ Oceanog Instit Mem.* 97:1–158.
- Gordon DP, Mawatari SF. 1992. *Atlas of Marine Fouling Bryozoa of New Zealand Ports and Harbours*. New Zealand Oceanographic Institute, Miscellaneous Publications 107: 52 pp.
- Gosliner TM, Griffiths RJ. 1981. Description and revision of some South African Aeolidacean Nudibranchia (Mollusca, Gastropoda). *Ann S Afr Mus.* 84:105–150.
- Gosliner T. 1982. A new record of the nudibranch gastropod *Polycera hedgpethi* Marcus, from the Indian Ocean of South Africa. *J Moll Stud.* 48:30–35.
- Gosliner T (1987). *Nudibranchs of Southern Africa: A Guide to Opisthobranch Molluscs of Southern Africa*. Monterey, CA: Sea Challengers, 136 pp.
- Grant WS, Cherry MI, Lombard AT. 1984. A cryptic species of *Mytilus* (Mollusca: Bivalvia) on the west coast of South Africa. *S Afr J Mar Sci.* 2:149–162.
- Griffiths CL. 1974. The Amphipoda of Southern Africa Part 4: The Gammaridea and Caprellidea of the Cape Province east of Cape Agulhas. *Ann S Afr Mus.* 65(9):251–336.
- Griffiths CL. 1975. The Amphipoda of Southern Africa Part 5: The Gammaridea and Caprellidea of the Cape Province west of Cape Agulhas. *Ann S Afr Mus.* 67(5):91–181.
- Griffiths CL. 2000. Overview of current problems and future risks. In: Preston G, Brown G, van Wyk E, editors. *Best Management Practices for Preventing and Controlling Invasive Alien Species*. Cape Town: Working for Water Programme, p. 235–241.
- 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.
- Griffiths CL, Kruger LM, Smith EC. 1996. First record of the sea anemone *Metridium senile* from South Africa. *S Afr J Zool.* 31:157–158.
- Griffiths CL, Mead A, Robinson TB. 2010. A brief history of marine bio-invasions in South Africa. *Afr Zool* 44:241–247.
- Griffiths CL, Robinson TB, Mead A. 2009. The status and distribution of marine alien species in South Africa. In: Rilov G, Crooks JA, editors. *Biological invasions in marine ecosystems*. Berlin, Heidelberg: Springer-Verlag. p. 393–408.
- Haghebaert G. 1989. Coleoptera from marine habitats. In: Wouters K, Baert L, editors. *Proceedings of the Symposium Invertebrates of Belgium*. Brussels: Royal Belgian Institute of Natural Sciences. p. 301–308.
- Hagström JO (1916) *Critical researches on the Potamogetons*. Kungl Svenska Vetenskapsakad Handl 55(5):1–281.
- Hallegraeff GM. 1998. Transport of toxic dinoflagellates via ships' ballast water: bioeconomic risk assessment and efficacy of possible ballast water management strategies. *Mar Ecol Prog Ser.* 168:297–309.
- Hammersley-Heenan RH. 1893. A short account of the attacks of the *Teredo navalis* and *Chehura terebrans* upon greenheart (*Nectandra rodioei*) and Sneezewood (*Pteroxylon utile*) timbers. *Trans S Afr Philos Soc.* 5(2):313–317.
- Hammersley-Heenan RH. 1897. The harbour of Algoa Bay, Cape Colony. *Minutes of Proc Inst Civil Engin.* (London). 130:263–275.

- Hampton S, Griffiths CL. 2007. Why *Carcinus maenas* cannot get a grip on South Africa's wave exposed coastline. *Afr J Mar Sci* 9:123–126.
- Harmer SF. 1926. The Polyzoa of the Siboga Expedition. Part II. Cheilostomata Anasca. *Mon Siboga Exped Leiden*. 28b:181–487.
- Harrison K, Holdich DM. 1984. Hemibranchiate sphaeromatids (Crustacea: Isopoda) from Queensland, Australia with a world-wide review of the genera discussed. *Zool J Linn Soc*. 81:275–387.
- Hartmeyer R. 1913. Tunicata. Zoologische und Anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika. Jena: 125–144.
- Haupt TM, Griffiths CL, Robinson TB, Tonin AFG. 2010a. Oysters as vectors of marine aliens, with notes on four introduced species associated with oyster farming in South Africa. *Afr Zool*. 45(1):52–62.
- Haupt TM, Griffiths CL, Robinson TB, Tonin AFG. 2010b. History and status of oyster exploitation and culture in South Africa. *J Shellfish Res*. 29:151–159.
- Henry DP, McLaughlin PA. 1975. The barnacles of the *Balanus amphitrite* complex (Cirripedia, Thoracica). *Zool Verhandelingen*. 141:1–254.
- Henschel JR, Cook PA, Branch GM. 1990. The colonization of artificial substrata by marine sessile organisms in False Bay. I. Community development. *S Afr J Mar Sci*. 9:289–297.
- Henzler CM, Ingolfsson A. 2008. The biogeography of the beachflea, *Orchestia gammarellus* (Crustacea, Amphipoda, Talitridae), in the North Atlantic with special reference to Iceland: a morphometric and genetic study. *Zool Scripta*. 37:57–70.
- Hertling UM, Lubke RA. 1999a. Use of *Ammophila arenaria* for dune stabilization in South Africa and its current distribution – perceptions and problems. *Env Man*. 24:467–482.
- Hertling UM, Lubke RA. 1999b. Indigenous and *Ammophila arenaria*-dominated dune vegetation on the South African Cape coast. *App Veg Sci*. 2:157–168.
- Hertling UM, Lubke RA. 2000. Assessing the potential for biological invasion – the case of *Ammophila arenaria* in South Africa. *S Afr J Sci*. 96:520–527.
- Hewitt CL, Campbell ML, Thresher RE, Martin RB, Boyd S et al. 2004. Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Mar Biol*. 144:183–202.
- Hewitt CL, Gollasch S, Minchin D. 2009. The vessel as a vector – biofouling, ballast water and sediments. In: Rilov G, Crooks JA, editors. *Biological invasions in marine ecosystems*. Berlin, Heidelberg: Springer-Verlag. p. 117–132.
- Hincks T. 1880. *A History of the British Marine Polyzoa*. London: Van Vorst. 601 pp.
- Hoppe, KN. 2002. *Teredo navalis*: the cryptogenic shipworm, in: Leppäkoski, E. et al. (Ed.) (2002). *Invasive aquatic species of Europe: distribution, impacts and management*. pp. 116–119.
- Howes S, Herbinger CM, Darnell P, Vercaemer B. 2007. Spatial and temporal patterns of recruitment of the tunicate *Ciona intestinalis* on a mussel farm in Nova Scotia, Canada. *J Exp Mar Biol Ecol*. 342:85–92.
- Hughes RN. 1979. South African populations of *Littorina rudis*. *Zool J Linn Soc*. 65:119–126.
- Jeong SJ, Yu OH, Suh HL. 2007. Life history and reproduction of *Jassa slatteryi* (Amphipoda, Ischyroceridae) on a seagrass bed (*Zostera marina* L.) in southern Korea. *J Crust Biol*. 27:65–70.
- Jerling HL. 2008. The zooplankton community of Richards Bay harbour and adjacent Mhlathuze Estuary, South Africa. *Afr J Mar Sci*. 30:55–62.
- Kalejta B, Hockey PAR. 2008. Distribution of shorebirds at the Berg River estuary, South Africa, in relation to foraging mode, food supply and environmental features. *Ibis* 136: 233–239.
- Kaplan Z. 2008. A taxonomic revision of *Stuckenia* (Potamogetonaceae) in Asia, with notes on the diversity and variation of the genus on a worldwide scale. *Folia Geobot*. 43:159–234.
- Kensley B. 1978. *Guide to the Marine Isopods of Southern Africa*. Trustees of the South African Museum Cape Town. pp. 173.

- Kilburn RN. 1972. Taxonomic notes on South African marine Mollusca (2), with the description of new species and subspecies of *Conus*, *Nassarius*, *Vexillum* and *Demoulia*. *Ann Natal Mus.* 21:391–437.
- Kilburn R, Rippey E. 1982. *Sea Shells of Southern Africa*. Macmillan, Johannesburg. pp. 249.
- Kittlein MJ. 1991. Population biology of *Sphaeroma serratum* Fabricius (Isopoda, Flabellifera) at the Port of Mar del Plata, Argentina. *J Nat Hist.* 25:1449–1459.
- Knevel IC, Lans T, Menting FBJ, Hertling UM, van der Patten WH. 2004. Release from native root herbivores and biotic resistance by soil pathogens in a new habitat both affect the alien *Ammophila arenaria* in South Africa. *Oecologia* 141:502–510.
- Knight AJ, Hughes RN, Ward RD. 1987. A striking example of the founder effect in the mollusc *Littorina saxatilis*. *Biol J Linn Soc.* 32:417–426.
- Knight-Jones P, Knight-Jones EW. 1974. Spirorbinidae (Serpulidae: Polychaeta) from South Africa, including three new species. *Mar Biol.* 25:253–261.
- Knight-Jones P, Knight-Jones EW, Kawahara T. 1975. A review of the genus *Janua*, including *Dexiospira* (Polychaeta: Spirorbidae). *Zool J Linn Soc.* 56:91–129.
- Korringa P. 1956. Oyster culture in South Africa. Hydrographical, biological and osteological observations in the Knysna Lagoon, with notes on conditions in other South African waters. *Invest Rep Div Sea Fish S Afr.* 20:84–102.
- Kott P. 1985. The Australian Ascidiacea, Part 1. Phlebobranchia and Stolidobranchia. *Mem Qld Mus.* 23:1–438.
- Laird MC, Griffiths CL. 2008. Present distribution and abundance of the introduced barnacle *Balanus glandula* in South Africa. *Afr J Mar Sci.* 30(1):93–100.
- Lambert CC, Lambert G. 1998. Non-indigenous ascidians in southern California harbors and marinas. *Mar Biol.* 130:675–688.
- Lambert CC, Lambert G. 2003. Persistence and differential distribution of nonindigenous ascidians in harbors of the Southern California Bight. *Mar Ecol Prog Ser.* 259:145–161.
- Lamy ME. 1931. Voyage de MP Lesne dans l’Afrique du Sud, 1928–1929. Mollusques marins. *Bull Mus Nat Hist (Paris) Ser2* 3:304–307.
- Leliaert F, Coppejans E. 2003. The marine species of *Cladophora* (Chlorophyta) from the South African east coast. *Nova Hedwigia* 76:45–82.
- Leppakoski E, Shiganova S, Alexandrov B. 2009. European enclosed and semi-enclosed seas. In: Rilov G, Crooks JA, editors. *Biological invasions in marine ecosystems*. Berlin, Heidelberg: Springer-Verlag. p. 529–547.
- Lewis JT, Kraft GT. 1979. Occurrence of a European red alga (*Schottera nicaeensis*) in Australian waters. *J Phys.* 15:226–230.
- Lily EL, Halanynch K M, Anderson DM. 2005. Phylogeny, biogeography, and species boundaries within the *Alexandrium minutum* group. *Harmful Algae* 4:1004–1020.
- Lily EL, Halanynch KM, Anderson DM. 2007. Species boundaries and global biogeography of the *Alexandrium tamarense* complex (Dinophyceae). *J Phycol.* 43:1329–1338.
- Lindqvist C, De Laet J, Haynes RR, Aagsen L, Keener BR, Albert VA. 2006. Molecular phylogenetics of an aquatic plant lineage, Potamogetonaceae. *Cladistics* 22:568–588.
- Lindstrom SC, Gabrielson PW. 1989. Taxonomic and distributional notes on northeast Pacific Antithamnionaceae (Ceramilales: Rhodophyta). *Jap J Phycol.* 37:221–235.
- Lombard AT. 2004. Marine Component of the National Spatial Biodiversity Assessment for the Development of South Africa’s National Biodiversity Strategic and Action Plan. National Botanical Institute. pp. 101.
- López-Legentil S, Turon X, Planes S. 2006. Genetic structure of the star sea squirt, *Botryllus schlosseri*, introduced in southern European harbours. *Mol Ecol.* 15:3957–3967.
- Loyola e Silva J de. 1960. Sphaeromatidae do litoral Brasileiro (Isopoda – Crustacea). *Bol Univ Parana, Zool.* 4:1–182.

- Mackie JA, Keough MJ, Norman JA, Christidis L. 2001. Mitochondrial evidence of geographical isolation within *Bugula dentata* Lamouroux. In: Wyse-Jackson PN, Buttler CJ, Spencer JME, editors. Bryozoan Studies, Proceedings of 12th International Bryozoology Association Conference, Balkema, Lisse, Netherlands: p. 199–206.
- Macnae W. 1954. On some aolidacean nudibranchiate molluscs from South Africa. *Ann Natal Mus.* 13:1–50.
- Mader E, Van Vierssen W, Schwenk K. 1998. Clonal diversity in the submerged macrophyte *Potamogeton pectinatus* L. inferred from nuclear and cytoplasmic variation. *Aquat. Bot.* 62, 147–160.
- Maggiore F, Fressi E. 1984. Presence of *Dynamene bidentata* (Adams, 1880) in the Mediterranean (Isopoda). *Crustaceana* 46:309–313.
- Marques AC, Pena Cantero AL, Vervoort W. 2000. Mediterranean species of *Eudendrium* Ehrenberg, 1834 (Hydrozoa, Anthomedusae, Eudendriidae) with the description of a new species. *J Zool.* 252: 197–213.
- Marshall DJ, Keough MJ. 2003. Effects of settler size and density on early post-settlement survival of *Ciona intestinalis* in the field. *Mar Ecol Prog Ser.* 259:139–144.
- Matthews SG, Pitcher GC. 1996. Worst recorded marine mortality on the South African coast. In: Yasumoto T, Oshima Y, Fukuyo Y, editors. Harmful and Toxic Algal Blooms. Paris: Intergovernmental Oceanographic Commission of UNESCO. p. 89–92.
- Mayer C. 1903. Die Caprellidae der Siboga-Expedition. *Siboga Expedition* 34: 160pp
- McCain JC. 1968. The Caprellidae (Crustacea: Amphipoda) of the Western North Atlantic. *US Nat Mus Bull.* 278: 147 pp
- McDonald GR. 2007. Sarcoglossa and Nudibranchia. In: Carlton JT, editor. *The Light and Smith Manual. Intertidal Invertebrates from Central California to Oregon.* Berkeley and Los Angeles: University of California Press. p. 788–807.
- Mead A, Carlton JT, Griffiths CL, Rius M. 2011. Revealing the scale of marine bioinvasions in developing regions. *Biol Inv.* 16: DOI 10.1007/s10530-011-0016-9.
- Michaelsen VW. 1927. Einige neue westaustralische Ptychobranchiate Ascidien. *Zool Anz.* 71:193–203.
- Michaelsen VW. 1934. The Ascidians of the Cape Province of South Africa. *Trans Roy Soc S Afr.* 22(2):129–163.
- Mikkelsen PM, Bieler R. 2008. Seashells of southern Florida. Living marine mollusks of the Florida Keys and adjacent regions. *Bivalves.* Princeton, Oxford: Princeton University Press. 503 pp.
- Millar RH. 1955. On a collection of ascidians from South Africa. *Proc Zool Soc Lon.* 125: 169–221.
- Millar RH. 1962. Further descriptions of South African ascidians. *Ann S Afr Mus.* 46:113–221.
- Millard N. 1952. Observations and experiments on fouling organisms in Table Bay Harbour, South Africa. *Trans Roy Soc S Afr.* 33 (4):415–445.
- Millard NAH. 1959. Hydrozoa from ships' hulls and experimental plates in Cape Town docks. *Ann S Afr Mus.* 45:239–256.
- Millard NAH. 1970. A new record of a moerisiid hydroid from South Africa. *Afr Zool.* 5: 275–276.
- Millard NAH. 1975. Monographs on the Hydroida of southern Africa. *Ann S Afr Mus.* 68: 1–513.
- Millard NAH. 1978. The geographical distribution of Southern African hydroids. *Ann S Afr Mus.* 74(6):159–200.
- Minchin D, Gollasch S, Cohen AN, Hewitt CL, Olenin S. 2009. Characterizing vectors of marine invasions. In: Rilov G, Crooks JA, editors. *Biological invasions in marine ecosystems.* Berlin, Heidelberg: Springer-Verlag. p. 109–116.
- Miranda N. 2009. The invasive gastropod *Tarebia granifera* in the Isimalingo Wetland Park. The Aardvark. *Zool Soc S Afr.* April: 7.

- Moll F, Roch F. 1931. The Tereidinidae of the British Museum, the natural history museums at Glasgow and Manchester, and the Jeffreys collection. *Mal Soc Lon Proc.* 19:201–218.
- Monniot C, Monniot F, Griffiths CL, Schleyer M. 2001. South African ascidians. *Ann S Afr Mus.* 108(1):141 pp.
- Nel R, Coetzee PS, Van Niekerk G. 1996. The evaluation of two treatments to reduce mud worm (*Polydora hoplura* Claparede) infestation in commercially reared oysters (*Crassostrea gigas* Thunberg). *Aquaculture* 141:31–39.
- Nelson WA, Maggs CA. 1996. Records of adventive marine algae in New Zealand: *Antithamnionella ternifolia*, *Polysiphonia senticulosa* (Ceramiales, Rhodophyta), and *Striaria attenuata* (Dictyosiphonales, Phaeophyta). *New Zeal J Mar Freshw Res.* 30: 449–453.
- Noble J. 1886. Official handbook. History, productions, and resources of the Cape of Good Hope. Cape Town: W. A. Richards and Sons. 308 pp.
- Norris RE, Aken ME. 1985. Marine benthic algae new to South Africa. *S. afr. J. Bot.* 51: 55–65.
- Nunez MA, Pauchard A. 2010. Biological invasions in developing and developed countries: does one model fit all? *Biol. Inv.* 12:707–714.
- O'Donoghue CH, de Waterville D (1935). A collection of Bryozoa from South Africa. *J Linn Soc (London)* 39:203–218.
- O'Donoghue CH, de Waterville D. 1944. Additional notes on South African Bryozoa. *Ann Natal Mus.* 10:407–432.
- Okamoto K., Kobayashi Y, Ishida H. 2007. Changes in the species composition and the abundance of phytoplankton in ballast water. *Bull Plankton Soc Jap.* 54(1):42–49 (in Japanese).
- Panning A. 1924. Beitrage zur Kenntnis der Land- und Sueswasserfauna Deutsch-Suedwestafrika (Zur Zeit Mandat Suedwest-Afrika). *Ergebnisse der Hamburger deutsch-suedwestafrikanischen Studienreise 1911*, herausgegeben von W. Michaelsen, Hamburg, 2(3) Isopoda: 167–201.
- Peart RA. 2004. A revision of the *Cymadusa filosa* complex (Crustacea: Amphipoda: Corophioidea: Ampithoidae). *J Nat Hist.* 38:301–336.
- Peterson K. 1990. Evolution and taxonomy in capitate hydroids and medusae (Cnidaria: Hydrozoa). *Zool J Linn Soc.* 100:101–231.
- Pierce SM. 1982. What is *Spartina* doing in our estuaries? *S Afr J Sci.* 78(6):229–230.
- Pillai NK. 1961. Monograph. Wood-boring Crustacea of India. Government of India Press. 61 pp.
- Pitcher GC, Cembella AD, Joyce LB, Larsen J, Probyn T A, Sebastian CR. 2007. The dinoflagellate *Alexandrium minutum* in Cape Town harbour (South Africa): Bloom characteristics, phylogenetic analysis and toxin composition. *Harmful Algae* 6:823–836.
- Pitcher GC, Horstman DA, Calder D, De Bruyn JE, Post BJ. 1993. The first record of diarrhetic shellfish poisoning on the South African coast. *S Afr J Sci.* 89:512–514.
- Poluzzi A, Sabelli B. 1985. Polymorphic zooids in deltaic species populations of *Conopeum seurati* (Canu, 1928) (Bryozoa, Cheilostomata). *Mar Ecol.* 6:265–284.
- Primo C, Vázquez E. 2004. Zoogeography of the southern African ascidian fauna. *J Biogeog* 31:1987–2009.
- Prins AJ. 1984. Morphological and biological notes on some South African arthropods associated with decaying organic matter. Part 2. The predatory families Carabidae, Hydrophilidae, Histeridae, Staphylinidae and Silphidae (Coleoptera). *Ann S Afr Mus.* 92:295–356.
- Provan J, Booth D, Todd NP, Beatty GE, Maggs CA. 2008. Tracking biological invasions in space and time: elucidating the invasive history of the green alga *Codium fragile* using old DNA. *Div Dist.* 14:343–354.
- Provan J, Murphy S, Maggs CA. 2005. Tracking the invasive history of the green alga *Codium fragile* ssp. *tomentosoides*. *Mol Biol.* 14:189–104.

- Read GB. 1975. Systematics and biology of polydorid species (Polychaeta: Spionidae) from Wellington Harbor. *J Roy Soc N Z.* 5:395–419.
- Reid DG. 1996. Systematics and Evolution of *Littorina*. London: The Ray Society. 463 pp.
- Ribeiro MA, Alcantara-Filho GP, Fantinato FM, Tommasi, LR. 1982. Sobre a ocorencia de Pantopoda na regio da Baia de Santos, Sao Paulo (Brasil). *Dusenja* 13:37–40.
- Richards A. 1990. Muricids: a hazard to navigation? *Hawaiian Shell News* 38(5):10.
- Riddin T, Adams JB. 2008. The seed banks of two temporarily open/closed estuaries in South Africa. *Aquat Bot.* 90:328–332.
- Rius, M., Branch, GM, Griffiths, CL & Turon, X. 2010. Relating settlement patterns to adult distribution: the effects of larval behaviour on gregarious ascidians. *Mar Ecol Prog Ser* 418:151–163.
- Rius M, McQuaid CD. 2009. Facilitation and competition between invasive and indigenous mussels over a gradient of physical stress. *Basic Appl Ecol.* 10:607–613
- Rius M, Pascual M, Turon X. 2008. Phylogeography of the widespread marine invader *Microcosmus squamiger* (Asciacea) reveals high genetic diversity of introduced populations and non-independent colonizations. *Div Dist.* 14:818–828.
- Rius M, Pineda MC, Turon X. 2009a. Population dynamics and life cycle of the introduced ascidian *Microcosmus squamiger* in the Mediterranean Sea. *Biol Inv.* 11:2181–2194.
- Rius M, Turon X, Marshall DJ. 2009b. Non-lethal effects of an invasive species in the marine environment – the importance of early life-history stages. *Oecologia* 159:873–882.
- Robinson TB, Branch GM, Griffiths CL, Govender A, Hockey PAR. 2007. Changes in South African rocky intertidal invertebrate community structure associated with the invasion of the mussel *Mytilus galloprovincialis*. *Mar Ecol Prog Ser.* 340:163–171.
- Robinson TB, Griffiths CL, Kruger N. 2004. Distribution and status of marine invasive species in and bordering the West Coast National Park. *Koedoe*, 47:79–87.
- Robinson TA, Griffiths CL, McQuaid CD, Rius M. 2005. Marine alien species of South Africa – status and impacts. *Afr J Mar Sci.* 27:297–306.
- Robinson TB, Griffiths CL, Tonin A, Bloomer P, Hare MP. 2005. Naturalized populations of oysters, *Crassostrea gigas* along the South African Coast: distribution, abundance and population structure. *J Shellfish Res.* 24 (2):443–450.
- Rocha RM, Kremer LP. 2005. Introduced ascidians in Paranaguá Bay, Paraná, Southern Brazil. *Rev Brasil Zool.* 22:1170–1184.
- Rodriguez SR. 2003. Consumption of drift kelp by intertidal populations of the sea urchin *Tetrapygyus niger* on the central Chilean coast: possible consequences at different ecological levels. *Mar Ecol Prog Ser.* 251:141–151.
- Rodriguez SR, Ojeda FP. 1993. Distribution patterns of *Tetrapygyus niger* (Echinodermata: Echinoidea) off the central Chilean coast. *Mar Ecol Prog Ser.* 101:157–162.
- Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AJ. 2000. Invasion of coastal marine communities in North America: apparent patterns, processes and biases. *Annu Rev Ecol Syst.* 31:481–531.
- Ryland JS. 1974. Bryozoa in the Great Barrier Reef Province. In: Proceedings of the Second International Coral Reef Symposium. Brisbane, Australia: Great Barrier Reef Committee. p. 341–348.
- Ryland JS. 1974. Behaviour, settlement and metamorphosis of bryozoan larvae: a review. *Thalass Jugosl.* 10:239–262.
- Ryland JS, Hayward PJ. 1977. British Anascan Bryozoa. London: Academic Press. 188 pp.
- Samaai T, Gibbons MJ. 2005. Demospongiae taxonomy and biodiversity of the Benguela region on the west coast of South Africa. *Afr. Nat. Hist.* 1:1–96.
- Santamaria L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecol.* 23:137–154.
- Sapeika N. 1948. Mussel poisoning. *S Afr Med J.* 22:337–338.

- Schalke HJWG. 1973. The Upper Quaternary of the Cape Flats area (Cape Province, South Africa). *Scripta Geologica* 15:1–57.
- Schlacher TA, Wooldridge TH. 1996. How sieve mesh size affects sample estimates of estuarine benthic macrofauna. *J Exp Mar Biol Ecol.* 201:159–171.
- Schuchert P. 2004. Revision of the European athecate hydroids and their medusae (Hydrozoa, Cnidaria): families Oceanidae and Pachycordylidae. *Rev Suisse Zool.* 111:315–369.
- Schuchert P. 2005. Species boundaries in the hydrozoan genus *Coryne*. *Mol Phylo Evol.* 36: 194–199.
- Sebastian CR, Etheridge SM, Cook PA, O’Ryan C, Pitcher GC. 2005. Phylogenetic analysis of toxic *Alexandrium* (Dinophyceae) isolates from South Africa: implications for the global phylogeography of the *Alexandrium tamarense* species complex. *Phycologia* 44:49–60.
- Schoonbee HJ. 1991. Biological control of fennel-leaved pondweed, *Potamogeton pectinus* (Potamogetonaceae), in South Africa. *Agr Eco Env.* 37:231–237.
- Siddall SE. 1980. A clarification of the genus *Perna* (Mytilidae). *Bull Mar Sci* 30(4):858–870.
- Silva PC, Basson PW, Moe RL. 1996. Catalogue of the benthic marine algae of the Indian Ocean. University of California Publications in Botany 79:1–1259.
- Simon CA, Booth AJ. 2007. Population structure and growth of polydorid polychaetes that infest the cultured abalone, *Haliotis midae*. *Afr J Mar Sci.* 29:499–509.
- Simon CA, Ludford A, Wynne S. 2006. Spionid polychaetes infesting cultured abalone *Haliotis midae* in South Africa. *Afr J Mar Sci.* 28:167–171.
- Simon CA, Thornhill DJ, Oyarzun F, Halanych KM. 2009. Genetic similarity between *Boccardia proboscidea* from Western North America and cultured abalone, *Haliotis midae*, in South Africa. *Aquaculture* 294:18–24.
- Simon-Blecher N, Granevitza Z, Achituv, Y. 2008. *Balanus glandula* from North-West America to the west coast of South Africa. *Afr J Mar Sci.* 30:85–92.
- Singer BS. 2005. *Thais sacellum* and *Ergalatax obscura*, new immigrants to northern Israel. *Triton* 12:2.
- Skelton P. 2001. A complete guide to the freshwater fishes of Southern Africa. 2nd edition. Cape Town: Struik Publishers. 395 pp.
- Sluiter CP. 1898. Beiträge zur Kenntnis der Fauna von Südafrika. II. Tunicaten. *Zool Jahrb (Systematik).* 11:1–64.
- Smith EA. 1910. On South African marine Mollusca, with descriptions of new species. *Ann Natal Mus.* 2(2):175–220.
- Soot-Ryan T. 1955. A report of the Family Mytilidae (Pelecypoda). Allan Hancock Pacific Expeditions 20:1–174.
- Stebbing TRR. 1888. Amphipoda. Report of the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76. 29:1–1737.
- Stebbing TRR. 1910. General Catalogue of South African Crustacea (Part V. of S.A. Crustacea, for the marine investigations in South Africa). *Ann S Afr Mus.* 6(4):281–599.
- Stebbing TRR. 1917. The Malacostraca of Durban Bay. *Ann Durban Mus.* 1(5):435–450.
- Stechow E. 1925. Hydroiden der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer “Valdivia” 1898–1899*, 17: 383–546.
- Stegenga H, Bolton JJ, Anderson RJ. 1997. Seaweeds of the South African west coast. *Contributions from the Bolus Herbarium.* 18:3–637.
- Stenton-Dozey JME, Griffiths CL. 1983. The fauna associated with kelp stranded on a sandy beach. *Dev Hydrobiology* 19:557–568.
- Steyn DG, Lussi M. 1998. Marine Shells of Southern Africa. Hartebeesport: Ekoguide Publishers.
- Stock JH. 1954. Pycnogonida from Indo-West Pacific, Australian and New Zealand waters. *Papers from Dr. Th. Mortensen’s Pacific Expedition 1914–1916. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn.* 116:1–168.

- Stock JH. 1957. Contributions to the knowledge of the Red Sea. No. 2. Pycnogonida from the Gulf of Aquaba. Bull Sea Fish Res Stat. 13:13–14.
- Stock JH. 1959. On some South African Pycnogonida of the University of Cape Town Ecological Survey. Trans Roy Soc S Afr. 35(5):549–567.
- Tan KS, Sigurdsson JB. 1996. Two new species of *Thais* (Mollusca: Neogastropoda: Muricidae) from peninsular Malaysia and Singapore, with notes on *T. tissoti* (Petit, 1852) and *T. blanfordi* (Melville, 1893) from Bombay, India. Raffles Bull Zool. 44:77–107.
- Tarjuelo I, Posada D, Crandall K, Pascual M, Turon X. 2001. Cryptic species of *Clavelina* (Asciacea) in two different habitats: harbours and rocky littoral zones in the northwestern Mediterranean. Mar Biol. 139:1432–1793.
- Teske PR, Wooldridge TH. 2002. What limits the distribution of subtidal macrobenthos in permanently open and temporarily open/closed South African estuaries? Salinity vs. sediment particle size. Est Coastal Shelf Sci. 57:225–238.
- Teske PR, Wooldridge TH. 2004. Affinities of some common estuarine macroinvertebrates to salinity and sediment type: empirical data from Eastern Cape estuaries, South Africa. Afr Zool. 39:183–192.
- Thornton JA, Beekman H, Boddington G, Dick R, Harding WR, Lief M, Morrison IR, Quick AJR. 1995. The ecology and management of Zandvlei (Cape Province, South Africa), an enriched shallow African estuary. In: McComb AJ, editor. Eutrophic Shallow Estuaries and Lagoons. Inc Boca Raton, FL: CRC Press. p. 109–128.
- Trowbridge CD. 1998. Ecology of the green macroalga *Codium fragile* (Suringar) Hariot 1889: invasive and non-invasive subspecies. Annu Rev Oceanog Mar Biol. 36:1–64.
- Turner RD. 1966. A Survey and Illustrated Catalogue of the Tereidinidae (Mollusca: Bivalvia). Mus. Comp. Zool. Harvard University. 265 pp.
- Turon X. 1988. Some ascidians from Namibia (SW Africa). Monogr Zool Mar. 3:267–291.
- Turon X, Nishikawa T, Rius M. 2007. Spread of *Microcosmus squamiger* (Asciacea: Pyuridae) in the Mediterranean Sea and adjacent waters. J Exp Mar Biol Ecol. 342:185–188.
- Uriz MZ. 1990. Possible influence of trawl fishery on recent expansion in the range of *Suberites tylobtusa* in the southeast Atlantic. In: Rützler K. editor. New perspectives in sponge biology. Washington DC: Smithsonian Institution Press. p. 309–315.
- Van Name WD. 1936. The American land and fresh-water isopod Crustacea. Bull Am Mus Nat Hist. 71, 535 pp.
- Vasquez JA, Buschmann A. 1997. Herbivore-kelp interactions in Chilean subtidal communities: a review. Rev Chil Hist Nat. 70:41–52.
- Vasquez JA, Santelices B. 1990. Ecological effects of harvesting *Lessonia* (Laminariales, Phaeophyta) in central Chile. Hydrobiologia 204/205:41–47.
- Vega JMA, Vasquez JA, Buschmann AH. 2005. Population biology of the subtidal kelps *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales, Phaeophyceae) in an upwelling ecosystem of northern Chile: interannual variability and El Niño 1997–1998. Rev Chil Hist Nat. 78:33–50.
- Vivier L, Cyrus DP. 1999. The zoobenthic fauna of the Nhlabane coastal lake system, KwaZulu-Natal, South Africa, 20 years after construction of a barrage. Water SA 25:533–542.
- Waldron FW. 1904a. The destruction of timber on the South African coast by marine wood-borers. Min Proc Cape Soc Civil Engin. 2(8):1–6.
- Waldron FW. 1904b. The destruction of timber on the South African coast by marine wood-borers. Min Proc Cape Soc Civil Engin. 2(12):5–6.
- Warren E. 1906. On *Halocordyle cooperi* sp. nov., a hydroid from the Natal coast. Ann Natal Govt Mus. 1:73–81.
- Warren E. 1907. Note on the variation in the arrangement of the capitate tentacles in the hydroid, *Halocordyle cooperi* Warren. Ann Natal Govt Mus. 1:209–213.
- Willan RC. 1984. Nudibranchs of Australasia. New edition. Sydney, Australia: Australasian Marine Photographic Index. 56 pp.

- Wilson N. 2006. New record of the nudibranch *Polycera hedgpethi* Er. Marcus, 1964, in South Australia, with a discussion of its occurrence in Australia. *Records W Aust Mus Suppl.* 69:137–140.
- Winston JE. 1982. Marine bryozoans (Ectoprocta) of the Indian River area (Florida). *Bull Am Mus Nat Hist.* 173:99–176.
- Winston JE. 1995. Ectoproct diversity of the Indian River coastal lagoon. *Bull Mar Sci.* 57: 84–93.
- Wollaston EM. 1968. Morphology and taxonomy of southern Australian genera of Crouanieae Schmitz (Ceramiaceae: Rhodophyta). *Aust J Bot.* 16:217–417.
- Wyatt ASJ, Hewitt CL, Walker DI, Ward TJ. 2005. Marine introductions in the Shark Bay World Heritage Property, Western Australia: A preliminary assessment. *Div. Dist.* 11:33–44.
- Yannic G, Baumel A, Ainouche ML. 2004. Uniformity of the nuclear and chloroplast genomes of *Spartina maritima* (Poaceae), a salt marsh species in decline along the western European coast. *Heredity* 93:182–188.
- Zvyagintsev A Yu. 2003. Introduction of species into the northwestern Sea of Japan and the problem of marine fouling. *Russ J Mar Biol.* 29:(suppl. 1):S10–S21.