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# **Climate and Bioinvasives: Drivers of Change on South African Rocky Shores?**

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**Thesis presented for the degree of Doctor of Philosophy**

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I, **ANGELA MEAD**, hereby declare that:

- (i) the above thesis is my own unaided work, both in concept and execution, and that apart from the normal guidance from my supervisor, I have received no assistance except as stated below:

**Chapter 2: Appendix A: Vignettes for inventory – research and writing of vignettes was a collaboration between A Mead (lead author and researcher), JT Carlton, CL Griffiths and M- Rius**

- (ii) neither the substance nor any part of the above thesis has been submitted in the past, or is being, or is to be submitted for a degree at this University or at any other University.

**Signed:**

Signed by candidate

**DATE: 8<sup>th</sup> February 2011**

*For my boys...the constant compass in my life*

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## Abstract

The overall aims of the thesis were to assess spatio-temporal change in macro species assemblages at sites located around the South African coast. Detected changes were considered in parallel with regional patterns of bioinvasion and climate change driven shifts in temperature trends over comparable time scales. Marine introductions were re-evaluated through field surveys, examination of historic literature and improved taxonomic resolution. In this way the numbers of introduced and cryptogenic species were enormously increased, from 22 and 18 to 85 and 40, respectively. The majority of introductions originated from the Eastern Atlantic, were vectored primarily by ballast water and found within harbours, with patterns emulating four centuries of shipping history. Few open coast introductions were evident. Long-term changes in the species composition of macro-assemblages were investigated through comparing site data from historical (1933-1944; 1989-1992; 1987) and contemporary (2007-2009) sampling periods. Multivariate analyses revealed significant temporal change in species assemblages both within and between all biogeographic regions in the low and mid-intertidal. Across the cool and warm-temperate regions (west and south coast), species richness was reduced. Cool- and warm-water adapted species numbers increased and decreased respectively, leading to homogenization of assemblages across regions. Within the sub-tropical and tropical regions (east coast), assemblage similarity, species richness and the number of warm-water adapted species increased. Particularly notable was a range contraction in the southern range limit of a native mussel, *Perna perna* on the west coast. All detected changes coincided with regional changes in sea temperature, driven by altered upwelling regimes and the warming of the Agulhas Current. The establishment and spread of a relatively cool-adapted, introduced mussel, *Mytilus galloprovincialis*, contributed significantly to the range contraction, species compositional changes and increasing similarities between assemblages on the west and south coast. Experimental manipulation and immuno-assay revealed significant differences in the plasticity of the heat-stress response within the two mussel species. Differences in induction thresholds and thermotolerance were identified indicating the ecological energetics of the introduced mussel were unlikely to be negatively impacted by near-shore cooling in comparison to the native mussel. This could translate into the observed distributional shifts.

## Chapter 1: Introduction

Rocky intertidal communities occupy what is essentially a narrow, linear strip snaking along the coastline. Located between low and high tide marks, these ocean-margin systems straddle the ever-moving interface between marine and terrestrial ecosystems (Stephenson and Stephenson 1972). Intertidal communities are composed of diverse groups of algae and fauna, ranging from micro to mega size classes. The majority of species present have pelagic larval life stages, but live as sessile or sedentary juveniles and adults on the rocky shore following recruitment. Each species present has a contributing role to the overall structure and functioning of an intertidal community.

Although most intertidal organisms are ectotherms that have their evolutionary roots in marine habitats, they must tolerate short-term cycles of aerial exposure (emersion). During emersion, temperatures that the organisms experience are elevated in comparison to immersion temperatures experienced when the organisms are covered by turbulent waters (Helmuth *et al.* 2002). Thus they have adapted physiological mechanisms to cope with temperature fluctuations over a variety of temporal scales (Hoffman and Parsons 1997). Besides physiological stress, intertidal organisms adapt to cope with a range of physical stressors (Somero 2002; Helmuth and Denny 2003; Witman and Smith 2003; Davenport and Davenport 2005; Kitzes and Denny 2005; Leslie *et al.* 2005), one example

being exposure to wave action (Bustamante and Branch 1996b; Hampton and Griffiths 2007).

As a result, rocky shore habitats are considered amongst the most physiologically and physically stressful on earth (Connell 1972; Paine 1983; 1994; Helmuth and Hoffman 2001; Scavia *et al.* 2002; Prezeslawski *et al.* 2005). The combination of physiological and physical stressors in a given region form an underlying vertical environmental gradient from low- to high-shore. This dictates the well-established biotic interactions present (Southward 1958; Connell 1972; Wethey 1984; 1985; Paine 1994), as well as behaviour and the variable biodiversity of intertidal communities that exists at any point in time from shore to shore (Menge and Olsen 1990; Bertness *et al.* 1999; Chapman *et al.* 1995; Raffaelli and Hawkins 1996; Tomanek and Helmuth 2002).

Temporal change in both sea temperature (hereafter referred to as immersion temperature) and air temperature (hereafter referred to as emersion temperature) have been documented from region to region and where there is a persistent directional trend this is considered to be a function of global climate change (IPCC 2001; Scavia *et al.* 2002; Kruger and Shongwe. 2004; IPCC 2007). Besides impacting intertidal organisms at a physiological level, long-term shifts in temperature regime will also alter the underlying environmental gradient indirectly. Indirect effects include altered precipitation levels, atmospheric pressure and wind direction or strength (Reason and Rouault 2005; Trenberth *et al.* 2007; Rouault *et al.* 2009), as well as increases in the size, frequency and

intensity of coastal storms, sediment transportation, wave action and upwelling systems (Pollack and Shannon 1987; Bakun 1990; Shannon *et al.* 1991; Scavia *et al.* 2002). Ultimately, this translates into spatial and temporal changes in the physical stressors experienced by organisms within intertidal communities.

Rocky intertidal communities have been identified as model systems in terms of their potential to detect climate change driven shifts in temperature regimes (Helmuth *et al.* 2006; Mieszkowska 2009). Besides being easily accessible and globally distributed, intertidal organisms within these systems are often living close to their physiological tolerance limits (Hoffman and Parsons 1997; Helmuth *et al.* 2002; Stillman and Somero 1996). Moreover, they comprise of relatively short-lived, sessile organisms, that cannot easily escape from changing environmental conditions (Brown 1984; Helmuth *et al.* 2006; Mieszkowska 2009). As such, strong responses have both been predicted (Paine 1994; Walther *et al.* 2002; IPCC 2007) and observed (Fields *et al.* 1993; Lubchenco *et al.* 1993; Southward *et al.* 1995; Sagarin *et al.* 1999; Hawkins *et al.* 2003; Harley *et al.* 2006; Mieszkowska *et al.* 2006; Rosenzweig *et al.* 2008).

Climate is one determinate of the edges of a specie's range. Based on a 'climate envelope' model (Pearson and Dawson 2003), long-term change in underlying environmental gradients, such as immersion and emersion temperature, could fall within or outside of the physiological tolerance range of a species living within a rocky intertidal ecosystem. If the shift is significant, or fast enough to favour

population-level increases or decreases over species acclimation or genetic adaptation, then the result would be range extensions or contractions, respectively (Helmuth *et al.* 2002; Mieszkowska 2009). However, range extensions would depend on species interactions within an assemblage, habitat type or connectivity and larval dispersal mechanisms, in order for niche realisation to occur (Helmuth *et al.* 2002; Walther *et al.* 2002; Pearson and Dawson 2003; Mieszkowska 2009).

A number of shifts in the distributional ranges of intertidal species have been detected, the outcome being either species loss from, or addition into, communities (Helmuth *et al.* 2006). Changes have been linked to altered immersion and emersion temperature trends over a range of spatio-temporal scales (Helmuth *et al.* 2006, Mieszkowska, 2009). In temperate regions, poleward range extensions in warm-water affinity species have been described at rates of 16-20 km per year, far exceeding terrestrial equivalents (Weslawski *et al.* 1997, Parmesan and Yohe, 2003, Zacherl *et al.* 2003, Berge *et al.* 2005). Conversely, in Chile, range contractions in cold-water affinity species have been reported, albeit in the same northerly direction (Rivadeneira and Fernandez, 2005). In California, warm- and cold-water adapted species have increased and decreased abundance respectively, in concert with warming immersion and emersion temperatures (Sagarin *et al.* 1999).

Besides range edge effects, impacts have been predicted to occur within the geographical ranges of species, particularly those which have obligate cold- or warm-water affinities (Helmuth *et al.* 2002; 2005; 2006; Parmesan *et al.* 2005; Lima *et al.* 2006; Sagarin and Somero 2006; Sagarin *et al.* 2006; Moore *et al.* 2007). It has been established that within-range shifts have resulted in the creation of 'hot-spots' and 'cold-spots' (Sagarin and Gaines 2002; Sagarin *et al.* 2006; Mieszkowska 2009), as well as pocket extinctions (Sagarin and Somero 2006), for rocky intertidal species. In addition, emersion temperatures are expected to alter vertical zonation on the shore, dictating where species are found and how they interact with each other (Harley 2003). Warming emersion temperatures could squeeze the upper limits of high- and mid-shore species (Wetthey 1984; Somero 2002; Harley and Lopez 2003; Davenport and Davenport 2005).

Climate change driven temperature shifts may also increase the vulnerability of natural communities to marine introductions (Carlton 1996; 2009). Following the establishment of introductions, alterations in the structure and functioning of indigenous communities and ecosystems can be expected (Occhipinti-Ambrogi 2007). Introduced organisms may alter productivity, nutrient retention and cycling, habitat structure, biodiversity and community stability (Grosholz 2002; Castilla *et al.* 2004; Ruesink *et al.* 2006; Robinson *et al.* 2007).

Species creep refers to both indigenous and introduced intertidal species naturally extending their range within old and into new regions, thus representing new influxes of species into communities (Barry *et al.* 1995; Kendall *et al.* 2004; Helmuth *et al.* 2006; Shinen and Morgan 2009). Just as changes in immersion temperature have resulted in the range expansion of indigenous species (Firth *et al.* 2009; Ling *et al.* 2009), so too have they been implicated in the successful spread of marine introductions (Bachelet *et al.* 2004). Temperature-driven extinctions, range recessions and within-range impacts potentially open resource niches that would promote successful establishment of bioinvaders (Kennedy *et al.* 2002; Stachowicz and Byrnes 2006; Occhipinti-Ambrogi 2007). For example, the recruitment and survival of introduced populations of the Japanese oyster *Crassostrea gigas* within natural habitats globally has been attributed to unprecedented increases in water temperature (Shatkin *et al.* 1997).

Climate-driven changes in the underlying environmental gradient, such as altered temperature trends, can potentially impact the physiological mechanisms of individual organisms within a species. Physiological mechanisms impact on important life processes, such as reproduction, dispersal, recruitment and mortality (Lindquist 1986; Mieszkowska 2009). If significant enough, this may scale-up to a population-level change, ultimately altering community structure or functioning (Helmuth *et al.* 2006). For example, a population-level shift of a key structural or functional species would significantly alter the composition and dynamics of a community (Hawkins and Hartnoll 1982; Barry *et al.* 1995;

Southward *et al.* 1995; Sagarin *et al.* 1999; Walther *et al.* 2002; Simkanin *et al.* 2005; Harley *et al.* 2006; Mieszkowska 2009; Keith *et al.* in press). Thus temperature shifts are considered as a potential driver of change within intertidal ecosystems (Helmuth *et al.* 2006).

An integrated approach that investigates both individual (physiological) and population-level responses would be more effective in understanding climate change impacts on intertidal communities (Southward 1991; Menge *et al.* 2002; Helmuth *et al.* 2006; Drinkwater *et al.* 2009) and has been effectively demonstrated (Southward *et al.* 1995; Dahlhoff *et al.* 2002; Tomanek and Helmuth 2002; Helmuth *et al.* 2005; Moore *et al.* 2007). As molecular-based bio-indicator technologies have advanced rapidly over the last decade, the underlying 'individualistic' responses to environmental change are being effectively identified. One such technique is the utilization of a group of molecular chaperones, termed the 'heat shock' proteins (hereafter referred to as stress protein or HSP70). Additional examples include monitoring heart rate in response to thermal fluctuation and the use of protein-labelling using 'gene chips' to detect impacts of temperature on different metabolic pathways (Dahlhoff *et al.* 2002; Braby and Somero 2006a; 2006b; Field *et al.* 2006).

Within stress protein families, such as HSP70, there are inducible forms that express across the physiological temperature range tolerated by the intertidal organisms studied. Their role is to facilitate refolding or recycling of heat damaged proteins within cells (Hofmann and Parsons 1997). Thus, they have

been used as a proxy measure of thermo-tolerance across a wide range of intertidal species (Hofmann and Somero 1996; Hofmann and Parsons 1997; Chapple *et al.* 1998; Tomanek and Somero 1999; Buckley *et al.* 2001; Hofmann *et al.* 2002; Tomanek and Sandford 2003; Sagarin and Somero 2006; Snyder and Rossi 2004; Jansen *et al.* 2007).

The existence of quality historic data sets pertaining to species distributions have enabled researchers to establish the latitudinal biogeographic limits of a range of taxa. This information has been used to defined major marine biogeographic regions (Setchell 1920; Hutchins 1947; Southward 1958; Luning 1990; Vermeij 1992). For example, several surveys conducted in the 1950's have defined the biogeographical provinces that comprise the coastlines of Britain and Ireland (Southward and Crisp 1954 a; 1954 b; Crisp and Southward 1958; Crisp *et al.* 1959). In order to assess potential climate driven impacts, such as temperature, on intertidal communities across time, baseline and contemporary data sets need to be assessed for change and compared with environmental data over similar time frames (Mieszkowska 2009). To date, significant shifts in the distribution and abundance of rocky shore species and subsequent correlation with shifts in temperature regimes have been identified across a range of regions, using the aforementioned approach (Kendall 1986; Kendall and Lewis 1987; Tegner *et al.* 1996; Lima *et al.* 2006; Mieszkowska *et al.* 2006). A spatio-temporal approach becomes even more vital when one considers that not all predicted responses to

climate are expected to occur evenly through time and space (Rivadeneira and Fernandez 2005; Keith *et al.* 2009).

Following a massive ecological survey of the South African rocky intertidal region conducted between 1933 –1944, numerous unpublished data records on the distribution patterns of intertidal marine species are preserved within the Iziko South African Museum marine collections in Cape Town. The data available comprise surveys of more than 25 sites along the South African coast and described species distributions, as well as analyses of community compositions (Isaac 1937(a); 1937(b); 1938; 1949; Stephenson *et al.* 1937; 1938; 1939; 1940; Bright 1938; Eyre and Stephenson 1938; Eyre *et al.* 1938; Eyre 1939; Stephenson *et al.* 1940; Stephenson 1944; 1948). The comprehensive 'presence/absence' data contained within the archived databases have served as benchmark information that has been utilized to establish the biogeographic ranges of species around the South African coast (Brown and Jarman 1978; Bolton 1986; Stegenga and Bolton 1992; Bustamante and Branch 1996a; Bolton and Anderson 1997; Gibbons *et al.* 1999; Turpie *et al.* 2000; Stegenga and Bolton 2002; Bolton *et al.* 2004). As a result, the biogeographical ranges of both cool- and warm-water adapted macro fauna and algae are relatively well known (Branch *et al.* 2010).

In addition, a variety of authors have used the historical data to define biogeographic regions around the South African coastline (Emanuel *et al.* 1992;

Bustamante and Branch 1996a; Bolton and Anderson 1997; Awad et al. 2002; Lombard 2004; Sink *et al.* 2005). Between two and five broad biogeographic regions have been recognized by these authors, with discrepancies regarding the naming of the areas, levels of dissimilarity between regions, region boundaries and recognition of overlap zones. Lombard (2004) synthesised all existing information and through extensive expert input recognised five coastal regions, which have been slightly modified, to incorporate the work of Sink *et al.* (2005), for the purposes of this report (Figure 1.1). The regions are each defined by 'suites' of species, in combination with changes in the underlying environmental gradient, as viewed from an atmospheric and oceanographic perspective. The cool-temperate region (CTP) on the west coast and warm-temperate region (WTP) on the south coast are divided by a broad overlap zone (False Bay) which will be termed transition zone 1 (TZ1). On the east coast, the subtropical region (STP) merges in the north with a tropical region (TP) that extends into Mozambique. There is a second transition zone between the WTP and the STP (East London), which will be termed transition zone 2 (TZ2).

Intertidal climate change research within South African has developed slowly over the years. Initially, MacDonald *et al.* (1988) recognized the importance of a focus on connecting marine biosphere and atmospheric interactions. He suggested utilizing long-term data sets to achieve this and that it should form the South African national contribution to the 'International Geosphere-Biosphere Programme' (IGBP). Griffiths *et al.* (2004) took an important step forward,

formulating predictions that linked shifts in atmospheric and oceanic regimes with anticipated intertidal community responses. Broad changes were indicated and future predictions discussed on the basis of the evidence available. Predictions included altered wind and rainfall patterns, intensified upwelling and concurrent warming of both immersion and emersion temperatures (Griffiths *et al.* 2004). In addition, it was predicted that, as a result of temperature shifts, cool-water adapted species may become restricted in their distribution and warm-water species may expand their ranges southward and westward.

Branch (1984) considered the impacts of an extreme weather pattern anomaly which resulted in a short-term increase in temperature along the west and southwest coast. This study used both quantitative and qualitative data as a benchmark and detected different responses across intertidal organisms. Whereas mass mortalities of the indigenous black mussel, *Choromytilus meridionalis*, were recorded, the warm-water affinity gastropod, *Oxysteles tabularis*, and limpet, *Scutellastra longicosta*, both underwent a south-westerly range extension. Recruitment patterns shifted for the limpet, *Scutellastra oculus*, and a recruitment failure was recorded at the range edge of the limpet, *Scutellastra granatina*.

There exists a body of peer-reviewed published work that has established important baseline information related to South African ocean margin communities. They explore species interactions and individual species

responses, although the questions investigated do not directly address climate change issues. The results and outcomes of these studies will compliment research that does specifically frame climate change based research questions within intertidal systems, providing key insights that will facilitate overall interpretation. For example, two major gradients have been established horizontally along South African rocky shores. Productivity and biomass decreases from the CTP to the TP and biodiversity increases from the TP to the CTP – a response to wave action (McQuaid and Branch 1984; Bustamante and Branch 1996; Bustamante *et al.* 1997; Awad *et al.* 2002). McQuaid and Branch (1985), followed by Bustamante *et al.* (1995), established that the dominance of functional feeding groups within rocky shore communities is also linked to wave action.

Mussels have been established as key structural and functional components of rocky intertidal communities (McQuaid and Phillips 2000; 2006; Porri *et al.* 2006; Nicastro *et al.* 2008) and several studies have focused on species level interactions and their mediation by physical stressors (Hammond and Griffiths 2004, Steffani and Branch 2005; Bownes and McQuaid 2006; Rius and McQuaid 2006; Zardi *et al.* 2006, 2007; Xavier *et al.* 2007). Several studies experimentally quantified the impacts of temperature on the energetics of mussel species present on South African shores (Hockey and Van Erkom Schurink 1990; Van Erkom Schurink and Griffiths 1991; 1992; 1993). These results indicated that the introduced mussel, *Mytilus galloprovincialis*, partitions its energy budget

differently to *Perna perna*, an indigenous mussel. There is a positive correlation between temperature, growth rates and reproductive output in *M. galloprovincialis*, which outperforms *P. perna* at all temperatures. To date, these are the only studies of this nature that relate to the physiological performance of introduced and indigenous mussels in relation to temperature effects.

Investigations into the status and scale of marine introductions within South Africa have evolved over time. Several publications have attempted to quantify numbers of introduced and cryptogenic species within South Africa (Griffiths *et al.* 1992; Griffiths 2000; Robinson *et al.* 2005; Griffiths *et al.* 2009). Prior to this thesis, the number of known marine introductions and cryptogenics was relatively low and stood at 10 and 22 respectively (Griffiths *et al.* 2009). These figures make an assessment of spatial and temporal patterns and processes for marine bioinvasion in South Africa difficult to assess (Wonham and Carlton, 2005, Carlton 2009).

In South Africa, immersion temperature is influenced by seasonal interactions between the cold Benguela and warmer Agulhas Currents, both of which are fed by larger off-shore water bodies (McQuaid and Branch 1984; Shannon *et al.* 1991; Emanuel *et al.* 1992; Bustamante *et al.* 1997; Schumman *et al.* 2005; Rouault *et al.* 2009). Figure 1.2 illustrates a 4 x 4 km resolution linear decadal trend in AVHRR SST (sea-surface temperature) data ( $^{\circ}\text{C}$ ) for the South African region between 1985 and 2007. The major change in the region is the warming

of the Agulhas Current system, due to its intensification in response to changing wind patterns in the South Indian Ocean (Rouault *et al.* 2009).

The AVHRR data indicate that within the CTP, near-shore SST is cooling by -0.2 to -0.5<sup>0</sup>C per decade. There are isolated small-scale pockets of cooling in the region Cape Agulhas to Cape St Francis (WTP) of approximately -0.2<sup>0</sup>C per decade. A larger region of cooling, ranging from -0.2 to -0.7<sup>0</sup>C is evident at Port Elizabeth, centred in the Port Alfred dynamic upwelling cell (located in the WTP). Starting at TZ2 a very thin strip of near-shore water is cooling at a rate of -0.6 to -0.8<sup>0</sup>C per decade as far as Port St. John (STP). North of Port St. John, within the TP, near-shore SST's are warming by +0.2 to +0.4<sup>0</sup>C.

Kruger and Shongwe (2004) demonstrated clearly that South African air (emersion) temperatures have warmed up over the past 70 years, but this factor alone does not explain the large-scale changes in wind speed shown in Figure 1.2 by the geostrophic velocity vector overlay. Recently, significant changes to southerly and westerly wind regimes have been reported in South Africa (Reason and Rouault 2005; Rouault *et al.* 2009). Shifts in westerly wind patterns are a well-know feature of global climate change (Trenberth *et al.* 2007). Linear trends in surface wind speed from 1982 to 2007 are shown in Figure 1.3, as measured using ERA40, a satellite based method. It is clear from these data that winds favouring upwelling have increased in the region. The coastal changes can

therefore be explained with a combination of (i) change in wind speed and (ii) intensification of the Agulhas Current system. Both of these effects are being created by a shift of westerly wind and an intensification of the Atlantic and Indian high-pressure system (Rouault *et al.* 2009).

To summarize:

- a. Cooling trends are evident in the CTP, caused by an increase in the intensity and frequency of upwelling from April - August.
- b. Minor cooling is evident along the south east coast (WTP) caused by an increase in easterly winds from April - August.
- c. A cooling trend is evident in the Port Alfred upwelling cell (located within the WTP) caused by a combination of an intensification of the Agulhas Current and an increase in easterly wind. The minor band of coastal cooling that seems to extend as far as Port St. John within the STP is probably due to intensification of the Agulhas Current.
- d. Warming in the Agulhas Current system occurs for all months of the year and warming is evident at the near-shore, north of Port St. John within the TP.

Interestingly, the localized cooling of near-shore waters goes against the global increasing trend indicated by the IPCC report (2007). Comparitively, the rate of temperature change within the region is fast compared to the global average increase (IPCC 2007).

Given that studies specifically framing climate change questions in relation to shifts in intertidal communities are being conducted globally, the availability of archived data for the South African region and the fact that environmental change is evident around the South African coast, the overarching aims of the thesis are:

- (i) Apply a combination of approaches in order to reassess current lists of marine introduced and cryptogenic species within the South African region.
- (ii) Test if patterns of marine bioinvasion differ between the biogeographic regions of South Africa.
- (iii) Test if long-term changes in biodiversity have occurred within the macrofaunal and macroalgal component of rocky intertidal communities along the South African coast.
- (iv) Identify correlations between change in the macrofaunal and macroalgal component of rocky intertidal communities, patterns of bioinvasion and climate change driven temperature shifts over comparable spatio-temporal scales.
- (v) Using heat shock proteins, test for differences in the physiological responses of an introduced and indigenous intertidal mussel species to a range of temperature treatments.

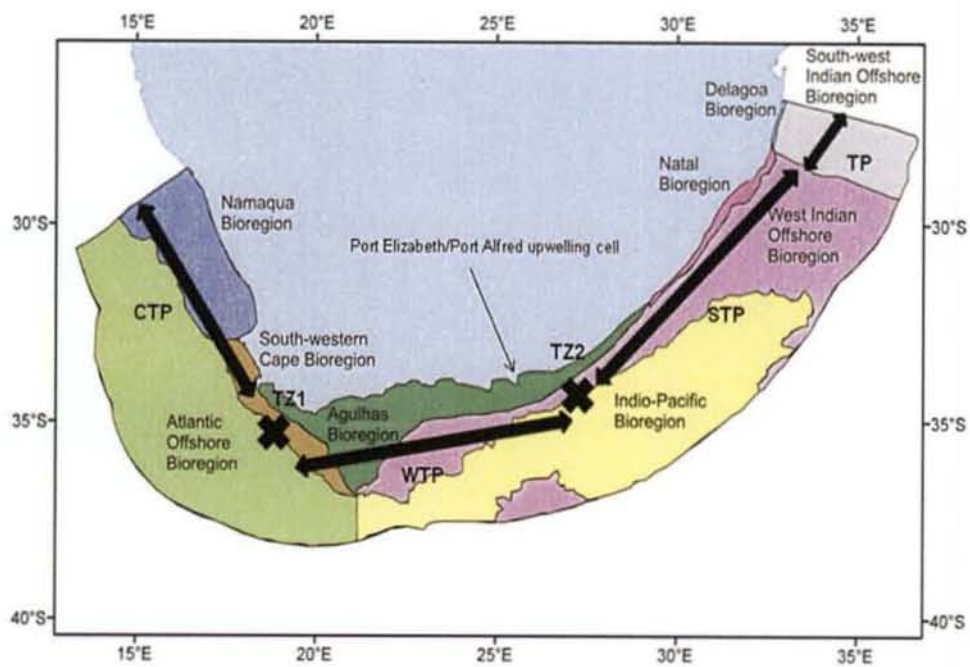


Figure 1.1: Biogeographic provinces of the South African coast. Note: CTP = cool-temperate province, TZ1 = transition zone 1, WTP = warm-temperate province, TZ2 = transition zone 2, STP = sub-tropical province and TP = tropical province. (Modified after Lombard 2004 and Sink *et al.* 2005)

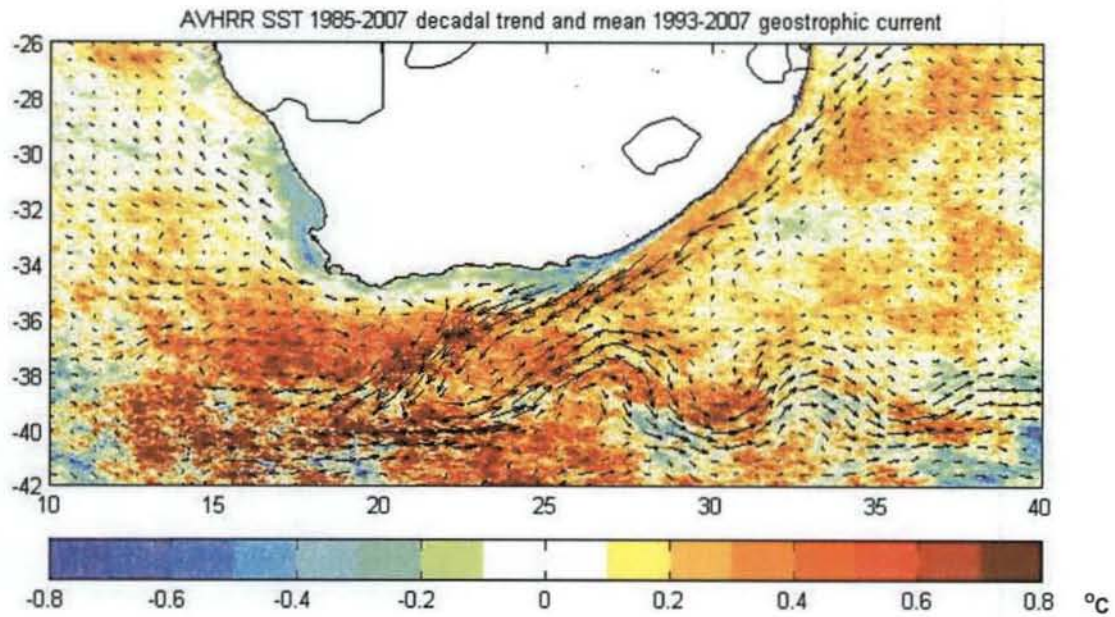


Figure 1.2: Satellite derived AVHRR data depicting the decadal linear trend for sea surface temperature from 1985 to 2007 for the South African region. Mean 1993-2007 absolute geostrophic velocity vectors, derived from combined altimeter readings, are superimposed (From Rouault *et al.* 2009).

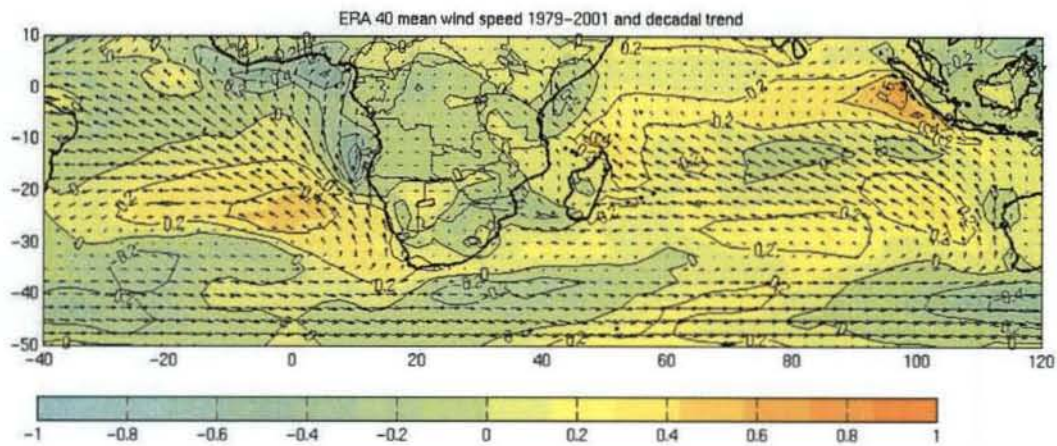


Figure 1.3: Satellite derived ERA 40 data depicting decadal linear trends in surface wind speed between 1982-2007. Mean wind speed and direction is super-imposed (arrows).

## **Chapter 2: Revealing the scale of South African marine bioinvasions.**

### **Introduction**

Within this body of work, the terms 'bioinvader', 'bioinvasive' 'introduced species', 'introduction' and 'non-native' refer to marine organisms whose natural biogeographic range does not extend to South Africa. Through various vectors, these species have arrived on South African shores and established populations that have persisted up to the present date. In the context of this thesis, the term 'invasive' is only applied in the case of the introduced mussel, *Mytilus galloprovincialis*, when the spatial spread and increasing dominance of an introduced species has been monitored and quantified over time (Robinson 2007). This species has been documented as having both negative and positive affects on different components of intertidal communities (Robinson et al. 2005).

The frequency of human-mediated marine introductions is increasing globally, and their role and importance as agents of global change is becoming ever more apparent (Ruiz et al. 1997; Sala et al 2000; Wonham and Carlton 2005). As a result, considerable resources have been directed into research on this topic. However, a few regions, such as Europe and Australia, dominate the literature in terms of reporting the presence and impacts of marine introduced species at a variety of spatial scales (Carlton 1996; Ruiz *et al.* 1997; 1999; 2000; Leppakoski and Olenin 2000; Sala *et al.* 2000; Levings *et al.* 2002; Hewitt *et al.* 2004). In part, this domination is due to the greater availability of financial, scientific and in

particular taxonomic resources in these regions.

Obtaining a realistic 'fix' on the number of marine introductions within a region can be a challenging task (Carlton 2009) and in some cases may not be possible. However, it has been attempted across a number of studies, inclusive of Carlton (1987), Eno *et al.* (1997), Coles *et al.* (1999) Ruiz *et al.* (2000), Orensanz *et al.* (2002), Hewitt *et al.* (2004), Castilla and Neill (2009) and Leppakoski *et al.* (2009). Ruiz *et al.* (2000) recorded 298 marine and estuarine introduced species in North America, a comparatively well-known region. However, the authors suggest that the real number of introductions could easily be 600–900 species and thus the reported figure should not be interpreted as accurate and final. Coles *et al.* (1999) reported 101 introduced species from Pearl Harbour on Oahu Island, Hawaii. Ten years later, Carlton and Eldredge (2009) reported nearly twice that number for Pearl Harbor, based almost entirely on retrospective historical analysis and greater taxonomic resolution, rather than on new introductions that had taken place since 1999. Thus, even in well-studied areas, the diversity of introduced species is rarely adequately resolved.

The situation is of even greater concern in regions of the world where the state of knowledge of the marine biota remains relatively poor, or where there has been less historical interest in marine introductions, the result of several confounding reasons (Nuñez and Pauchard 2009). Such reasons include (i) systematic and taxonomic challenges, (ii) access issues in order to undertake new sampling

surveys across a variety of marine habitats and (iii) availability of historic records (Carlton 1996; 2003; 2009; Wonham and Carlton 2005). Denmark, South Africa , Japan, Uruguay / Argentina, the Azores and Chile have recently reported totals of 18, 22, 25, 31, 33 and 51 marine introductions, respectively (Orensanz *et al.* 2002; Hewitt *et al.* 2004; Otani 2004; Jensen and Knudsen 2005; Castilla and Neill 2009; Griffiths *et al.* 2009). Based on the aforementioned reasons, Carlton (2009) suggests that the actual number of introductions in these regions is probably 5-10 times the number reported.

There are regions where the number of reported bioinvasions is sufficiently high to facilitate a spatio-temporal bioinvasive patterns analysis. To date, these have been conducted at both local and pan-regional scales (Carlton 2003; Wonham and Carlton 2005; Castilla and Neill 2009; Fofonoff *et al.* 2009; Hayden *et al.* 2009; Rilov and Galil 2009; Sliwa *et al.* 2009). These analyses are an important step toward understanding the patterns and processes behind successful introductions (Carlton 1996; Ruiz and Hewitt 2002; Occhipinti-Ambrogi 2003; 2007; Byers 2009; Lonhart 2009; Olyarnik *et al.* 2009).

Vector types, dispersal pathways, source regions, taxonomic composition, spatial distribution, receiving habitat types, measured impacts and rates of successful introduction have all been investigated in order to elucidate bioinvasion patterns (Ruiz and Hewitt 2002; Carlton 2003; Wonham and Carlton 2003; Wilson *et al.* 2008; Carlton 2009; Hewitt *et al.* 2009; Miller and Ruiz 2009; Minchin *et al.*

2009). Through establishing bioinvasion patterns for various regions across the globe, it is envisaged that cross-regional comparisons will become possible, and that these will facilitate bioinvasion predictions and the formulation of effective management policies (Carlton 1996; 2009; Kolar and Lodge 2001; Bax et al. 2003). However, it is recognized that sound interpretation is dependent on the quality of baseline knowledge available. In the interim assessing spatio-temporal patterns using the uneven data available needs to be undertaken with caution (Ruiz and Hewitt 2002).

Species that are neither clearly indigenous nor introduced are termed cryptogenic (Carlton 1996). Denmark (Jensen and Knudsen 2005), Japan (Otani 2004) and Chile (Castilla and Neill 2009) are among several regions that have yet to report numbers of cryptogenic species. Cryptogenic species are in fact 'red lights' within biodiversity assessments, not secondary citizens, as they emphasize the potential depth and breadth of a region's cryptic introduction history. It is critical to call attention to the many species that have been assumed to be indigenous without compelling evidence (Carlton 1996; 2009). Without due attention to cryptogenic species, substantial underestimates will be made of the potential scale of regional and global bioinvasions (Carlton 2009).

In South Africa, there has been limited long-term historical focus on bioinvasions in the marine environment. Although several ecological studies have examined conspicuous introductions, such as that of the western European crab *Carcinus*

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

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

difficult to know the composition of the indigenous or indeed introduced marine biota during these early colonization phases. In addition, despite many South African species being given European names, and thus having remarkably disjunct distributions, taxonomists working in South Africa in the 19th and 20th centuries rarely considered that these species might be introduced, with Millard's (1959; 1975; 1978) work on hydroids being a notable exception.

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

In order to improve the quality of the South African knowledge base with regard to marine bioinvasives, this chapter has the following aims:

- (i) Application of a wider range of investigatory approaches in order to determine a more realistic estimate of the known diversity of introduced and cryptogenic species and
- (ii) Analysis of spatial differences in the patterns of bioinvasion

evident along the coast.

## **Materials and Methods**

### **Re-assessment of the South African bioinvasions inventory**

A combination of approaches were employed to examine in detail the potential biogeographic histories and affinities of taxa. The aim was to reassess the current inventory of introduced and cryptogenic species in South Africa (Griffiths *et al.* 2009) through expanding the types of approach that had previously been applied. The approaches were as follows:

#### *Comparative invasion biogeography*

The aim was to reveal species that were recognized as bioinvasions elsewhere, but had not yet been recognized as introduced in South Africa. Lists of known South African species were compared with lists of species considered to be introduced in other comparable climatic regimes. This included regions at similar latitudes in the southern hemisphere, for example Australia, New Zealand, and South America, but also in northern latitudes, such as North America and Europe. If the same species was present in South Africa, the criteria of Carlton (1996), Chapman (1988) and Chapman and Carlton (1991) were applied to determine if they should be classified as introduced or cryptogenic. These included evidence derived from palaeontological, archaeological, historic, biogeographic, genetic and systematic studies. Species were assigned indigenous, introduced, or cryptogenic status based on these analyses. Some

taxa recognized in other southern hemispheric countries as 'introduced' were not pursued at this time, due to a lack of evidence pertaining to their South African status.

#### *Disjunct distributions*

The question was posed as to whether selected taxa recognized in South Africa, whose systematic status appeared to be reasonably resolved, had highly disjunct global distributions. The aforementioned decision criteria were implemented. It should be noted that large suites of microscopic species (protozoans, nematodes, rotifers, diatoms, dinoflagellates) do not lend themselves to this approach, as their global status has largely been defined based upon the morphospecies concept, rather than on verification through genetic work.

#### *Under-considered habitats and rapid assessment surveys*

Numerous introductions are found in habitats that are rarely or insufficiently explored (Carlton 2009). This is particularly the case in South Africa (Robinson *et al.* 2005). Through rapid assessment surveys, the aim was to reveal species that were recognizable as bioinvasions. Sampling was conducted in September 2008 at locations on the southern and western coasts of South Africa. These were (i) Table Bay Harbour, Cape Town, (ii) Milnerton Lagoon, Table Bay, (iii) Langebaan Lagoon, Saldanha Bay and (iv) Zandvlei Lagoon, False Bay, Cape Town. For new species records, the date of first collection was recorded as the sampling date (September 2008).

The first habitat sampled was the fouling and wood-boring communities in Table Bay Harbour (Cape Town). The emphasis was placed on fauna associated with gribble (*Limnoria*)-infested wood. Several pieces of wood (5 x 10 x 5 cm) were removed from wooden structures (n=10) within the harbour. Wood samples were returned to the laboratory and organisms across all size ranges extracted and identified through examination under microscopes. Voucher specimens were preserved in 70% ethanol for long-term archival purposes and where necessary, for distribution to systematists.

At Milnerton Lagoon, Table Bay, 0.25 m<sup>2</sup> quadrats (n=10) were placed randomly along the strandline habitat located in the supralittoral zone. All debris (inclusive of decomposing kelp) and samples of sand from within the quadrats were removed and returned to the laboratory. At Langebaan Lagoon, Saldanha Bay, 0.25 m<sup>2</sup> quadrats were placed randomly along sandy beach (n=10) and marsh (n=10) habitats. Organic material and samples of sand/mud from within the quadrats were removed and returned to the laboratory. Organisms across all size ranges were extracted from all samples and identified through examination under microscopes. Voucher specimens were preserved in 70% ethanol for long-term archival purposes and where necessary, for distribution to systematists

At Zandvlei Lagoon, False Bay, Cape Town, the emphasis was on the tubeworm *Ficopomatus enigmaticus* and the associated biota found within the reefs formed by the tubeworm. Several small sections of reef were removed from within the

water. Samples were returned to the laboratory. Organisms across all size ranges, inclusive of the tubeworm, were extracted and identified through examination under microscopes. Voucher specimens were preserved in 70% ethanol for long-term archival purposes and for distribution to systematists.

Taxa identified included harpacticoid copepods, protists, bryozoans, amphipods (including *Chelura*), isopods and polychaetes. It should be noted that full taxonomic identifications have yet to be completed on a number of species found within the wood samples.

#### *Additional records since 2005*

Additional records of recently-detected, previously unrecorded, introduced species between 2005 and 2010 were included within this treatment. Date of first collection was obtained from the primary literature (peer reviewed publications) and voucher specimens held within the Iziko South African Museum Marine Collection, Cape Town.

#### *Expanded review of literature and museum collections*

The previous work of Griffiths *et al.* (2009) was expanded to capture additional 19th century literature (inclusive of peer reviewed publications, monographs, government reports and maritime records – Appendix A; Appendix B). Grey literature sources were used judiciously and only when the levels of expertise and scholarship could be adequately assessed. Voucher specimens and species

records stored within the Iziko South African Museum Marine Collection, Cape Town were examined to identify and establish dates of first collection across all species with a historical record.

The five aforementioned approaches were bundled into three major categories: (i) taxonomic-biogeographic resolution, (ii) field surveys and (iii) exploration of historical literature. Based on these categories, the revisionary work led to allocation of 'introduced' or 'cryptogenic' status to various candidate species. If evidence warranted it, a species was similarly removed from the inventory. *Indigenous regions* were first determined from the peer-reviewed and often highly specialized taxonomic literature (Appendix A; Appendix B). This said, indigenous ranges are often erroneously reported, or are conflicting in the literature, and thus multiple sources were used when available to assess indigenous areas in addition to other evidence, such as biogeographic patterns of sister taxa. For cosmopolitan species, the indigenous region or origin was classified as 'unknown.' *Transport vectors* are based on life history knowledge and date/site of introduction in South Africa, extracted from literature records (Appendix A; Appendix B).

### **Temporal and spatial patterns analysis**

Relevant data were extracted from the vignettes detailed for each species, following re-assessment of the bioinvasions inventory (Appendix A). Temporal and distributional patterns were elucidated using introduced species counts. Rate of discovery, regional distributions, indigenous regions, taxonomic groups,

vector pathways and habitat type were investigated. Assessments were based on a range of 72-85 records for individual species found within marine and brackish environments. Groups of organisms included in each treatment covered invertebrates, phytoplankton, algae, a coastal insect, a fish and vascular plants (inclusive of a terrestrial plant occupying salt marshes). Cryptogenic species were excluded.

Temporal analyses are currently confounded by a lack of ability to accurately assess 'date of introduction'. For most of the species records, date of first collection could be accurately determined, rather than a date of actual successful introduction. For the majority of species it was not possible to demonstrate prior absence or presence beyond this date, although such species may have been present in South Africa for decades, or even centuries, before collection. Regarding those species for which prior absence could be argued, this mostly involved assignation of a window of arrival close to the era of introduction. Moreover, South African bioinvasions were first collected by taxonomists working on specific taxa at a time when specimens were not recognized as 'introductions' at the time of collection. However, in order to assess the effectiveness of the methods presented here, collection dates were used in order to determine how discovery rates are changing over time.

#### *Rate of discovery*

Species counts were regressed against collection year since 1840 (earliest first collection record known). This analysis was based on 73 of the possible 85

species records, as date of first collection could not be determined for 12 species. Three alternative models were compared in order to best describe the temporal change in the cumulative number of reported bioinvasions (Wonham and Carlton 2005). The first model was a linear regression fit to untransformed data ( $y = \alpha + \beta x$ ), the second quadratic fit to square-root ( $x$ ) transformed data ( $y = \alpha + \beta x^2$ ) and the third, exponential fit to  $\ln(x)$ -transformed data ( $y = \exp(\alpha + \beta x)$ ). These models described a constant rate, constant increasing rate and accelerating rate of discovery, respectively (Wonham and Carlton 2005).  $R^2$  values were compared and although all analyses yielded values that explained the variance well ( $R^2 = 0.88-0.95$ ), the best fit model is reported. In addition, the mean number of introduced species collected per decade was calculated across thirty year periods, in order to compare discovery rates during periods where introductions were collected as a by-product of maritime surveys or indigenous biodiversity surveys (1840 to 1990) relative to where introductions were collected as a product of focused bioinvasive research (1990-2010).

Two surveys which have progressively re-assessed the bioinvasions inventory for South Africa were conducted by Robinson et al. (2005) and Griffiths et al. (2009) over the period of one year, as per the current re-assessment. All three re-assessments separate introduced and cryptogenic species. Based on the number of introduced species revealed within each re-assessment the percentage of introductions revealed is calculated for each study, as a proportion of number of introductions revealed in total, as an indicator of the effectiveness

of the current methodologies.

### *Distribution analysis*

This was based on literature records as described under 're-assessment of the South African bioinvasions inventory' (Appendix A; Appendix B). Continuous distribution ranges were distinguished from single point location records, in order not to assume that a species occurs between two known points, such as two ports. The coastline of South Africa can be divided into separate biogeographical regions separated by transition zones (Table 2.1). The provinces are defined as per chapter 1, based on species suites present in combination with physical environmental conditions (Bolton 1986; Emanuel *et al.* 1992; Steggena and Bolton 1992; Bustamante and Branch 1996b; Steggena and Bolton 2002; Lombard 2004; Sink *et al.* 2005). Species were placed into each province category where they had a recorded presence. Four species were excluded, as their distribution had yet to be determined. Therefore regional comparisons were based on information available for 81 individual listed species.

Species uniqueness per biogeographic region or transition zone was determined. The number of species shared between regions and those that were unique to a specific region were identified and tallied. The Jaccard Similarity Index was used to identify similarity between regions (%) based on the numbers of shared and unique species. The following formula was applied:

$$S_{AB} = A_n B / A_u B$$

where  $S$  = Similarity,  $A$  and  $B$  represent regions or transition zones,  $A_nB$  represents the total number of unique species found across both region  $A$  and  $B$  and  $A_uB$  represents the total number of shared species found in both region  $A$  and  $B$ .

### *Regional comparison*

For comparisons across the biogeographic regions and transition zones that form the South African coastline (Table 2.1), data were extracted from the species vignettes (Appendix A) as to the indigenous region of origin, vector pathway and habitat for each species present within each biogeographic region or transition zone. Extracted data were arranged into contingency tables and the *Chi-squared* statistic applied (Zar 1999: attributed to Pearson (1904) and Fisher (1922)). The aim was to test if the frequency of successful introductions per region varied significantly ( $P < 0.05$ ) when tested against indigenous region of origin, vector pathway, habitat or species number (Wonham and Carlton 2005).

### *Additional analyses*

Data for taxonomic group, habitat type, known impacts and species with mono and polyvetric invasion pathways were identified, based on 81-85 individual species records using the species vignettes (Appendix A). Where information related to a specific analysis was not available, the species in question was assigned to an 'unknown' category. Based on South African studies listing the taxonomic diversity and species richness of marine species in South Africa

(Gibbons *et al.* 1999; Griffiths *et al.* 2010), the scale of bioinvasions was calculated as a percentage of total known marine biodiversity for the region (85 species).

## **Results**

A species-by-species treatment of the introduced and cryptogenic biota is presented in Appendix A. Each vignette details the history, systematics and biogeography of a specific introduced and cryptogenic species found within marine and estuarine habitats along the South African coast. Evidence and literature that led to status allocation is highlighted within this monographic style treatment and key reference material is summarized in Appendix B. Initial spatio-temporal patterns of marine bioinvasions in South Africa are also presented.

### **Re-assessment of the South African bioinvasion inventory**

In total, 85 introduced and 40 cryptogenic marine and estuarine species in South Africa were identified (Table 2.2). This is a major re-assessment of the previous inventory and expands substantially on the 22 and 18 respective species reported previously (Griffiths *et al.* 2009). Of the 64 newly resolved introduced species, 57% were sourced from within the historic literature, 11% were identified following field surveys conducted in 2008 and 13% were revealed following taxonomic resolution. Of the 22 newly resolved cryptogenic species, 64% were sourced from within the historic literature, 14% were identified following field surveys conducted post 2007, and 22% were revealed following taxonomic resolution (Figure 2.1). All taxa were identified to species level.

No fewer than 15 of the species in Table 2.2 were originally mistakenly re-described as new endemic species after they had arrived in South Africa (Table 2.3). Five species in the South African marine fauna were tentatively retained, although they were last collected over 50 years ago. This decision was taken as they are in locations or habitats that have not been thoroughly re-explored since the original record, therefore it would be an unjustified assumption to remove them at this stage (Table 2.4). Two additional species are recognized as introductions, but to date are present only within closed aquaculture facilities (Table 2.2). One bryozoan species *Membranipora membranacea* was removed from previous lists of introduced species (Robinson *et al.* 2005; Griffiths *et al.* 2009). Following taxonomic resolution and genetic analysis, it is now recognized as a previously undescribed indigenous species, *M. rustica* (Florence *et al.* 2008).

## **Temporal and spatial patterns of bioinvasion**

### *Rate of discovery*

The variance in the rate of discovery of marine introductions in South Africa is best explained by a quadratic polynomial model ( $R^2 = 0.96$ ; Figure 2.2). This indicates a constant increase in the rate of discovery. With the exception of 90-110 years post 1840, species collection rates were lower in periods where introductions were collected as bi-products of maritime or indigenous biodiversity surveys, compared to focused bioinvasive research (1990-2010). During the

maritime and biodiversity surveys, the species collection rate increased progressively from 0.6 and 2.6 species per decade between 30 to 50 and 60 to 80 years after the earliest collection record to 8.3 and 1 species per decade between 90 to 110 and 120 to 140 years after 1840. During the period of focused invasive research, between 150 to 170 years after 1840, the species addition rate was 8.3 species per decade. Of the total known number of marine introductions to date (85 species), Robinson (2005) revealed 11.7%, Griffiths et al. (2009) revealed 14.1% and the current re-assessment revealed 74.2%.

#### *Regional comparison*

The highest numbers of introductions were reported from the cool-temperate region (CTP) on the west coast (55 species) and the lowest from the tropical region (TP) on the northeast coast (15 species) (Table 2.5; Table 2.6; Figure 2.3). According to *Chi-square* analysis, indigenous regions, invasion pathways, habitat type, taxonomic groupings and shared or unique species differed significantly among regions ( $P < 0.001$ ; Table 2.7). The CTP has the highest proportion of introductions unique to the region (42%; 55 species), followed by the sub-tropical region (STP) on the east coast (26%; 31 species).

The transition zones located in between the biogeographic regions (TZ1; TZ2) have the highest proportion of shared species, with 94% (35 species) and 100% (21 species) respectively (Table 2.6; Figure 2.3). The Jaccard Similarity Index revealed that there were dissimilarities between regions based on respective

shared and unique species compositions (Table 2.8). The CTP shared the highest similarities (40-60%) with all other biogeographic regions and transition zones (Table 2.8). The CTP similarity values increased with increasing distance along the coast from west (TZ1) to east (TP). Similarity between all other regions and transition zones was low, ranging from 4-24% (Table 2.8). The transition zones, TZ1 and TZ2, were the most dissimilar to each other (96%) and the STP and TZ2 were highly dissimilar (92% respectively), when compared with the TP (Table 2.8). The STP was most similar to TZ1 (20%) and TZ2 (20%) in comparison to all other biogeographic regions (Table 2.8).

#### *Areas of origin and vector pathways*

The majority of introduced species were native to the northern hemisphere, with 30% originating from the Eastern Atlantic. A further 15% originated from the southern hemisphere (Table 2.9; Figure 2.4a). Northern hemispheric species all established within the cool- and warm-temperate regions and the transition zones between them. Conversely, the majority of southern hemispheric species have established within the STP and TP of the east coast (Table 2.9; Figure 2.4b).

An overwhelming proportion of species (94%) were introduced unintentionally, with only 6% being imported intentionally, or specifically for mariculture purposes (Table 2.10; Figure 2.5a). In terms of possible vector pathways, 51% of species arrived on the South African coastline through polyvector channels. Ship fouling and ballast water were the dominant vectors of marine introduced species to the

South African coast (88%). The CTP and adjacent transition zone (TZ1) hosted species introduced by all the vectors listed, inclusive of introduction through fishery activity and oil rigs (Table 2.10; Figure 2.5b). Ship-boring species had arrived predominantly within the TP, the CTP and TZ1, although in relatively low numbers, compared to the other listed vectors (Table 2.10; Figure 2.5b). The warm-temperate region has received the highest number of species via the mariculture industry, reflective of the number of mariculture facilities.

#### *Habitat and taxonomic distribution*

Marine introduced species in South Africa are currently known from 11 habitats (Table 2.11). A large proportion of introductions (53%) were found within harbours, with a further 30% found in rocky shores and estuaries (Table 2.11; Figure 2.6; Figure 2.7a). Within the CTP on the west coast, introduced species were found distributed across all 11 habitats. Offshore species were found within the CTP, warm-temperate region (WTP) and TZ1 habitat separates them (Table 2.11; Figure 2.7b). Whereas introduced species found on rocky shores were evident consistently across all regions, estuarine species were concentrated within the STP and TP of the east coast.

Marine introduced species were distributed over 17 taxonomic groups (Table 2.12). Cnidarians, annelids, crustaceans, molluscs and chordates accounted for over three quarters of the species (Figure 2.8a; Figure 2.8b). The cnidarians (13 species) included both anthozoans (2 species) and hydrozoans (11 species). The molluscs (12 species) included both gastropods (7 species) and bivalves (5

species). The crustaceans (17 species) primarily consisted of isopods (6 species) and amphipods, 11 species (Table 2.12). There was one fish, an estuarine species, *Cyprinus carpio* and the echinoderms included the urchin species, *Tetrapyrgus niger*. Algal records consisted of two green algae plus three red algae and there was one flowering plant reported, the dune dwelling *Ammophila arenaria* (Table 2.12).

The earliest collection records of introduced species in South Africa were of the crustacean, *Chelura terebrans*, the bryozoans, *Bugula flabellata* and *Bugula dentata*, the estuarine fish, *Cyprinus carpio*, the green alga, *Cladophora prolifera* and the dune plant, *Ammophila arenaria*, which were all reported between 1846 and 1888 (Table 2.12). Impacts are only known for 5% of all the bioinvaders listed within the current inventory, with the majority of studies concentrating on just one or two of the more conspicuous species, specifically the mussel, *Mytilus galloprovincialis* and crab *Carcinus maenas* (Appendix A). The total number of marine introduced species within the current inventory represents 0.7% of the total known marine biodiversity for South Africa (Griffiths et al. 2010).

## **Discussion**

The most important lessons to take away from this assessment were that (i) expanding the approaches used within the methods resulted in a substantive increase in the number of introduced and cryptogenic species recognized within the South African region and (ii) initial spatial assessments revealed differences within the patterns of bioinvasion from region to region.

### **The South African bioinvasion inventory: a temporal perspective**

Since the first formal attempt at assessing the bioinvasive inventory within the South African region (Griffiths *et al.* 1992), the number of known marine introduced and cryptogenic species within South Africa has increased rapidly. In addition, the earliest collection date for an introduced species has been pushed back to 1846, over a century earlier than the previous reported date of 1955 (Griffiths *et al.* 2009). This clearly indicates that marine introductions started establishing in the South African marine environment a long time ago, comparable to the earliest records of Denmark (1895), the Azores (1887) and Chile (1864) (Carlton 2009).

Based on a model developed by Wonham and Pachevsky (2006), which incorporates first collection dates, the expected (null) trend was evident for the majority of regional data tested, indicating an exponential increase in invasion records and rates over time. However, Wonham and Pachevsky (2006) recognize that data sets spanning short temporal periods may not reveal the 'true' best fit model, due to record limitation. In the case of South Africa, based on the current inventory, a constant, rather than exponential, increase was the 'best fit' for discovery rate. However, all three models, inclusive of the exponential model, explained variance well. This may indicate that as more introduced species are added to the South African inventory, the expected null trend may be observed.

Through model manipulation, Solow and Costello (2004) effectively demonstrate that it is possible to have an accelerating rate of detection without an increasing rate of introduction. Therefore, the former does not necessarily prove or indicate the latter. Wonham and Pachevsky (2006) point out that even establishing an exponential increase in invasion rate does not necessarily indicate an increasing invasion success. Thus, the constantly increasing rate of detection revealed within the South African region indicates very little about invasion rates or success. However, it does reveal important information related to the effectiveness of an increase in effort per unit time. The number of species revealed within thirty year periods peaked twice, once 90-110 years post 1840 and once 150-170 years post 1840. The former period (1930's to 1950's) coincides with a historic high in the number of prominent taxonomists working and publishing within the region (Appendix A) and the commencement of a number of extensive biological surveys undertaken within marine habitats (Isaac 1937(a); 1937(b); 1938; 1949; Stephenson *et al.* 1937; 1938; 1939; 1940; Bright 1938; Eyre and Stephenson 1938; Eyre *et al.* 1938; Eyre 1939; Stephenson *et al.* 1940; Stephenson 1944; 1948). The latter period (1990's to 2009) represents a period of focused bioinvasive research within marine habitats, inclusive of this re-assessment (Griffiths 2000; Griffiths *et al.* 1992; 2009; Robinson *et al.* 2005).

The design and implementation of a well-planned investigative programme has paid dividends, in terms of making dramatic progress within a short space of time. The current re-assessment revealed three quarters of the known

introduced species within South Africa. It has increased the known resolution of both introductions (85 species) and cryptogens (40 species) by over four- and two- fold respectively since the last publication (Griffiths *et al.* 2009). Formal research into marine bioinvasive research has been conducted since 1992 when 15 species were reported, however, introduced and cryptogenic species were not distinguished at that point in time (Griffiths *et al.* 1992). Robinson *et al.* (2005) and Griffiths *et al.* (2009) each spent one year re-assessing the bioinvasive inventory and separated cryptogens from introductions. Robinson *et al.* (2005) report 10 introductions, whereas Griffiths *et al.* (2009) report 22 introductions. In comparison to these previous endeavours, although spanning a comparable research period of one year, the current re-assessment widened the search for historical literature to include documents and voucher specimens from the 1800's, taxonomic expertise of international researchers in order to resolve taxonomic and biogeographic issues and conducted 'rapid assessment' field surveys within habitats previously not assessed. Through this approach, it became possible to reveal the presence of previously misidentified, overlooked, or new introductions, as well as to resolve the status of several cryptogenic species.

According to Carlton (2009), the number of introductions within the South African region could be as high as 220 species, which is 10 times higher than the 22 species previously recorded (Griffiths *et al.* 2009). Through continued use of the methods applied within this re-assessment, it may be possible to reveal these

introductions within a 2-3 year period, based on the fact 64 introduced species were added in one year. In comparison, New Zealand added 40 introduced and 27 cryptogenic species over a period of nine years between 1998 and 2007 (Hayden *et al.* 2009), coincided with the commencement of targeted surveillance aimed at identifying marine introduced species (Hewitt *et al.* 2004). This represents a rate of 4.4 introduced species and 1.8 cryptogens added per year. Australia increased the number of introductions two-fold over a period of 14 years, from 68 to 129, following the establishment of the CSIRO Centre for Research on Introduced Marine Pests (CRIMP) in 1994 (Sliwa *et al.* 2009). This represents a rate of 4.3 introduced species added per year, with both regions falling substantively below the 64 introduced and 22 cryptogenic species per year revealed by the current re-assessment. This provides strong motivation for other regions to initiate similar programs aimed at effectively and efficiently detecting marine introductions and cryptogenic species.

Despite the progress made, it needs to be emphasized that the current re-assessment remains preliminary work, in which only a proportion of the 'true' number of introductions and cryptogenics within South Africa have been identified. For example, a great many more species of sponges, hydroids, flatworms, polychaetes, bryozoans, and other taxonomically-challenging groups (Gibbons *et al.* 1999) are neither clearly recognised as indigenous nor introduced at this stage. Through continued application of the current methodologies, combined with with finer-scale morphological and genetic taxonomic work, it is

predicted that many more such species will be discovered within the region, in line with the predictions of Carlton (2009). Thus, those making global assessment must avoid concluding that the number of introduced marine species in South Africa is sufficiently well-known to invite comparisons with other regions without applying caution when interpreting patterns (such as attempted by Molnar *et al.* 2008).

A recent study by Nuñez and Pauchard (2009) revealed that the challenge in forming global strategies to deal with bioinvasions is the fact that there are major differences in data quality and availability between developed and developing regions. This confounds comparative analyses, limiting the ability of scientists to fully understand the potential depth and breadth of this striking global phenomenon (Carlton 2009; Nuñez and Pauchard 2009). It is imperative that the key issues of (i) commitment to monitoring and vigilance (Campbell 2009) and (ii) implementation of standardized assessments across areas (Hewitt *et al.* 2009; Sliwa *et al.* 2009) are addressed. Based on the success of the comprehensive approach utilized within the current re-assessment, there is potential that such standardised protocols can be implemented in both developed and developing regions. Once regions have adequately resolved the true scale of marine bioinvasions, accurate cross-regional assessments may be possible.

### **Spatial patterns of bioinvasion**

The patterns analyses conducted to date for the South Africa region represent a

coarse measure at this time, due to the fact the bioinvasive inventory for the region is incomplete. However, the results do provide clues and suggestions of possible bioinvasion patterns for the region. One such outcome has been the identification of the northern hemisphere as the main source of introduced species into South Africa. Interestingly, the majority of these species are located within the cool- and warm-temperate regions (CTP; WTP). In contrast, those species originating from other southern hemisphere regions appear to have had more success establishing in the sub-tropical (STP) and tropical (TP) regions, despite the fact there are major ports located all along the coastline that would have been exposed to centuries of shipping history from all global regions.

A number of introduced species that are shared across the biogeographic regions. The majority of these species are found within the CTP, the biogeographic region with the highest number of introductions, and within the transitional zones, where there is a well-documented regional overlap in indigenous species (Griffiths and Branch 1991). More than half of the introduced species present within the CTP have established across a wide range of biogeographic regions with very different climatic and oceanographic conditions, which explains the comparatively high similarity of the CTP with the other biogeographic regions. The observed South African distributions appear to suggest that there are introduced species which can exhibit high levels of plasticity and adapt to a wide range of conditions, increasing invasion success (Occhipinti-Ambrogi 2007). In contrast, there are also a large number of

introductions that are unique to the CTP, all of which are of northern hemispheric origin. The restricted distribution of these species may indicate they are adapted to specific climatic or oceanographic conditions (Occhipinti-Ambrogi 2007; Mieszkowska 2009). Alternatively shipping history and reproductive strategies have been demonstrated to limit arrival and subsequent spread along the coast (Carlton 2003; Wilson 2008).

As with other regions, the chances of an introduction having been introduced via certain vector pathways will have varied over time (Wonham and Carlton 2005). Wilson *et al.* (2008) attempted to represent the temporal windows and peaks of various vectors within South Africa. There are some discrepancies between their estimated windows and what is known from South African shipping history, suggesting they have estimated likely vector pulses. In South Africa, wooden ships carrying boring species would have been operational from the 1600's to early 1900's (a 300 year window) and dry ballast was used up until the 1940's and 50's, whereas mariculture is a relatively new phenomena (last few decades) on South African shores (Haupt *et al.* 2010). One needs to be aware of the adaptive nature of introduced species with regards to invasive pathways. For example, the boring bivalve, *Martesia striata*, has recently been shown to be capable of boring into ABS (Acrylonitrile butadiene styrene) pipes, as well as wood (Jenner *et al.* 2003). In addition, pelagic plastics are fast becoming an increasing concern as the latest modern vector for bryozoans (Florence pers.comm.). The fact that ship fouling (since 1600's) and ballast water (since

1880's) are the dominant vector pathways within South Africa is not unexpected, given the region's rich shipping history. It is interesting that as mariculture expands as an industry within South Africa, mariculture as a vector of invasive species has become more prominent (Haupt *et al.* 2010).

In the CTP, introductions appear to have arrived by all possible pathways at one point or another, whereas other provinces appear to be more 'pathway' selective. This pattern is also reflected in habitat occupation, with estuarine introductions flourishing in the STP and TP, where there are far more estuaries relative to the west coast. In contrast, the CTP has introduced species present within all habitats sampled. One could speculate that spatial and temporal patterns in the shipping industry would reveal higher levels of overall shipping and industrial activity on the west and south coast, as opposed to the east coast. This would allow for arrival by a higher number of pathways, as well as easier dispersal into a range of habitats. This could be achieved through analyses of historical shipping records for the South African region. Interestingly, Preisler *et al.* (2009) hint at the possibility that estuarine invaders are more successful than open coast invaders, but a more thorough, comparative survey of estuarine and coastal systems spanning all the provinces is needed before that can be established for the South African region.

The majority of the introduced species recorded are invertebrates, which is consistent with other studies (Cohen and Carlton 1998; Ruiz *et al.* 2000; Wonham

and Carlton 2005). Based on modified figures of known marine species per taxonomic group (Gibbons *et al.* 1999), the current bioinvader inventory indicates that introductions form a very small proportion (less than 1%) of total South African marine biodiversity, in terms of numbers. At this stage, this cannot be interpreted as a 'true' representation of the proportion of introduced species present within the region. For example, the low number of macro-algal species identified is most probably due to current low sampling intensity within harbours, especially given the high algal diversity reported in the STP and TP of the east coast, due to extensive coastal sampling (Steegena *et al.* 1997). Many taxa that are not represented within the current inventory are likely to be the result of sampling and taxonomic bias. Before focused bioinvasive research was initiated, this is indicated when the spread of introduced species across the different taxa is compared with the expertise of the taxonomists from which introduction were first collected (Appendix A; Appendix B). Many taxa, such as Nematoda, are under-surveyed, or have not been surveyed at all, due to the lack of taxonomic expertise (Gibbons *et al.* 1999) and introduced species certainly lie undetected within such groups (Carlton 2009).

Although South African bioinvasions are not sufficiently well known to invite conclusive comparisons with other regions, preliminary comparisons with similar assessments reveal some interesting concurrences and contrasts between regional bioinvasion patterns. Rilov and Galil (2009) report that up to 95% of Mediterranean bioinvaders have tropical (Indo-Pacific) origins, which is in line

with that region's shipping history. South African bioinvasions originate from regions with which there has been a long history of shipping trade, such as Europe. Hayden *et al.* (2009) reported that the discovery rate of marine introductions was on the increase within New Zealand, with ballast water and ship fouling as major vector pathways, statements that are in agreement with preliminary South African findings. As in South Africa, mariculture is recognized as an emerging vector pathway in Korea, with increases in ballast water introductions attributed to an increase in global shipping trade to the region over time (Seo and Lee 2009). Interestingly, range extensions across regional borders, a result of shifting climate corridors, are noted as being important invasive vector pathways in the South East Pacific (Castilla and Neill 2009) and in Korea (Seo and Lee 2009), whereas to date, there are no recorded South African marine introductions that have been vectored in this manner. The majority of Australian and South East Pacific bioinvaders are annelids, molluscs, crustaceans and chordates (Castilla and Neill 2009; Sliwa *et al.* 2009), which concurs with the findings for South Africa, despite possible differences in taxonomic expertise. Such apparent commonalities and differences warrant additional investigation as regional inventories, inclusive of South Africa, become more accurate and comprehensive.

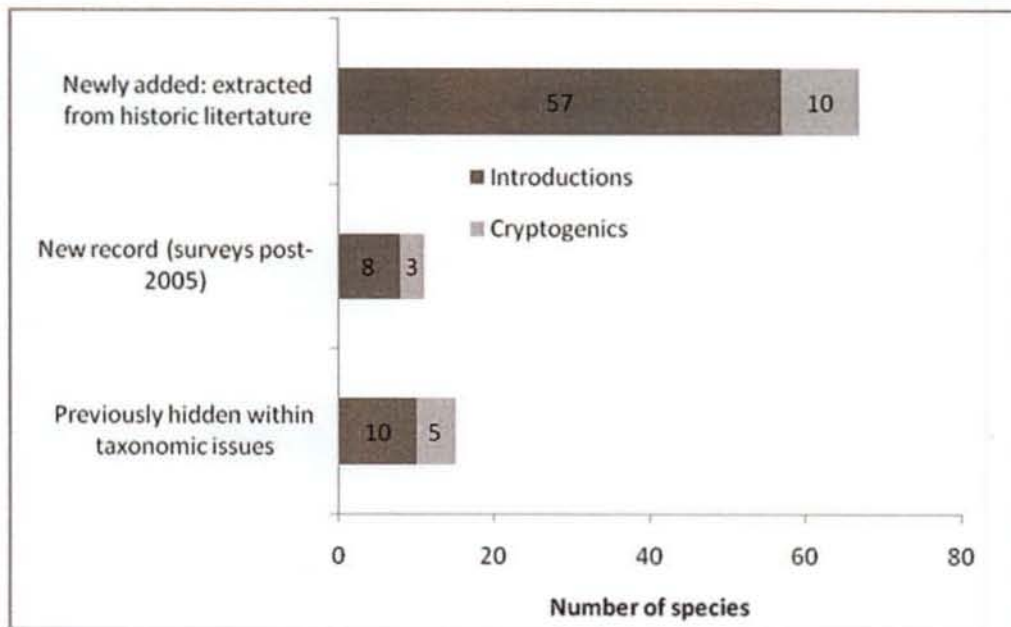


Figure 2.1: Sources for new additions to the updated South African inventory of marine introduced and cryptogenic species (given as species number).

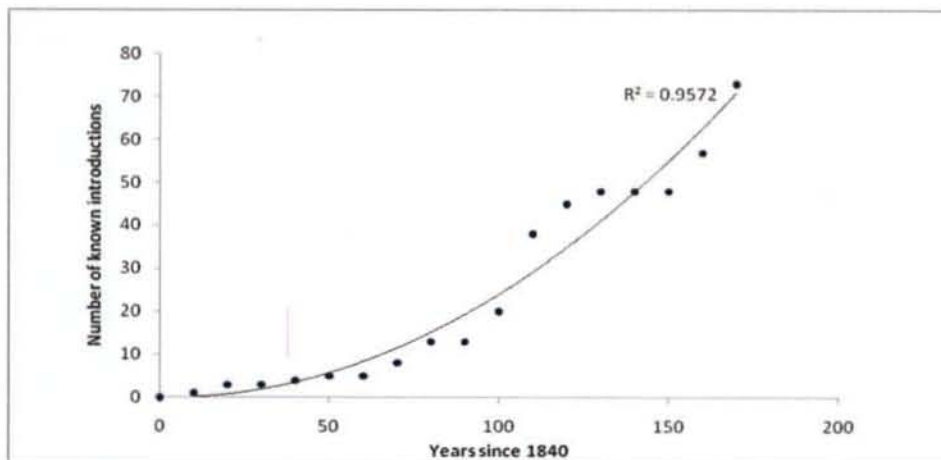


Figure 2.2: Cumulative number of South African marine introductions indicating the rate of discovery in years since 1840.

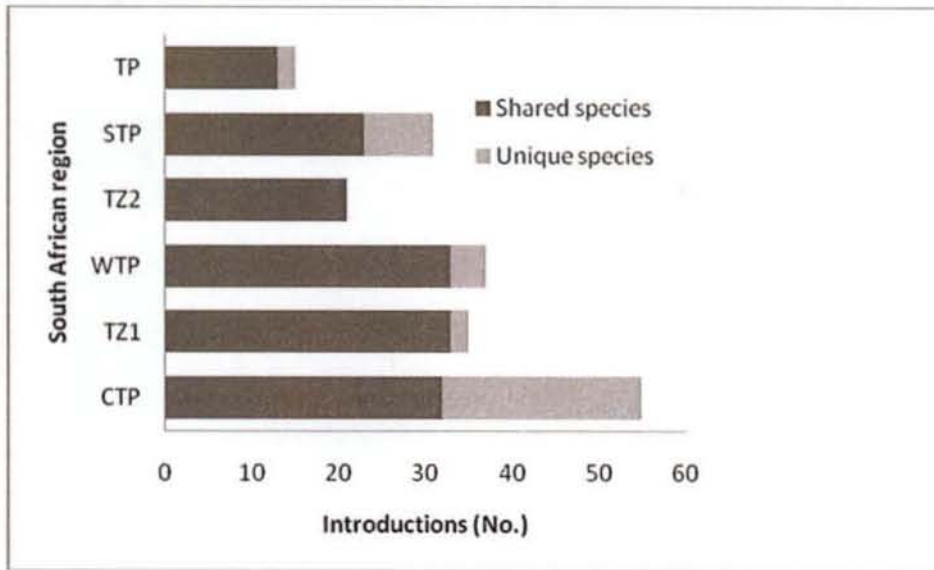
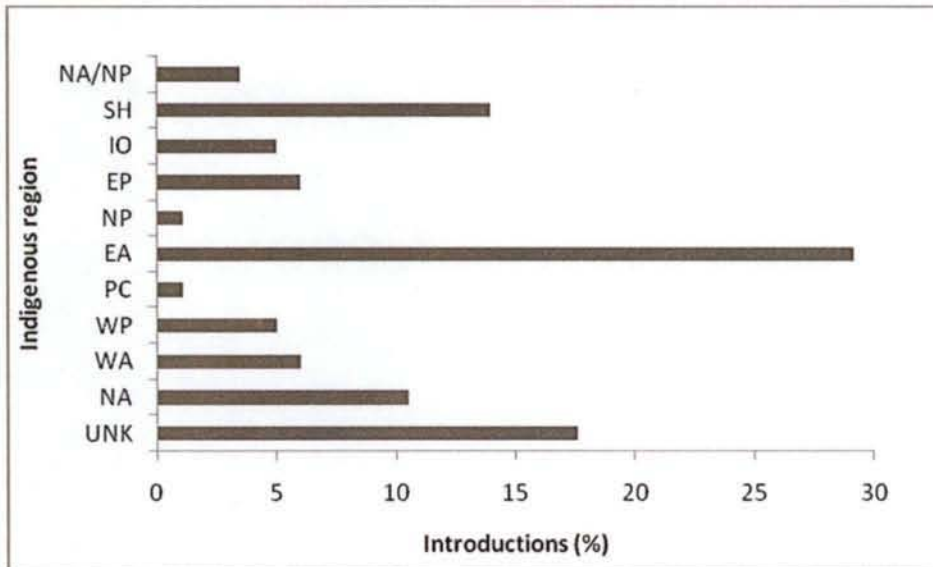


Figure 2.3: Marine introductions (number) per biogeographic region of South Africa.

(a)



(b)

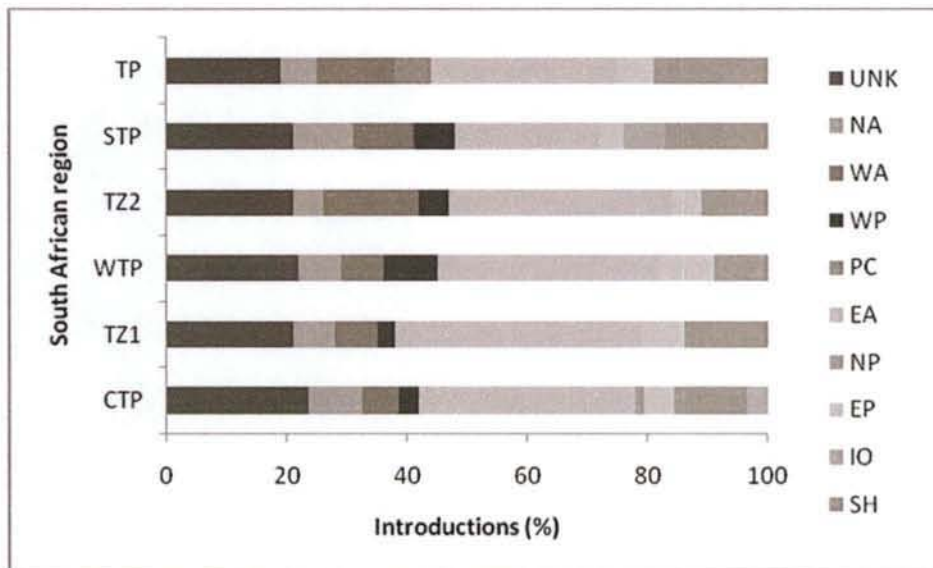
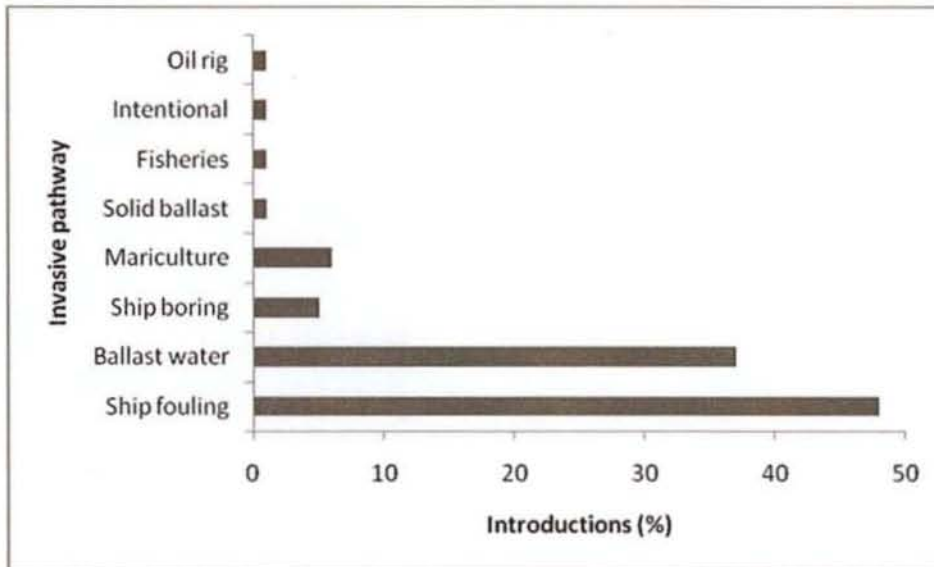


Figure 2.4a: Marine introductions (%) arriving from different points of origin and 2.4b: Marine introductions (%) arriving from different points of origin per biogeographic region of South Africa. For regional codes refer to Table 2.1. For origin codes refer to Table 2.8.

(a)



(b)

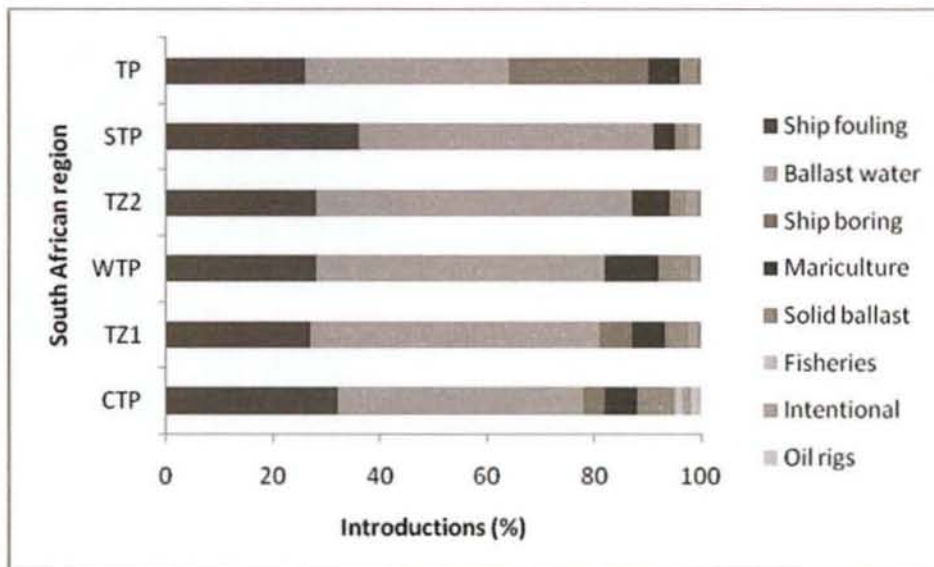


Figure 2.5a: Marine introductions (%) vectored by different invasive pathways and 2.5b: Marine introductions (%) vectored by different invasive pathways per biogeographic region of South Africa. For regional codes refer to Table 2.1.

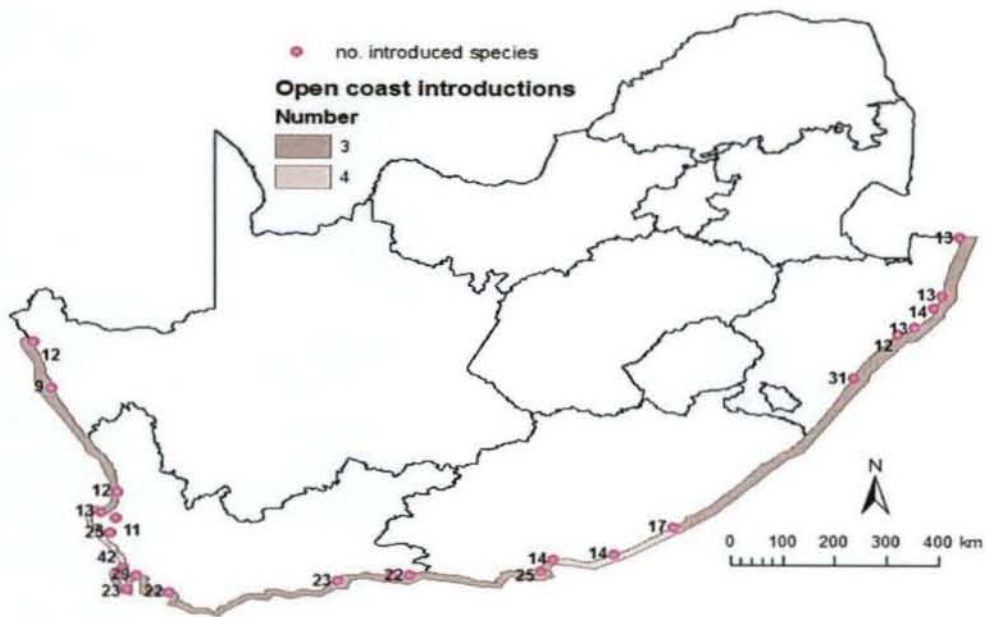
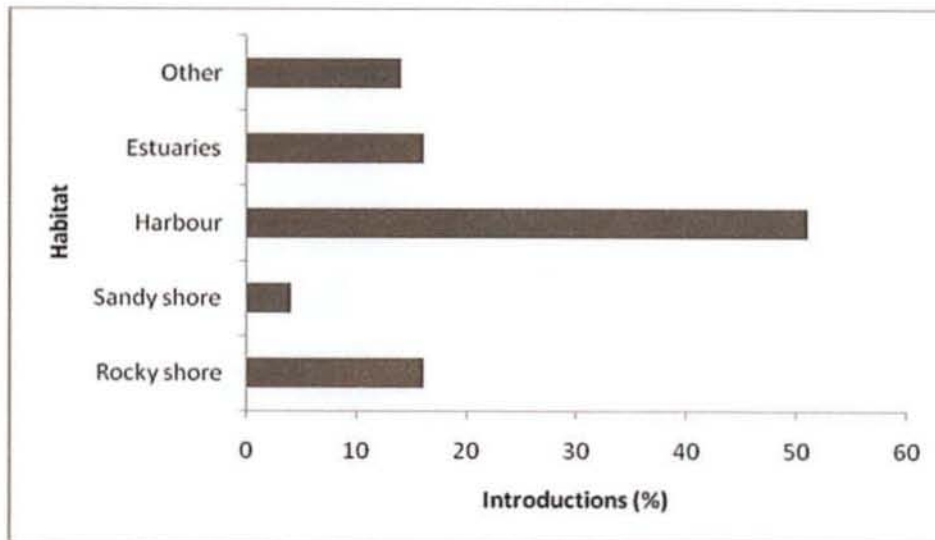


Figure 2.6: Number of marine introduced species recorded from major towns, harbours, and estuaries, and along the open coast of South Africa in 2010.

(a)



(b)

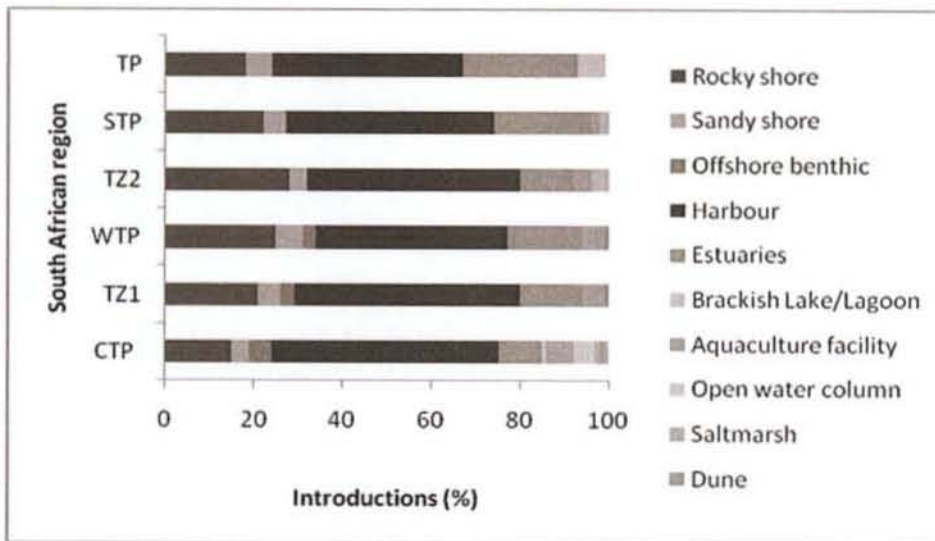
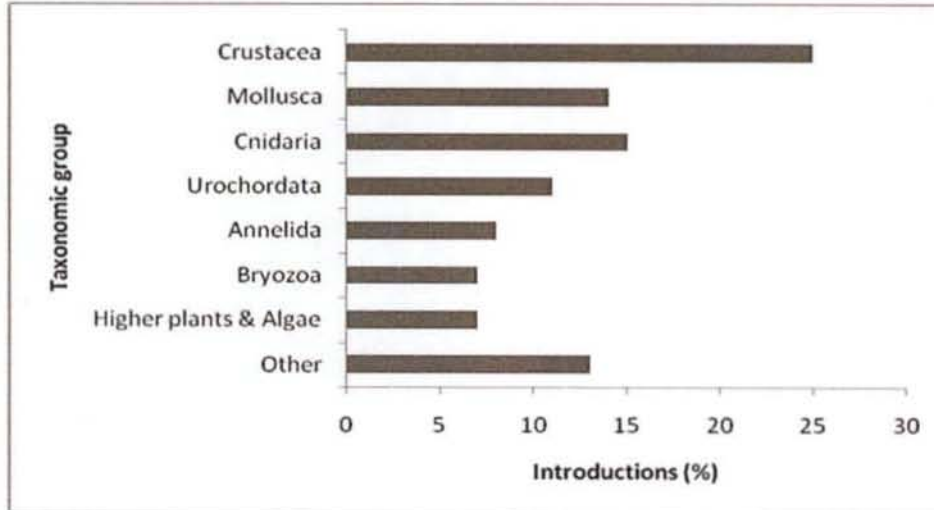


Figure 2.7a: Marine introductions (%) within different habitats and 2.7b: Marine introductions (%) within different habitats per biogeographic region of South Africa. For regional codes refer to Table 2.1.

(a)



(b)

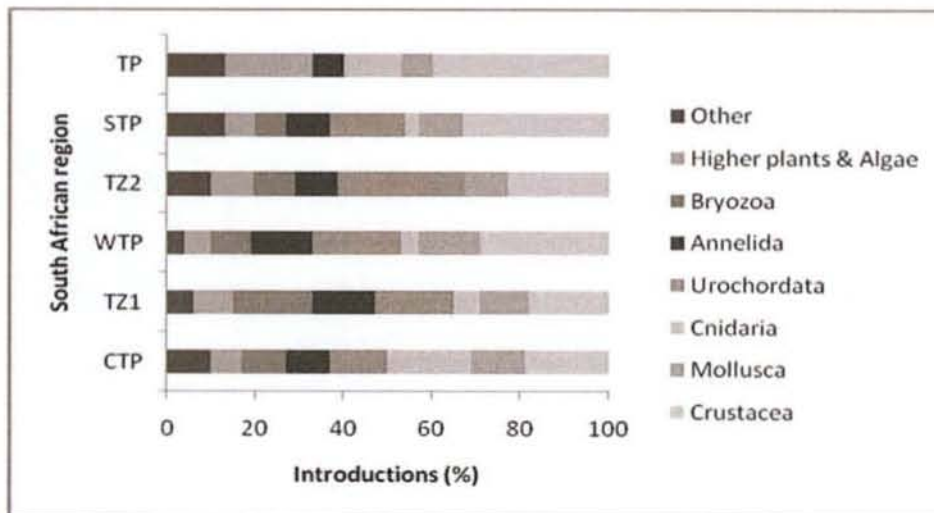


Figure 2.8a: Marine introductions (%) within different taxonomic groups and 2.8b: Marine introductions (%) within different taxonomic groups per biogeographic region of South Africa. For regional codes refer to Table 2.1.

Table 2.1: Biogeographic regions and transition zones of South Africa (modified after Lombard 2004).

Region	Definition	Code
Cool-temperate (west coast)	Alexander Bay (23° 38.1' S, 16° 27.2' E) to Cape Point (34° 21.4' S, 18° 29.8' E)	CTP
False Bay transition zone (south-west coast)	Cape Point (34° 21.4' S, 18° 29.8' E) to Cape Hangklip (34° 22.6' S, 18° 49.6' E)	TZ1
Warm-temperate (south-east coast)	Cape Hangklip (34° 21.6' S, 18° 49.6' E) to Port Elizabeth (33° 58.1' S, 25° 38.1' E)	WTP
East London transition zone (south-east coast)	Port Elizabeth (33° 58.1' S, 25° 38.1' E) to East London (33° 01.5' S, 27° 54.8' E)	TZ2
Sub-tropical (east coast)	East London (33° 01.5' S, 27° 54.8' E) to Durban (29° 45.3' S, 31° 03.5' E)	STP
Tropical (north-east coast)	Durban (29° 45.3' S, 31° 03.5' E) to Kosi Bay (26° 53.5' S, 32° 52.8' E)	TP

Table 2.2: Marine and estuarine introductions of South Africa. NOTE: \*Two species only found within closed aquaculture facilities to date.

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

Taxon	Status	First Collection Date	Biogeographic Origin	Region	Vector
<b>PROTOCTISTA</b>					
<i>Mirofolliculina limnoriae</i>	I	2008	unknown	--	SB
<i>Zoothamnium</i> sp.	C	NDD	unknown	--	SF
<b>DINOFLAGELLATA</b>					
<i>Alexandrium tamarense</i> -complex:	I	1948	N Atlantic/N Pacific	NA / NP	BW
<i>Alexandrium minutum</i>	I	2003	Europe	EA	BW
<i>Dinophysis acuminata</i>	I	1991	Europe	EA	BW
<b>PORIFERA</b>					
<i>Suberites ficus</i>	I	1998	Europe	EA	SF

**CNIDARIA****Anthozoa**

<i>Sagartia ornata</i>	I	1955	Europe	EA	SF/BW
<i>Metridium senile</i>	I	1995	N Atlantic/N Pacific	NA / NP	SF/OR

**Hydrozoa**

<i>Eudendrium carneum</i>	C	NDD	unknown	--	SF/BW
<i>Pachycordyle navis</i>	I	1958	Europe	EA	SF/BW
<i>Coryne eximia</i>	I	1946	N Atlantic/N Pacific	NA / NP	SF/BW
<i>Coryne pusilla</i>	C	NDD	unknown	--	SF/BW
<i>Moerisia maeotica</i>	I	1965	Ponto-Caspian	PC	SF/BW
<i>Pennaria disticha</i>	I	1901	unknown	--	SF/BW
<i>Pinauay larynx</i>	I	1947	North Atlantic	NA	SF/BW
<i>Pinauay ralphi</i>	I	1947	North Atlantic	NA	SF/BW
<i>Laomedea calceolifera</i>	I	1948	North Atlantic	NA	SF/BW
<i>Gonothyraea loveni</i>	I	1946	North Atlantic	NA	SF/BW
<i>Obelia bidentata</i>	I	1948	unknown	--	SF/BW
<i>Obelia dichotoma</i>	I	1938	unknown	--	SF/BW
<i>Obelia geniculata</i>	I	1934	unknown	--	SF/BW

**ANNELIDA****Polychaeta**

<i>Boccardia proboscidea*</i>	I	2006	Eastern Pacific	EP	M
<i>Neanthes succinea</i>	I	1947	North Atlantic	NA	SF/BW
<i>Capitella</i> sp. / spp. complex	C	NDD	unknown	--	SF/BW
<i>Polydora hoplura</i>	I	1947	Europe	EA	
SF/BW/M					
<i>Dodecaceria fewkesi</i>	I	2007	North American Pacific	EP	BW
<i>Ficopomatus enigmaticus</i>	I	1951	Australia	SH	SF/BW
<i>Hydroides elegans</i>	I	1970	Indo-Pacific	SH	SF/BW
<i>Neodexiospira brasiliensis</i>	I	1953	Indo-Pacific	SH	SF/BW
<i>Janua pagenstecheri</i>	I	1955	Europe	EA	SF/BW
<i>Simplicaria pseudomilitaris</i>	C	NDD	unknown	--	SF/BW

**CRUSTACEA**

**Cirripedia**

<i>Balanus glandula</i>	I	1992	North American Pacific	EP	SF/BW
<i>Amphibalanus venustus</i>	I	1938	Western North Atlantic	WA	SF

**Copepoda**

<i>Acartia spinicauda</i>	I	2003	Southeast Asia	SH	BW
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**Isopoda**

<i>Dynamene bidentata</i>	I	2006	Europe	EA	SF/BW
<i>Sphaeroma serratum</i>	I	1950	Europe	EA	SF/BW
<i>Sphaeroma annandalei</i>	C	1926	unknown	--	SF/BW
<i>Sphaeroma terebrans</i>	C	1908	Northern Indian Ocean	IO	SF/BW
<i>Sphaeroma walkeri</i>	I	1915	Northern Indian Ocean	IO	SF/BW
<i>Paracerceis sculpta</i>	I	2007	Northeast Pacific	EP	SF/BW
<i>Synidotea hirtipes</i>	C	1897	Indian Ocean	IO	SF/BW
<i>Synidotea variegata</i>	C	1940	Indo-Pacific	SH	SF/BW
<i>Ligia exotica</i>	C	NDD	unknown	--	SB
<i>Limnoria quadripunctata</i>	I	NDD	unknown	--	SB
<i>Limnoria tripunctata</i>	I	NDD	unknown	--	SB

**Amphipoda**

<i>Chelura terebrans</i>	I	1888	Pacific Ocean	SH	SF/SB
<i>Ischyrocerus anguipes</i>	I	1916	North Atlantic	NA	SF/BW
<i>Erichthonius brasiliensis</i>	I	1910	North Atlantic	NA	SF/BW
<i>Cymadusa filosa</i>	C	1913	unknown	--	BS
<i>Caprella equilibra</i>	C	NDD	unknown	--	SF/BW
<i>Caprella penantis</i>	C	NDD	unknown	--	SF/BW
<i>Paracaprella pusilla</i>	C	1955	unknown	--	SF/BW
<i>Corophium triaenonyx</i>	C	1931	Asia	WP	SF/BW
<i>Apocorophium acutum</i>	I	1915	North Atlantic	NA	SF/BW
<i>Monocorophium acherusicum</i>	I	1915	North Atlantic	NA	SF/BW
<i>Melita zeylanica</i>	C	NDD	Indian Ocean/Australia	IO/SH	SF/BW
<i>Jassa marmorata</i>	I	NDD	North Atlantic	EA	SF/BW
<i>Jassa morinoi</i>	I	NDD	North Pacific	EP	SF/BW
<i>Jassa slatteryi</i>	I	NDD	North Pacific	EP	SF/BW
<i>Orchestia gammarella</i>	I	1949	Europe	EA	BS

<i>Platorchestia platensis</i>	I	1904	unknown	--	BS
<i>Cerapus tubularis</i>	I	1901	North American Atlantic	WA	BS
<b>Decapoda</b>					
<i>Xantho incisus</i>	I	2008	Europe	EA	M
<i>Carcinus maenas</i>	I	1983	Europe	EA	SF/BW/OR
<hr/>					
<b>PYCNOGONIDA</b>					
<i>Ammothella appendiculata</i>	I	1951	Western Pacific	WP	SF/BW
<hr/>					
<b>INSECTA</b>					
<b>Coleoptera</b>					
<i>Cafius xantholoma</i>	I	1936	Europe	EA	BS
<hr/>					
<b>MOLLUSCA</b>					
<b>Gastropoda</b>					
<i>Littorina saxatilis</i>	I	NDD	Europe	EA	BS
<i>Thais blanfordi</i>	I	1950	Indian Ocean	IO	SF/BW
<i>Thais tissoti</i>	I	1950	Indian Ocean	IO	SF/BW
<i>Tarebia granifera</i>	I	2005	South-East Asia	SH	SF/BW
<i>Catriona columbiana</i>	I	1972	North Pacific	NP	SF/BW
<i>Polycera hedgpethi</i>	C	1980	Pacific Ocean	NP	SF/BW
<i>Thecacera pennigera</i>	C	NDD	unknown	--	SF/BW
<i>Anteaeolidiella indica</i>	C	1927	unknown	--	SF/BW
<b>Bivalvia</b>					
<i>Mytilus galloprovincialis</i>	I	1979	Europe	EA	SF/BW
<i>Ostrea edulis</i>	I	2007	Europe	EA	M
<i>Perna viridis</i>	I	2009	Indo-Pacific	IP	SF/BW
<i>Semimytilus alcosus</i>	I	2009	Europe	EA	SF/BW
<i>Crassostrea gigas</i>	I	2001	Japan	WP	M
<i>Hiatella arctica</i>	C	NDD	unknown	--	SF
<i>Teredo navalis</i>	I	NDD	Europe	EA	SB
<i>Lyrodus pedicellatus</i>	I	NDD	unknown	--	SB

<i>Bankia carinata</i>	C	NDD	unknown	--	SB
<i>Bankia martensi</i>	C	NDD	unknown	--	SB
<i>Dicyathifer manni</i>	C	NDD	unknown	--	SB
<i>Teredo somersi</i>	C	NDD	unknown	--	SB
<i>Martesia striata</i>	C	1910	unknown	--	SB
<b>BRACHIOPODA</b>					
<i>Discinisca tenuis*</i>	I	2008	Namibia	SH	M
<b>BRYOZOA</b>					
<i>Watersipora subtorquata</i>	I	1937	Caribbean	WA	SF
<i>Bugula neritina</i>	I	1944	unknown	--	SF
<i>Bugula flabellata</i>	I	1880	unknown	--	SF
<i>Bugula dentata</i>	I	1852	Indo-Pacific	SH	SF
<i>Conopeum seurati</i>	I	2001	Europe	EA	SF
<i>Cryptosula pallasiana</i>	I	1947	Europe	EA	SF
<b>ECHINODERMATA</b>					
<i>Tetrapyrgus niger</i>	I	2007	Chile	SH	M
<i>Ophiactis savignyi</i>	I	1968	Indo-West Pacific	SH	SF
<i>Marthasterias glacialis</i>	C	1842	Europe / North Africa	EA	SF/BW
<b>CHORDATA</b>					
<b>Ascidiacea</b>					
<i>Ascidia sydneiensis</i>	I	1932	Pacific Ocean	SH	SF
<i>Ascidiella aspersa</i>	I	2001	Europe	EA	SF
<i>Botryllus schlosseri</i>	I	1946	unknown	--	SF
<i>Ciona intestinalis</i>	I	1955	unknown	--	SF
<i>Clavelina lepadiformis</i>	I	2001	Europe	EA	SF
<i>Cnemidocarpa humilis</i>	I	2001	unknown	--	SF
<i>Corella eumyota</i>	C	1898	unknown	--	SF
<i>Cystodytes dellechiaiei</i>	C	1877	unknown	--	SF
<i>Didemnum granulatum</i>	C	2007	unknown	--	SF

<i>Didemnun rodriguessi</i>	C	2007	unknown	--	SF
<i>Diplosoma listerianum</i>	I	1949	Europe	EA	SF
<i>Microcosmus squamiger</i>	I	1950	Australia	SH	SF
<i>Polycarpa insulsa</i>	C	2007	unknown	--	SF
<i>Styela canopus</i>	C	1955	South Pacific	SH	SF
<i>Styela plicata</i>	I	1951	Asia	WP	SF
<i>Tridemnun cerebriforme</i>	C	1913	unknown	--	SF
<i>Didemnun psammathodes</i>	C	2001	unknown	--	SF
<i>Symplegma brakenhielmi</i>	C	1952	unknown	--	SF
<hr/>					
<b>PISCES</b>					
<i>Cyprinus carpio</i>	I	1860	Eurasia	EA	M
<hr/>					
<b>RHODOPHYTA</b>					
<i>Schimmelmanna elegans</i>	I	2002	Tristan da Cunha	WA	BW
<i>Schottera nicaeensis</i>	I	NDD	Mediterranean	WA	SF/BW
<i>Antithamnionella ternifolia</i>	C	NDD	Australia	SH	SF/BW
<i>Antithamnionella spirographidis</i>	I	1989	North Pacific	NP	SF/BW
<b>CHLOROPHYTA</b>					
<i>Cladophora prolifera</i>	I	1846	Europe	EA	SF
<i>Ulva fasciata</i>	C	NDD	Europe	EA	SF
<i>Codium fragile fragile</i> ( <i>tomentosoides</i> strain)	I	1937	Japan	WP	SF
<hr/>					
<b>VASCULAR PLANTS</b>					
<i>Ammophila arenaria</i>	I	1876	Europe	EA	I
<i>Spartina maritima</i>	C	1840	Europe	EA	BS
<i>Stuckenia pectinata</i>	C	1896	unknown	--	BS/BW

Table 2.3: Marine introduced and cryptogenic species in South Africa, mistakenly redescribed as new endemic species.

Species	Origin	Redescribed from South Africa as	Synonymy
<b>CNIDARIA</b>			
<b>Hydrozoa</b>			
<i>Pinauay ralphi</i>	North Atlantic	<i>Tubularia ralphi</i> Ewer 1953	Peterson 1990
<i>Pennaria disticha</i>	Unknown	<i>Halocordyle cooperi</i> Warren 1906	Millard 1975
<b>CRUSTACEA</b>			
<b>Amphipoda</b>			
<i>Cymadusa filosa</i>	Unknown	<i>Grubia australis</i> Barnard 1916	Barnard 1955
<i>Orchestia gammarella</i>	North Atlantic	<i>Talorchestia inaequalipes</i> Barnard, 1951	Griffiths 1975
<b>MOLLUSCA</b>			
<b>Bivalvia</b>			
<i>Lyrodus pedicellatus</i>	Unknown	<i>Teredo robsoni</i> Roch 1931	Turner 1966
<i>Bankia martensi</i>	Unknown	<i>Bankia capensis</i> Calman 1920	Turner 1966
<i>Teredora princesae</i>	Unknown	<i>Teredo alfredensis</i> van Hoepen 1941	Turner 1966
<i>Dicyathifer manni</i>	Unknown	<i>Teredo ancila</i> Barnard 1964	Turner 1966
<i>Teredo somersi</i>	Unknown	<i>Teredo radialis</i> Moll 1937	Turner 1966
<b>Gastropoda</b>			
<i>Thecacera pennigera</i>	Unknown	<i>Thecacera lamellata</i> Barnard 1933	Gosliner 1987
<i>Anteaeolidiella indica</i>	Unknown	<i>Aeolidiella saldanhensis</i> Barnard 1927 <i>Aeolidiella multicolor</i> Macnae 1954	Gosliner and Griffiths 1981
<b>ASCIDIACEA</b>			
<i>Styela canopus</i>	Western Pacific	<i>Styela stephensoni</i> Michaelsen 1934	Monniot <i>et al.</i> 2001

**ECHINODERMATA**

<i>Marthasterias glacialis</i>	Europe	<i>Asteracanthion africanus</i> Muller and Troschel 1842	Clark and Courtman-Stock 1976
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**PLANTS**

<i>Spartina maritima</i>	North Atlantic	<i>Spartina capensis</i> Nees 1841	Pierce 1982
<i>Stuckenia pectinata</i>	Unknown	<i>Potamogeton pectinata unguulatus</i>	Kaplan 2008

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Table 2.4: Marine introduced species retained as members of the South African marine fauna, albeit collected more than 50 years ago (see text discussion).

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

Table 2.5: South African distribution of marine and estuarine introductions with a summary of key references revealing important information establishing the introduced status of each species. For province codes refer to Table 2.1. For reference key: see Appendix B.

Taxon	South African regional distribution						References revealing status
	CTP	TZ1	WTP	TZ2	STP	TP	
<b>PROTOCTISTA</b>							
<i>Mirofolliculina limnoriae</i>	X						-
<b>DINOFLAGELLATA</b>							
<i>Alexandrium tamarense</i> -complex:			unknown				1, 2, 3
<i>Alexandrium minutum</i>	X						4
<i>Dinophysis acuminata</i>	X						4
<b>PORIFERA</b>							
<i>Suberites ficus</i>	X						5
<b>CNIDARIA</b>							
<b>Anthozoa</b>							
<i>Sagartia ornate</i>	X						6, 7
<i>Metridium senile</i>	X						8
<b>Hydrozoa</b>							
<i>Pachycordyle navis</i>	X						9, 10
<i>Coryne eximia</i>	X						9, 11
<i>Moerisia maeotica</i>						X	9, 12
<i>Pennaria disticha</i>					X	X	9, 13, 14
<i>Pinauay larynx</i>	X	X					9, 15, 16, 17
<i>Pinauay ralphi</i>	X				X		9, 16, 18
<i>Laomedea calceolifera</i>	X						9, 15, 19, 20
<i>Gonothyraea loveni</i>	X						9, 15, 19, 20
<i>Obelia bidentata</i>	X						9
<i>-Obelia dichotoma</i>	X	X	X				9

<i>Obelia geniculata</i>	X						9
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**ANNELIDA**

**Polychaeta**

<i>Boccardia proboscidea*</i>			X				21, 22, 23
<i>Neanthes succinea</i>			X		X		24, 25
<i>Polydora hoplura</i>	X	X	X				21, 22, 25, 26, 27
<i>Dodecaceria fewkesi</i>	X						-
<i>Ficopomatus enigmaticus</i>	X	X	X	X	X	X	25, 28, 29, 30
<i>Hydroides elegans</i>		X					17
<i>Neodexiospira brasiliensis</i>	X	X	X				25, 31, 32, 33
<i>Janua pagenstecheri</i>	X	X	X	X	X		32, 33

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**CRUSTACEA**

**Cirripedia**

<i>Balanus glandula</i>	X						34, 35
<i>Amphibalanus venustus</i>			X	X	X	X	36, 37

**Copepoda**

<i>Acartia spinicauda</i>					X		38
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**Isopoda**

<i>Dynamene bidentata</i>			X				-
<i>Sphaeroma serratum</i>					X		24, 39
<i>Sphaeroma walkeri</i>					X		-
<i>Paracerceis sculpta</i>			X				-
<i>Limnoria quadripunctata</i>	X	X	X				40, 41
<i>Limnoria tripunctata</i>	X						-

**Amphipoda**

<i>Chelura terebrans</i>	X	X	X				42
<i>Ischyrocerus anguipes</i>	X	X	X	X	X	X	43
<i>Erichthonius brasiliensis</i>	X	X	X	X	X	X	42
<i>Apocorophium acutum</i>			unknown				44
<i>Monocorophium acherusicum</i>					X		43
<i>Jassa marmorata</i>	X				X	X	45
<i>Jassa morinói</i>		X	X	X	X	X	45

<i>Jassa slatteryi</i>	X	X	X				45
<i>Orchestia gammarella</i>	X	X	X				39, 46, 47
<i>Platorchestia platensis</i>			X				47
<i>Cerapus tubularis</i>	X	X	X	X	X	X	43, 48
<b>Decapoda</b>							
<i>Xantho incisus</i>	X						49
<i>Carcinus maenas</i>	X						50
<hr/>							
<b>PYCNOGONIDA</b>							
<i>Ammothella appendiculata</i>					X		51, 52, 53
<hr/>							
<b>INSECTA</b>							
<b>Coleoptera</b>							
<i>Cafius xantholoma</i>	X	X	X	X	X	X	54, 55
<hr/>							
<b>MOLLUSCA</b>							
<b>Gastropoda</b>							
<i>Littorina saxatilis</i>	X		X				56, 57, 58
<i>Thais blanfordi</i>					X		59, 60
<i>Thais tissoti</i>					X		59, 60
<i>Tarebia granifera</i>						X	61
<i>Catriona columbiana</i>	X						62, 63, 64
<i>Tritonia nilsodhneri</i>	X	X					63, 65
<i>Kaloplocamus ramosus</i>		X	X	X	X		63, 66, 67
<b>Bivalvia</b>							
<i>Mytilus galloprovincialis</i>	X	X	X	X			50, 68
<i>Ostrea edulis</i>	X						49, 69
<i>Crassostrea gigas</i>	X		X				50
<i>Teredo navalis</i>			X				70, 71, 72
<i>Lyrodus pedicellatus</i>		X					73
<hr/>							
<b>BRACHIOPODA</b>							

<i>Discinisca tenuis*</i>	X							-
<b>BRYOZOA</b>								
<i>Watersipora subtorquata</i>	X	X						74, 75, 76
<i>Bugula neritina</i>	X	X	X	X	X			76, 77, 78
<i>Bugula flabellata</i>	X	X	X					76, 78, 79
<i>Bugula dentata</i>		X	X	X	X			76, 80
<i>Conopeum seurati</i>	X	X						81, 82, 83
<i>Cryptosula pallasiana</i>	X	X						26, 76, 83
<b>ECHINODERMATA</b>								
<i>Tetrapyrgus niger</i>	X							49, 84, 85
<i>Ophiactis savignyi</i>					X			24
<b>CHORDATA</b>								
<b>Asciidiacea</b>								
<i>Ascidia sydneiensis</i>	X							86, 87
<i>Ascidiella aspersa</i>	X	X	X					87
<i>Botryllus schlosseri</i>	X	X	X	X	X			88, 89
<i>Ciona intestinalis</i>	X	X	X	X	X	X		87, 88
<i>Clavelina lepadiformis</i>	X	X	X	X				87
<i>Cnemidocarpa humilis</i>	X							87
<i>Diplosoma listerianum</i>	X	X	X	X	X			87, 88
<i>Microcosmus squamiger</i>	X	X	X	X	X	X		87, 88, 89, 90
<i>Styela plicata</i>			X	X	X			88, 89
<b>PISCES</b>								
<i>Cyprinus carpio</i>	X	X	X	X	X	X		91
<b>RHODOPHYTA</b>								
<i>Schimmelmannia elegans</i>	X							92

<i>Schottera nicaeensis</i>					X	X	92, 93
<i>Antithamnionella spirographidis</i>			unknown				94
<b>CHLOROPHYTA</b>							
<i>Cladophora prolifera</i>						X	95
<i>Codium fragile fragile</i> ( <i>tomentosoides</i> strain)	X	X	X				94, 96, 97
<b>HIGHER PLANTS</b>							
<i>Ammophila arenaria</i>	X	X	X	X	X		98, 99, 100

Table 2.6: Marine introductions with a unique or shared presence recorded (%) per biogeographic region of South Africa. For regional codes refer to Table 2.1.

Species Number	Introductions by South African province					
	CTP	TZ1	WTP	TZ2	STP	TP
<b>Total Numbers</b>	<b>55</b>	<b>35</b>	<b>37</b>	<b>21</b>	<b>31</b>	<b>15</b>
Unique species (%)	42	6	11	0	26	14
Shared species (%)	58	94	89	100	74	86

Table 2.7: Summary of *Chi-squared* statistic testing differences in the numbers of marine introductions as categorized by region of origin, invasion pathway, habitat and species uniqueness. Key: df (v) = degrees of freedom; Chi crit = critical *Chi-squared* value; Chi obs = observed *Chi-squared* value; P = significance level.

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

Table 2.8: Similarity (%) based on shared and unique species between biogeographic regions and transition zones, as calculated using the Jaccard Index. For regional codes refer to Table 2.1.

Similarity (%)						
	CTP	TZ1	WTP	TZ2	STP	TP
CTP	X	40	40	45	60	60
TZ1		X	9	4	20	10
WTP			X	7	24	15
TZ2				X	20	8
STP					X	8
TP						X

Table 2.9: Indigenous regions of origin for marine introduced species recorded (%) per biogeographic region of South Africa. For regional codes refer to Table 2.1.

Indigenous region	Introductions by South African province (%)					
	CTP	TZ2	WTP	TZ2	STP	TP
Unknown (UNK)	23.5	21	22	21	21	19
Northern Atlantic (NA)	9	7	7	5	10	6
Western Atlantic (WA)	6	7	7	16	10	13
Western Pacific (WP)	3.5	3	9	5	7	0
Ponto-Caspian (PC)	0	0	0	0	0	6
Europe (E)	36	41	37	37	24	31
Northern Pacific (NP)	1.5	0	0	0	0	0
Eastern Pacific (EP)	5	7	9	5	4	6
Indian Ocean (IO)	0	0	0	0	7	0
Southern Hemisphere (SH)	12	14	9	11	17	19
North Atlantic/North Pacific (NA/NP)	3.5	0	0	0	0	0

Table 2.10: Invasive pathways of established marine introductions recorded (%) per biogeographic region of South Africa. For regional codes refer to Table 2.1.

Invasive Pathway	Introductions by South African province (%)					
	CTP	TZ2	WTP	TZ2	STP	TP
Ship fouling	32	27	28	28	36	26
Ballast water	46	54	54	59	55	38
Ship boring	4	6	0	0	0	26
Mariculture	6	6	10	7	4	6
Solid ballast	7	4.5	6	3	2.5	4
Fisheries	1.5	0	0	0	0	0
Intentional	1.5	2.5	2	3	2.5	0
Oil rigs	2	0	0	0	0	0

Table 2.11: Habitat types of established marine introductions recorded (%) per biogeographic region of South Africa. For regional codes refer to Table 2.1.

Habitat	Introductions by South African province (%)					
	CTP	TZ2	WTP	TZ2	STP	TP
Rocky shore	15	21	25	28	22	18
Sandy shore	4	5	6	4	5	6
Offshore benthic	5	3	3	0	0	0
Harbour	51	51	43	48	47	43

Estuaries	10	14	17	12	22	26
Brackish lakes & lagoons	1	0	0	0	0	6
Aquaculture facility	6	3	3	0	0	0
Open water column	5	0	0	0	0	0
Saltmarsh	1	0	0	0	0	0
Dune	1	3	3	4	2	0
Mangrove	1	0	0	4	2	0

Table 2.12: Taxonomic groups of marine introduced species recorded (%) per biogeographic region of South Africa (%). For regional codes refer to Table 2.1.

Taxonomic Group	Introductions by South African province (%)					
	CTP	TZ2	WTP	TZ2	STP	TP
Crustacea	19	18	29	23	33	40
Mollusca	12	11	14	9.5	10	7
Cnidaria	19	6	4	0	3	13
Urochordata	13	18	20	29	17	0
Annelida	10	14	14	9.5	10	7
Bryozoa	10	18	9	9.5	7	0
Higher plants & algae	7	9	6	9.5	7	20
Other	10	6	4	10	13	13

## **Appendix A: The Introduced and Cryptogenic Marine Fauna and Flora of South Africa**

### **Protoctista**

Numerous species of protists, ranging from free-living hypotrichous ciliates to ectocommensal and endosymbiotic taxa, have likely 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. I thus note only two (of what may be scores) of potentially introduced and cryptogenic species here.

### **Ciliophora**

#### **Heterotrichida Folliculinidae**

*Mirofolliculina limnoriae* (Giard 1883)

**Introduced**

This tiny green folliculinid protist lives on the dorsal surface of the pleotelson of the wood-boring isopod (gribble) *Limnoria* (Delgery *et al.* 2006). I found this species in September 2008 on *L. tripunctata* collected from wooden pilings in Table Bay Harbour, Cape Town. It has doubtless been present in South Africa for a very long time. I regard it as a co-introduction with *L. tripunctata*. However, the biogeographic origins of both host and commensal remain unknown.

#### **Peritricha 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 indigenous, they were likely introduced centuries ago with ship fouling. Modern era introductions have no doubt been supplemented by means of ballast water.

### **Dinoflagellata (Dinophyceae)**

A thorough review of the Biogeographic and evolutionary history of dinoflagellates in South Africa still remains to be done. I identify three taxa that I 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.

### **Peridiniales**

#### **Gonyaulacaceae**

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

**Introduced**

Saxitoxin-producing *Alexandrium* dinoflagellates are responsible for paralytic

shellfish poisoning (PSP), 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 PSP incidents in South Africa, as early as 1888 (Sebastian *et al.* 2005; see also 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 *A. catenella*. It seems probable that the modern-day (20th century) occurrences of *A. 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 on the occasion of its forming 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 indigenous 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 *A. minutum* in South African waters represents a new introduction to the region." Nevertheless, I am 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.

### **Dinophysaceae**

*Dinophysis acuminata* (Claparède and Lachmann 1859) **Introduced**

*Dinophysis acuminata*, the cause of diarrhetic shellfish poisoning (DSP), was long known from Europe, where it was first described from Norway in the mid-19th century. Reported World-wide 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). I regard it as transported by ballast water, in which it has been found (Okamoto *et al.* 2007).

### **Porifera**

#### **Demospongiae**

##### **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. However, it is now recognized as a mis-identification and is therefore not introduced (Uriz; pers. comm. 2009). I follow

the World Porifera Database in the spelling of the species name.

*Suberites ficus* (Esper 1958)

**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.

**Cnidaria**

**Anthozoa**

**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 amongst the 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 it can reach numbers of hundreds per m<sup>2</sup>. However, I take the first record to be 1955, when Day (1955) reported a *Sagartia*-like species from the same location. No other indigenous South African sea anemone could be confused with this distinctive species. The first museum records are from Langebaan in 1963 (SAM collections: catalogue number H1579

and H1594). Ship fouling and ballast water are the most probable vectors.

*Metridium senile* (Linnaeus 1767)

**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 6–12 m depth. In 2006 photographic evidence was presented to the authors of a deep water population of *M. 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 harbor population.

### **Hydrozoa**

As with other challenging groups, I can only make a first approximation of the numbers of introduced hydroids, especially since these invasions may have commenced in the 1600s. I 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), I 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 require 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. Thus, missing from our assessment are Pacific taxa (for example, Japan or the western Americas). 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 thus cryptogenic) hydrozoan element present in South Africa. For all the examples presented, I consider ship fouling and ballast water the most probable vectors.

### **Anthoathecata (Atheicata)**

#### **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.

#### **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.

### **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. Since this taxon represents multiple species (Schuchert 2005) no origin can be assigned. Embedded within one or more clades may be introduced port and harbor

populations, therefore South African material requires molecular and morphological re-examination.

### **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 *M. maeotica* were distributed by ships did not apply to these South African lakes. Other dispersal vectors are thus involved that would bring this European species to African shores. Further knowledge of the biota of these brackish lakes would clarify these vectors. *M. maeotica* was first collected in 1965.

### **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 in 1906 (Warren 1906, 1907) and were mistakenly re-described as an indigenous 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).

## **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, as the recorded depth of 126 m is not probable for this species (Millard 1975, Peterson, 1990). I thus 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)  
(= *Ectopleura ralphi*; = *Tubularia warreni*)

**Introduced**

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 (1914) record 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," thus I do not further consider that record here. Peterson (1990) synonymised Ewer's *T. warreni* with *Pinauay ralphi* (as *Ectopleura ralphi*), known only from harbours in Australia and South Africa. As Peterson noted, *P. 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 done. *P. ralphi* is a member of the Northern Hemisphere ectopleuras (Peterson, 1990) and is clearly indigenous specifically to the North Atlantic, as is its sister (or identical) species *P. crocea*. Presciently, Millard (1959) recognized that *T. warreni*, albeit ostensibly endemic to South Africa, might not be specifically distinct from *T. crocea* and speculated that it might be introduced from Europe. I retain *P. ralphi* as a distinct species here and presume that Millard's (1952) record of *T. crocea*, collected in 1947-1949, from Table Bay Harbour, is this species. Thus I take 1947 as the first record of this species from South Africa.

## **Leptothecata (Thecata)**

### **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 by Millard (1975) as *Eulaomedea calceolifera*. Millard (1959) and Millard (1978, as *Campanularia calceolifera*) regarded it as introduced by ships to South Africa. Zvyagintsev (2003) discusses its anthropogenic dispersal out of the North Atlantic Ocean since the 19th century. Stechow's (1925) record of this species from 70 m in Simon's Bay (False Bay) is in doubt (Millard 1978) and I do not include it here. Thus, the first South African collections of *L. calceolifera* were made in 1948 (Millard 1957).

*Gonothyreaa 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 I 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 1957, 1959).

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

**Introduced**

I recognize the harbor, 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, I reserve judgment on the biogeographic status of the populations of *Obelia* from other than harbours until genetic data are in hand. The first collections of which I am 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 the South African distribution as Durban to the Mozambique border on the east coast. In the absence of global population molecular genetics, the biogeographic origins of this and the following two *Obelia* spp. remain unknown.

*Obelia dichotoma* (Linnaeus 1758)

**Introduced**

As noted above, I regard inshore populations as the probable introduced 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*, *Lepas* sp. and *Caretta caretta*. It is very common in dock areas on pylons and ships' hulls." I suggest that these non-harbor habitats may represent indigenous *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*." I suggest that the deep-water populations, including those on the rock-lobster *Jasus*, may not be genetically identical to global harbor populations of this species. The first collections that have come to my attention are those from 1934 collected from Oudekraal, on the Cape Peninsula. Millard (1975) gives the South African distribution as Lambert's Bay on the west coast to Cape Town Docks.

## **Annelida**

### **Polychaeta**

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

### **Nereidae**

*Neanthes succinea* (Frey and 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 south east coast, as well as Durban (Day 1967).

### **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 introduced. 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 (for example; Schlacher and Wooldridge 1996, Teske and Wooldridge 2003, 2004).

### **Cirratulidae**

*Dodecaceria fewkesi* (Berkeley and Berkeley 1954)

**Introduced**

This polychaete constructs large, grayish, 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 4-5 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 indigenous 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 1 m 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 (JT. Carlton, personal observations) on open coasts, not in estuaries or bays. Its presence on harbor 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 I thus predict it will make its way out of Table Bay in due course.

### **Spionidae**

*Polydora hoplura* (Claparede 1870)

**Introduced**

This well-known European mud worm was first reported from the southern hemisphere by Millard (1952) 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 from South Africa. I 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 blusters and infestations by *P. 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 and Booth 2007).

*Boccardia proboscidea* (Hartman 1940)

**Within aquaculture facilities**

*B. proboscidea* is a tube-dwelling polychaete often found on the surfaces of oysters, abalone 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, *B. proboscidea* has been collected from abalone farms in Jakobsbaai (near Saldahna Bay) and Hermanus. Subsequently, *B. proboscidea* has been found embedded within oyster shells from farms in Knysna and Alexander Bay (T. Haupt, pers comm. 2009). To date, wild populations have not been identified (Simon and Booth 2007, Simon *et al.* 2009), thus 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 of aquaculture facilities.

### **Serpulidae**

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

**Introduced**

This well-known tubeworm constructs large reefs of entwined calcareous tubes; the animals' 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 meters. *F. enigmaticus* ranges from Milnerton Lagoon (Table Bay) on the west coast to Kosi Bay on the east coast and was introduced by ship fouling. *Ficopomatus reefs* 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 this worm may play within estuaries, in terms of reducing particle loads. For example, in the Zandvlei system *F. 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. While this could be described as a "positive" effect relative to apparent water quality, I 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, *F. enigmaticus* may be competing with indigenous 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 (South African Museum collection).

*Neodexiospira brasiliensis* (Grube 1872)  
(= *Janua brasiliensis*; = *Spirorbis foraminosus*)

**Introduced**

This Indo-Pacific polychaete was originally misidentified and recorded as present in South Africa as *S. foraminosus* by Day in 1961, based on specimens collected in 1953 (SAM collection). In 1967, Day noted the presence of *N. brasiliensis*, again as *S. 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* (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 *J. pagenstecheri*.

*Simplicaria pseudomilitaris* (Thiriot-Quévieux 1965)  
(=*Pileolaria pseudomilitaris*)

**Cryptogenic**

As with *J. 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.

## **Crustacea**

### **Cirripedia**

#### **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. I 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). Its South African distribution ranges from Hermanus on the south coast to Mozambique (east coast) and I considered ship fouling to be the vector.

## **Copepoda**

### **Calanoida**

#### **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). I consider this species to be a ballast water introduction.

## **Isopoda**

### **Sphaeromatidae**

*Dynaneme bidentata* (Adams 1800)

**Introduced**

*Dynaneme 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 in Port Elizabeth harbour on the southeast coast. Maggiore and Fresi (1984) record it as indigenous to the Atlantic coast of Europe and as possibly introduced in the Mediterranean. I consider ship fouling and ballast water as the vectors.

*Sphaeroma serratum* (Fabricius 1787)

**Introduced**

This intertidal isopod is especially common on mangroves, yet it is indigenous to Europe, where mangroves are not found. Thus, it would appear to be an example of utilization of a novel habitat. It was 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). I 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 indigenous 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 e Silva, 1960). I consider *S. 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 1899)

**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 1926. 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, thus 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 2006. 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 Herndricks 2002). I consider it a ship fouling and ballast water introduction.

### **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. I 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, prior to the advent of interoceanic shipping, are not known. To list all of these here would virtually comprise another monograph. *S. variegata*, for example, occurs both in fouling communities and in littoral algal communities from the Indo-Pacific to the west coast of Africa (Carlton and Chapman 1991). It occurs as far north as Cameroon and Namibia in 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). *S. 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 many centuries ago.

### **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 indigenous range is not yet known, pending global genetic analyses. Given its semi-terrestrial nature, I consider dry ballast or dunnage to be the most likely vectors since the earliest days of wooden sailing vessels.

### **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-19th 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. Since at least two species of introduced limnoriids now occur in South Africa, re-examination of museum material held in both Europe and South Africa is required to establish distribution and temporal records. Kensley (1978) reported *L. quadripunctata* as occurring from Table Bay to Port Elizabeth (on the

southeast coast). The origins of *L. quadripunctata* and *L. 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**

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

## **Amphipoda**

### **Cheluridae**

*Chelura terebrans* (Phillipi 1839)

**Introduced**

*Chelura terebrans* is a cosmopolitan reddish wood-boring amphipod, which 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 collected in 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.

## **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 K.H. 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 synonymised with the older name *C. 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, *C. 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 *C. filosa*, is in South Africa, or whether another species is involved.

## **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). *C. 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. I 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 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. *A. acutum* was first collected in South Africa in Durban in 1915 (Barnard 1916, as *Corophium acherusicum*, partim.). Crawford (1937) noted that Barnard's material contained mixed *A. acutum* and *M. acherusicum*, with the smaller specimens being *A. acutum*. Although there are no post-1915 records, I tentatively retain it in the fauna, presuming that it remains present, mixed with *M. ascherusicum* populations. The South African distribution is thus unknown.

*Monocorophium acherusicum* (Costa 1857)  
(= *Corophium acherusicum*)

**Introduced**

This amphipod has a similar habitat to *C. 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 indigenous 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. While 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.

### **Melitidae**

*Melita zeylanica* (Stebbing 1904)  
(= *Melita inaequistylis* (of Barnard 1916 not Dana 1852))

**Cryptogenic**

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 amongst 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 *M. zeylanica* is now abundant did not find this species. Barnard (1916) thus reported

*Austrochiltonia capensis* (as *Chiltonia capensis*) from Milnerton in 1898 and 1913, in "brack[ish]-waters among green weeds," while the first specimens of *M. 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 *M. inaequistylis* in 1897 and 1914, but by 1940 he judged these to belong to either a new species (*M. orgasmos*), or to *M. zeylanica* (which in 1916 he had treated as a junior synonym of *inaequistylis*). While Barnard (1940) referred to his *M. inaequistylis* of 1916 as being in part referable to *M. zeylanica*, he did not indicate which locations of the 1898 or 1914 material might be *zeylanica*. Although compelled by the apparent absence of *M. zeylanica* from the locations that produced *Austrochiltonia*, I treat *Melita* as cryptogenic, in part pending re-examination of this earlier material. Ship fouling and ballast water are the likely vectors.

### **Ischyroceridae**

*Ischyrocerus anguipes* (Kroyer 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 *J. falcata*, but in a major review of the genus, Conlan (1990) described several new species and re-allocated South African material amongst 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 *J. 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). Thus, cited below are only the locations given by Conlan (1990). Of interest is that Stebbing (1888) reported "*Podocerus falcatus*" (= *J. 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)  
(= *Jassa falcata* partim)

**Introduced**

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, pers. comm., February 2009), Durban and KwaZulu-Natal (east coast). As noted above, I do not take 1948 as the first date of record, pending re-examination of K. Barnard's early 20th century *Jassa*

material.

*Jassa morinoi* (Conlan 1990)  
(= *Jassa falcata* partim)

**Introduced**

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" 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, thus I 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, pers. comm., February 2009), Port Elizabeth (southeast coast) and on the east coast in KwaZulu-Natal (Conlan 1990).

*Jassa slatteryi* (Conlan 1990)  
(= *Jassa falcata* partim)

**Introduced**

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, pers. comm., 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 *C. abditus* by Barnard (1916), based on specimens collected off KwaZulu-Natal in 1901. *C. abditus* was subsequently synonymised with *C. 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.

### **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 *O. gammarella* by Griffiths (1975). It is locally common along the drift-line (under rocks and on debris) and amongst dune vegetation. It is known in South Africa from Langebaan (Barnard 1951), Table Bay (from 2008 collections at Milnerton Lagoon) and from 1949, in Knysna Estuary on the southeast coast (Griffiths 1974). I regard it as an early introduction with solid (dry) ballast.

*Platorchestia platensis* (Kroyer 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 post 1904 and thus there is no evidence that populations of *P. 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, I regard it as introduced to South Africa because of its highly restricted distribution and its known "weed" status. As with *O. gammarella*, I consider it to be an early introduction with solid ballast.

### **Caprellidae**

*Caprella equilibra* (Say 1818)

**Cryptogenic**

This amphipod clings tightly to hydroids, algae and other typical fouling species, leading to easy transportation by shipping. Thus I consider ship fouling and ballast water as the most probable vectors. The origin of *C. 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 fishes. 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 *C. 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 *C. equilibra*, it is now widely distributed and is found in Hawaii, Japan, Australia, New Zealand and on both coasts of the USA, where it was one of the most common caprellids (McCain 1968) prior to the arrival of *Caprella muticum* (Carlton unpublished), a species I 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 due to the large triangular projection on the front of pereonite 2. The origin of *P. 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, I regard ship fouling and ballast water are the most probable vectors.

## **Decapoda**

### **Xanthidae**

*Xantho incisus* (Leach 1814)

**Introduced**

This European crab has distinctive chelipeds, which are large and heavy with black tips. It is found amongst 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.* 2010). I consider this an introduction with oyster spat imported from France.

### **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, *C. 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). The same pertains 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 (south-west coast). It was first collected from Table Bay Docks in 1983, where it has established dense populations and has decimated shellfish populations (Robinson *et al.* 2005). I consider that it was probably introduced by ship fouling, ballast water or oil rigs.

## **Pycnogonida**

### **Ammonotheidae**

*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 *A. indica*, a species described from Singapore and was synonymised with *A. appendiculata* by Bamber (2000). The port-dwelling sea spiders of South Africa have not been resurveyed in recent decades, but I have no reason to suspect that *A. appendiculata* no longer occurs in Durban Bay, and I retain it on the South African faunal list. *A. appendiculata* was described from the Mediterranean, where it still occurs, but is otherwise patchily distributed around the Atlantic rim, being recorded, for example, outside of the Mediterranean from the West Indies and Florida (Child 1974) and Brazil (Ribeiro *et al.* 1982). In contrast, largely under the name *A. 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. I tentatively suggest that it may be indigenous 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.

## **Insecta**

The historical biogeography of the beach and maritime shore insects of South Africa remains to be explored. I suspect that a number of shore insects were introduced from the 1600s to 1800s with beach ballast from around the world. I identify one common European strand beetle as an example of such an introduction.

## **Coleoptera**

### **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. I 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.

## **Mollusca**

### **Gastropoda**

#### **Caenogastropoda**

#### **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, especially in light of the fact it is considered to be a complex, not just a single species. 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 *L. punctata* in Langebaan (west coast) by Barnard (1963) and from the Berg River Estuary (west coast) and Knysna Lagoon (southeast 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 since 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 *L. 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 *L. 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 (B.P.), and the other with an age range of 40,500 to 36,500 B.P. Strata level ages were determined from radiocarbon datings and pollen analyses, but the *L. saxatilis* shells themselves were not aged.

Hughes (1979, as *Littorina rudis*) then reported on further details of morphology, color, and reproduction of the Langebaan and Knysna populations, and on searches for *L. saxatilis* at other than these two sites (none was found). Knight *et al.* (1987) undertook genetic analyses of the South African populations, comparing them to both North American and European material; South African *L. 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 *L. 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 *L. 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.

I consider that the most probable origin of the modern-day populations of *L. 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, both to determine possible origin, but also to determine if, and if so how many, unique haplotypes exist in the former, in order to determine (by molecular clock estimations) how long this snail has been in the southern hemisphere. While 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 and these would bear re-

examination and verification as *L. saxatilis*, and it would be of no small interest to perform radiocarbon testing on the shells. Even if these prove to be *L. saxatilis* with good stratigraphic control, I suspect there is no link between these fossils and modern-day populations in South Africa. Had *L. 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, *L. saxatilis* are transported by floating materials, for example, or simply expand their range by moving along coastlines for eons); instead, it remains highly restricted to a few locations, suggestive of relatively recently-established populations.

I have as yet no first date of record of living *L. saxatilis* populations in South Africa. The dates of collection of Barnard's (1963) specimens identified as *L. 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 *L. punctata* and other names as well).

## **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, I am compelled by the evidence that a number of Indo-Pacific *Thais* have been, and are being, transported by human means. Both *T. sacellum* and *T. lacera* have been introduced to the Mediterranean (Gofas and Zenetos 2003;

Singer 2005) and *T. 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 I further expect that more northern species may now be extending their ranges south with coastal warming.

I treat two species, *T. blanfordi* and *T. tissoti* as introductions. In addition, *T. lacera* (Born 1778, Kilburn and Rippey 1982), *Stramonita haemastoma* (Linnaeus 1767, Kilburn and Rippey 1982 as *T. haemastoma*), *T. aculeata* (Deshayes 1844, Steyn and Lussi 1998) and *T. sacellum* (Gmelin 1791, G. Branch, personal communication, 2009), have all been reported from South African coasts, but their distribution and current status requires further study.

*Thais blanfordi* (Melvill 1893)

**Introduced**

I tentatively admit this well-known muricid as a introduced 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 *T. 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 I consider ship fouling and ballast water to be the likely vectors.

*Thais tissoti* (Petit 1852)

**Introduced**

As with *T. 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) noted 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 I also consider ship fouling and ballast water to be the likely vectors for this species.

### **Thiaridae**

*Tarebia granifera* (Lamarck 1816)

**Introduced**

A freshwater prosobranch originating from South-East Asia, *T. granifera* can tolerate high salinities for relatively long periods of time and is thus 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).

## **Opisthobranchia**

### **Nudibranchia**

#### **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). I recognize that this is a variable species with many synonyms (McDonald 2007). In South Africa it has only been recorded in Cape Town Docks and thus I concur with Gosliner (1987) that it represents an introduction, likely to have arrived in South Africa through ship fouling and ballast water.

#### **Polyceridae**

*Polycera hedgpethi* (Marcus 1964)

**Cryptogenic**

Records collated by 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 south-east coast). Willan and Coleman (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) **Cryptogenic**  
(= *Thecacera lamellata* (Barnard 1933))

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, *T. 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 harbor, 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. Thus the occurrence of this species at distant points does not argue against its being introduced.

#### **Aeolidiidae**

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

Likely transported by shipping globally, this species 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 theater. 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, *A. 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, *A. indica* feeds on the presumably-indigenous sea anemone *Anthothoe chilensis* (a species which itself may represent a complex or two or more taxa).

## **Bivalvia**

### **Mytilidae**

*Mytilus galloprovincialis* (Lamarck, 1891)

**Introduced**

The Mediterranean mussel forms dense beds in the mid to low intertidal zone. 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. It was first collected in Saldanha Bay, South Africa in 1979 with genetic confirmation of the identification published five years later (Grant and Cherry 1984). It is now the most significant marine introduction on rocky intertidal shores, ranging from central Namibia (west coast)

to East London on the east coast (Robinson *et al.* 2005). There have been several studies into a variety of ecological impacts, including competitive interactions, provision of habitat for infaunal species and provision of additional food for predators. It is commercially cultured and exploited by recreational and subsistence fishers (Robinson *et al.* 2005, 2007).

*Perna viridis* (Linnaeus 1758)

**Introduced**

We identified large green mussels collected from East London Harbour in 2010 as *P. 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 *P. perna*. To date there is no evidence of spread onto the open coast, but if this occurs there is potential for hybridisation with native *P. perna*. *P. viridis* is native to India and Southeastern Asia, but it has been widely introduced to Australia, Japan, the Caribbean, Gulf of Mexico and southeast US. 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 *S. algosus* is currently recognised 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 or a newly introduced population.

### **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 *et al.* 2005). It was intentionally introduced to Knysna in 1946 without success (Korringa 1956). Surveys in 2008 found a reproducing population in the Alexander Bay oyster dams on the west coast of South Africa (Haupt *et al.* 2010).

*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 *et al.* 2005). It is known from the Breede, Goukou and Knysna Estuaries along the southern coast and was introduced via mariculture.

### **Hiatellidae**

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

**Cryptogenic**

This small clam is recorded from fouling communities around the world, and likely consists of multiple species (Coan *et al.* 2000, Mikkelsen and Bieler 2008). I 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 *S. 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, I would regard *H. arctica* as introduced.

## **Teredinidae**

The biogeographic origins of many species of shipworms are now obfuscated by centuries of global shipping. I identify two teredinids here as introduced, but note that there are several additional cryptogenic species. I 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 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 *T. 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 *T. navalis* were "exceptionally virulent" on the Port Elizabeth breakwater (southeast coast). Waldron (1904) 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 *T. navalis* on a jetty at Knysna, based on a 10-year study. The distribution of *T. 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 *T. 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 south west coast, but this cannot be taken as the first date of occurrence of *L. pedicellatus* in South Africa.

*Bankia carinata* (Gray 1827)

**Cryptogenic**

*Bankia martensi* (Stempell 1899)  
(= *Bankia capensis* (Calman 1920))

**Cryptogenic**

*Dicyathifer manni* (Wright 1866)  
(= *Teredo ancila* (Barnard 1964))

**Cryptogenic**

*Teredo somersi* (Clapp 1924)  
(= *Teredo radialis* (Moll 1937))

**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 indigenous 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 harbor pilings or in ships' hulls.

## **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 *B. 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.

## **Brachiopoda**

### **Discinidae**

*Discinisca tenuis* (Sowerby 1847)

**Introduced**

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.* 2010). These oysters were translocated from Namibia. I also have unsubstantiated reports that *D. tenuis* has been seen on the shells of oysters reared in Algoa Bay (south-east 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, *D. tenuis* has not yet been found outside oyster farms, thus 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 confirmed example to date of an introduction in South Africa originating from a neighbouring country (*Semimytilus algosus* – see above - being another possible example). I consider mariculture to be the most probable vector.

## **Bryozoa**

### **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 in fact represent an endemic, previously undescribed species (newly named as *M. rustica*).

*Conopeum seurati* (Canu 1908) **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 of the European theater, *C. 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). Winston 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). This species has probably been introduced to, and overlooked in, many estuaries around the world. It is thus 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 (south-west coast). These populations appear similar if not identical to *C. seurati*, but this identification requires confirmation. I regard it as a ship-fouling invasion from Europe. It may have been present in South Africa for decades or centuries.

### **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 (1937) as *W. cucullata* and later synonymised by Florence *et al.* (2007) with *W. subtorquata*, based on identical morphological characteristics described by Gordon (1989). Florence *et al.* (2007) report its South African distributional as Saldanha Bay (west coast) to False Bay (south-west coast). There is some question as to whether *W. subovoidea* and *W. subtorquata* are separate species, due to the weak characterization of the former. Thus in order to establish the species boundaries within the genus, molecular techniques need to be applied (Florence *et al.* 2007).

## **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 in South Africa by O'Donoghue and de Waterville in 1944, but was probably a very early introduction. 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, *B. 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 (Florence *et al.* 2007, Harmer 1926, Mackie *et al.* 2002, Ryland 1974). It was first collected and reported from South Africa by Busk (1852). It ranges from Cape Point to Durban. As with *B. neritina*, it is likely to have been a very early introduction in ship fouling.

### **Cryptosulidae**

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

**Introduced**

I tentatively admit this European fouling bryozoan (Ryland and Hayward 1977) to the list of introduced 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 1947-1949 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 19th 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 it's "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.

## **Echinodermata**

### **Echinoidea**

#### **Arbaciidae**

*Tetrapyrgus niger* (Molina 1782)

**Introduced**

This 'black sea urchin' actually has a distinctive purple test, unlike any other species of urchin found in South Africa. Indigenous 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 during a survey of the Alexander Bay oyster dams in 2007. During the survey, it was noted that a breeding population, composed of both adults and juveniles was evident (Haupt *et al.* 2010). *T. 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, due to its grazing impact upon species of kelp (Rodriguez, 2003, Vasquez and Santelices 1990, Vasquez and Buschmann 1997, Vega *et al.* 2005). I consider

the most probable vector to have been import with the *C. gigas* spat, for mariculture purposes.

## **Ophiuroidea**

### **Ophiactidae**

*Ophiactis savignyi* (Muller and Troschel 1842)

**Introduced**

This small six-armed brittlestar is common in fouling communities and I thus 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.

## **Asteroidea**

### **Asteriidae**

*Marthasterias glacialis* (Linnaeus 1758)  
(= *Asteracanthion africanus* (Muller and Troschel 1842))

**Cryptogenic**

The large spiny seastar *M. glacialis* has its origin in Europe and the Mediterranean. The first South Africa record is from the 'Cape of Good Hope' where it was reported as *Asteracanthion africanus* by Muller and Troschel (1842). South African populations are a different colour and have different spination (several spines on some plates) than European populations. Some workers have thus assigned African populations to a subspecies, *M. glacialis africana*, but the systematic status of these populations as true subspecies has yet to be established genetically. The South African *M. glacialis* population is

confined to the South Western Cape, where it is a conspicuous predator in near-shore habitats, taking mostly mussels, but also gastropods, barnacles and ascidians (Penney and Griffiths 1984).

## **Chordata**

### **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 the majority of the species identified here as introduced have their origins in Europe, I 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 marinas and harbours (Rius *et al.* 2009b) and mussel farms (Heasman 1996) 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.

### **Polycitoridae**

*Cystodytes dellechiaiei* (Della Valle 1877)

**Cryptogenic**

An ascidian of unknown origin, first reported in South Africa by Millar (1962) from the Mozambique border. In 2001, Monniot *et al.* 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, 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).

### **Clavelinidae**

*Clavelina lepadiformis* (Müller 1776)

**Introduced**

This European fouling ascidian is colonial and has a characteristic transparent tunic that embeds the individual 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. This species has also been found in Saldanha Bay, Hout Bay and Table Bay on the west coast and East London on the south-east coast (M. Rius, unpublished). Colonies are often found attached to the undersides and sides of boats and jetties.

### **Didemnidae**

*Didemnum granulatum* (Tokioka 1954)

**Cryptogenic**

First found in South Africa by Monniot *et al.* (2001), from samples collected in Port Elizabeth on the south-east coast and KwaZulu-Natal (Isipingo) 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 me to suspect it is cryptogenic.

*Didemnun 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 *D. granulatum*, the origin of this species is unknown; however it is widely distributed around the world, thus I suspect it to be cryptogenic.

*Didemnun rodriguesi* (Rocha and Monniot 1993)

**Cryptogenic**

*Didemnun rodriguesi* represents another ascidian of unknown origin, due to a global distribution throughout tropical seas and thus I suspect it is 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); I thus 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 this 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. *D. 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 it 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).

### **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. It now occurs in temperate waters worldwide (Clarke and Castilla 2000, Howes *et al.* 2007, Lambert and Lambert 1998, Marshall and Keough 2003). It was first collected in Durban (Millar 1955). *C. intestinalis* can cause severe damage to mussel farms which results in important economic losses (Howes *et al.* 2007, Robinson *et al.* 2005).

### **Corellidae**

*Corella eumyota* (Traustedt 1882)

**Cryptogenic**

Found among other ascidians species in harbor communities as a fouling organism. *C. eumyota* is considered a cosmopolitan (Primo and Vázquez 2004) or circumpolar (Turón 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 I consider it as cryptogenic. *C. 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 Saldahna Bay (west coast), Table Bay (south east coast) and East London on the east coast (M. Rius unpublished).

### **Asciidiidae**

*Ascidia sydneyensis* (Stimpson 1855)

**Introduced**

This solitary ascidian can reach up to 100 mm and has a semitransparent tunic that can be covered by mud and epibionts. It is commonly found on pontoons and jetties, where it lives within a matrix of fouling organisms. Primo and Vasquez (2004) considered *A. sydneyensis* a cosmopolitan species, due to 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 (south-west coast) in 1932. Since then, it has been found in Port Elizabeth on the south-east coast (M. Rius, unpublished). It is usually a dominant fouling organism in harbor communities.

*Asciidiella aspersa* (Müller 1776)

**Introduced**

The tunic of this abundant European ascidian is transparent and can reach up to 80 mm. The mantle is normally white with pale red siphons, thus it is easily identified on ropes, tyres and pontoons within harbours (M. Rius, unpublished).

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 south-west coast.

### **Styelidae**

*Botryllus schlosseri* (Pallas 1766)

**Introduced**

This colonial ascidian forms very characteristic star-shaped zooid systems. It was first recorded by Millar (1955), based on specimen collected in 1946 from Durban harbour on the east coast. *B. schlosseri* is found in many South African harbours as a fouling organism, from Alexander Bay (west coast) to Port Elizabeth on the south-east coast (M. Rius, unpublished). There is some concern as to unknown impacts on indigenous kelp species, as *B. schlosseri* often colonizes these species when they are present in harbours. Griffiths *et al.* (2009) also recognize the potentially negative impact of *B. schlosseri* on the eelgrass *Zostera capensis* (mistakenly referred to as *Spartina maritima* therein).

*Cnemidocarpa humilis* (Heller 1878)

**Introduced**

This solitary ascidian has a leathery tunic and adults normally measure 40-50 mm. It can be found attached to floating pontoons and harbour ropes (Monniot *et al.* 2001, M. Rius, unpublished). 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 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. *C. humilis* is found in Alexander Bay (west coast) and Table Bay harbour on the south west coast (M. Rius, unpublished).

*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).

*Styela plicata* (Lesueur 1823)

**Introduced**

This solitary western Pacific ascidian has a characteristic thick, tough tunic and a body length up to 80-90 mm. Commonly found attached to floating pontoons and harbour ropes, it can compete with and displace indigenous species (Rius *et al.* 2009a). It is one of the most common harbour ascidian species worldwide (Lambert and Lambert 2003, Rocha and Kremer 2005, Wyatt *et al.* 2005). *S. 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) found this species to be very abundant in several locations along the South African coast. It ranges from Mossel Bay to Port Elizabeth (south-east coast) and is also reported from Durban on the east coast (M. Rius, unpublished).

*Styela canopus* (Savigny 1816)

**Cryptogenic**

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

This small (20-30 mm) 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 first recorded *S. canopus* as *S. stephensoni* (a South African endemic) in 1934 and Millar subsequently recorded it as *S. marquesana* in 1955. This species is found in Durban on the east coast.

*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 Australia (Monniot *et al.* 2001). First recorded by Millar (1955) as *S. viride*, Monniot *et al.* (2001) recognized that the specimens collected from Durban Harbor (east coast) in 1952 were *S. brakenhielmi*. Its distribution remains on the east coast (M. Rius, unpublished), concurring with Millar (1962) who attributed it as a warm-water component of the South African ascidian fauna.

### **Pyuridae**

*Microcosmus squamiger* (Michaelsen 1927)

**Introduced**

A highly successful fouling organism, this solitary ascidian has a maximum body length of 50 mm and can form dense monospecific clumps within its introduced range (Rius *et al.* 2009b). The tunic is generally covered by mud and epibionts, which makes its identification in the field considerably more difficult. As many studies have wrongly identified *M. squamiger* as *M. 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 (Kott 1985, Michaelsen 1927, Monniot *et al.* 2001) and genetic (Rius *et al.* 2008) studies indicate that the origin of *M. 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 *M. 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 *M. exasperatus* or *M. squamiger*. As no *M. exasperatus* have been found in recent surveys (Monniot *et al.* 2001, M. Rius, unpublished), I assume that the specimens collected by Millar were *M. squamiger* and thus I take the first collection of this species in South Africa as 1950. *M. squamiger* occurs at Alexander Bay (west coast) and Cape Town Docks (south-west coast). The reports of *M. squamiger* in Alexander Bay and Table Bay by Griffiths *et al.* (2009) were misidentifications of another introduced ascidian, *Cnemidocarpa humilis*. In addition to being a harbor species, *M. squamiger* has been found in open coast locations, where it covers all available substrata, achieving densities of up to 2 300 individuals m<sup>-2</sup> and displacing indigenous communities (Rius *et al.* 2009b).

## **Pisces**

### **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. 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, due to grubbing in sediments for food, and is considered a pest by conservation authorities.

## **Algae**

### **Rhodophyta**

#### **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 harbor 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.

#### **Phylloporaceae**

*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. I am 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 Reunion 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.

### **Ceramiaceae**

*Antithamnionella ternifolia* (Lyle 1922)  
(= *A. tasmanica* (Wollaston 1968))

**Cryptogenic**

This southern hemisphere (Eno *et al.* 1997) alga was first described from the tip of South America, was much later recorded from Australia (Silva *et al.* 1996, as *A. 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 invasion. 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, I consider it cryptogenic. Stegenga *et al.* (1997, as *A. 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* (Wollaston 1968)

**Introduced**

A North Pacific alga (Lindstrom and Gabrielson 1989) that has been introduced to Europe (Eno *et al.* 1997), Australia (Wollaston 1968) and elsewhere. In South Africa it is 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). I regard it as a ship-fouling introduction, likely via Australasia, rather than directly from the North Pacific.

## **Chlorophyta**

### **Cladophoracea**

*Cladophora prolifera* (Roth 1797) (Kützting 1843)

**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 *C. rugulosa* may be a South African endemic. While noting that records of *C. prolifera* in South Africa date back to the 1840s, they suggest that such early records may also have been confused with *C. rugulosa* (thus 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. I tentatively accept

the designation of Hewitt *et al.* (2004) that this alga has been introduced from the Mediterranean to the southern hemisphere.

### **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 yet determine its origins (for example, *U. fasciata* is said to be the commonest species of *Ulva* in the Hawaiian Islands, where *C. 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 to occur from False Bay to tropical East Africa, noting it is considered a pan tropical species.

### **Codiaceae**

*Codium fragile fragile* (Suringar 1867) (Hariot 1889)  
(= invasive strain *tomentosoides* (van Goor) (PC. 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 (Ribera and Boudouresque 1995, Provan *et al.* 2004), 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 introduced *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). Begin and Scheibling (2003), however, 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 *C. 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 rock pools 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, and I thus retain it in the South African invasive algal flora pending further collections from the Melkbosstrand and other regions.

## Higher Plants

### Poaceae

*Ammophila arenaria* (Linnaeus 1758)

**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, England, to stabilize sand dunes and thus for drift sand control (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, *A. 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 indigenous (European) root herbivores and biotic resistance by soil pathogens affect the invasiveness of *Ammophila* in South

Africa.

*Spartina maritima* (Curtis 1787) (Fernald 1916)  
(= *Spartina capensis* (Nees 1841))

**Cryptogenic**

*Spartina maritima* is widely distributed through western and southern Europe, northwest Africa, and also occurs on the west coast of South Africa (Chevalier, 1923, who suggested that this species is indigenous to South Africa). Pierce (1982) argued that *S. maritima* is a European introduction. Adams *et al.* (1999) noted that the status of *S. 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 *S. maritima*, although not on populations from South Africa. *S. maritima* was first described from South Africa as *S. 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](http://www.aluka.org); accessed August 2009). Pending further genetic evidence, we consider *S. maritima* as cryptogenic, and possibly introduced by solid ballast. If so, it would be one of South Africa's first recorded marine invasions.

### **Potamogetonaceae**

*Stuckenia pectinata* (Linnaeus 1753) (Borner 1912)  
(= *Potamogeton pectinatus*; = *P. pectinatus unguilatus* (Hagstrom 1916))

**Cryptogenic**

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 *S. pectinata*). Nevertheless, the ancestral distribution of the genus is rooted, as it were, in the northern hemisphere (Lindqvist *et al.* 2006), and *S. pectinata*, while widespread in northern waters, is highly patchy and isolated in the southern hemisphere (Santamaria 2002, figure 2, page 139), 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 inter hemisphere 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 (2009). While on the one hand *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 indigenous aquatic flora or infauna, impacted sediment dynamics or nutrient turnover. Relative to the latter, *S. pectinata* appears to be important in estuarine phosphorus cycles (Thornton *et al.* 1995, Adams *et al.* 1999). The earliest record I have found to date is that of Hagstrom (1916), who described *Potamogeton pectinatus* var. *ungulatus* (now regarded as a synonym of *S. pectinata*; Kaplan 2008), from the Koude River, Cape Province ([www.aluka.org](http://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, I have no doubt that earlier records will surface.

**Appendix B: Guide to referencing key used in Table 4 which indicates the main references that reveal the status of an introduced or cryptogenic organism within South Africa.**

Reference no.	Authors and publication year
1	Sapeika, 1948
2	Sebastian <i>et al.</i> 2005
3	Lilly <i>et al.</i> 2007
4	Pitcher <i>et al.</i> 2007
5	Samaai and Gibbons, 2005
6	Day, 1955
7	Acuna <i>et al.</i> 2004
8	Griffiths <i>et al.</i> 1996
9	Millard, 1975
10	Schuchert, 2004
11	Schuchert, 2005
12	Millard, 1970
13	Warren, 1906
14	Warren, 1907
15	Millard, 1959
16	Peterson, 1990
17	Henschel, 1990
18	Ewer, 1953
19	Millard, 1957
20	Millard, 1978
21	Simon <i>et al.</i> 2006
22	Simon and Booth, 2007
23	Simon <i>et al.</i> 2009
24	Day and Morgans, 1956
25	Day, 1967
26	Millard, 1952
27	Nel <i>et al.</i> 1996
28	Day, 1955
29	Blaber <i>et al.</i> 1974
30	ten Hove and Weerdenburg, 1978
31	Day, 1961
32	Knight-Jones and Knight-Jones, 1974
33	Knight-Jones and Knight Jones, 1975
34	Laird and Griffiths, 2008
35	Simon-Blecher <i>et al.</i> 2008
36	Henry and McLaughlin, 1975
37	Carlton and Newman, in prep
38	Jerling, 2008
39	Barnard, 1951
40	Hammersley-Heenan, 1897
41	Kensley, 1978
42	Stebbing, 1910

43	Barnard, 1916
44	Barnard, 1915
45	Conlan, 1990
46	Griffiths, 1974
47	Griffiths, 1975
48	Barnard, 1962
49	Haupt and Griffiths, in press
50	Robinson <i>et al.</i> 2005
51	Stock, 1954
52	Stock, 1959
53	Bamber, 2000
54	Prins, 1984
55	Stenton-Dozey and Griffiths, 1983
56	Barnard, 1963
57	Kilburn, 1972
58	Reid, 1996
59	Kilburn and Rippey, 1982
60	Tan and Sigurdsson, 1996
61	Miranda, 2009
62	Gosliner and Griffiths, 1981
63	Gosliner, 1987
64	McDonald, 2007
65	Jones, 2008
66	Cattaneo-Vietti and Sordi, 1988
67	Jensen, 2000
68	Grant <i>et al.</i> 1984
69	Korringa, 1956
70	Noble, 1886
71	Hammersley-Heenan, 1893
72	Waldron, 1904
73	Moll and Roch, 1931
74	O'Donoghue and de Waterville, 1937
75	Gordon, 1989
76	Florence <i>et al.</i> 2008
77	O'Donoghue and de Waterville, 1944
78	Gordon & Mawatari, 1992
79	Hinks, 1880
80	Busk, 1852
81	Winston, 1982
82	Winston, 1995
83	Awad <i>et al.</i> 2005
84	Rodriguez, 2003
85	Vega <i>et al.</i> 2005
86	Michaelsen, 1934
87	Monniot <i>et al.</i> 2001
88	Millar, 1955
89	Rius <i>et al.</i> in press
90	Turon <i>et al.</i> 2007
91	Skelton, 1991
92	De-Clerck <i>et al.</i> 2002
93	Norris and Aken, 1985
94	Stegegna <i>et al.</i> 1997
95	Leliaert and Coppejans, 2003
96	Provan <i>et al.</i> 2005
97	Provan <i>et al.</i> 2008
98	Hertling and Lubke, 1999a

99  
100

Hertling and Lubke, 1999b  
Hertling and Lubke, 2000

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## **Chapter 3: Spatio-temporal change in South African rocky intertidal species assemblages.**

### **Introduction:**

Impacts of global change on the biogeography of rocky intertidal species assemblages have been both predicted (Walther *et al.* 2002; IPCC 2007) and detected in many regions worldwide, across a wide range of spatio-temporal scales (Hawkins *et al.* 2003; Harley *et al.* 2006; Helmuth 2006; Mieszkowska *et al.* 2005; 2006; 2007; Mieszkowska 2009). Moreover, changes that have been reported correlate with long term shifts in environmental temperature regimes (Helmuth *et al.* 2006; Mieszkowska 2009) and have been documented as significantly impacting the structure and functioning of species assemblages (Southward *et al.* 1995; Tomanek and Helmuth 2002; Moore *et al.* 2007; Hawkins *et al.* 2008).

Detected changes linked to temperature shifts include range extensions and contractions (Barry *et al.* 1995; Sagarin *et al.* 1999; Kendall *et al.* 2004; Mieszkowska *et al.* 2005; 2006; 2007; Shinen and Morgan 2009) and fluctuations in the numbers of cold- and warm-water adapted species present within specific regions (Helmuth *et al.* 2006). In temperate regions, pole-ward range extensions in warm-water adapted species have been described at rates of 16-20 km per year, far exceeding terrestrial equivalents (Weslawski *et al.* 1997, Parmesan and Yohe, 2003, Zacherl *et al.* 2003, Berge *et al.* 2005). Conversely, in Chile, range contractions in cool-water adapted species have been reported, albeit in the

same northerly direction (Rivadeneira and Fernandez, 2005). Besides range edge effects, pocket extinctions (Sagarin et al. 2006) and several within-range impacts (Helmuth *et al.* 2006; Lima *et al.* 2006; Moore *et al.* 2007) have been documented.

Besides being an integral element of global change (Sala et al. 2000; Occhipinti-Ambrogi and Savini 2003; Wonham & Carlton 2005), it has been suggested that the vulnerability of natural communities to marine introduced species may be increased as a result of climate driven regime shifts (Occhipinti-Ambrogi and Savini 2003; Occhipinti-Ambrogi 2007; Byers 2009; Lonhart 2009; Olyarnik *et al.* 2009). Temperature-driven migrations of native species populations can potentially open resource niches that could facilitate successful establishment of bioinvaders (Kennedy et al. 2002, Stachowicz and Byrnes 2006, Occhipinti-Ambrogi 2007), ultimately altering species composition, structure and functionality of communities (Grosholz, 2003, Castilla *et al.* 2004, Ruesink *et al.* 2006 Robinson *et al.* 2007). For example, in California, a relatively warm-adapted invasive mussel, *Mytilus galloprovincialis*, has proliferated over indigenous cool-water adapted *M. trossolus* and *M. californianus* in concert with warming immersion and emersion temperatures (Sagarin *et al.* 1999).

Historically, South African studies into rocky shore biogeography have concentrated on identifying spatial patterns of distribution for algal and faunal species that comprise intertidal assemblages. Early studies forming part of the

University of Cape Town Ecological Surveys were conducted from 1933 to 1944 (Isaac 1937(a); 1937(b); 1938; 1949; Stephenson *et al.* 1937; 1938; 1939; 1940; Bright 1938; Eyre and Stephenson 1938; Eyre *et al.* 1938; Eyre 1939; Stephenson *et al.* 1940; Stephenson 1944; 1948). The primary goal of the intertidal program was to survey an extensive range of sites spanning the coastline, from Port Nollath on the northwest coast to St. Lucia on the northeast coast. Data generated were descriptive accounts and lists containing species incidence data (presence/absence). The resultant species inventories (historical baseline data) arising from these surveys formed the basis for defining the biogeographic regions that constitute the coastline (Stephenson 1944; Emanuel *et al.* 1992). In addition, voucher specimens, currently housed within the Iziko South African Museum, Cape Town, contributed to important early monographs (Day 1969) and biodiversity assessments (Gibbons *et al.* 1999) of marine species within South Africa.

The more contemporary studies to have been conducted were all quantitative in design. However, few covered the entire coastline, or incorporated sub-regional comparisons. Of those that did (McQuaid and Branch 1984; McQuaid 1985; Bolton 1986; Emanuel *et al.* 1992; Stegegna and Bolton 1992; Bustamante *et al.* 1996a; Stegegna and Bolton 2002; Sink *et al.* 2005) several attempted to link species distributions to trends in environmental data, inclusive of temperature (McQuaid and Branch 1984; McQuaid 1985; Bolton 1986; Stegegna and Bolton 1992; Stegegna and Bolton 2002).

As a result of these more rigorous analyses, the original biogeographic delimitation proposed in the 1930-40s was progressively refined (Emanuel *et al.* 1992, Bustamante and Branch, 1996b, Stegogna and Bolton, 2002, Lombard, 2004, Sink *et al.* 2005). The currently accepted delimitation description has evolved from a combination of these studies. It recognises a cool-temperate region (CTP) on the west coast and a warm-temperate region (WTP) on the south/south east coast. These biogeographic regions are separated by a transition zone (TZ1: False Bay), located on the south west coast. Beyond the WTP lies a sub-tropical region (STP) stretching up the east coast until it becomes a tropical province (TP) in the extreme northeast. A second transition zone (TZ2: East London), is located between the WTP and STP (modified after Lombard 2004 and Sink *et al.* 2005).

Within the local literature, there have been a number of peer-reviewed publications recognizing that knowledge of biogeographic delimitations and how they have changed over time is essential when defining conservation areas (Attwood *et al.* 1997; Hockey and Branch 1997; Awad *et al.* 2002; Sink *et al.* 2005). However, such changes have yet to be assessed for marine habitats within the South African region. Moreover, post the historical intertidal surveys conducted between 1933 and 1944, regional shifts in environmental conditions that may impact species assemblages and species distributions have been recorded. This includes rising air (emersion) temperatures (Kruger and Shongwe

2004) and changes in sea surface (immersion) temperatures (Chapter 1: Figure 1.2; Rouault *et al.* 2009). In addition, an increasing number of bioinvasive species within rocky intertidal habitats has been recorded post 1846 (Chapter 2). As environmental change and bioinvasives have been clearly demonstrated to alter intertidal communities across regions globally, it can be expected, *a priori*, that changes within South African intertidal species assemblages are highly likely to have occurred and the altered composition of species may have implications for the structure and functioning of intertidal communities.

Based on multivariate analysis of the historical baseline and contemporary data sets the following will be tested in this chapter: South African macroalgal and macrofaunal rocky intertidal species assemblages and distributions have changed significantly over time. In addition, evidence pertaining to patterns of bioinvasion and climate change driven temperature shifts will be considered in parallel with any significant changes detected within species assemblages over comparative time frames.

## **Materials and Methods:**

### **Historic data extraction**

Incidence data (presence/absence) were extracted from raw databases and peer reviewed publications generated from the UCT Ecological Survey of 1933-44 and housed within the marine collection, Iziko South African Museum, Cape Town (historical baseline data). Data were extracted for sites spanning the entire

South African coastline, incorporating the west coast (Bright 1937a; 1937b; Stephenson *et al.* 1940), False Bay (Bokenham 1938; Bokenham and Neugebauer 1938), southeast coast (Stephenson and Stephenson 1936; Eyre and Stephenson 1938), East London (Eyre *et al.* 1938) and the northeast coast (Stephenson *et al.* 1938). In addition, incidence and biomass data were extracted for matched sites using a database generated following surveys conducted from 1989 to 1992 (Bustamante 1994; Bustamante and Branch 1996a).

### **Contemporary sampling design**

Contemporary sampling surveys were conducted between 2007 and 2009. Sites were matched across the three temporal sampling periods using a combination of GPS co-ordinates (Table 3.1), written descriptions, ink drawings and photographic evidence. Sites were distributed across four pre-defined biogeographical regions that form the South African coastline and the two major transition zones located between them (Table 3.1; Figure 3.1). All sites were located at distance from pollution outfall pipes and industrial/harbour developments. Comparative data across the three sampling periods were available for a total of 12 sites located across the cool-temperate region of the west coast (CTP: 3), transition zone 1 (TZ1: 1), warm-temperate region of the southeast coast (WTP: 3), transition zone 2 (TZ2: 2), sub-tropical region on the east coast (STP: 2) and tropical region on the northeast coast (TP: 1) sampled in identical months and following comparative survey methods.

Sampling protocols followed a modified version of the NaGISA protocol description for rocky intertidal sites (Rigby *et al.* 2007) and was comparable across the three sampling periods. The shore was divided into four intertidal zones (low, lower-mid, upper-mid and high). Ten transect lines were run vertically from the mean high water spring tide mark (MHWS) to the mean low water spring tide mark (MLWS). They were set 10 m apart, spanning a horizontal distance of 100 m. Along each transect line, 1 m<sup>2</sup> quadrats were randomly placed within each intertidal zone. Therefore, there were 10 replicate quadrats in total per intertidal zone, per site. Tide pools or gullies were avoided. The use of replicate vertical transect lines (and therefore replicate quadrats) has been demonstrated to improve accuracy when estimating intertidal species richness and cover at a reasonable level of sampling effort (Whitman-Miller and Ambrose 2000). Within each quadrat, percentage cover of macroalgal and colonial species was recorded. Macrofaunal abundance (species counts) for sedentary and low mobility species were also recorded for all organisms greater than 1 mm in size. Although macroalgal and macrofaunal sampling underestimates total species richness, it provides information that is comparable between sites and across temporal periods (Bustamante and Branch 1996a).

At each site surveyed from 1989 to 1992 (Bustamante and Branch 1996a), a mean whole wet biomass value (g) was obtained for each species through destructive sampling. Means were calculated using 50 individuals spanning the full range of sizes present at each site. The data are available in Bustamante

(1994). This method was applied by Robinson (2007) when obtaining mean values for the wet biomass of mussel species. Therefore, the same method was applied during the 2007-2009 sampling period at each site. When comparing data sets from all three sampling periods, data were expressed as species incidence (presence/absence). In addition, data from the 1989-1992 and 2007-2009 sampling periods were expressed in terms of wet biomass ( $\text{Kg/m}^2$ ) for each species recorded, per intertidal level and site.

## **Data analysis**

### ***Spatio-temporal assessment of species biodiversity and distribution***

Multi-site comparisons of incidence and biomass data ( $\text{Kg/m}^2$ ) were used to determine if the composition of species assemblages had significantly changed over time. A whole intertidal approach was applied to the incidence data whereas the low, lower-mid, upper-mid and high intertidal zones were treated separately for biomass data ( $\text{Kg/m}^2$ ).

In order to assess similarities between sites, biological data were arranged into rectangular matrices (cases = species, samples = sites) and transformed to (i) reducing the weighting of abundant species and (ii) ensure that significant differences existing in the variability between comparative data sets were removed (see 'data considerations' below; Appendix C(i)). When similarity is assessed using the Bray-Curtis measure, the similarity coefficient is invariant to this level of transformation (Field *et al.* 1982).

The Bray-Curtis similarity index was applied to the species-sample matrices and hierarchical agglomerative cluster analyses performed using group average linkage. SIMPROF was used to test the structure of the data based on deviation ( $\rho_i$  statistic) of sample profiles from a mean calculated resemblance profile. Significant differences ( $P < 0.05$ ) were established between samples (sites) within subsets of data corresponding to each branch of the dendrogram. Red dotted lines on the cluster diagram indicated that significant differences were not detected ( $P > 0.05$ ). In addition to classification of the different samples, data were subjected to non-metric multi-dimensional scaling (MDS), with resemblance levels indicated. This produced a graphic representation in two dimensions of the similarity between groups. Both hierarchical cluster analysis and non metric MDS ordinations were used to compare species composition within assemblages across spatial and temporal scales for incidence and biomass-based data (Bray-Curtis 1957; Kruskal and Wish 1978; Field *et al.* 1982).

Significant dissimilarities ( $P < 0.05$ ,  $R < 1.0$ ) among sample groups (sites) within each sampling period were tested for using a permutation based one-way analysis of similarities (ANOSIM) for both incidence and biomass data. ANOSIM is an analogue of univariate ANOVA. To detect which species were responsible for contributing both similarities and dissimilarities between groups, Similarity Percentages (SIMPER) was applied. In each group comparison, an average Bray-Curtis dissimilarity ( $D$ ) value (%) was calculated. The average contribution of each species to the overall dissimilarity was ranked ( $D_i$ ) and the ratio between

overall dissimilarity ( $D$ ) and the standard deviation ( $SD$ ) of the species ranking ( $D_i$ ) calculated ( $D/SD(D_i)$ ). The cumulative percentage contribution of each species to the overall dissimilarity between groups was calculated as  $\sum D_i\%$ . An average Bray-Curtis similarity ( $s$ ) value (%) was also calculated for group comparisons. The average contribution of each species to the overall similarity was ranked ( $S_i$ ) and the ratio between overall similarity ( $S$ ) and the standard deviation ( $SD$ ) of the species ranking ( $S_i$ ) calculated ( $S/SD(S_i)$ ). The cumulative percentage contribution of each species to the overall similarity between groups was calculated as  $\sum S_i\%$ .

All multivariate analyses were completed using the Plymouth Routines in Multivariate Ecological Research (PRIMER) version 6.1 (Clarke and Warwick 1994).

### ***Spatio-temporal assessment of taxonomic structure***

There are two main measurements that can be applied in order to detect temporal shifts in taxonomic structure (TAXDTEST). Both are a measure of diversity and community structure and are relatively uninfluenced by sample size and sampling effort (Price *et al.* 1999). Taxonomic distinctness ( $\Delta^+$ ) compares the number of higher taxa present within samples over time ( $y = \text{lambda (+)}$ ). Variation in taxonomic distinctness ( $\text{var}\Delta^+$ ) compares the spread of species between higher taxa within samples over time ( $y = \text{delta (-)}$ ). Both measures take into account the taxonomic level at which any two species are related through the application of a simple linear weighting factor, therefore the average (weighted)

path length is represented (see Price *et al.* (1999) for a full worked statistical explanation).

Analyses rely on the full taxonomic classification (Kingdom to Species) of each species within the data sets being known. This information was obtained using WoRMS, an on-line classification database for marine species (Appeltans *et al.* 2009). The resultant inventory (or species aggregation file) was used by TAXDTEST to test for significant differences in taxonomic structure across time. Macroalgae and macrofauna were analyzed separately based on aggregation files of 86 and 110 species respectively. Firstly, taxonomic distinctness ( $\Delta^+$ ) and variation in taxonomic distinctness ( $\text{var}\Delta^+$ ) was determined for species assemblages located at sites sampled in 1989-1992 and 2007-2009. The resultant values were then compared to a funnel plot constructed from the historical baseline data (1933-44). Sites falling outside of the funnel were taxonomically distinct.

All TAXDTEST analyses were completed using the Plymouth Routines in Multivariate Ecological Research (PRIMER) version 6.1 (Clarke and Warwick 1994).

### ***Species-level analyses***

Individual species appearing (+) and disappearing (-) from sites were tallied to establish an overview of regional species richness, temperature tolerance amongst species, algal structural groups and functional feeding groups. Counts

were based on lists of distinguishing species (contributing to 90% of the dissimilarity) generated from Similarity Percentages (SIMPER) analysis which compared species assemblages at sites across sampling periods. Results were averaged per biogeographic region, or for the transition zones in-between.

#### *Species richness*

The number of species appearing (+) and disappearing (-) across sampling periods was determined.

#### *Temperature tolerance*

Species were allocated cool-water (CW), warm-water (WW) and cosmopolitan status (C), according to their biogeographic distribution along the South African coast (Branch *et al.* 2010). The number of CW-, WW- and C-adapted species appearing (+) and disappearing (-) across sampling periods were determined.

#### *Algal structural groups*

The macroalgal component of data sets was extracted. Species were pooled into algal groups based on the following structural groups: leathery (L), foliose (Fo), articulate calcified (AC), crustose (Cr), corticated (C) and filamentous (F). The number of species appearing (+) and disappearing (-) across sampling periods was determined for each group within each group.

#### *Functional feeding groups*

The macrofaunal component of data sets was extracted. Species were pooled into groups based on dominant feeding mechanism which was categorised as:

primary producers (PP), grazers (G), suspension feeders (SF), predators (P) and omnivores (O). The number of species appearing (+) and disappearing (-) across sampling periods was determined for each group within each group. .

### **Data considerations**

The three data sets (1933-1944, 1989-1992 and 2007-2009) span a period of 76 years in total. Although they do not represent a continuous time series, with long periods where data are not available, all surveys were conducted in identical sampling months. One assumption made in interpreting apparent differences in species assemblages across these sampling periods has been that occupancy status does not significantly fluctuate over shorter, unmeasured time scales as a result of seasonal changes or species turnover. In addition, it is assumed that climax assemblages (in terms of succession) have been surveyed, thus an element of caution has been applied when interpreting detected changes.

There is local evidence that seasonal effects along the southeast and east coast of South Africa are negligible (McQuaid and Branch 1984; Dye 1998). In addition, although seasonal fluctuations are evident within west coast assemblages (McQuaid and Branch 1984; Bustamante and Branch 1985; McQuaid 1985; Bustamante and Branch 1996a), Robinson et al. (2007) established that climax assemblages are reached within a relatively short space of time (months) and can remain persistent over long periods.

Observed species richness within habitats (alpha diversity) is dependent on sample size (Gotelli and Colwell 2001). Therefore, biases in sampling effort could lead to significant variation in species richness recorded per sampling period (Gotelli and Colwell 2001; Ugland et al. 2003; Colwell *et al.* 2004). Although survey sites, methods and sampling months were identical, it was important to establish if sampling was adequate across time periods to allow for valid species assemblage comparisons. Thus an assessment of sampling representivity, based on species richness, was required (Gotelli and Colwell 2001; Ugland et al. 2003; Colwell *et al.* 2004).

As the data sets consisted of replicated, multi-individual samples, sample-based species accumulation curves were selected (a type of taxon sampling curve). Based on successive pooling of samples (censused quadrats) from each sample set (sampling period), accumulation curves were constructed to determine if asymptote species richness had been reached for the sample effort used (Appendix C(i)). Generally, species accumulation curves rise rapidly at first as additional individuals are revealed with consecutive sampling and added to the pool of all previously observed individuals. This slows as increasingly rare species are added, until an asymptote is reached (Gotelli and Colwell 2001). This is particularly the case when the species can be easily observed and identified and it is possible to count all of the species present (Ugland *et al.* 2004). As the intertidal surveys were focused on highly visible macro components of assemblages, estimates of total species richness were not

required (Ugland *et al.* 2004) and an asymptote was reached within each sampling period (Appendix C(i) a-c).

Another possible source of bias within the data was the scaling up of the 1989-1992 quadrats ( $0.5 \text{ m}^2$ ) to facilitate comparative analyses with the  $1 \text{ m}^2$  quadrats used within the other two sampling periods. A larger variance term would be expected for the smaller compared to the larger quadrat size. To ensure detected changes between 1944-1989 and 1989-2007 were a function of temporal change, rather than quadrat size, data were interrogated by testing for differences between variances (see Zar (1999) for a full worked statistical explanation). Intertidal levels were analyzed separately and analyses were based on total biomass ( $\text{Kg/m}^2$ ) per quadrat for matched sites within each sampling period (Appendix C(ii)). A total of 11/15 analyses across all intertidal zones were not significantly different ( $P > 0.05$ ). In comparison, 4/15 analyses revealed significant differences ( $P < 0.05$ ). However, in 3/4 cases, the variance was higher in the 2007-2009 sample data, with the upper-mid intertidal level at Port Nollath being the only case where variance was higher for the 1989-1992 sample data (Appendix C(ii)). In all four cases, log transformation resolved significant differences between variance values (Appendix C(ii)).

Finally, the use of incidence data in conjunction with ANOSIM may be less robust than using biomass data, as both rare and abundant species are given equal weighting. However, when incidence and biomass based sample (site) data

were analysed separately, data classification was in strong agreement (Appendix C(iii) and results section below). In addition, plotting species richness onto MDS ordinations (Clarke, pers.comm.) revealed that there was no clear correlation between species richness, sampling periods or similarity groupings (Appendix C(iv)).

### **Results:**

Significant changes in species assemblages were detected at rocky intertidal sites located within and in-between biogeographic regions from 1933 to 2009 (Figure 3.1a and b). Incidence and biomass ( $\text{kg/m}^2$ ) based analyses were in strong agreement, revealing similar temporal and spatial trends (Appendix C(iii): Figure C3.1a and b; Figure C3.2a and b; Figure C3.3a and b). The overall agreement indicated that both types of data were equally robust.

Hierarchical cluster analysis revealed that sites sampled in 1989-1992 and 2007-2009 were classified separately (formed discrete groups) from sites sampled in 1933-1944 (Figure 3.1a). Multi dimensional scaling (MDS) ordination paralleled hierarchical cluster analysis, yielding the same assemblages with low stress (2D stress = 0.09) indicative of strong grouping (Figure 3.2b). Analysis of similarities (ANOSIM) indicated that detected changes in species assemblages among sites across the different sampling periods were significantly different ( $R=0.62$ ;  $P=0.001$ ). Testing the data structure (species composition) for each sample site subset corresponding to a branch of the dendrogram (SIMPROF) revealed there

were two major groups within the cluster analysis (Figure 3.1a) that were not significantly different ( $P > 0.05$ ).

### **Changes at Transition Zones and Adjacent Provincial Sites**

The first major group that was not significantly different, according to cluster analysis and SIMPER, shared 53% similarity (Figure 3.1a) and consisted of species assemblages sampled at sites across both contemporary sampling periods, located within the cool- and warm-temperate (CTP; WTP) regions, the False Bay transition zone (TZ1) and the East London transition zone (TZ2). In contrast, species assemblages sampled at WTP and TZ2 sites during the baseline survey (1933 to 1944) were significantly different ( $P < 0.05$ ) from assemblages sampled at the CTP and TZ1 sites and from each other (Figure 3.1a). Thus, all changes occurred between 1944 and 2009.

Based on biomass data ( $\text{Kg/m}^2$ ) for hierarchical cluster analysis, TZ1 and WTP sites sampled at all intertidal levels during 1989-1992 and 2007-2009 were classified separately (formed a discrete group sharing higher similarity) compared to CTP sites, although all three regions formed a discrete cluster at a similarity of 24-34% (Appendix C: Figure C3.1a; Figure C3.2a; Figure C3.3a). Multi dimensional scaling (MDS) ordination paralleled hierarchical cluster analysis, yielding the same assemblages with low stress (2D stress = 0.04-0.08) indicative of strong grouping (Appendix C: Figure C3.1b; Figure C3.2b; Figure

C3.3b). Analysis of similarities (ANOSIM) indicated that detected changes were significantly different ( $R=0.61-0.87$ ;  $P=0.001$ ).

According to cluster analysis and SIMPER, species assemblages sampled at sites across both contemporary sampling periods, located within the warm-temperate region (WTP) and the East London transition zone (TZ2) shared 55% similarity (Figure 3.1a). In contrast, species assemblages sampled at TZ2 sites during the baseline survey (1933 to 1944) were significantly different ( $P<0.05$ ) from WTP sites (Figure 3.1a), sharing a 43% similarity with assemblages at sites located in the sub-tropical (STP) region (Figure 3.1a).

Based on counts of species contributing to dissimilarity between groups, (according to Similarities Percentage analysis: SIMPER), species richness decreased in the CTP, TZ1 and WTP, whilst increasing in TZ2 (Figure 3.3). Moreover, there was a net gain of cool-water adapted species within assemblages at sites within the CTP, TZ1 and WTP from 1933-2009 (Figure 3.3). Conversely, there was a net loss of warm-water adapted species within assemblages at sites within TZ1 and the WTP over the same period (Figure 3.3). Within TZ2, there was a net increase of cosmopolitan species (Figure 3.3).

SIMPER results indicated that species assemblages located at sites within the CTP and TZ1 had an overall reduction in average dissimilarity of 15% between 1933 and 2009 (Figure 3.4). In parallel, an average dissimilarity reduction of 8%

was evident for assemblages located at sites within TZ1 and the WTP over the same time period (Figure 3.4). In addition, SIMPER analysis revealed that species assemblages located at sites within the WTP and TZ2 had undergone temporal variation over the 76 year period, reducing average dissimilarity by 36% (Figure 3.4). Conversely, average dissimilarity increased between assemblages located at sites in TZ2 and the STP by 17% (Figure 3.4). Temporal variation was evident within each biogeographic region and the transition zones in-between, ranging from 38 to 63% with highest variation within the CTP region (63%) and TZ2 (61%) regions (Figure 3.5).

Changes in species assemblages were accompanied by changes in taxonomic structure. Species assemblages located at sites sampled in 1989-1992 and 2007-2009 within the CTP and TZ1 were not taxonomically distinct when compared with the historical baseline data (1933-1944). All contemporary sites within these regions fell within the funnel formed by the historical data (Table 3.2; Figure 3.6a, b, c and d). However, change in the taxonomic structure of macroalgal species within assemblages was detected at sites located in the WTP. Sites sampled in both 1989-1992 and 2007-2009 fell outside of the funnel, indicating changes had occurred over a 76 year period (Table 3.2; Figure 3.6a and b). In Figure 3.6a, contemporary sites were located below the funnel, indicating the number of higher algal taxa had decreased. In Figure 3.6b, contemporary sites were located above the funnel, indicating algal species were distributed more unevenly between higher taxa. Changes in taxonomic structure

were accompanied by shifts in the types of algal structural groups present within WTP assemblages. Based on species counts contributing to dissimilarity between groups (according to SIMPER analysis), there was a net increase in leathery and crustose algae, paralleled by a net decrease in foliose species over a comparable time scale (Figure 3.7).

Significant temporal changes in faunal taxonomic structure were detected in TZ2 for assemblages at sites sampled in 2007-2009. TZ2 sites sampled in 1989-1992 fell within the funnel formed by the historical baseline data (1933-1944) and therefore were not taxonomically distinct. This indicated change had occurred over the last 17 years. In Figure 3.6c, contemporary sites were located above the funnel, indicating the number of higher faunal taxa had increased. In Figure 3.6d, contemporary sites were located above the funnel, indicating faunal species were distributed more unevenly between higher taxa. Changes in taxonomic structure were accompanied by shifts in the types of algal structural groups present within TZ2 assemblages. Based on species counts contributing to dissimilarity between groups (according to SIMPER analysis), there was a net increase in suspension feeders (Figure 3.8).

### **Additional Change Within and Between Provinces**

The second major group that was not significantly different, according to SIMPROF ( $P > 0.05$ ) shared 55% similarity (Figure 3.1a) and consisted of species assemblages sampled at sites across both contemporary sampling periods,

located within the sub-tropical (STP) and tropical (TP) regions, located on the northeast coast. In contrast, species assemblages sampled at STP sites during the baseline survey (1933 to 1944) were significantly different ( $P < 0.05$ ) from sampling conducted in 2007-2009 (Figure 3.1a). Thus changes occurred between 1944 and 2009.

Based on biomass data ( $\text{Kg/m}^2$ ) for hierarchical cluster analysis, TP sites sampled at low and upper-mid intertidal levels during 1989-1992 and 2007-2009 formed a discrete group sharing 37-38% similarity (Appendix C: Figure C3.1a; Figure C3.3a). Multi dimensional scaling (MDS) ordination paralleled hierarchical cluster analysis, yielding the same assemblages with low stress (2D stress = 0.06-0.08) indicative of strong grouping (Appendix C: Figure C3.1b; Figure C3.3b). Analysis of similarities (ANOSIM) indicated that detected changes were significantly different ( $R = 0.83-0.87$ ;  $P = 0.001$ ).

Based on counts of species contributing to dissimilarity between groups, (according to Similarities Percentage analysis: SIMPER), species richness increased in both the STP and TP (Figure 3.3). Moreover, there was a net gain of warm-water adapted species within assemblages located in both regions from 1933-2009 (Figure 3.3). SIMPER results revealed temporal variation was evident within assemblages located at sites within the STP and TP, with average dissimilarity values of 48 and 38% respectively from 1933 to 2009 (Figure 3.5).

Changes in species assemblages were accompanied by changes in taxonomic structure. Change in the taxonomic structure of faunal species was detected within assemblages at sites located in the STP (Table 3.2; Figure 3.6c and d). In Figure 3.6c, contemporary sites were located above the funnel, indicating the number of higher faunal taxa had increased post 1933-1944. However, Figure 3.6d indicates there was no temporal change within the number of faunal species distributed between higher taxa, as sites fell within the funnel. Based on species counts contributing to dissimilarity between groups (according to SIMPER analysis), there was a net increase in suspension feeders, grazers and omnivores (Figure 3.8).

### **Characteristic Species**

Contemporary characteristic species lists (2007-2009), generated following SIMPER analyses, compared species assemblages at sites within each biogeographic region or transition zone, across intertidal levels (Table 3.3; Table 3.4). Averaged similarity values ( $S$ ) for sites within all regions were consistently high across all intertidal levels ( $S = 54.86-83.84$ ) indicative of low variability (Table 3.3; Table 3.4).

All species contributing to average similarity ( $S$ ) in the CTP, TZ1 and WTP are cosmopolitan or cool-water adapted according to biogeographic distribution. A number of ranked species contributing to average similarity ( $S$ ) are shared across the three provinces and intertidal zones (Table 3.3). Most notable is the

relatively cool-water adapted introduced mussel, *Mytilus galloprovincialis*, which is the most characteristic species present in lower-mid intertidal assemblages within all three regions (Table 3.3). Interestingly, SIMPER analyses comparing 1933-1944 and 2007-2009 assemblages revealed *M. galloprovincialis* as a key distinguishing species, having appeared in the contemporary assemblages. In parallel, a native warm-water adapted mussel, *Perna perna*, was revealed as a key distinguishing species as, at sites sampled within the CTP between 2007 and 2009, it was absent. However, between 1933 and 1944, *P. perna* had previously been recorded in the low and mid-intertidal.

In addition, the leathery alga, *Ecklonia maxima*, crustose alga, *Spongites yendoii* and the articulate calcified alga, *Corallina officinalis* are common in the low-intertidal of the CTP, TZ1 and WTP, as are the limpet, *Scutellastra granularis* and gastropod, *Oxystele variegata* within the upper-mid intertidal. These species are consistently characteristic at these sites, based on high ratio  $S_i/SD(S_i)$  values.

Species contributing to average similarity ( $S$ ) in the STP and TP are a mixture of warm-water adapted and cosmopolitan species. A number of ranked species contributing to average similarity ( $S$ ) are shared across the two regions within all three intertidal zones (Table 3.4). In the low-intertidal, the indigenous warm-water adapted mussel, *P. perna* is consistently characteristic of assemblages across the STP, TP and TZ2. In the low and upper-mid-intertidal, barnacles such as *Octomeris angulosa*, *Tetraclita serrata* and *Chthamalus dentatus* are

consistently present within each region (Table 3.4). Conversely, TZ2 shared very few species with either the STP or TP, having more species in common with the WTP (Table 3.5).

### **Discussion:**

As with the studies conducted by Southward *et al.* (1995) and Sagarin *et al.* (1999) indicating changes in intertidal assemblages have occurred over 70 and 60 year periods respectively, this study has revealed that South African intertidal species assemblages have changed over the past 76 years. However, although significant shifts in assemblage composition have been detected at sites sampled within and between biogeographic regions, the degree of change differs spatially. Regional changes in assemblage composition will be discussed with specific reference to correlations with trends in sea surface temperature, patterns of bioinvasion and biogeographic delimitations over comparable periods.

### **Sea temperature trends and assemblage changes**

Land based air temperatures are well documented as increasing across the entire land mass of South Africa (Kruger and Shongwe 2004). In parallel, 4 km resolution AVHRR data collated from 1985-2007 (Chapter 1: Figure 1.2) and optimally interpolated (OI) data collated from 1982-2007 (Figure 3.9) both indicate clear decadal trends in near-shore sea temperatures that correlate with the detected changes in species assemblages.

The net increase in the numbers of cool-water adapted species and reciprocal net decrease in the numbers of warm-water adapted species at sites located the

cool- (CTP) and warm-temperate (WTP) region and False Bay transition zone (TZ1) in-between have contributed to the significant differences detected within species assemblages and correlate with regional cooling. Near-shore cooling is occurring at a rate of  $-0.2$  to  $-0.5$  °C per decade (Chapter 1: Figure 1.2; Figure 3.9: SST1 and SST2), attributed to changes in local climatology (Chapter 1), such as wind patterns (Chapter 1: Figure 1.3) and altered pressure systems, which ultimately has led to increased upwelling activity within the region (Reason and Rouault 2005; Schumann *et al.* 2005; Trenberth *et al.* 2007; Rouault *et al.* 2009). Specifically, the upwelling centre located at Port Elizabeth appears to have intensified (Chapter 1: Figure 1.2) as a result of the Agulhas Current speeding up over time and removing larger bodies of surface water at the retroflect on the southeast coast (Schumman *et al.* 2005; Rouault *et al.* 2009; pers comm.). These shifts are in line with predictions for upwelling regions globally (Bakun 1990).

The net increase in warm-water adapted species at sites located within the subtropical (STP) tropical (TP) regions correlates with increased near-shore temperatures within these regions, evident in the AVHRR data (Chapter 1: Figure 1.2) and OI data (Figure 3.9: SST4 and SST5). Rouault *et al.* (2009) attribute decadal warming in the range of  $+0.2$  to  $+0.4$ °C to warming of the Agulhas current on the east coast above Port St. Johns (Chapter 1: Figure 1.2; Figure 3.9: SST6).

Comparative changes in the temperature affinities of macro-species within rocky intertidal assemblages have been observed in other regions globally (Helmuth et al. 2006; Mieszkowska 2009). For example, in the UK, Southward *et al.* (1995) reported an increase in the abundance of warm-water adapted species in response to a  $\pm 0.5^{\circ}\text{C}$  immersion temperature increase between 1920 and 1980. Post 1980, near-shore temperatures cooled, accompanied by an increase in the abundance of cool-water adapted species. Similarly in Ireland, Simkanin *et al.* (2005) coupled a reduction in cool-water adapted species with warming temperatures, whereas warm-water adapted species proliferated. In the Mediterranean, Bianchi and Morri (2000) reported an increase in warm-water adapted species within the Ligurian Sea from 1985 onward that were in concert with warming trends in sea temperatures. Across in California, Sagarin *et al.* (1999) detected shifts in the proportions of cool and warm-water adapted species, with the latter increasing in line with increasing near-shore temperatures over comparable time frames. Given the global and local evidence, it can be speculated that shifts in temperature, a response to climate change, have a role in driving long-term change in the species composition found within the rocky intertidal macro-assemblages of South Africa.

### **Patterns of bioinvasion and assemblage changes**

The most characteristic and distinguishing species present within species assemblages sampled in 2007-2009 for the CTP, TZ1 and WTP was identified as

the cool-water adapted mussel, *Mytilus galloprovincialis*. This is an introduced species which arrived post 1944 (*circa* 1979) and spread along approximately 1,500km of South African rocky shore over a 30 year period (Chapter 2: Figure 2.6; Appendix A). Locally, *M. galloprovincialis* has been established as an ecosystem engineer and dominant space occupier (Van Erkom Schurink and Griffiths 1990; 1991a; 1991b; 1992; Robinson 2007; Wallentinus and Nyberg 2007) with the ability to modify environments both structurally and functionally (McQuaid and Phillips 2000; 2006; Porri *et al.* 2006; Nicastro *et al.* 2008). This is attributed to its substantive competitive advantages (Bownes and McQuaid 2006; Rius and McQuaid 2006; Xavier *et al.* 2007; Zardi *et al.* 2006; 2007) and interestingly, the presence of *M. galloprovincialis* has greatly changed infaunal communities, due to the provision of a complex biogenic habitat (Hammond and Griffiths 2004).

In Southern California, arrival of *M. galloprovincialis* led to the displacement of indigenous populations of congeners *M. trossolus* and *M. californianus*, impacting the southern range of *M. trossolus* as the result of interference competition (Geller 1999; Sagarin *et al.* 2006; Shinen and Morgan 2009). Large scale extinctions were evident from a number of locations along the coast attributed to smothering, reduced filtration rates and restricted growth effects exerted by *M. galloprovincialis* on the indigenous mussels (Sagarin *et al.* 2006). A clear hybrid zone now separates *M. galloprovincialis* and *M. trossolus* populations (Braby and Somero 2006). Given that it is recognized cascaded

change within species assemblages is linked to changes in key habitat forming taxa (Schiel *et al.* 2004), it is not surprising that the results of this study indicate *M. galloprovincialis* has played a role in reshaping South African species macro-assemblages post arrival and that its spread coincides with the recorded disappearance of the native mussel, *Perna perna* from TZ1.

Given the ability of *M. galloprovincialis* to modify habitats and dominate space, this could explain the shift in algal taxonomic structure observed within assemblages located at sites in the WTP. Algal species changed from foliose species, requiring space for their holdfasts, to crustose species that can overgrow mussel beds. Thus, alterations in algal taxa present, driven by the dominance of the bioinvader, could have impacted overall community dynamics, which has led to the increased similarity with the CTP and TZ1 regions. This would be an example of a cascade effect as described by Scheil *et al.* (2004). Such effects are being reported globally, for example, within UK intertidal assemblages a temperature driven reduction in an algal species, *Fucus vesiculosus*, led to the decline of a grazing limpet, *Patella vulgata*, which utilized *F. vesiculosus* as a shelter (Moore *et al.* 2007).

Simkanin *et al.* (2005) recorded that the arrival and dominance of an introduced barnacle, *Elminius modestus*, post 1955, was partially responsible for observed shifts in species assemblages. They speculated that although this may be due to competitive advantages, on the basis of rising sea temperatures and

complimentary shifts in the abundance of cool-water and warm-water adapted species, climate may be acting in synergy with patterns of bioinvasion in altering species composition. That climate change impacts are likely to be superimposed on ecosystem stressors, such as bioinvasives, has been advocated by a number of researchers (Scavia *et al.* 2002, Stachowicz *et al.* 2002; Occhipinti-Ambrogi and Savini 2003; Drinkwater *et al.* 2009). Changes in environmental temperature could lead to conferral of a competitive advantage from one species to another where species pairs overlap (Bianci and Morri 2000). This was the case in New Zealand, where a native mussel, *Perna canaliculus*, due to its inability to tolerate changing temperatures, was outcompeted by an invasive mussel belonging to the genus *Mytilus* (Petes *et al.* 2007) and may well be the case between *M. galloprovincialis* and *P. perna* within the CTP.

### **Biogeographic delimitations and assemblage change**

Historically, False Bay (TZ1) has been considered a strong transitional zone between the CTP and WTP regions (Emanuel *et al.* 1992; Bustamante and Branch 1996a). As sea temperatures were within an intermediate range in comparison to the biogeographic regions on either side, the Bay supported a mixture of warm-water adapted and cool-water adapted species (Griffiths and Branch 1991). Many species within TZ1 were described as located at the edge of their distributional range (Eyre 1939; Stephenson and Stephenson 1972; McQuaid and Branch 1984; 1985; Bolton 1986; Griffiths and Branch 1991, Emanuel *et al.* 1992; Awad *et al.* 2002) and a large number of endemic species were recognized (McQuaid and Branch 1984; Griffiths and Branch 1991).

The increased similarity between sites located within the CTP, TZ1 and WTP, a result of significant changes in species assemblages over a 79 year period, suggests that the two biogeographic regions and the Bay are merging. Interestingly, the existence of a separate CTP and WTP region has been debated within the literature. Several authors promote them as separate provinces (Stephenson 1939; 1944; Stephenson and Stephenson 1972; Emanuel *et al.* 1992; Bustamante and Branch 1996a), whereas algal ecologists advocate the idea of one 'mega region' incorporating both the west and south coast (Bolton 1986; Stegogna and Bolton 2002). The results of the current study indicate that the formation of one large 'mega-region' is a strong possibility, should homogenization of species assemblages continue.

In addition, the results of this study suggest that species assemblages located within the East London transition zone (TZ2), dividing the WTP and STP, have significantly altered over time. Species compositions are currently more typical of the WTP, whereas historically, they have more closely resembled STP assemblages. If changes continue along the same trend, TZ2 may actually shift, north of its current East London location. Results also indicate that intertidal assemblages located at STP and TP sites have become more similar over a comparable time period. Interestingly, Emanuel *et al.* (1992) utilized the regional descriptions of Stephenson (1944) and agreed there was a 'biogeographic break' between Durban and sites just North of Durban. Utilizing data from 1997

surveys, Sink *et al.* (2005) failed to detect this transitional zone and attributed it to the fact that Emanuel *et al.* (1992) had incorporated sub-tidal surveys into their data sets. According to this study, it may be that the transition zone disappeared due to a merging of the STP and TP, which suggests that the window within which these two regions have merged may lie between 1933 and 1997.

Climate change and bioinvasives, identified as having a role in the observed changes, have been implicated as synergistically altering communities through 'unprecedented rates of species homogenization' (Braby and Somero 2006a). In light of the increasing similarities evident within intertidal assemblages along the coast, and apparent shifts in biogeographic delimitation, this appears to be the case in South Africa. Continued monitoring will be essential in order to assess further changes and review the current biogeographic delimitation with added confidence, given the importance of this information for conservation policy.

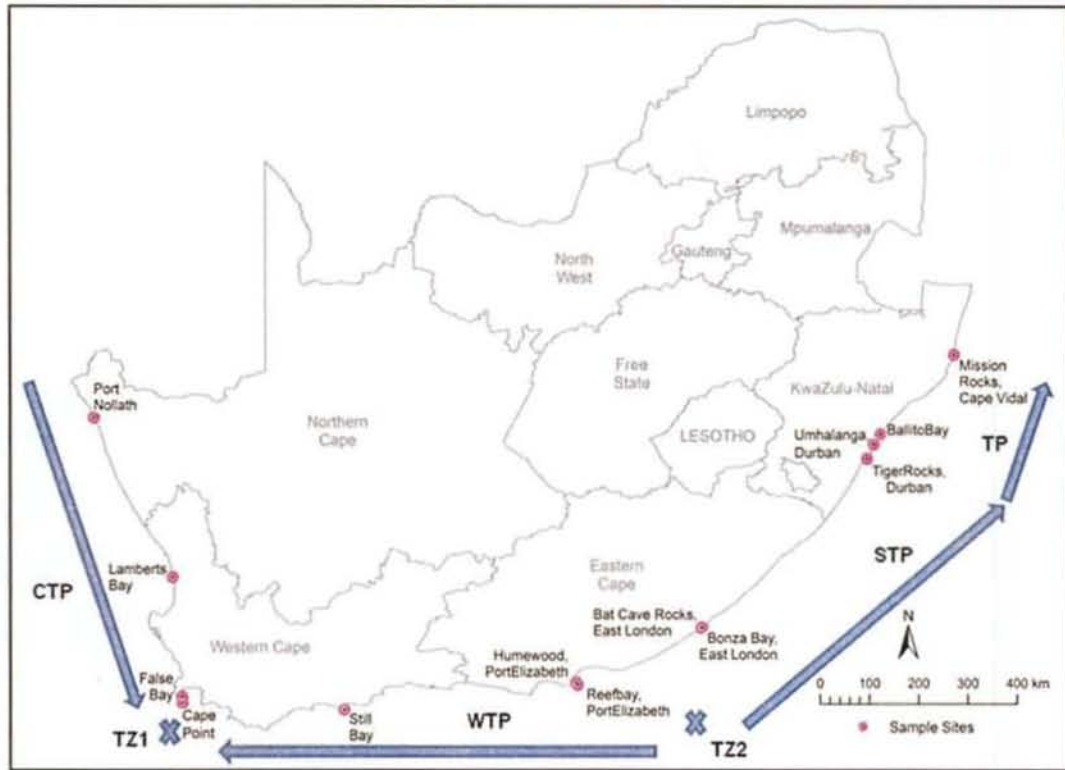


Figure 3.1: Outline of the Southern African shoreline south of 25°S indicating 12 rocky intertidal sites sampled across three periods (1933-44, 1989-1992 and 2007-2009). Sites are distributed across different biogeographic regions (blue arrows) and two major transition zones located in-between (blue crosses). Refer to Table 3.1 for regional codes. (Modified after Lombard 2004 and Sink *et al.* 2005).

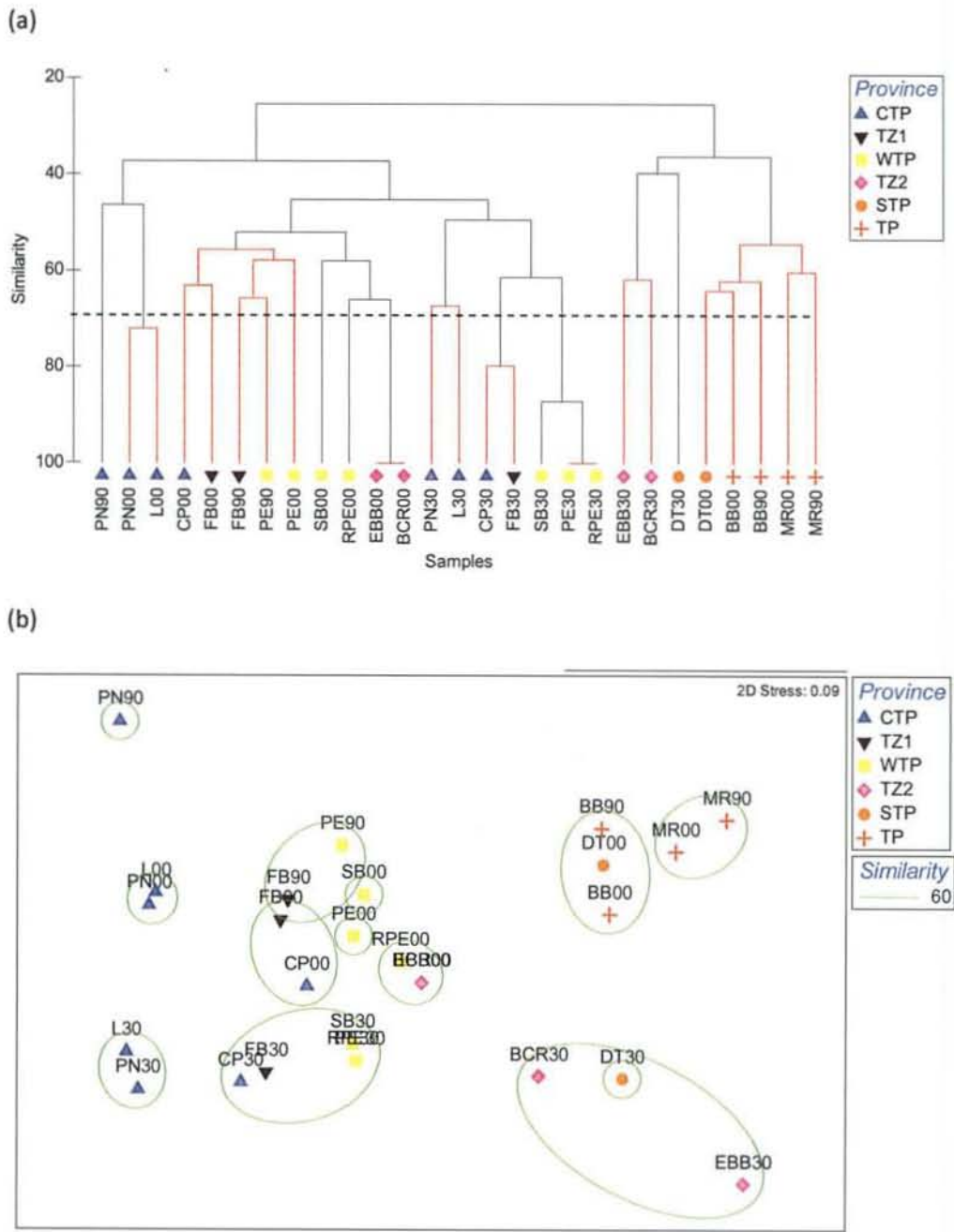


Figure 3.2a: Based on the Bray-Curtis similarity index, data classification by hierarchical cluster analysis (SIMPROF: significant differences between sample groups indicated by black solid lines ( $P < 0.05$ )) and 3.2b: Non-metric MDS ordination (2D stress: 0.09) for intertidal sites sampled in 1933-1944 (30), 1989-1992 (90) and 2007-2009 (00). ANOSIM:  $R = 0.62$ ;  $P = 0.001$ . refer to Table 3.1 for site and regional codes.

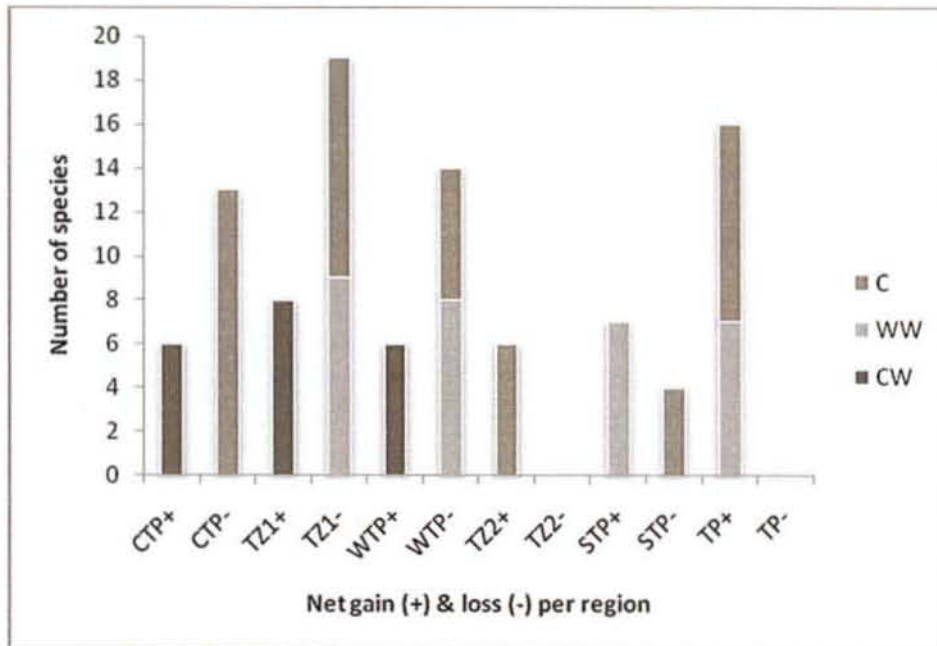


Figure 3.3: Net number of cool-water adapted (CW), warm-water adapted (WW) and cosmopolitan (C) species appearing (+) and disappearing (-) from South African biogeographic regions and transition zones in-between from 1933-2009. Refer to Table 3.1 for site distribution within regions and regional codes.

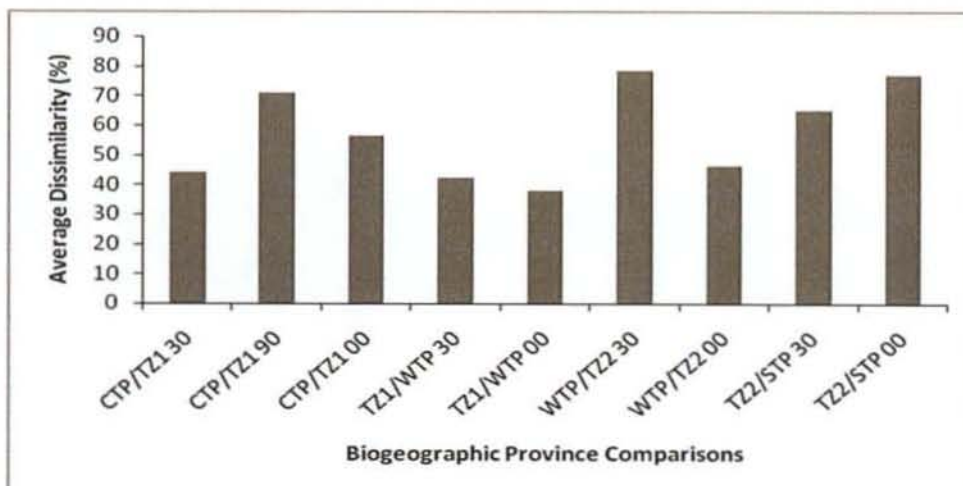


Figure 3.4: Bray-Curtis average dissimilarity (%D) between the biogeographic regions of South Africa and the transition zones in-between for the 1933-1944 (30), 1989-1992 (90) and 2007-2009 (00) sampling periods. Refer to Table 3.1 for site distribution within regions and regional codes.

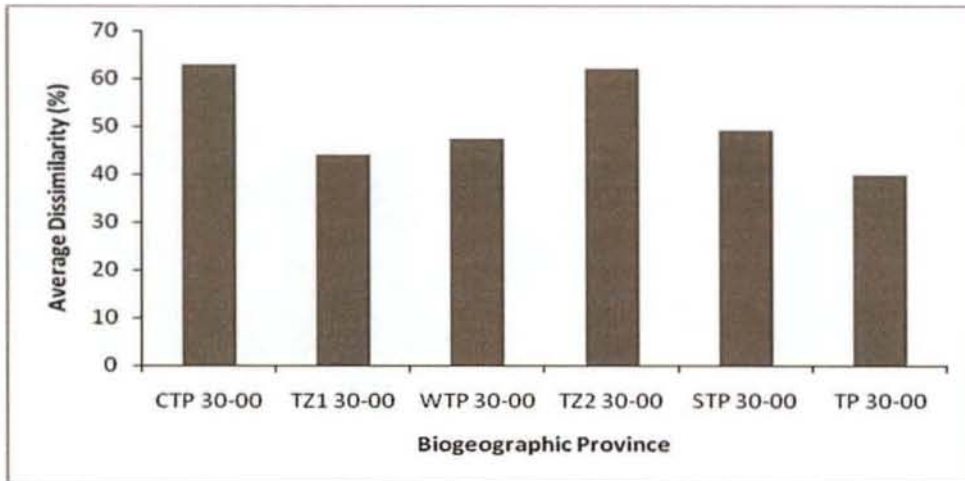


Figure 3.5: Bray-Curtis average dissimilarity (%*D*) per South African biogeographic region from 1933 (30) to 2009 (00). Refer to Table 3.1 for site distribution within regions and regional codes.

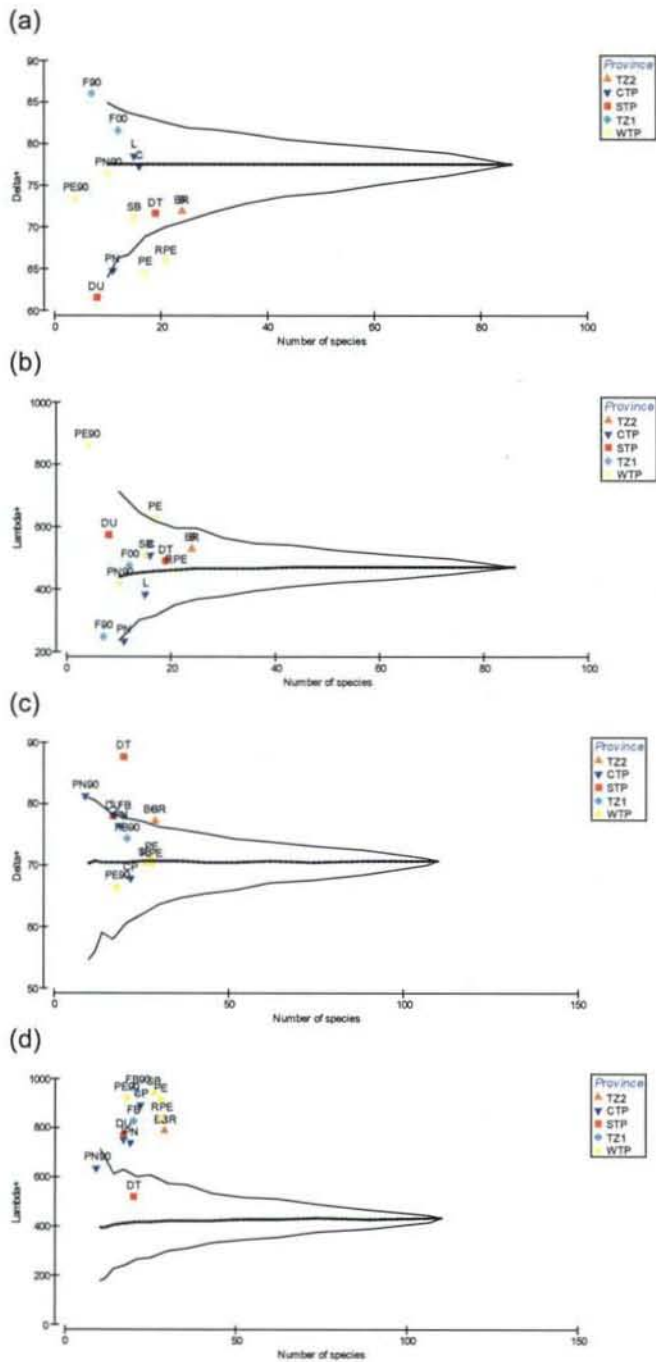


Figure 3.6a and c: Taxonomic distinctness ( $\Delta^+$ ) and 3.6b and d: Variation in taxonomic distinctness ( $\Delta^+$ ) at sites sampled in 1989-1992 and 2007-2009 as compared to historical baseline data (1933-1944) forming the funnel in each plot. Macroalgal (a and b) and macrofaunal (c and d) assemblages were analyzed separately. Refer to Table 3.1 for site and regional codes.

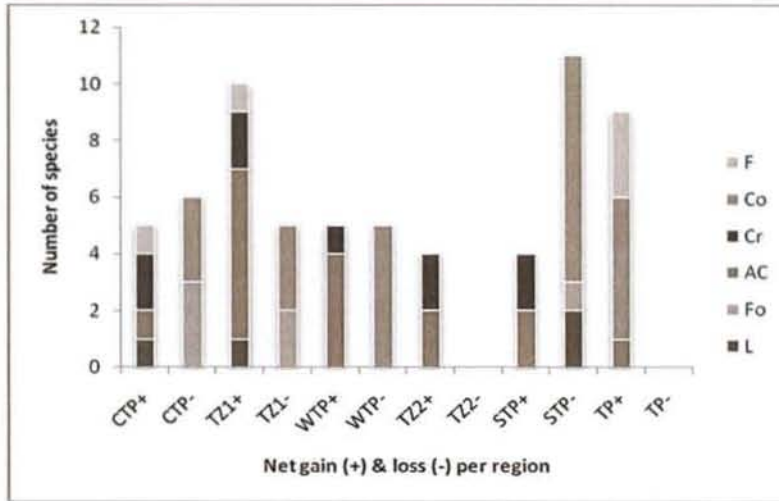


Figure 3.7: Net number of filamentous (F), corticated (Co), crustose (Cr), articulate calcified (AC), foliose (Fo) or leathery (L) macroalgal species appearing (+) and disappearing (-) from South African biogeographic regions and transition zones in-between from 1933 - 2009. Refer to Table 3.1 for site distribution within regions and regional codes.

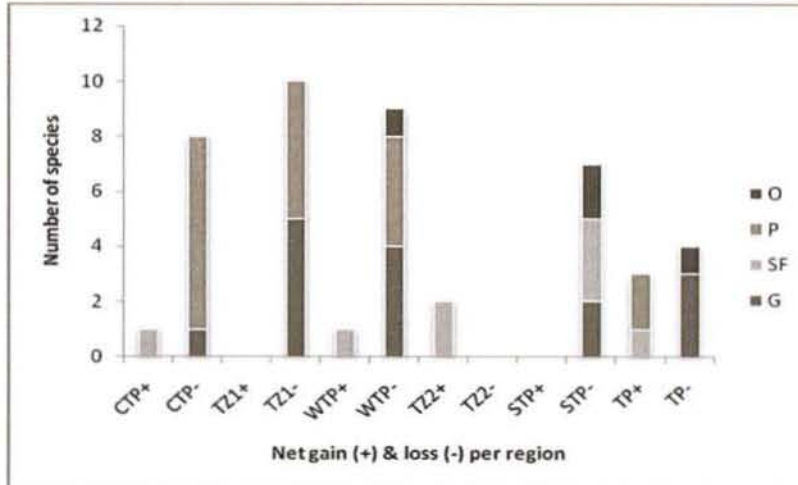


Figure 3.8: Net number of macrofaunal species within different functional feeding groups (omnivore (O), predator (P), suspension feeder (SF) or grazer (G)) appearing (+) and disappearing (-) from South African biogeographic regions and transition zones in-between from 1933 to 2009. Refer to Table 3.1 for site distribution within regions and regional codes.

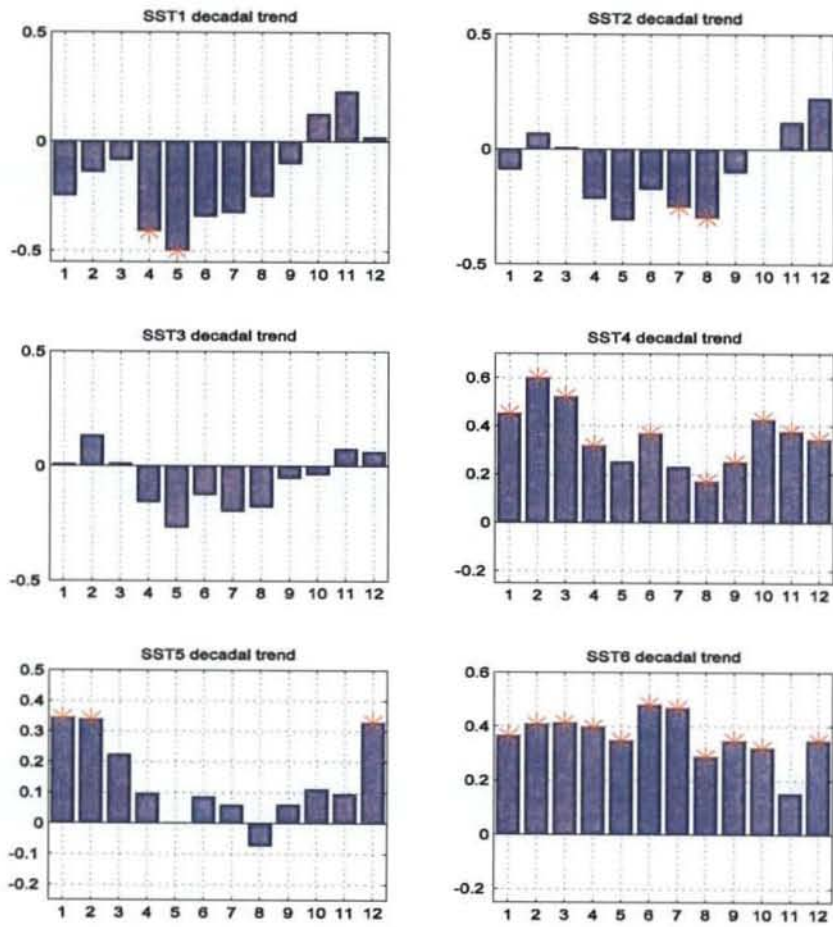


Figure 3.9: Linear trend ( $^{\circ}\text{C}$  per decade) for each month of the year derived using optimally interpolated (OI) sea surface temperature data series from 1982 to 2007. Regions assessed are the CTP (SST1), TZ1 and WTP (SST2), Port Elizabeth/Port Alfred (SST3), STP (SST4), Durban (SST5) and the Agulhas Current system (domain from  $36^{\circ}\text{S}$  to  $42^{\circ}\text{S}$  and  $10^{\circ}\text{E}$  to  $35^{\circ}\text{E}$ : SST6). Statistically significant trends are highlighted with a star symbol.

Table 3.1: South African exposed rocky intertidal sites sampled in 1933-44, 1989-9292 and 2007-2009. Regional allocation, GPS co-ordinates and site codes are indicated.

Site name	Region	Latitude	Longitude	Site code
Port Nolloth	CTP	29° 15' 10.9" S	16° 52' 01.4" E	PN
Lamberts Bay	CTP	32° 05' 46.9" S	18° 18' 05.7" E	L
Cape Point	CTP	34° 20' 49.0" S	18° 28' 54.0" E	CP
False Bay	TZ1	34° 14' 22.6" S	18° 28' 36.8" E	FB
Still Bay	WTP	34° 28' 28.3" S	21° 25' 43.0" E	SB
Reef Bay, Port Elizabeth	WTP	34° 01' 45.4" S	25° 41' 04.6" E	RPE
Humewood, Port Elizabeth	WTP	33° 58' 52.2" S	25° 39' 18.3" E	PE
Bat Cave Rocks, East London	TZ2	33° 00' 10.0" S	27° 56' 29.0" E	EBB
Bonza Bay, East London	TZ2	32° 59' 40.4" S	27° 56' 57.9" E	BCR
Tiger Rocks, Durban	STP	29° 59' 01.5" S	30° 58' 02.2" E	DT
Ballito Bay	TP	29° 32' 38.9" S	31° 12' 46.2" E	BB
Mission Rocks, Cape Vidal	TP	28° 07' 37.2" S	28° 07' 37.2" E	MR

Table 3.2: Summary of change (X) in taxonomic distinctness (TD ( $\Delta^+$ )) and variation in taxonomic distinctness (varTD ( $\Delta^+$ )) at sites sampled in 1989-1992 (90) and 2007-2009 (00) compared to historical baseline data (1933-1944). Refer to Table 3.1 for site and regional codes.

Region	Site	Sample period	Macroalgal Species		Macrofaunal Species	
			TD( $\Delta^+$ )	varTD( $\Delta^+$ )	TD( $\Delta^+$ )	varTD( $\Delta^+$ )
	PN	90				
	PN	00				X
	L	00				X
<b>CTP</b>	CP	00				X
	FB	90				X
<b>TZ1</b>	FB	00				X
	SB	90				X
	PE	90		X		X
	PE	00	X	X		X
<b>WTP</b>	RPE	00	X			X
	EBB	00			X	X
<b>TZ2</b>	BCR	00			X	X
	DT	00			X	
<b>STP</b>	DU	00				X



<i>Spongites yendoi</i>	4.49	0.99	49.84	<i>Oxystele sinensis</i>	9.64	9.97	30.05	<i>Chthamalus dentatus</i>	3.87	1.41	26.49
<i>Scutellastra granularis</i>	2.89	0.63	60.06	<i>Cymbula oculus</i>	7.95	8.52	40.09	<i>Spongites yendoi</i>	3.53	1.23	35.12
<i>Cladophora capensis</i>	1.50	0.44	65.36	<i>Bifurcaria</i>				<i>Scutellastra granularis</i>	2.71	1.36	41.74
<i>Oxystele variegata</i>	1.08	0.59	69.20	<i>brassicaeformis</i>	7.34	6.90	50.13	<i>Perna perna</i>	2.71	0.83	48.35
<i>Aulactinia reynaudi</i>	0.94	0.38	72.54	<i>Oxystele tigrina</i>	7.27	5.05	59.68	<i>Gelidium pristoides</i>	2.00	0.70	53.24
<i>Oxystele tigrina</i>	0.93	0.48	75.84	<i>Gibbula multicolor</i>	5.25	5.69	66.58	<i>Burnupena lagenaria</i>	1.33	0.81	56.48
<i>Ulva rigida</i>	0.87	0.40	78.91	<i>Spongites yendoi</i>	4.71	3.49	72.76	<i>Actinia equina</i>	1.31	0.82	59.69
<i>Chiton nigrovirescens</i>	0.87	0.21	81.98	<i>Oxystele variegata</i>	3.55	8.20	77.42	<i>Tetracita serrata</i>	1.23	0.56	62.68
<i>Cymbula granatina</i>	0.69	0.40	84.42	<i>Sarcothalia stiriata</i>	3.18	5.61	81.61	<i>Gibbula multicolor</i>	1.12	0.83	65.41
<i>Siphonaria capensis</i>	0.59	0.32	86.50	<i>Ralfsia verrucosa</i>	3.05	2.76	85.61	<i>Cymbula oculus</i>	0.95	0.59	67.74
<i>Burnupena lagenaria</i>	0.58	0.37	88.54	<i>Ulva rigida</i>	2.47	7.27	88.85	<i>Caulacanthus ustulatus</i>	0.82	0.40	69.75
<i>Caulacanthus ustulatus</i>	0.50	0.32	90.31	<i>Siphonaria capensis</i>	1.84	1.15	91.26	<i>Scutellastra longicosta</i>	0.73	0.40	71.52
								<i>Siphonaria serrata</i>	0.71	0.63	73.26
								<i>Onithochiton literatus</i>	0.71	0.59	74.98
								<i>Corallina officinalis</i>	0.67	0.31	76.62
								<i>Sargassum elegans</i>	0.60	0.49	78.08
								<i>Nucella dubia</i>	0.58	0.70	79.50
								<i>Jania intermedia</i>	0.55	0.32	80.84
								<i>Octomeris angulosa</i>	0.52	0.32	82.12
								<i>Laurencia natalensis</i>	0.51	0.40	83.37
								<i>Cymbula sanguinans</i>	0.51	0.32	84.61
								<i>Helcion dunkeri</i>	0.49	0.55	85.82
								<i>Oxystele sinensis</i>	0.44	0.40	86.89
								<i>Scutellastra barbara</i>	0.44	0.30	87.96
								<i>Hymeniacedon perlevis</i>	0.40	0.31	88.94
								<i>Bostrychia mixta</i>	0.37	0.32	89.86
								<i>Splachnidium rugosum</i>	0.35	0.32	90.71
<b>Upper-mid intertidal CTP (S=54.86)</b>				<b>Upper-mid intertidal TZ1 (S=83.84)</b>				<b>Upper-mid intertidal WTP (S=66.93)</b>			
<b>Characteristic Species</b>	<b>S<sub>i</sub></b>	<b>S<sub>i</sub>/SD(S<sub>i</sub>)</b>	<b>∑ S<sub>i</sub>%</b>	<b>Characteristic Species</b>	<b>S<sub>i</sub></b>	<b>S<sub>i</sub>/SD(S<sub>i</sub>)</b>	<b>∑ S<sub>i</sub>%</b>	<b>Characteristic Species</b>	<b>S<sub>i</sub></b>	<b>S<sub>i</sub>/SD(S<sub>i</sub>)</b>	<b>∑ S<sub>i</sub>%</b>
<i>Scutellastra granularis</i>	9.28	0.87	37.34	<i>Tetracita serrata</i>	17.41	12.79	20.77	<i>Scutellastra granularis</i>	4.93	1.89	13.36
<i>Oxystele variegata</i>	2.36	0.57	46.81	<i>Scutellastra granularis</i>	10.90	13.92	32.80	<i>Chthamalus dentatus</i>	4.36	0.63	25.17
<i>Champia lumbricalis</i>	2.26	0.24	55.90	<i>Oxystele variegata</i>	7.98	17.83	42.31	<i>Tetracita serrata</i>	4.07	1.26	36.20
<i>Helcion pectunculus</i>	2.02	0.55	64.03	<i>Spongites yendoi</i>	7.96	10.32	51.81	<i>Helcion pectunculus</i>	2.93	1.97	44.14
<i>Burnupena lagenaria</i>	1.94	0.48	71.85	<i>Octomeris angulosa</i>	6.54	4.29	59.60	<i>Siphonaria serrata</i>	2.32	1.08	50.42
<i>Porphyra capensis</i>	1.26	0.31	76.91	<i>Cymbula granatina</i>	6.17	16.16	66.97	<i>Acanthochiton garnoti</i>	1.98	0.66	55.77
<i>Siphonaria capensis</i>	1.07	0.31	81.22	<i>Siphonaria serrata</i>	5.92	9.62	74.03	<i>Gelidium pristoides</i>	1.79	0.69	60.62
<i>Aeodes orbitosa</i>	1.06	0.17	85.48	<i>Hymeniacedon perlevis</i>	5.31	1.15	80.37	<i>Spongites yendoi</i>	1.43	0.48	64.49
<i>Cymbula oculus</i>	0.86	0.24	88.95	<i>Gelidium pristoides</i>	4.61	11.83	85.88	<i>Burnupena lagenaria</i>	1.42	0.54	68.33
<i>Siphonaria serrata</i>	0.78	0.24	92.10	<i>Porphyra capensis</i>	2.88	7.95	89.31	<i>Caulacanthus ustulatus</i>	1.36	0.49	72.00
				<i>Cymbula oculus</i>	2.31	0.62	92.07	<i>Pomatoleios kraussii</i>	1.12	0.32	75.05

							<i>Burnupena cincta</i>	1.10	0.45	78.01
							<i>Siphonaria capensis</i>	1.06	0.66	80.89
							<i>Cymbula oculus</i>	1.00	0.58	83.60
							<i>Oxystele variegata</i>	0.72	0.47	85.56
							<i>Ulva rigida</i>	0.60	0.39	87.17
							<i>Bostrychia mixta</i>	0.58	0.24	88.74
							<i>Actinia equina</i>	0.57	0.39	90.29

Table 3.4: 2007-2009 characteristic species assemblages within the low, lower-mid and upper-mid intertidal along the southeast and east coast of South Africa as determined by Similarities Percentage (SIMPER) analyses (based on 90% of species contributing to Bray-Curtis average similarity ( $S$ )). Ranking ( $S_i$ ) is determined by the average contribution of each species to overall average similarity ( $S$ ).  $S_i/SD(S_i)$  is the ratio between the ranking ( $S_i$ ) and standard deviation ( $SD$ ) of  $S_i$ .  $\sum S_i\%$  represents the cumulative percentage contribution of each species to the overall similarity ( $S$ ). Analyses based on biomass data ( $\text{Kg/m}^2$ ). KEY: species shared between TZ2 and STP, STP and TP and all provinces. Refer to Table 3.1 for site and regional codes.

Low intertidal TZ2 (S=55.45)				Low intertidal STP (S=50.55)				Low intertidal TP (S=59.18)			
Characteristic species	$S_i$	$S_i/SD(S_i)$	$\sum S_i\%$	Characteristic species	$S_i$	$S_i/SD(S_i)$	$\sum S_i\%$	Characteristic species	$S_i$	$S_i/SD(S_i)$	$\sum S_i\%$
<i>Gunnarea capensis</i>	7.56	0.30	21.31	<i>Perna perna</i>	14.97	4.20	29.61	<i>Jania intermedia</i>	7.82	4.07	19.96
<i>Spongites yendoi</i>	4.91	0.91	35.16	<i>Ralfsia expansa</i>	7.24	3.48	43.94	<i>Hypnea spicifera</i>	4.12	1.23	30.47
<i>Ralfsia verrucosa</i>	4.17	0.90	46.92	<i>Ulva rigida</i>	3.89	0.90	51.62	<i>Spyridia hypnoides</i>	3.62	1.24	39.71
<i>Pomatoleios kraussii</i>	2.91	0.53	55.14	<i>Gunnarea capensis</i>	3.82	1.13	59.19	<i>Cheilosporum cultratum</i>	3.35	0.91	48.26
<i>Jania adhaerans</i>	2.85	0.53	63.16	<i>Gelidium foliaceum</i>	3.58	0.89	66.27	<i>Perna perna</i>	2.39	0.53	54.36
<i>Scutellastra cochlear</i>	2.73	0.90	70.87	<i>Hypnea spicifera</i>	3.53	0.91	73.25	<i>Sargassum elegans</i>	1.79	0.52	58.91
<i>Ulva rigida</i>	2.15	0.90	76.94	<i>Pomatoleios kraussii</i>	3.13	0.53	79.44	<i>Helcion dunkeri</i>	1.25	0.90	62.12
<i>Laurencia natalensis</i>	1.04	0.52	79.88	<i>Jania intermedia</i>	3.03	0.91	85.43	<i>Tetraclita squamosa</i>			
<i>Callithamnion stuposum</i>	1.00	0.39	82.70	<i>Jania verrucosa</i>	1.95	0.63	89.29	<i>rufotincta</i>	1.18	0.52	65.12
<i>Gibbula multicolor</i>	0.97	0.52	85.40	<i>Chthamalus dentatus</i>	0.83	0.50	90.94	<i>Hypnea rosea</i>	1.01	0.46	67.69
<i>Aulactinia reynaudi</i>	0.97	0.53	88.17					<i>Plocamium corallorhiza</i>	1.00	0.51	70.25
<i>Perna perna</i>	0.79	0.53	90.40					<i>Laurencia natalensis</i>	1.00	0.67	72.80
								<i>Gelidium foliaceum</i>	0.93	0.60	75.16
								<i>Jania verrucosa</i>	0.83	0.53	77.28
								<i>Ralfsia expansa</i>	0.82	0.41	79.38
								<i>Gelidium abbotiorum</i>	0.82	0.52	81.48

									<i>Arthrocardia flabellata</i>	0.82	0.37	83.57
									<i>Polyzonia elegans</i>	0.79	0.38	85.59
									<i>Padina boryana</i>	0.77	0.53	87.55
									<i>Oxystele tabularis</i>	0.69	0.52	90.11
<b>Lower-mid intertidal TZ2 (S=56.53)</b>				<b>Lower-mid intertidal STP (S=59.25)</b>				<b>Lower-mid intertidal TP (S=55.13)</b>				
<b>Characteristic species</b>	<b>S<sub>i</sub></b>	<b>S<sub>i</sub>/SD(S<sub>i</sub>)</b>	<b>∑ S<sub>i</sub>%</b>	<b>Characteristic Species</b>	<b>S<sub>i</sub></b>	<b>S<sub>i</sub>/SD(S<sub>i</sub>)</b>	<b>∑ S<sub>i</sub>%</b>	<b>Characteristic species</b>	<b>S<sub>i</sub></b>	<b>S<sub>i</sub>/SD(S<sub>i</sub>)</b>	<b>∑ S<sub>i</sub>%</b>	
<i>Caulacanthus ustulatus</i>	9.70	3.78	17.23	<i>Chthamalus dentatus</i>	9.43	3.79	15.92	<i>Jania intermedia</i>	9.58	1.18	31.80	
<i>Spongites yendoii</i>	8.13	8.17	31.65	<i>Octomeris angulosa</i>	9.05	3.17	31.20	<i>Perna perna</i>	1.89	0.50	38.08	
<i>Ulva rigida</i>	5.22	6.15	40.92	<i>Saccostrea cucullata</i>	8.62	1.39	45.74	<i>Zoanthus durbanensis</i>	1.82	0.51	44.12	
<i>Burnupena lagenaria</i>	5.13	4.42	50.03	<i>Ralfsia expansa</i>	7.58	3.36	58.54	<i>Pomatoleios kraussii</i>	1.76	0.50	49.97	
<i>Siphonaria capensis</i>	3.45	4.06	56.15	<i>Ulva rigida</i>	4.95	3.86	66.90	<i>Tetraclita serrata</i>	1.54	0.51	55.08	
<i>Gibbula multicolor</i>	2.67	7.14	60.88	<i>Tetraclita serrata</i>	3.36	0.90	72.56	<i>Ralfsia expansa</i>	1.47	0.51	59.95	
<i>Pomatoleios kraussii</i>	2.26	0.89	64.89	<i>Spongites yendoii</i>	2.84	0.75	77.35	<i>Octomeris angulosa</i>	1.39	0.51	64.57	
<i>Ralfsia spp.</i>	2.22	0.53	68.83	<i>Perna perna</i>	2.71	0.52	81.92	<i>Halimeda cuneata</i>	1.15	0.51	68.38	
<i>Jania adhaerans</i>	2.00	0.53	72.37	<i>Oxystele tabularis</i>	1.80	0.90	84.96	<i>Laurencia natalensis</i>	1.10	0.49	72.04	
<i>Siphonaria oculus</i>	1.92	1.79	75.79	<i>Morula granulata</i>	1.53	0.53	87.54	<i>Gelidium foliaceum</i>	0.99	0.43	75.34	
<i>Tetraclita serrata</i>	1.47	0.74	78.40	<i>Fissurella natalensis</i>	1.26	0.88	89.66	<i>Chthamalus dentatus</i>	0.93	0.51	78.42	
<i>Octomeris angulosa</i>	1.05	0.52	80.27	<i>Gunnarea capensis</i>	1.21	0.39	91.70	<i>Spyridia hypnoides</i>	0.93	0.38	81.49	
<i>Acanthochiton garnoti</i>	0.93	0.39	81.92					<i>Scutellastra pica</i>	0.59	0.38	83.44	
<i>Siphonaria serrata</i>	0.92	0.53	83.55					<i>Palythoe natalensis</i>	0.58	0.38	85.37	
<i>Aulactinia reynaudi</i>	0.92	0.53	85.18					<i>Oxystele tabularis</i>	0.55	0.39	87.20	
<i>Cellana capensis</i>	0.91	0.53	86.79					<i>Zoanthus natalensis</i>	0.40	0.15	88.54	
<i>Corallina spp</i>	0.86	0.39	88.32					<i>Dasya scoparia</i>	0.40	0.15	89.88	
<i>Laurencia natalensis</i>	0.83	0.39	89.80					<i>Ulva rigida</i>	0.11	0.40	91.21	
<i>Hymeniacedon perlevis</i>	0.34	0.79	91.19									
<b>Upper-mid intertidal TZ2 (S=51.16)</b>				<b>Upper-mid intertidal STP (S=76.30)</b>				<b>Upper-mid intertidal TP (S=57.22)</b>				
<b>Characteristic Species</b>	<b>S<sub>i</sub></b>	<b>S<sub>i</sub>/SD(S<sub>i</sub>)</b>	<b>∑ S<sub>i</sub>%</b>	<b>Characteristic Species</b>	<b>S<sub>i</sub></b>	<b>S<sub>i</sub>/SD(S<sub>i</sub>)</b>	<b>∑ S<sub>i</sub>%</b>	<b>Characteristic Species</b>	<b>S<sub>i</sub></b>	<b>S<sub>i</sub>/SD(S<sub>i</sub>)</b>	<b>∑ S<sub>i</sub>%</b>	
<i>Tetraclita serrata</i>	12.3	4.52	24.03	<i>Saccostrea cucullata</i>	23.26	5.96	30.49	<i>Saccostrea cucullata</i>	18.6	3.20	32.66	
<i>Helcion pectunculus</i>	4.71	7.00	33.24	<i>Perna perna</i>	19.56	7.00	56.12	<i>Tetraclita serrata</i>	12.5	6.08	54.57	
<i>Siphonaria serrata</i>	4.04	7.64	41.14	<i>Chthamalus dentatus</i>	13.06	9.71	73.25	<i>Chthamalus dentatus</i>	9.25	1.72	70.74	
<i>Spongites yendoii</i>	4.04	1.18	49.05	<i>Tetraclita serrata</i>	9.93	10.83	86.26	<i>Siphonaria serrata</i>	4.28	5.07	78.22	
<i>Arthrocardia flabellata</i>	3.21	0.91	55.32	<i>Afrolittorina africana</i>	1.67	0.91	88.45	<i>Tetraclita squamosa</i>				
<i>Chthamalus dentatus</i>	2.62	1.15	60.45	<i>Helcion pectunculus</i>	0.17	1.61	90.57	<i>rufotincta</i>	3.85	0.53	84.95	
<i>Nucella dubia</i>	2.22	1.25	64.79					<i>Gelidium foliaceum</i>	2.16	0.53	88.72	
<i>Cymbula oculus</i>	1.97	0.88	68.64					<i>Bryopsis flanaganii</i>	1.92	0.51	92.07	
<i>Gelidium foliaceum</i>	1.70	0.53	71.96									
<i>Helcion concolor</i>	1.39	0.65	74.68									
<i>Ulva rigida</i>	1.25	0.53	77.13									

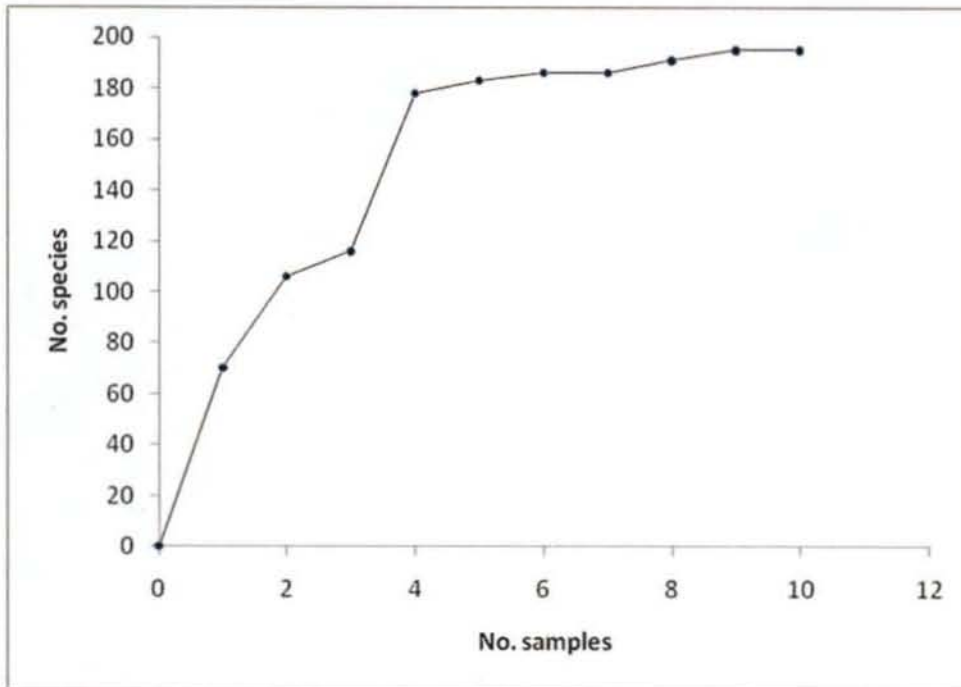
<i>Siphonaria oculus</i>	1.21	1.23	79.49							
<i>Oxystele variegata</i>	1.21	0.53	81.85							
<i>Oxystele tigrina</i>	1.19	0.51	84.18							
<i>Mytilus galloprovincialis</i>	0.95	0.52	86.05							
<i>Patirella exigua</i>	0.95	0.53	87.91							
<i>Burnupena lagenaria</i>	0.84	0.39	89.54							
<i>Cheilosporum cultratum</i>	0.80	0.26	91.10							

Table 3.5: Shared characteristic species between biogeographical regions for the South African coast (2007-2009). Refer to Table 3.1 for regional codes.

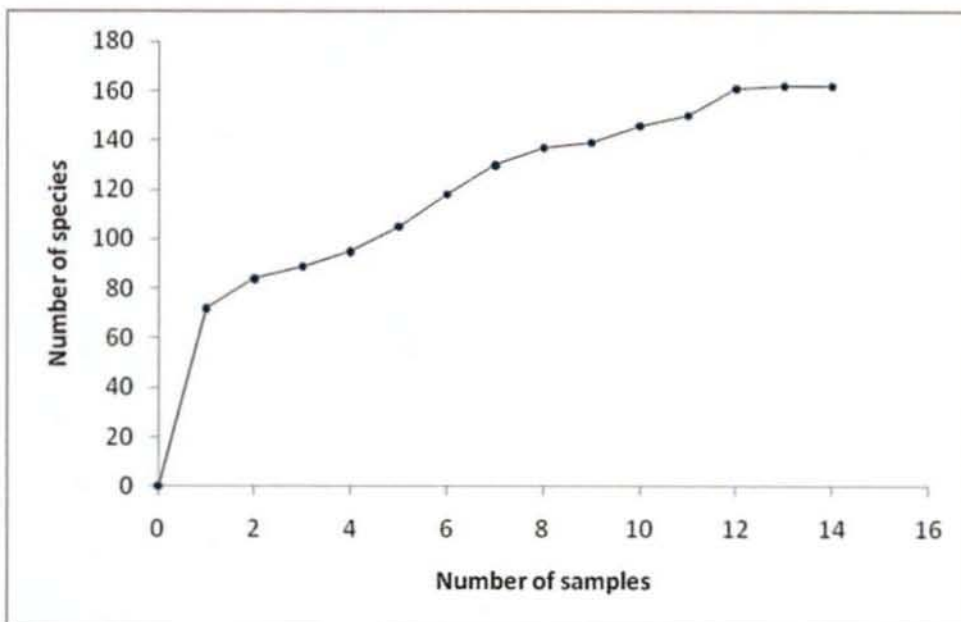
Regional Comparison	No. Shared Species / Intertidal Zone			Total No. Species
	Low	Lower-mid	Upper-mid	
CTP/TZ1	3	5	1	9
TZ1/WTP	4	3	2	9
CTP/WTP	2	1	4	7
CTP/TZ1/WTP	3	1	2	6
WTP/TZ2	4	8	9	21
TZ2/STP	3	1	1	5
STP/TP	5	4	1	10
TZ2/STP/TP	1	3	2	6

**Appendix C(i): Assessment of sampling representivity (species accumulation curves) for each sampling period.**

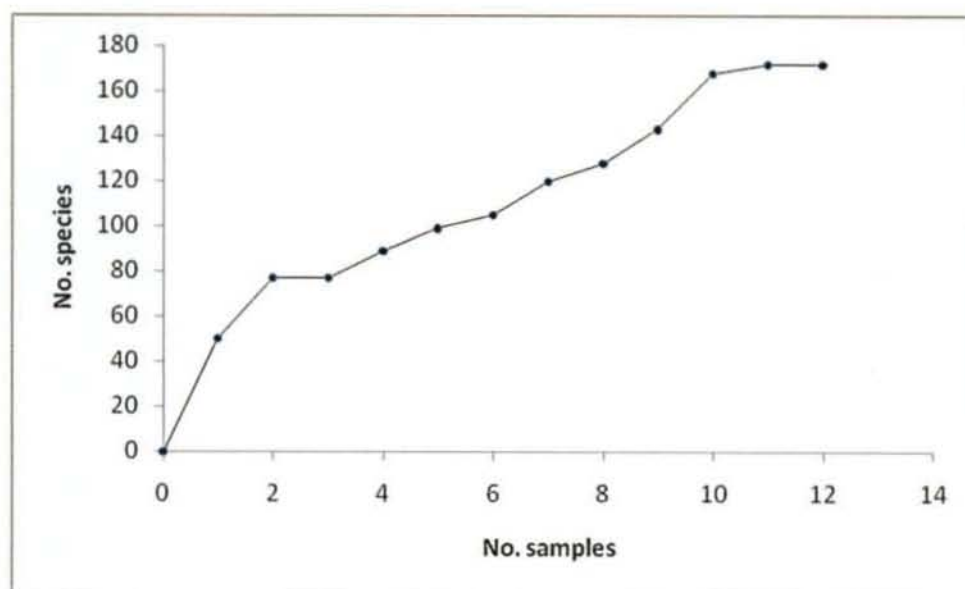
(a) 1933-1944



(b) 1989-1992



(c) 2007-2009



**Appendix C(ii): Assessment of differences in variance between 1989-1992 and 2007-2009 sampling data.**

Intertidal level	Site*	Variance (s): total biomass (Kg/m <sup>2</sup> ) values				F-crit (F <sub>0.05,9,9</sub> )	F	P < 0.05	Pooled variance (s <sub>p</sub> )
		1990	2000	ln1990	ln2000				
Low	PN	0.29	1.83	0.001	0.001	6.23	4.03	0.011	X
	FB	0.73	0.21	X	X	3.53	4.03	0.073	0.521
	PE	0.35	3.09	0.011	0.019	8.61	4.03	0.003	X
	BB	3.19	0.09	X	X	0.03	4.03	1.999	0.182
	MR	0.08	0.06	X	X	1.17	4.03	0.811	0.008
Lower-mid	PN	2.64	0.91	X	X	2.89	4.03	0.129	0.197
	FB	1.28	0.48	X	X	3.15	4.03	0.102	0.094
	PE	0.51	2.02	X	X	3.96	4.03	0.052	0.141
	BB	1.24	0.32	X	X	3.82	4.03	0.058	0.087
	MR	0.39	0.06	X	X	0.16	4.03	1.987	0.025
Upper-mid	PN	6.02	0.51	0.042	0.113	6.23	4.03	0.001	X
	FB	0.14	0.07	X	X	3.53	4.03	0.288	0.012
	PE	0.03	0.31	0.001	0.003	8.61	4.03	0.004	X
	BB	0.67	1.55	X	X	0.03	4.03	0.228	0.123
	MR	0.11	0.42	X	X	1.17	4.03	1.945	0.022

\*For site codes refer to Table 3.1

**Appendix C(iii): Biomass (Kg/m<sup>2</sup>) based hierarchical cluster analyses and non-metric MDS ordinations.**

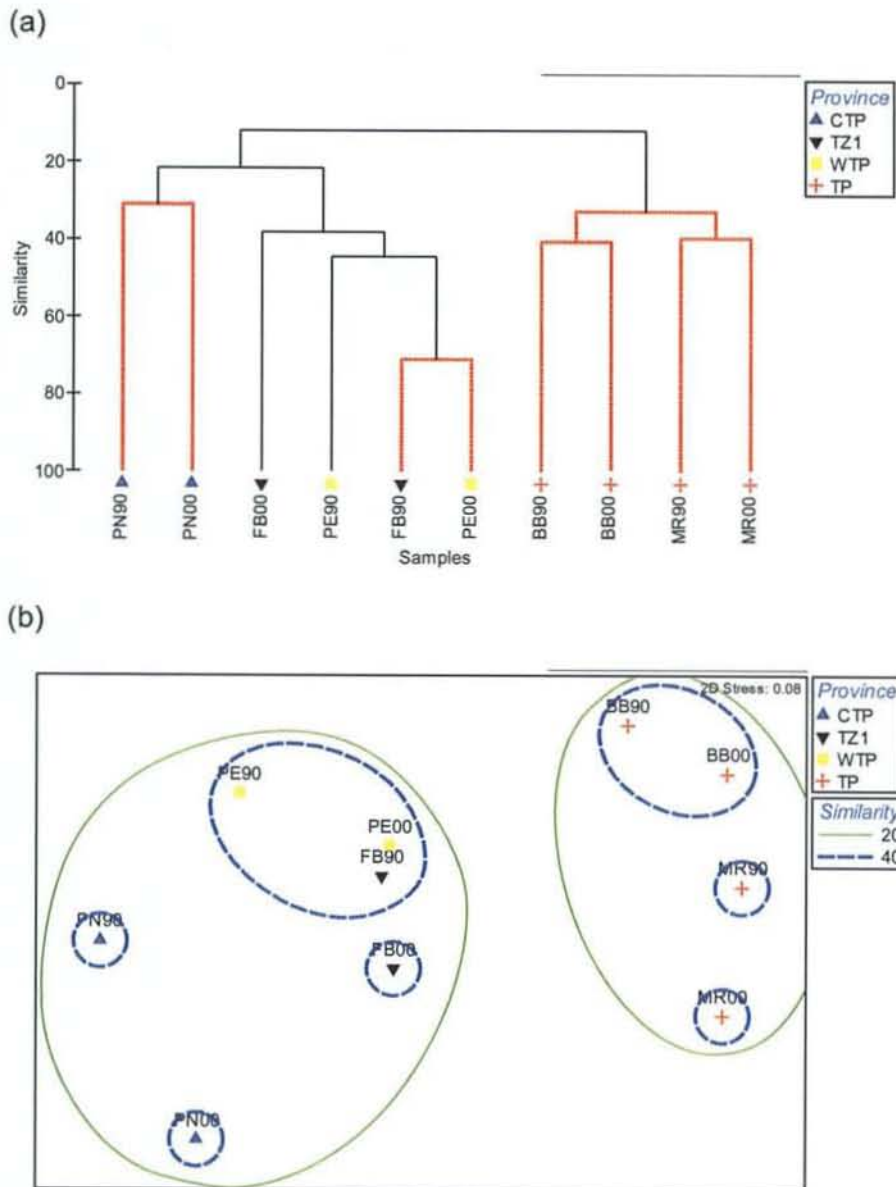


Figure C3.1a: Based on the Bray-Curtis similarity index, data classification by hierarchical cluster analysis (SIMPROF: significant differences between sample groups indicated by black solid lines ( $P < 0.05$ )) and C3.2b: Non-metric MDS ordination (2D stress: 0.08) for low-intertidal sites sampled in 1989-1992 (90) and 2007-2009 (00). Analyses based on biomass data (Kg/m<sup>2</sup>). ANOSIM:  $R=0.83$ ;  $P=0.001$ . Refer to Table 3.1 for site and regional codes.

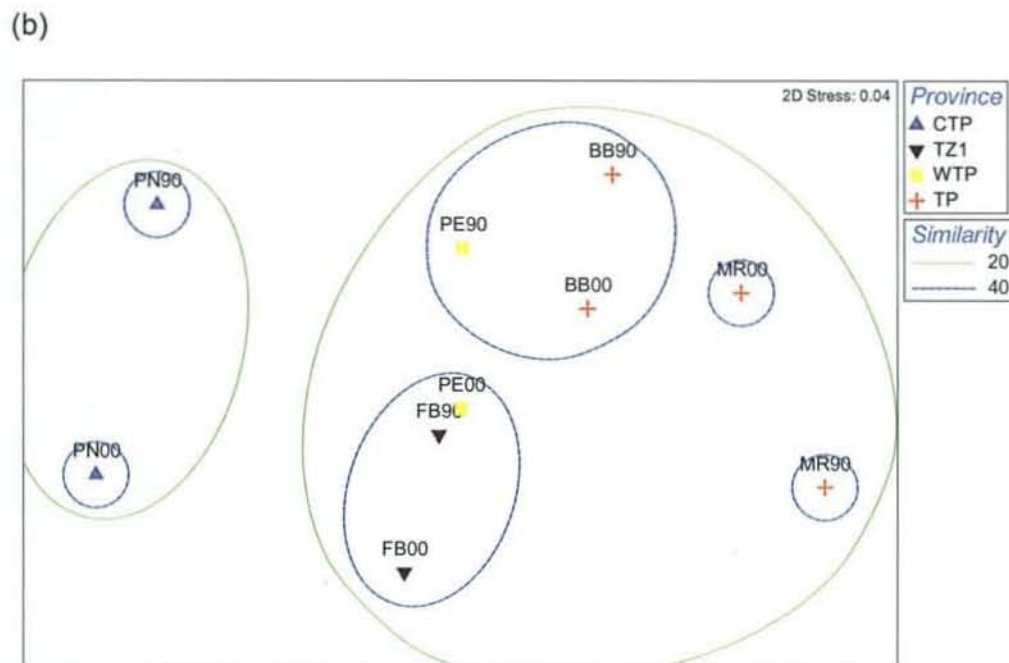
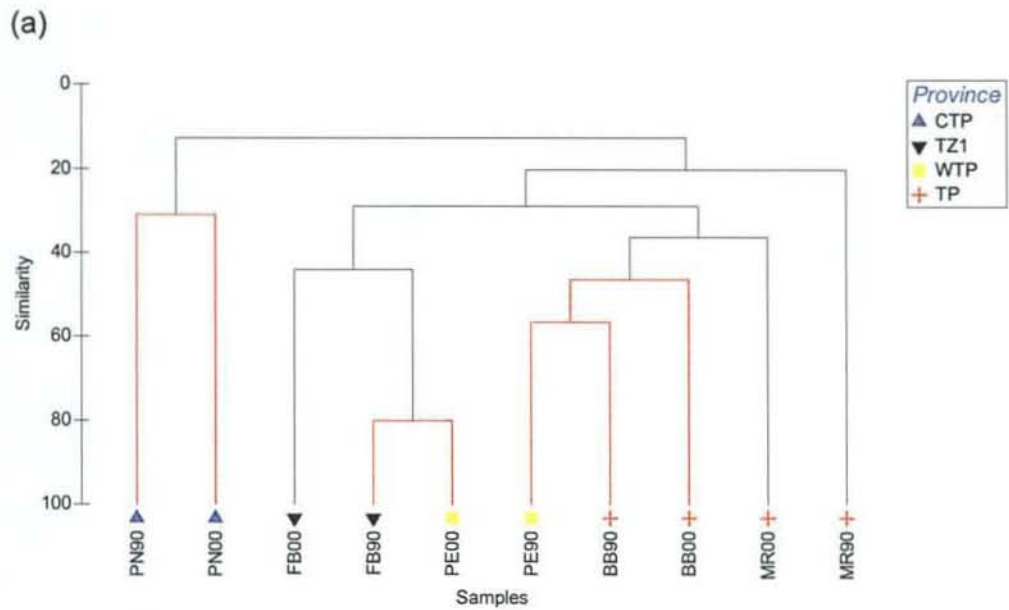


Figure C3.2a: Based on the Bray-Curtis similarity index, data classification by hierarchical cluster analysis (SIMPROF: significant differences between sample groups indicated by black solid lines ( $P < 0.05$ )) and C3.2b: Non-metric MDS ordination (2D stress: 0.04) for lower-mid intertidal sites sampled in 1989-1992 (90) and 2007-2009 (00). Analyses based on biomass data ( $\text{Kg/m}^2$ ). ANOSIM:  $R=0.61$ ;  $P=0.001$ . Refer to Table 3.1 for site and regional codes.

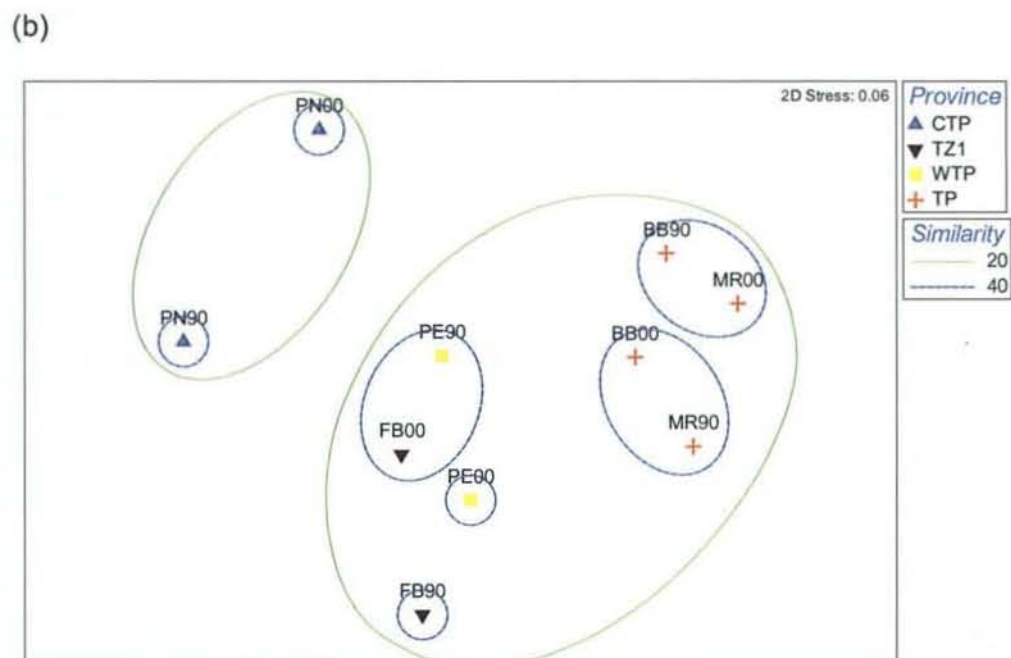
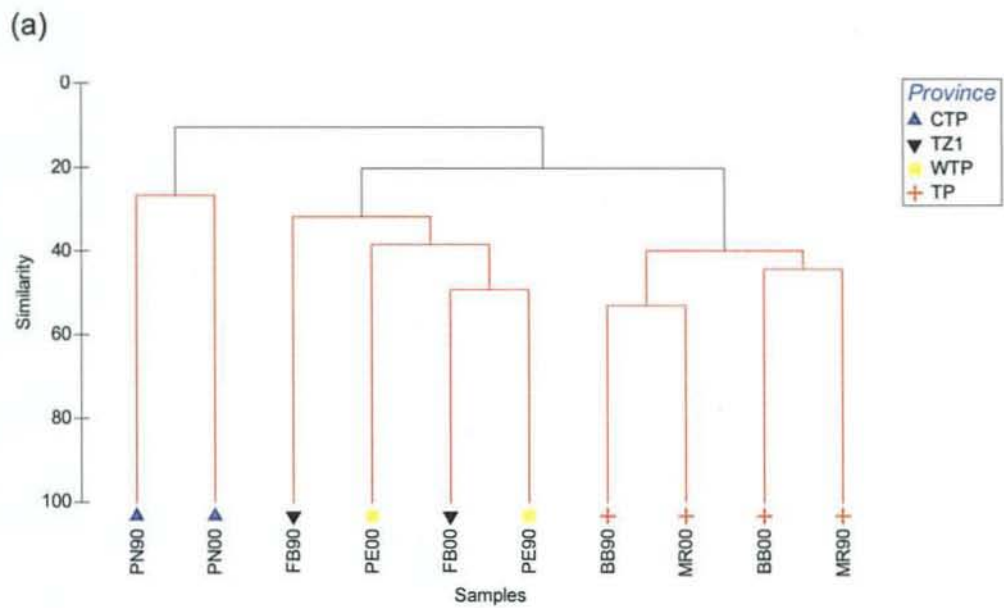
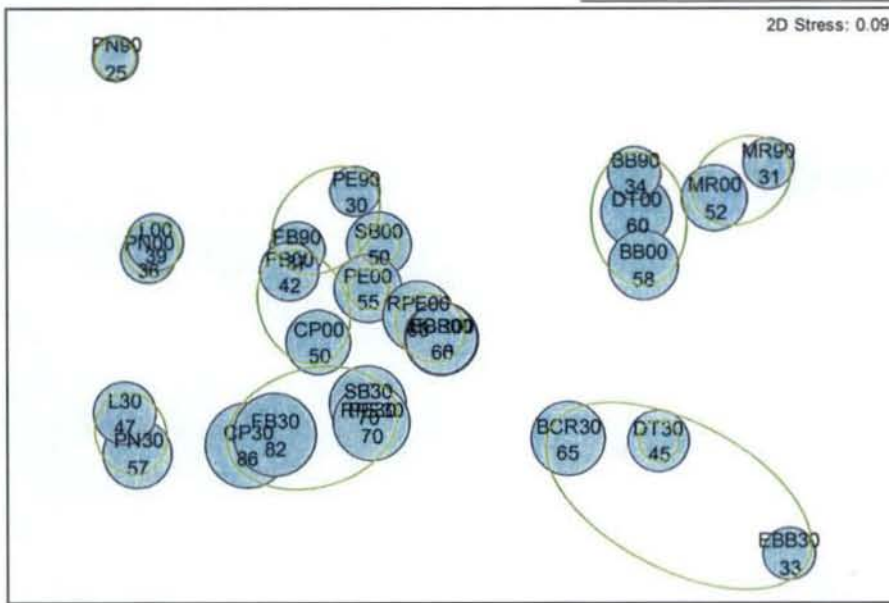


Figure C3.3a: Based on the Bray-Curtis similarity index, data classification by hierarchical cluster analysis (SIMPROF: significant differences between sample groups indicated by black solid lines ( $P < 0.05$ )) and C3.2b: Non-metric MDS ordination (2D stress: 0.06) for upper-intertidal sites sampled in 1989-1992 (90) and 2007-2009 (00). Analyses based on biomass data ( $\text{Kg/m}^2$ ). ANOSIM:  $R=0.87$ ;  $P=0.001$ . Refer to Table 3.1 for site and regional codes.

## Appendix C(iv):



Appendix C(iv): species richness values per site for 1933-1944 (30), 1989-1992 (90) and 2007-2009 (00) sampling periods, as overlaid on the non-metric MDS ordination generated from species assemblage comparisons based on the Bray-Curtis similarity index. Refer to Table 3.1 for site codes.

## Chapter 4: Times of change: a biogeographic range shift in False Bay, South Africa.

### Introduction

Based on local climatic regimes and resultant species suites, the South African coastline has been divided into distinct biogeographic regions, separated by transition zones (Emanuel *et al.* 1992; Bustamante and Branch 1996b; Stegegna and Bolton 2002; Lombard 2004; Sink *et al.* 2005). At 900 km<sup>2</sup>, False Bay is the largest bay present along the coast (Grundlingh and Largier 1991). It forms part of a transition zone (TZ1) separating the cool- and warm-temperate regions of the west and south coast respectively.

As a result, the Bay supports a rich diversity of marine life. This incorporates both warm- and cool-temperate species components (Griffiths and Branch 1991) many of which are located at their southeastern or southwestern distributional extremes respectively (Eyre 1939; Stephenson and Stephenson 1972; McQuaid and Branch 1984; 1985; Bolton *et al.* 1991; Emanuel *et al.* 1992; Awad *et al.* 2002). Additionally, approximately 60.9% of the species within the Bay are endemic to South Africa (Bolton *et al.* 1991; Griffiths and Branch 1991; Awad *et al.* 2002). There are a number of peer-reviewed publications that describe oceanographic conditions within the Bay in some detail (Grundlingh and Largier 1991; Spargo 1991).

Several temporal shifts in species composition have been qualitatively documented within the Bay over time. Day (1968) described the presence of *Ecklonia maxima*, which was previously recorded as absent by Eyre (1939). This cool-temperate laminarian has since persisted into contemporary survey periods in a limited number

of locations along the Bay (Bolton and Anderson 1987). The native warm-water adapted mussel, *Perna perna*, albeit at the southwestern most extreme of its South African distribution (Van Erkom Shcurink and Griffiths 1990), was described as 'dense and extensive' by Eyre *et al.* (1939) and as 'abundant' by Day (1968). However, the relatively cool-water adapted, Mediterranean mussel, *Mytilus galloprovincialis* was noted as a 'potentially dominant species within the Bay' by several authors who worked in the area subsequent to its arrival and spread along the South African coast *circa* 1979 (Chapter 2: Figure 2.6; Appendix A). Such observations suggest that the intertidal biota within the Bay has been changing over time.

Interestingly, through the use of mathematical modelling, Roy (2001) identified that transition zones will be particularly vulnerable to climate-driven temporal change within species assemblages, due to the convergence of high numbers of species that are located at the distributional limits of their biogeographic range. Globally, a number of shifts in the distributional ranges of intertidal species have been detected, the outcome being species loss from, and addition into, species assemblages in concert with shifting temperature trends and the arrival of bioinvasive species (Helmuth *et al.* 2006; Mieszkowska 2009).

Following a regional analysis, spanning a period of 76 years, significant changes within intertidal species assemblages located in False Bay were evident (Chapter 3). The increasing similarity with assemblages located in the adjacent cool- and warm-temperate regions was in concert with regional cooling and the arrival of *M. galloprovincialis*. The introduced mussel was the most characteristic species within

contemporary assemblages, whereas a major distinction between historic and contemporary species assemblages was the apparent disappearance of the native mussel, *P. perna* (Chapter 3).

The focus of this study is to (i) quantitatively document significant change in macroalgal and macrofaunal assemblages located within the Bay at a finer resolution of sampling (over 50 km) and (ii) establish the spatial extent of the respective appearance and disappearance of *M. galloprovincialis* and *P. perna*, for comparison with regional findings. This will be achieved through comparisons of archive and contemporary data sets spanning a 25 year period. Evidence pertaining to local patterns of bioinvasion and climate change driven temperature shifts will be considered in parallel with detected changes in species composition.

## **Materials and methods**

### **Biological sampling design**

Historical (1987) and contemporary (2007 to 2009) biodiversity data collected from low and mid-intertidal sites within the False Bay (TZ1) transition zone (Chapter 3: Figure 3.1) were compared. Ten sites (Table 4.1; Figure 4.1) were matched across sampling periods, using a combination of GPS co-ordinates, permanent shore markers and photographic evidence. Bi-monthly surveys were conducted at all sites from January to December in 2008 and 2009, in order to record mussel abundance for the introduced mussel, *Mytilus galloprovincialis* and native mussel, *Perna perna*. Twenty 1 m<sup>2</sup> quadrats were randomly placed within the low- and mid-intertidal at each site and numbers of mussels recorded. Counts were converted using wet biomass values obtained for each species, per site. The sampling protocol for

species assemblages was identical to the design used for the regional study, across both sampling periods (refer to Chapter 3 for details). Wet biomass values were calculated for both sampling periods using a destructive sampling method used by Bustamante and Branch (1996a), described in Chapter 3

## **Data analysis**

### ***Spatio-temporal changes in species assemblages***

Multi-site comparisons of species assemblages across both sampling periods were based on biomass data ( $\text{Kg/m}^2$ ). The same analyses were performed as per Chapter 3. The Bray-Curtis index was applied. Data were classified using hierarchical agglomerative cluster analysis, data structure was tested using SIMPROF ( $P < 0.05$ ), a graphic representation of the classified data was generated using a non-metric multi dimensional scaling (MDS) ordination. Analysis of similarities (ANOSIM:  $P < 0.05$ ) tested the significance of detected differences between groups compared. Similarities percentage (SIMPER) calculated the average Bray-Curtis similarity (%S) and dissimilarity (%D) between groups. SIMPER was used to detect the species responsible for both similarities (characteristic species) and dissimilarities (distinguishing species). For a full description of each test, refer to chapter 3.

All multivariate analyses were completed using the Plymouth Routines in Multivariate Ecological Research (PRIMER) version 6.1 (Clarke and Warwick 1994).

### ***Mussel Biomass***

The mean biomass ( $\text{Kg/m}^2$ ) of each mussel species was calculated ( $\pm$  SD) for each site, per sampling period.

## ***Species-level analyses***

Species level analyses were performed as per Chapter 3 for thermotolerance of species, algal structure and functional feeding groups.

### **Data considerations**

Biases in sampling effort could lead to significant variation in species richness recorded per sampling period (Gotelli and Colwell 2001; Ugland et al. 2003; Colwell *et al.* 2004). Although survey sites, methods and sampling months were identical, it was important to establish if sampling was adequate across time periods to allow for valid species assemblage comparisons (refer to Chapter 3). Thus an assessment of sampling representivity, based on species richness, was required (Gotelli and Colwell 2001; Ugland et al. 2003; Colwell *et al.* 2004). Species accumulation curves were calculated for each sampling period, based on successive pooling of samples (Appendix D). As the intertidal surveys were focused on highly visible macro components of assemblages, estimates of total species richness were not required (Ugland *et al.* 2004) and an asymptote was reached within each sampling period (Appendix D).

## **Results**

### **Temporal site comparisons**

Significant changes in species assemblages were detected at rocky intertidal sites located within the False Bay (TZ1) transition zone between 1987 and 2009. Hierarchical cluster analysis revealed that sites sampled in 2007-2009 were classified separately (formed discreet groups) from sites sampled in 1987 in the low and mid intertidal (Figure 4.1a; 4.2a). Multi-dimensional scaling (MDS) ordination paralleled hierarchical cluster analysis for both intertidal levels, yielding the same

assemblages with low stress (0.12-0.18) indicative of strong grouping (Figure 4.1b; 4.2b). Analysis of similarities (ANOSIM) indicated that detected changes in species assemblages across the different sampling periods were significantly different within the low-intertidal ( $R=0.43$ ,  $P=0.001$ ) and mid-intertidal ( $R=0.63$ ,  $P=0.001$ ). Testing the data structure (species composition) for each sample site subset corresponding to a branch of the dendrogram (SIMPROF) revealed that the separate groups formed within the cluster analysis (4.1a; 4.2a) were not significantly different ( $P>0.05$ ).

In the low-intertidal, Similarities Percentage (SIMPER) analyses revealed dissimilarity between the two sampling periods was 61.26% in the low-intertidal and 67.96% in the mid-intertidal. There was an overall decrease in species richness at both intertidal levels, with the net number of cool-water adapted species increasing at all sites between 1987 and 2009 (Figure 4.3). Conversely, there was a net loss of warm-water adapted and cosmopolitan species at both intertidal levels over the same time period (Figure 4.3). Corticated and foliose algal species were lost from species assemblages located at both intertidal levels between 1987 and 2009 (Figure 4.5), whereas in the low-intertidal, there was a net gain in leathery algal species (Figure 4.5). The number of suspension feeders increased between 1987 and 2009, at both intertidal levels, with a reciprocal decrease in grazer numbers (Figure 4.6).

### **Characteristic and distinguishing species**

According to SIMPER, similarity values (S) of all sites increased in both the low- and mid-intertidal between 1987 and 2008-2009 (Table 4.2). This indicated that species assemblages sampled across sites in 2007-2009 were more homogenous when compared to the 1987 sampling period (Table 4.2). Characteristic species within

each intertidal zone changed between 1987 and 2007-2009. The cool-water adapted bioinvasive mussel, *Mytilus galloprovincialis*, increased in biomass, which resulted in higher  $S_i/SD(S_i)$  values and therefore strengthened its ranking as the most characteristic species within the low- and mid-intertidal (Table 4.2). Four additional species of suspension feeder, the polychaete, *Gunnarea capensis*, and three barnacles, *Chthamalus dentatus*, *Notomegabalanus algicola* and *Octomeris angulosa*, ranked higher due to increased  $S_i/SD(S_i)$  values, indicating their increased dominance within both zones by 2007-2009 (Table 4.2). By 2007-2009 the cool-temperate adapted laminarian, *Ecklonia maxima*, became more consistent across low-intertidal sites, thus achieving a higher characteristic ranking. However, the warm-water mussel, *Perna perna*, was no longer characteristic within either intertidal level (Table 4.2). Mussel species accounted for the majority of dissimilarity in community assemblages across time in both the low- and mid-intertidal. The two key distinguishing species were *M. galloprovincialis* and *P. perna* (Table 4.3).

### **Changes to mussel biomass**

Average biomass of *M. galloprovincialis* increased between 1987 and 2008-2009, from 2.9 to 5.9 Kg/m<sup>2</sup> in the low-intertidal (Figure 4.7a and b) and from 1.4 to 10.9 kg/m<sup>2</sup> in the mid-intertidal (Figure 4.7e and f). Conversely, over the same time period, *P. perna* disappeared completely from all six sites where it had been previously recorded in both the low- and mid-intertidal (Figure 4.7c, d, g and h). The average biomass of *P. perna* decreased enormously at the one site (Baileys Cottage) where it was still present, declining from 2.7 to 0.2 Kg/m<sup>2</sup> in the low-intertidal and 1.3 to 0.09 Kg/m<sup>2</sup> in the mid-intertidal (Figure 4.7c, d, g and h). Between 2008 and 2009, additional bi-monthly surveys monitoring mussel biomass revealed these changes to be persistent and the biomass of *P. perna* also declined

over the year from 0.21 to 0.17 kg/m<sup>2</sup>. The remaining population at Bailey's Cottage were composed of large adults, with no evidence of recruitment (personal observation), suggesting that this is a relict population undergoing slow decline and is likely to disappear completely within the next few years.

## **Discussion**

Results indicate species assemblages at sites sampled within the False Bay (TZ1) transition zone have significantly changed over the past 25 years. Despite the higher site resolution, all observed changes are in strong agreement with the results of the regional analyses (Chapter 3). A species range contraction and changes in species assemblage composition will be discussed with specific reference to correlations with trends in local sea surface temperature and patterns of bioinvasion.

### **Range contraction**

The disappearance of the warm-water adapted mussel, *Perna perna*, from all sites sampled in 2007-2009, with the exception of the relict population at Bailey's Cottage, represents a range contraction of 50 km over a 25 year period (an average rate of 2 km per year). This comprises a substantive range contraction from its southern most distributional limit in South Africa.

In the UK, Mieszkowska *et al.* (2005) reported a 120 km range contraction in a cold-water adapted species, *Alaria esculenta*, over a 14 year period, representing an average contraction rate of 8.5 km per year. This is currently over four times higher than the range contraction reported for South Africa. However, qualitative investigation revealed that dense *P. perna* populations were only evident in intertidal zones located over 350 km northeast of False Bay, well within the warm-temperate

biogeographic region (personal observation). This merits further stochastic quantification of *P. perna* populations along its full distributional range, in order to establish the full spatial extent and persistence of the range contraction.

### **The synergistic effect of a bioinvader and climate change**

Bioinvasive species are a well-known threat to the biodiversity and ecological functioning of marine ecosystems, potentially displacing native equivalents within community assemblages (Seed and Suchanek 1992; Cohen and Carlton 1993; Carlton 1996; 2009; Mack *et al.* 2000; Grosholz 2003; Occhipinti-Ambrogi 2007). *Mytilus galloprovincialis* is one of three bioinvaders known from rocky intertidal habitats along the coasts of South Africa (Chapter 2: Figure 2.6; Appendix A). As an eco-system engineer, dominant space occupier and provider of biogenic habitat with substantive competitive advantages, *M. galloprovincialis* has the ability to significantly modify environments (Van Erkom Schurink and Griffiths 1990; 1991; 1992; 1993; Hammond and Griffiths 2004; Robinson *et al.* 2007; Wallentinus and Nyberg 2007). It is highly likely that the observed range recession, reduced macro-species richness, changes in species composition and increasing similarity or 'homogenization' of species assemblages at sites within False Bay are linked to the arrival and spread of this dominant introduced species. Based on increasing biomass and an increased presence across all sites it has become the most dominant species within the low- and mid-intertidal of this transition zone, since first reports of its arrival post-1979. Its dominant presence supports early predictions that it would substantively modify intertidal communities (McQuaid and Branch 1984; 1985; McQuaid *et al.* 1985; Van Erkom-Schurink and Griffiths 1990; Griffiths and Branch 1991).

Based on 4 km resolution AVHRR satellite data collected between 1987 and 2007 (Chapter 1: Figure 1.2), there is good evidence of an overall decadal cooling trend of approximately  $-0.5$  to  $-0.8^{\circ}\text{C}$  along the west coast, and specifically within False Bay (Figure 4.8a). Linear trend optimally interpolated (OI) SST data analyzed for a location within the Bay indicated a similar trend (Figure 4.8b). The increasing trend in upwelling intensity, frequency and season length, predicted (Bakun 1990; Lutjeharms and Stockton 1991; Scavia *et al.* 2002) and reported (Reason and Rouault 2005; Trenberth *et al.* 2007; Rouault *et al.* 2009) for the Benguela region over the past four decades, is highly likely to be driving the observed near-shore cooling (Rouault *et al.* 2009).

In Northern-hemispheric regions, range contractions of cool-water species and expansions of warm-water species are coupled with increases in warm-water adapted species and reciprocal decreases in cool-water adapted species (Weslawski *et al.* 1997, Sagarin *et al.* 1999, Zacherl *et al.* 2003, Berge *et al.* 2005, Rivadeneira and Fernandez, 2005). In contrast, the range contraction reported here is a possible response to cooling waters and is accompanied by corresponding increases in cool-water and decreases in warm-water adapted species within intertidal species assemblages. For example, the cool-water adapted laminarian, *Ecklonia maxima*, appears more consistently within low-intertidal assemblages within the Bay, post surveys conducted by Bolton and Anderson (1987). The successful dominance of *M. galloprovincialis* within the Bay may be linked to its ability to adapt to local decreases in immersion temperatures.

Competitive interactions between species along the coast of South Africa that, in themselves regulate species assemblages and distribution (Connell 1972), are regulated by a range of environmental factors, specifically sea surface (immersion) temperature, operating over a variety of temporal and spatial scales (McQuaid and Branch 1984; 1985; Bustamante and Branch 1996a; Bustamante *et al.* 1997; Steffani and Branch 2003a; 2003b, Braby and Somero 2006; Rius and McQuaid 2006). Global climate change scenarios imply temporal shifts in the underlying signals influencing temperature, which have now been linked to measurable range-related shifts between competing species within marine communities (Sagarin *et al.* 1999; Zacherl *et al.* 2003; Mieszkowska *et al.* 2005, 2006, 2007; 2009; Helmuth *et al.* 2006; Lima *et al.* 2006; Moore *et al.* 2007; Petes *et al.* 2007; Jones *et al.* 2009). In addition, it is predicted that climate change will facilitate the arrival, spread and dominance of bioinvasive species (Occhipinti-Ambrogi and Savini 2003; Stachowicz *et al.* 2003; Occhipinti-Ambrogi 2007; Carlton 2009; Drinkwater *et al.* 2009), which has been observed within intertidal systems in Ireland (Simkanin *et al.* 2005), California (Braby and Somero 2006a) and New Zealand (Petes *et al.* 2007).

As *M. galloprovincialis* and *P. perna* occupy the same ecological niche, the competitive relationship between *these two mussel species* has been investigated from a number of experimental perspectives, with several studies indicating that *M. galloprovincialis* has the potential to outcompete *P. perna* (Griffiths *et al.* 1992; Hockey and Van Erkom Schurink 1992; Van Erkom Schurink and Griffiths 1992; Zardi *et al.* 2007). Experiments demonstrate that *M. galloprovincialis* had a consistently large scope for growth over a range of immersion and emersion temperatures. In contrast the scope for growth in *P. perna* was consistently lower

than *M. galloprovincialis* at all intertidal levels and negatively correlated with decreasing water temperature. Moreover, fecundity and successful recruitment rates in *M. galloprovincialis* are very high compared to *P. perna* (Van Erkom Schurink and Griffiths 1991; Griffiths *et al.* 1992), as is resistance to desiccation (Hockey and Van Erkom Schurink 1992). The outcomes of this study suggest *M. galloprovincialis* has realized its potential as a competitive dominant over *P. perna* in False Bay.

In summary, Eyre (1939) described False Bay community assemblages as similar to the warm-temperate region with 'an element of the cooler west coast' and it has been described as a 'strong biogeographic breakpoint' (transition zone) between the cool and warm-temperate regions within the literature (Stephenson and Stephenson 1972; Bolton 1986; Griffiths and Branch 1991; Emanuel *et al.* 1992). Long-term shifts in the physical environment and species assemblage change, as revealed through this study and within Chapter 3, support the model-based suggestion that transition zones are vulnerable to global change (Roy, 2001). The implications are that climate and bioinvaders have played a role in altering species composition and distributions to the point where assemblages are more representative of the adjacent cool-temperate region, diminishing the historic role of False Bay as a transition zone between biogeographic regions.

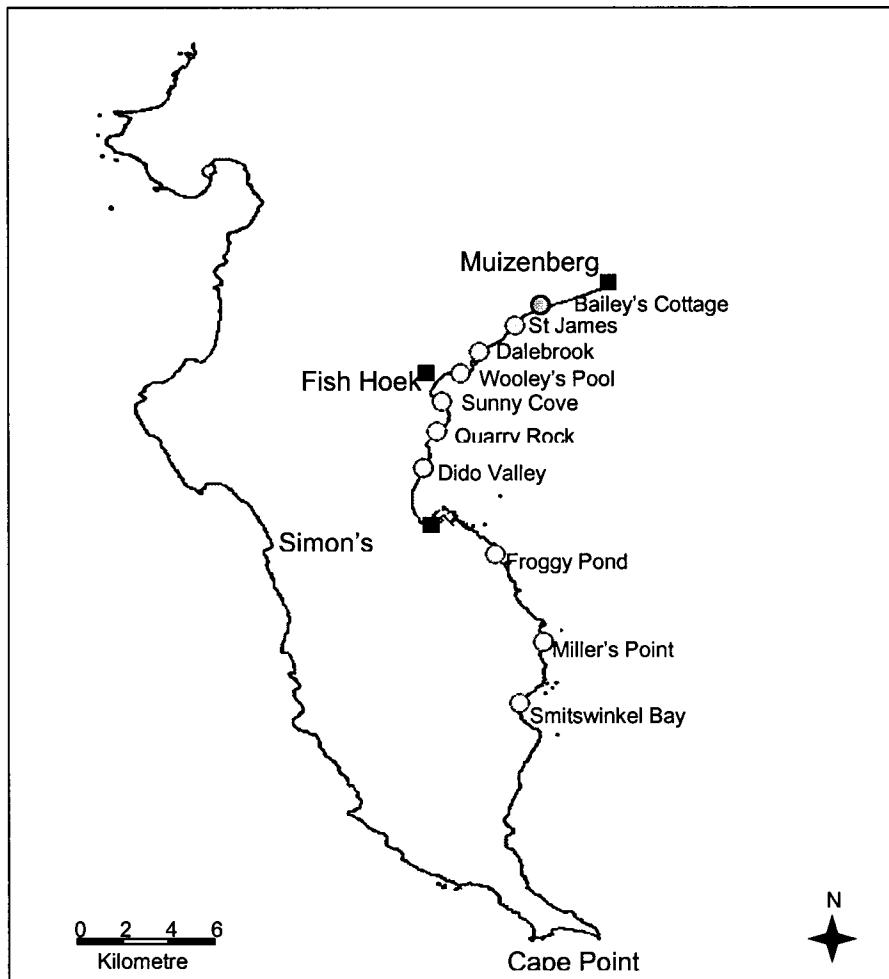


Figure 4.1: Spatial distribution of rocky intertidal sites sampled in 1987 and 2008-2009 in False Bay (TZ1), South Africa. For site GPS co-ordinates, refer to Table 4.1.

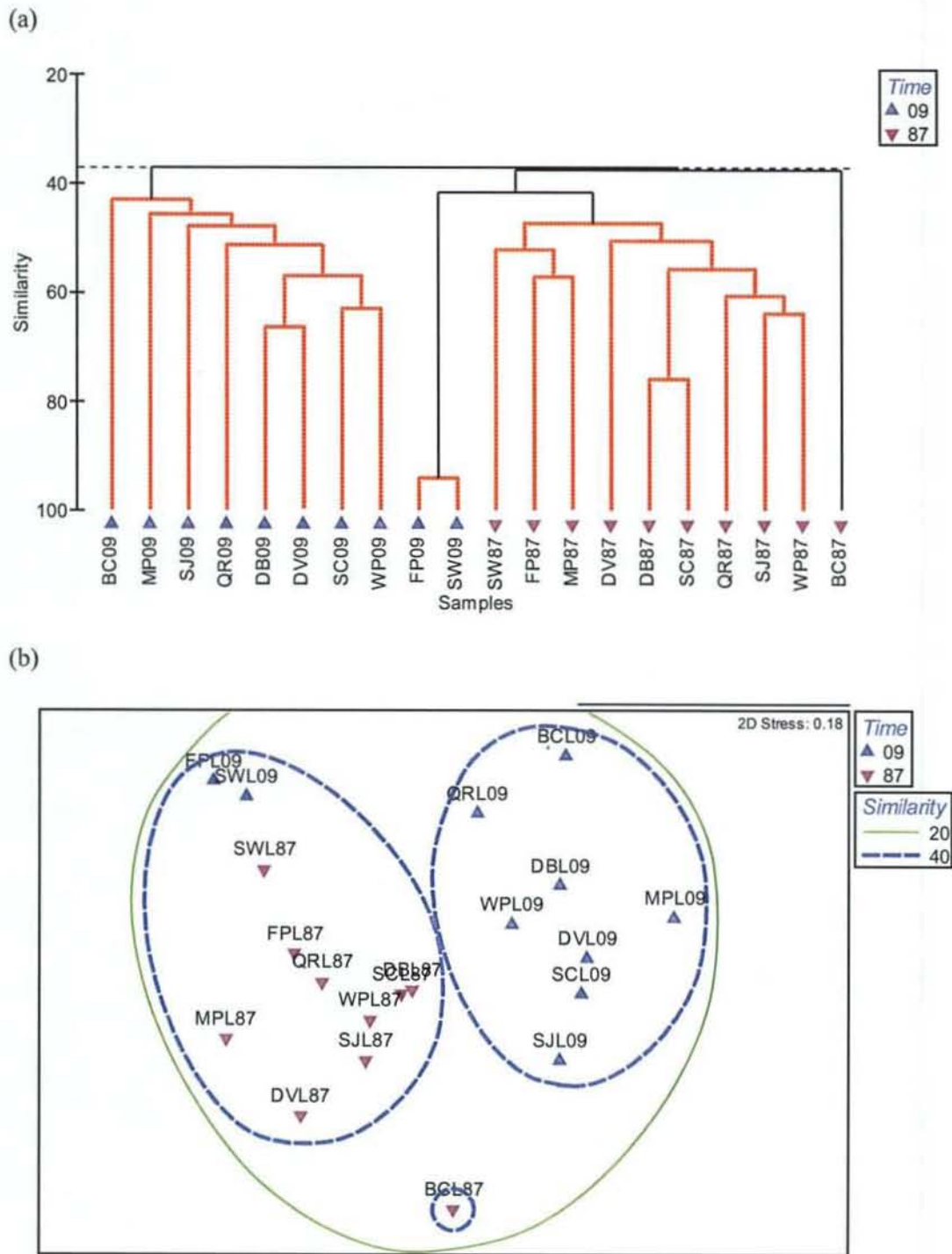


Figure 4.2a: Based on the Bray-Curtis similarity index, low-intertidal data classification by hierarchical cluster analysis (SIMPROF: significant differences between sample groups indicated by black solid lines ( $P < 0.05$ )) and 4.2b: Non-metric MDS ordination (2D stress: 0.18) for intertidal sites sampled in 1987 (87) and 2007-2009 (09). ANOSIM:  $R = 0.62$ ;  $P = 0.001$ . Refer to Table 4.1 for site codes. ANOSIM ( $R = 0.43$ ;  $P = 0.001$ ).

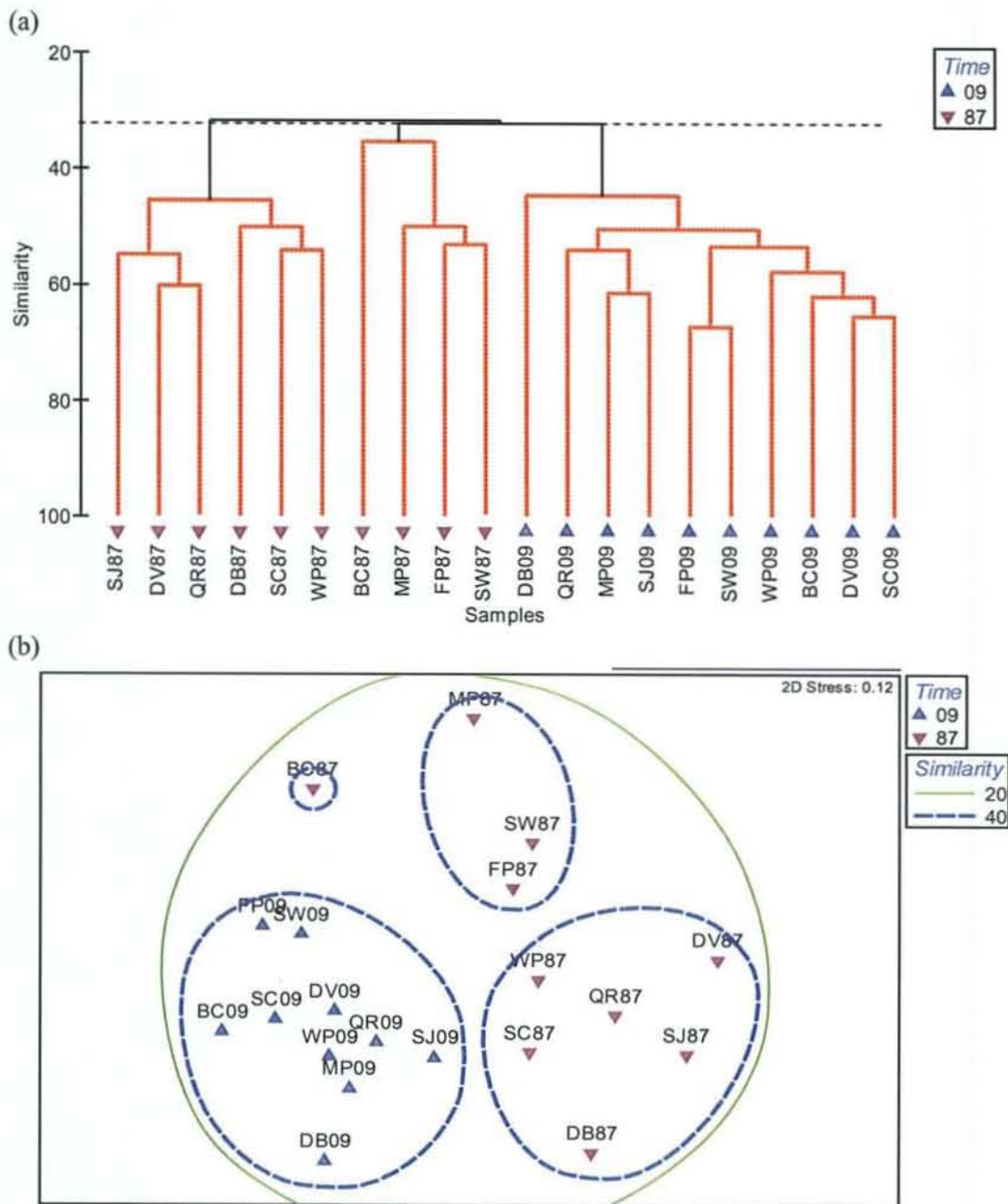


Figure 4.3a: Based on the Bray-Curtis similarity index, low-intertidal data classification by hierarchical cluster analysis (SIMPROF: significant differences between sample groups indicated by black solid lines ( $P < 0.05$ )) and 4.3b: Non-metric MDS ordination (2D stress: 0.12) for intertidal sites sampled in 1987 (87) and 2007-2009 (09). ANOSIM:  $R = 0.62$ ;  $P = 0.001$ . Refer to Table 4.1 for site codes. ANOSIM ( $R = 0.63$ ;  $P = 0.001$ ).

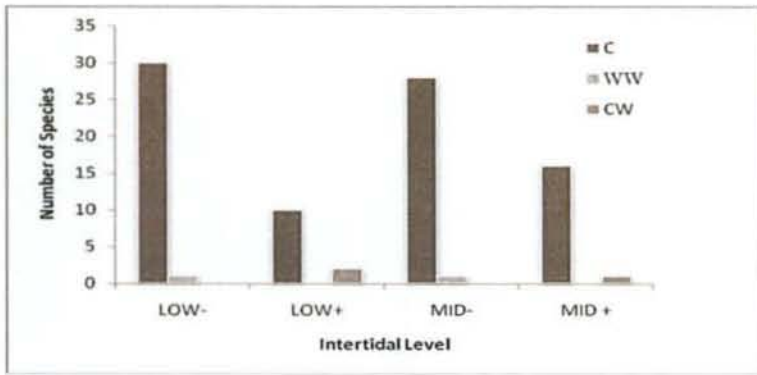


Figure 4.4: Net number of cool-water adapted (CW), warm-water adapted (WW) and cosmopolitan (C) species appearing (+) and disappearing (-) from the False Bay (TZ1) transition zone from 1987-2009.

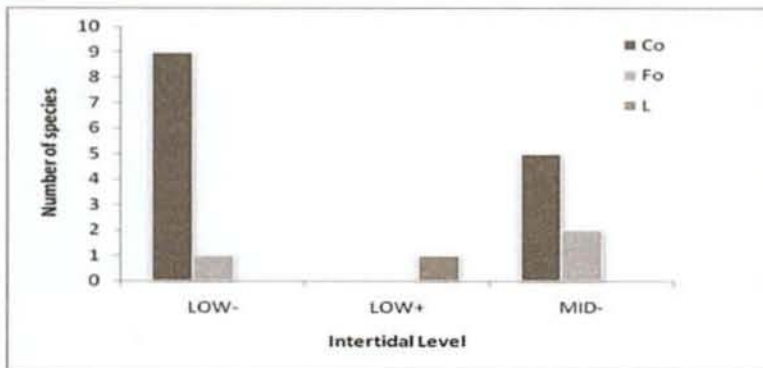


Figure 4.5: Net number of corticated (Co), foliose (Fo) or leathery (L) macroalgal species appearing (+) and disappearing (-) from the False Bay (TZ1) transition zone from 1987-2009.

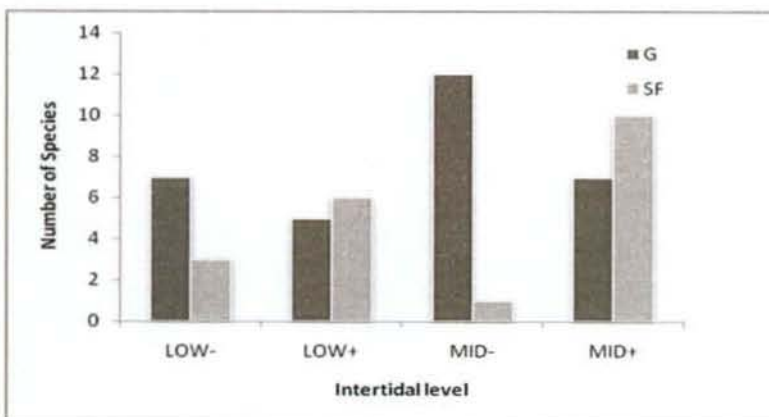
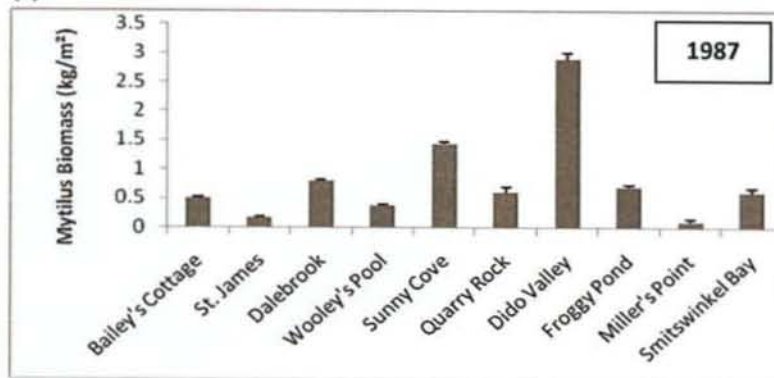
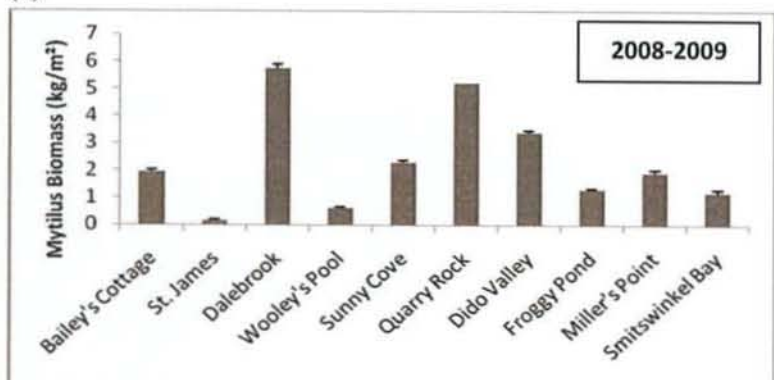


Figure 4.6: Net number of macrofaunal species within different functional feeding groups (suspension feeder (SF) or grazer (G)) appearing (+) and disappearing (-) from the False Bay (TZ1) transition zone from 1987-2009.

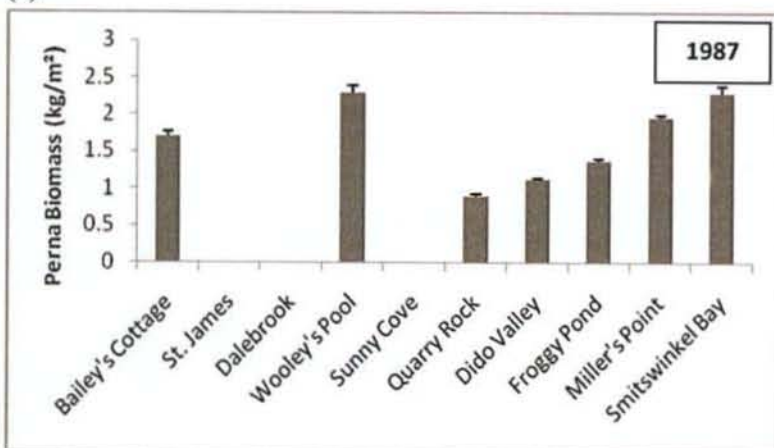
(a)



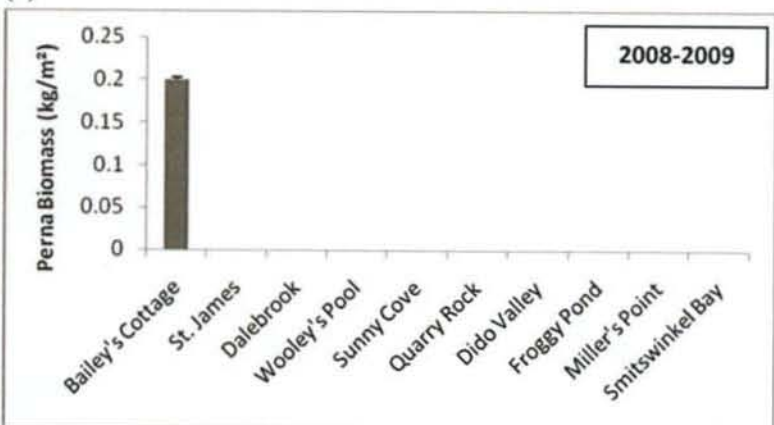
(b)



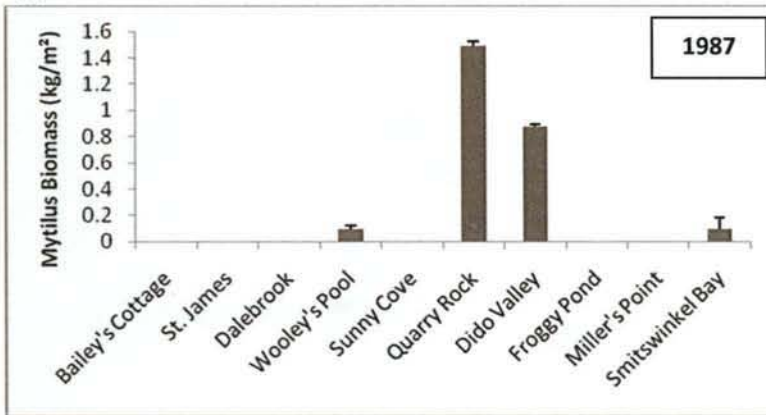
(c)



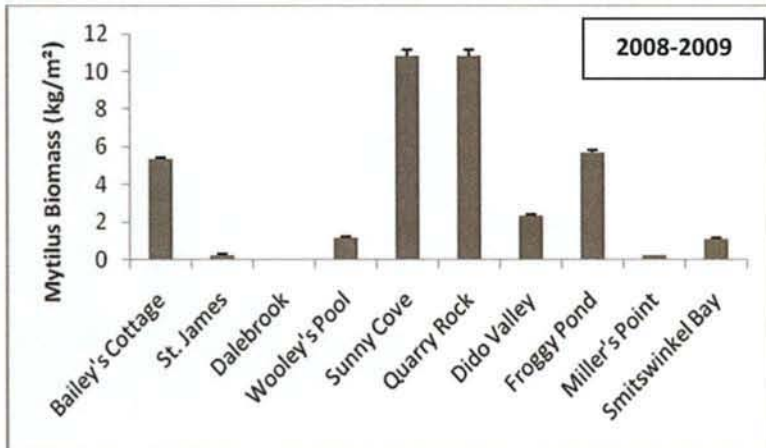
(d)



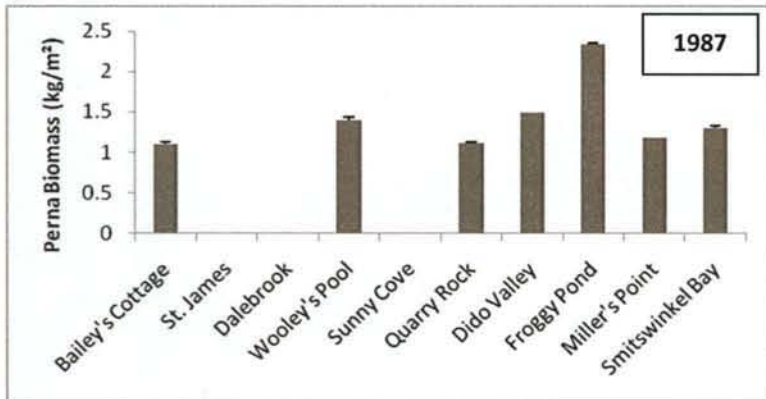
(e)



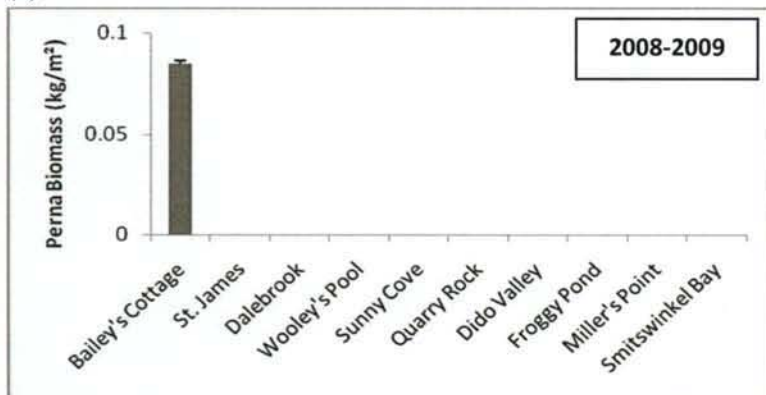
(f)



(g)



(h)



Continued....

Figure 4.7a and b, c and d: Biomass ( $\text{Kg/m}^2 + \text{SD}$ ) of *Mytilus galloprovincialis* and *Perna perna* respectively at low-intertidal sites and 4.7d and e, f and g: Biomass ( $\text{Kg/m}^2 + \text{SD}$ ) of *Mytilus galloprovincialis* and *Perna perna* respectively at mid-intertidal sites in False Bay, South Africa.

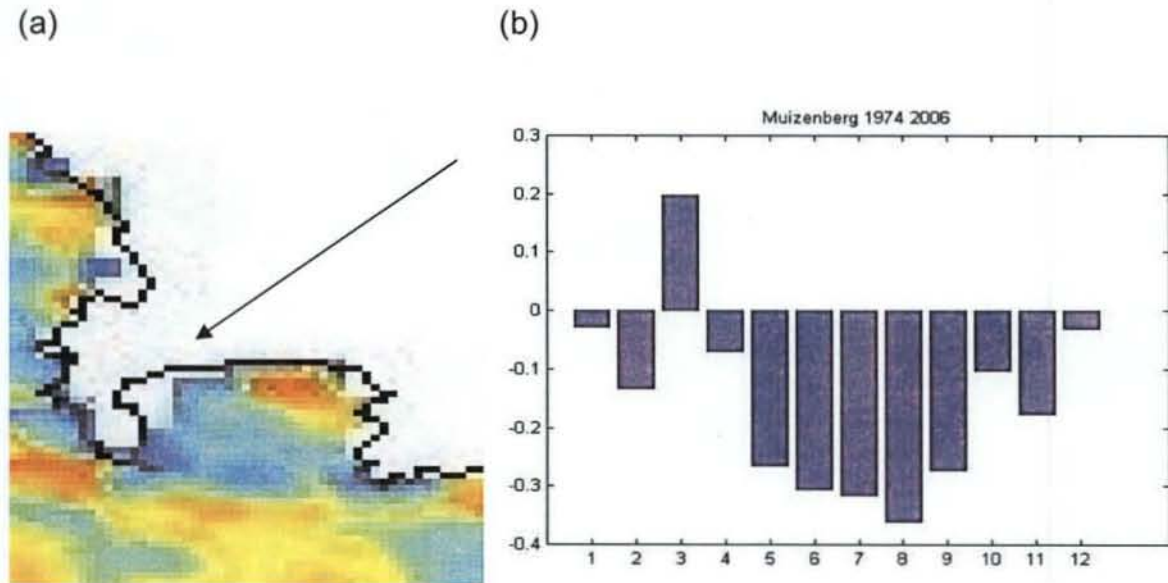


Figure 4.8a: 4 km by 4 km AVHRR satellite data within the False Bay (TZ1) transition zone, South Africa, indicating decadal cooling (blue) in sea surface temperature (SST) within the Bay between 1985 and 2007. 4.8b: Corresponding cooling in SST based on in-situ optimally interpolated (OI) SST data within Muizenberg, False Bay (obtained from South African Weather Services) from 1974 to 2006.

Table 4.1: GPS location of rocky intertidal sites sampled in 1987 and between 2008-2009, False Bay, South Africa.

Site	GPS coordinates
Bailey's Cottage (BC)	S 34 06'48.5" E 18 27'58.8"
St James (SJ)	S 34 06'59.7" E 18 27'42.0"
Dalebrook (DB)	S 34 07'28.1" E 18 27'08.5"
Wooley's Pool (WP)	S 34 07'57.9" E 18 26'41.7"
Sunny Cove (SC)	S 34 08'38.5" E 18 26'14.7"
Quarry Rock (QR)	S 34 09'21.9" E 18 26'09.6"
Dido Valley (DV)	S 34 10'12.5" E 18 25'49.4"
Froggy Pond (FP)	S 34 12'16.6" E 18 27'30.7"
Miller's Point (MP)	S 34 14'22.6" E 18 28'36.8"
Smitswinkel Bay (SW)	S 34 15'51.5" E 18 28'04.2"

Table 4.2: 1987 and 2007-2009 characteristic species assemblages within the low- and mid-intertidal in False Bay, as determined by Similarities Percentage (SIMPER) analyses (based on 70% of species contributing to Bray-Curtis average similarity (S)). Ranking (S<sub>i</sub>) is determined by the average contribution of each species to overall average similarity (S). S<sub>i</sub>/SD(S<sub>i</sub>) is the ratio between the ranking (S<sub>i</sub>) and standard deviation (SD) of S<sub>i</sub>.  $\sum S_i\%$  represents the cumulative percentage contribution of each species to the overall similarity (S). Analyses based on biomass data (Kg/m<sup>2</sup>).

1987 Low-intertidal (S= 39.02)				2007-2009 Low-intertidal (S= 43.87)			
Characteristic species	S <sub>i</sub>	S <sub>i</sub> /SD(S <sub>i</sub> )	$\sum S_i\%$	Characteristic species	S <sub>i</sub>	S <sub>i</sub> /SD(S <sub>i</sub> )	$\sum S_i\%$
<i>Mytilus galloprovincialis</i>	5.58	3.29	11.31	<i>Mytilus galloprovincialis</i>	8.92	3.40	20.33
<i>Perna perna</i>	3.26	0.91	34.53	<i>Ecklonia maxima</i>	2.58	1.08	45.19
<i>Scutellastra argenvillei</i>	1.42	0.90	70.36	<i>Gunnarea capensis</i>	2.53	0.71	50.95
				<i>Chthamalus dentatus</i>	2.36	1.25	56.33
				<i>Notomegabalanus algicola</i>	1.01	0.64	66.47
				<i>Octomeris angulosa</i>	0.94	0.66	70.86
1987 Mid-intertidal (S= 43.38)				2007-2009 Mid-intertidal (S= 52.05)			
Characteristic species	S <sub>i</sub>	S <sub>i</sub> /SD(S <sub>i</sub> )	$\sum S_i\%$	Characteristic species	S <sub>i</sub>	S <sub>i</sub> /SD(S <sub>i</sub> )	$\sum S_i\%$
<i>Perna perna</i>	4.54	0.88	11.64	<i>Mytilus galloprovincialis</i>	9.20	2.47	17.68
<i>Tetraclita serrata</i>	2.71	1.00	34.67	<i>Tetraclita serrata</i>	7.22	3.56	31.55
<i>Octomeris angulosa</i>	0.77	0.49	79.94	<i>Chthamalus dentatus</i>	1.95	1.06	66.83
				<i>Octomeris angulosa</i>	1.91	0.75	74.17

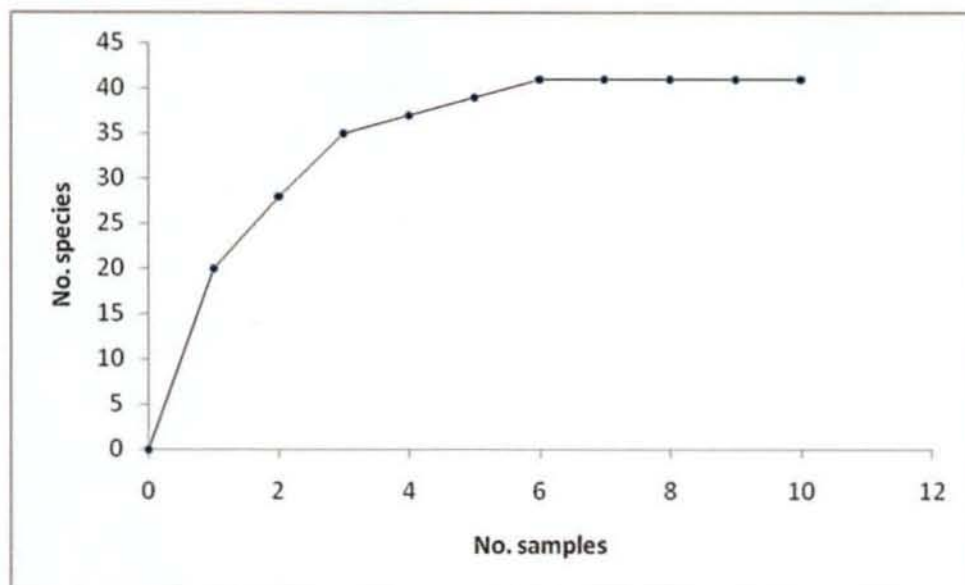
Table 4.3: 1987 and 2009 distinguishing species assemblages within the low- and mid-intertidal in False Bay, as determined by Similarities Percentage (SIMPER) analyses (based on 55% of species contributing to Bray-Curtis average dissimilarity (D)). Ranking determined by D<sub>i</sub>, the average contribution of each species to D. D<sub>i</sub>/SD(D<sub>i</sub>) equals the ratio between D<sub>i</sub> and SD(D<sub>i</sub>), the standard deviation of D<sub>i</sub>.  $\sum D_i\%$  represents the cumulative percentage contribution of each species to the overall dissimilarity (D). Analyses based on biomass data (kg/m<sup>2</sup>).

1987 and 2009 Low-intertidal (D= 61.26)				1987 and 2009 Mid-intertidal (D= 67.96)			
Distinguishing species	D <sub>i</sub>	D <sub>i</sub> /SD(D <sub>i</sub> )	$\sum D_i\%$	Distinguishing species	D <sub>i</sub>	D <sub>i</sub> /SD(D <sub>i</sub> )	$\sum D_i\%$
<i>Perna perna</i>	2.91	1.41	4.75	<i>Mytilus galloprovincialis</i>	5.46	1.46	8.04
<i>Gunnarea capensis</i>	2.35	1.11	8.59	<i>Perna perna</i>	4.00	1.39	13.93
<i>Corallina officinalis</i>	2.27	1.49	12.28	<i>Gigartina polycarpa</i>	2.49	1.27	17.59
<i>Ulva rigida</i>	2.10	1.23	15.71	<i>Ulva rigida</i>	1.99	1.07	20.52
<i>Bunodosoma capensis</i>	1.74	1.28	18.55	<i>Gelidium pristoides</i>	1.98	1.09	23.43
<i>Scutellastra cochlear</i>	1.65	1.13	21.25	<i>Tetraclita serrata</i>	1.96	1.44	26.31
<i>Bifurcariopsis capensis</i>	1.64	0.91	23.92	<i>Oxystele variegata</i>	1.82	1.01	28.99
<i>Bifurcaria brassicaeformis</i>	1.56	1.08	26.47	<i>Gunnarea capensis</i>	1.75	0.98	31.56
<i>Gelidium pristoides</i>	1.51	1.55	29.02	<i>Octomeris angulosus</i>	1.74	1.18	34.13

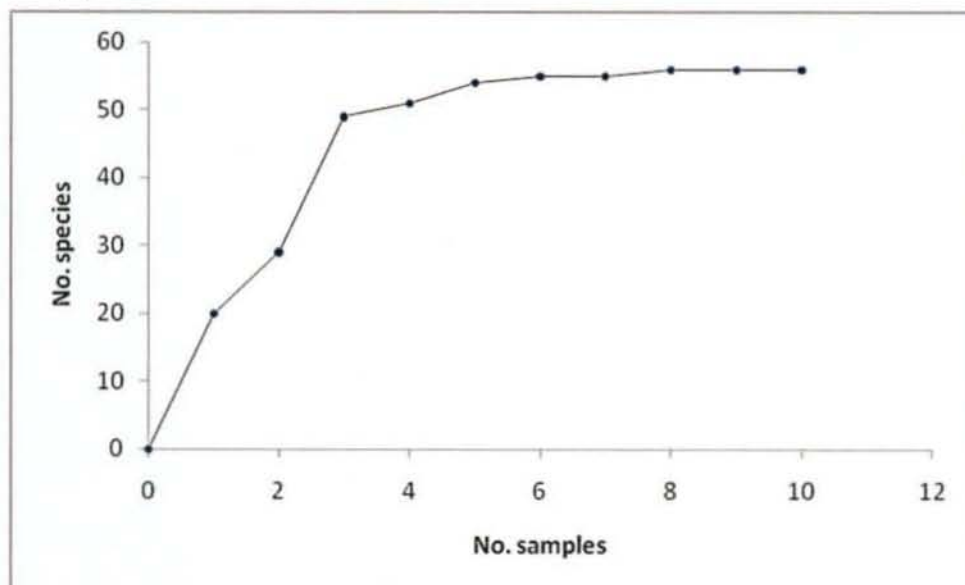
<i>Gigartina polycarpa</i>	1.49	1.00	31.47	<i>Scutellastra granularis</i>	1.60	1.33	36.49
<i>Mytilus galloprovincialis</i>	1.48	1.42	33.91	<i>Chthamalus dentatus</i>	1.57	1.17	38.80
<i>Anthopleura michaelseni</i>	1.47	1.01	36.32	<i>Oxystele sinensis</i>	1.56	1.09	41.09
<i>Nothogenia erinacea</i>	1.28	0.37	38.71	<i>Bunodosoma capensis</i>	1.48	0.80	43.27
<i>Octomeris angulosa</i>	1.22	1.13	40.81	<i>Siphonaria serrata</i>	1.46	1.57	45.42
<i>Helcion dunkeri</i>	1.19	0.67	42.80	<i>Hildenbrandia lecanellierii</i>	1.43	1.21	47.53
<i>Scutellastra argenvillei</i>	1.18	1.19	44.74	<i>Burnupena lagenaria</i>	1.36	1.83	49.53
<i>Burnupena lagenaria</i>	1.10	1.21	46.66	<i>Siphonaria capensis</i>	1.27	1.31	51.40
<i>Scutellastra granularis</i>	1.08	1.22	48.46	<i>Ralfsia verrucosa</i>	1.27	1.65	53.27
<i>Parechinus angulosus</i>	1.05	1.09	50.22	<i>Cymbula oculus</i>	1.23	1.11	55.08
<i>Chthamalus dentatus</i>	0.99	1.34	51.94	<i>Scutellastra longicosta</i>	1.20	0.98	56.84
<i>Cymbula granatina</i>	0.99	1.27	53.56	<i>Anthopleura michaelseni</i>	1.16	0.60	58.55
<i>Ecklonia maxima</i>	0.97	0.94	55.17	<i>Cymbula granatina</i>	1.14	1.43	60.22
<i>Notomegabalanus algalicola</i>	0.94	1.04	56.75	<i>Spongites yendoi</i>	1.14	1.31	61.90

**Appendix D: Assessment of sampling representivity (species accumulation curves) for each sampling period.**

(a) 1987



(b) 2007-2009



## **Chapter 5: Stressed Out! Comparative responses of a native and bioinvasive mussel to immersion and emersion temperature treatments.**

### **Introduction**

Analyses based on ecological and environmental information have demonstrated that population and community level biological impacts are occurring in response to regional climate change signals (Easterling *et al.* 2000; Hughes 2000; McCarty 2001; Walther *et al.* 2000; 2002). Marine responses that have been reported include climate-related mortality events (Heogh-Guldberg 1999; Hughes *et al.* 2003; Pandolfi *et al.* 2003), changes in the abundance of cold and warm-adapted species (Barry *et al.* 1995; Sagarin *et al.* 1999; Moore *et al.* 2007) and shifts in species range boundaries (Southward *et al.* 1995; Hawkins *et al.* 2003; Zacherl *et al.* 2003; Berge *et al.* 2005; Mieszkowska *et al.* 2005; Rivadeneira and Fernandez 2005). Such studies are indicators as to 'what' is happening at a population level but are usually reported post-change.

Certainly, several impacts have been in line with predicted trends on a global scale (Scavia *et al.* 2002; Walther *et al.* 2002; IPCC 2007). For example, respective range contractions and expansions have been reported for cold- and warm-water adapted species in response to warming across a number of regions within the northern hemisphere (Helmuth *et al.* 2006; Meiszkowska 2009). However, identifying global wide patterns of change is complicated by the variation in temperature signals and associated ecological impacts observed at local and regional scales (Helmuth 1998; Sagarin 1999; Helmuth and Hofmann 2001; Halpin *et al.* 2002; Helmuth *et al.* 2002; 2006). Through the identification of cellular-level mechanisms being impacted by

environmental signals, more confidence can be attached to explanations 'why' population responses occur over a range of spatio-temporal scales (Halpin *et al.* 2002; Helmuth *et al.* 2002). To date, the integration of environmental, ecological and physiological evidence has been instrumental in explaining temporal and spatial shifts in the distributional limits of intertidal species (Helmuth 2002; Menge *et al.* 2002; Tomanek and Helmuth 2002; Helmuth *et al.* 2005; Hofmann 2005; Sagarin *et al.* 2006).

Molecular and bio-indicator technologies have advanced rapidly over the last couple of decades and can effectively provide insight into individual level responses to environmental cues (Feder and Hofmann 1999; Halpin *et al.* 2002; Helmuth *et al.* 2002). An effective technique is the use of a group of molecular chaperones, known as 'heat shock' (hereafter stress proteins), to elucidate individual and species level responses to thermal based stress (Feder and Hofmann 1999). Stress proteins, such as the Hsp70 family, include inducible isoforms that express at threshold temperatures representing extremes of the physiological temperature range tolerated by those intertidal organisms within their natural environments. Therefore, they can be and have been used as a measure of thermo-tolerance within a species (Hofmann and Somero 1996; Chapple *et al.* 1998; Tomanek and Somero 1999; Buckley *et al.* 2001; Hofmann *et al.* 2002; Tomanek and Sandford 2003; Snyder and Rossi 2004; Sagarin and Somero 2006). Moreover, inducible stress proteins have been demonstrated to be effective at detecting and identifying the thermal stress response of mussels belonging to the genus *Mytilus* (Hofmann and Somero 1995; 1996; Buckley *et al.* 2001; Halpin *et al.* 2002), for example, the stress response in *Mytilus trossulus*, *M. galloprovincialis* and *M. californianus* was found to be strongly

influenced by thermal history of the individuals (Hofmann and Somero 1995; Buckley *et al.* 2001).

Expression is related to the role of inducible stress proteins in refolding (effectively 'rescuing') thermally denatured cell proteins or preventing cytotoxic aggregations within cells following thermal stress (Parsell and Lindquist 1993; Feder and Hofmann 1999; Hofmann and Somero 1995; Buckley *et al.* 2001). The physical production of stress proteins has important bio-energetic budget implications that require a redirection of energy resources from other cellular activities (Feder and Hofmann 1999). Firstly, ATP hydrolysis is required during up-regulation of stress proteins (Hofmann and Somero 1995; Ciechanover 1998; Feder and Hofmann 1999; Anestis *et al.* 2007) and secondly, increases in stress protein production have been positively correlated with a cascaded expression of additional molecules within cells (Buckley *et al.* 2001; Anestis *et al.* 2007). Examples include pyruvate kinase, p38 MAPK and ubiquitin, a molecule responsible for removing stressed proteins that are beyond repair in the form of ubiquitin conjugates (Hofmann and Somero 1995; Buckley *et al.* 2001; Anestis *et al.* 2007). Thirdly, Buckley *et al.* (2001) established that stress protein production does not completely eliminate irreversible damage to cellular proteins, the degradation and *de novo* synthesis of which requires additional ATP hydrolysis. Overall, stress responses could exert a negative effect on the finely balanced ecological-energetic relationships of a species, leading to reductions in energy resources directed toward growth and fecundity (Hofmann and Somero 1995; 1996; Chapple *et al.* 1998; Feder and Hofmann 1999; Tomanek and Somero 1999; Buckley *et al.* 2001).

It is highly likely that extreme levels of individual stress in response to environmental temperature cues could instigate and perpetuate population-level distributional shifts (Hofmann and Somero 1995; 1996; Chapple *et al.* 1998; Tomanek and Somero 1999). Species located within transition zones between biogeographic provinces are often at the edge of their distributional range, where physiological thresholds of temperature tolerance are already limiting their distributions (Griffiths and Branch 1991). In these regions, models and predictions concur in that they state species are more likely to be impacted within these vulnerable regions (Roy 2001; Walther *et al.* 2002). A range contraction of 2 km per year was detected in the False Bay transition zone (TZ1) located in-between the cool- and warm-temperate biogeographic regions of South Africa (Chapter 4). This represented a substantive contraction from the southern distributional limit of a native, warm-water adapted mussel, *Perna perna* (Chapter 4). Conversely, the introduced mussel species, *Mytilus galloprovincialis*, a relatively cool-water adapted species on South African shores proliferated throughout the same region and beyond over a similar time scale (Chapters 3; Chapter 4). AVHRR satellite and *in-situ* data indicate that near-shore sea surface temperature (SST) has decreased by up to 0.5°C per decade in TZ1 (Chapter 1; Figure 1.3; Reason and Rouault 2005; Trenberth *et al.* 2007; Rouault *et al.* 2009), thus altering the immersion temperatures experienced by intertidal organisms. In addition, ambient air temperatures, which are important for intertidal organisms during emersion periods, have been increasing (Kruger and Shongwe 2004).

The plasticity of the heat-shock response within populations of the native mussel, *P. perna*, and the introduced mussel, *M. galloprovincialis*, located within TZ1 will be

investigated. Specifically the expression of Hsp72, an inducible isoform belonging to the Hsp70 family (hereafter referred to as inducible Hsp70), will be measured post exposure to a range of immersion and emersion temperature cycles. It is hypothesized that there will be significant differences in the overall induction thresholds and concentrations of inducible Hsp72 produced by the introduced and native mussels, influenced by thermal history. Results will be considered within the context of mussel energetics, regional temperature shifts and the observed distributional shifts.

## **Materials and Methods:**

### **Specimen Collection and Acclimation**

Adult specimens of both *Mytilus galloprovincialis* and *Perna perna* (60.0-70.0 mm and 70.0-80.0 mm length, respectively) were collected from the low-intertidal of False Bay, South Africa (Bailey's Cottage: S 34 06'48.5" E 18 27'58.8") in early September. The temperature of the seawater was 12°C and the air temperature was 18°C. Mussels were immediately transported in seawater to the Marine Biology Research Centre (University of Cape Town) where they were placed into aquaria. In total, 70 specimens of each mussel species were placed into a series of aquaria that formed each 'treatment' or 'control' group. The aquaria contained aerated, filtered habitat water. Mussels within each aquarium were distributed over mesh bags similar to those used in mariculture (mesh size 10 mm<sup>2</sup>) and fed using mixed algal cultures that were added to each aquarium at regular intervals, in equal concentrations and volume. Throughout the experiment, oxygen, salinity and pH levels were kept constant within each aquarium.

Aquaria within each group were set at one of four pre-selected acclimation (immersion) temperatures (group 1: 12.0°C (field control group); group 2: 9.0°C; group 3: 12.0°C; group 4; 15.0°C; group 5: 18.0°C  $\pm$  0.1°C). Different water temperatures were achieved and maintained using chillers and heaters within separate aquaria, prior to the water entering the habitat aquaria. For the duration of the experiments, habitat water was drained away and replaced over a three hour period. This occurred twice during each 24 hour period (controlled by electronic timers attached to pump mechanisms) and simulated maximal emersion periods experienced by low-intertidal mussels during South African spring tidal cycles.

During a ten week acclimation period, the air (emersion) temperature was maintained at 18°C (field control temperature). Background levels of inducible Hsp70 were quantified for both species at all acclimation (immersion) temperatures using the methodology detailed below. This continued for the control group (group 1) where emersion conditions were not varied from the field control temperature for the duration of the experiment. During acclimation, no Hsp70 was induced across the four immersion temperature groups. The control group produced no Hsp70 for the duration of the experiment. Moreover, Hsp half life has been established at 1-2 days within the cells of invertebrates and other organisms (Landry *et al.* 1982; Chen *et al.* 1990). Therefore any inducible Hsp70 detected can be classed as a positive response to variations in emersion temperature.

### **Treatments**

A subset (N=8) of mussels were randomly selected from aquaria within each treatment group were selected and exposed to a range of emersion temperatures ranging from 24-36°C (Figure 5.1). Following emersion, the mussels were marked

and re-immersed in the habitat water temperatures maintained within each aquarium, a process that was repeated over ten tidal cycles, in order to simulate a typical South African low spring tidal cycle. The difference between the acclimation (immersion) and treatment (emersion) temperatures created a range of differential temperature treatments (Table 5.1). Following treatment, gill tissue was removed from each mussel and ground over liquid nitrogen. Resultant tissue powders were stored at  $-80^{\circ}\text{C}$  prior to Hsp analysis.

### **Mortality levels**

Throughout the experiment, mussels were observed for mortality (classified as mussels that did not close their shells in response to stimulation or 'gaped'). No mussel mortality was observed.

### **Stress Protein labelling**

The overall protocol was adapted from Hofmann and Somero (1995; 1996) and Buckley *et al.* (2001).

### *Tissue Preparation*

In preparation for electrophoresis and immunoassay, 100-200 mg of each tissue sample was homogenized in four volumes (w/v) of phosphate buffered saline (PBS:  $10\text{ mM l}^{-1}$  sodium phosphate and  $150\text{ mM l}^{-1}$  sodium chloride (pH7.6)) containing one dissolved protease inhibitor cocktail tablet per 10 ml PBS (Roche Applied Science: Complete Mini: Cat. No. 04 693 124 001: containing EDTA and for inhibition of serine, cysteine and metalloproteases). The homogenate was centrifuged at  $16\ 000\text{ g}$  for 5 min at  $4^{\circ}\text{C}$ . From the resultant supernatant, a sample was removed for total protein concentration determination (modified Bradford Protein Assay: Pierce

Coomassie Plus). Post determination, the supernatant was further diluted with PBS (pH7.6) and SDS sample buffer (50 mmol l<sup>-1</sup> Tris-HCl (pH6.8), 10% glycerol, 2% 2-mercaptoethanol) containing 10% SDS (sodium dodecyl sulphate) and 5% bromophenol blue. This was to ensure equal loading of total protein for electrophoresis (10 µg/ 15µl). The resultant mixture was boiled at 100°C for 5 min and stored at -20°C prior to electrophoresis.

### *Electrophoresis*

Relative levels of the stress protein, inducible Hsp70, were determined using western blot analysis of the gill extracts prepared as described above. Equal amounts of gill protein (10µg/15µl) in addition to an Hsp70 standard (1 µg/15µl; >95%; from bovine brain; SIGMA-ALDRICH: Cat. No. H9776) and pre-stained protein markers to monitor western transfer efficiency (PeqGOLD Pre-stain Protein Marker IV: cat. No. 17188) were electrophoresed on a 10% SDS-polyacrylamide gel for 1.5 h at 120 V. The separated proteins were then transferred to nitro-cellulose membrane via semi-dry electrophoretic transfer at 100 V and 300 mA for 1 h using a transfer buffer composed of 192 mM l<sup>-1</sup> glycine, 25 mM l<sup>-1</sup> Tris base and 20% methanol. Transfer conditions were optimized to ensure complete transfer of proteins in the 70 kDA region.

### *Immunoblot analysis*

Western blotting was performed using an enhanced chemiluminescence protocol. Following transfer, the membrane was blocked overnight with 5% nonfat dry milk in PBS (blocking solution (pH7.6)). After three 5 min washes in Tris buffered saline (TBS: 50 mM l<sup>-1</sup> Tris base and 150 mM l<sup>-1</sup> sodium chloride (pH7.5)) containing 0.2%

Tween-20, the blot was incubated for 1 h in the primary antibody solution composed of a monoclonal mouse anti-HSP 70 antibody (SIGMA-ALDRICH: Cat. No. H5147) diluted 1:5 000 in blocking solution. The blot was washed three times for 5 min with PBS/0.2% Tween-20, incubated for 1 h in secondary antibody (rabbit anti-mouse IgG; SIGMA-ALDRICH: Cat. No. A9044) diluted 1: 6 000 in blocking solution and then washed three times for 5 min with PBS/0.2% Tween-20. The western blot was developed using chemiluminescence-based detection following the manufacturer's instruction (Amersham ECL Advance Western Blotting Detection Kit, GE Healthcare).

### **Analysis**

Hsp70 protein synthesis patterns were identified using western-blotting techniques, in gill tissue isolated from both species (Figure 5.2a; Figure 5.3a). Inducible Hsp70 bands were analyzed densitometrically using Bio-Rad Quantity One 4.4.1. This measures the pixel intensity of the bands within a set area (INT/mm<sup>2</sup>). The pixel density (INT/mm<sup>2</sup>) of expressed inducible Hsp70 was load adjusted using an internal control protein band (42kDa: Figure 5.2b; Figure 5.3b) before conversion into Hsp70 concentrations (µg/µl). No inducible Hsp70 was expressed in acclimated mussels maintained at the field control temperature or within the control group for the duration of the experiment. Therefore levels of inducible Hsp72 bands present post treatment were not adjusted for background expression. Densities were converted to concentration values (µg/µl) relative to the loaded Hsp70 standard. Data shown are averaged per immersion/emersion temperature treatment group (N=8).

An analysis of variance, ANOVA ( $P < 0.05$ ) was used to identify the significance level of detected differences in Hsp70 expression between different treatments and species.

## **Results:**

The monoclonal antibody used in the immunoblot analysis detected an inducible form of Hsp70 (Hsp72) within the tissue of both mussels, *Mytilus galloprovincialis* and *Perna perna*, post treatment. Expression of inducible Hsp70 was strongly influenced by thermal history, with consistent results amongst individuals tested from each species. Whereas both species responded similarly to increasing emersion temperatures, differences were found in the response to immersion temperatures.

*M. galloprovincialis* synthesized inducible Hsp70 at all immersion temperatures post treatment, the intensity of which was up-regulated with increasing emersion temperatures (Figure 5.4). The overall intensity of expression (density) ranged from 2343-3510 INT/mm<sup>2</sup>, which equates to a concentration range of 0.053-0.071 µg/µl (Table 5.2; Figure 5.5). The induction threshold for Hsp70 expression was regulated by immersion temperature. Whereas the induction threshold was set at an emersion temperature of 30°C when the mussels were acclimated to immersion temperatures of 9-15°C, it shifted upward to 32°C when immersion temperatures were increased to 18°C. The concentration range of inducible Hsp70 correlated negatively with increasing immersion temperature. Mussels exposed to 9 and 12°C immersion temperatures differed significantly from those exposed to 15 and 18°C immersion temperatures, producing concentrations of 0.053-0.071 µg/µl and 0.047-0.064 µg/µl respectively (Table 5.2; Figure 5.2a; Figure 5.4; Figure 5.5).

*Perna perna* synthesized inducible Hsp70 at all immersion temperatures post treatment, the intensity of which was up-regulated with increasing emersion temperatures (Figure 5.4). The intensity of expression (density) ranged from 968-1620 INT/mm<sup>2</sup>, which equates to a concentration range of 0.024- 0.04 µg/µl (Table 5.2; Figure 5.5). The induction threshold for Hsp70 expression appeared to be regulated by immersion temperature. Whereas the induction threshold was set at the maximal emersion temperature of 34°C when the mussels were acclimated to immersion temperatures of 9-12°C, it shifted upward to a 36°C when immersion temperatures were increased to 15°C which was maintained at 18°C immersion. The concentration range of inducible Hsp70 correlated positively with increasing immersion temperature. Mussels exposed to 9 and 18°C immersion temperatures differed significantly, producing maximal concentrations of 0.032 µg/µl and 0.04 µg/µl respectively (Table 5.2; Figure 5.3a; Figure 5.4; Figure 5.5).

When compared, there are significant differences between the induction threshold and concentrations of inducible Hsp70 produced within the gill tissue of the two mussel species, post thermal treatment. The Hsp70 induction thresholds for *P. perna* (34-36°C) were higher than those of *M. galloprovincialis* (30-32°C). In addition, *P. perna* produced significantly lower concentrations of inducible Hsp70 compared to *M. galloprovincialis* (a ratio of 1:2) for the combined immersion and emersion temperature ranges tested. Both species did not express inducible Hsp70 until induction thresholds were reached, although the differential between immersion and emersion temperatures were identical for several temperature treatment combinations below and above the threshold value.

## Discussion

The aim of the present study was to establish if local changes in environmental temperature have the potential to impact the underlying physiological mechanisms of individuals, translating into population level responses in the intertidal zone. Through examining the plasticity of the heat-stress response in two mussels that occupy the same ecological niche, several similarities and significant differences were identified in their thermal responses. In combination, immersion and emersion temperature have been identified as playing a pivotal role in setting the induction threshold for inducible Hsp70 expression, as well as controlling the up-regulation of Hsp70 in *M. galloprovincialis* and *P. perna*, albeit differently.

Threshold temperature for Hsp70 induction displayed intraspecific and interspecific plasticity, being strongly influenced by the thermal history of individuals. Warmer acclimated individuals belonging to both species exhibited a higher induction threshold. However, *M. galloprovincialis* had an overall lower induction threshold of 30-32°C compared to *P. perna* which was 34-36°C and which may be attributable to their respective cooler and warmer-adaptive natures (Bustamante *et al.* 2010). Thus *M. galloprovincialis* is the more thermosensitive of the two species.

A great deal of plasticity has been reported for the induction threshold of inducible Hsp70 production across a number of studies involving ectotherms. The outcomes of several of these studies concur with the results presented here (Hoffman and Somero 1995; 1996; Feder and Hofmann 1999; Tomanek and Somero 1999; Buckley *et al.* 2001). Tomanek and Somero (1999) established that when individuals of the intertidal snail, *Tegula brunnea*, were acclimated to warmer temperatures, the

induction threshold (termed  $T_{on}$ ) upshifted. A similar study involving the mussel genus *Mytilus*, demonstrated that increasing acclimation temperature upshifted the induction threshold in *M. californianus* and *M. trossulus* when field acclimated mussels collected in summer were compared to specimens collected in winter or laboratory acclimated to lower temperatures (Roberts *et al.* 1997; Buckley *et al.* 2001).

In general, organisms from warmer environments do appear to induce HSPs at higher temperatures compared to congeners or competitive equivalents from colder environments (Buckley *et al.* 2001). Tomanek and Somero (1999) established that a sub-tropical intertidal species (warm-adapted) *Tegula rugosa*, had a much higher induction threshold temperature compared to a cool-temperate (cold-adapted) intertidal congener, *T. brunnea*. In addition, Hoffman and Somero (1996) established that the induction threshold was lower in the northern occurring *M. trossulus* (23°C) compared to the southern occurring *M. galloprovincialis* (25°C). Both mussel species found in South Africa appear to be able to adapt their ability to start expressing inducible Hsp70 according to thermal history and the resultant degree of stress experienced. However, it would appear that as for the genera *Tegula* (Tomanek and Somero 1999) and *Haliotis* (Dahlhoff and Somero 1993) this adaptation occurs over a narrow range of emersion temperatures, compared to the full range that would be experienced within their natural habitats.

The present study has established that both immersion and emersion temperature appeared to control up-regulation of inducible Hsp70 expressed by each species differently. Whereas increasing emersion temperatures created higher levels of

heat-stress for both mussel species, irrespective of immersion temperature, the role of immersion temperature is more complex in each species. Whereas Hsp70 production in *M. galloprovincialis* negatively correlated with increasing immersion temperature, Hsp70 production in *P. perna* positively correlated with increasing immersion temperature. However, the overall intensity (concentration range) of the heat-stress response was much greater in *M. galloprovincialis* compared to *P. perna* across the complete range of immersion and emersion temperatures tested. Thus, the cool-adapted species, *M. galloprovincialis* is more thermosensitive, as its proteins are more unstable under thermal stress at lower temperatures. However the results indicate it has the capacity to up-regulate enough Hsp70 to repair and rescue comparatively high levels of reversible protein damage (Feder and Hofmann 1999).

According to the findings of Tomanek and Somero (1999) for the snail genus *Tegula*, the retention of interspecific differences in induction threshold, thermosensitivity and thermotolerance between *M. galloprovincialis* and *P. perna* is possibly due to differences in the thermal stability of the cellular proteins found within each species and/or that there are genetic differences influencing the differential factors listed. Hofmann and Somero (1996) established that significant interspecific differences existed in the heat-stress responses of two congener mussels that had established populations occupying different latitudes of the Pacific coast of North America. The northern occurring, cold-water adapted mussel, *Mytilus trossulus*, was more thermosensitive at lower temperatures than the southern occurring, relatively warm-water adapted mussel, *M. galloprovincialis*, attributable to variation in protein stability and thermotolerance. Therefore two relatively cold-water adapted species, *M.*

*trossulus* on the Pacific coast and *M. galloprovincialis* on the South African coast, produced higher concentrations of Hsp70 at lower acclimation temperatures. This is in line with

The results of the present study implies that although the introduced mussel *M. galloprovincialis* is more thermotolerant than *P. perna* over a range of immersion and emersion temperatures, the former species is comparatively more susceptible to reversible protein damage at lower immersion temperatures, whereas the latter species is more susceptible to reversible protein damage at higher immersion temperatures. The results indicate beyond a doubt that *M. galloprovincialis* and *P. perna* are adapted to respond differently to heat-stress, but how does this relate to the observed population level range expansion and recession in the face of decreasing immersion and increasing emersion temperatures in the habitat environment? Mussels are as energetically efficient as the environment allows them to be (Jansen *et al.* 2007). Van Erkom Schurink (1992) conducted a study into the physiological energetics of *M. galloprovincialis* and *P. perna* on South African shores. Significant differences in the filtration, respiration, excretion and absorption rates of both species were reported, with *M. galloprovincialis* ultimately having higher metabolic rates and a larger scope for growth that increased with warm-water acclimation. Interestingly, scope for growth increased with warm-water acclimation in *P. perna*, although it was consistently higher in *M. galloprovincialis*.

A parallel study investigating spawning events and reproductive output in the two congeners revealed that whereas *M. galloprovincialis* had a higher ratio of females and two protracted spawning periods (in summer and winter), *P. perna* had a higher

ratio of males and one extended spawning season over winter and spring. It was concluded that the introduced mussel had a higher reproductive output compared to the indigenous mussel (Van Erkom Schurink and Griffiths 1991a). Similar energetic relationships have been established between *M. galloprovincialis* and *M. trossulus* along the Pacific coast, which have afforded the introduced mussel a competitive edge over the indigenous *M. trossulus* (Shinen and Morgan 2009).

Whereas Hsp70 expression is a good measure of reversible protein damage during heat-stress, irreversible damage also occurs to the cellular protein pool and inducible Hsp70 cannot 'rescue' and 'refold' all of these proteins which are ultimately 'tagged' for proteolytic degradation by a low molecular inducible protein, ubiquitin (see review: Ciechanover 1998; Buckley *et al.* 2001). The degree of irreversible protein damage can be measured using concentrations of ubiquitin conjugates. Measurements of ubiquitin conjugates in latitudinally divided populations of *Mytilus* revealed that concentrations were consistently and significantly higher in the warm-water adapted species at all temperatures (Hofmann and Somero 1996). Buckley *et al.* (2001) corroborated that increasing levels of Hsp70 expression in *Mytilus* species correlated with higher levels of ubiquitin conjugate within cells and that warm-adapted species tend to sustain more damage to their protein pool, as indicated by the higher overall levels of irreversible protein damage compared to cold-adapted species exposed to identical environmental temperatures.

Although the introduced mussel is producing more Hsp70 at lower immersion temperatures, this does not necessarily imply a negative impact for *M. galloprovincialis*, due to enhanced thermosensitivity and thermotolerance, combined

with a much larger energetic budget. Firstly, intense expression of Hsp70 indicates a higher proportion of reversible protein damage is being repaired. Secondly, given that *M. galloprovincialis* is a cold-water adapted species, measurements of ubiquitin conjugates may reveal that compared to *P. perna*; it sustains less irreversible damage at reducing immersion temperatures. Alternatively, even if high levels of protein damage are sustained, the introduced mussel is likely to have the capacity to repair, degrade and re-synthesize proteins even at lower habitat temperatures, processes that require a great deal of metabolic energy. In parallel it is likely that *M. galloprovincialis* will be able to continue to maintain high levels of reproductive output, facilitating successful recruitment and spread of populations.

Conversely, it has been demonstrated that at lowered habitat temperatures, *P. perna* has a highly limited energy budget and reduced levels of reproductive output which may be intensified by cold-shock and cold coma during immersion, severely depressing metabolic activity (Jansen et al. 2007). Although *P. perna* is producing reduced concentrations of Hsp70 at lowered immersion temperatures, it is still susceptible to low level reversible protein damage post an induction threshold of 34°C. This temperature is well within the range of typical summer emersion temperatures for the region (South African Weather Services). Given that *P. perna* is warm-water adapted, the levels of irreversible protein damage may exceed those experienced by *M. galloprovincialis* at comparable habitat temperatures, despite comparably lower HsP70 expression. A lack of energetic resources to degrade ubiquitin conjugates leads to cytotoxicity and a reduced ability to repair and re-synthesize proteins will lead to reduced physiological functionality of cells (Buckley et al. 2001). Alternatively, it can be inferred that the metabolic cost of diverting energy

to these processes would negatively impact reproductive output and therefore recruitment success (Hofmann and Somero 1995).

In conclusion, the bioinvasive and indigenous mussels, *M. galloprovincialis* and *P. perna*, have responded to decreasing immersion and increasing emersion temperatures differently at a physiological level. Given the overall increased thermotolerance, cold-water adapted heat-stress response and substantially larger energy budget available to the introduced mussel, this could have viably tipped the competitive balance between *M. galloprovincialis* and *P. perna*, resulting in the observed changes in distributional range limits observed over the past quarter century.

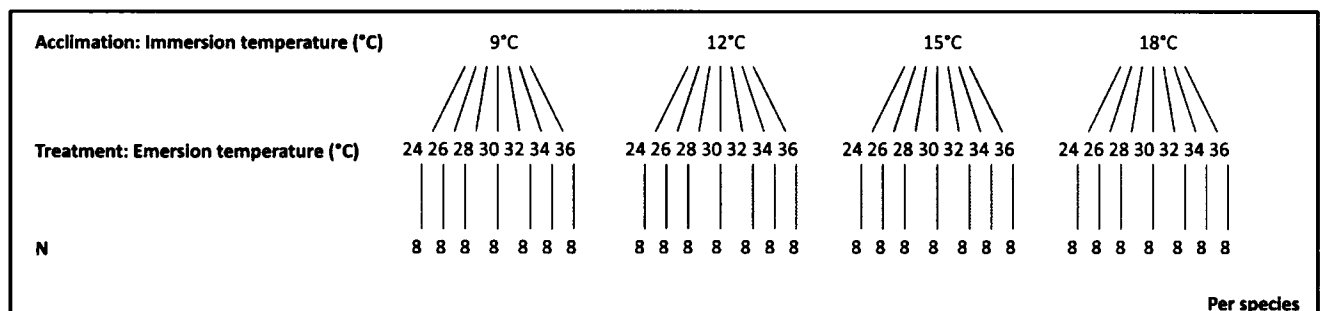


Figure 5.1: Schematic diagram of experimental design.

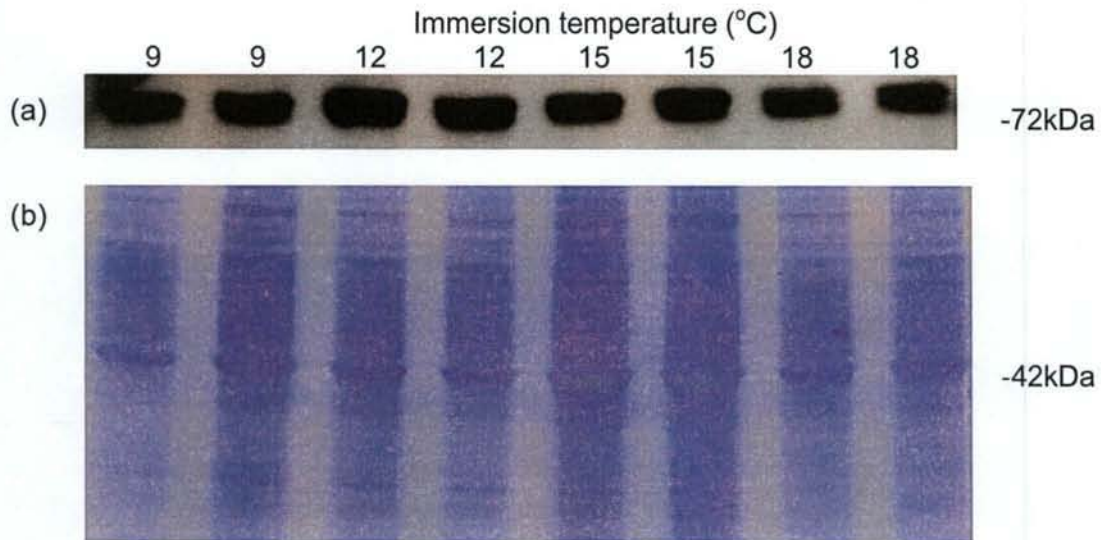


Figure 5.2(a): Western blot indicating densities of inducible Hsp70 (72kDa) produced in *Mytilus galloprovincialis*, post acclimation (immersion) in water temperatures (9-18°C: N=2 per blot) and cyclical exposure to a treatment (emersion) temperature of 36°C. 5.3(b): SDS-Page indicating intensities of the internal control protein band (42kDa), following identical treatment.

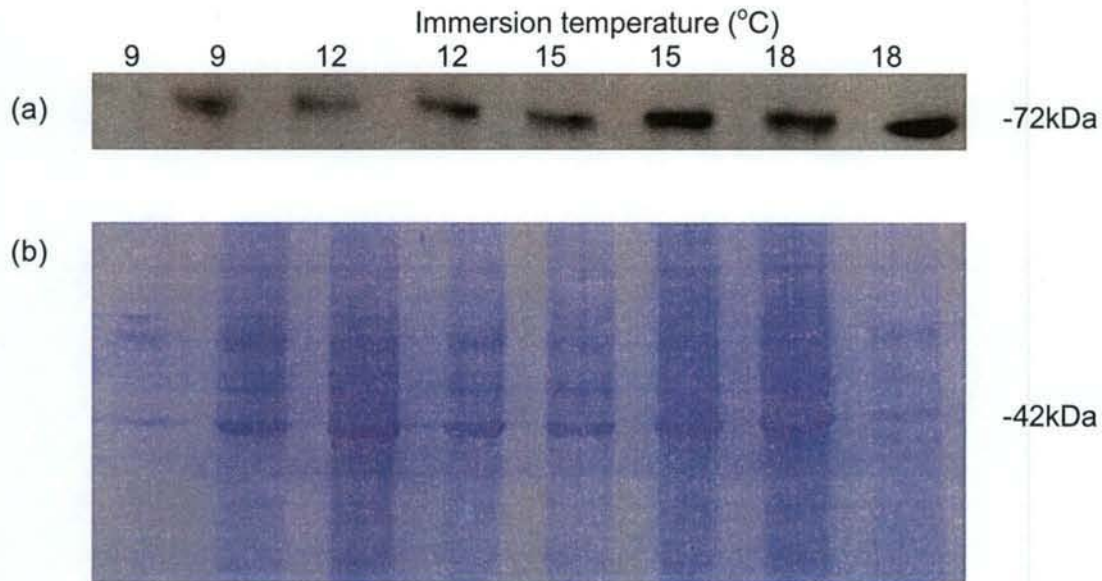


Figure 5.3(a): Western blot indicating densities of inducible Hsp70 (72kDa) produced in *Perna perna*, post acclimation (immersion) in water temperatures (9-18°C: N=2 per blot) and cyclical exposure to a treatment (emersion) temperature of 36°C. 5.3(b): SDS-Page indicating intensities of the internal control protein band (42kDa), following identical treatment.

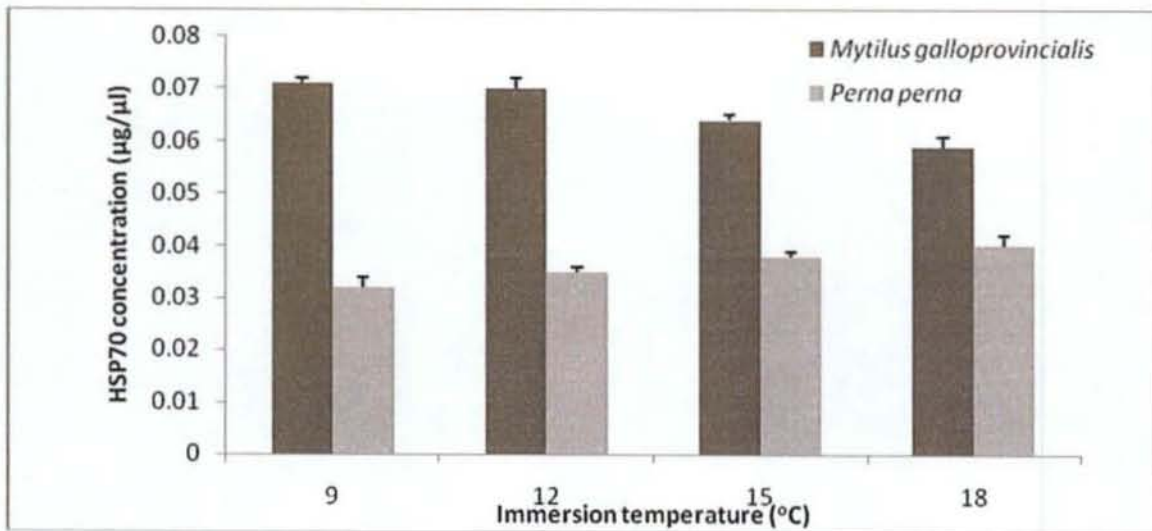


Figure 5.4: Mean ( $\pm$ SD) concentration of inducible Hsp70 ( $\mu\text{g}/\mu\text{l}$ ), expressed by the mussels *Mytilus galloprovincialis* and *Perna perna*, per acclimation (immersion) and emersion temperature treatment.

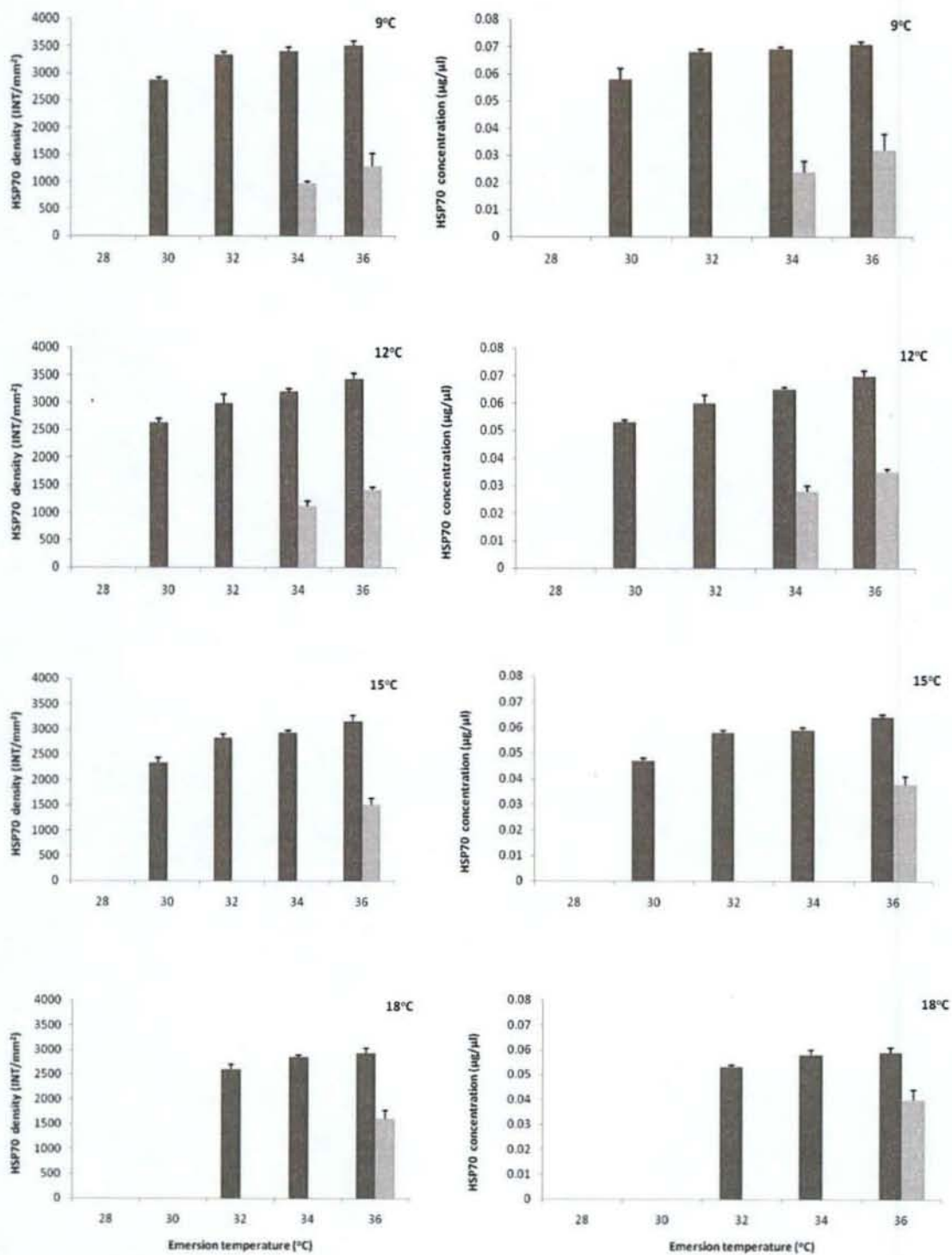


Figure 5.5 Left hand column: mean ( $\pm$ SD) inducible Hsp70 densities (INT/mm<sup>2</sup>). Right hand column: mean ( $\pm$ SD) concentration of inducible Hsp70 ( $\mu$ g/ $\mu$ l) expressed by the mussels, *Mytilus galloprovincialis* (black columns) and *Perna perna* (grey columns), per acclimation (immersion) temperature and emersion temperature treatment.

Table 5.1: Differential between immersion and emersion temperatures (°C). Key: differentials equal.

Immersion temperature (°C)	Emersion water temperature (°C)						
	24	26	28	30	32	34	36
9	15	17	19	21	23	25	27
12	12	14	16	18	20	22	24
15	9	11	13	15	17	19	21
18	6	8	10	12	14	16	18

Table 5.2: Mean ( $\pm$ SD) concentration of inducible Hsp70 ( $\mu\text{g}/\mu\text{l}$ ) produced by the mussels, *Mytilus galloprovincialis* and *Perna perna*, per acclimation (immersion) temperature and emersion temperature treatment.

Immersion (°C)	Emersion (°C)	Hsp70 concentration ( $\mu\text{g}/\mu\text{l}$ )			
		<i>M. galloprovincialis</i>	SD $\pm$	<i>P. perna</i>	SD $\pm$
9	28	0	0	0	0
	30	0.058	0.004	0	0
	32	0.068	0.001	0	0
	34	0.069	0.001	0.024	0.004
	36	0.071	0.001	0.032	0.006
12	28	0	0	0	0
	30	0.053	0.001	0	0
	32	0.06	0.003	0	0
	34	0.065	0.0008	0.028	0.002
	36	0.07	0.002	0.035	0.001
15	28	0	0	0	0
	30	0.047	0.001	0	0
	32	0.058	0.001	0	0
	34	0.059	0.001	0	0
	36	0.064	0.001	0.038	0.003
18	28	0	0	0	0
	30	0	0	0	0
	32	0.053	0.001	0	0
	34	0.058	0.002	0	0
	36	0.059	0.002	0.04	0.004

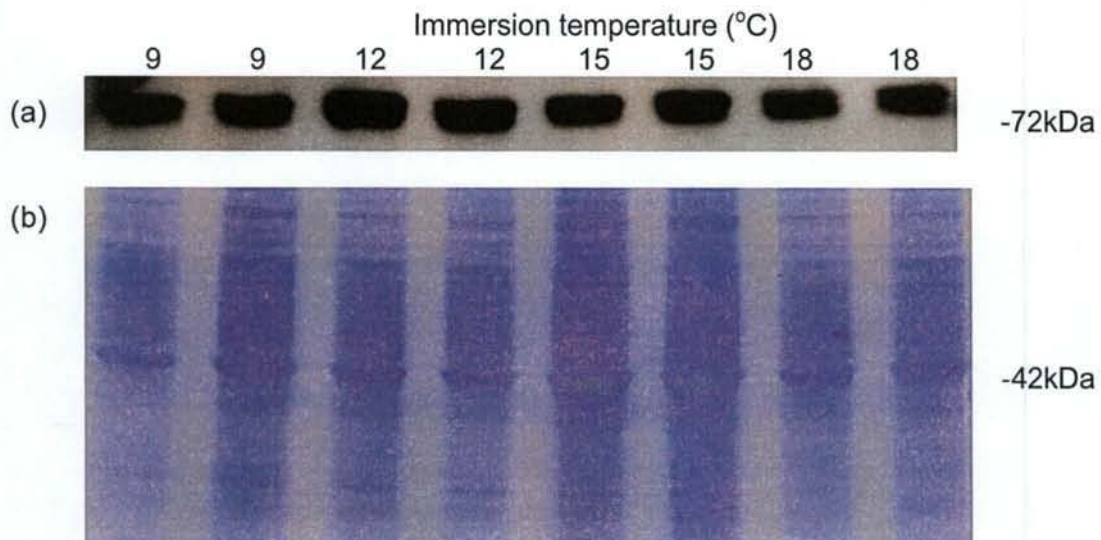


Figure 5.2(a): Western blot indicating densities of inducible Hsp70 (72kDa) produced in *Mytilus galloprovincialis*, post acclimation (immersion) in water temperatures (9-18°C: N=2 per blot) and cyclical exposure to a treatment (emersion) temperature of 36°C. 5.3(b): SDS-Page indicating intensities of the internal control protein band (42kDa), following identical treatment.

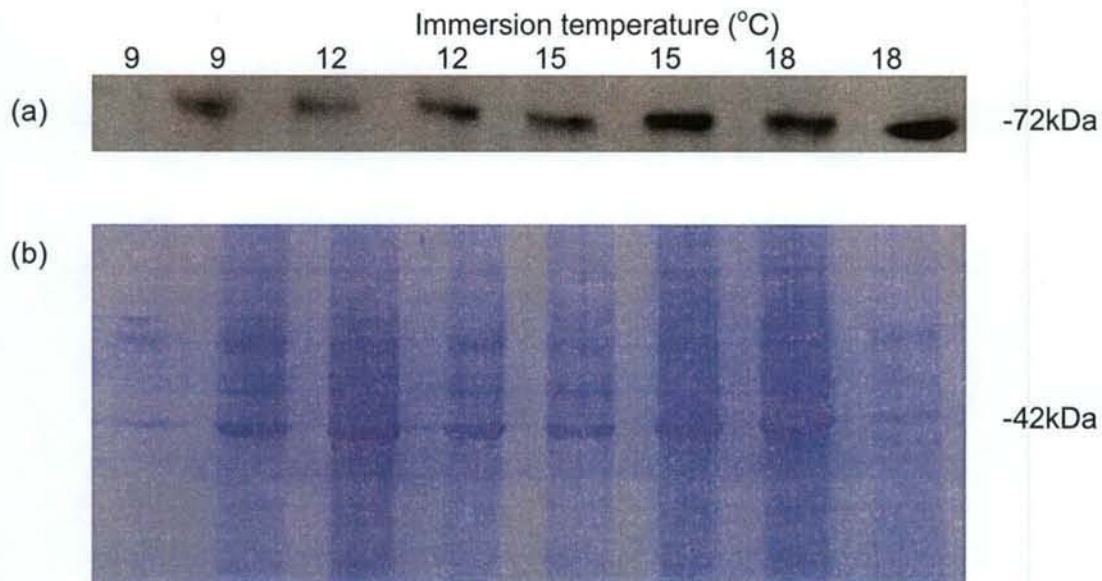


Figure 5.3(a): Western blot indicating densities of inducible Hsp70 (72kDa) produced in *Perna perna*, post acclimation (immersion) in water temperatures (9-18°C: N=2 per blot) and cyclical exposure to a treatment (emersion) temperature of 36°C. 5.3(b): SDS-Page indicating intensities of the internal control protein band (42kDa), following identical treatment.

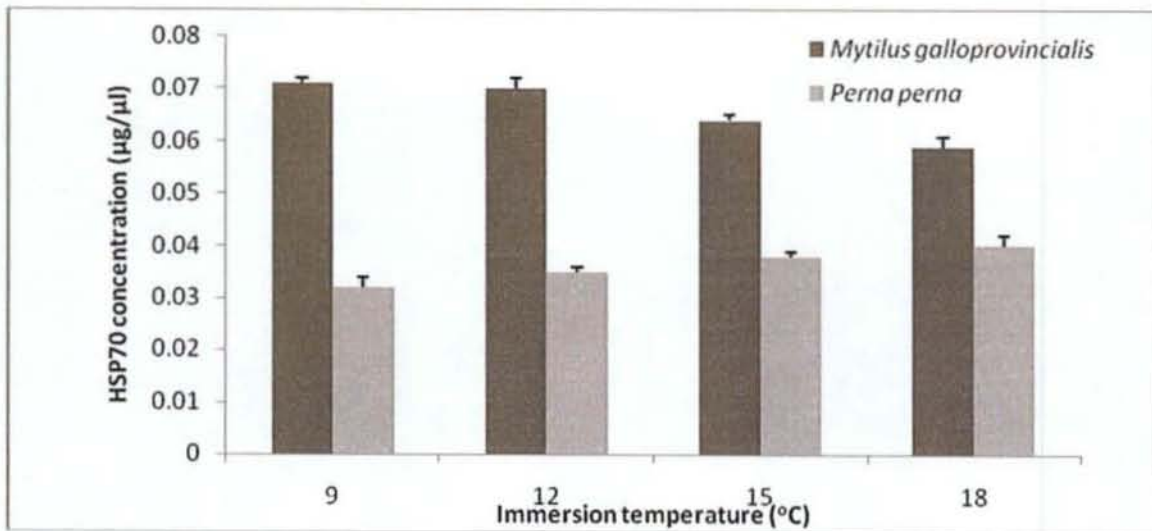


Figure 5.4: Mean ( $\pm$ SD) concentration of inducible Hsp70 ( $\mu\text{g}/\mu\text{l}$ ), expressed by the mussels *Mytilus galloprovincialis* and *Perna perna*, per acclimation (immersion) and emersion temperature treatment.

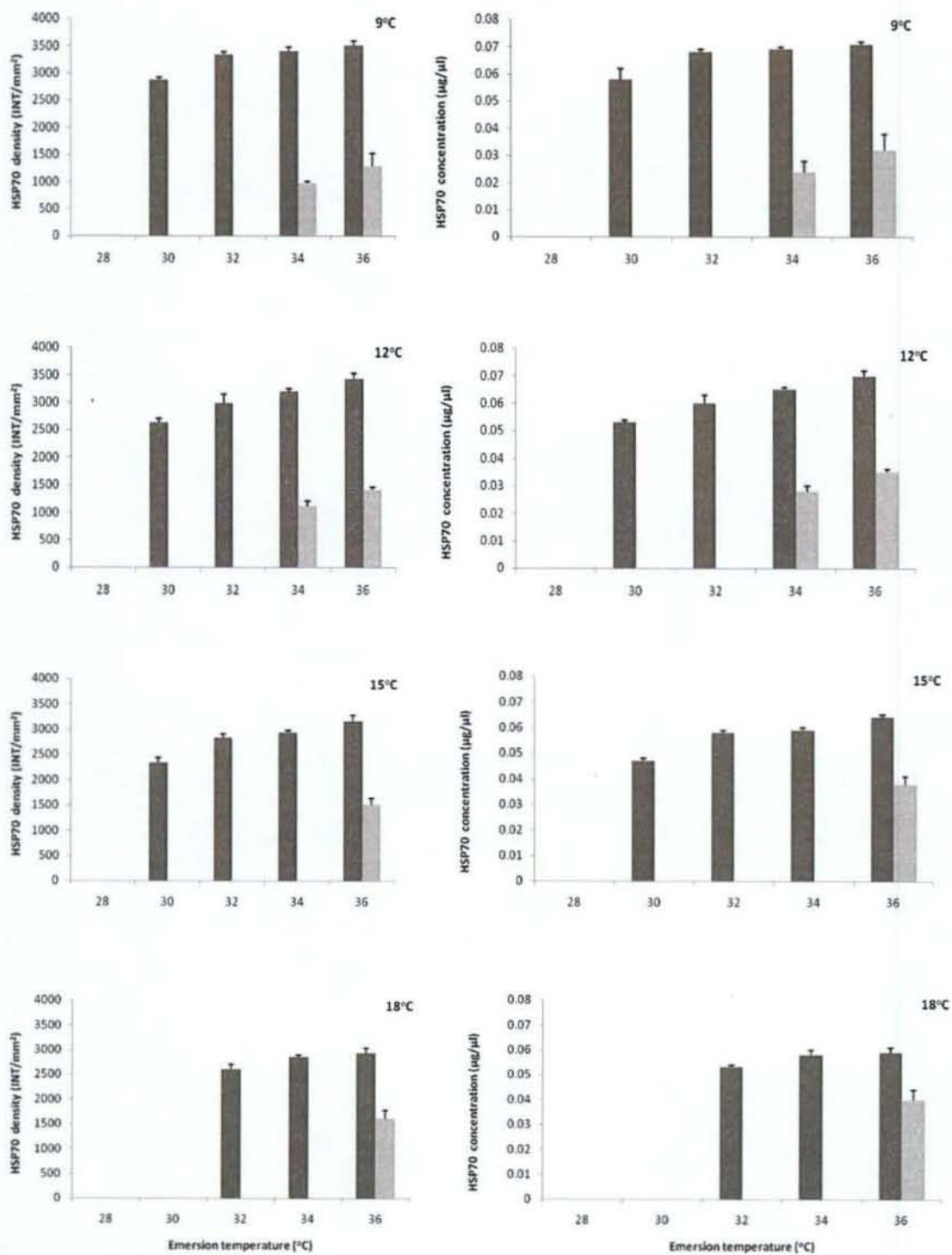


Figure 5.5 Left hand column: mean ( $\pm$ SD) inducible Hsp70 densities (INT/mm<sup>2</sup>). Right hand column: mean ( $\pm$ SD) concentration of inducible Hsp70 ( $\mu$ g/ $\mu$ l) expressed by the mussels, *Mytilus galloprovincialis* (black columns) and *Perna perna* (grey columns), per acclimation (immersion) temperature and emersion temperature treatment.

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18	6	8	10	12	14	16	18

Table 5.2: Mean ( $\pm$ SD) concentration of inducible Hsp70 ( $\mu\text{g}/\mu\text{l}$ ) produced by the mussels, *Mytilus galloprovincialis* and *Perna perna*, per acclimation (immersion) temperature and emersion temperature treatment.

Immersion (°C)	Emersion (°C)	Hsp70 concentration ( $\mu\text{g}/\mu\text{l}$ )			
		<i>M. galloprovincialis</i>	SD $\pm$	<i>P. perna</i>	SD $\pm$
9	28	0	0	0	0
	30	0.058	0.004	0	0
	32	0.068	0.001	0	0
	34	0.069	0.001	0.024	0.004
	36	0.071	0.001	0.032	0.006
12	28	0	0	0	0
	30	0.053	0.001	0	0
	32	0.06	0.003	0	0
	34	0.065	0.0008	0.028	0.002
	36	0.07	0.002	0.035	0.001
15	28	0	0	0	0
	30	0.047	0.001	0	0
	32	0.058	0.001	0	0
	34	0.059	0.001	0	0
	36	0.064	0.001	0.038	0.003
18	28	0	0	0	0
	30	0	0	0	0
	32	0.053	0.001	0	0
	34	0.058	0.002	0	0
	36	0.059	0.002	0.04	0.004

## Chapter 6: Synthesis

This thesis uses a multi-faceted approach to assess spatio-temporal change in intertidal species macro assemblages at rocky sites located along the coast of South Africa. Detected changes in species composition were considered alongside patterns of bioinvasion, assessed within this thesis and evidence pertaining to climate driven temperature shifts over comparable time scales. The aims were achieved as follows:

- (1) A thorough assessment of the status of rocky-intertidal research with respect to intertidal community structure, biogeographic delimitations patterns of bioinvasion and climate change was conducted from both the international and local perspective.
- (2) The status of marine introduced and cryptogenic species was re-assessed and the resultant inventory analyzed for spatio-temporal patterns of bioinvasion across the marine and estuarine habitats of South Africa.
- (3) Historic and contemporary sampling data were compared to identify significant spatio-temporal changes in the composition of species assemblages within and between the biogeographic regions of South Africa and on a finer spatial scale within a transition zone between biogeographic regions, located on the west coast.
- (4) Detected changes were compared to patterns of bioinvasion established in (2) above and evidence for climate driven temperature shifts within the different regions.
- (5) The physiological temperature response of an introduced, cool-water adapted mussel, *Mytilus galloprovincialis*, and native, warm-water adapted mussel, *Perna perna*, following evidence that the former had proliferated contributing

to dissimilarities in species assemblages and the latter had experienced a significant range contraction.

Intertidal systems are located at the interface between oceanographic and atmospheric regimes. In order to relate climate and ecosystem change over comparable time frames, sea and ambient air temperatures were selected as indicators of how climate change may be impacting near-shore systems. Through collaboration with oceanographers and climatologists, it was possible to identify relevant data sets and modify these to establish decadal trends. In order to understand why temperature changes were occurring, it was important to reference the decadal data with regional and global climate change theories. The major trends identified using a combination of AVHRR and *in-situ* data were that (a) near-shore cooling was evident in the cool and warm-temperature regions on the west and south coast – the result of changes in wind and upwelling regimes and (b) the sub-tropical and tropical regions on the east coast were experiencing warming trends, influenced by changes to the overall temperature of the Agulhas Current.

It was recognized that, although there had been a great deal of progress in the field of marine bioinvasion research in South Africa over recent decades, knowledge was still limited. In order to assess the role of bioinvasions as potential drivers of change in intertidal systems, a spatial and temporal analysis was essential in establishing an overall status benchmark for the region. Given the rich shipping history of the region and numbers of bioinvasions that had been recorded in comparative, but developed regions, it was anticipated *a priori* that the full scale of introductions was probably being underestimated. A protocol was developed in order to identify introduced

species hidden within historical literature, undersurveyed habitats and unresolved taxonomic issues. Within a period of less than a year, the number of marine introductions and cryptogenic species has been increased four and two-fold from 22 and 18 to 85 and 40 respectively. This was a large step toward revealing the true scale of bioinvasions in South Africa, although there is still much work to be done. Through continued application of the protocol to a wider range of habitats, phyla and historic documents, it is predicted that the inventory will continue to expand.

Whereas temporal analysis of the introductions data was limited to assessing rates of discovery, the increase in the number of known introductions facilitated a spatial analysis – the first of its type to be applied in the South African region. This revealed several interesting patterns of bioinvasion. For example, the origin of the majority of introductions was identified as the Eastern Atlantic, vectored primarily by ballast water. Provincial differences in bioinvasion pattern were also evident, with the cool-temperate province and transitional zones in-between supporting the highest numbers and diversity of introductions. The majority of introductions appeared to be concentrated around harbour areas, although a few open coast invaders, which have the potential to impact rocky intertidal communities, were evident. This body of work has provided a sound baseline of information from which (a) initial patterns of bioinvasion can be elucidated, (b) knowledge gaps can be identified, (c) re-analyses and new analyses can be conducted as the inventory continues to grow and (d) information imparted to the international community that may eventually facilitating global wide comparisons.

In order to assess spatio-temporal changes in species assemblages, relevant historic information spanning 76 years were data mined from a range of databases generated through sampling in 1933-1944, 1989-1992 and 1987. Sites spanned the biogeographic regions of the coast and transitional zones in-between. Contemporary surveys of macro-assemblages (macroalgae and macrofauna) were conducted across comparative sites. Significant differences in the composition of species assemblages were found across all biogeographic regions. However, the three major changes were as follows:

- (a) Species composition changed within the cool (CTP) and warm-temperate (WTP) regions in line with localized cooling of near-shore waters. Species richness was reduced and cool-water adapted species replaced warm-water adapted species. The most characteristic species on the shore was the introduced mussel, *Mytilus galloprovincialis*. The overall effect of these changes was increased homogenization of rocky intertidal communities across these regions.
- (b) Species composition changed within the sub-tropical (STP) and tropical (TP) regions in line with localized warming of near-shore waters. Species richness increased, as did the number of warm-water adapted species.
- (c) Within the False Bay (TZ1) transition zone located between the CTP and WTP, a range contraction was observed in a warm-water, indigenous mussel, *Perna perna*. The contraction was quantified as a 50 km retreat over a period of two decades. However, it was qualitatively assessed to be in the region of approximately 400 km. This was paralleled by the proliferation of the cool-water adapted, introduced mussel.

In the context of global climate change scenarios, the observed distributional shifts support climate change predictions forecasted for the intertidal zone. As far as the author is aware, this is one of only a few examples from the southern hemisphere that report biogeographic changes, potentially driven by climate change. Interestingly, the range contraction represents an equator-ward compression of the southern range limit of a warm-water species – a possible response to near-shore cooling.

Data collated and added through this study provides an excellent local 'baseline' from which the collection, collation and analysis of comprehensive data time series can evolve to form part of a longer-term monitoring program aimed at continued detection, quantification and forecasting of assemblage shifts that are linked to patterns of bioinvasion and shifts in temperature trends.

The establishment and spread of a relatively cool-adapted, introduced mussel, *Mytilus galloprovincialis*, contributed significantly to the range contraction, species compositional changes and increasing similarities between assemblages on the west and south coast. Experimental manipulation and immuno-assay were combined in order to measure inducible Hsp70 expression over a range of immersion and emersion temperatures. Analyses revealed significant differences in the plasticity of the heat-stress response within the two mussel species. Differences in induction thresholds, and thermotolerance were identified indicating the ecological energetics of the introduced mussel were unlikely to be negatively impacted by near-shore cooling in comparison to the native mussel. This could translate into the observed distributional shifts. The experiment was the first of its kind to be conducted in South

Africa, for the species selected and was therefore novel in both its design and application.

To conclude, significant spatial-temporal changes are evident within the species composition of assemblages located at sites along the South African coast. The results of the study indicate that both climate and bioinvasions are influential in altering species assemblages across a variety of temporal and spatial scales. In addition, physiological evidence identified that introduced and native species respond differently to temperature pressure. All aims were achieved, the outcomes of which will contribute substantially to this field of research both locally and internationally.

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