

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

**HISTORY AND STATUS OF OYSTER EXPLOITATION AND
CULTURE IN SOUTH AFRICA, AND THE ROLE OF OYSTERS AS
VECTORS FOR MARINE ALIEN SPECIES**

Tanya M. Haupt

This thesis is submitted for the degree of
Master of Science

Zoology Department and Marine Biology Research Centre,
University of Cape Town

JULY 2009

Supervisors: C. L. Griffiths

T. B. Robinson

DECLARATION

I hereby declare that all the work presented in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted for a degree at any other university.

Signed by candidate

.....
Tanya M. Haupt

30.06.07

.....
Date

ACKNOWLEDGEMENTS

My supervisors Charles Griffiths and Tamara Robinson are thanked for their guidance and input. I am especially grateful to the manager of the Striker Fishing Oyster Company, Antonio Tonin, for his input, as well as allowing visits to his farm. The staff of Marine and Coastal Management (Department of Environmental Affairs and Tourism) and Paul de Bruyn from the Oceanographic Research Institute are thanked for their provision of data. Lastly, thanks to my family and friends (Angela Mead, Candice Lyons, Lizelle Odendaal) for their support. A special thanks to Dwayne Phillips and Louise Lange for their unconditional support and assistance during laboratory and fieldwork.

Financial support was provided by the Centre of Invasion Biology (CIB) – a joint venture between the National Research Foundation (NRF) and Department of Science and Technology (DST).

TABLE OF CONTENTS

ABSTRACT	1
AIMS AND OBJECTIVES	3
PART 1:	
CHAPTER 1. History and status of oyster exploitation and culture in South Africa	4

PART 2:	
CHAPTER 2. Oysters as vectors of marine aliens with notes on four newly-recorded marine alien species associated with oyster farming in South Africa	26
CHAPTER 3. Intra-regional translocations of epi-and infaunal species associated with the pacific oyster <i>Crassostrea gigas</i>	44

CHAPTER 4. Summary and Conclusions	66
LITERATURE CITED	69

ABSTRACT

In South Africa, both wild and cultivated oysters are consumed. Edible wild oysters include *Striostrea margaritacea*, *Saccostrea cucullata*, *Ostrea atherstonei* and *O. algoensis* and all occur along the South and East coasts. These oysters were, or are, exploited commercially, recreationally and via subsistence fishers with *S. margaritacea* being the most targeted species. The commercial harvesting areas are along the Southern Cape coast and in KwaZulu-Natal. The Southern Cape coast is the largest harvesting area with 102 of the 145 pickers employed in the region. Commercial and recreational harvesting is managed by the Marine and Coastal Management Branch of the Department of Environmental Affairs and Tourism. Data on the total annual catch of oysters in these provinces are minimum estimates, as collectors do not always comply with the harvesting regulations. Subsistence harvesting is largely unmanaged, except in KZN, and is particularly rife in the Eastern Cape Province. The culture of oysters is dependent on importing *Crassostrea gigas* spat mostly from Chile. Oyster production statistics are only available since 1985, but approximately two million *Crassostrea gigas* oysters were produced annually throughout the seventies and early eighties. Since then, production has fluctuated over the years with an approximate increase of six million between 1985 and 1991, a decrease of five million between 1991 and 1998, and is presently stable. The establishment and closure of a highly productive farm in the late eighties and early nineties respectively, as well as improved production in recent years, has resulted in these trends. Although the market for oysters has grown, production has not kept up with demand, due to a lack of suitable locations for mariculture purposes. Finding suitable sites for oyster cultivation along the Northern Cape coast and establishing local oyster hatcheries for *C. gigas* oysters is suggested as the way forward. The latter would also prevent associated marine alien species from being imported with spat. Globally, oysters are well known vectors of marine alien species and despite oyster imports as early as 1894 into South Africa, this topic has been afforded little or no local attention. A visit to various oyster farms in South Africa resulted in the discovery of four newly-recorded alien species: the black sea urchin *Tetrapygus niger*, from Chile, the European flat oyster *Ostrea edulis*, thought to be locally extinct following its intentional introduction into

South Africa in 1946, Montagu's crab *Xantho incisus*, from Europe, and the brachiopod *Discinisca tenuis*, from neighbouring Namibia. Oyster imports are suggested as their most likely vector into South Africa and the biological attributes of some emphasizes the possible threat and the need to limit or prevent their spread. Local or intraregional translocation of *C. gigas* and associated species, including aliens colonizing the area, may aid in this spread. Oysters host a diverse community of epi- and infaunal fouling taxa, which can be accidentally translocated along with their hosts in the course of commercial oyster trade. Thus, the types and quantities of fouling taxa occurring on farmed *Crassostrea gigas* were examined. How effectively these taxa are removed by standard cleansing techniques and whether those that persist after washing, survived intraregional translocation, were also examined. Cleaning and translocating oysters significantly reduced both the quantity (by more than 30 and 40 times respectively) and variety of fouling taxa. Although the mean abundance (A) or biomass (B) of taxa in uncleansed oysters (A: 79.48 ± 233.10 (SD), B: 0.034 ± 0.314 (SD)) were greatly reduced in cleansed oysters (A: 2.30 ± 7.65 (SD), B: 0.0003 ± 0.002 (SD)), small quantities still managed to survive translocation (A: 1.87 ± 7.43 (SD), B: 0.006 ± 0.020 (SD)). Thus, the effectiveness of exposing oysters to freshwater or heated seawater as a more thorough cleansing regimen, to prevent the translocation of such taxa, were examined. Results indicated that oysters were able to survive for a longer time in freshwater (0% mortalities after 18 h) than in heated seawater (26.7% mortalities after 40 sec), but most taxa were eliminated more effectively by the latter treatment (e.g. 88.5% of the mudworm *Polydora hoplura* died after 20 sec compared to 97.5% after 18 h in freshwater). However, only a single reproductive individual of an alien species may be required for a successful introduction, and soaking for 20 sec in heated seawater would still be ineffective. An alternative treatment of 18 h in freshwater and 20 sec in heated seawater or freshwater, is suggested as a more effective treatment.

AIMS AND OBJECTIVES

The overall aim of this thesis is to document the history of oyster exploitation and culture in South Africa and to investigate the role of this industry in the introduction and spread of marine alien species. In pursuit of these objectives the dissertation is presented in two parts:

Part 1 reviews the history and current status of the oyster fishery and culture industry in South Africa and is dealt with in Chapter 1. Attention is given to the harvesting practices and yields of the four naturally occurring oyster species harvested along our coast, as well as the necessity of introducing an alien oyster species to meet increasing demand and the development and status of this industry. This chapter is designed for publication in the *Journal of Shellfish Research*, where it will form a parallel to a similar well-cited publication on the exploitation and culture of mussels in the region. No similar review currently exists.

Part 2 of the thesis, comprising Chapters 2 and 3 focuses on introduced oysters as possible vectors for marine alien species. Chapter 2 provides a review of the history of oyster movements worldwide and an account of alien species introduced to various localities through oyster culture. This review brings attention to the absence of such studies being conducted in South Africa, compared to the extensive literature which exists for many parts of the world. Thus, Chapter 2 also examines oyster farms in the region in a directed effort to detect unrecorded marine alien species that might have been introduced via the oyster trade. Chapter 3 examines the spread of organisms, particularly marine alien species, through the intraregional transportation of introduced oysters hence aiming to identify the types and quantities of organisms transported via the oyster trade. The chapter also devises and tests mechanisms for minimizing translocation by treating oysters either with hot or fresh water prior to shipping. Both chapters are presented in the format of papers for later publication.

PART 1

University of Cape Town

CHAPTER 1

University of Cape Town

HISTORY AND STATUS OF OYSTER EXPLOITATION AND CULTURE IN SOUTH AFRICA

INTRODUCTION

The South African coastline is divided into three biogeographical provinces and extends from the Namibian border (28°S16°E) in the West, to that of Mozambique (26°S32°E) in the East, a distance of 3100 km. The main features of this coastline are the cold Benguela Current of the West coast and the warm Agulhas Current of the South and East coasts. These two major current systems determine the distribution patterns of many marine organisms (Brown & Jarman 1978, Branch & Griffiths 1988, Emanuel *et al.* 1992).

Various families of oysters occur along this coastline and are listed in Kilburn & Rippey (1982); however only members of the family Ostreidae are of commercial interest in this region, which is too temperate for the culture of pearl oysters of the family Pteriidae. Four indigenous or “wild” species of Ostreidae are recognised from South Africa, these belonging to three genera: *Striostrea*, *Saccostrea* and *Ostrea*. *Striostrea margaritacea* and *Saccostrea cucullata* were previously known as *Crassostrea margaritacea* and *C. cucullata* respectively. *Ostrea atherstonei* and *O. algoensis* represent the genus *Ostrea*, also known as ‘flat oysters’ (Kilburn & Rippey 1982). In addition to these indigenous species, the introduced Pacific oyster *Crassostrea gigas* is widely farmed and has become naturalized in several estuaries along the South coast (Robinson *et al.* 2005a).

DISTRIBUTION PATTERNS, SPECIES CHARACTERISTICS AND HABITAT PREFERENCES

Striostrea margaritacea (False Bay to Mozambique)

S. margaritacea, the Cape rock oyster (Fig. 1.1), is a large, heavy oyster, which can grow up to 180 mm shell length (Branch *et al.* 2005). Individuals have a deep, multi-layered, cup-shaped lower valve cemented to the substratum and a thin flat upper valve, usually with fine radially striated conchiolin on the exterior (Kilburn & Rippey

1982). This conchiolin, together with the iridescent mother-of-pearl to gold shell interior and the smooth valve margins with no distinct colour, are characteristics that distinguish this species from *S. cucullata* (Robinson *et al.* 2005a). It is common on rocky reefs from low water to about 5 m depth (Kilburn & Rippey 1982). *S. margaritacea* is the most common indigenous oyster species in the Western Cape and also the most economically important native oyster in this region (Branch *et al.* 2005).

Saccostrea cucullata (Algoa Bay to KwaZulu-Natal)

S. cucullata, the Natal rock oyster (Fig. 1.1), is smaller than *S. margaritacea*, growing to only 70 mm shell length (Branch *et al.* 2005, Robinson *et al.* 2005a). The lower valve is deeply hollowed below the hinge and cemented to the rock, while the upper valve is relatively flat. Unlike *S. margaritacea*, the radial threads are absent, the shell interior is a non-iridescent whitish grey and the valve margins are black, with undulating folds (Kilburn & Rippey 1982). Individuals form a conspicuous belt on rocks in the upper mid-tidal zone where they settle on shells and are known to thrive under muddy conditions, the roots of mangrove trees and even reeds (Kilburn & Rippey 1982, Branch *et al.* 2005).

Ostrea atherstonei (Saldanha Bay to South coast of KwaZulu-Natal)

O. atherstonei, the red oyster (Fig. 1.1), has a shallow lower valve that is not hollowed below the hinge and its colouring ranges from purplish-brown to wine-red with a maximum shell length of 105 mm. Individuals inhabit sheltered reefs on the open coast, mainly below the low tide level. *O. atherstonei* provides excellent eating, but does not form beds and is therefore of little commercial importance (Kilburn & Rippey 1982, Branch *et al.* 2005).

Ostrea algoensis (False Bay to East London)

O. algoensis, the Cape weed oyster (Fig. 1.1), is relatively small, often delicate and flattened, and grows to only 45 mm shell length. The internal margin bears distinct chomata in the hinge region and the exterior is either smooth, or has weak radial folds. The exterior colouring is yellow or yellowish-grey with black or purplish rays and the interior is a very pale brownish-yellow to greenish-grey. *O. algoensis* is found in pools or in the mouths of estuaries and is often attached to the underside of intertidal rocks (Kilburn & Rippey 1982).

Crassostrea gigas

C. gigas, the introduced Pacific oyster (Fig. 1.1), is the most important commercially marketed oyster globally and in South Africa. It is quite similar in appearance to *S. cucullata* and *S. margaritacea* and is often confused with them. It is characterised by a non-iridescent white to off-white shell interior, has at least one adductor scar purple in colour and undulating valve margins that show no colouration, although a few may be mauve-black (Robinson *et al.* 2005a). *C. gigas* is usually larger than *S. cucullata* and *S. margaritacea*, reaching a maximum size of 200 mm. Naturalized populations have recently been found in the Breede, Goukou and Knysna Estuaries on the Southern Cape coast (Fig. 1.1). The Breede Estuary supported the largest population of $184\,206 \pm 21\,058.9$ compared to 876 ± 604.2 and 1228 ± 841.8 for the Goukou and Knysna Estuaries respectively (Robinson *et al.* 2005a). In the Breede River Estuary, the origins of *C. gigas* are unknown, but it is possible that it became established as a result of trial introductions carried out in Southern Cape estuaries by the Division of Sea Fisheries of the Department of Trade and Industries. Another possible source of introduction could be that this species has expanded its range from oyster farms in the East (e.g. Knysna) (Tonin 2001). Individuals inhabit the low intertidal zone and are found to a depth of 1 m (Robinson *et al.* 2005a).

OYSTER EXPLOITATION

South African shellfish resources have been exploited by indigenous people for many thousands of years (Bigalke 1973, Volman 1978, Avery & Siegfried 1980, Siegfried *et al.* 1985, Hockey & Bosman 1986, Hockey *et al.* 1988, Van Erkom Schurink & Griffiths 1990, Lasiak 1991, Dye *et al.* 1994a, Kyle *et al.* 1997), as evidenced by the occurrence of shell remains in prehistoric middens (Thackeray 1988, Van Andel 1989). Harvesting occurred all along the coast, with the oldest evidence being from the Eastern Cape. Molluscan faunal remains excavated from here provide evidence that Middle Stone Age inhabitants from the Late Pleistocene period exploited shellfish in this area (Thackeray 1988, Van Andel 1989). Archaeological evidence on the West coast, however, provides a more detailed account of prehistoric exploitation. The volume of the midden deposited is an indication of the intensity of harvesting. Taking the latter into account, middens deposited on the West coast indicate a low level of

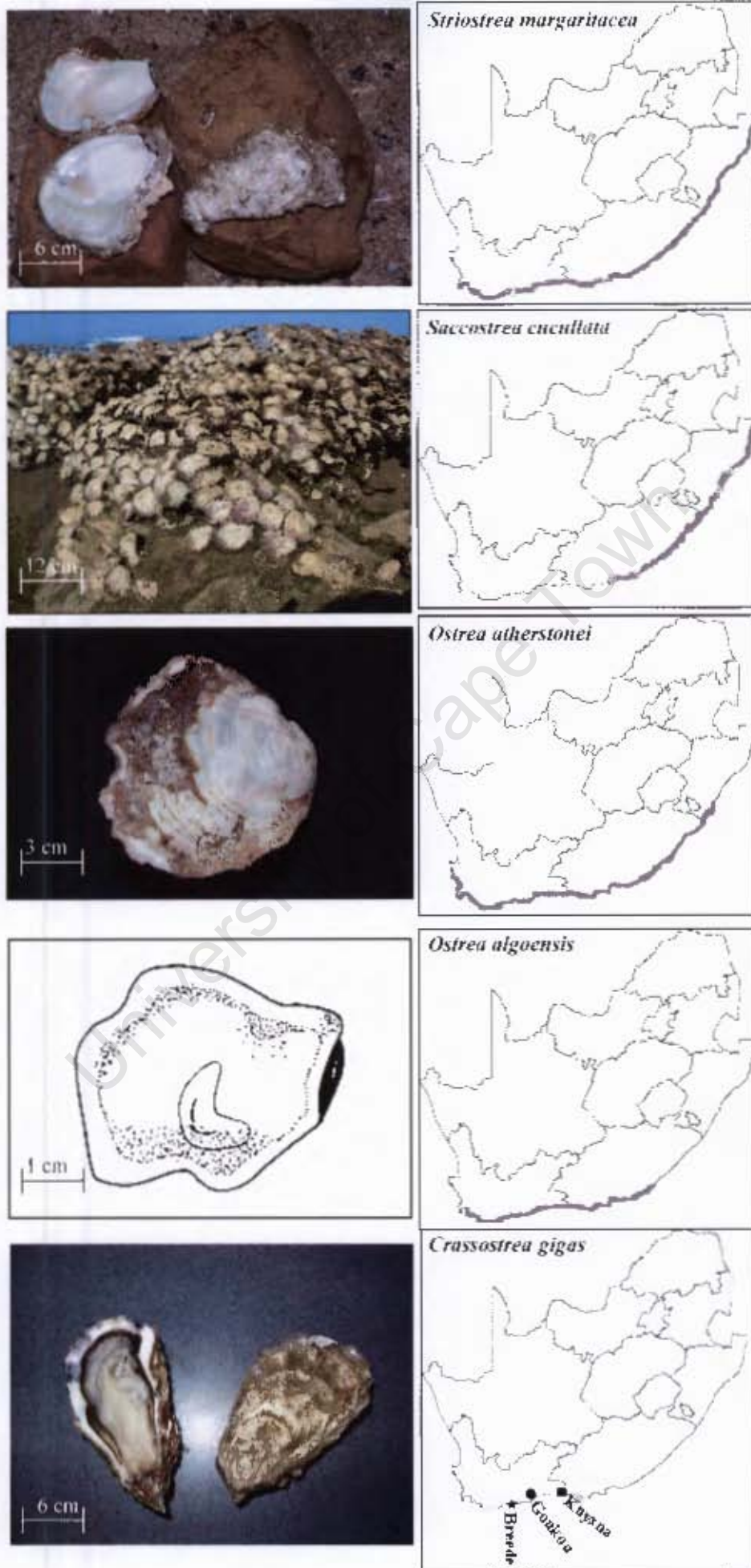


Figure 1.1. Appearance and distribution of wild and introduced oysters in South Africa

exploitation between 15 000 and 2 900 years B.P. A dramatic change took place between 2 900 and 2 100 B. P. when “megamiddens” (huge open deposits of up to 30 000 m³) were created (Buchanan 1988, Jerardino & Yates 1996). According to Henshilwood *et al.* (1994), charcoal remains in megamiddens suggest that shellfish were dried and stored. This phase ceased around 2 100 B.P., after pastoralism was introduced as an alternative food resource, as distance to the sea probably increased significantly due to sea level changes and widening coastal plains (Van Andel 1989, Sealy & Yates 1994). This resulted in a decline of human activities on the coast. However, according to Griffiths & Branch (1997), even with the occurrence of megamiddens, prehistoric consumption and population densities were low by modern standards. Prehistoric middens are mainly composed of marine species such as the black mussel *Choromytilus meridionalis*, the white sand mussel *Donax serra* and the brown mussel *Perna perna*. Limpets such as *Scutellastra granularis*, *S. granatina* and *S. argenvillei*, as well as whelks *Burnupena spp*, were also found in middens (Parkington *et al.* 1988, Thackeray 1988, Jerardino & Yates 1996, Halkett *et al.* 2003, Jerardino *et al.* 2008). Oysters do not, however, appear to have been targeted at this time, as the occurrence of oyster shells has not been reported from these middens.

In the modern era, commercial, recreational and subsistence harvesting of wild oysters occurs along the Southern Cape coast and in KwaZulu-Natal (KZN). *Striostrea margaritacea*, with its extensive distribution range, is targeted commercially, while other species, mainly *Saccostrea cucullata*, are harvested for recreational and subsistence purposes. The Directorate of Marine and Coastal Management (MCM) of the Department of Environment Affairs and Tourism (DEAT), is the primary institution responsible for the management of both the recreational and commercial oyster fisheries along the Southern Cape coast. In KZN, Ezemvelo KwaZulu-Natal Wildlife (EKZNW) is responsible for management of these fisheries on behalf of MCM. Prior to 2002, the South African oyster fishery was managed as two separate entities, according to their areas of operation, namely KwaZulu-Natal and the Southern Cape. Presently, both fisheries are managed as a single national fishery and four commercial oyster-harvesting areas are recognised, i.e. Southern Cape coast, Port Elizabeth, KZN North and KZN South (DEAT 2006) (Fig. 1.2). No legally sanctioned commercial harvesting occurs along the remainder of the South and East coasts, although oysters do occur there (Fig. 1.1). Recreational

collectors (e.g. holiday-makers) have to apply for a permit and are allowed a maximum of 25 oysters per day, which can be collected by hand, or with an implement (e.g. blade or flat edge not exceeding 40 mm and not less than 1 m in length) (DEAT 2008/2009). Details of the spatial and temporal exploitation and patterns of each species are given below:

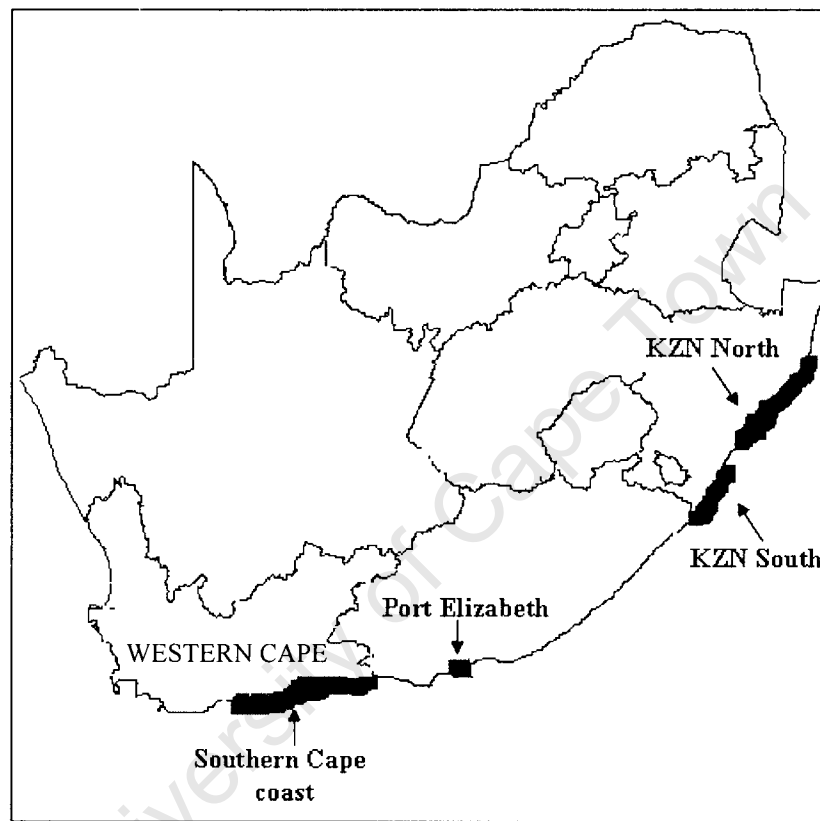


Figure 1.2. Map of South Africa showing provincial boundaries and the four legally recognized commercial oyster harvesting zones, the Southern Cape coast, Port Elizabeth, KZN North and KZN South.

Striostrea margaritacea

(a) Southern Cape coast and Port Elizabeth

S. margaritacea is collected for small-scale commercial, recreational and subsistence use along the Southern Cape coast and throughout the Eastern Cape (Cockcroft *et al.* 2002) (Fig. 1.2). Previously, regulations were implemented for harvesting oysters along the Southern Cape coast (e.g. 25 oysters per picker per day), but the fishery was still poorly managed, as no licensing, or submission of catch returns were implemented (Dye *et al.* 1994b). Presently, a licence is required to harvest oysters commercially and the Southern Cape houses the majority of pickers, i.e. 102 of the

145 pickers employed in South Africa. Commercial pickers are also expected to complete catch return forms on a regular basis, indicating the number of oysters collected and the number of outings undertaken. These forms are then collected by Marine and Coastal Management inspectors. Commercial harvesting of oysters is managed by means of limiting the number of pickers, with no daily bag limit, and effort is split across areas according to the extent of accessible oyster reef (DEAT 2006). The fishery is further controlled by a closed season from 15 December – 05 January, in order to limit conflict between recreational harvesters and the commercial oyster sector (DEAT 2006).

There are only three legal commercial pickers in Port Elizabeth (Fig. 1.2), and no harvesting of the oyster beds is practised, as only washed-up oysters are being collected (DEAT 2006). Levels of exploitation, are, however, still high in the rest of the Eastern Cape due to recreational and mostly subsistence harvesting (Kiepiel & Quinlan 1997, Robertson & Fielding 1997, Britz *et al.* 2001, Cockcroft *et al.* 2002).

Figure 1.3 shows that the total commercial catch of oysters per annum along the Southern Cape coast and Port Elizabeth region has decreased since the earliest record in 1972 till present. Reasons for this decline could be either a decrease in stocks of *S. margaritacea*, due to over exploitation, or stricter regulations being implemented. These figures are not, however, entirely reliable, as pickers often fail to submit catch return forms (L. Madikaza, MCM pers. comm). Thus, the total annual catch is probably higher than is actually presented by the results.

Subsistence harvesting of *S. margaritacea* also occurs to some degree along the Southern Cape coast, without any firmly enforced conservation legislation (Siegfried *et al.* 1994, Griffiths & Branch 1997). The oysters are not usually consumed by fishers themselves, but are rather sold to generate an income. It was therefore suggested that people undertaking these activities should be considered as small-scale commercial fishers, rather than subsistence fishers (Branch *et al.* 2002, Clark *et al.* 2002). Thus, in 2002, limited commercial oyster rights were allocated to empower a number of former subsistence fishers, who were previously prevented from legally selling their harvests (DEAT 2006).

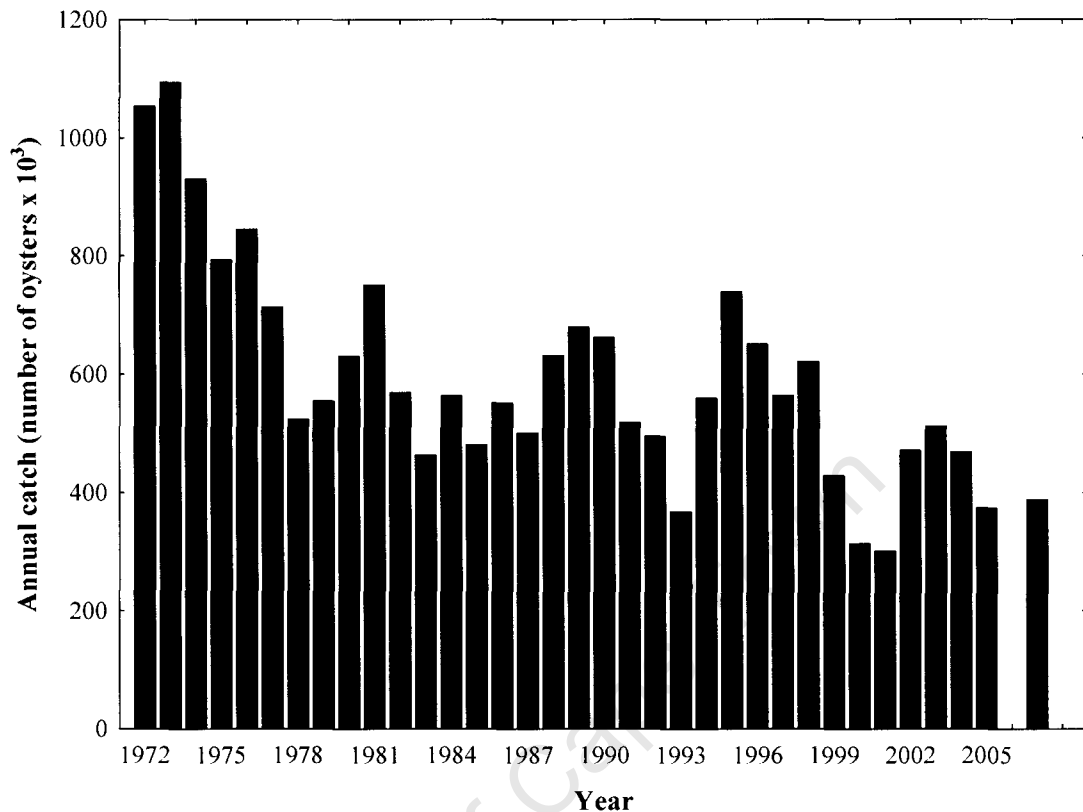


Figure 1.3. Annual commercial catches of *Striostrea margaritacea* between 1972 – 2007 from the Southern Cape coast and Port Elizabeth regions (Data sourced from L. Madikaza, MCM, DEAT).

b) KwaZulu-Natal

In KZN, *S. margaritacea* is collected for small-scale commercial, recreational and subsistence purposes (Cockcroft *et al.* 2002). The most important beds occur on the North coast, with 25 pickers, compared to only 15 on the South coast (Schleyer & Kruger 1990, DEAT 2006) (Fig. 1.2). The oyster fishery in this province has operated for over a century and evidence of harvesting comes from as early as 1894 (Thompson 1913). The fishery is separated into a local trade (commercial) fishery and a “visitor” (recreational) fishery. The former is currently the only commercial intertidal fishery along the KZN coast (De Bruyn 2006).

The commercial fishery was initially managed by dividing the coastline into three separate harvesting regions. In the mid-1950s, these regions were divided into nine zones (De Bruyn 2006). In 1998 this was again revised, reducing the three regions to two with five zones in each, following recommendations from Schleyer (1988) and

Schleyer & Kruger (1991) (Fig. 1.4). Harvesting is controlled by a rotational system that operates over a five-year period. Two adjacent zones are consecutively harvested, each for one year, first by recreational, then by commercial fisheries and then left fallow for the following three years (De Bruyn 2006).

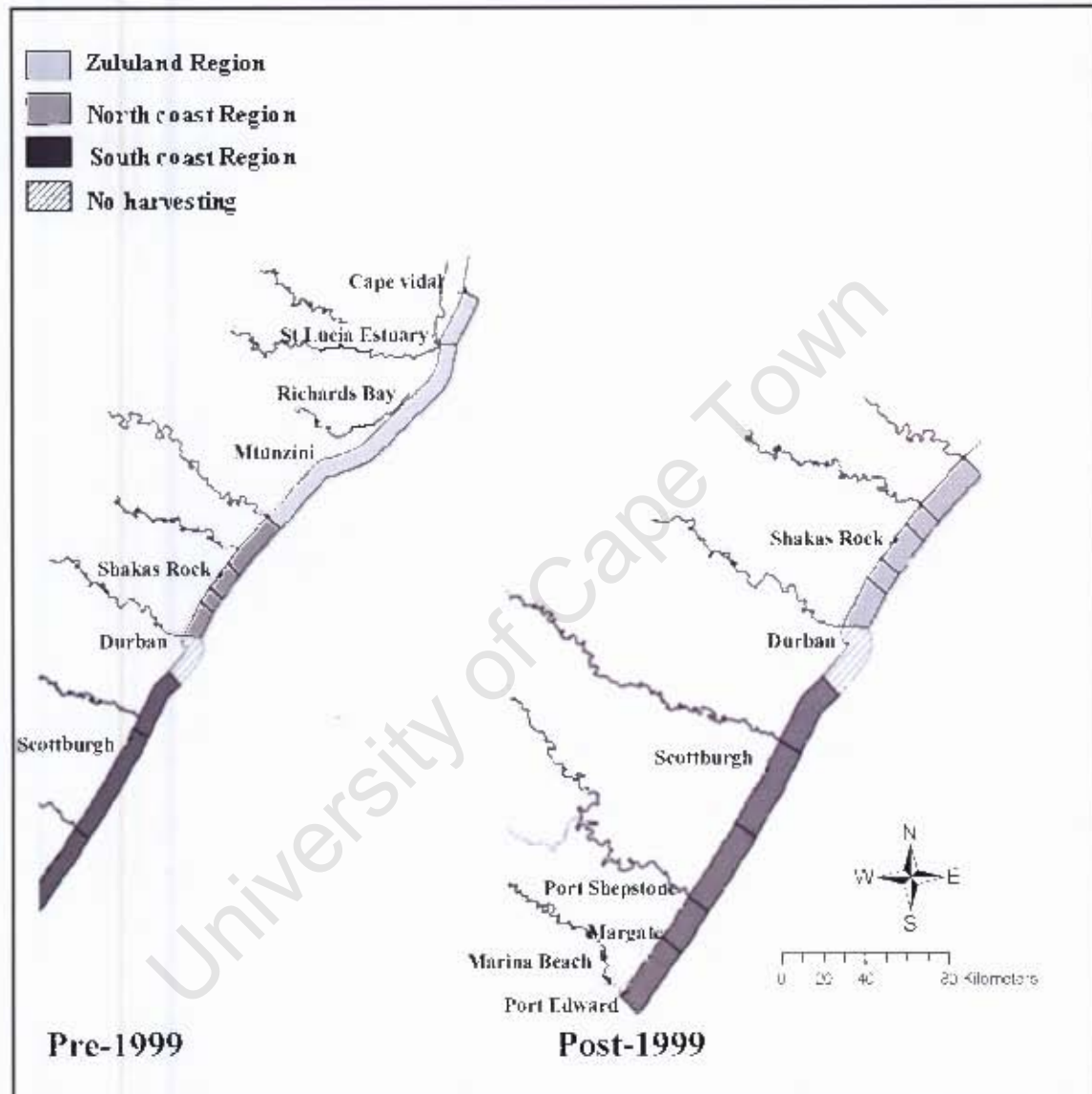


Figure 1.4. Commercial oyster harvesting zones along the KZN coast prior to and after 1999. The Zululand region, used for oyster harvesting prior to 1999, is no longer being exploited (Map sourced from De Bruyn 2006).

Both commercial and recreational fisheries are managed by licences, subject to the submission of catch returns, which provide useful statistics for managers. Prior to 1998, a daily bag limit of 50 oysters per recreational permit per day was allowed, but this has since been reduced to 25 oysters per permit per day, in an effort to prevent overexploitation. The commercial regulations have also changed. Prior to 1999, five

pickers per licence were allowed, after which ‘half’ and ‘full’ licences allowing between five and twelve pickers were issued. Presently, pickers themselves are registered directly, doing away with full and half licenses. As a result of this change, commercial bag limits per license per day have decreased from 960 oysters to 190 oysters per picker per day. The gear and instruments used have also changed. Historically, women and girls harvested oysters by entering the water to depths not greater than their chests and prying oysters from the rocks with a 1 m implement having a flattened end no wider than 4 cm. Oysters were located by feeling them on rocks and by sight, if the water was clear. The use of diving gear was prohibited. Thus, only oyster populations found in the intertidal and near-subtidal zones were exploited during spring low tides. Harvesting now occurs predominantly by males, who use masks and snorkels and hence are able to exploit oysters in slightly deeper water (1.5 m). Divers are, however, still restricted from using fins and flotation devices. This prevents the subtidal “seed” stock or “mother beds” from being exploited (Dye *et al.* 1994b, De Bruyn 2006).

Prior to the implementation of the new zonation system in 1998, stocks of *S. margaritacea* were diminishing in KZN. Over-fishing, due to an increase in the annual commercial catches (Fig. 1.5) and other factors, such as cyclical population changes and environmental changes, may have all played a role in this decline (Schleyer & Kruger 1990). De Bruyn *et al.* (2008) found that the abundance of the stock has increased since the new rotational harvesting system was introduced in 1998, indicating a recovery. Nevertheless, Figure 1.5 indicates that the total annual commercial catches of *S. margaritacea* have decreased from 1981-2007. This trend flattened between 1998 and 2005, with catches being relatively stable. However, in 2007, a further decline was seen. The lower catches are a result of lower effective effort.

Apart from the commercial and recreational oyster fisheries, subsistence harvesting of *S. margaritacea* and other oysters, such as *S. cucullata*, also exists in KZN (Kyle *et al.* 1997). Data relating to such informal fishing activities are unavailable, because no control has been implemented in the past. Presently, however, a management plan for subsistence fisheries in KZN has been drawn up, and controls are in the process of being implemented.

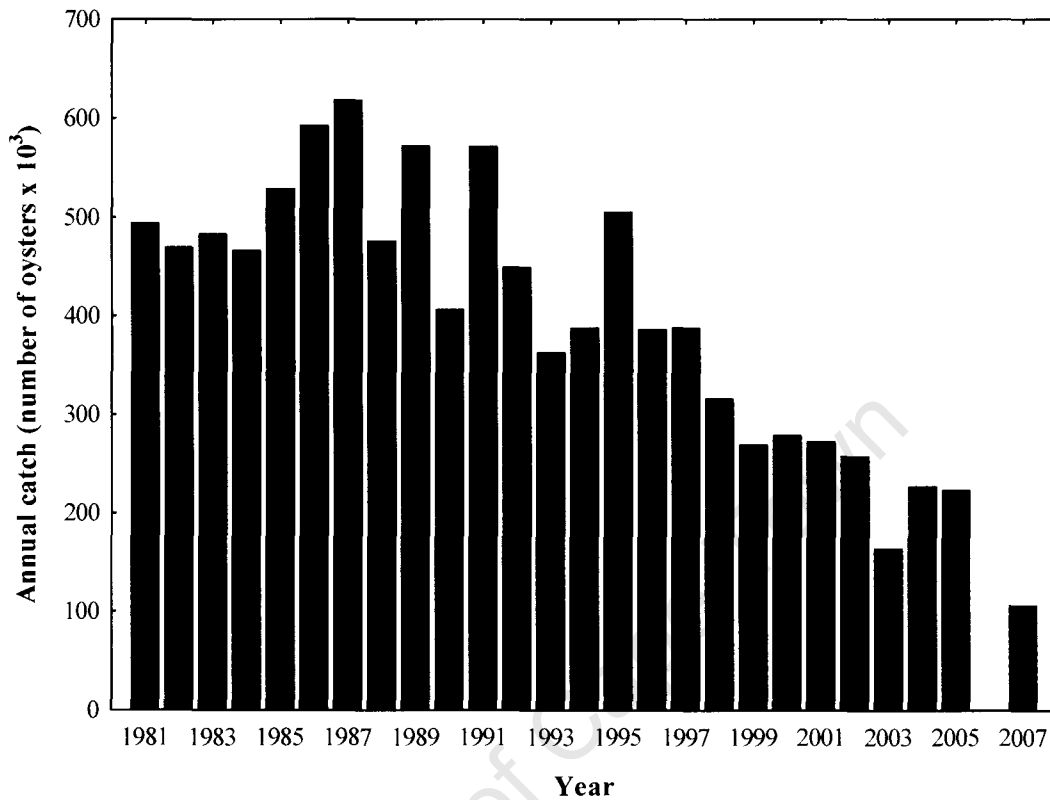


Figure 1.5. Annual commercial catches of *Striostrea margaritacea* between 1981-2007 in KwaZulu-Natal (Data sourced from MCM, DEAT).

Saccostrea cucullata

(a) Eastern Cape Province

The majority of subsistence fishing in South Africa is carried out along the heavily-populated East coast (Clark *et al.* 2002, Cockcroft *et al.* 2002). This coast is relatively undeveloped and the unspoilt nature of the surroundings has attracted many visitors and tourists, who encourage subsistence fisheries by creating a market for resources, such as oysters (Kiepiel & Quinlan 1997, Robertson & Fielding 1997). *S. cucullata* have been heavily exploited by only subsistence and recreational fisheries along this coastline (Kyle *et al.* 1997, Cockcroft *et al.* 2002). Hockey & Bosman (1986) compared exploited sites with protected sites (i.e. reserves) and found that exploited sites had greater species richness, but the size and density of exploited species, including *S. cucullata*, were diminished in exploited areas. The removal rates of this species have been estimated at 9-11 m⁻² y⁻¹ (Dye 1989). Dye (1990), found *S. cucullata* to be good recruiters and suggested that, if exploitation had to cease, a three

year period would be necessary for populations to recover. However, in later work, Dye *et al.* (1994b) suggested that the recruitment of this species in the Eastern Cape Province was so poor that no exploitation should be permitted. In the past decade, exploitation levels of *S. cucullata* in the Eastern Cape Province have been moderate compared to those of *S. margaritacea*, which are collected commercially as well. In 2001, the stock status of *S. cucullata* was considered to be variable to good and the species was therefore not viewed as an immediate research priority in this province (Britz *et al.* 2001).

(b) KwaZulu-Natal

S. cucullata occurs in great densities in KZN, but is only targeted by recreational and subsistence fishers (Cockcroft *et al.* 2002). Subsistence fishers exploit this resource for a variety of purposes, including food, ornamentation and traditional medicine. Harvesting is carried out mostly by women or children and, although oysters are not collected as often as mussels, it is still one of the main species harvested. For example, five tonnes of *S. cucullata* and *S. margaritacea* were collected in KZN North between 1988 and 1994 (Kyle *et al.* 1997). However, only *S. margaritacea* may be harvested commercially (De Bruyn 2006).

Ostrea atherstonei* and *Ostrea algoensis

These oysters are not currently exploited in any significant numbers, although failed attempts at culturing both species have been made in the past (Korringa 1956). They occur in KZN, but numbers are too scarce to warrant targeted collection (M. Schleyer, pers. comm.). In Langebaan Lagoon, deposits of *O. atherstonei* shells have fossilized, forming extensive oyster beds (Grindley 1969, Compton 2001), indicating that these oysters must have occurred in great numbers in this area in the past. Changes in the flow patterns of ocean currents, brought about by a fall in the sea level, are thought to be the reason for their mass mortality (Scott 1951). The gravel oyster bed extends throughout the lagoon and into areas of Saldanha Bay below a thin sand layer (Compton 2001). The gravel bed is best developed along the eastern half of the Lagoon, where it was dredged commercially for agricultural lime in the past. Three million tonnes of lime were processed by an oyster shell factory that no longer operates today (Tankard 1976).

Crassostrea gigas

Wild populations of *C. gigas* have recently been reported in estuaries along the Southern Cape coast. Holidaymakers have been observed collecting *C. gigas* in the Breede River Estuary (Robinson *et al.* 2005a), although exploitation rates have not been quantified. Conservation legislation currently protects these populations. However, even though the authorities are aware of its invasive nature, no action has been taken.

From the above, it is evident that, although commercial and recreational harvesting of oysters in South Africa are controlled to a variable extent, the subsistence sector, which is an active role player in contributing to the exploitation of stocks, has been largely ignored. In the past, subsistence fishers had no legal access to marine resources and were therefore classified as poachers (Cockcroft *et al.* 2002). This changed with the introduction of the White Paper on Fisheries and the Marine Living Resources Act (MLRA) in 1998, which recognised subsistence fishing for the first time in South Africa (Anon 1997, 1998). Authorities have, however, only recently started managing the subsistence sector, although this fishery is still uncontrolled along large parts of the South African coastline, notably, in most of the Eastern Cape (i.e. former Transkei). In the early 1990s, the government of Transkei obtained funding for the Transkei Inshore Fisheries Support Programme, and one of their aims concentrated on the sustainable exploitation of marine resources, such as oysters (Fielding *et al.* 1994). However, despite such efforts, Marine and Coastal Management currently only actively controls the south-western half of the province around Port Elizabeth, and fishery managers, or even researchers, are not based in most of the relatively inaccessible and underdeveloped eastern area, where poaching of marine resources remains rife (Britz *et al.* 2001).

OYSTER CULTURE

Aquaculture in South Africa's marine environment is underdeveloped compared to harvest fisheries. This is largely due to the generally linear and wave-exposed nature of the coastline, which contains few significant estuaries or embayments suitable for culture operations. Until recently, there has also been a lack of government

investment and promotion. However, aquaculture facilities for high value species, such as oysters, have become relatively well established through private sector initiatives (Britz *et al.* 2001). These ventures were, however, not easily established, and oyster culture in South Africa has a long history, fraught with many difficulties.

European settlers arriving in the Cape noticed the masses of indigenous oysters (probably *Striostrea margaritacea*) along the coast (Korringa 1956). Attempts at culturing oysters were therefore made as early as 1673, but it was not until 1948, after the Division of Sea Fisheries realized the benefits of mariculture, that the first commercial company was founded in Knysna, along the South coast, and attempts at farming *S. margaritaceae* were made (Hecht & Britz 1992).

During these pioneer stages, the majority, if not all attempts at establishing the culture of *S. margaritacea* failed, particularly in incidences where this species was relocated to where it did not occur naturally. On the Cape Peninsula, for example, attempts at transporting oysters from the Southern Cape coast to Cape Town were unsuccessful (Thompson 1913). Reasons for these failures were the lack of knowledge of the conditions required by *S. margaritacea* for growth, fattening, and reproduction (Korringa 1956). In 1882, a similar attempt was made in the Eastern Cape Province and oysters were relocated to the Kowie River from further down the coast. However, it is presumed that fresh water intrusion and shifting sands resulted in failure of this attempt (Thompson 1913). Fortunately, these failed attempts did not completely discourage early pioneers and in 1888, the “Act to promote the cultivation of oyster fisheries and the discovery of pearl-bearing oysters” was established (Korringa 1956).

The main problem during these early periods of oyster culture appeared to be insufficient knowledge on culturing indigenous oysters, such as *S. margaritacea*. Thus, in 1894, a representative from the United Kingdom with ample knowledge on oyster culture visited South Africa. Soon after, exotic oysters, such as the European flat oyster *Ostrea edulis*, were imported. These early attempts at introducing exotic oysters to both the East and West coasts of South Africa were, however, unsuccessful. The majority of the imported oysters died shortly after arrival, probably due to poor shipping conditions and predation in their new environment. These failed attempts

proved discouraging and oyster culture ventures were subsequently delayed for a long period (Korringa 1956).

In 1946, interest was renewed in the Knysna Estuary as a suitable location for oyster culture, the main driving force being a growing local demand for oysters, as the supply of indigenous oysters taken from the rocks was proving insufficient. Artificial collectors (stakes and asbestos roofing tiles) were first set out and results appeared promising, as *S. margaritacea* spat began to settle on the collectors, with two tiles carrying as many as 50 oysters. No natural beds of oysters occurred within the estuary and oyster larvae were washed in from the sea. These promising results led to the formation of the Knysna Oyster Company, Ltd. However, too little was known about the biology of *S. margaritacea* and importing exotic oysters of known quality seemed more viable. *O. edulis* and the Portuguese oyster *Crassostrea angulata*, were therefore imported from Europe. This was unsuccessful, however, as sand apparently penetrated the oysters' delicate tissues and choked their filtering mechanism (Korringa 1956).

After years of experimental trials of importing exotic oysters, South Africa now follows the global trend of importing the much hardier Pacific oyster *Crassostrea gigas*. Spat have been imported from France, England and Chile, but are presently only being imported from Chile. Imports from France have recently been banned, as a result of the contagious herpes virus affecting oysters in France (T. Tonin, pers. comm.). *C. gigas* spat was imported to the Knysna Estuary as early as 1973 and this species has since become the only oyster cultured on a commercial scale (Hecht & Britz 1992). The main reason for its preference over *S. margaritacea* is its faster growth rate (Hecht & Britz 1992). *C. gigas* can attain market size within 9-11 months from two gram seed, whereas *S. margaritacea* takes three years (DEAT 2006, De Bruyn 2006). This is, however, site dependent, as *C. gigas* reaches market size only after 24 months on intertidal racks at Knysna.

Oyster farms and nurseries require a permit from Marine and Coastal Management before any activities are undertaken. Details and locations (Fig. 1.6), of current oyster nurseries and marine and estuarine farms are given below.

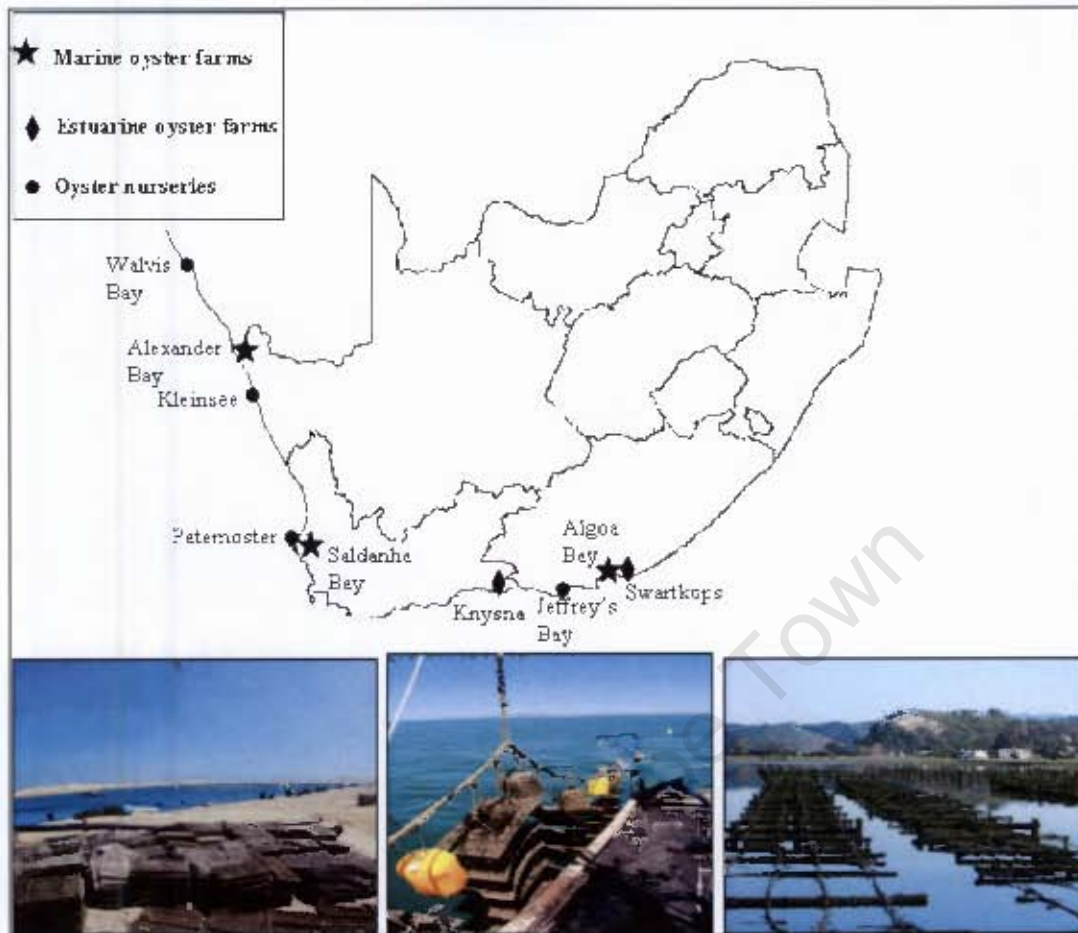


Figure 1.6. The location of marine and estuarine oyster farms and oyster nurseries in South Africa and illustrations of oyster farms located in Alexander Bay, Saldanha Bay and Knysna Estuary (left to right).

NURSERIES

Oyster nurseries located in Walvis Bay (Namibia), Kleinsee, Paternoster and Jeffrey's Bay (Fig. 1.6) have been in existence for approximately five years. These nurseries import *C. gigas* spat of less than 5 mm in length from Chile, after which they are kept in an upwelling facility for approximately two months. When they reach a length of approximately 20-25 mm, they are placed in plastic mesh cages, which are suspended in the upper part of the water column in dams and ponds (in the case of Kleinsee and Paternoster), or in the sea (Walvis Bay). These seed oysters are rigorously cleansed and graded until they reach the required size for translocation to the various growout farms. This can take anything from 3-8 months, depending on site and season-specific environmental conditions.

MARINE OYSTER FARMS

Three marine-based farms are currently operational in the region. Oyster farming activities in Alexander Bay (Fig. 1.6) commenced in 1994. The farm is situated inside Alexkor, a state-owned diamond mining company in the Northern Cape Province. Two dams are present on the farm and *C. gigas* oysters are grown in baskets from seed to market size in the 3.5 ha South dam adjacent to the sea. Water is pumped from the sea into the dam, which is raised 10 m above sea level, from where the water is drained to a lower dam and from there to the sea. Due to technical difficulties, the farm ran at a loss until the engagement of Mariculture Development Services (MDS) in 2003. The aim of involving MDS was for the farm to become a major player in South African oyster production, as well as an important source of revenue and jobs in Alexander Bay. Average monthly production of oysters is 65 000 and oysters are sold all over South Africa under different labels. The current aim is to increase these numbers by using the larger 8 ha lower dam also for oyster production. Oysters of 25-30 g will be grown in this dam to the desired market size of 60-80 g (total wet weight) (Alexkor Limited 2003). Alexander Bay has also recently begun operating as a nursery, supplying part-grown oysters to the farm in Algoa Bay.

In Saldanha Bay (Fig. 1.6), the Fisheries Development Corporation ran an oyster farm in Langebaan Lagoon but this was closed down approximately 20 years ago as a result of the establishment of the West Coast National Park. Trials in the main bay and the artificially created dam adjacent to the ore-loading jetty began around the same time. The dam-based operation was commercialized and operated until 2005. The current operation in the bay began in 2005. This bay is the only sheltered bay along the South African West coast and its mariculture potential was recognized approximately 20 years ago. It has since become prominent in this industry (Jackson & McGibbon 1991, Tonin 2001). Since 1985, mussel cultivation has been the main mariculture activity in this area. However, three established oyster farms currently exist (Probyn *et al.* 2001, Tonin 2001). The culture cycle at the biggest farm begins with the purchase of *C. gigas* juveniles (25-35 g in total wet weight each) from nurseries, after which they are placed in specially designed plastic mesh cages, and suspended in the upper few metres of the water column in the southern, more exposed part of the bay. The oysters are removed from the sea on a regular two month cycle, size-graded and cleaned of fouling organisms which could inhibit growth. It takes on average 3-4

months for these juvenile oysters to attain market size which ranges from 45-120 g (total wet weight), depending on specific market preferences.

Oyster farming activities in Algoa Bay (Fig. 1.6) were initiated in the late 1980s. Activities at this farm begin with the translocation of juvenile oysters, approximately four months old, from the Knysna Estuary (Fig. 1.6). Oyster operations in the bay, as well as in Knysna, are owned by the same South Cape Oysters Company. The reason for the translocation of oysters from Knysna Estuary relates to unfavourable conditions, such as floods, which result in low salinity levels (Warman 2001). Oysters are therefore only grown here for four months, after which they are translocated to Algoa Bay, where conditions are considered more suitable. In the bay, oysters are cultured via a longline system moored in 10 m of water. Ropes of 150 m long are strung with stacks of approximately five bags each at 1 m intervals. Of the 250 ha of sea area set aside for maricultural purposes, 52 ha are leased to oyster farmers (Tonin 2001). Oysters grown in these waters reach market size after only three to four months and are then returned to Knysna Estuary and kept in holding tanks until purchased.

ESTUARINE OYSTER FARMS

South Africa has very few large, permanently open estuaries suitable for mariculture. Oyster culture in the Knysna Estuary (Fig. 1.6) was initiated in 1946 and efforts were concentrated on the indigenous *S. margaritacea*. A hatchery was developed and the first batch of *S. margaritacea* was reared in 1970. However, due to subsequent problems and the extremely slow growth rate of this species (three years to reach market size), the hatchery was closed and it was decided to import *C. gigas* spat (M. B. Solomons, pers. comm.). As recently as 2001, 18 ha of the Estuary were used for the cultivation of *C. gigas* and it was regarded as the centre of oyster production in South Africa (Tonin 2001). Since then, oyster production in Knysna has declined and has instead become concentrated in Saldanha Bay and Algoa Bay. Oyster spat are purchased from the Jeffrey's Bay nursery and grown on racks in 6 mm mesh bags for the first 2-4 months. They are then brought back to land, where they are mechanically size-graded and sorted into new bags with the appropriate mesh size (i.e. small enough to hold the oysters and large enough to allow maximum water circulation), after which they are translocated to Algoa Bay. The Knysna Oyster Co. is therefore no

longer a significant producer and functions only as a nursery farm for the Algoa Bay operation. Most of the 18 ha previously leased for cultivation are no longer being used.

The oyster farm in the Swartkops Estuary (Fig. 1.6) is comprised of floating wooden lattices in a tidally flushed pond that is linked to the main estuary via a shallow sandy channel. The seed oysters are glued individually to the wooden laths, and these are nailed together in a lattice which is floated in the pond. The oysters are then allowed to grow to market size before the lattices are pulled ashore and the oysters removed.

HISTORY OF OYSTER PRODUCTION

Approximately two million *Crassostrea gigas* oysters were produced annually throughout the seventies and early eighties (Hecht & Britz 1992). However, oyster production statistics are only available since 1985 (South African Molluscan Shellfish Monitoring and Control Programme database). Overall oyster production in South Africa has fluctuated considerably over that time. Production increased by approximately six million between 1983 and 1991, decreased by approximately five million between 1991 and 1998, and has been relatively stable over the last decade (Fig. 1.7) (T. Tonin pers. comm.). In the late 1980s, a productive farm was established in Algoa Bay that operated for a few years, producing a few million oysters a year before it closed in the early nineties. This, together with the significant decline in production in the Knysna Estuary, resulted in the decrease in production observed in Figure 1.7. After this period, the new farm in Algoa Bay, along with improved production on the West coast (i.e. Alexander Bay and Saldanha Bay oyster farms), offset the earlier declines and led to a stabilization in total production (T. Tonin pers. comm.). According to Alexkor Limited (2003), the market for cultivated oysters in South Africa has grown steadily over the last decade. However, production has not kept up with demand. Compared to production in other countries, South Africa is a minor producer, the main reason for this being that relatively few places along the coastline are suitable for culturing oysters. Saldanha Bay, for example, is situated in the centre of an industrial harbour, where unmonitored pollution occurs. For example, tributyl-tin (TBT) originating from anti-fouling paints causes shell deformation (Probyn *et al.* 2001, Britz *et al.* 2001).

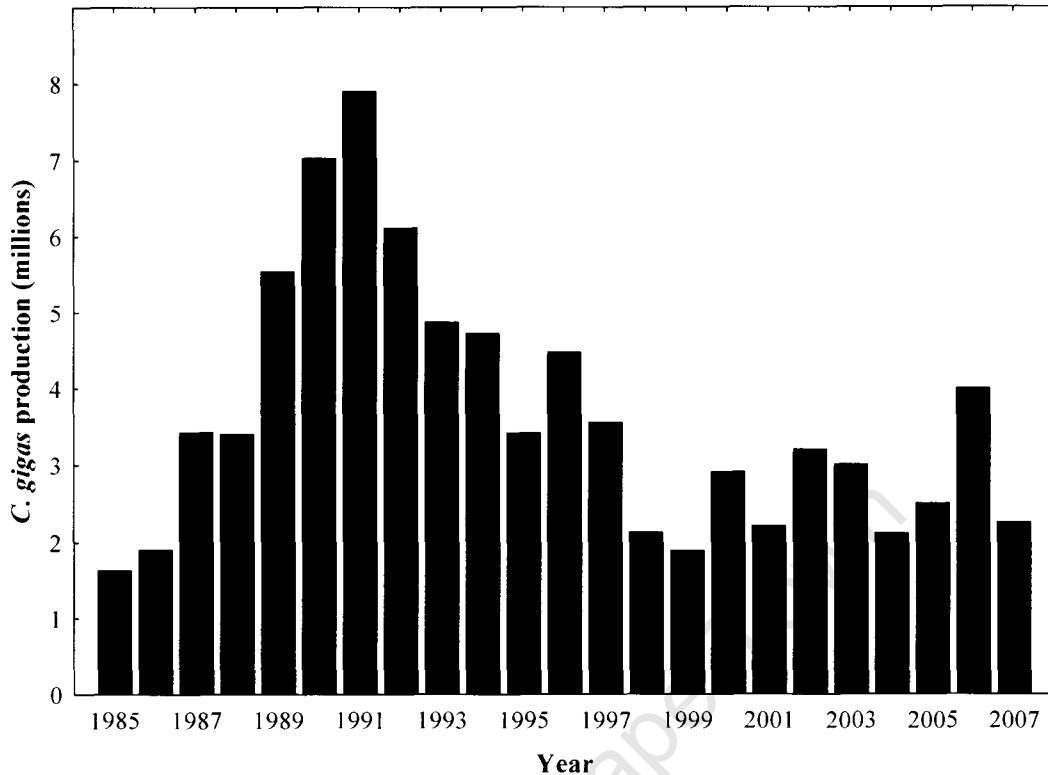


Figure 1.7. South African production of farmed Pacific oyster, *Crassostrea gigas*, 1985-2007 (data sourced from the South African Molluscan Shellfish Monitoring and Control Programme database).

CONCLUSION

The four indigenous oyster species, *Striostrea margaritacea*, *Saccostrea cucullata*, *Ostrea atherstonei* and *Ostrea algoensis*, that are, or were, of commercial interest in South Africa, all occur along the South and East coasts, with none occurring along the West coast. Native oysters are exploited commercially, recreationally and by subsistence fishers, with *S. margaritacea* being the main target species. The commercial and recreational sectors along the Southern Cape coast and Port Elizabeth in the Eastern Cape are managed and controlled by Marine and Coastal Management officials, while Ezemvelo KwaZulu-Natal Wildlife manages KwaZulu-Natal on behalf of Marine and Coastal Management. The majority of commercial oyster harvesting takes place along the Southern Cape coast, with 102 pickers, compared to 3, 15 and 25 pickers in Port Elizabeth, KZN South and KZN North respectively. Data on the total annual catch of oysters in these provinces are minimum estimates, as collectors do not always comply with the harvesting regulations, frequently failing to

hand in forms with their total oyster catches to officials. Thus, exploitation levels of *S. margaritacea* may be higher than indicated by the results.

The management of South African oyster fisheries has concentrated on the commercial and recreational harvesting of *S. margaritacea*, while subsistence harvesting of these oysters, as well as other species, such as *S. cucullata*, has been and still is to some degree, largely ignored in most harvesting areas. This lack of sufficient management may be detrimental to oyster stocks, as subsistence harvesting may be having substantial impacts on the stock. Subsistence fishers are also the most difficult to manage, as coastal dwellers have collected marine resources freely without restrictions for many decades. In KZN, regulations for the subsistence sector are in the process of being implemented, for example the conversion of the previous fishery to one of right's holders i.e. transfer to the pickers. However, the subsistence sector in most of the Eastern Cape remains largely unmanaged. Management plans for resource use, as well as levels of enforcement and monitoring capacity, are better developed in KZN than in the Eastern Cape. Thus, management of subsistence fisheries in KZN may differ from what is practical in the Eastern Cape. For example, daily bag limits of *S. margaritacea* or *S. cucullata* may be appropriate and enforceable in KZN, whereas an overall limit on a basket of resources (e.g. oysters, mussels and limpets), may be more practical and enforceable in the Eastern Cape (Cockcraft *et al.* 2002). If it was decided to manage the subsistence sector of the Eastern Cape, additional resources would be required, as there is a severe shortage of reliable and trustworthy enforcement officers. Tourists in the area should also be discouraged from purchasing illegally collected resources, and this would lower the demand on already exploited stocks. Marine and Coastal Management is currently developing a system to ensure that the data from subsistence fisheries are recorded.

The culture of oysters can be viewed as an activity that can provide additional socio-economic benefits from marine resources. This is particularly important as most wild fisheries in South Africa are maximally exploited and offer little opportunity for growth. Efforts should be concentrated on finding more suitable sites for farming *C. gigas*. Many argue that the South African coastline is too exposed to the elements for aquaculture purposes. However, abandoned diamond mining dams along the Northern Cape coastline have long been regarded as having significant potential for

mariculture, but there has been little progress towards realising this potential. The primary reasons for this are a shortage of available expertise, failure to attract investors to the area, the remote location and distance to market (Alexkor Limited 2003). Setting up oyster farms in popular tourist spots such as Gansbaai along the South coast is almost impossible, due to public pressure, as holiday makers do not look favourably on unsightly mariculture operations in these areas (Warman 2001). These very same tourists, however, contribute to the demand for oysters in South Africa. Estuaries situated in impoverished coastal areas along the Southern Cape coast also constitute promising sites for oyster farming and could play a role in making rural communities meaningful role-players in South African oyster production.

There is an obvious demand for both wild and cultivated oysters. Establishing local hatchery facilities with introduced *C. gigas* oysters might be the way forward for oyster culture in South Africa. This would also prevent marine alien species associated with oysters from being accidentally introduced into South African waters. Oyster imports and translocations are well known vectors of marine alien species in many regions of the world. This issue is addressed in the following two chapters.

PART 2

University of Cape Town

CHAPTER 2

University of Cape Town

OYSTERS AS VECTORS OF MARINE ALIENS
WITH NOTES ON FOUR NEWLY-RECORDED MARINE ALIEN
SPECIES ASSOCIATED WITH OYSTER FARMING IN SOUTH
AFRICA

INTRODUCTION

Many species of commercially-cultured shellfish, particularly mussels, oysters, clams and scallops, have been intentionally transported around the globe to establish or enhance aquaculture ventures (Chew 1990). However, shellfish imported in this way can also facilitate introduction of marine alien species. Such introductions can compromise the introduced aquaculture species themselves, epi- or infaunal organisms associated with the imported species, or species introduced accidentally along with them. Live shellfish often contain a variety of associated organisms, including disease microorganisms and multicellular parasites (Carriker 1992; Naylor *et al.* 2001).

The oyster trade in particular, has been responsible for the distribution of many unwanted species (Minchin 1996; Ruesink *et al.* 2005). Oysters have been widely transported since Roman times, due to their inherent ability to withstand long journeys out of water (Andrews 1980). Modern transport methods, such as airfreight, have allowed for their further and faster dispersal across the globe. The contribution of this activity to marine invertebrate introductions and invasions has long been evident and, as early as the 1950's, Charles Elton famously stated "The greatest agency of all that spreads marine animals to new quarters of the world must be the business of oyster culture" (Elton 1958).

According to Minchin (1996) and Wolff & Reise (2002), the main reasons for the importance of oysters in the translocation of alien species are the long history of the trade and the large quantities of oysters shipped. Another contributing factor is that oysters do not bury into the substratum, thus remaining exposed to colonisation by fouling organisms, which are also difficult to remove due to the rugose nature of oyster shells

(Minchin 1996, Wolff & Reise 2002). Awareness of the potential risks associated with the accidental translocation of such fouling organisms has grown significantly in many countries, but large quantities of shellfish, especially oysters, are still being traded without application of adequate biocontrol measures (Wolff & Reise 2002).

Overall, oysters have been introduced to 79 countries outside their native ranges, 66 of these introductions were of the Pacific oyster *Crassostrea gigas* (Ruesink *et al.* 2005). As a result, this species is now one of the most cosmopolitan of all marine invertebrates (Ruesink *et al.* 2005). Besides the Atlantic coast of North America, areas of oyster production in Europe, Western North America and Australasia all depend on *C. gigas* (Andrews 1980). This species is large-bodied, long-lived and able to adapt to a wide range of environmental situations (Chew 1990). The importation of *C. gigas* to various countries was mostly driven by the diminishing populations of native organisms due to over-harvesting, disease and adverse weather conditions (Chew 1990, Miossec & Gouilletquer 2007, Padilla & Gray 2007). For example, in North America and France, *C. gigas* was introduced from Japan, following the decline of the native Olympia oyster *Ostrea lurida* and the native Portuguese oyster *C. angulata* respectively. In Australia, *C. gigas* was introduced due to its ability to reach marketable size in only 18 months, much faster than the 3-4 years of the native Sydney Rock oyster *Saccostrea commercialis* (Chew 1990, Chew 2001, Nell 2002). Other widely introduced oyster species include *Crassostrea virginica*, *Ostrea edulis* and *Saccostrea commercialis* (Ruesink *et al.* 2005).

Ruesink *et al.* (2005) documented a total of 78 alien marine algae, invertebrates, and protozoan species introduced to nine regions (Argentina, Gulf USA, the Baltic Sea, New Zealand, Australia, East USA, West USA, French Atlantic and the North Sea) through oyster culture. Regions in which a wider variety of oyster species are cultured also have a larger number of associated alien species (Ruesink *et al.* 2005). In North Western Europe, at least five alien species have been introduced via imports of *C. virginica*: the slipper limpet *Crepidula fornicata*, the American tingle or predatory oyster drill *Urosalpinx cinerea*, the false angel wing *Petricola pholadiformis*, the polychaete *Clymenella torquata*, and the ostracod *Eusarsiella zostericola* (Andrew 1980, Wolff & Reise 2002).

U. cinerea, *C. torquata* and *E. zostericola* were restricted to estuaries in Europe (Andrews 1980, Utting & Spencer 1992), whereas *C. fornicata* and *P. pholadiformis* spread and colonized large parts of the European seas. *C. fornicata* has become widely dispersed via a combination of larval transport, transport by floating objects (seaweeds attached to shells) and transport with oysters translocated to new sites for relaying (Wolff & Reise 2002). Other alien species that were probably introduced with *C. virginica* include the bivalve *Mya arenaria* and a mud crab *Rithropanopeus harrisi*, both of which have spread extensively in Northern Europe (ICES 1972). *C. gigas* imports occurred on an even larger scale and more than 20 invasive species accompanied oyster imports in France alone. However, only four or five of these have spread and become established: the anthozoan *Aiptasia pulchella*, the polychaete *Hydroides ezoensis*, the barnacles *Balanus albicostatus* and *Balanus amphitrite amphitrite*, and the bivalve *Anomia chinensis* (Grizel & Heral 1991). Grizel & Heral (1991) also reported two Japanese algae species, *Laminaria japonica* and *Undaria pinnatifida*, which had become established after the importation of *C. gigas*. Other invasive species, such as the parasitic copepods *Mytilicola orientalis* and *Myicola ostrea*, as well as the well-known algal species *Sargassum muticum*, may also have been introduced via *C. gigas* imports (Andrews 1980, Wolff & Reise 2002). Critchley & Dijkema (1984) found that *Sargassum muticum* can be transferred with half-grown oysters, whilst this brown alga is in the small inconspicuous stages of development.

In Western North America, the local establishment of *C. gigas* spat and the development of hatcheries resulted in the widespread culture of this species along the Pacific coastline (Quayle 1969, Drinkwaard 1999). This, as well as the long time period over which oyster importations have occurred, has offered many opportunities for alien species accompanying *C. gigas* to become established (Andrews 1980). The scale of such introductions is far greater on the Pacific than on the Atlantic and Gulf coasts of North America. This is due to the absence of large scale importations of commercial oysters, or other shellfish, into the latter areas (Carlton 1992). In the past, shipments of oysters were not checked for invasive species and boxes containing *C. gigas* spat could hold up to 22 species of mollusc shells (Hanna 1966). Molluscs introduced via shipments of oysters

include *Cecina manchurica*, the Japanese false cerith *Batillaria attramentaria*, the convex slippersnail *Crepidula convexa*, *C. fornicata*, the Eastern white slippersnail *Crepidula plana*, the Japanese oyster drill *Ceratostoma inornatum/Ocenebra japonica*, the Atlantic oyster drill *Urosalpinx cinerea*, the channelled whelk *Busycotypus canaliculatus*, the Eastern mudsnail *Ilyanassa obsoleta*, Japanese nassa *Nassarius fraterculus*, European ovatella *Ovatella myosotis*, *Musculista senhousia*, the ribbed mussel *Geukensia demissa*, the Chinese jingle *Anomia chinensis*, the Atlantic rangia *Rangia cuneata*, the Baltic macoma *Macoma 'balthica'*, the Japanese trapezium *Trapezium liratum*, the Japanese littleneck *Venerupis philippinarum*, *Gemma gemma*, the false angelwing *Petricola pholadiformis*, softshell *Mya arenaria* and *Lyrodus takanoshimensis* (Carlton 1992). Nine of these species originate from Japan and 13 from the Atlantic coast of North America (Carlton 1992). *Venerupis japonica* is by far the most significant alien mollusc species associated with oyster imports. This clam has become widely distributed and is used for human consumption in its introduced range (Andrews 1980). Non-molluscan species include two serious Japanese parasites of oysters: - the flatworm predator *Pseudostyochus ostreophagus*, as well as *Mytilicola orientalis*, which is also evident in European waters (Andrews 1980).

Marine alien species that have been imported with cultured oysters may have significant ecological impacts in areas where they have become established. Amongst many other factors, they are able to alter the trophic structure of the invaded area and change the disturbance regime (Vitousek 1990). It has been suggested that large densities of these alien species could interfere in trophic energy flow (Minchin 1996). *C. fornicata* compete with native organisms for food and space and can alter the benthic community structure of silty waters through their feeding activities and excretions (Kaiser *et al.* 1998). The spread of *S. muticum* has resulted in the interference with the commercial algal species *Chondrus crispus* (Andrews 1980).

In Western North America, studies of all but one of the introduced molluscs, *O. myosotis*, have demonstrated dramatic impacts on native communities. They are known to compete with native species and alter the physical appearance and ecological structure of the

invaded habitat (Carlton 1992). The great densities of *G. demissa*, *M. senhousia*, *M. arenaria*, *V. philippinarum* and *G. gemma*, are responsible for the alteration of benthic communities (Carlton 1992). *I. obsoleta* is known to limit the distribution of the native mudsnail *Cerithidea californica*, by preying on its egg capsules (Race 1982), and *B. attramentaria* excludes similar-sized individuals of the native Pacific coast snail *Cerithidea* which feeds on diatoms of the same size (Whitlatch & Obrebski 1980, Byers 2000). Carlton (1992) suggested that the extensive populations of molluscs associated with oyster imports that have not been studied may also have had, or are having, significant ecological impacts. Ecological impacts of some species such as *C. fornicata* have been well documented (Blanchard 1997, de Montaudouin *et al.* 1999, de Montaudouin & Sauriau 1999), but further studies on other abundant and harmful species are needed.

In addition to free-living associated species, parasites of introduced oysters can also infest native species. In North Western Europe, *M. orientalis* is a common parasite in the gut or mantle cavity of native oysters (Andrews 1980, Minchen 1996). In Western North America, the parasite *M. orientalis* results in mortalities of oyster spat and is hard to control (Andrews 1980). Another economically important pest of oysters is the shell-boring sabellid polychaete, *Terebrasabella heterouncinata*, introduced with *C. gigas* to California. This parasite infested cultured red abalone, *Haliotis rufescens*, but has since been successfully eradicated (Kuris & Culver 1999). In Australia, introduced parasites of oysters include the mudworms *Polydora websteri* and *Boccardia knoxi* (Nell 2002). High infestations of these worms are associated with increased mortality and reduced condition in their mollusc hosts (Leonart *et al.* 2003, Simon *et al.* 2006). These burrowers penetrate the inner surface of mollusc shells, which the host then repairs with nacre, forming a blister (Stephen 1978), which when punctured, releases anaerobic metabolites, such as hydrogen sulphide. This lowers the market value of oysters considerably (Handley 1995).

Examples of diseases associated with imported oysters and that have effects on native communities also exist (e.g. Malpeque Bay disease in Canada 1914, Delaware Bay

disease on the Mid-Atlantic coast of North America 1957) (Andrews 1980). *C. gigas* was blamed for the outbreak of a protozoan *Bonamia ostrea*, which affected the cultivation of *O. edulis* oysters in the Netherlands and North-Western Europe in 1981 (Chew 1990, Nehring 2006). This disease resulted in a serious decline of *O. edulis* and was most prevalent in mature oysters that suffered mortalities of 50-80 % (Minchin & Rosenthal 2002). It is currently present in Spain, France, Britain and Ireland (Balseiro *et al.* 2006). Although these speculations of shellfish diseases being imported with *C. gigas* oysters exist, there is no clear evidence that this is in fact the cause (Wolff & Reise 2002).

From the above, it is evident that considerable research has been carried out on the introduction of alien species associated with oyster imports in foreign countries, although more work is required to determine the possible ecological impacts of some of these species. In South Africa however, this problem has been recognised, but little or no attention has been afforded to documenting it.

South Africa lies on one of the world's major shipping routes and has thus been exposed to marine introductions since the late 10th century (Yap & Man 1996). However, despite the considerable research undertaken on marine invasions in Australia, the United States of America and Europe (Orensanz *et al.* 2002), this topic has only recently received attention in South Africa. The most recent published reviews of marine alien species in South Africa are those of Robinson *et al.* (2005b) and Griffiths *et al.* (2008). Both studies recognised approximately 20 confirmed extant species from the region, most of which are restricted to sheltered bays, estuaries and harbours. Only the Mediterranean mussel *Mytilus galloprovincialis* and the recently reported barnacle *Balanus glandula* (Laird & Griffiths 2008) are known to have spread extensively along the open wave-exposed coastline. The number of marine introductions recorded in South Africa is small compared to other regions of the world - for example, 298 marine alien species are recorded along North American shores (Ruiz *et al.* 2000). However, large areas of the South African coast remain relatively unexplored for alien species and taxonomy of certain marine groups, specifically alien species, is also poorly developed (Robinson *et al.* 2005b). It is thus highly likely that the presently recorded number of introduced

species is a severe underestimate of actual introductions. Indeed a still unpublished study by Mead *et al.* (*in prep.*) has already resulted in the recognition of at least 70 additional marine alien species from this area.

In Chapter 1, the reliance of the South African oyster industry on commercially importing spat of the Pacific oyster *Crassostrea gigas* was discussed. This activity might very well have lead to the unintentional introduction of marine aliens. Oyster farms in this region have not previously been sampled in a directed effort to detect such bioinvasions. This chapter therefore examines marine alien species that might have been introduced via the oyster trade in these areas

METHODS

Three oyster farms along the West and East coast of South Africa, in Alexander Bay, Saldanha Bay and Knysna respectively (Fig 1.6, Chapter 1), were surveyed, specifically searching for new marine alien species, although known marine alien species were also noted. Due to the variable nature of the three farms (Chapter 1), sampling techniques differed substantially. For example, in Alexander Bay, the layout of the farm allowed for a complete survey of the oyster operation as the dams are isolated from the sea, whereas the oyster farms in Saldanha Bay and Knysna form part of a harbour and an estuary respectively, which did not allow for complete surveillance within the scope of this study. Thus, sampling of the latter two farms targeted only *Crassostrea gigas* oysters, oyster baskets and other structures associated with the farming operation. However, the general habitats in both Saldanha Bay and Knysna Estuary have recently been surveyed for alien species (Robinson *et al.* 2004, Griffiths *et al.* 2008) and the introduced species previously recorded there are included in the listings below.

Alexander Bay

The survey of Alexkor Ltd. in Alexander Bay was carried out in March 2007. Two dams exist on the farm, of which only one is in operation (Chapter 1). Both dams were surveyed and each dam was divided into five sites. At each site, five samples of each

type. i.e. push-net (soft-substratum), core (soft-substratum) and general (hard-substratum, i.e. rocks, oysters and oyster racks) were collected. Push-net samples were carried out using a large net with a wooden board placed horizontally at the front, to displace organisms from the sandy bottom into the net. The push-net was dragged along the sandy bottom for 10 m at each site. Contents were then transferred to a 1 mm mesh sieve and after most of the sand and debris were washed away, the remaining samples were transferred to sorting trays. Core samples were carried out using a specially adapted box-coring spade (20 x 10 cm). At each site, the spade was pushed into the sandy bottom three times with the contents being placed in a sieve. General samples involved collecting any organisms on hard substrata such as rocks, oysters and oyster racks at each site. Soft substrata or hard substrata were not found at every site, in these cases, only the possible type of sampling was carried out. Trek-net samples were also carried out by pulling a net (20 m long with 1cm mesh) three times at appropriate locations (i.e. deep sandy bottomed areas) in each dam.

Saldanha Bay

The survey at the Striker Fishing Oyster Company in Saldanha Bay was carried out in August 2007. Thirty market size oysters (>50 g total wet weight), collected from the same stock of Chilean oysters, were collected. Oysters of each set were made up from three sub-samples of ten oysters each, taken from three separate baskets on the same culture rope. A scrape of organisms residing on the oyster baskets (1 x 3) were also collected to represent any species not residing on the oysters.

Knysna Estuary

The survey at the Knysna Oyster Company was carried out in August 2008. At Knysna, oysters are grown on racks in 6 mm mesh bags (Chapter 1). Racks are distributed in different areas of the estuary. Thirty *C. gigas* oysters were collected in total. These were divided into three sub-samples of 10 oysters each, taken from three different sites in the estuary. The first site was situated deep into the estuary and accommodated juvenile oysters purchased from Jeffrey's Bay Nursery, which were approximately 2-3 months old. The second site was nearby the latter, however, oysters were approximately six

months old and formed part of a pilot study which would determine the growth rate of oysters which are not relocated to Port Elizabeth (Chapter 1). The third site was situated closer to the mouth of the estuary where oysters were exposed to greater salinities. This site accommodated juvenile oysters of 2-3 months, which were purchased from Jeffrey's Bay nursery. A scrape of any additional organisms residing on the mesh bags and on the racks were taken at each site.

Samples collected from Alexander Bay, Saldanha Bay and the Knysna Estuary were preserved in 70% ethanol and brought back to the laboratory at the University of Cape Town. Oyster samples collected from Saldanha Bay and Knysna were thoroughly searched for organisms on and in the grooves of oyster shells. Organisms were identified to species level.

RESULTS

The focus of this chapter was to survey oyster farms for all alien species and elaborate on new discoveries. Ten alien species occurred in Alexander bay while 15 occurred in Saldanha Bay and seven in the Knysna Estuary (Table 1).

Table 1. Alien species occurring at Alexander Bay, Saldanha Bay and Knysna oyster farms.

TAXON	ALEXANDER BAY	SALDANHA BAY	KNYSNA
CNIDARIA			
<i>Sagartia ornata</i>		√	
POLYCHAETA			
<i>Boccardia proboscidea</i>		√	
<i>Polydora hoplura</i>		√	
CRUSTACEA			
<i>Balanus glandula</i>		√	
<i>Carcinus maenas</i>		√	
<i>Monocorophium acherusicum</i>	√		
<i>Jassa slatteryi</i>		√	√
BRYOZOA			
<i>Bugula neritina</i>	√	√	√
BRACHIOPODA			
<i>Discinisca tenuis</i>		√	
MOLLUSCA			
<i>Crassostrea gigas</i>	√	√	√
<i>Littorina saxatilis</i>		√	√
<i>Mytilus galoprovincialis</i>	√	√	√
<i>Ostrea edulis</i>	√		
ECHINODERMATA			
<i>Tetrapygyus niger</i>	√		
ASCIDIACEA			
<i>Asciella aspersa</i>		√	
<i>Botryllus schlosseri</i>	√	√	
<i>Ciona intestinalis</i>	√	√	
<i>Diplosoma listerianum</i>	√	√	√
<i>Microcosmos squamiger</i>	√		√

The following account only details newly recorded alien species found in the course of these surveys and which appear to have been introduced as a result of oyster importation. Three such species were found: *Tetrapygyus niger*, *Ostrea edulis* and *Discinisca tenuis*. In

addition to these, a sample of a crab *Xantho incisus*, was sent to the University of Cape Town from Kleinsee oyster nursery (Fig. 1.6, Chapter 1) along the West coast during the course of this study, and appears certain to have been introduced there with oyster spat. These four newly recorded species are described and illustrated below.

***Tetrapygus niger*, Molina 1782 (Class Echinoidea, Family Arbaciidae)**

The natural range of the black sea urchin *T. niger* (Fig 2a) is along the temperate Pacific coast of South America from Northern Peru to the Strait of Magallanes in southern Chile. No previous history of invasion exists for this species. It is identified by its typically depressed purplish test, which is quite different from the round, green test of *Parechinus angulosus*, the only common coastal urchin native to the west coast of South Africa. *T. niger* was first collected from Alexander Bay oyster farm in 2007. A breeding population of hundreds or more individuals, consisting of both juveniles and adults, was recorded. Individuals were scattered on the bottom and in oyster baskets within the two oyster dams on the farm, being particularly common amongst *C. gigas* within oyster baskets.

***Ostrea edulis*, Linnaeus 1758 (Class: Bivalvia, Family: Ostreidae)**

The European flat oyster *O. edulis* (Fig. 2b) originates from Europe and has a global distribution from Norway to Morocco in the North-Eastern Atlantic, extending into the Mediterranean. Additional naturalized populations exist where this species has been introduced for aquaculture purposes (e.g. Eastern North America, Canada and British Columbia). It is identified by its rounded shell, which differs from the flat shells of native *Ostrea* species. In South Africa, *O. edulis* was first recorded in the Knysna Estuary in 1946, with subsequent introductions known to have occurred in Saldanha Bay and St Helena Bay in the 1980's and 90's (T. Tonin, pers. comm.). Recent publications have, however, regarded the population as locally extinct (Robinson et al. 2005). During the course of this study an extant and naturalised population was rediscovered in the Alexander Bay oyster farm along the West coast in 2007. Both adults and juveniles were recorded occurring amongst *C. gigas* oysters and on stones and other structures within both dams of the Alexander Bay oyster farm indicating the presence of a significant breeding population.

Xantho incisus, Leach 1814 (Phylum: Crustacea, Family: Xanthidae)

X. incisus (Fig. 2c) commonly known as Montagu's crab, originates from Europe and is distributed in the Mediterranean, Atlantic and English Channel. No previous invasion history exists for this species. The large, dark coloured pincers, compared to the paler body colouring, distinguish *X. incisus* from other South African crab species found along the Atlantic coast. A single individual was collected on the banks of the Kleinsee oyster nursery by a resident of the area, Andre van Wyk, in January 2008. The manager of the nursery, Quiryn Snethlage, reports first observing this species approximately three years ago, but has not collected any other individuals. The only confirmed specimen is thus the single specimen reported here, although earlier visual observations suggest a breeding colony seems likely.

Discinisca tenuis, Sowerby 1847 (Phylum: Brachiopoda, Family: Discinidae)

D. tenuis (Fig. 2d) is reported in the literature as native and endemic to Namibia, although shells have frequently been found washed ashore in Alexander Bay, just across the Namibian border into South Africa (T. Tonin pers, comm.). No previous history of invasion exists for this brachiopod. The unusual transparent, hairy, fringed shell makes this species easily distinguishable from the few native South African brachiopod species. The first South African record of live *D. tenuis* was made in Saldanha Bay in 2008, where numerous living individuals were found attached to the shells of *C. gigas* oysters grown in suspended culture. An average of one individual per oyster was found in a batch of 150 oysters inspected. Several previous surveys of the fauna of Saldanha Bay (Day 1958, Chrisie & Moldan 1977, Robinson *et al.* 2004, Awad *et al.* 2005) have failed to detect this conspicuous species, making it highly unlikely that it occurred naturally in the region at that time. We therefore deduce that it has recently been introduced, along with the cultured oysters with which it was associated.

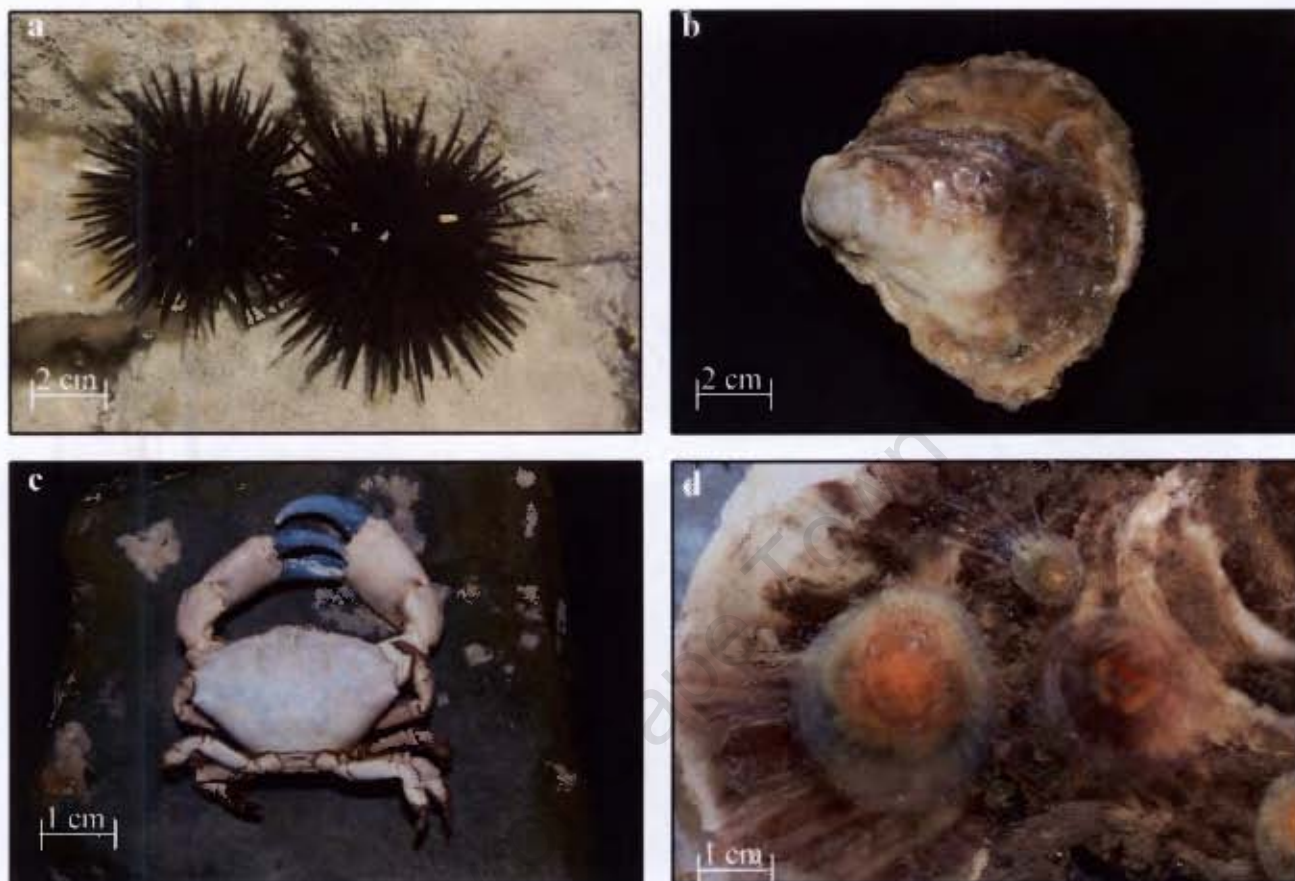


Figure 2. Appearance of *Tetrapygus niger* (a), *Ostrea edulis* (b), *Xantho incisus* (c) and *Discinisca tenuis* (d).

DISCUSSION

The aim of this chapter was to identify unfamiliar alien species that might have been introduced via the oyster trade in South Africa. Known alien species from the study sites: Alexander Bay, Saldanha Bay and the Knysna Estuary, were also listed. These three areas are clearly hot spots of invasion along the coast, most of the open coast being invaded by only one of two widespread species, *Mytilus galloprovincialis* and *Balanus glandula*. Of the three sheltered sites examined here Saldanha Bay hosted the largest number of aliens (Table 1). Interestingly, the occurrence of similar numbers of alien species in Alexander Bay, which is isolated from any boat traffic or international harbours, must be due to

oyster culture activities. Only the four newly discovered marine alien species recorded in the course of this study are discussed in detail below.

Tetrapyrgus niger is the most abundant sea urchin in its area of origin along the central Chilean coast (Rodriguez & Ojeda 1993). The most likely vector of this species into Alexander Bay oyster farm is the introduction of juveniles along with spat of *Crassostrea gigas* imported from Chile. The farm is isolated from any harbours and shipping activities making it most likely that shipping could not have acted as a vector for this introduction.

A population of *Ostrea edulis* also occurred in the same oyster dams at Alexander Bay. This species was first introduced to the Knysna Estuary in 1946 (Korringa 1956) and has since then thought to have become locally extinct (Griffiths 2000, Robinson et al 2005). This discovery thus marks its re-inclusion onto the list of extant alien species reported from South Africa. The population occurring at the farm could have been accidentally introduced along with consignments of *C. gigas* spat from Chile or France, but more likely were deliberately translocated from other oyster farms elsewhere in South Africa, where relict populations may have survived undetected since the early days of experimental oyster farming in the region.

Oyster imports from France might also have resulted in the introduction of the alien crab species *X. incisus*, found at Kleinsee oyster nursery. Like Alexander Bay, Kleinsee is isolated from any international harbours or boat traffic, which could act as alternative vectors.

The discovery of the brachiopod *D. tenuis* further down the West coast in Saldanha Bay is the first example of an alien marine species in South Africa originating from a neighbouring country. Individuals were found attached to shells of *C. gigas*. The most likely vector of this species is *C. gigas* oyster spat translocated from the oyster nursery in Walvis Bay, Namibia. No evidence was found of this species occurring on substrata other than oysters, indicating that the species may not yet have established self-sustaining populations off the original substratum on which they were introduced. Interestingly this

species has very recently also been noted on oysters for sale on a Cape Town supermarket and reputedly cultured in Algoa Bay from spat purchased from Alexander Bay (T. Tonin, pers comm.), suggesting that this species has also been introduced to other localities outside its native range.

Possible impacts:

The impacts of alien species fall into one of three categories: they may have no detectable or significant effect, they may be advantageous if they are commercially exploitable, or they might have negative ecological or economical impacts (Griffiths 2000). Of particular concern are species known to be a problem either in their area of origin, or in other invaded habitats.

Some echinoid species are already known to have a significant ecological impact as they play an important role as habitat engineers. *Parcentrotus lividus* has been described as an important habitat modifier of immediate sublittoral areas in Europe (Kitching *et al.* 1983). Himmelman *et al.* (1971), has discussed *Strongylocentrotus drobachiensis* in the North Western Atlantic causing a series of changes in the dynamics of the biota and in the North Eastern Pacific there are studies on *S. franciscanus* and its influence on offshore kelp-beds (Dean *et al.* 1983). Similarly, *T. niger* is a well known ecosystem engineer and has become an economic and ecological pest in its areas of origin. In Northern Chile, *T. niger* is the most conspicuous benthic grazer and has recently quadrupled in abundance, resulting in catastrophic effects on associated flora (Vasquez & Buschmann 1997, Vega *et al.* 2005, V. Haeussermann, pers. comm.). Larvae of this species settle in beds of the kelps *Lessonia nigrescens* and *L. trabeculata*, which are regularly exported from Chile as raw materials for alginate production (Vasquez & Santelices 1990, Rodriguez & Ojeda 1993). These kelps are an important food resource for *T. niger*, and make up 68% of its diet (Rodriguez 2003). Increased grazing from the urchins has reduced the recruitment of both *Lessonia* species and has modified the morphology of *L. trabeculata* by grazing on the holdfast. This weakens individuals, making them susceptible to drag forces and increasing mortality from water movement (Vasquez & Santelices 1990). Ojeda & Santelices (1984) showed that in the absence of

the dominant canopy species *L. nigrensis*, algal species such as *Gelidium chilense* are unable to increase their cover, or monopolize the substratum, due to predation by *T. niger*. The increase in abundance of *T. niger* has also resulted in local extinctions of the kelp *Macrocystis integrifolia* due to overgrazing (Vega *et al.* 2005). These ecological impacts illustrate the possible impacts of *T. niger* along the west coast of South Africa, which is also dominated by extensive and commercially valuable kelp- bed ecosystems (Branch & Griffiths 1988).

A well-established population of *O. edulis* occurs in the same oyster dams at Alexander Bay. Although *O. edulis* has been deliberately introduced to South Africa several times (Korringa 1956) the origins of this particular population are unknown. Globally this species has been used to boost aquaculture in many regions (Askew 1972, Mann 1983, Shpigel 1989, Chew 1990, Drinkwaard 1999) and the negative impacts of these introductions have been extensively documented. These include the genetic loss of native oyster species due to the exchange of *O. edulis* oyster stocks and the potential of *O. edulis* as a vector for the oyster disease *Bonamia ostreae* and oyster pathogen *Marteilia refringens* in Europe (van Banning 1991, Cigarria & Elston 1997, Le Roux *et al.* 2005). If the population size of *O. edulis* escalated it could compete with *C. gigas*, which is cultured in the dams. Densities of *C. gigas* however, currently far outweigh those of *O. edulis*. If populations of *O. edulis* manage to establish in surrounding coastal waters, impacts such as competition with native bivalve species could also occur.

Literature on the crab *X. incisus* focuses on its biology, distribution, spatial and temporal settlement patterns and association with other fauna, rather than its impacts as an invader (Crothers 1970, Wirtz 1997, Flores *et al.* 2002, Flores & Paula 2002). The discovery of this crab in South Africa thus appears to be its first record as an alien species. Being a powerful predator this species could cause considerable damage to the shellfish industry by consuming *C. gigas* or other shellfish. Although no such incidents have been recorded, further studies should be conducted to determine the density, distribution, habitat and diet at this site in order to determine whether the crabs are limited to the oyster farm, or have

spread into surrounding coastal waters. This is, however, unlikely given the isolation of this particular dam from the open sea.

Literature on the brachiopod *D. tenuis* is limited. Its distribution and biology are noted by Branch *et al.* (2005) and its occurrence in Namibia discussed by Brunton & Hiller (1990), Hiller (1990) and Nemliher & Kallaste (2002). It is unknown whether *D. tenuis* has managed to spread to substrata other than that of cultured *C. gigas* oysters in Saldanha Bay. Brachiopods are sessile filter-feeding organisms and might therefore compete with native fauna for food and space. Their unsightly appearance may also have a negative impact on consumers of shellfish farmed in the bay. Although oysters are cleansed prior to purchase, not all associated fouling organisms are removed and *D. tenuis* are especially resistant, as they are flat and attach via threads to the oyster shells.

Because the ecological impacts of these alien species are unknown in the South African context, precautions should be taken to prevent their further spread in South African waters. At present, the populations of *T. niger* and *O. edulis* are thought to be restricted to the oyster dams at Alexander Bay. Juveniles of both species were found during sampling indicating that the populations are able to successfully reproduce in their new environment. Of concern is the possibility of these species establishing outside of the oyster dams on the open coast. The cleansing procedure of the oysters at the farm entails jet-spraying with seawater to remove any fouling species. This water, along with any excess debris and fouling species, is returned to the surrounding sea via an unfiltered and untreated run-off system. The occurrence of the urchins and oysters outside the oyster dam, as well as their density inside the dams, remains to be determined. Should either species be detected in the open ocean, a suitable eradication programme to eliminate them and prevent their spread should be urgently initiated. Olenin *et al.* (2007) have recently published a method for quantifying alien impacts and this might be considered in terms of the potential risks of *T. niger* to the South African kelp-beds and their associated and specialised biota. In the interim, measures to prevent the transfer of *T. niger* and *O. edulis* from the dam to the open sea should be initiated.

The density of *X. incisus* in Kleinsee is not known, as to date, only a single dead specimen on the littoral fringe of the cultivation dam has been collected. Setting out crab traps would be the best way to determine their density and also control and even eliminate this species, without any harm to the cultured oysters.

The brachiopods *D. tenuis* are not easily removed from oyster shells due to their flat and inconspicuous nature. Thus, a more thorough cleansing regime, for example soaking oyster spat in freshwater or heated seawater before translocation to farms, should be instituted to prevent further introductions along with imported Namibian spat.

This chapter emphasizes the increasing role played by the oyster industry in introducing marine alien species to South Africa. From the track record of some of these aliens, it is evident that these species could pose a real threat. The extent of these invasions need to be assessed and actions taken to limit their spread. The local, or intraregional, translocation of cultured oysters is a common activity, which often occurs between farms and nurseries and may aid in the spread of alien species within South Africa. The following chapter examines the spread of fouling organisms, particularly marine alien species, associated with translocating *C. gigas* oysters within the region. Preventative measures, such as a more thorough cleansing regime to eliminate these organisms before translocation, are also examined.

CHAPTER 3

University of Cape Town

INTRA-REGIONAL TRANSLOCATIONS OF EPI- AND INFAUNAL SPECIES ASSOCIATED WITH THE PACIFIC OYSTER *CRASSOSTREA GIGAS*

INTRODUCTION

The previous chapter highlighted the role that oysters have played in the introduction of marine alien species in regions where oysters are imported for commercial purposes. For example, South Africa has imported *Crassostrea gigas* spat from Chile, France and England, which has most probably resulted in the introduction of at least four newly-recorded alien species. In this chapter, the focus shifts from intercontinental, to local, or intraregional translocation of species associated with *C. gigas* in South Africa. After the intercontinental translocation of oysters, further regional spread can occur through additional translocation mechanisms (Buchan & Padilla 1999, Bossenbroek *et al.* 2001, Johnson *et al.* 2001). Most often, once an introduced species is brought into a region, no political constraints or economic boundaries are implemented preventing further spread within the region (Miller *et al.* 2001). Thus, local or intraregional translocation of oysters has become increasingly problematic in the spread of fouling organisms, particularly alien species (Wasson *et al.* 2001). Intraregional translocation of commercially imported oysters and associated alien species are common, but have received little attention in the literature.

Overland translocation is a common occurrence in mollusc culture, as spat are often grown-out in different areas to those where adults are farmed (Minchin 2007). For example, seed mussels of *Perna canaliculus* are transported from the North Island to the South Island in New Zealand, and cultured scallops *Patinopecten yessoensis* are distributed within Japan (Ventilla 1982). This rapid overland transport facilitates the survival of in- or epifaunal species associated with the transported molluscs, and these can include economically and ecologically significant pests, parasites and diseases (Minchin 2007). Often, these movements have resulted in the unintentional spread of species. For example, salmon fingerlings *Salmo salar*, transported from Swedish hatcheries to Norway in 1974, resulted in the introduction of the helminth parasite *Gyrodactylus salaricus*, which subsequently caused population declines of salmon in

Norway (Johnsen & Jensen 1991). In certain cases, the aquaculture species may spread and become invasives themselves. Such an example can be seen in the invasion of the Columbia River by Asian freshwater clam *Corbicula fluminea*. It is thought that a few individuals of this species were imported initially as live food, but gave rise to a full scale invasion (Chapman *et al.* 2003).

In the oyster industry, local or intraregional translocation may involve the exchange of commercial oyster stock and spat by growers and nurseries in different areas (Wasson *et al.* 2001). Such translocations of oysters are common, but are rarely documented (J. Carlton, pers. comm.). Wasson *et al.* (2001) indicated that 18 or more alien species, from a total of over 50 found in the Elkhorn Slough Estuary in central California, had the potential to be transported with oysters through intraregional translocation. A similar situation exists in North-Western Europe, where consignments of oysters transported overland within mesh bags could be the cause of the spread of the Asian crab *Hemigrapsus penicillatus* and the predatory snail *Ocenebrellus inornatus* (Minchin 2007). Another example is the spread of the brown alga *Undaria pinnatifida*, from harbour to harbour in Europe, possibly through local maritime transport associated with translocated oysters (Voisin *et al.* 2005). The initial introduction of this species in Europe was through consignments of oyster spat imported from Japan (Ohno & Largo 1998, Wolff & Reise 2002).

In South Africa, a unique system of translocation and local exchange between oyster farms, nurseries, retailers and customers exists. Oyster nursery facilities in Walvis Bay (Namibia), Kleinsee, Paternoster and Jeffery's Bay import oyster spat from hatcheries in Chile, France and the UK. These are grown in the nurseries for two months, after which they are transported to various oyster farms, where they are grown to adult or market size (Chapter 1). In some incidences, juveniles are also translocated to neighbouring farms, where waters are better suited for growth, and returned once market size is reached. From the farms, they are purchased by supermarkets, restaurants or directly by the general public. Since oysters are consumed alive, they are kept in holding tanks upon arrival at supermarkets and restaurants. Many of these retailers are located at or near the sea and a flow-through system between holding tanks and the ocean may exist, to supply oysters with a continuous flow of fresh seawater. Occasionally, oysters purchased by the general

public may even be stored in nearby seawater (e.g. suspended from a local jetty), together with their associated fouling organisms. Once the oysters are consumed, the shells, with their live associated fauna, may also be disposed of into local water bodies. In this way, alien species present on *C. gigas*, as well as the oysters themselves, may expand to new sites and biogeographic regions (Chapman *et al.* 2003, Robinson *et al.* 2005a). Although oysters are usually cleansed before leaving nurseries or farms, hitchhiking organisms are still found on and in between the grooves of oyster shells, or even in the mantle cavity (Basson 2003). It is important to note that species transported in this way are not necessarily imported with the oyster spat, but may colonize the growing oysters in the oyster farm, following which they may be translocated to other sites, expanding the native range, or setting up a new nucleus of invasion.

The oyster operation located in the Knysna Estuary provides one such interesting case study for the intraregional translocation of *C. gigas* and its associated organisms. Juvenile *C. gigas* are purchased from a nursery in Jeffrey's Bay, which in turn imports oyster spat from Chile and France. In the Estuary, the juveniles are grown for four months, after which they are transported to Algoa Bay oyster farm, where the conditions for growth of oysters are considered more suitable (Chapter 1). Oysters grown in these waters reach market size after only a further three to four months and are then returned to the Knysna Estuary and kept in holding tanks until purchased (M. B. Solomons, pers. comm.). Such oyster movements may thus well result in the translocation of fouling species in both directions between these two areas.

The standard cleansing procedure prior to translocation involves manually removing fouling organisms from the oyster shells, after which oysters are jet blasted with seawater. At the Cape Knysna Oyster Co., the mesh bags in which juvenile oysters are held are merely shaken off in the estuarine water to remove excess mud, before being translocated to Algoa Bay (A. Malgraaf, pers. comm.). Consignments of oysters are not inspected for associated species.

The translocation of fouling organisms still persisting after the cleansing procedure can be reduced or eliminated by a more thorough cleansing regimen (Wasson *et al.* 2001). Nel *et al.* (1996) suggested the treatment of commercially reared *C. gigas* in

freshwater for 12 h, or heated sea water at 70°C for 40 sec, to reduce the numbers of the mud worm *Polydora hoplura*. Korringa (1976) also suggested that immersing oysters in heated seawater at 70°C for 20 sec would eradicate external fouling organisms, with no injury to the oysters.

This chapter examines the type and quantities of fouling species occurring on *C. gigas*, how effectively these are removed by the standard cleansing procedure of manually removing fouling organisms and jet-blasting oysters with seawater, and if species still persist, whether or not they survive translocation. The effectiveness of exposing *C. gigas* to freshwater, or heated seawater, as a suitable further cleansing regimen to eliminate any remaining fouling species was also tested. Results from this study quantify the risks associated with translocating oysters and aim to suggest mechanisms for reducing the translocation of indigenous species beyond their natural range and the spread of marine alien species associated with oysters.

METHODS

Cultured *Crassostrea gigas* oysters were collected from the Striker Fishing Oyster Company in Saldanha Bay in August 2007. Three replicate samples of 30 oysters each were examined to evaluate the numbers and densities of species present at three stages in the collection and shipping process, uncleansed, cleansed (i.e. after manual removal of fouling organisms and jet-blasting) and following translocation. The three samples of oysters were all of market size (>50 g: total wet weight) and were collected from the same stock of Chilean oysters, but from different parts of the farm. Oysters of each sample were made up of three sub-samples of 10 oysters, each taken from three separate baskets on the same culture rope. For the 30 oysters representing the uncleansed stage, each oyster was placed into a separate plastic bag, which was later filled with 70% formalin. Organisms residing on the shells and in the grooves of individual oysters were counted (solitary organisms) or weighed (colonial organisms) and identified to species, or when not possible, family level. The two samples of 30 oysters each, representing the cleansed and translocated stages, underwent the standard cleansing procedure of manually removing visually obvious organisms residing on the oyster shells and jet-spraying with sea water (Fig. 3.1 a & b). Individual oysters from the cleansed treatment were placed in separate plastic bags

and covered with 70% formalin. Counts of organisms and types of species still remaining on cleansed oysters were obtained by searching for organisms on the shell and in the grooves. For the translocation stage, oysters were packaged with ice in polystyrene boxes exactly as for commercial shipment and transported to the University of Cape Town, where they were kept in this state for 24 h to replicate the time and conditions under which oysters are kept during normal commercial operations. After this period, individual oysters were placed in containers of seawater and examined microscopically for live organisms. Survival was assessed for Polychaeta by movement of tentacles, for Cnidaria by movement of tentacles or expansion, for Mollusca by closure of their shells, for Crustacea by movement of appendages and for Porifera by retention of colour and form.



A

B

Figure 3.1 Market-sized *C. gigas* are manually cleansed of organisms and debris (A) after which they are jet-sprayed with sea water (B), before being packed in polystyrene boxes for shipping.

The effectiveness of submerging *C. gigas* in freshwater and heated seawater in order to decrease or eliminate fouling species that survive cleansing was also tested. In

October 2008, oysters were collected from the Striker Fishing Oyster Company in Saldanha Bay where they were cleansed before translocation to the University of Cape Town, where experiments were carried out. Oysters weighed an average of 63.71 g in total wet weight. The time periods 3, 6, 9, 12, 15 and 18 h were chosen for soaking oysters in freshwater and 20, 40 and 60 sec for immersion in heated seawater. These time periods were chosen as a previous preliminary study by Nel *et al.* (1996) in which oysters were treated with freshwater for 12 h, or heated seawater (70°C) for 40 sec, significantly reduced numbers of, but did not completely eliminate, fouling organisms.

Freshwater experiment

Salinity was measured using an ATAGO S/Mill Salinity 0 - 100% hand-held refractometer and remained at 0‰ throughout the experimental period. For each time period, 15 oysters were soaked in individual containers of freshwater. Following the treatment, oysters were transferred to individual containers of seawater overnight (12 h) to recover (Nel *et al.* 1996). After the recovery period, oyster survival was tested for by observing if contraction of the mantle edge occurred after mechanical stimulation. Epi-faunal organisms were examined under a dissecting microscope and survival noted if feeding activity, or retraction in response to stimulation, occurred. Polychaete survival was difficult to examine visually as they often retreated into their burrows. After the 12 h recovery period in seawater, oysters were thus transferred to individual containers of 0.05% phenol solution in seawater overnight (12 h). This vermifuge is used to extract burrowing polychaetes from bivalve shells (Handley 1995). A control group of 15 untreated oysters was also placed in 0.05% phenol solution for 12 h to obtain an initial polychaete count. The average number of polychaetes that emerged from untreated oysters (control) was then compared to the number of polychaetes that emerged from oysters treated with freshwater to determine percentage survival.

Heated seawater experiment

For this experiment, three samples of 15 oysters each were placed in a warm water bath set at 70°C following Nel *et al.* (1996) for either 20, 40 or 60 sec. Thereafter, oysters and associated organisms were treated in the same manner as above.

Statistical analyses

Statistical analyses were carried out using Statistica 8. The abundance of solitary fouling taxa, or biomass of colonial fouling taxa, occurring per oyster and numbers of fouling species occurring per oyster were compared between uncleaned, cleaned and translocated stages using a non-parametric Kruskal-Wallis one-way ANOVA test, followed by Multiple Comparisons of mean ranks. In instances where a taxon present in the uncleaned and cleaned stages was absent in the translocated stage, a non-parametric Mann-Whitney test was used to compare the abundance or biomass of fouling taxa per oyster and the numbers of species per oyster among uncleaned and cleaned stages. If a taxon occurred in one treatment only, statistical analyses were not applicable (NA). Analyses were conducted separately for the different taxa. As species found in some taxa were both solitary and colonial, measurements and graphs are presented for both abundance (solitary organisms) and biomass (colonial organisms).

RESULTS

Uncleaned oysters had a significantly higher mean abundance or mean biomass of all taxa tested compared to cleaned and translocated oysters (Table 2a, Table 3, Fig. 3.2 a, b & c, Fig. 3.3 a, b & c). Most of these differences occurred between uncleaned and cleaned oysters and uncleaned and translocated oysters (Table 2a). The mean abundance (A) or biomass (B) of overall taxa per oyster was more than 30 times greater in uncleaned (A: 79.48 ± 233.10 (SD), B: 0.034 ± 0.314 (SD)) compared to cleaned (A: 2.30 ± 7.65 (SD), B: 0.0003 ± 0.002 (SD)) oysters and more than 40 times greater than in translocated (A: 1.87 ± 7.43 (SD), B: 0.006 ± 0.020 (SD)) oysters (Table 4). Taxa which occurred in great abundance on uncleaned oysters included the crustaceans *Jassa slattery* and *Anatanaïs gracilis* (342.37 ± 480.8 (SD) & 53.07 ± 61.41 (SD) per oyster respectively), the polychaete *Polydora hoplura* (115.77 ± 84.42 (SD)) and the introduced mussel *Mytilus galloprovincialis* (69.23 ± 36.29 (SD)). Most of the species that survived cleaning also had a 100% survival rate following translocation, except for the barnacle *Notomegabalanus algicola* (62.5%) and *M. galloprovincialis* (50%). Significant differences were also found in the number of species of all taxa per oyster among uncleaned, cleaned and translocated treatments (Table 2b). A higher

number of species for the majority of taxa occurred on uncleansed oysters, compared to cleansed and translocated ones (Fig. 3.4 a, b & c).

The percentage survival of different epi- and infaunal taxa, as well as of *C. gigas* oysters themselves, after soaking in freshwater and heated seawater for variable time periods are illustrated in Figure 3.5 a, b & c. Oysters survived with no mortalities after 18 h in fresh water (Fig. 3.5 a & b). However, survival in heated seawater decreased by 26.7 % after 40 sec and 86.7% after 60 sec (Fig. 3.5c). In freshwater, cnidarians (*Aulactinia reynaudi*) and brachiopods (*Discinisca tenuis*) did not survive at all, whereas the polychaete *P. hoplura* showed a steady decrease in survival through time, with almost complete mortality at 97.5% after 18 h (Fig. 3.5a). Other polychaete species, *Cirriformia capensis*, *C. tentaculata*, *Lepidonatus semitectus clava*, *Loimia medusa*, *Nereis sp*, *Platynereis dumerilii*, and *Syllis sp*, maintained a stable percentage mortality through time at 22.7% (Fig. 3.5a). Crustaceans *Anatanais gracilis*, *Austromegabalanus cylindricus*, *Jassa slattery*, and *Notomegabalanus algicola*, did not survive after 6 and 9 hrs in freshwater, but 23.5%, 4.9% and 12% survived for 12, 15 and 18 h respectively (Fig. 3.5b). The molluscs *Aulacomya ater* and *M. galloprovincialis* survived for 6 h in freshwater, after which survival decreased by 55.6% after only 9 h, although only 27.3% died after 18 h (Fig. 3.5b). Echinoderms (*Thyone aurea*), all died after soaking for longer than 9 h in freshwater. Ascidians (*Ascidia sp*) survived with no mortalities for 6 h in freshwater, after which survival decreased steadily, but complete mortality was not achieved even after 18 h, when 46.2% of individuals still survived (Fig. 3.5b). In heated seawater, 88.5% of *P. hoplura* and 66.7% of crustaceans died after only 20 sec, and both were completely eliminated after 60 and 40 sec respectively. Brachiopods, molluscs and ascidians did not survive even the shortest immersion in heated seawater (Fig. 3.5c).

Table 2. Results of statistical tests analysing (a) abundance or biomass* and (b) the numbers of species occurring per oyster among uncleaned, cleaned and translocated stages. Significant differences among groups are indicated by UC (uncleaned), C (cleaned) and T (translocated). NA = Not Applicable, Sol = solitary, Col = colonial.

(a)

TAXON	H - STATISTIC	DEGREES OF FREEDOM (df)	SIGNIFICANCE LEVEL	MULTIPLE COMPARISONS
Porifera*	11.12	2	<0.05	
Sol Cnidaria	2.22	1	<0.05	
Col Cnidaria*	NA			
Unsegmented worms	NA			
Polychaeta	58.14	2	<0.05	(UC&C) (UC&T)
Arthropoda	NA			
Crustacea	69.81	2	<0.05	(UC&C) (UC&T)
Bryozoa*	NA			
Mollusca	64.64	2	<0.05	(UC&C) (UC&T)
Echinodermata	6.39	1	<0.05	
Sol Ascidiacea	14.32	2	<0.05	(UC&T)
Col Ascidiacea*	NA			

(b)

TAXON	H - STATISTIC	DEGREES OF FREEDOM (df)	SIGNIFICANCE LEVEL	MULTIPLE COMPARISONS
Porifera	9.44	2	<0.05	
Cnidaria	3.56	1	<0.05	
Unsegmented worms	NA			
Polychaeta	46.85	2	<0.05	(UC&C)(UC&T)
Arthropoda	NA			
Crustacea	69.43	2	<0.05	(UC&C) (UC&T)
Bryozoa	NA			
Mollusca	57.35	2	<0.05	(UC&C)(UC&T)
Echinodermata	5.99	1	<0.05	
Ascidiacea	16.05	2	<0.05	(UC&T)

Table 3. Means and standard deviations of abundance (solitary organisms: SOL) or biomass * in grams (colonial organisms: COL) of taxa per oyster in uncleaned, cleaned and translocated stages.

TAXON	UNCLEANSED	CLEANSED	TRANSLOCATED
Porifera*	0.117±0.623	0.001±0.003	0.023±0.037
Sol Cnidaria	0.90±1.60	0.07±0.36	0±0
Col Cnidaria*	0.002±0.009	0±0	0±0
Unsegmented worms	2±1.96	0±0	0±0
Polychaeta	135.17±88.85	14.03±16.62	14.20±16.53
Arthropoda	0.03±0.18	0±0	0±0
Crustacea	411.43±539.52	1.97±5.25	0.17±0.65
Bryozoa*	0.003±0.011	0±0	0±0
Mollusca	73.57±35.62	1.77±2.81	0.57±1.01
Echinodermata	11.80±8.92	0.10±0.40	0±0
Sol Ascidiacea	0.97±1.40	0.50±1.46	0.03±0.18
Col Ascidiacea*	0.01±0.07	0±0	0±0

Table 4. Epi- and infaunal species present in uncleansed, cleansed and translocated oysters. Figures given are mean abundance (#) and standard deviation (SD) of solitary taxa per oyster or mean biomass (g) and standard deviation (SD) of colonial taxa per oyster. Alien species are in bold.

TAXON	UNCLEANSED (MEAN ± SD)		CLEANSED (MEAN ± SD)		TRANSLOCATED (MEAN±SD)	
	Abundance (#)	Biomass (g)	Abundance (#)	Biomass (g)	Abundance (#)	Biomass (g)
PORIFERA						
Knobbly-orange sponge		0.114±0.624		0		0
<i>Leucosolenia</i> sp		0.003±0.009		0.001±0.003		0.023±0.036
CNIDARIA						
<i>Aulactinia reynaudi</i>	0.90±1.60		0.07±0.36		0	
<i>Eudendrium</i> spp		0.002±0.009		0		0
<i>Virgularia schultzei</i>		0.0002±0.00		0		0
UNSEGMENTED WORMS						
<i>Malacobdella grossa</i>	1.73±1.89		0		0	
<i>Planocera gilchristi</i>	0.27±0.52		0		0	
POLYCHAETA						
<i>Cirriatulidae</i> spp	0.03±0.18		0		0	
<i>Flabelligiridae</i> spp	0.03±0.18		0		0	
<i>Nereidae</i> spp	0.83±2.11		0.03±0.18		0.03±0.18	
<i>Nereis</i> spp	0.17±0.75		0		0	
<i>Lepidonotus semitectus clava</i>	0.27±0.69		0.03±0.18		0.03±0.18	
<i>Loimia medusa</i>	0.53±0.73		0.1±0.31		0.17±0.38	
<i>Platynereis dumerilii</i>	10.47±0.18		0.03±0.18		0.03±0.18	
<i>Polydora hoplura</i>	115.77±84.42		13.5±16.66		13.53±16.65	
<i>Pseudopotamilla reniformis</i>	0.03±0.18		0		0	
<i>Sabellidae</i> spp	0.03±0.18		0		0	
<i>Sillidae</i> spp	1.47±4.66		0		0	
<i>Spionid</i> spp	0.03±0.18		0		0	
<i>Syllis</i> spp	4.97±4.26		0.3±0.65		0.37±0.67	
<i>Terebellidae</i> spp	0		0.03±0.18		0	
<i>Typhloscolecidae</i> spp	0.07±0.25		0		0	
ARTHROPODA						
<i>Tanystylum brevipes</i>	0.03±0.18		0		0	
CRUSTACEA						
<i>Anatanais gracilis</i>	53.07±61.41		1.03±2.09		0.03±0.18	
<i>Austromegabalanus cylindricus</i>	0.5±0.63		0		0	
<i>Dexamine spiniventris</i>	10.7±16.66		0		0	
<i>Hymenosoma orbiculare</i>	0.9±1.77		0		0	

Table 4 continued

TAXON	UNCLEANSED (MEAN ± SD)		CLEANSED (MEAN ± SD)		TRANSLOCATED (MEAN±SD)	
	Abundance (#)	Biomass (g)	Abundance (#)	Biomass (g)	Abundance (#)	Biomass (g)
<i>Jassa slatteryi</i>	342.37±480.8		0.8±3.31		0.07±0.37	
<i>Jasus lalandi</i>	0.03±0.18		0		0	
<i>Notomegabalanus algicola</i>	3.83±3.50		0.13±0.34		0.07±0.37	
<i>Paridotea ungulata</i>	0.03±0.18		0		0	
BRYOZOA						
<i>Bowerbrankia imbricata</i>		0.001±0.003		0		0
<i>Bugula avicularia</i>		0.002±0.011		0		0
MOLLUSCA						
<i>Aulacomyer ater</i>	0.13±0.34		0		0.07±0.25	
<i>Mytilus galloprovincialis</i>	69.23±36.29		1.77±2.81		0.5±1.01	
<i>Venerupis corrugatus</i>	4.2±7.05		0		0	
ECHINODERMATA						
<i>Thyone aurea</i>	11.8±8.92		0.1±0.40		0	
ASCIDIACEA						
<i>Ascidia</i> sp	0.9±1.35		0.5±1.46		0.03±0.18	
<i>Ciona intestinalis</i>	0.03±0.18		0		0	
<i>Diplosoma listerianum</i>		0.01±0.07		0		0
<i>Pyura stolonifera</i>	0.03±0.18		0		0	
MEAN & SD OF TOTAL TAXA (PER OYSTER)	79.48±233.10	0.034±0.314	2.30±7.65	0.0003±0.002	1.87±7.43	0.006±0.020

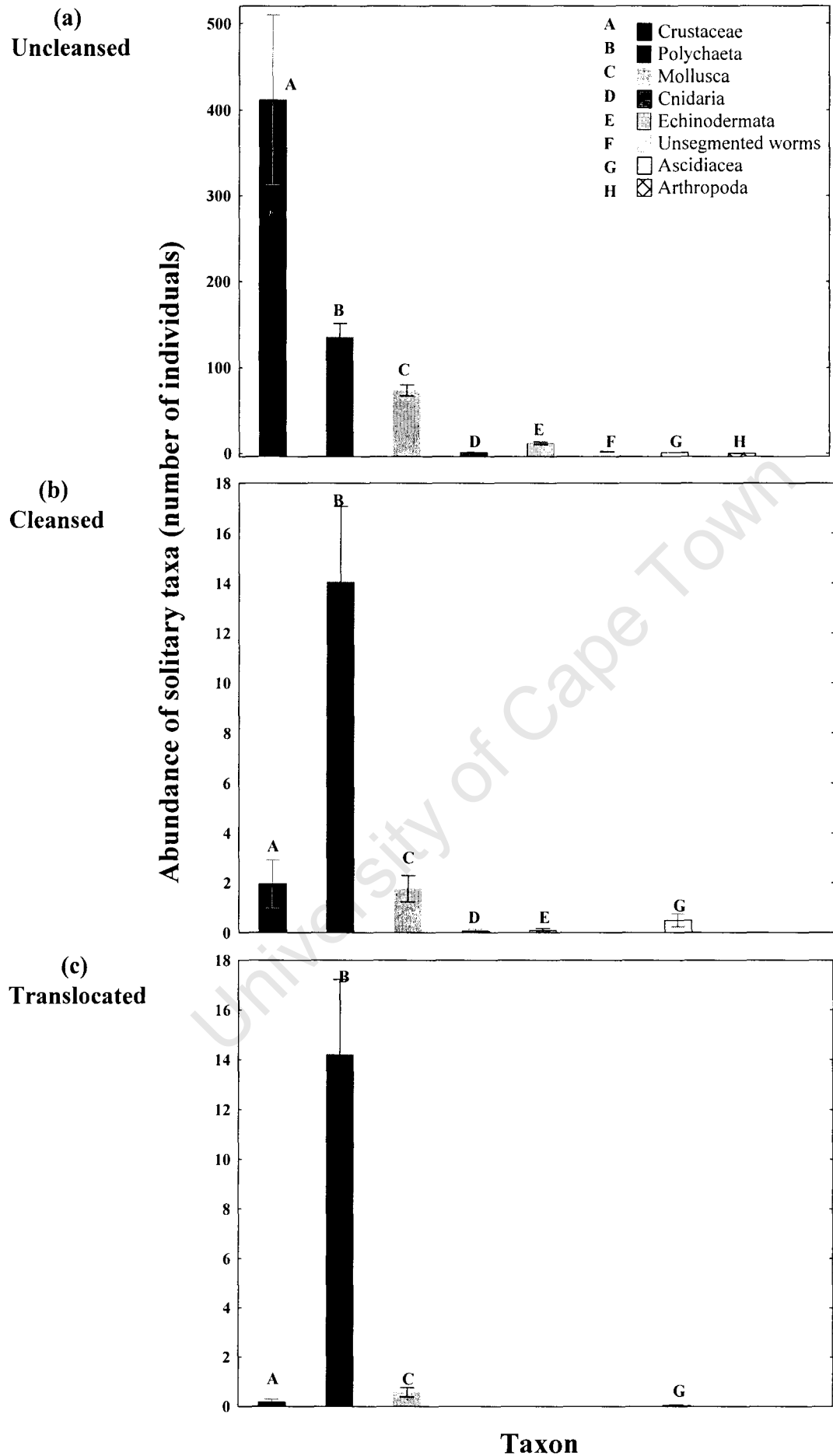


Figure 3.2. Mean abundance of solitary taxa (number of individuals) per oyster in (a) uncleaned, (b) cleansed and (c) translocated stages (note differences in scale between graphs). Standard error is shown.

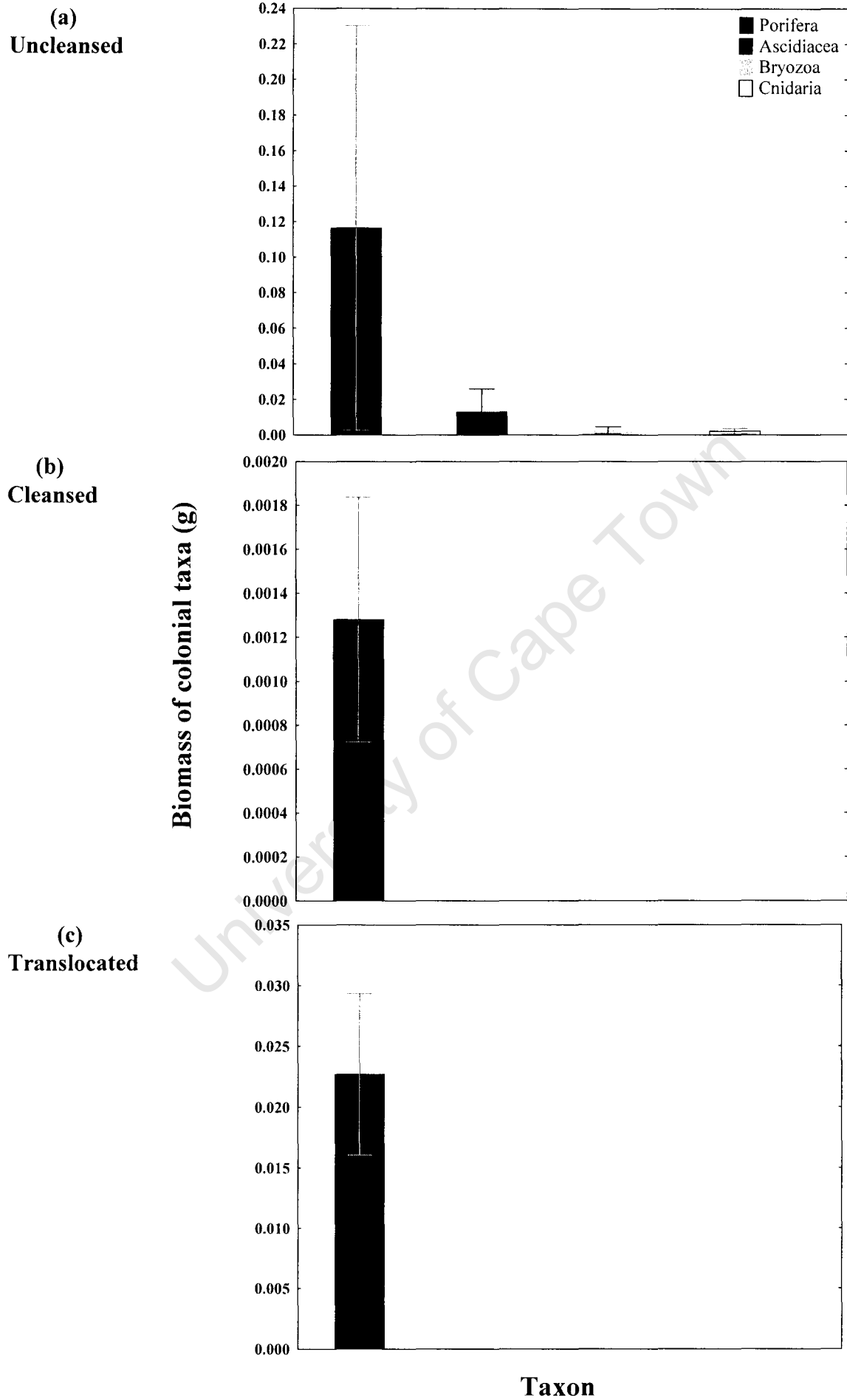


Figure 3.3. Mean biomass (g) of colonial taxa per oyster in (a) uncleaned, (b) cleansed and (c) translocated stages (note differences in scale between graphs). Standard error is shown.

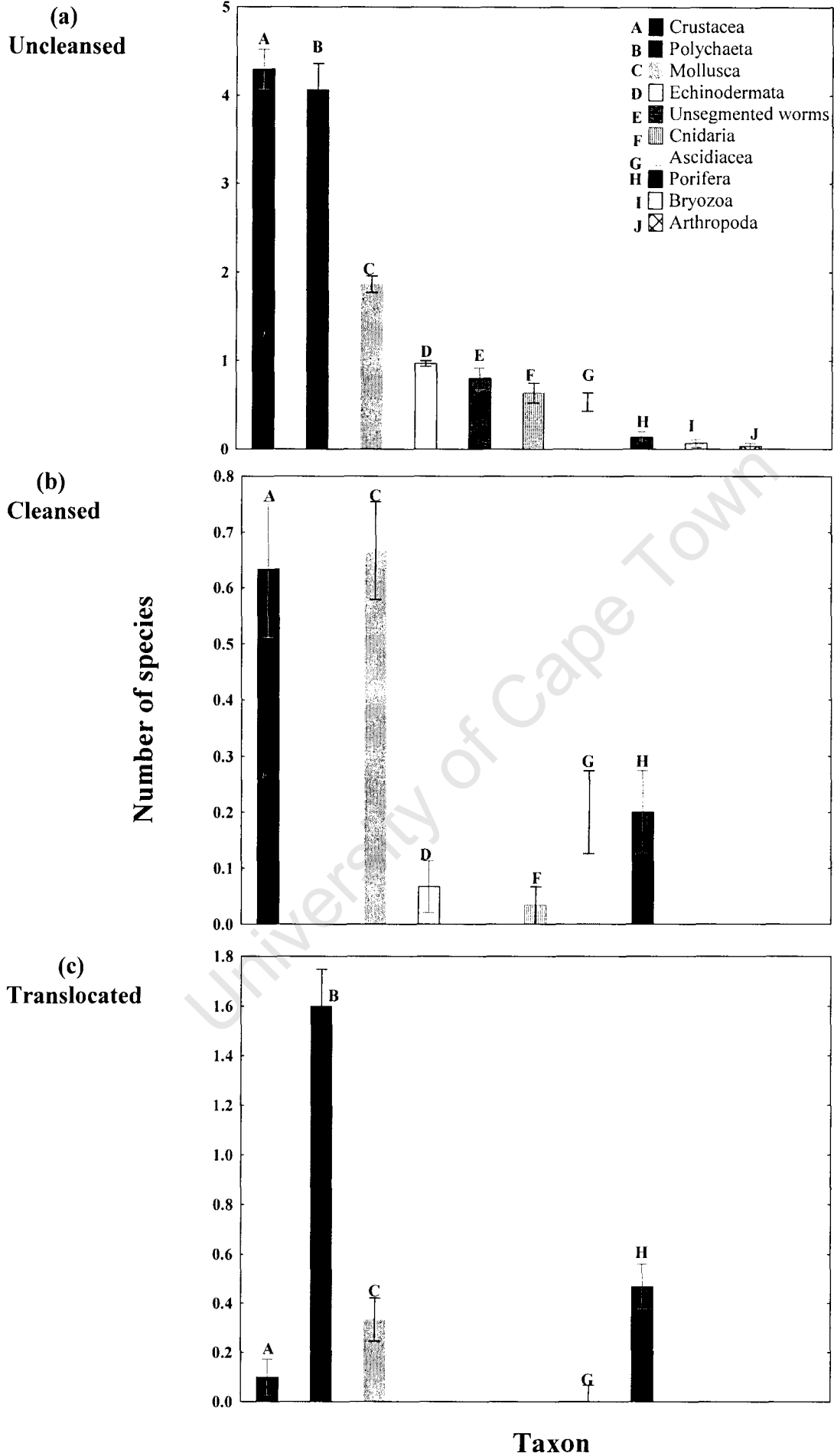


Figure 3.4. Mean number of species per oyster in (a) uncleaned, (b) cleaned and (c) translocated stages (note differences in scale between graphs). Standard error is shown.

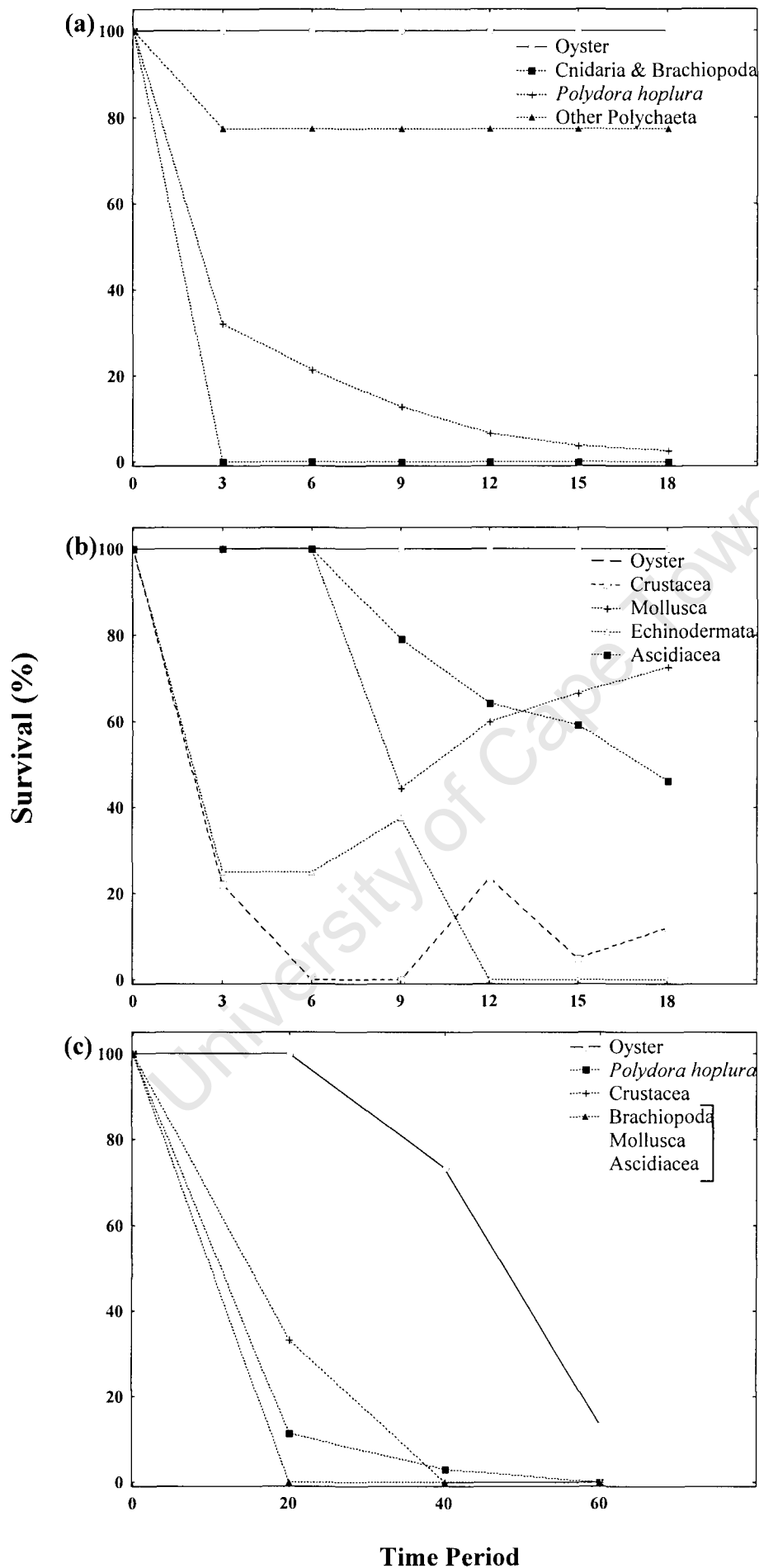


Figure 3.5. Percentage survival of taxa after soaking in freshwater (a & b) (hours) and heated seawater (c) (seconds) for variable time periods. Survival of oysters under the same treatments are also represented. Note: for the freshwater treatment, taxa were divided into two graphs (a) and (b) for better illustration

DISCUSSION

The aim of this chapter was to examine the types and quantities of fouling species occurring on farmed *Crassostrea gigas*, how effectively these were removed by standard cleansing techniques and whether species that persisted after washing, survived intraregional translocation. The effectiveness of exposing these oysters to freshwater or heated seawater to prevent the translocation of fouling species was also examined.

It is evident that cleansing and translocating oysters, significantly reduces both the quantities and variety of fouling species occurring or surviving on *C. gigas* oysters (Table 2 a&b). The quantities (i.e. abundance and biomass) were reduced by more than 30 times after cleansing, and by more than 40 times after translocation, when compared to uncleansed oysters (Table 3, Table 4, Fig. 3.2 a, b & c, Fig. 3.3 a, b & c). The numbers of species of most taxa occurring per oyster were also greater in uncleansed, compared to cleansed and translocated oysters (Fig. 3.4 a, b & c).

Those species that persisted, usually occurred on *C. gigas* in relatively large numbers or biomass before the cleansing procedure (Table 4), or were those that penetrated into the shell. For example, the invasive burrowing polychaete species, *Polydora hoplura*, was the most abundant polychaete species in the uncleansed, cleansed and translocated stages (Table 4). These mudworms are noted pests of cultured molluscs and considerable research has been done on their impact (Blake & Evans 1972, Handley 1995, Handley & Bergquist 1997, Leonart *et al.* 2003, Tinoco-Orta & Caceres-Martinez 2003, Simon *et al.* 2006). At Saldanha Bay Oyster Farm, *C. gigas* are reared using an off-bottom culture system in which oysters are permanently submerged, enabling faster growth (Wisely *et al.* 1979). This method allows fouling organisms such as *P. hoplura* to attach to oysters and by so doing, escape siltation and predators which occur on the ocean floor (Blake & Evans 1972). The cleansing procedure at the farm reduced numbers of *P. hoplura* in cleansed, compared to uncleansed stages, but a few individuals still persisted and survived translocation (Table 4). The persistence of the remaining individuals was probably due to their burrowing nature, as burrowing organisms are not as effectively removed during the cleansing procedure as those occurring externally on the oyster shells.

The crustaceans *Anatanaia gracilis*, *Dexamine spiniventris* and the alien species *Jassa slattery*, also occurred in large numbers on uncleaned oysters, but their numbers were greatly reduced by the cleansing procedure and some still persisted after translocation (Table 4). These crustaceans often secrete tubes on the shells of *C. gigas*, or occur in the grooves of the oyster shells, which could explain their resilience to cleansing. The indigenous tanaid species, *A. gracilis*, and the alien amphipod species, *J. slattery*, survived translocation. *A. gracilis* ranges from Lamberts Bay on the West coast to Durban on the East coast and could be spread beyond this range through the translocation of *C. gigas* oysters (Day 1974). *J. slattery* can be found in Langebaan Lagoon along the West coast and False Bay and Knysna along the South coast (Conlan 1990). Although this alien species was probably introduced by shipping rather than with *C. gigas*, the translocation of oysters may aid in its further dispersal. The indigenous white dwarf barnacle, *N. algicola*, only had a 50% survival after translocation. However, this species may well disperse to areas in South Africa where it does not naturally occur, such as along the KwaZulu-Natal coastline.

The alien mussel *Mytilus galloprovincialis* occurred in large numbers on uncleaned *C. gigas* and persisted after cleansing and translocation (Table 4). This species has an extremely high settlement rate along the West Coast of South Africa (Robinson *et al.* 2005b), which could explain its great abundance on *C. gigas*. Because mussels are visible, manually removing them is relatively easy and numbers were greatly reduced by the cleansing procedure. Individuals that persisted after cleansing were usually juveniles found in the grooves of *C. gigas* shells, where they were difficult to remove. Although the percentage survival of this species was only 62.5% after translocation, molluscs are quite hardy, and can remain out of water for long periods. *M. galloprovincialis* is the dominant intertidal mussel throughout the West coast (Van Erkom Schurink & Griffiths 1990), and translocation of this species East of East London via consignments of *C. gigas* could expand its already extensive range.

Colonial Cnidaria (*Eudendrium spp* and *Virgularia schultze*), unsegmented worms (*Malacobdella grossa* and *Planocera gilchristi*), the arthropod *Tanystylum brevipes*, the alien bryozoans *Bowerbankia imbricate* and *Bugula avicularia*, and the alien colonial ascidian, *Diplosoma listerianum*, found on uncleaned oysters, were absent

from both cleansed and translocated oysters (Table 4). A significant difference in abundance of solitary alien ascidians, *Ascidia* sp., *Ciona intestinalis* and the indigenous *Pyura stolonifera*, occurred between uncleansed, cleansed and translocated oysters (Table 2a). These species occurred on uncleansed oysters, but only *Ascidia* sp. persisted after cleansing and translocation (Table 4), and therefore posed the risk of its spread via the translocation of *C. gigas*.

From the above, it is evident that, even though the cleansing procedure significantly reduced both quantities and numbers of species of fouling taxa, small numbers of certain species still persisted and survived translocation. Treating oysters with freshwater or heated seawater is thus suggested as a more thorough cleansing regimen to remove these fouling species. It is important that the cleansing regime is not harmful to the oysters, as this would be unprofitable for the commercial oyster operations.

C. gigas oysters soaked in freshwater all survived up to 18 h (Fig. 3.5 a & b). These results were inconsistent with Nel *et al.* (1996), who showed oyster survival of 91.2, 84.8, 87.1 and 95.8% for 3, 6, 9 and 12 h respectively, in freshwater. This treatment was most effective for the removal of brachiopods and cnidarians, neither taxon surviving even the shortest soak time (Fig. 3.5a). The brachiopod, *Discinisca tenuis*, is an alien species originally from Namibia and has not been recorded in Saldanha Bay before (Chapter 2). The most likely vector of this species into Saldanha Bay is *C. gigas* oyster spat translocated from an oyster nursery in Walvis Bay. Although oyster spat are said to be rigorously cleansed before leaving the nursery, the flat juveniles or larvae of *D. tenuis* may be easily overlooked.

Soaking in freshwater decreased the percentage survival of the polychaete *P. hoplura* by 97.5% after 18 h (Fig. 3.5a). This result is consistent with Nel *et al.* (1996), who found that numbers of *P. hoplura* were significantly reduced, but individuals were not completely eradicated, when treated for 12 h in freshwater. However, unlike in the present study, they treated worms after extraction from their burrows. Thus, the time periods they recommended might be biased, as they did not take into consideration the protection afforded to the worms by their mud-enclosed burrows. In this study, other species of polychaetes seemed relatively unaffected by the treatment and maintained a

average survival of mudworms (1.13 per oyster) compared with freshwater treatment (1.59 per oyster). They suggested soaking oysters for 40 sec in heated seawater at 70°C as the most practical time, as their results showed greater percentage oyster mortality at 45 sec (i.e. 8.7%). Oyster mortality was much higher after only 40 seconds in our study, i.e. 26.7% (Fig. 3.5c). However, a shorter soak time of 20 sec with no oyster mortalities, did not completely eradicate all fouling taxa (e.g. 11.5% of *P. hoplura* and 33.3% of crustaceans still survived). Soaking for a shorter time would therefore not be efficient, as the survival of only a few individuals of an alien species is required for a successful introduction. Perhaps a combination of 18 h in freshwater and 20 sec in heated sea or fresh water would be a more effective treatment. Soaking oysters for 18 h in freshwater did not completely eradicate fouling taxa in the present study, but the percentage survival of most taxa decreased substantially. An additional soak in heated water afterwards might be sufficient to eliminate all fouling taxa, although the effectiveness of such combined treatment was not tested in this study.

Alternative measures to rid oysters of fouling taxa have also been documented. Schleyer (1991) found that intertidal rearing of oysters yielded lower *P. hoplura* infestation when compared to subtidal oysterbeds. The reason for this is that newly-settled juvenile and adult mudworms are susceptible to desiccation (Wisely *et al.* 1979). Thus, an alternative method for eradicating fouling organisms is periodic drying by exposing oysters to air for three days. Wisely *et al.* (1979) showed that this method was successful in killing most encrusting fouling organisms, but not mudworms. Nel *et al.* (1996) suggest that this was due to the treatment being administered after a three and a half month grow-out period, by which time newly-settled mudworms had already excavated a protective burrow. Thus, care should be taken as to when the treatment is carried out. The literature suggests that treatment for mudworms is best carried out before settlement in their burrows. Zottoli & Carrier (1974) found that free-living mudworms only start to excavate burrows after one month in the laboratory, while De Keyser (1987) reported incidental infestations in *C. gigas* after two months. Thus, submerged oysters should be treated at monthly or bimonthly intervals (Nel *et al.* 1996). Oysters should not, however, be left out of the water for long periods, as growth would then be slower than if they were submerged. This may, however, be countered by the fact that oysters cleansed of fouling organisms generally have a higher growth rate (Wisely *et al.* 1979).

Results from this study quantify the risks associated with the intraregional translocation of *C. gigas* oysters. It is evident that given current cleaning procedures, intraregional translocation of oysters may aid in transporting indigenous species beyond their natural range, as well as facilitating the spread of marine aliens. Although a more thorough cleansing regime of treating oysters with either freshwater or heated seawater is possible, additional preventative measures, such as inspecting for fouling species before leaving oyster operations, and public awareness of the risks associated with temporally storing *C. gigas* oysters in nearby seawater, are required. This study provides us with a better understanding of the pathways and vectors involved, and proposes new management codes and regimes to reduce unwanted impacts in aquaculture. Further studies could examine the potential benefits of combined treatments of periodic air-drying, a freshwater soak and a short heat treatment to eradicate all fouling organisms.

SUMMARY AND CONCLUSIONS

The objectives of this thesis were to review current knowledge on the exploitation and culture of oysters in South Africa, and the role of imported *Crassostrea gigas* as a vector for marine alien species. Chapter 1 reviewed the history and status of oyster exploitation and culture in South Africa, as no such literature exists in contrast to similar fisheries such as mussels or abalone, which have been well documented. Little potential exists to expand commercial oyster fisheries in South Africa and efforts should rather be concentrated on effective management to avoid overexploitation of indigenous stocks. Besides for KZN, more effort should be applied to proper monitoring or management of subsistence fisheries, which have received little attention to date. The demand for cultured oysters, namely imported *C. gigas*, has grown with the increase in tourism, however, production has been relatively stable over the past decade and demands are not always met. Many oyster farmers blame the wave exposed coastline, or unfavourable coastal conditions, for the failure of past oyster establishments and the difficulty in setting up new ones. Finding new sites for oyster culture, for example, along the unexplored Northern Cape coast and establishing local hatchery facilities for *C. gigas* oysters are suggested as a way forward. This would discontinue the importation of *C. gigas* spat and also avoid the possible transfer of their associated marine alien species.

Chapter 2 reviewed the role of oyster imports in the introduction of alien species and discussed four newly-recorded marine alien species for which the oyster trade is the most likely vector. The black sea urchin *Tetrapygus niger*, the European flat oyster *Ostrea edulis* and Montagu's crab *Xantho incisus*, were probably imported along with consignments of oyster spat from either Chile, or France and England respectively, while the brachiopod *Discinisca tenuis* originated from our neighbouring country, Namibia. Organisations such as the ICES (The Code of Practice of the International Council for the Exploration of the Sea) are used to prevent such introductions in certain countries where oyster culture is practiced. This Code of Practice on the Introduction and Transfers of Marine Organisms first evolved in the late 1970s. Later versions include advice on the management of parasites, disease agents and genetically-modified organisms. The ICES

rules prevent harmful introductions through the importation of exotic organisms, including oysters. Some basic rules are the periodic inspection (including microscopic examination) of material prior to importation, disinfection, and quarantine in the receiving country, to confirm that there are no associated organisms (ICES 2005).

ICES is an intergovernmental organisation and although South Africa is not one of its 20 member countries, it is affiliated to ICES. The Code of Practice has not been rigorously followed with regard to oyster spat import, as South African operations are not required to quarantine, disinfect or treat spat in any way. However, the hatcheries from which spat are imported are required to produce health certification approved by their authorities. This is largely aimed at preventing the spread of oyster diseases, rather than alien introductions. Unfortunately, there is no industry-wide initiative in South African marine aquaculture to address alien introductions. Oyster operations are therefore adopting their own approach. Larger spat which may have been exposed to the natural environment in the country of origin and have a high likelihood of contamination by organisms are no longer being imported. Nurseries also import smaller spat than in the past, and these have been cultured in a controlled hatchery environment, isolated from the natural environment and thereby at low risk of alien species contamination. It is a primary objective of at least one of these nurseries to develop a hatchery in South Africa. The development of hatchery facilities of *C. gigas* should be considered as an alternative to mass importations. One such operation using *C. gigas* larvae was under development in Algoa Bay along the South coast, but has since failed, as a result of the current global economic downturn. However, the oyster nursery in Patermoster is scheduled to establish a hatchery during the course of 2009. The official policy should be that only larvae and spat from strictly controlled and monitored foreign hatcheries should be allowed, and that no spat which has been exposed to its natural environment in its country of origin should ever be imported. South African oyster operations and their suppliers overseas have started taking proactive steps by working together towards the elimination of imports, which they believe should become official state and industry policy. It is important, however, that the process is properly phased and managed to ensure that the industry is

not irreparably harmed by blanket bans on spat imports before a reliable domestic supply is assured (T. Tonin, pers. comm.).

Until then, a suitable eradication program to permanently eliminate these newly recorded marine alien species, and possible others that still remain undetected, should be considered, before further intraregional spread occurs via the local translocations of imported oysters. After initial importation, translocations of oysters are unconstrained by political or economic boundaries, and therefore become the concern of entire biogeographic regions. Oysters can host a diverse community of epi-and infaunal fouling taxa, including alien species, which can be accidentally translocated along with their hosts. Chapter 3 examined the types and quantities of such taxa, which are translocated via a system of local exchange between oyster farms, nurseries, retailers and customers in South Africa. Oysters are cleansed before leaving farms or nurseries, but some species, such as the alien brachiopod *D. tenuis*, may be easily overlooked and translocated along with consignments of oysters, resulting in further dispersal. The chapter also devises and tests mechanisms for minimizing translocation by treating oysters prior to shipment, either with hot or fresh water. Soaking oysters for up to 18 h in freshwater, or 20 sec in heated seawater, with no oyster mortalities, were insufficient to eliminate all fouling taxa. As the survival of only a single reproductive alien species is required for a successful introduction, an alternative treatment of 18 h in freshwater and 20 sec in heated seawater or freshwater, is suggested as a possibly more effective treatment.

As long as there is a demand for oysters in South Africa, this industry, with, or without, associated alien species, is likely to continue. Perhaps a closer relationship between scientists and industry, as well as a more informed public, is needed to develop early warning networks, and a shared responsibility. An approach such as this may very well stem the rising tide of aquaculture derived biological invasions in South Africa.

LITERATURE CITED

- ALEKKOR LIMITED. 2003. Oyster farming. In: *Annual Alexkor Report*, pp. 142-145.
- ANDREWS, J.D. 1980. A review of introductions of exotic oysters and biological planning for new importations. *Marine Fisheries Review* **42(12)**: 1-11.
- ANON. 1997. *White Paper. A marine Fisheries Policy for South Africa*. Department of Environmental Affairs and Tourism, Cape Town.
- ANON. 1998. Marine Living Resources Act, 1998 (Act. No. 18 of 1998). *Government Gazette, South Africa* **395**.
- ASKEW, C.G. 1972. The growth of oysters *Ostrea edulis* and *Crassostrea gigas* in Emsworth Harbour. *Aquaculture* **1**: 237-259.
- AVERY, G. & SIEGFRIED, W.R. 1980. Food gatherers along South Africa's seashores. *Oceans* **13**: 33-37.
- AWAD, A., GREYLING, L., KIRKMAN, S., BOTES, L., CLARKE, B., PROCHAZKA, K., ROBINSON, T., KRUGER, N. & JOYCE, L. 2005. Port Biological Baseline Survey Drat Report of Saldanha bay, South Africa. Unpublished report.
- BALSEIRO, P., CORCHAS, R.F., MONTES, J., GAMEZ-LEAN, J., NOVOA, B. & FIGUERAS, A. 2006. Comparison of diagnosis techniques for the protozoan parasite *Bonamia ostreae* in flat oyster *Ostrea edulis*. *Aquaculture* **261(4)**: 1135-1143.
- BASSON, J. 2003. Translocations of species associated with commercial movements of Pacific oysters, *Crassostrea gigas*. Unpublished Honours project, Zoology Department, University of Cape Town, Cape Town, South Africa.
- BIGALKE, E.H. 1973. The exploitation of shellfish by coastal tribesmen of the Transkei. *Annals of the Cape Provincial Museum* **9**: 159-175.

- BLAKE, J.A. & EVANS, W.J. 1972. *Polydora* and related genera as borers in mollusc shells and other calcareous substrates (Polychaeta: Spionidae). *Veliger* **15**: 235-249.
- BLANCHARD, M. 1997. Spread of the slipper limpet *Crepidula fornicata* (L.1758) in Europe. *Scientia Marina* **61**: 109-118.
- BOSSENBROEK, J.M., KRAFT, C.E. & NEKOLA, J.C. 2001. Prediction of long-distance dispersal using gravity models: zebra mussel invasion of inland lakes. *Ecological Applications* **11** (6): 1778–1788.
- BRANCH, G.M. & GRIFFITHS, C.L. 1988. The Benguela ecosystem part V. The coastal zone. *Oceanography and Marine Biology Annual Review* **26**: 395-486.
- BRANCH, G.M., HAUCK, M., SIQWANA-NDULO, N. & DYE, A.H. 2002. Defining fishers in the South African context : subsistence, artisanal and small-scale commercial sectors. *South African Journal of Marine Science* **24**: 475-487.
- BRANCH, G.M., GRIFFITHS, C.L., BRANCH, M.L. & BECKLEY, L.E. 2005. *Two Oceans: A Guide to the Marine Life of Southern Africa*. David Philip Publishers, Cape Town & Johannesburg.
- BRITZ, P.J., SAUER, W.H.H., MATHER, D., OELLERMAN, L.K., COWLEY, P.D., TER MORSHUIZEN, L. & BACELA, N. 2001. Baseline study of the utilisation of living marine resources in the Eastern Cape Province. Report, Department of Ichthyology and Fisheries Science, Rhodes University, South Africa.
- BROWN, A.C. & JARMAN, N. 1978. Coastal marine habitats. In: *Biogeography and Ecology of Southern Africa*, (eds), M.J.A. Werger & A.C. van Bruggen, pp. 1241-1277. Weiner, Junk, The Hague.
- BRUNTON, C.H.C. & HILLER, N. 1990. Late Cainozoic brachiopods from the coast of Namaqualand, South Africa. *Paleontology* **33**(2): 313–342.

- BUCHANAN, W.F. 1988. *Shellfish in prehistoric diet: Eland's Bay, south western Cape coast, South Africa*. British Archaeological Reports, Oxford.
- BUCHAN, L.A.J. & PADILLA, D.K. 1999. Estimating the probability of long-distance overland dispersal of invading aquatic species. *Ecological Applications* **9(1)**: 254-265.
- BYERS, J.E. 2000. Competition between two estuarine snails: implications for invasions of exotic species. *Ecology* **81(5)**: 1225-1239.
- CARLTON, J.T. 1992. Introduced marine and estuarine molluscs of North America: An end-of-the-20th – century perspective. *Journal of Shellfish Research* **11(2)**: 489-505.
- CARRIKER, M.R. 1992. Introductions and transfers of molluscs: risk considerations and implications. *Journal of Shellfish Research* **11(2)**: 507-510.
- CHAPMAN, J.W., MILLER, T.W. & COAN, E.V. 2003. Live seafood species as recipes for invasion. *Conservation Biology* **17 (5)**: 1386-1395.
- CHEW, K.K. 1990. Global bivalve shellfish introductions. *World Aquaculture* **21(3)**: 9-22.
- CHEW, K.K. 2001. Shellfish: Worldwide statistics for oysters and clams. *Aquaculture Magazine* **27(3)**: 72-76.
- CHRISTIE, N.D. & MOLDAN, A. 1977. Distribution of benthic macrofauna of Langebaan Lagoon. *Transactions of the Royal Society of South Africa* **42**: 273-284.
- CIGARRIA, J. & ELSTON, R. 1997. Independent introduction of *Bonamia ostrea*, a parasite of *Ostrea edulis*, to Spain. *Diseases of Aquatic Organisms* **29(2)**: 157-158.
- CLARK, B.M., HAUCK, M., HARRIS, J.M., SALO, K. & RUSSELL, E. 2002. Identification of subsistence fishers, fishing areas, resource use and activities along the South African coast. *South African Journal of Marine Science* **24**: 425-437.

- COCKCROFT, A.C., SAUER, W.H.H., BRANCH, G.M., CLARK, B.M., DYE, A.H. & RUSSELL, E. 2002. Assessment of resource availability and suitability for subsistence fishers in South Africa, with a review of resource management procedures. *South African Journal of Marine Science* **24**: 489-501.
- COMPTON, J.S. 2001. Holocene sea level fluctuations inferred from the evolution of depositional environments of the southern Langebaan Lagoon salt marsh, South Africa. *The Holocene* **11(4)**: 395-405.
- CONLAN, K.E. 1990. Revision of the crustacean amphipod genus *Jassa* (Corophioidea: Ischyroceridae). *Canadian Journal of Zoology* **68**: 2031-2075.
- CRITCHLEY, A.T. & DIJKEMA, R. 1984. On the presence of the introduced brown alga *Sargassum muticum* attached to commercially imported *Ostrea edulis* in the SW Netherlands. *Botanica marina* **27(5)**: 211-216.
- CROTHERS, J.H. 1970. The distribution of crabs on rocky shores around the Dale Peninsula. *Field Studies* **3**: 263-274.
- DAY, J.H. 1958. The biology of Langebaan Lagoon : a study of the effect of shelter from wave action. *Transactions of the Royal Society of South Africa* **26**: 475-515.
- DAY, J.H. 1974. Crustacea: Order Tanaidacea. In: *Marine life on South African Shores*, pp. 93-94, A.A. Balkema, Cape Town, Rotterdam.
- DEAN, T.A., SCHROETER, S.C. & DIXON, J.D. 1983. Effects of grazing by two species of sea urchins (*Strongylocentrotus franciscanus* and *Lytechinus anamesus*) on recruitment and survival of two kelp species (*Macrocystis pyrifera* and *Pterygophora californica*). *Marine Biology* **78(3)**: 301-313.
- DEAT REPORT. 2006. General reasons for the decisions on the allocation of rights in the oyster fishery. *General Published Reasons: Oysters*, South Africa.

- DEAT. 2008/2009. Marine recreational activity. *Information Brochure*, Department of Environmental Affairs and Tourism, South Africa.
- DE BRUYN, P. 2006. A novel application of operational management procedures in the fisheries management of the oyster (*Striostrea margaritacea*) in Kwazulu-Natal, South Africa. Ph. D. thesis, University of KwaZulu-Natal, South Africa.
- DE BRUYN, P., MOLONEY, C.L. & SCHLEYER, M.S. 2008. Application of age-structured production models to assess oyster *Striostrea margaritacea* populations managed by rotational harvesting in KwaZulu-Natal, South Africa. *ICES Journal of Marine Science* **66**: 408-419.
- DE KEYSER, J.M.N. 1987. Growth of the Pacific oyster *Crassostrea gigas* (Mollusca: Bivalvia) in the Blue Hole (Swartkops Estuary), Port Elizabeth, South Africa. M.Sc thesis, University of Port Elizabeth, Port Elizabeth, South Africa.
- DE MONTAUDOUIN, X., AUDEMARD, C. & LABOURG, P.J. 1999. Does the slipper limpet (*Crepidula fornicate*, L.) impair oyster growth and zoobenthos biodiversity? A revised hypothesis. *Journal of Experimental Marine Biology and Ecology* **235**: 105-124.
- DE MONTAUDOUIN, X. & SAURIAU, P.G. 1999. The proliferating Gastropoda *Crepidula fornicate* may stimulate macrozoobenthic diversity. *Journal of the Marine Biological Association of the UK* **79**: 1069-1077.
- DRINKWAARD, A.C. 1999. Introductions and developments of oysters in the North Sea area: a review. *Helgoland Marine Research* **52**: 301-308.
- DYE, A.H. 1989. Studies on the ecology of *Saccostrea cucullata* (Born, 1778) (Mollusca: Bivalvia) on the east coast of southern Africa. *South African Journal of Zoology* **24(2)**: 110-115.
- DYE, A.H. 1990. Episodic recruitment of the rock oyster *Saccostrea cucullata* (Born, 1778) on the Transkei coast. *South African Journal of Zoology* **25(3)**: 185-187.

- DYE, A.H., SCHLEYER, M.H., LAMBERT, G. & LASIAK, T.A. 1994a. Intertidal and subtidal filter-feeders in Southern Africa. In: *Rocky Shores: Exploitation in Chile and South Africa*, (ed) W. Siegfried, pp. 57-74, Springer-Verlag, Berlin.
- DYE, A.H., BRANCH, G.M., CASTILLA, J.C. & BENNETT, B.A. 1994b. Biological options for the management of the exploitation of intertidal and subtidal resources. In: *Rocky Shores: Exploitation in Chile and South Africa*, (ed) W. Siegfried, pp. 131-154, Springer-Verlag, Berlin.
- ELTON, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen Ltd, London, England.
- EMANUEL, B.P., BUSTAMANTE, R.H., BRANCH, G.M., EEKHOUT, S. & ODENDAAL, F.J. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *South African Journal of Marine Science* **12**: 341-354.
- FIELDING, P.J., ROBERTSON, W.D., DYE, A.H., TOMALIN, B.J., VAN DER ELST, R.P., BECKLEY, L.E., MANN, B.Q., BIRNIE, S., SCHLEYER, M.H. & LASIAK, T.A. 1994. Transkei coastal fisheries. *Special publication (Oceanographic Research Institute (South Africa))* **3**: 1-175.
- FLORES, A.A.V., CRUZ, J. & PAULA, J. 2002. Temporal and spatial patterns of settlement of brachyuran crab megalopae at a rocky coast in Central Portugal. *Marine Ecology Progress Series* **229**: 207-220.
- FLORES, A.A.V. & PAULA, J. 2002. Sexual maturity, larval release and reproductive output of two brachyuran crabs from a rocky intertidal area in central Portugal. *Invertebrate Reproduction & Development* **42(1)**: 21-34.
- GRIFFITHS, C.L. & BRANCH, G.M. 1997. The exploitation of coastal invertebrates and seaweeds in South Africa: historical trends, ecological impacts and implications for management. *Transactions of the Royal Society of South Africa* **52 (1)**: 121-148.

- GRIFFITHS, C. 2000. Overview on current problems and future risks. In *Best Management Practices for Preventing and Controlling Invasive Alien Species*, (eds) G. Preston, G. Brown, E. van Wyk, pp. 235-241. The Working for Water Programme, Cape Town.
- GRIFFITHS C.L., ROBINSON T.B. & MEAD, A. 2008. The status and distribution of marine alien species in South Africa. In: Rilov, G. & Crooks, J.A. *Biological Invasions in Marine Ecosystems*. Ecological Studies 204. Springer-Verlag, Berlin, Heidelberg. pp 393-408.
- GRINDLEY, J.R. 1969. Quaternary marine palaeoecology in South Africa. *Archaeological Bulletin* **24**: 151-157.
- GRIZEL, H. & HERAL, M. 1991. Introduction into France of the Japanese oyster (*Crassostrea gigas*). *The ICES Journal of Marine Science* **47**: 399-403.
- HALKETT, D., HART, T., YATES, R., VOLMAN, T.P., PARKINGTON, J., ORTON, J., KLEIN, R.G., CRUZ-URIBE, K. & AVERY, G. 2003. First excavation of intact Middle Stone Age layers at Ysterfontein, Western Cape Province, South Africa: implications for Middle Stone Age ecology. *Journal of Archaeological Science* **30(8)**: 955-971.
- HANDLEY, S.J. 1995. Spionid polychaetes in Pacific oysters, *Crassostrea gigas* (Thunberg) from Admiralty Bay, Marlborough Sounds, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **29**: 305-309.
- HANDLEY, S.J. & BERGQUIST, P.R. 1997. Spionid polychaete infestation of intertidal pacific oysters *Crassostrea gigas* (Thunberg), Mahurangi Harbour, northern New Zealand. *Aquaculture* **153**: 191-205.
- HANNA, G.D. 1966. Introduced molluscs of western North America. *Occasional Papers of the California Academy of Sciences* **48**: 1-108.

- HECHT, T. & BRITZ, P.J. 1992. The current status, future prospects and environmental implications of mariculture in South Africa. *South African Journal of Science* **88**: 335-342.
- HENSHILWOOD, C.S., NILSSEN, P. & PARKINGTON, J. 1994. Mussel drying and food storage in the late Holocene, SW Cape, South Africa. *Journal of Archaeology* **21**: 103-109.
- HILLER, N. 1990. The Southern African recent brachiopod fauna. In: *Brachiopods Through Time*, (eds) D.I. MacKinnon, E. Dahne & J. Lee, pp. 439-445, CRC Press, Balkema, Rotterdam.
- HIMMELMAN, J.H. & STEELE, D.H. 1971. Foods and predators of the green sea urchin *Strongylocentrotus droebachiensis* in Newfoundland waters. *Marine biology* **9(4)**: 315-322.
- HOCKEY, P.A.R. & BOSMAN, A.L. 1986. Man as an intertidal predator in Transkei: disturbance, community convergence and management of a natural food resource. *Oikos* **46**: 3-14.
- HOCKEY, P.A.R., BOSMAN, A.L. & SIEGFRIED, W.R. 1988. Patterns and correlates of shellfish exploitation by coastal people of Transkei: an enigma of protein production. *Journal of Applied Ecology* **25**: 353-364.
- ICES. 1972. Report of the working group on the introduction of non-indigenous marine organisms. International Council for the Exploration of the Sea, Cooperation Research Report. Copenhagen.
- ICES. 2005. Code of Practice on the Introductions and Transfers of Marine Organisms. International Council for the Exploration of the Sea, Cooperation Research Report Copenhagen.

- JACKSON, L.F. & MCGIBBON, S. 1991. Human activities and factors affecting the distribution of macrobenthic fauna in Saldanha Bay. *South African Journal of Aquatic Science* **17**(1/2): 89-102.
- JERARDINO, A. & YATES, R. 1996. Preliminary results from excavations at Steenbokfontein Cave: implications for past and future research. *South African Archaeological Bulletin* **51**: 7-16.
- JERARDINO, A., BRANCH, G.M. & NAVARRO, R. 2008. Human impact on precolonial West coast marine environments of South Africa . In: *Human Impacts on Ancient Marine Ecosystems: a Global Perspective*, (eds) T.C. Rick & J.M. Erlandson, pp. 279-296. University of California Press, Berkley.
- JOHNSEN, B.O. & JENSEN, A.J. 1991. The *Gyrodactylus* story in Norway. *Aquaculture* **98**: 289-302.
- JOHNSON, L.E., RICCIARDI, A. & CARLTON, J.T. 2001. Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. *Ecological Applications* **11**(6): 1789-1799.
- KAISER, M.J., LAING, I., UTTING, S.D. & BURNELL, G.M. 1998. Environmental impacts of bivalve mariculture. *Journal of Shellfish Research* **17** (1): 59-66.
- KIEPIEL, J. & QUINLAN, T. 1997. Micro-tourism and future development of resource utilisation along the Transkei coast. In: *Transkei Coastal Fisheries Resources: Phase 2- Resource Utilisation, Development and Tourism*, (eds) W.D. Robertson & P.J. Fielding, pp. 107-166. The Oceanographic Research Institute, Durban, South Africa.
- KILBURN, R. & RIPPEY, E. 1982. The autobranch bivalves. In: *Sea Shells of Southern Africa*, (ed) E.M. Cadell, pp. 154-205, Macmillan South Africa, Johannesburg.
- KITCHING, J.A., THAIN, F.R.S. & THAIN, V.M. 1983. The ecological impact of the sea urchin *Paracentrotus lividus* (Lamarck) in Lough INE, Ireland. *Philosophical Transactions of the Royal Society of London* **300**(1101): 513-552.

- KORRINGA, P. 1956. Oyster culture in South Africa: hydrographical, biological and osteological observations in the Knysna Lagoon, with notes on conditions in other South African waters. *Investigational Report of the Division of Fisheries* **20**: 1-86.
- KORRINGA, P. 1976. Farming the Cupped Oyster of the Genus *Crassostrea*: A Multidisciplinary Treatise. In: *Developments in Aquaculture and Fisheries Science* **2**. Elsevier Scientific Publishing Company, Amsterdam.
- KURIS, A. M. & CULVER, C.S. 1999. An introduced sabellid polychaete pest infesting cultured abalones and its potential spread to other California gastropods. *Invertebrate Biology* **118**: 391-403.
- KYLE, R., PEARSON, B., FIELDING, P.J., ROBERTSON, W.D. & BIRNIE, S.L. 1997. Subsistence shellfish harvesting in the Maputland Marine Reserve in northern KwaZulu-Natal, South Africa: Rocky shore organisms. *Biological Conservation* **82**: 183-192.
- LAIRD, M.C. & GRIFFITHS, C.L. 2008. Present distribution and abundance of the introduced barnacle *Balanus glandula* in South Africa. *African Journal of Marine Science* **30(1)**: 93-100.
- LASIAK, T. 1991. The susceptibility and/or resilience of rocky littoral molluscs to stock depletion by the indigenous coastal people of Transkei, southern Africa. *Biological Conservation* **56**: 245-264.
- LE ROUX, F., LORENZO, G., PEYRET, P., AUDEMARD, C., FIGUERAS, A., VIVARES, C., GOUY, M. & BERTHE, F. 2005. Molecular evidence for the existence of two species of *Marteillia* in Europe. *Journal of Eukaryotic Microbiology* **48(4)**: 449-454.
- LLEONART, M., HANDLINGER, J. & POWELL, M. 2003. Spionid mudworm infestation of farmed abalone (*Haliotis spp.*). *Aquaculture* **221**: 85-96.

- MANN, R. 1983. The role of introduced bivalve mollusc species in mariculture. *Journal of the World Mariculture Society* **14**: 546-559.
- MEAD, A., CARLTON, J., GRIFFITHS, C.L. & RIUS, M. 2008. What's new in the Zoo? Marine introductions of South Africa. Manuscript in prep.
- MILLER, T.W., CHAPMAN, J.W. & COAN, E.V. 2001. Live seafood: a recipe for biological and regulatory concern? In *Marketing and Shipping Live Aquatic Products*, (eds) B.C. Paust & A.A. Rice, pp. 249-256. University of Alaska Sea Grant Program, Seattle Washington.
- MINCHIN, D. 1996. Management of the introduction and transfer of marine molluscs. *Aquatic Conservation: Marine and Freshwater Ecosystems* **6**: 229-244.
- MINCHIN, D. & ROSENTHAL, H. 2002. Exotics for stocking and aquaculture, making correct decisions. In *Invasive Aquatic Species of Europe*, (eds) E. Leppakoski, S. Gollasch & S. Olenin, pp. 206-216. Kluwer Academic Publishers, Netherlands.
- MINCHIN, D. 2007. Aquaculture and transport in a changing environment: overlap and links in the spread of alien biota. *Marine Pollution Bulletin* **55**: 302-313.
- MIOSSEC, L. & GOULLETQUER, P. 2007. The Pacific oyster *Crassostrea gigas*: An introduced species for aquaculture in European waters in the 1970s became an invasive species in the late 1990s. Oral presentation at the 5th International Conference on Marine Bioinvasions. Boston, USA.
- NAYLOR, R.L., WILLIAMS, S.L. & STRONG, D.R. 2001. Aquaculture - A gateway for exotic species. *Science* **294**: 1655-1656.
- NEHRING, S. 2006. NOBANIS – Invasive alien species fact sheet – *Crassostrea gigas*. Online database of Northern European and Baltic network on invasive alien species. NOBANIS www.nobanis.org. Accessed on 01.07.2008.

- NEL, R., COETZEE, P.S. & VANNIEKERK, G. 1996. The evaluation of two treatments to reduce mud worm (*Polydora hoplura* Claparede) infestation in commercially reared oysters (*Crassostrea gigas* Thunberg). *Aquaculture* **141**: 31-39.
- NELL, J. 2002. The Australian oyster industry. *World Aquaculture* **613**: 8-10.
- NEMLIHER, J. & KALLASTE, T. 2002. Secondary alterations of the shell apatite of *Discinisca tenuis* from Luderlitz, Namibia. *Lithology & Mineral Resources* **37 (1)**: 18-24.
- OHNO, M. & LARGO, D.B. 1998. The seaweed resources of Japan. In: *Seaweed Resources of the World*, (eds) A.T. Critchley & M. Ohno, pp. 1-14. Japanese International Cooperation Agency, Yokosuka, Japan.
- OJEDA, F.P. & SANTELICES, B. 1984. Ecological dominance of *Lessonia nigrescens* (Phaeophyta) in central Chile. *Marine Ecology Progress Series* **19**: 83-91.
- OLENIN, S., MINCHIN, D. & DAUNYS, D. 2007. Assessment of biopollution in aquatic ecosystems. *Marine Pollution Bulletin* **55(7-9)**: 379-394.
- ORENSANZ, J.M., SCHWINDT, E., PASTORINO, G., BORTOLUS, A., CASAS, G., DARRIGRAN, G., ELIAS, R., LOPEZ GAPPA, J.J., OBENAT, S., PASCUAL, M., PENCHASZADEH, P., LUZ PIRIZ, M., SCARABINO, F., SPIVAK, E.D. & VALLARINO, E.A. 2002. No longer the pristine confines of the world's ocean: a survey of exotic marine species in the southwestern Atlantic. *Biological Invasions* **4**: 115-143.
- PADILLA, D.K. & GRAY, S. 2007. Invading ecosystem engineering dramatically alters benthic communities in and out of marine reserves. Oral presentation at the 5th International Conference on Marine Bioinvasions. Boston, USA.
- PARKINGTON, J., POGGENPOEL, C., BUCHANAN, B., ROBEY, T., MANHIRE, T. & SEALY, J. 1988. Holocene coastal settlement patterns in the Western Cape. In: *The*

Archaeology of Prehistoric Coastlines, (eds) G. Bailey & J. Parkington, pp. 22-41. Cambridge University Press, Cambridge.

PROBYN, T., PITCHER, G., PIENAAR, R. & NUZZI, R. 2001. Brown tides and mariculture in Saldanha Bay, South Africa. *Marine Pollution Bulletin* **42 (5)**: 405-408.

QUAYLE, D.B. 1969. Pacific oyster culture in British Columbia. *Bulletin of the Fisheries Research Board of Canada* **167**: 1-68.

RACE, M.S. 1982. Competitive displacement and predation between introduced and native mud snails. *Oecologica* **54**: 337-347.

ROBERTSON, W.D. & FIELDING, P.J. 1997. Patterns and economics of resource utilisation and tourism along the Transkei coast. In: *Transkei Coastal Fisheries Resources: Phase 2- Resource Utilisation, Development and Tourism*, (eds) W.D. Robertson & P.J. Fielding, pp. 5-105. The Oceanographic Research Institute, Durban, South Africa.

ROBINSON, T.B., GRIFFITHS, C.L. & KRUGER, N. 2004. Distribution and status of marine invasive species in and bordering the West Coast National Park. *Koedoe* **47(1)**: 79-87.

ROBINSON, T.B., GRIFFITHS, C.L., TONIN, A., BLOOMER, P. & HARE, M.P. 2005a. Naturalized populations of oysters, *Crassostrea gigas* along the South African coast: Distribution, abundance and population structure. *Journal of Shellfish Research* **24(2)**: 443-450.

ROBINSON, T.B., GRIFFITHS, C.L., MCQUAID & RUIS, M. 2005b. Marine alien species of South Africa – status and impacts. *African Journal of Marine Science* **27 (1)**: 297-306.

- RODRIGUEZ, S.R. & OJEDA, F.P. 1993. Distribution patterns of *Tetrapygyus niger* (Echinodermata: Echinoidea) off the central Chilean coast. *Marine Ecology Progress Series* **101**: 157-162.
- RODRIGUEZ, S.R. 2003. Consumption of drift kelp by intertidal populations of the sea urchin *Tetrapygyus niger* on the central Chilean coast: possible consequences at different ecological levels. *Marine Ecology Progress Series* **251**: 141-151.
- RUESINK, J.L., LENIHAN, H.S., TRIMBLE, A.C., HEIMAN, K.W., MICHELI, F., BYERS, J.E. & KAY, M.C. 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual Review of Ecology and Evolutionary Systems* **36**: 643-689.
- RUIZ, G.M., FOLONOFF, P.W., CARLTON, J.T., WONHAM, M.J. & HINES, A.H. 2000. Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics* **31**: 481-531.
- SCHLEYER, M.H. 1988. Recommended change in the rotation of commercial oyster harvesting zones in Natal. Unpublished ORI report No. 52. Oceanographic Research Institute, Durban.
- SCHLEYER, M.H. 1991. Shell-borers in the oyster, *Striostrea margaritacea*: pests or symbionts? *Symbiosis* **101**: 135-144.
- SCHLEYER, M.H. & KRUGER, A. 1990. Historical trends in the exploitation of the oyster *Striostrea margaritacea*, presented at Oceans '90, the Seventh National Oceanographic Conference, San Lameer, South Africa.
- SCHLEYER, M.H. & KRUGER, A. 1991. A study of the oyster *Striostrea margaritacea* (Lamarck). Unpublished ORI report No. 70. Oceanographic Research Institute, Durban. 7-17.
- SCOTT, P. 1951. Inshore fisheries of South Africa. *Economic Geography* **27**: 123-147.

- SEALY, J.C. & YATES, R. 1994. The chronology of the introduction of pastoralism in the Cape, South Africa. *Antiquity* **68**: 58-67.
- SHPIGEL, M. 1989. Gametogenesis of the European flat oyster (*Ostrea edulis*) and Pacific oyster (*Crassostrea gigas*) in warm water in Israel. *Aquaculture* **80**: 343-349.
- SIEGFRIED, W.R., HOCKEY, P.A.R. & CROWE, A.A. 1985. Exploitation and conservation of brown mussel stocks by coastal people of Transkei. *Environmental Conservation* **12**: 91-104.
- SIEGFRIED, W.R., HOCKEY, P.A.R. & BRANCH, G.M. 1994. The exploitation of intertidal and subtidal resources of rocky shores in Chile and South Africa – an overview. In: *Rocky Shores: Exploitation in Chile and South Africa*, (ed) W.R. Siegfried, pp. 1-15, Springer-Verlag, Berlin.
- SIMON, C.A., LUDFORD, A. & WYNNE, S. 2006. Spionid polychaetes infesting cultured abalone *Haliotis midae* in South Africa. *African Journal of Marine Science* **28** (1): 167-171.
- STEPHEN, D. 1978. Mud blister formation by *Polydora ciliate* in the Indian backwater oyster *Crassostrea madrasensis* (Preston). *Aquaculture* **13**: 347-350.
- TANKARD, A.J. 1976. Pleistocene history and coastal morphology of the Ysterfontein-Eland's Bay area, Cape Province. *Annals of the South African Museum* **69**: 73-119.
- THACKERAY, J.F. 1988. Molluscan fauna from Klasies River, South Africa. *The South African Archaeological Bulletin* **43**: 27-32.
- THOMPSON, C.W. 1913. Sea Fisheries of the Cape Colony from Van Riebeeck's Days to the Eve of the Union, with a Chapter on Trout and other Freshwater Fishes. Maskew Miller, Cape Town.

- TINOCO-ORTA, G.D. & CACERES-MARTINEZ, J. 2003. Infestation of the clam *Chione fluctifraga* by the burrowing worm *Polydora sp. nov.* in laboratory conditions. *Journal of Invertebrate Pathology* **83**: 196-205.
- TONIN, A. 2001. CPPP small research farmer oyster cultivation project: A survey of possible oyster cultivation sites on the western and eastern Cape coasts. *Mariculture Development Services*. Monthly report **1**.
- UTTING, S.D. & SPENCER, B.E. 1992. Introductions of marine bivalve molluscs into the United Kingdom for commercial culture- case histories. *ICES Marine Science Symposium* **194**: 84-91.
- VAN ANDEL, T.H. 1989. Late Pleistocene sea levels and the human exploitation of the shore shelf of southern South Africa. *Journal of Field Archaeology* **16(2)**: 133-155.
- VAN BANNING, P. 1991. Observations on the bonamiasis in the state of the European flat oyster, *Ostrea edulis*, in the Netherlands, with special reference to the recent developments in Lake Grevelingen. *Aquaculture* **93(3)**: 205-211.
- VAN ERKOM SCHURINK, C. & GRIFFITHS, C.L. 1990. Marine mussels of southern Africa – their distribution patterns, standing stocks, exploitation and culture. *Journal of Shellfish Research* **9**: 75-85.
- VASQUEZ, J.A. & SANTELICES, B. 1990. Ecological effects of harvesting *Lessonia* (Laminariales, Phaeophyta) in central Chile. *Hydrobiologia* **204-205**: 41-47.
- VASQUEZ, J.A. & BUSCHMANN, A. 1997. Herbivore-kelp interactions in Chilean subtidal communities: a review. *Revista Chilena de Historia Natural* **70**: 41-52.
- VEGA, J.M.A., VASQUEZ, J.A. & BUSCHMANN, A.H. 2005. Population biology of the subtidal kelps *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales, Phaeophyceae) in an upwelling ecosystem of northern Chile: interannual variability and El Niño 1997-1998. *Revista Chilena de Historia Natural* **78**: 33-50.

- VENTILLA, R.F. 1982. The scallop industry in Japan. *Advances in Marine Biology* **20**: 309-382.
- VITOUSEK, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* **57**: 7-13.
- VOISIN, M., ENGEL, C.R. & VIARD, F. 2005. Differential shuffling of native genetic diversity across introduced regions in a brown alga: Aquaculture vs. maritime traffic effects. *Ecology* **102 (15)**: 5432-5437.
- VOLMAN, T.P. 1978. Early archaeological evidence for shellfish collecting. *Science* **201**: 911-913.
- WARMAN, G. 2001. Mariculture offers growth potential. In *Fishing Industry News Southern Africa*, pp. 10-12, (ed) C. Attwood, George Warman Publications, Cape Town, Johannesburg, South Africa.
- WASSON, K., ZABIN, C.J., BEDINGER, L., DIAZ, M.C. & PEARSE, J.S. 2001. Biological invasions of estuaries without international shipping: the importance of intraregional transport. *Biological Conservation* **102(2)**: 143-153.
- WHITLATCH, R.B. & OBREBSKI, S. 1980. Feeding selectivity and coexistence in two deposit-feeding gastropods. *Marine Biology* **67**: 187-192.
- WIRTZ, P. 1997. Crustacean symbionts of the sea anemone *Telmatactis cricoids* at Madeira and the Canary Islands. *Journal of Zoology* **242 (4)**: 799-811.
- WISELY, B., HOLLIDAY, J.E. & REID, B.L. 1979. Experimental deepwater culture of the Sydney rock oyster (*Crassostrea commercialis*). *Aquaculture* **17**: 25-32.
- WOLFF, W.J. & REISE, K. 2002. Oyster imports as a vector for the introduction of alien species into Northern and Western European coastal waters. In *Invasive Aquatic Species of Europe*, (eds) E. Leppakoski, S. Gollasch & S. Olenin, pp. 193-205. Kluwer Academic Publishers, Netherlands.

YAP, M. & MAN, D.L. 1996. *Colour, Confusion and Concessions: the History of the Chinese in South Africa*. Hong Kong University Press, Hong Kong.

ZOTTOLI, R.A. & CARRIKER, M.R. 1974. Burrow morphology, tube formation, and microarchitecture of shell dissolution by the spionid polychaete *Polydora websteri*. *Marine Biology* **27**: 307-316.

University of Cape Town