The foraging ecology, demographics and conservation of African Black Oystercatchers *Haematopus moquini* in Namibian nursery areas.

by

Antje Leseberg

Thesis submitted for the degree of
Master of Science

Percy FitzPatrick Institute of African Ornithology
Department of Zoology

Faculty of Science
University of Cape Town
September 2001

To my parents

"Anyone seeing a Black Oystercatcher for the first time might be inclined to laugh at its grotesque and rather comic appearance. Its outsize red bill is impossibly bright, the eyes are red-ringed, and the pallid fleshy feet bring to mind a seaside bather who has taken off his shoes and socks. When the bird nods and utters a piercingly loud whinny, the observer is convinced that it is simple as well as strange looking"

J. F. Lansdowne, referring to the American Black Oystercatcher in
Birds of the West Coast, 1976.

DECLARATION

This thesis reports the results of original research which I carried out under the auspices of the Percy FitzPatrick Institute of African Ornithology, University of Cape Town. All assistance I received has been fully acknowledged. This work has not been submitted for a degree at any other university.

signature removed

Antje Leseberg

03/12/2001

Date

TABLE OF CONTENTS

ABSTRACT

Leseberg, A. 2001. The foraging ecology, demographics and conservation of African Black Oystercatchers *Haematopus moquini* in Namibian nursery areas. M.Sc. thesis, Percy FitzPatrick Institute of African Ornithology, University of Cape Town.

The African Black Oystercatcher *Haematopus moquini* is one of the world's rarest and most range-restricted oystercatcher species: its global population stands at less than 5000 individuals. African Black Oystercatchers are susceptible to human disturbance during the breeding season and are facing ever-increasing pressure from rapid coastal development. In 1998 the first juvenile oystercatcher nursery was discovered at Walvis Bay/Swakopmund, Namibia. The discovery of three additional Namibian (two near Lüderitz and one at the Hoanib River mouth) and one Angolan (Baia dos Tigres) nursery soon followed. All these nurseries are located outside the adult breeding range and together they support *ca.* 400 juvenile oystercatchers. Ring resightings prove that nurseries support juveniles from all regions of the adults' breeding range, although birds from the Eastern Cape Province were under-represented at the Walvis Bay/Swakopmund nursery. Infrequent resightings of ringed Namibian juveniles suggest that they may target nurseries closer to their natal sites near Lüderitz and that South African juveniles, having further to travel and arriving later in Namibia, must continue to more northern nurseries. Juveniles first arrive at nurseries in May–June and by winter (Aug/Sep) numbers are highest – moult ratios indicate that 50% of the Walvis Bay roost comprises first-year birds. A minimum of two years is spent at a nursery, whereupon 2–3 year old birds return to natal sites in early summer (the start of the breeding season). Resightings of colour-ringed juveniles suggest that 42% of South African juveniles disperse to a nursery. The remainder undertake short-distance movements (usually < 150 km) and remain near natal sites. These juveniles are scattered along the coast and do not form discrete nurseries. No equivalent example of a dichotomous post-fledging dispersal pattern has yet been found in another bird species. Neither body condition at fledging (hypothesis: only larger juveniles have enough of an energetic "cushion" to migrate to nurseries) nor hatching date (hypothesis: later-fledged juveniles are forced to migrate to nurseries because habitats near natal sites are already filled with older juveniles) were significantly different between short- and long-distance dispersers.

Research was carried out at the Walvis Bay/Swakopmund nursery during four visits between Aug/Sep 1999 and May/Jun 2000. The study aimed to quantify seasonal and tidal patterns of habitat use and responses to changes in prey abundance, and to investigate whether nurseries provide favourable foraging conditions and high energetic returns for juvenile oystercatchers.

In contrast to adult oystercatchers, juveniles at Walvis Bay display a wide dietary spectrum and foraging activity is opportunistic and in response to local changes in prey abundance and availability. A large proportion of their prey is washed up and therefore available at all stages of the tidal cycle. At Swakopmund, foraging activity follows a strict tidal regime. Habitat diversity is low and birds move little between areas in response to prey abundance. Focal animal observations revealed seasonal fluctuations in intake rates – most pronounced at Walvis Bay, where prey density correlates with the intensity and duration of wash-up events. At both sites daily energy intake (DEI) compares well with the predicted DEI for the African Black Oystercatcher. At Swakopmund, nocturnal foraging was observed and intake rates were similar to those attained by adults in the breeding range. At Walvis Bay, non-tidal foraging allowed oystercatchers to meet energy demands during daylight hours and there was no evidence of nocturnal foraging. At this site, diurnal foraging activity peaked in the early morning and late afternoon and evening. The midday period was spent roosting, regardless of tidal state, and birds generally returned to the roost soon after sunset. There was no evidence of an age-related dominance hierarchy at the nursery. Observations suggest that conditions at the nursery are not conducive to intra-specific kleptoparasitism and instances of interference and food stealing were infrequent. Cape Gulls did on occasion steal prey from oystercatchers but for the majority of the study these losses represented less than 1% of oystercatcher intake rates.

Evidence from this study suggests that the Walvis Bay/Swakopmund nursery provides a favourable environment for inexperienced juvenile African Black Oystercatchers. Foraging habitats are abundant, offering diverse prey that are easily accessible and processed. Because nurseries are located outside the breeding range, there is no interference from adults and juveniles are able to improve their foraging efficiency without interference. There is no evidence that the Walvis Bay/Swakopmund nursery is currently at carrying capacity. Rocky stretches of coast, with abundant food, between Swakopmund and Walvis Bay are under-utilised by the oystercatchers and provide an important resource should primary foraging areas fail. If conservation measures implemented in the South African breeding range to boost oystercatcher productivity are successful, more juveniles may migrate to nurseries in the future.

ACKNOWLEDGEMENTS

Firstly I would like to thank Prof. Phil Hockey for supervising and guiding this project and for giving me the opportunity to research exciting new findings concerning oystercatcher biology. His quick and constructive comments on numerous earlier drafts were greatly appreciated. Mark Boorman and Sandra Dantu, and Keith and Gail Wearne provided me with a home away from home while in Swakopmund and Walvis Bay and I treasure their friendship. Without their support those would have been long days on the wind-swept mudflats of Walvis Bay and I thank them for showing me the beauty of Namibia. Jeanne Meintjes of Eco Marine Kayak Tours generously offered me lifts to Pelican Point and saved me from long hikes with tripod and telescope. Alison Sakko, John Paterson and Yves Chesselet all provided valuable information regarding the other oystercatcher nurseries and Jean-Paul Roux and Rob Simmons are thanked for surveying the two Lüderitz nurseries under rather trying conditions. Rob Simmons provided much unpublished information and data for this study and I wish to thank him for a fantastic trip to Sandwich Harbour. Anton Wolfaardt, Jane Turpie and Margit Wilhelm provided unpublished data from various regions in South Africa. A special thank you to Douglas Loewenthal for the use of unpublished results and for his support and friendship over the years. The oystercatcher ringers and participants of the Oystercatcher Conservation Programme, too numerous to mention here, are thanked for the valuable data they have collected since the start of the Programme.

WWF-SA, the Tony and Lisette Lewis Foundation and the Total Foundation are thanked for the financial support they provided throughout this study. Mazda Wildlife generously provided the Programme with a vehicle that never let me down in 16 000 km of travels. The National Research Foundation provided me with a post-graduate bursary for two years. Lastly, I wish to thank the Walvis Bay Municipality for providing aerial photographs, the Ministry of Environment and Tourism of Namibia for making this study possible and the Walvis Bay Salt Refinery (Roy Stanton) for allowing me to work on their property.

General Introduction

GENERAL INTRODUCTION

The African Black Oystercatcher *Haematopus moquini* has a breeding range extending from Lüderitz (26°38'S, 15°10'E) on the central Namibian coast to Mazeppa Bay (32°29'S, 28°39'E) on the East Cape coast of South Africa (Hockey 1983a). There have been a few extralimital breeding records, including two nests found at the Hoanib River mouth, about 800km north of Lüderitz in 1984 (Braine 1987), as well as at least two pairs suspected of breeding near Easter Cliffs in December 2000, approximately 170 km north of Lüderitz (R.E. Simmons, pers. comm.). Furthermore, in the KwaZulu/Natal province of South Africa, one pair has bred at Port Edward (M. Tyass *in litt.*). On the west coast there have been records of non-breeding birds as far north as Lobito, Angola (Summers & Cooper 1977). The most easterly record is of a single bird at Inhaca Island, Mozambique, in December 1996 (de Boer & Bento 1999).

Roughly 75% of the global African Black Oystercatcher population, presently estimated at under 5000 birds, is found in South Africa (Hockey 1983a), making it the third rarest, as well as one of the most range-restricted oystercatcher species in the world (BirdLife International 2000). Adults are sedentary and territorial and breed on the open coast and at off-shore islands during the austral summer – November to March (Hockey 1983b). Their breeding activities coincide with peak recreational use of the coastline, making oystercatchers susceptible to human disturbance and reducing breeding success (Leseberg *et al.* 2000). Surveys during the 1996/97 breeding season indicated that over large areas of the species' west coast range breeding success was below that required to maintain a stable population and that in areas of the Eastern Cape Coast there was no evidence of successful breeding. Furthermore, with rapid coastal development, concern grew that the African Black Oystercatcher was facing a conservation crisis. Africa's only other oystercatcher species, the Canarian Black Oystercatcher *Haematopus meadewaldoi*, is presumed to have gone extinct due to ever increasing levels of human disturbance and competition with man for food. It has not been seen on the Canary Islands since 1931 (Hockey 1987).

In the light of perceived threats to the African Black Oystercatcher, the Oystercatcher Conservation Programme was launched in January 1998, run under the auspices of the Percy FitzPatrick Institute of African Ornithology at the University of Cape Town. Based on an assessment of population trends over the past 25 years and ongoing monitoring of breeding success around the South African coast, the programme is in the process of developing a conservation strategy for the species, as well as population dynamics models that will be used to predict future changes in the population under a range of development and conservation scenarios. The Programme has also succeeded in increasing public awareness of concerns about the African Black Oystercatcher and plans to use the bird as a flagship species to highlight other coastal conservation issues in South Africa.

However, while results from the population model (Loewenthal 1998 & unpubl. data), together with other studies (Wilhelm 1999, Leseberg *et al.* 2000) increased our knowledge of oystercatcher breeding biology, foraging performance and the effects of human disturbance, very little was known about juvenile movements between the times of fledging and breeding. Female and male oystercatchers become sexually mature at three and four years respectively (Hockey 1996a); however, on average, birds only acquire a territory and begin breeding when about six years old (Loewenthal 1998 & unpubl. data). In the early 1980s it was concluded that juvenile oystercatchers did not disperse far from their natal sites – a few hundred kilometres at most (Hockey 1983a, Hockey 1986), and the maximum measured dispersal distance was 650 km (Hockey 1996b). However, in February 1998, a juvenile ringed at Knysna on the south coast of South Africa was recaptured in Swakopmund, Namibia (Tree 1998), more than 2500 km from its birthplace. Immediate visits to Walvis Bay and Swakopmund confirmed the presence of several other South African colour-ringed juveniles. Walvis Bay and Swakopmund were unequivocally identified as key nursery areas for juvenile and immature African Black Oystercatchers.

Since then, four other juvenile nurseries have been discovered along the west coast of southern Africa. The term 'nursery' is used here to describe specific habitats that are targeted by aggregations of juvenile oystercatchers and where they gather for 2–3 years before returning to natal sites. The term does not imply any parental care, because these sites fall outside of the adult oystercatcher breeding range, nor does it imply that juveniles require these areas to survive. Although the importance of these nurseries to the conservation of the African Black Oystercatcher was intuitively clear, almost nothing was known about habitat use, diet or foraging performance of oystercatchers at these sites. Because the Walvis Bay/Swakopmund nursery is one of the largest and certainly the most accessible of the five oystercatcher nurseries it was chosen for this study.

The Walvis Bay/Swakopmund nursery was visited on four separate field trips in August/September and November/December 1999 and in February/March and May/June 2000. Each visit was of approximately six weeks duration. A short follow-up visit was made to Walvis Bay and Sandwich Harbour (a large, undisturbed wetland 50 km to the south) in July 2001.

This study has the following objectives:

- To record all colour-ringed juvenile oystercatchers observed at the Walvis Bay/ Swakopmund nursery and to compare the seasonal numbers and the age structure of the two nursery populations – **Chapter 1**.
- To determine the proportion of South African oystercatchers that undertake long-distance migrations to nurseries – **Chapter 1**.
- To identify the key foraging habitats, as well as the diet and foraging behaviour of oystercatchers at Walvis Bay and Swakopmund – **Chapter 2**.
- To determine seasonal patterns of prey abundance and availability and how this affects oystercatcher numbers and distribution – **Chapter 2**.
- Through focal animal observations, to quantify foraging performance (foraging effort, intake rates and prey size choice) and to investigate any variation in performance in relation to seasonal prey availability/abundance and habitat type. Using instantaneous scan techniques, to quantify tidal activity rhythms and overall foraging time – **Chapter 3**.
- To evaluate the conservation implications of the juvenile dispersal strategies of the African Black Oystercatcher and to assess the threats that juvenile oystercatchers may face at the Walvis Bay/Swakopmund nursery – **Chapter 4**.

In satisfying these objectives, the study aims to test following key hypotheses:
Young oystercatchers target specific nursery sites along the west coast of southern Africa because these areas meet important ecological requirements of juvenile birds – hypothesised to be the following:

- For juveniles to avoid competition and aggression from territorial adults, they should aggregate where adults are absent (outside the breeding range) or where adults occur at low densities (Hockey 1983a).
- Because juveniles oystercatchers are considered less efficient foragers than adults (Norton-Griffiths 1969), nurseries must provide easily accessible and plentiful food resources. Furthermore, a lower foraging proficiency may lead to longer foraging times to meet daily energetic requirements.

Chapter 1

CHAPTER 1

The origins, numbers and demographics of juvenile African Black Oystercatchers at Namibian nurseries.

Introduction

Prior to the discovery of the Namibian nurseries, colour-ringed oystercatchers had only been resighted in South Africa. Throughout this time the existence of juvenile roosts was anticipated on the basis of exclusion of juveniles from adult territories, but the failure to locate any such roosts in South Africa was puzzling. It is now clear that this failure was the result of an inadequate search radius. Walvis Bay, 1600 km north of Cape Town, was never even considered a possibility and no searches were made here for colour-ringed birds. Oystercatchers observed there in the past were assumed to be Namibian non-breeding adults. Only once an intensive chick ringing operation was initiated as part of the Oystercatcher Conservation Programme (OCP) did long-distance movements of juvenile oystercatchers become apparent.

This chapter summarises the movements and dispersal distances of colour-ringed oystercatchers around the coast of southern Africa between July 1998 and July 2001. The number of oystercatchers observed at Walvis Bay and Swakopmund during the study period and the age structure of the roost (based on moult ratios and ringed birds) are discussed and compared with historical count data from Walvis Bay and Sandwich Harbour. Finally, an attempt is made to calculate the overall proportion of South African juveniles that disperse to nurseries.

Materials and Methods

The OCP's ringing activities

Oystercatcher chick ringing began in the 1997/98 breeding season and the fourth ringing season was completed in March 2001. The South African section of the breeding range was divided into seven ringing regions, each being assigned a different colour code (Fig. 1.1). Within these regions the OCP's participating bird ringers ringed chicks with a standard metal ring, as well as two coloured plastic rings denoting ringing season and region. Since the 1998/99 season, larger, more robust plastic rings engraved with unique three-digit codes have been used to track

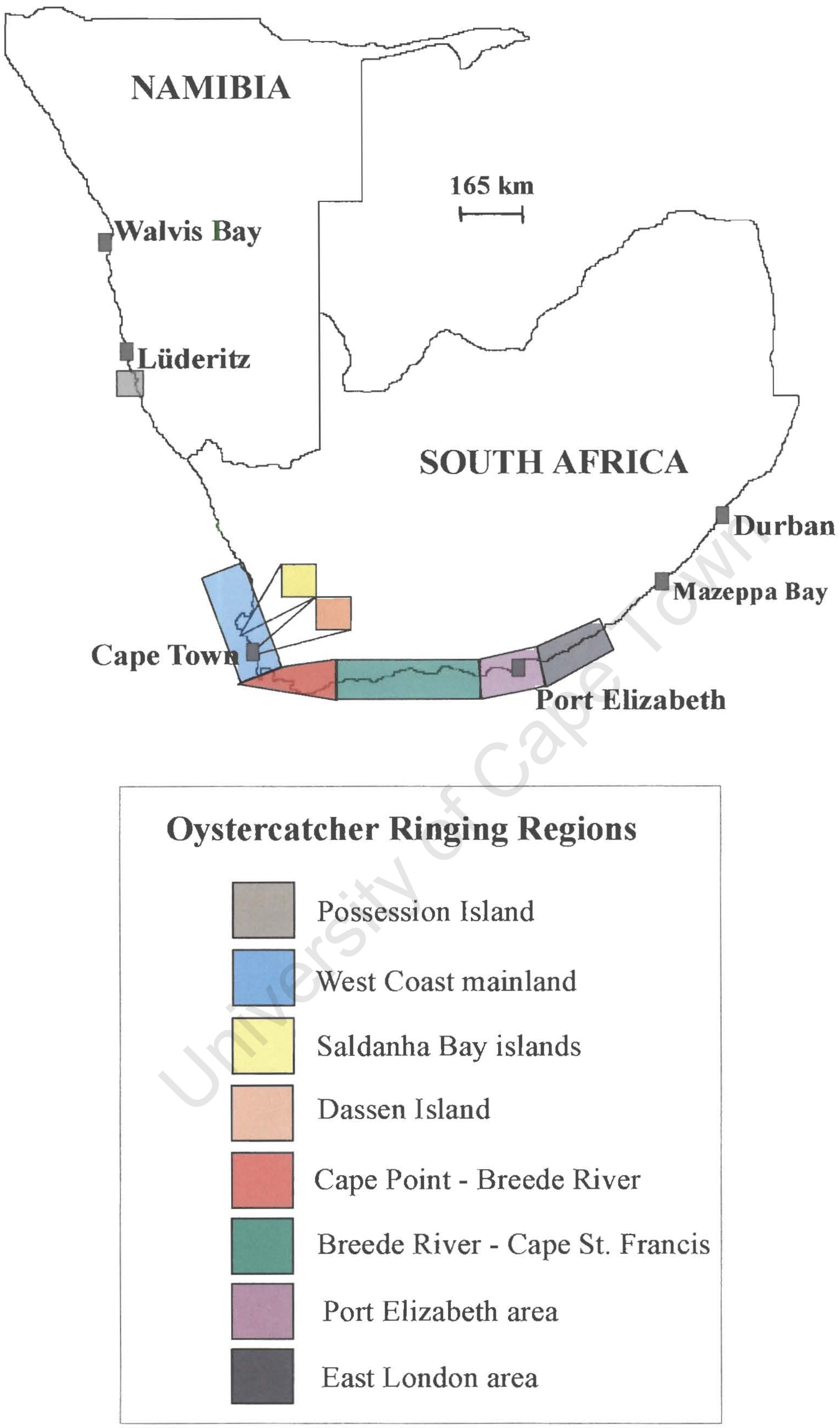


Figure 1.1. The geographic location and extent of the oystercatcher ringing regions in southern Africa.

individual juveniles. Since the start of the 1997/98 breeding season, 696 oystercatcher chicks have been colour-ringed, of which 357 (51%) are individually identifiable. Through public talks and newsletters, the OCP has made members of the public aware of colour-ringed birds and resightings from around the southern African coast are sent to the Programme on a continual basis.

Determining oystercatcher numbers and age classes at nurseries

During this study, roosting birds at Walvis Bay were counted whenever conditions were suitable, and at Swakopmund on a daily basis while at the site. It was difficult to count birds on a daily basis with 100% accuracy at Walvis Bay because there is movement between areas and because juveniles are flighty and difficult to approach. Oystercatcher numbers obtained during the study period were compared with historical oystercatcher counts at Walvis Bay, Swakopmund and Sandwich Harbour – a wetland area 55 km to the south.

Ageing birds

Birds in their first year are easily recognised by their reddish-brown eye colour with a narrow burnt orange eye ring, as well as greyish-pink legs, and bills that are distally dirty brownish (Hockey 1986). After their first year, however, ageing African Black Oystercatchers on soft-part coloration becomes difficult. By examining moult patterns in the primary feathers of juveniles of known age (colour–ringed and captive individuals) it was possible to determine the timing and duration of primary moult as a function of age. Oystercatchers, like all waders, shed their primaries in sequence from the innermost (P1), to the outermost feathers (P10 – Summers & Cooper 1977, Hale 1980). Thus, a bird showing a gap in the inner primaries is in the early stages of moult and *vice versa*.

On each field visit to the Walvis Bay/Swakopmund nursery, colour-ringed juveniles were located and checked for active primary moult when put to flight. The date of each observation (month) and, where possible, the position of the gap in the wing (outer, mid or inner primaries) was noted. As a result the periods of active primary moult for the years before a young oystercatcher enters the adult moult cycle were identified.

Determining the proportion of South African juveniles at nurseries

Whilst it is known how many oystercatcher chicks were ringed in South Africa over the seasons, not all of these chicks would have fledged successfully. Chick mortality between hatching and fledging could not be ignored and was calculated in order to estimate the number of ringed juveniles that survived to fledging. Chick mortality was determined for four ten-day age classes (0–10; 11–20; 21–30 and 31–40 days) from oystercatcher nest monitoring data carried out throughout South Africa as part of the Oystercatcher Conservation Programme. Oystercatchers fledge at 35–40 days (Hockey 1986). Data were collected from all regions in South Africa, as well as from protected and unprotected areas. Furthermore, all chicks ringed in South Africa in the 1997/98 and 1998/99 seasons (401 chicks in total) were aged according to measurements taken on the ringing day. Growth rates of wing, tarsus and culmen lengths, as well as chick mass obtained by Hockey (1984b) from wild chicks on the Saldanha Bay islands were used to allocate ringed chicks to the same ten day age classes as used to calculate mortality rates. The mortality rates were subsequently applied directly to the number of birds ringed in each of the four age classes.

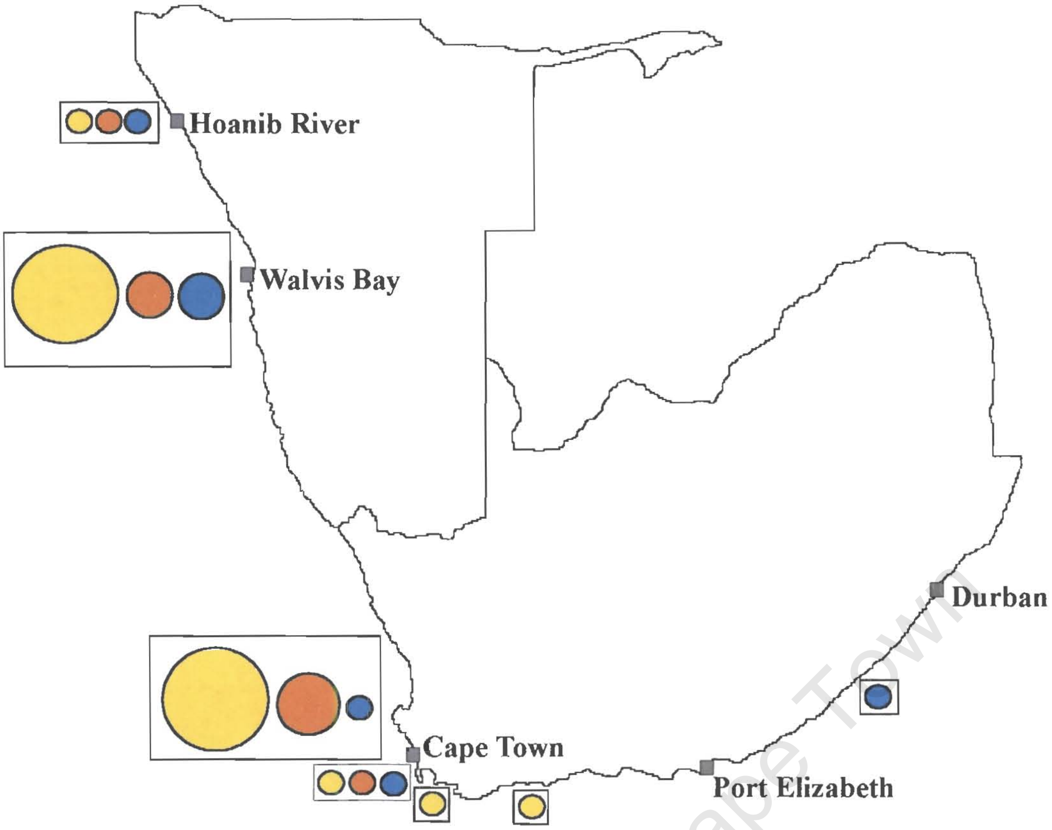
Results and Discussion

Juvenile movements and the locations of nurseries

Chick ringing effort has increased steadily since the first season of 1997/98, as has the frequency of resightings of colour-ringed birds around the southern African coast. These resightings are summarised in Figures 1.2 and 1.3.

Of the eight ringing regions (Fig. 1.1), Dassen Island and the islands in Saldanha Bay on South Africa's West Coast contribute the most ringed juveniles per season (65–165 p.a.) and account for the greatest number of resightings. The only chick colour-ringing carried out in Namibia has been on Possession Island near Lüderitz, where small numbers have been ringed (40). A few of these birds have been resighted at Walvis Bay, indicating that this nursery is used by Namibian as well as South African juveniles. The maximum dispersal distance to date (2800 km) was by a juvenile ringed near East London and resighted at Walvis Bay.

The distribution of resightings along the southern African coastline is to some extent a function of (unquantifiable) monitoring effort. Areas such as the Cape Peninsula and Saldanha Bay and

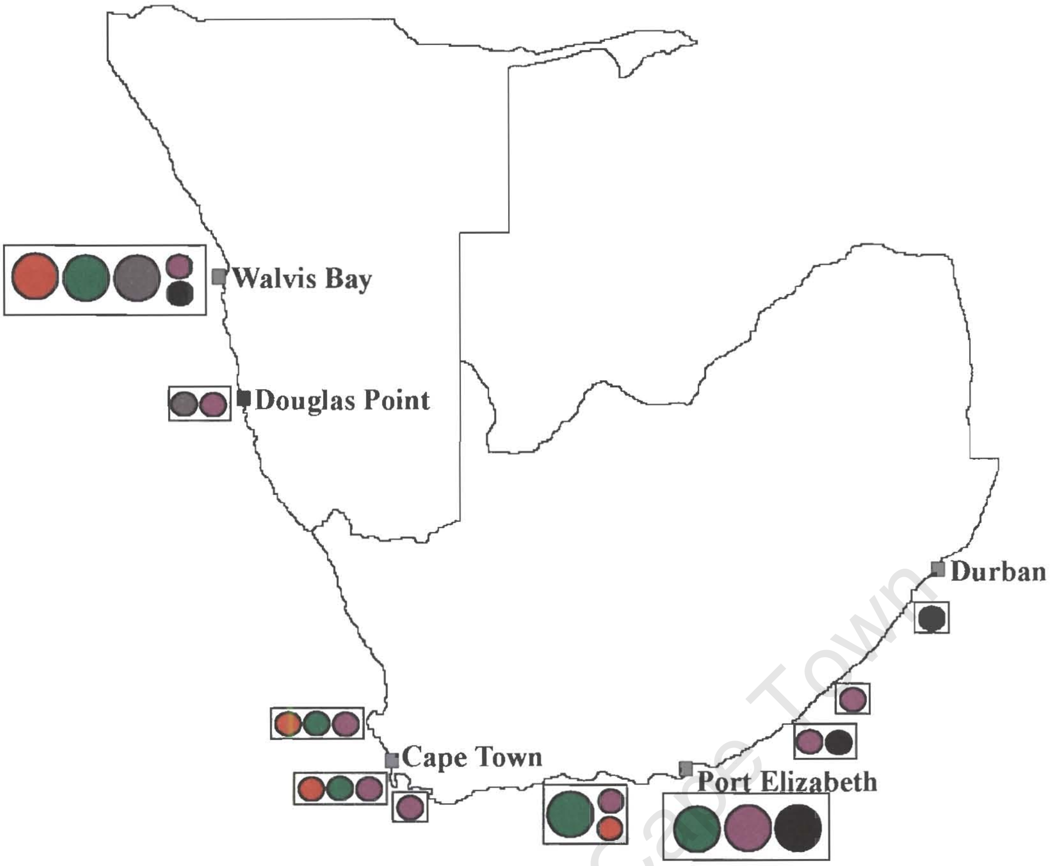


REGION	Numbers ringed (1997/98 - 2000/01)	Numbers re-sighted (July 1998 -July 2001)
Yellow	269	58
Orange	160	25
Blue	28	10

Numbers resighted

○	1 - 2
○	3 - 10
○	11 - 15
○	> 15

Figure 1.2. Colour resightings of juvenile African Black Oystercatchers along the southern African coastline and at Namibian nurseries between July 1998 and July 2001. Numbers ringed and subsequently resighted are shown for birds from the yellow, orange and blue ringing regions (Fig. 1.1).



REGION	Numbers ringed (1997/98 - 2000/01)	Numbers resighted (July 1998 - July 2001)
Red	37	10
Green	100	15
Purple	118	17
Black	25	5
Brown	41	5

Numbers resighted

○ 1 - 2

◯ 3 - 10

Figure 1.3. Colour resightings of juvenile African Black Oystercatchers along the southern African Coastline and at Namibian nurseries between July 1998 and July 2001. Numbers ringed and subsequently resighted are shown for birds from the red, green, purple, black and brown ringing regions (Fig. 1.1).

surrounds are monitored on a regular basis by staff and students of the OCP and have consequently yielded many resightings. Monitoring activity is much lower between Saldanha Bay and the Namibian border, where oystercatcher density is low, averaging 0.36 birds.km^{-1} (Hockey 1983a).

To date, four nursery areas have been identified in Namibia and one has been located in southern Angola. The most southerly is at Douglas Point, 55 km north of Lüderitz. In November 2000, 111 birds were counted here. Not all birds could be aged accurately, but 48 were unequivocally identified as first-year birds (R.E. Simmons & J.P. Roux *in litt.*). Thirty kilometres to the north at Hottentot Point is another nursery (104 birds in November 2000). Again, not all birds were aged accurately, but a minimum of 23 1–2 year old birds was seen. A group of 10 1–2 year old birds was seen during the same survey at Spencer Bay (17 km north of Hottentot Point), but it is uncertain whether these constitute an independent nursery (R.E. Simmons & J.P. Roux *in litt.*). The large oystercatcher nurseries north of Lüderitz are both located along stretches of rocky shore where the diet of the birds is likely to consist of limpets and mussels (Hockey & Underhill 1984). Douglas Point also lies close to Ichaboe Island and birds do fly across to the island to feed (Y. Chesselet, pers. comm.).

On the northern Namibian coast, at the Hoanib River (*ca.* 250 km south of the Angolan border), as well as at Möwe Bay, 10 km further south, an oystercatcher nursery regularly contains up to 35 birds – at least three different South African juveniles have been recorded at this site, where oystercatchers feed on a rocky section of coast with an abundance of mussels (J. Paterson *in litt*). The northern Namibian coastline consists largely of sandy shores; rocky outcrops such as the one at the Hoanib mouth are rare.

Up to 50 African Black Oystercatchers are present at Baia dos Tigres in southern Angola (A. Sakko *in litt.*). This is a very remote area of coast and this aggregation was only discovered in the mid-1990s. Although the birds have not been aged by experts, it is highly likely that they form a nursery for the following reasons: 1) The flock is present throughout the year; and 2) the birds are never seen in pairs and have not been observed in territorial defence or displaying any other behaviour characteristic of breeding adults. Prior to the discovery of this nursery, African Black Oystercatchers were thought to occur in Angola only as vagrants (Hockey 1983a). Baia dos Tigres is a complex system of sand banks and shallows and it is thought that the oystercatchers feed on sand mussels, polychaetes and other species associated with sandy shores (A. Sakko, pers. comm.).

There are many sightings of colour-ringed juveniles at sites other than nurseries (Figs. 1.2 & 1.3). With the exception of those moving in an easterly direction, there is always uncertainty as to whether birds were en route to a nursery or not. What is certain, however (and based on multiple resightings), is that some juveniles travel only short distances (usually less than 150 km and sometimes less than 10 km) from their natal sites. It appears, therefore, that African Black Oystercatchers (which are highly sedentary as adults) have a dichotomous post-fledging movement pattern. Some undertake 'typical' short-distance exploratory dispersal, whereas others undertake targeted longer-distance migration and both strategies are followed throughout the breeding range.

Numbers and demographics at nurseries on the central Namibian coast

Records of "large groups" of African Black Oystercatchers at Walvis Bay date back to the mid - 19th Century. In the 1850's, Andersson wrote 'This species is usually observed in pairs; but I have seen it in considerable flocks at Walwich Bay late in October and early in November: the birds composing these flocks are always too shy to be approached within gunshot' (Gurney 1872). Andersson's observations that the birds were a) in flocks and b) difficult to approach, conform precisely with characteristics of nurseries.

Annual shorebird counts over the last two decades have consistently recorded flocks of African Black Oystercatchers in the Walvis Bay area (Fig. 1.4a). Numbers increased in the 1990s, averaging 125, compared to an average of 38 recorded during the 1980s (R.E. Simmons, unpubl. data). These changes may be explained by birds moving to Walvis Bay from Sandwich Harbour – a wetland area 50 km to the south. In the early 1970s, groups of up to 130 birds were regularly recorded at Sandwich Harbour (Berry & Berry 1975). However, Sandwich Harbour is geomorphologically very active with constantly shifting sand bars and lagoons (Noli-Peard & Williams 1991, Simmons *et al.* 1998). In the 1970s, the northern wetland area of Sandwich Harbour consisted of extensive tidal mudflats rich in bivalves such as *Dosinia lupinus* (Kensley & Penrith 1977, R.E. Simmons, pers. comm.), a preferred prey species of oystercatchers at

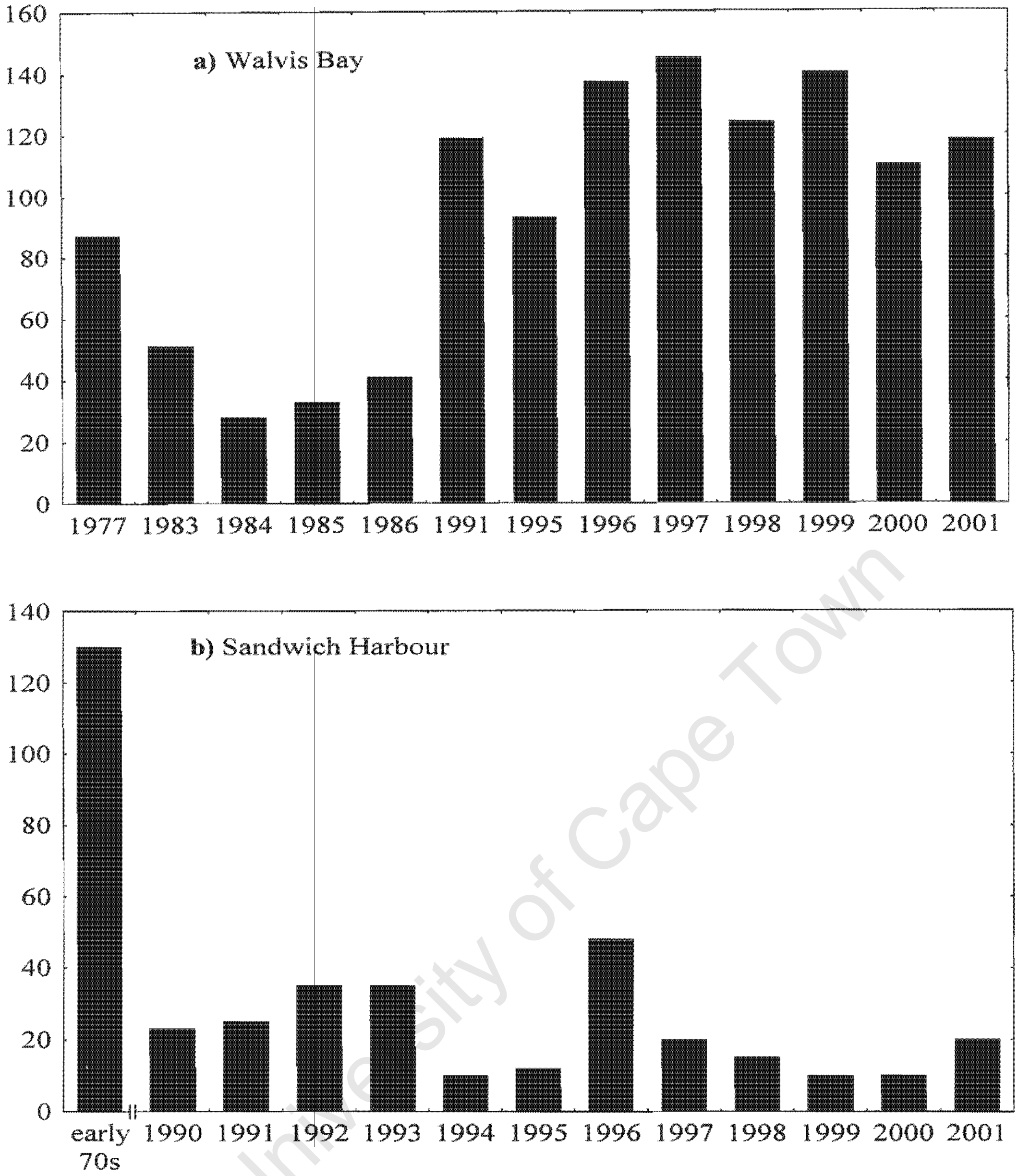


Figure 1.4. Total number of African Black Oystercatchers counted at Walvis Bay in 1977 and 1983–2001 and at Sandwich Harbour in the early 1970s (Berry & Berry 1975) and 1990–2001 (R.E. Simmons unpubl. data).

Walvis Bay (Chapter 2). However, this northern section has been much reduced in size, and has changed into a largely fresh water wetland since the early 1970s (Simmons *et al.* 1998), with a concomitant reduction in the availability of food for oystercatchers. In the 1990s, oystercatcher numbers at Sandwich Harbour fluctuated between 10–35 birds (Fig. 1.4b), although fewer than ten birds were recorded on several of the quarterly counts made during this time (R.E. Simmons, unpubl. data). To date five colour-ringed oystercatchers have been recorded at

Sandwich Harbour (one from the Port Elizabeth area, two from Dassen Island, one from Saldanha Bay and one from Possession Island).

Oystercatcher numbers at Walvis Bay and Swakopmund

Walvis Bay consistently supported more oystercatchers than Swakopmund (Table 1.1), averaging 125 whereas Swakopmund averaged 11. However, up to 60 birds have been recorded at Swakopmund in the past (M. Boorman & S. Dantu *in litt.*). Numbers at Swakopmund fluctuate seasonally, peaking in early winter (May and June – Fig. 1.5). In the summer months, numbers usually fall to below ten birds. This pattern is linked to the annual arrival of juveniles from their breeding grounds to the south. The first juveniles arrive at the Walvis Bay/Swakopmund nursery in May and June, about 14–18 weeks after the peak fledging time.

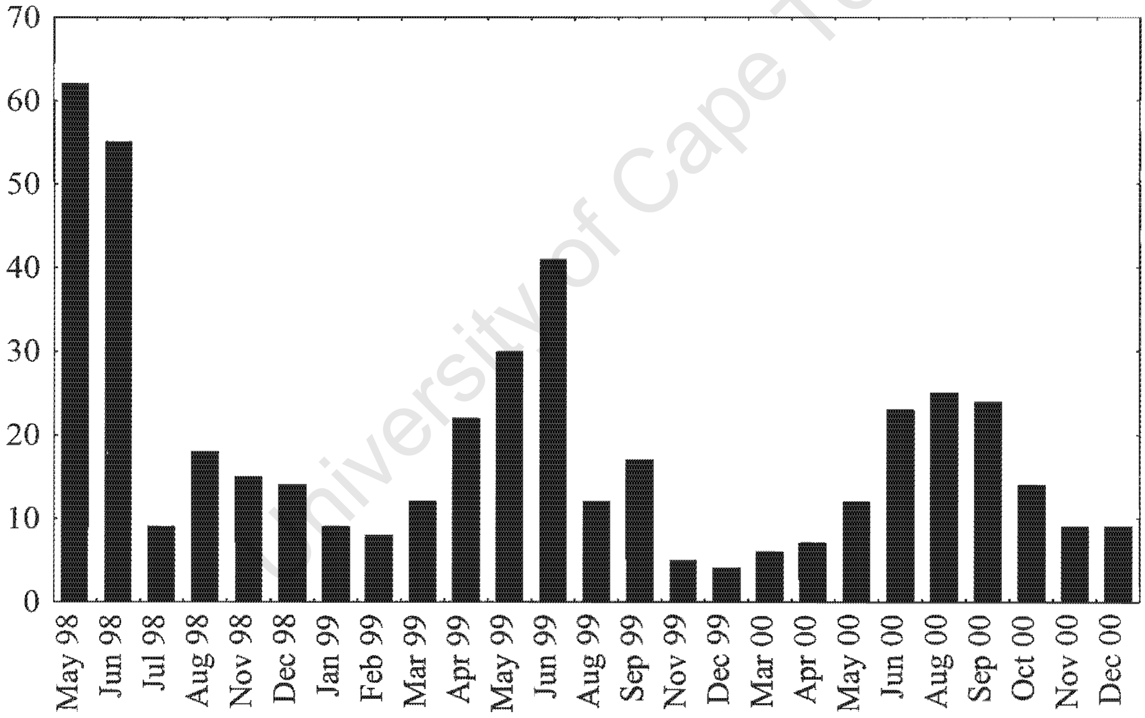


Figure 1.5. Average monthly numbers of African Black Oystercatchers at the Swakopmund roost between May 1998 and December 2000 (M. Boorman & S. Dantu, unpubl. data)

In the summer of 1999/00 the southwestern Cape Province of South Africa was characterised by unusually high temperatures – average daily maximum temperatures for December 99 and January 00 were 29.1° C and 28.4° C and both months were characterised by consecutive days where temperatures exceeded 30° C (SAWB 1999 & 2000). These high temperatures caused high egg mortality and repeated re-nesting resulted in late fledging and in juveniles arriving later than usual at nurseries. In 2000, numbers at Swakopmund peaked between June and September.

Table 1.1. Total numbers and proportion of ringed African Black Oystercatchers observed during the study period; WB – Walvis Bay SM – Swakopmund.

	Aug/Sep		Nov/Dec		Feb/Mar		May/Jun	
	WB	SM	WB	SM	WB	SM	WB	SM
Total number	160	13	120	5	120	6	100	19
Percentage ringed (sites combined)	19		16		14		24	

The reduction in numbers at the Walvis Bay nursery in early summer (Table 1.1) cannot be explained by a seasonally elevated mortality rate – no depredation of African Black Oystercatchers was ever observed at the nursery nor were any carcasses recovered. Rather, this change represents emigration. The oldest birds return south at this time (the start of the breeding season). Adult African Black Oystercatchers reach sexual maturity at three (females) to four (males) years old (Hockey 1996a), but many two-year old birds return to their natal areas. Four individuals, ringed as chicks on the Saldanha Bay islands in January 1999 and resighted during the study at Walvis Bay and/or Swakopmund have subsequently been recorded (January–May 2001) back at or very close to their natal sites in South Africa that they left two years previously (pers. obs.). This is the first conclusive evidence of individually marked African Black Oystercatchers completing their post-fledging movements and returning to natal sites. To date, 170 km represents the furthest distance an African Black Oystercatcher has been found breeding away from its birthplace (pers. obs). However, of 46 birds retrapped thus far, only three additional birds have been found breeding more than 5 km from their birthplace (D. Loewenthal, unpubl. data).

Transient juveniles that were observed for six weeks or less at the Walvis Bay/Swakopmund nursery (Table 1.2) are thought to use the area as a stop-over point on journeys to other

Table 1.2. The length of time colour-ringed oystercatchers spent at the Walvis Bay/ Swakopmund nursery and their age when first recorded.

Length of time spent at the nursery	No. of juveniles at the nursery that are either	
	< 1 year old	1–2 years old
> 12 months	4	1
7–12 months	2	4
3–6 months	1	——
< 3 months	——	——
< 6 weeks	2	2
not known	1	4

nurseries. As yet there is no record of an individually marked bird that has been observed both at Walvis Bay and at a nursery farther north. However, first-time sightings of 1–2 year old transient juveniles at Walvis Bay (Table 1.2), suggest that they had returned from northern nurseries and were travelling southwards to their natal sites.

Demographics of the nursery population

Based on observations of moulting birds at the Walvis Bay/Swakopmund nursery it was determined that a juvenile oystercatcher, which fledges between January and March, begins its first primary moult at the end of September of the same year and finishes by the end of the following March. This moult cycle is thus completely (6 months) out of phase with adult moult (Fig. 1.6). As the moult period straddles the breeding season of adults, the bird is in its second year at the end of moult. The second primary moult begins the following January, when the juvenile is entering its third year. This moult extends from January to June. Thus, African Black Oystercatchers complete only two full primary moults in their first three years. Only once the bird is in its fourth year is its moult fully synchronous with that of adults, beginning after the breeding season in March and ending in October. These results agree closely with Baker's (1975) findings regarding juvenile moult patterns in New Zealand's Variable

Oystercatcher *H. unicolor*. He concluded that first year birds moult in late (austral) spring and early summer and second year birds in summer, while adults start their moult in autumn.

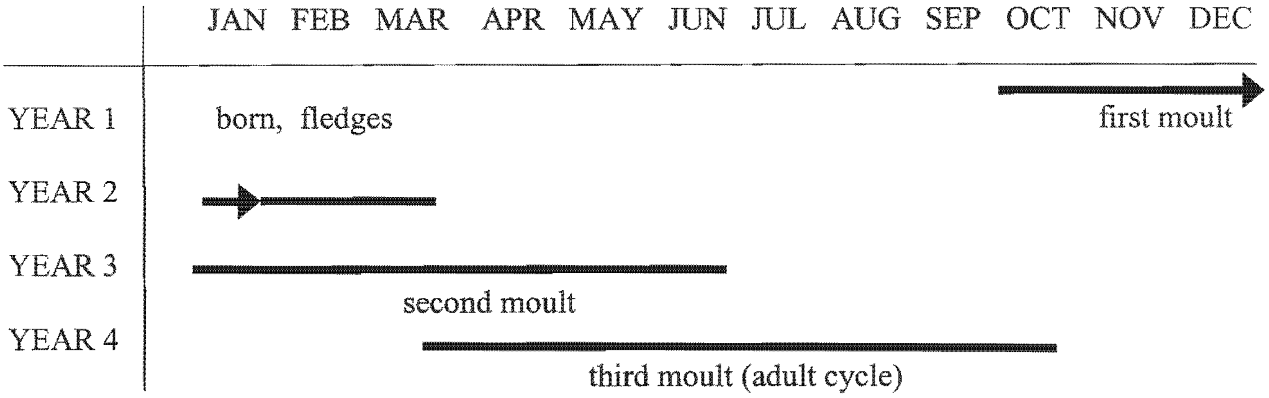


Figure 1.6. Duration of the first three primary moults of juvenile African Black Oystercatchers.

Thus, on a combination of the presence or absence of primary moult, and the stage of the moult, birds can be aged fairly accurately in the field up to November of their third year. However, whilst Figure 1.6 is a useful guideline for ageing birds, it is not possible to age all birds unequivocally at all times. Considering the presence or absence of moult alone, any bird in moult in November and December is a first year bird and any bird in moult between July and September is in it fourth year or older. Considering the stage of the moult cycle, any bird in late moult in February and March is a bird early in its second year (end of the first moult).

From this knowledge of periods of active primary moult of different age classes (Fig. 1.6) and overall moult ratios collected on each visit to Walvis Bay, the numbers and proportions of birds of different ages were calculated (Table 1.3). In Nov/Dec 99, 57% (71) of the oystercatchers at Walvis Bay were in moult, representing birds in their first year. During the previous visit in Aug/Sep 99, 22% (37) of the birds were in moult – birds in their third year or older. Numbers fell by approximately 50 individuals between Aug/Sep and Nov/Dec. Emigration of both second and third year birds (as shown by four ringed oystercatchers resighted back at their birthplace they had left two years previously) are thought to account for these changes. Whilst the moult ratios mentioned thus far are based on field observations of moulting birds of known age (indicated in bold in Table 1.3), the assumption was made that third year birds are twice as likely to leave Walvis Bay at this time of year (start of the breeding season) than are second year birds. For both age groups this represents a pre-moult migration, second year birds beginning their next (second) moult the following January and third year birds beginning their third moult at the end of the following March. When applying this probability ratio to the values for Aug/Sep, numbers of second year birds fell to 38 and third year birds to 16 individuals in Nov/Dec.

Table 1.3. The numbers and proportions of juveniles of different ages present at the Walvis Bay/Swakopmund nursery during the study period. Numbers in bold indicate oystercatchers in active moult and arrows indicate birds ageing one year and moving into the next age class.

	Aug/Sep 99		Nov/Dec 99		Feb/March 00		May/June 00	
	N	%	N	%	N	%	N	%
Birds in their first year	71	42	**71**	**57**	**0**	**0**	31	26
Birds in their second year	62	36	38	30	71	57	71	59
Birds in their third year and older	**37**	**22**	16	13	54	43	**18**	**15**
Overall proportion in moult	22		57		44		15	
Total number	170		125		125		120	

By February/March 00, all birds at the nursery have aged by one year. The 71 first year birds recorded in Nov/Dec have become second year birds, just as the 38 and 16 second and third year birds enter the third year and older group (54 birds). In Feb/Mar, no first year birds have yet arrived at Walvis Bay from natal sites to the south. During the last visit in May/June, 15% (18) of the birds were in moult, representing individuals in their third year or older – the only age group in moult at this time of year (Fig. 1.6). These 18 birds indicate that a further 36 third year plus birds had left the nursery between Feb/Mar and May/Jun. Assuming that the number of second year birds (71) remained the same, 31 new first year birds had arrived at the Walvis Bay nursery by the end of the study period in June 2000.

First year birds continue to arrive at the Walvis Bay/Swakopmund nursery until July/August. In Aug/Sep 99, the number of first year birds at the nursery was more than double that present in

May/June 2000. The pattern of arrival and departure times of different age classes at the nursery is directly dependent on fixed parameters such as the timing of fledging, primary moult and the onset of the breeding season.

Proportion of South African juveniles at nurseries

Only the 1997/98 and 1998/99 breeding seasons were included in this analysis as juveniles fledged during later years had not yet arrived at the nursery at the time of the study. During the last visit to Walvis Bay in May 2000 the first juveniles from the 1999/00 season were recorded. Figures 1.2 and 1.3 do, however, show all subsequent resightings until the 31st July 2001.

Analysis of 110 separate clutches and 190 hatchlings indicated that 79 (42%) of chicks fledged successfully, 24% of chicks died between 0–10 days, 23% between 11–20, 5% between 21–30 and 6% between 31–40 days.

After fledging, young oystercatchers remain close to their natal territories for approximately one month. This time period, together with the age of ringed chicks, a 35–40 day fledging period and the earliest resightings of individually colour coded juveniles at Walvis Bay, indicates a minimum travel time of two months to the nursery. Nothing is known about how foraging conditions and natural predation affect the survival of migrating juveniles during this time. Resightings of birds in transit are very rare, making it virtually impossible to determine a mortality rate between departure from the natal sites and arrival at a nursery. For the sake of this analysis it was assumed that juveniles do not experience any further mortality while travelling to a nursery. Conditions at the nurseries are favourable to inexperienced youngsters (Chapter 2) and mortality is very low (no dead birds were ever recovered at Walvis Bay) – possibly close to the annual adult mortality rate of 5% (D. Loewenthal, unpubl. data).

Of the 401 juveniles ringed in the 1997/98 and 1998/99 seasons, 327 were predicted to still be alive at ± 6 months. Of these, a minimum of 12.5% were resighted at the Walvis Bay/ Swakopmund nursery during this study (Table 1.4). However, the nursery represents only 30% of the total number of juveniles at Namibian nurseries (*ca.* 400). If 12.5% of surviving South African-ringed juveniles were present at Walvis Bay/Swakopmund alone, 42% of South African-ringed birds are predicted to be present in all five nurseries combined. This assumes that all nurseries support the same proportion of South African juveniles, which may not be the case if the two Lüderitz nurseries are dominated by Namibian juveniles (Chapter 4) – this will only be known once the two sites are thoroughly surveyed. Furthermore, because ringed and unringed oystercatchers are equally likely to migrate to a nursery, 42% can be considered the overall proportion of South African juvenile oystercatchers that follow the long-distance dispersal strategy.

During this study 50% of the oystercatchers at the Walvis Bay/Swakopmund nursery were first-year birds (i.e. the previous season's production). If this ratio is applied to all nurseries, 200 recently fledged juveniles (50% of a total of 400) arrive at nurseries each year. These juveniles will comprise both South African and Namibian birds.

Table 1.4. The number of oystercatcher chicks ringed between 1997 and 1999, the number predicted to be alive at 6 months and the proportions resighted at the Walvis Bay/Swakopmund nursery.

Origin	Number Ringed	Number predicted to be alive at 6 months	Number resighted at nursery	% resighted (based on predicted N)
[1] West Coast	249	202	30	14.9
[2] South Coast	66	52	10	19.2
[3] East Coast	86	73	1	1.4
TOTAL	401	327	41	12.5

[1] West Coast islands and mainland; [2] Cape Point to Cape St. Francis; [3] Port Elizabeth and East London areas.

Conclusions

1. Understanding of juvenile dispersal behaviour of African Black Oystercatchers has grown extensively with the discovery of at least four discrete nursery areas on the Namibian coast and one in southern Angola. Juveniles from throughout the South African breeding range travel to these nurseries, some covering a distance of > 2500 km to reach them. Historical records from Walvis Bay indicate that such nursery sites are traditional. Movement of individually identifiable juveniles between nurseries (other than between Walvis Bay and Swakopmund) has yet to be conclusively proved.

2. All the nurseries are located outside the breeding range of the adults. Juveniles first arrive at the Walvis Bay/Swakopmund nursery in May–June and they remain there for a minimum of two years. Numbers fall in early summer when birds return to natal sites in South Africa.

3. A dichotomous post-fledging dispersal pattern exists; not all juveniles move long distances. Several remain close to their natal sites, never moving further away than a few kilometres. Short-distance dispersers are scattered around the coast and do not form discrete nurseries. Rather, they aggregate with adults at high-tide roosts (Hockey 1983b).

4. Colour resightings at Walvis Bay indicate that 12.5% of ringed and successfully fledged South African juveniles reach Walvis Bay. If all nurseries support the same proportions of South African juveniles, a total of 42% of South African juvenile oystercatchers employ a long-distance dispersal strategy.

Chapter 2

CHAPTER 2

Foraging habitats and dispersion of juvenile African Black Oystercatchers at the Walvis Bay/Swakopmund nursery.

Introduction

The world's 11 extant oystercatcher species use both soft and hard substrata for foraging and their diets vary accordingly (Hockey 1996a,b). At the species level, oystercatchers feed on a variety of different prey items, predominantly molluscs, bivalves and polychaete worms (Hockey 1996b).

The African Black Oystercatcher inhabits both rocky and sandy shores throughout the year. It has one of the widest dietary spectra of any oystercatcher, feeding on at least 52 invertebrate species (Hockey & Underhill 1984, Hockey 1996b). On rocky shores, gastropods – notably mussels and limpets, as well as whelks and winkles, make up most of the diet. Since the early 1980s the rapid spread of the invasive Mediterranean Mussel *Mytilus galloprovincialis,* first introduced over 30 years ago and now the most abundant intertidal bivalve on the west coast of southern Africa (Hockey & van Erkom Schurink 1992), has led to a major shift in the diet of African Black Oystercatchers. The Ribbed Mussel *Aulacomya ater*, once dominant in the birds' diet, has been replaced by *Mytilus* along most of the west coast of South Africa and Namibia. In this region the Mediterranean mussel makes up 65–75% of the diet of oystercatchers (Hockey 1996b).

On the open sandy coasts of the Eastern Cape Province of South Africa, oystercatchers specialise on the bivalves *Donax serra* and *D. sordidus* (McLachlan *et al.* 1980, Ward 1990). Compared to other species such as the Eurasian Oystercatcher *H. ostralegus*, few adult African Black Oystercatchers forage on estuarine mudflats.

When foraging on rocky shores, African Black Oystercatchers search for gaping mussels and open them by severing the posterior adductor muscle that holds the two valves together (Hockey 1981b). The mussel is then either eaten *in situ* or removed from the mussel bed to be eaten higher up on the shore. In contrast, Eurasian Oystercatchers generally target closed mussels and open them using a hammering or stabbing technique (Goss-Custard & Sutherland

1984). These differences can be explained by the fact that African Black Oystercatchers experience a much smaller tidal range, and, because mussels grow in the mid to low intertidal zone, they remain damp and gaping for extended periods (Hockey 1981b). A larger tidal range, together with greater physiological stresses experienced in winter, force Eurasian Oystercatchers to target closed mussels. Limpets are dislodged from rocks by a sharp blow to the posterior section of the shell or are simply levered off the rock by inserting the lower mandible under the shell. The meat is cleaned from the limpet by a circular scissoring action (Hockey 1981b). This technique is broadly comparable to that used by other oystercatcher species.

Because the African Black Oystercatcher feeds exclusively in the intertidal zone, its foraging periods are tidally controlled, and foraging activity peaks just before low water (Hockey 1984a). Pairs are highly territorial for most of the year and tightly bound to a stretch of coastline, some as narrow as 20 m of shore. Their diet is directly dependent on the invertebrate species present within their territory, and differences in bill morphology between males and females result in some dietary segregation between them (Hockey & Underhill 1984). Foraging activity is thus controlled by the tide and diet is determined by the location and size of the territory.

The foraging ecology of juvenile oystercatchers is driven by different selective pressures. Young oystercatchers require several years to perfect the often complex techniques needed to catch and process different prey species (Norton-Griffiths 1969) and juvenile Eurasian Oystercatchers are considered less efficient foragers than adults (Goss-Custard & Durell 1987a, Goss-Custard *et al.* 1998). Their foraging inefficiency is reflected in the fact that when first arriving on the winter feeding grounds juveniles are very aggressive towards older and more proficient conspecifics and regularly attempt to steal food items from them (Goss-Custard & Durell 1987b). As their foraging efficiency increases, however, they become less aggressive, less successful in encounters and increasingly prone to interference from other birds (Goss-Custard & Durell 1987b). It becomes energetically more profitable for the juveniles to search for their own food than to steal it from conspecifics (Goss-Custard *et al.* 1998).

Another strategy employed by many juvenile Eurasian Oystercatchers is to target types of prey that are a) not taken by adults and b) easy to process (Goss-Custard & Durell 1983). As a result, the dietary spectrum of these oystercatchers narrows with age. While most adults feed in only one habitat and on one prey species, most commonly *Mytilus edulis,* juveniles typically forage in two or three different habitats, preferring species such as the ragworm *Nereis diversicolor* and the burrowing bivalve mollusc *Scrobicularia plana* (Goss-Custard & Durell 1983). Only once the prey handling techniques of juveniles have developed sufficiently, and they are mature enough to compete with adults successfully, will they begin foraging in adult-dominated habitats such as mussel beds. Amongst American Pied Oystercatchers *H. palliatus* feeding on oyster beds, juveniles scavenged more often than older birds on scraps of flesh left in shells or preyed on other invertebrates within the oyster beds (Cadman 1980).

Juvenile African Black Oystercatchers that disperse to Namibian nurseries do not experience any competition with adults (Chapter 1), but they are nonetheless inexperienced foragers and select habitats where food is abundant and easily processed. Just as young Eurasian Oystercatchers feed on a wide spectrum of prey species, it is predicted that juveniles at Namibian nurseries will utilise several different habitats and display an opportunistic foraging strategy. Because they are not concerned with breeding or holding a territory, their movements are likely to be a response to changes in prey availability and profitability.

This chapter describes the oystercatcher foraging habitats, behaviour and diet at the Walvis Bay/Swakopmund nursery. Seasonal patterns of prey abundance and the role they play in the distribution and number of oystercatchers at the two sites are discussed.

Materials and Methods

Description of study sites

1.) Walvis Bay

The town of Walvis Bay (22°59'S; 14°31'E) lies in the Kuiseb River Delta on the Namib Desert coast and its associated wetlands form one of Namibia's four Ramsar sites as Wetlands of International Importance (Simmons *et al.* 1998). The wetlands are situated to the south and west of the town, comprising extensive mudflats and intertidal areas along Walvis Bay Lagoon, the outer lagoon and continuing northwards along the eastern shore of Pelican Point (Fig. 2.1), a 10 km long sand spit (Noli-Peard & Williams 1991, Simmons *et al.* 1998).

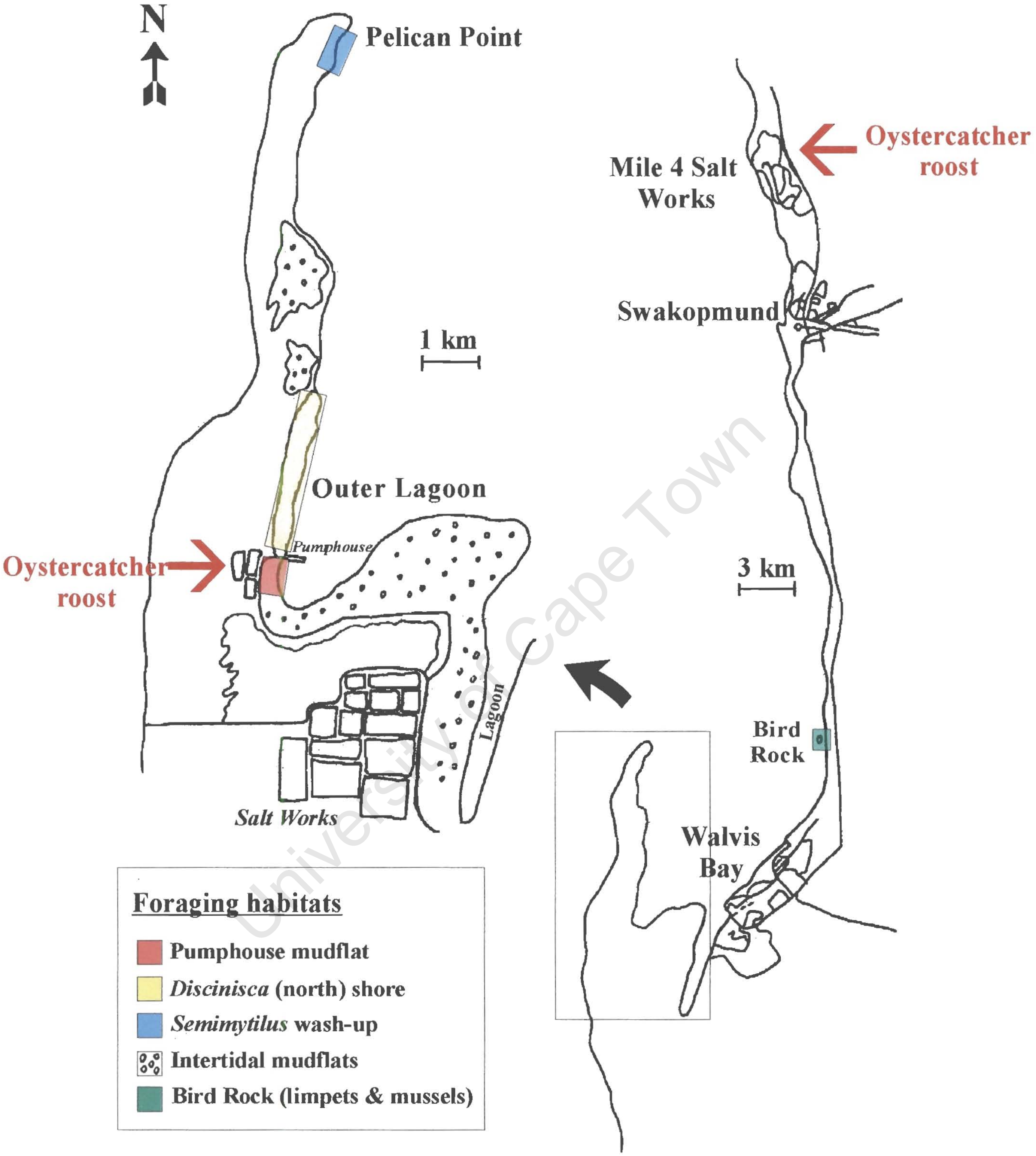


Figure 2.1. The Walvis Bay and Swakopmund oystercatcher roosts and surrounding foraging habitats.

The oystercatcher roost at Walvis Bay is situated near the north-western shore of the outer lagoon and at the site of the salt works' main pumpstation that supplies seawater to a gravity-fed system of evaporation pans (Fig. 2.1). The two pans nearest to the pumphouse have been set aside for oyster cultivation and both diurnal and nocturnal oystercatcher roosts form on the sand dykes that separate these pans. The primary foraging habitats are situated on either side of the 150 m long jetty that leads to the pumphouse (Fig. 2.1). To the south of the pumphouse is a tidal mudflat where the Heart Clam *Dosinia lupinus* is the dominant prey of the oystercatchers. The shoreline to the north of the pumphouse continues to the tip of Pelican Point, approximately 9 km away, but the birds fed primarily on the 150 m of shoreline immediately north of the jetty. This habitat comprises a thick shellbank at the high tide mark, consisting mostly of empty *Venerupis corrugatus* shells. The intertidal shoreline is made up of sandy and coarse sediments from which *Dosinia* is absent. Here juveniles foraged on washed up prey items. The Disc Lamp Shell *Discinisca tenuis,* a species of primitive brachiopod endemic to Namibia and with an average diameter of 20 mm (Branch *et al.* 1994), is washed up in vast quantities and constituted the primary prey in this habitat.

Secondary feeding habitats around Walvis Bay included areas near the tip of Pelican Point where the alien Bisexual Mussel *Semimytilus algosus* is washed ashore on a frequent but unpredictable basis (Fig. 2.1).

2.) Swakopmund

Swakopmund lies 30 km north of Walvis Bay. A few, small, natural wetlands are restricted to areas around the mouth of the Swakop River. However, only during very rare floods does water flow into the sea, and in most years the lower river is dry. Onshore waves sometimes form a lagoon behind the beach bar, attracting several waterbird species (Noli-Peard &Williams 1991). The other area near Swakopmund that supports large numbers of waterbirds is the site of the Mile 4 Salt Works (22° 39'S; 14° 33'E), about 7 km north of the town. This is also the location of the Swakopmund oystercatcher roost (Fig. 2.1). Mile 4 comprises a series of evaporation pans, as well as a large, wooden, commercial guano platform. The Mile 4 shoreline benefits from the nutrient rich waters of the Benguela upwelling system. Nutrients are brought to the surface and swept onshore by strong winds, making this coastline, in terms of invertebrate biomass, one of the richest shores in southern Africa (Simmons *et al.* 1998).

The oystercatcher roost at Mile 4 is comparable to the one at Walvis Bay as it is located on a sand dyke separating two evaporation pans. The coastline at Mile 4 utilised by the oystercatchers comprises stretches of rock separated by short sandy beaches: the total length of shore exploited by these birds is 2 km. In contrast to Walvis Bay, juveniles at Mile 4 can only forage when the intertidal zone is exposed. Brown Mussels *Perna perna* are, however, periodically ripped from the subtidal mussel beds during heavy seas and deposited above the high water mark, where they form a food source available to the birds at all stages of the tidal cycle.

The 30 km of coastline between Walvis Bay and Swakopmund is mostly sandy beach with a few isolated rocky outcrops. Although shorebird densities here are considered to be one of the highest on any open coastline in southern Africa (Simmons *et al.* 1998), this shoreline supported few oystercatchers during the study. The only section where foraging oystercatchers were observed was along a string of rocky outcrops opposite a guano platform ('Bird Rock'), 7 km north of Walvis Bay (Fig. 2.1). These rocks represent the only permanent food supply for oystercatchers in the Walvis Bay area but were rarely used. The only time when large numbers (up to 40 birds) were observed foraging at Bird Rock was in May/June 2000, when the birds also formed a diurnal high tide roost on the beach adjacent to the rocks. Being an exposed site, however, oystercatchers probably returned to the main roosts either at the Walvis Bay pumphouse or at Mile 4 at night. The intertidal area at Bird Rock supports dense mussel beds, and although there are a few similar areas along the rest of the coastline between Bird Rock and Swakopmund, it is likely that intense fishing and off-road vehicle pressure along this coastline precludes juvenile oystercatchers from using these areas. At Bird Rock, human disturbance by fishermen was low.

Measuring seasonal patterns of prey abundance

At Walvis Bay, the primary feeding habitats on either side of the pumphouse were sampled during each season. The pumphouse mudflat was 330 m long and had an average downshore width of 180 m. This area was divided into ten equidistant downshore transects, and along each transect six samples, 20–30 m apart, were taken. Each of the 60 samples was 300 x 300 mm in area and excavated to a depth of 150 mm. All clams recovered were counted, measured and collected for calorific analysis. Small polychaete worms that were on occasion eaten by the oystercatchers were very rarely encountered on the mudflat and were not sampled.

To the north of the pumphouse, mussels and *Discinisca* were washed up in a 2–3 m wide band. The number of each species recovered from 50 randomly positioned 500 x 500 mm quadrats was recorded and individual animals were measured. Only *Discinisca* was sufficiently abundant to be collected for calorific analysis. Because the washed up food was no longer fresh, but in varying stages of decay, only items containing fresh flesh were included in the sampling. *Semimytilus* wash-ups at Pelican Point were unpredictable and transient, and the area was never sampled.

The rocky shores at Mile 4 and Bird Rock were divided into two biotic zones, upper and lower. The upper zone was dominated by the limpets *Scutellastra granularis* and *Cymbula granatina* and scattered mussels, while the lower zone had far fewer limpets and was covered by mussel beds in the lowest 2–3 m of shore. *Cymbula miniata* was common low on the shore, but also occurred in upper shore rock pools. Bird Rock was only sampled in May/June 2000, but Mile 4 was sampled in all seasons. Both the upper and lower shore were sampled using randomly positioned 500 x 500 mm quadrats. A wire mesh divided the quadrats into 100 50 x 50 mm squares, and these were used to calculate mussel cover. The total number of limpets of each species in the quadrat was counted. On average, 60 samples were taken in each zone. Subsamples of all species were collected, measured and frozen for calorific analysis. The average downshore width of each zone was calculated from 12 independent measurements. At Mile 4, washed up *Perna perna* were sampled along the high water mark when present. All fresh mussels found within 50 500 x 500 mm quadrats were counted and measured.

Results and discussion

Juvenile foraging behaviour

Birds foraging on the mudflat locate *Dosinia* by surface pecking and single probing. When feeding in shallow water at low tide, juveniles employ a faster stitching action, where the bill is not withdrawn fully after each probe. A similar technique has been observed in Eurasian Oystercatchers feeding on cockles *Cardium edule* (Hulscher 1976). Although the mudflat extends over a large area (Fig. 2.1), birds never fed more than 300 m from the pumphouse.

On the shoreline to the north of the pumphouse, the abundance of *Discinisca* at certain times, together with the fact that the membranous shell halves are easily opened by the juvenile oystercatchers, makes it a favoured food resource for oystercatchers. Ruddy Turnstones *Arenaria interpres* and Sanderlings *Calidris alba* also fed on *Discinisca* (pers. obs.). Other washed up molluscs eaten on a regular basis by the oystercatchers on this shore are the indigenous Black Mussel *Choromytilus meridionalis* and the invasive *Mytilus galloprovincialis. Venerupis corrugatus* is very rarely washed up alive but some individuals become exposed low on the shore at spring low tides. Black mussels attached to the rocks along the edge of the pumphouse jetty are also eaten by the oystercatchers at low tide.

During the study period juvenile oystercatchers were also observed eating Kelp Lice *Paridotea ungulata* along the edge of pans, as well as barnacles attached to the wooden poles used for oyster cultivation. Oystercatchers were never observed feeding on the oysters themselves, as these were unavailable by virtue of their depth. On occasion birds scavenged on dead Crown Crabs *Hymenosoma orbiculare* and jellyfish, both washed up on either side of the pumphouse. New additions to the dietary spectrum of the African Black Oystercatcher include *Dosinia lupinus, Discinisca tenius* and *Semimytilus algosus*.

At Pelican Point, wash-ups of *Semimytilus* can provide enough food for several days and on several occasions a group of 20–30 juveniles fed and roosted at the Point for the duration of the wash-up event. After each spring tide, large areas along the Pelican Point peninsula are flooded. Standing water remains for several days and juveniles were observed feeding on *Dosinia* that had been washed into these temporary pans.

The oystercatchers at Mile 4 targeted mostly limpets and mussels. The Brown Mussel *Perna perna*, as well as *Mytilus galloprovincialis* and to a lesser extent *Choromytilus meridionalis* are all present on the rocky shores. Amongst the limpets, *Cymbula miniata* dominates the diet, although *C. granatina* and *Scutellastra granularis* are both more abundant on the shore. The prey handling techniques observed were similar to those described for adult birds by Hockey (1981b), except in a few instances where juveniles hammered through the side of mussel shells and extracted the meat through the resulting hole. Such behaviour has not previously been recorded for the African Black Oystercatcher, (although they do occasionally hammer through the shells of *C. granatina* – P.A.R. Hockey pers. comm.), but is the common method of opening mussels used by the Eurasian Oystercatcher. This hammering technique was only employed when attacking sparsely distributed mussels fairly high up on the shore. A closer inspection of these mussels revealed unusually thin and brittle shells, indicating an infestation by the blue-green alga *Mastigocoleus* sp. which is known to weaken the shells of several mussel species (Webb & Korrûbel 1994). These weakened mussel shells would be comparatively easy for oystercatchers to open using a hammering technique. Other species eaten on rare occasions at Mile 4 were whelks *Nucella squamosa* and winkles *Oxystele variegata*, as well as polychaete worms such as the Mussel Worm *Pseudonereis variegata* living amongst the mussel beds.

Prey abundance

In late winter (Aug/Sep), *Dosinia* abundance on the pumphouse mudflat was at the lowest level recorded and the average shell size was large (28.8 mm). By Nov/Dec the next cohort of small clams (5–10 mm) was present on the mudflat, increasing the overall abundance and reducing the average size (Table 2.1). During the last two visits in Feb/Mar and May/Jun *Dosinia* abundance remained high, although there was little change in either average or maximum size.

Table 2.1. Seasonal variation in *Dosinia* and *Discinisca* average shell length and abundance at Walvis Bay. Size ranges are given in brackets.

	Dosinia shell length (mm)	*Dosinia* density ($N.m^{-2}$)	*Discinisca* shell length (mm)	*Discinisca* density ($N.m^{-2}$)
Aug/Sep 99	28.8 (13–40)	7.6	20.2 (12–34)	80
Nov/Dec 99	23.2 (5–40)	16.3	19.4 (9–29)	40–0
Feb/March 00	23.6 (10–42)	22.6	20.8 (18–25)	0.08–0.8
May/June 00	23.7 (11–42)	22.2	20.2 (11–24)	26

Comparisons of *Discinisca* density during the four visits to Walvis Bay must be made with caution. The density of lamp shells was dependent on the length of time for which birds had been exploiting the resource since the last wash-up event. On two of the visits (Nov/Dec & Feb/Mar) *Discinisca* was sampled both at the beginning and at the end of the visit, and results show great variation in prey abundance (Table 2.1). However, it does seem that *Discinisca* was more abundant in late winter than at other times of the year. In mid-November, *Discinisca* density stood at 40 shells. m^{-2} (within a 3 m wide band), but by the end of the month it had decreased to zero. During the Feb/Mar visit *Discinisca* density was so low that it had became an unprofitable food source. The higher density in winter suggests that larger swells or currents dislodge *Discinisca* more often at this time of the year.

Table 2.2. Seasonal variation in the average density of limpets (N. m^{-1} shore), mussel cover (%) and washed up mussels (N. m^{-2}) at Mile 4. (U.S. & L.S. – Upper & Lower shore, N/C – not collected)

	Wash up (N. m^{-2})	Limpet density (N. m^{-1} shore)						Mussel cover (%)	
	Perna only	*C. granatina*		*S. granularis*		*C. miniata*		*Mytilus & Perna* combined	
	High water mark	U.S.	L.S.	U.S.	L.S.	U.S.	L.S.	U.S.	L.S.
Aug/Sep 99	6	49	3	567	33	N/C		0.6	6
Nov/Dec 99	5	228	40	428	108	22	5	0.9	7
Feb/Mar 00	N/C	73	89	1389	203	3	132	2.2	49
May/Jun 00	N/C	200	88	1170	225	6	75	4	26

Scutellastra granularis was by far the most abundant intertidal limpet throughout the study period, especially on the upper shore. On the lower shore this species was found attached to mussels. *Cymbula miniata* was the rarest of the limpet species present. This species has a patchy distribution, occurring in high densities in rock pools on the upper shore but being completely absent from the exposed rocks. Sampling was undertaken on a random basis, but the proportion of pools along the upper shore is small and it is possible that this micro-habitat was under-sampled.

Washed up *Perna perna* were sampled on two of the visits and the overall density was low (5–6 shells. m^{-2}). These brown mussels were, however, of a large average size (74 mm) and the shells are partially open when washed up, making this a potentially profitable food source for the birds.

Juvenile distribution and numbers in response to prey abundance and availability

The abundance and diversity of washed up food available to juvenile African Black Oystercatchers at Walvis Bay enabled them to forage largely independently of tidal fluctuations. Although the pumphouse mudflat was only accessible at low tide, several other feeding areas were available at high tide. Even at Mile 4, washed up mussels were regularly available at the high water mark. Being independent of the tides is an advantage to inexperienced foragers that require more time to meet their daily energetic demands.

Juvenile movements between foraging habitats evidenced a highly opportunistic foraging strategy. The reasons for shifts between habitats may be subtle, but are assumed to be responses to energetic profitability (Chapter 3). Several such habitat shifts were observed during the study, and on each of the four visits to Walvis Bay, the proportions of oystercatchers foraging in the primary feeding habitats were examined over ten (not necessarily consecutive) days. Daily proportions were based on the average number of oystercatchers observed throughout a particular day, and not on the overall number of birds spread around the entire Walvis Bay area in a particular season (Chapter 1, Table 1.1). There was much movement of oystercatchers between feeding areas and because of their inaccessibility not all areas could be observed at the same time. This led to far fewer oystercatchers being observed on some days than the numbers known to be at Walvis Bay.

At the beginning of August, most foraging activity was concentrated on the primary feeding areas on either side of the pumphouse. Sixty to eighty percent of the birds (based on daily bird numbers) fed north of the pumphouse and 10–20% fed on the mudflat (Fig. 2.2a). This was a response to high *Discinisca* and low *Dosinia* abundance at this time of year (Table 2.1). Towards the end of August one of the evaporation pans behind the roost was drained of most of its water, exposing a large 'artificial' mudflat. Immediately this happened, up to 80% of the oystercatchers moved to this new habitat (Fig. 2.2a) where they fed on large *Dosinia* and on polychaete worms. At this time, no birds foraged on the pumphouse mudflat (Fig. 2.2a), indicating that the food resources available in the pan were far more profitable than those on the mudflat (Chapter 3). Feeding in the pan continued for several days until it was refilled once more, at which time the dispersion of birds reverted to what it was prior to pan drainage (Fig. 2.2a).

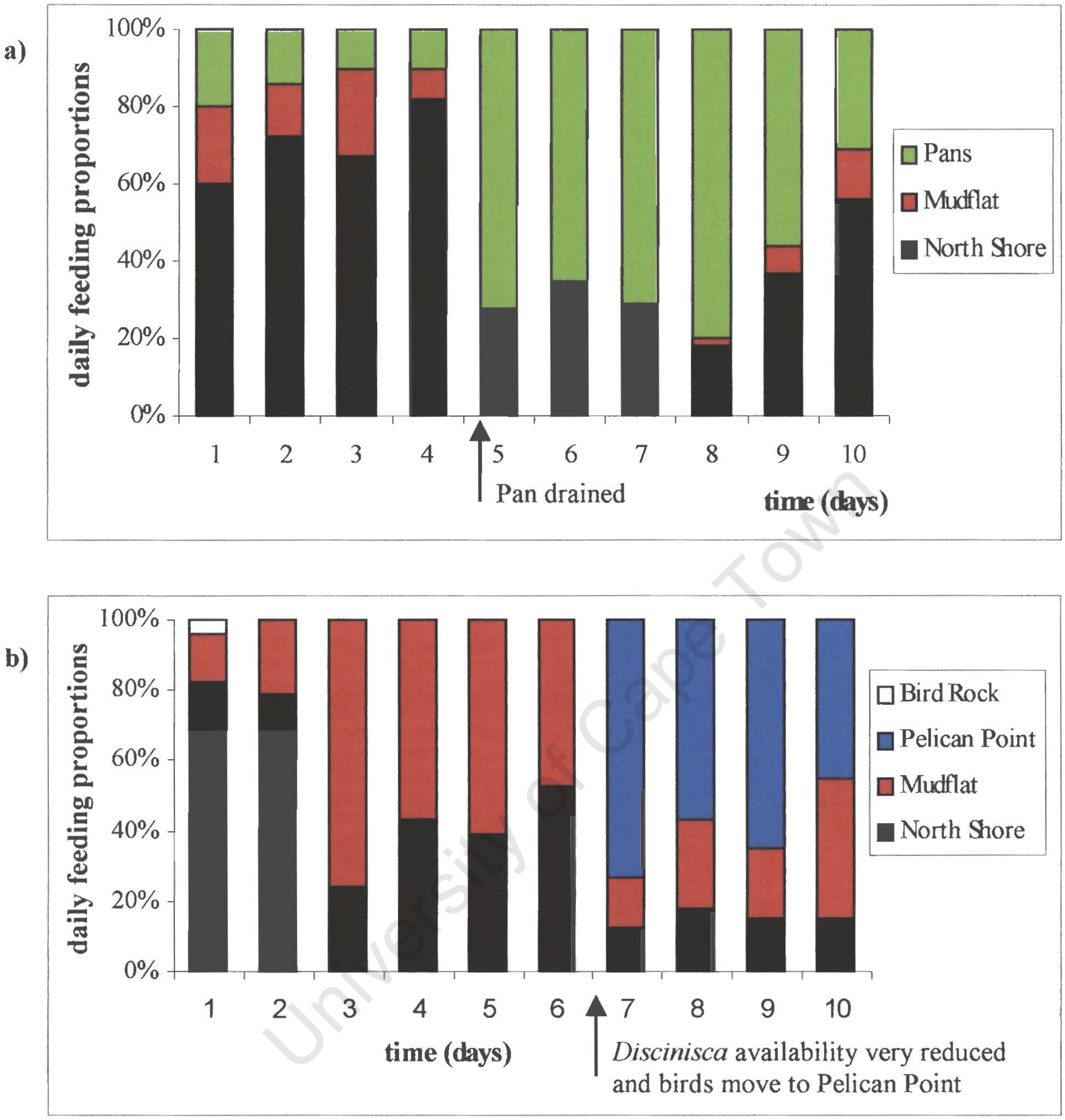


Figure 2.2. The daily proportions of oystercatchers foraging in different habitats at Walvis Bay during a) Aug/Sep and b) Nov/Dec 1999.

By Nov/Dec *Dosinia* abundance had doubled on the mudflat (Table 2.1), and the proportion of juveniles utilising this food source was greater than on the previous visit (Figs. 2.2a, b). By the end of November *Discinisca* had disappeared, and, at the same time, a group of around 30 oystercatchers was first observed roosting and foraging at Pelican Point. Food resources at

Pelican Point are ephemeral, indicating that a series of *Semimytilus* wash-ups must have occurred concurrently with the severely decreased availability of *Discinisca* on the shore north of the pumphouse.

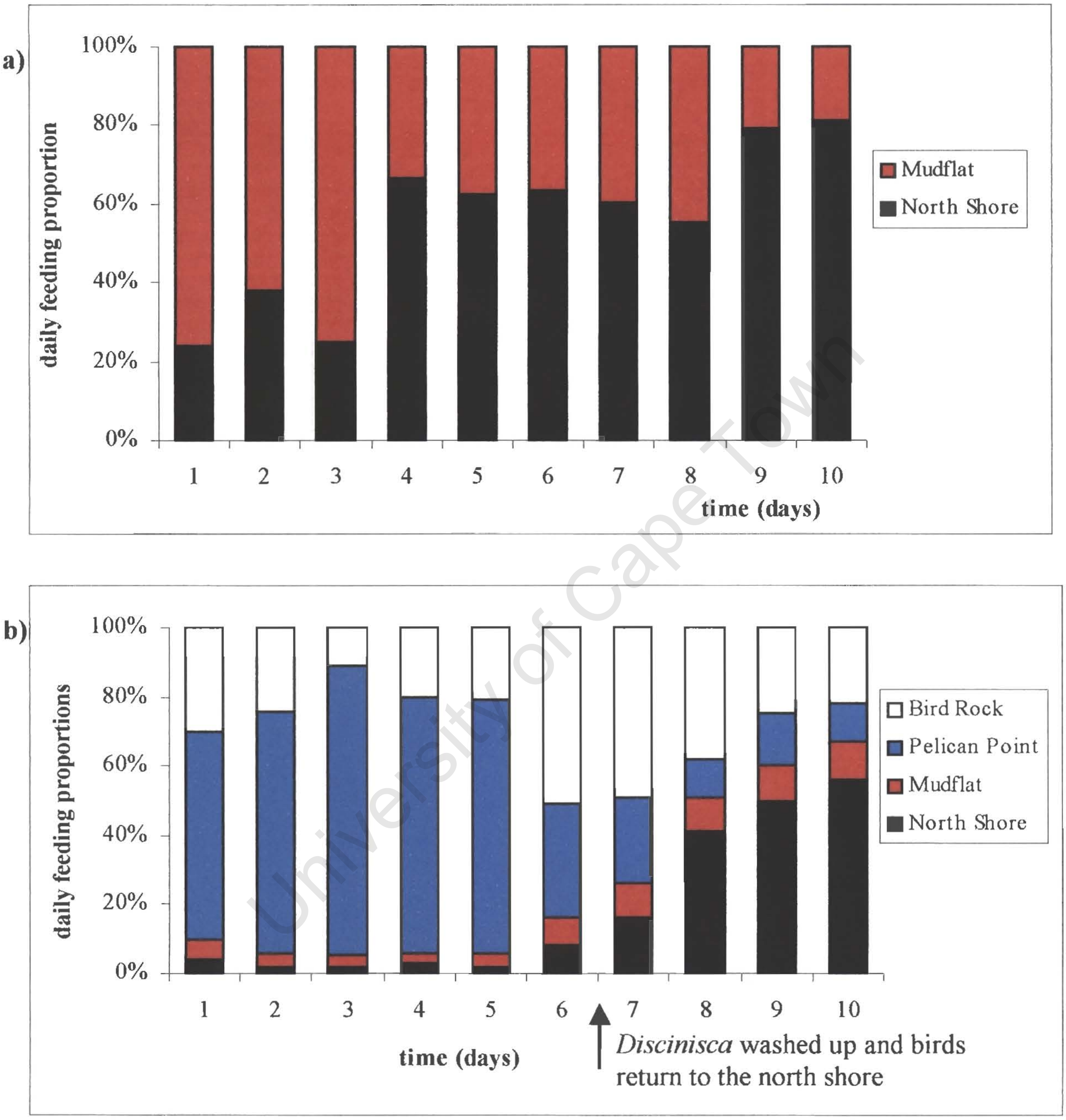


Figure 2.3. The proportions of oystercatchers foraging in different habitats at Walvis Bay during a) Feb/Mar and b) May/June 2000.

During Feb/March, *Dosinia* abundance was at its highest level, and early February was the only time during the study when a greater proportion of oystercatchers foraged on the pumphouse mudflat than on the north shore (Fig. 2.3a). *Discinisca* abundance was low throughout this period, increasing marginally at the beginning of March (Table 2.1). This coincided with increased use of the north shore by oystercatchers. It is likely that some oystercatchers were present at Pelican Point during the Feb/March visit (as they had been in Nov/Dec and May/June – Fig. 2.2b, 2.3b), but the Point is completely inaccessible without an off-road vehicle, which was not available at the time.

During the last visit in May/June, the distribution of juvenile oystercatchers at Walvis Bay was very different to previous visits. Large wash-ups of *Semimytilus* in May resulted in up to 80% of all birds feeding and roosting at Pelican Point (Fig. 2.3b). The rocky shore at Bird Rock was also an important feeding area for a short period. Very few oystercatchers were observed here on previous visits, but in May/June 10–50% of the birds foraged here on a daily basis. Numbers at the pumphouse roost were very low and hardly any feeding was observed on either the pumphouse mudflat or the *Discinisca* shore to the north. Only at the beginning of June did a major *Discinisca* wash-up event result in birds returning to this area (Fig. 2.3b). Although the density of *Dosinia* on the pumphouse mudflat was one of the highest recorded during the study, little feeding was observed here when *Discinisca* was abundant on the north shore.

The diversity of foraging habitats at the Swakopmund nursery is very limited and movements in response to prey availability were few. Oystercatchers were observed moving between Mile 4 and Bird Rock, but the amount of interchange between the two areas remains unclear because only a few of the ringed juveniles were individually identifiable. There was, however, seasonal variation in oystercatcher numbers at Swakopmund, with abundance peaking in winter (Chapter 1, Fig. 1.5). This pattern could be a result of i) seasonal variation in food abundance at Swakopmund and/or Walvis Bay, or ii) seasonal arrival and departure of birds to and from the nurseries.

At Swakopmund, washed up mussels were slightly more abundant in winter, but overall mussel and limpet densities on the shore cannot explain the large seasonal variation in oystercatcher numbers. Winter food abundance at Walvis Bay is also not a likely explanation as it is high at this time of year. Although *Dosinia* density was low in Aug/Sep, *Discinisca* formed an abundant and tidally independent food source for the birds. The most likely explanation for fluctuating oystercatchers numbers at Swakopmund is the seasonal arrival and departure of birds. Juveniles arrive at the nurseries from May onwards and numbers peak in winter. At the beginning of summer many immatures leave the nurseries to return to their natal sites for the start of the breeding season (Chapter 1). During the summer months oystercatcher numbers at Swakopmund were at their lowest level: this can be explained by emigration of birds either south to the breeding grounds or to Walvis Bay.

Conclusions

1. The Walvis Bay/Swakopmund nursery holds several advantages for inexperienced juvenile African Black Oystercatchers. They do not experience any competition with adults (Chapter 1), and many of their food resources are washed ashore and are therefore available at all stages of the tidal cycle. In addition, many washed up *Semimytilus* and *Discinisca* are partially open and therefore easy for juveniles to handle.

2. Foraging dispersion was opportunistic in response to seasonal variations in prey availability and abundance. Primary foraging habitats were identified in the Walvis Bay area, but as more profitable, albeit temporary, food resources became available elsewhere, primary habitats were temporarily abandoned.

3. At Swakopmund, juvenile movements were few because of low habitat diversity. Seasonal variation in oystercatcher numbers at this site could not be explained by fluctuations in food abundance at either Swakopmund or Walvis Bay but rather reflected seasonal arrival and departure of birds to and from the nurseries.

Chapter 3

CHAPTER 3

Activity rhythms and foraging performance of juvenile African Black Oystercatchers at the Walvis Bay/Swakopmund nursery.

Introduction

Activity rhythms and foraging performance of adult African Black Oystercatchers have been quantified in different seasons and habitats (Ryan 1983, Hockey 1984a, Ward 1990, Wilhelm 1999, Leseberg *et al.* 2000). However, nothing is known about the foraging performance of juvenile African Black Oystercatchers, although it has been shown that juveniles of other oystercatcher species are less proficient foragers than adults (Cadman 1980, Goss-Custard & Durell 1987a).

A large proportion of the diet of juvenile oystercatchers at Walvis Bay consists of prey species that are a) available at all stages of the tidal cycle and b) easy to capture and handle (Chapter 2). This, together with the fact that the birds moved opportunistically in response to seasonal variations in prey availability and abundance, suggests that juvenile foraging proficiency may be low. Other ways in which juveniles might compensate for low foraging proficiency is to steal food from conspecifics or to forage for longer to meet energy demands (Wunderle 1991).

The primary aim of this chapter is to assess the ease with which young oystercatchers at Walvis Bay and Swakopmund satisfy their daily energy demand at different times of year. Specifically, the chapter aims to:

a) Describe and explain the activity rhythms and foraging strategies of juvenile oystercatchers at the Walvis Bay/Swakopmund nursery and discuss any seasonal variation in foraging performance in relation to prey availability and/or abundance.
b) Compare intake rates and foraging effort of juvenile oystercatchers between different habitats at the nursery.
c) Test the hypothesis that juvenile oystercatchers are less proficient foragers than adults and must forage for longer to meet their daily energetic requirements.
d) Investigate the effects, if any, that intra- and/or interspecific kleptoparasitism have on the overall foraging performance of juvenile oystercatchers.

Materials and Methods

Activity rhythms

Both the Walvis Bay and Swakopmund roosts were visited on a daily basis. Except for days set aside for intertidal prey sampling and when adverse weather (regular fog and strong wind) prevented observations, oystercatchers were observed throughout daylight hours. At Walvis Bay numbers of oystercatchers moving in and out of the roost were recorded continuously, while numbers present in all areas (mudflat, *Discinisca* shore and roost) were counted at 30 minute intervals during the course of the day. Accurate foraging times were only obtained for birds at Swakopmund because there were fewer birds and activity patterns were easier to monitor. Foraging time was quantified using the instantaneous scan technique (Altmann 1974), where intertidal feeding habitats were scanned at five-minute intervals and bird numbers and activities were recorded. The average time spent foraging (Ft, in minutes) by an individual bird was calculated using the equation (Turpie & Hockey 1993): $Ft = \sum t_{i..j} [\ I\ (\ Ft_i\ /\ F_{max}\ )\ ]$, where t = time, I = count interval in minutes, and F = the number of feeding birds.

Nocturnal observations were attempted on several occasions at Swakopmund using a custom-built passive image intensifier with an infra-red image enhancer. Although the equipment was not powerful enough to allow for nocturnal foraging performance to be quantified, oystercatchers were observed leaving the roost at night on the falling tide, flying down to the shore and returning hours later. Thus nocturnal foraging was assumed to occur at Swakopmund. At Walvis Bay, however, the extent of nocturnal foraging was difficult to determine. On several occasions birds were heard flying around the area at night and a few were seen on the mudflat before dawn. However, because of the size of the study area, quantitative observations proved impossible.

Throughout these daily observations, whether on the foraging habitats or in the roost, intra- and interspecific interactions were noted. Although foraging behaviour and interactions were recorded for birds of known age (colour-ringed birds), individuals could not be sexed accurately from observations in this study and a possible sex skew in the nursery population could not be investigated. Pairs of adult African Black Oystercatchers can be sexed according to culmen length and morphology, with females having longer and more pointed bills than males (Hockey 1981a). However, it is difficult to apply this technique with confidence to flocks of juveniles.

Of six oystercatchers caught in mist-nets at Swakopmund (M. Boorman & T. Tree *in litt*) four were undoubtedly females and two were males (according to culmen lengths – Hockey 1981a).

Focal Animal Observations (FAOs)

Foraging oystercatchers were observed using a Kowa TSN-821 telescope fitted with a 32x wide-angle lens. Each FAO lasted 10 minutes and, while oystercatchers were foraging on the pumphouse mudflat, step rates and the number and sizes of *Dosinia lupinus* clams eaten were recorded. Step rates (a measure of foraging effort) were measured with a handheld counter, and *Dosinia* sizes were estimated as a percentage of exposed culmen length. FAOs on the north shore also recorded step rates and number of *Discinisca tenuis* eaten. Due to their small size, it was impossible to size individual *Discinisca* according to culmen length, and the average seasonal shell size from intertidal sampling (Chapter 2) was used for the energetic analysis. Towards the end of August, oystercatchers fed opportunistically for several days in a temporarily drained evaporation pan (Chapter 2) where an abundant *Dosinia* resource had become available. Both on the mudflat, the *Discinisca* shore and in the pan, polychaete and ribbon worms (Nemertea) were occasionally eaten by the oystercatchers, but they were extremely small (too small to size accurately) and were very seldom encountered during intertidal sampling. These worms were assumed to contribute very little to the energetic intake rates and were ignored in calculations of energy budgets. On rocky shores at both Bird Rock and Swakopmund, the number and sizes of limpets and mussels eaten were recorded, as were step rates. During FAOs all aggressive interactions and their outcomes were noted, and the frequency of inter- and/or intra-specific kleptoparasitism was recorded in all foraging habitats.

When the shell of a prey item could not be seen clearly, the lump of meat extracted was used to classify the item as either small, medium or large based on previous observations. In instances where the prey item was obscured entirely but the bird had clearly swallowed a limpet or mussel, the average observed prey size was used. At both the Walvis Bay *Dosinia* mudflat and at Swakopmund the majority of observations could be made from a vehicle at a distance of 50–75 m, with minimal disturbance to the birds. Observer distance was greatest when observing birds foraging on *Discinisca* (100–150 m). Foraging observations interrupted for longer than 30 seconds by repeated pauses in foraging, or where birds were obscured from view, were terminated.

Observer accuracy in estimating prey size from exposed culmen length was tested using a model oystercatcher with a culmen length of 67 mm (average length for both sexes combined, Hockey 1981). Thirty mussels, limpets and *Dosinia* spanning the size ranges taken by oystercatchers were presented on the tip of the bill in random sequence, and, using the same equipment and distances as in the field, their lengths were estimated. For each prey type the estimated shell lengths were regressed against the actual lengths and the resulting equations were used to calibrate field observations (Fig. 3.1).

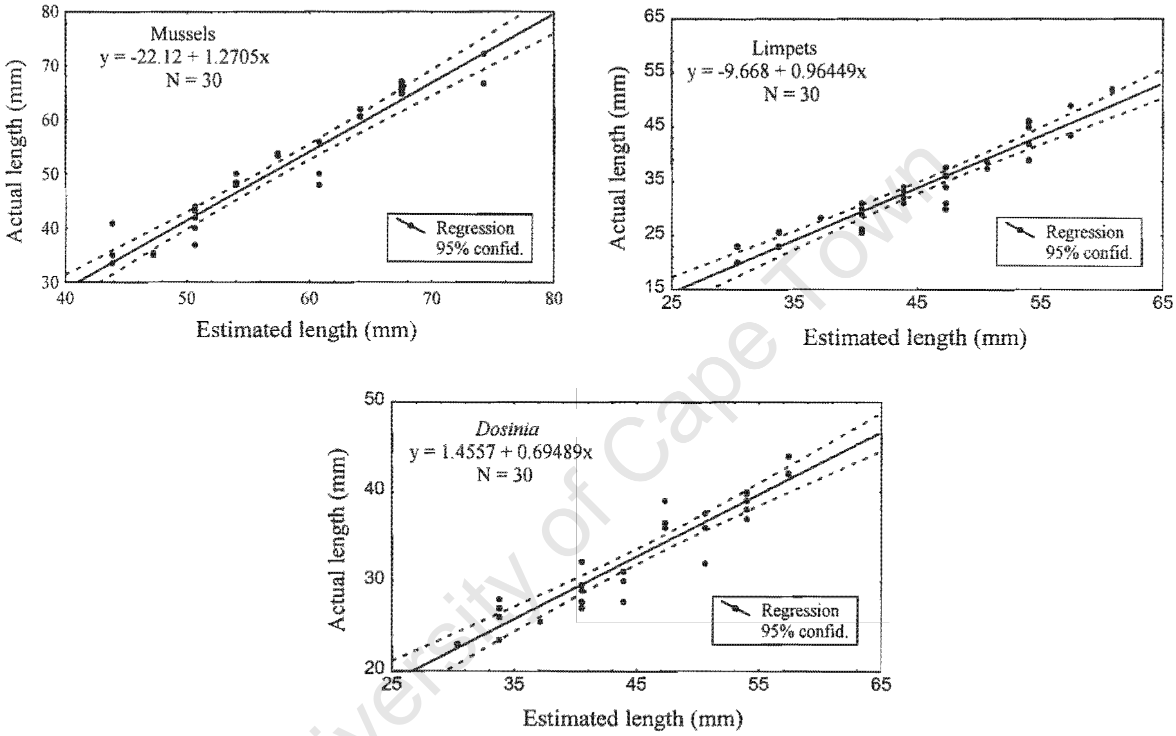


Figure 3.1. Regressions between actual and estimated shell lengths of mussels, limpets and clams (*Dosinia*).

Prey collection for calorific analysis

During each of the four visits to the study sites, 60 individuals of each prey species, spanning the entire size range available, were collected and frozen. In the lab, the flesh of each item was dried at 60° C for 3–4 days and the shell length was measured. Dried samples were weighed, ground to a fine powder and their energetic contents ($kJ.g^{-1}$) were determined using a CP 500 bomb calorimeter. Seasonal length–dry weight regressions were calculated for *Dosinia* and *Discinisca*. Since it was frequently impossible to identify the species of limpet or mussel eaten by oystercatchers during FAOs, data for all limpets, and those for all mussels were pooled into two regression equations for the calculation of energy intake rates.

In Nov/Dec and Feb/Mar, opened *Dosinia* shells were collected from the surface of the mudflat to relate oystercatcher prey size choice to seasonal prey density and size. The procedures for sampling *Dosinia* abundance are detailed in Chapter 2. Because no other bird species ate *Dosinia*, except for instances of kleptoparasitism of oystercatchers by gulls, all empty shells collected were assumed to have been of prey eaten by oystercatchers. No invertebrate predators were encountered during the sampling that could account for some of the emptied shells. On rocky shores, empty shells were quickly washed away by the incoming tide and insufficient numbers could be collected to make a similar comparison. In these instances, comparisons of the sizes of available and consumed prey rests on prey size estimates made during FAOs and their subsequent calibration.

Field metabolic rate and energetic intake rates of juvenile oystercatchers

No empirical information exists on the Field Metabolic Rate (FMR) of African Black Oystercatchers. Nagy *et al.* (1999), using doubly labeled water, calculated an allometric equation for the FMR of Charadriiformes, where FMR ($kJ.d^{-1}$) = 8.13 (mass, in g)$^{0.77}$. With an average mass of 666 g for juvenile oystercatchers at Walvis Bay/Swakopmund (based on the masses of six individuals caught at the nursery), FMR = 1214 $kJ.d^{-1}$. The mean assimilation efficiency ((energy in – energy out)/energy in) of a hand-reared juvenile African Black Oystercatcher fed on mussels and limpets has been calculated as 72.7% (Hockey 1984b). Therefore Nagy *et al.* 's equation predicts that a juvenile oystercatcher of 666 g must consume 1670 $kJ.d^{-1}$ in order to meet its energy demands. Kersten (1996) determined the FMR of breeding Eurasian Oystercatchers *H. ostralegus*, with an average mass of 530 g, to be 682 $kJ.d^{-1}$. There are some problems with the applicability of all these predictions to African Black Oystercatchers which are discussed later.

Seasonal energy intake rates ($kJ.min^{-1}$) were determined for juvenile oystercatchers foraging in all habitats from the number and sizes of prey items eaten during FAOs (sizes corrected for observer bias), together with the energetic content ($kJ.g$ dry $mass^{-1}$) of the prey ingested. Intake rates were compared between 1-year old and older birds on the north shore and the mudflat at Walvis Bay. One-year olds were either identified according to colour-ring combinations, or by their dusky bills, narrow eye rings and greyish-pink legs (Hockey 1986) in the case of unringed individuals. Any pseudo-replication of intake rates amongst colour-ringed birds was eliminated by determining an average intake rate for these individuals. However, because unringed birds were not individually identifiable, possible pseudo-replication could not be eliminated for this group. All statistical tests in this study were performed using STATISTICA 5.5 (2000) and Zar (1996).

Results

Activity rhythms and foraging times

At Walvis Bay activity patterns were independent of tidal rhythms and, during daylight hours, foraging activity peaked in the early morning and late afternoon and evening. In Nov/Dec and Feb/Mar, no foraging activity was consistently observed between 10:00 and 14–15:00 hours (Fig. 3.2b,c) and all the oystercatchers were in the roost. Individual birds did on occasion fly to the foraging areas during this time, but they never remained there for long and usually returned to the roost after only a few minutes. In Aug/Sep, a similar pattern was observed with foraging activity peaking before 10:00 in the morning and after 15:00 in the afternoon, but on most days small numbers of birds foraged throughout the midday period (Fig. 3.2a). While the availability of washed up food (*Discinisca*) at Walvis Bay was independent of tidal status, the pumphouse mudflat could only be utilised by the birds at low tide. However, when low tide coincided with the midday 'roosting period' the birds did not change their activity pattern, and the mudflat was ignored (Fig. 3.2d). When low tide was in the early morning and evening the mudflat was utilised extensively by the birds. Such a foraging pattern is unusual for the African Black Oystercatcher, elsewhere a strictly tidal forager, but was observed on a daily basis and on three of the four visits to Walvis Bay. In May/Jun, no comparable activity pattern was observed as the majority of the Walvis Bay oystercatchers switched their focus to Bird Rock, where foraging became tidally constrained and high tide periods were spent roosting on the adjacent beach (Chapter 2, Fig. 2.1).

The proportion of foraging oystercatchers at Walvis Bay fell after sunset (Fig. 3.2a-c), with birds returning to the roost. However, without powerful night-vision equipment is was difficult to ascertain how many birds remained on the feeding grounds after dark and for how long. The oystercatchers generally took less than 30 seconds to cover the distance between the roost and

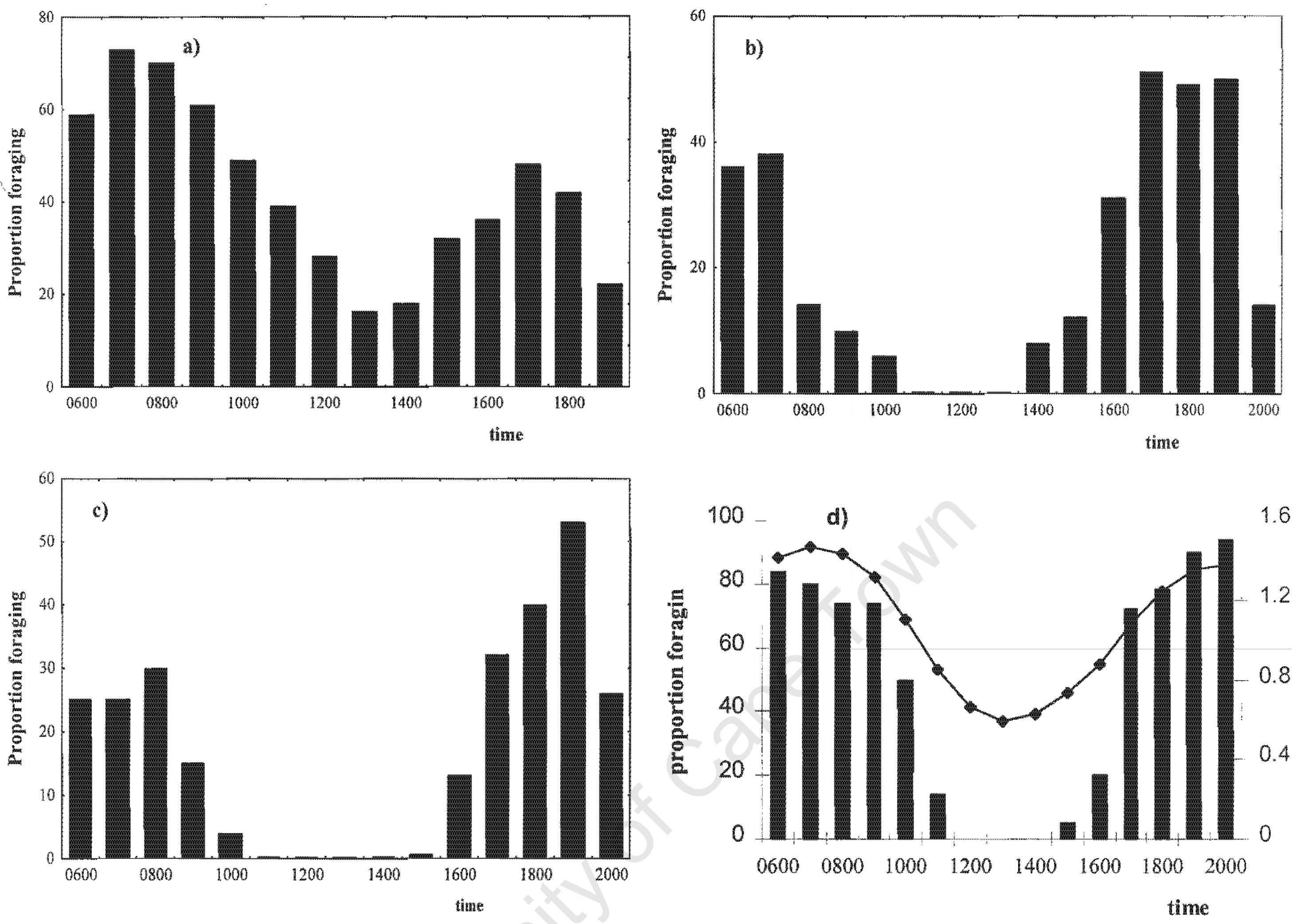


Figure 3.2. The daytime activity rhythms of oystercatchers at Walvis Bay in a) Aug/Sep, b) Nov/Dec, and c) Feb/Mar and d) oystercatcher foraging activity (bars) independent of tidal height (line).

the mudflat/north shore and were less vocal when flying at dusk; birds returning to the roost were therefore easily overlooked. On a few separate occasions, when conditions allowed, the mudflat was scanned at night using an image intensifier (see methods), but no birds were seen to be foraging.

At Walvis Bay, departure times from the roost to the feeding grounds in the afternoon varied by 1–2 hours between seasons. In Aug/Sep, although there were small numbers foraging throughout daylight hours, large-scale movement out of the roost occurred, on average, between 13:00 and 14:00 hours. In Nov/Dec and Feb/Mar, the oystercatchers left the roost between

14:00 and 15:00, and 15:00 and 16:30 respectively. There was no apparent difference in the morning arrival times at the roost between the seasons, and 10:00 was the average observed arrival time throughout the study. Sunset varied by about one hour between the summer and winter visits (19:15–19:40 in Nov/Dec and Feb/Mar and 18:40–18:55 in Aug/Sep), and foraging birds could be observed for longer in Nov/Dec and Feb/Mar.

At Swakopmund, the oystercatchers' activity rhythms were tidally controlled – birds foraged at low tide and roosted at high tide (Fig. 3.3). Whenever possible bird movements were recorded from sunrise to sunset, and the proportion of time spent in and out of the roost for all four visits combined was found to be almost equal over the daytime period (49% and 51% respectively). Oystercatchers, on average, entered the roost 191 ± 76 minutes before high tide and left it 190 ± 45 minutes before low tide. While on the shore, birds actively foraged for 57% of the time. On average, oystercatchers at Swakopmund fed for 234 ± 65 minutes during daylight hours.

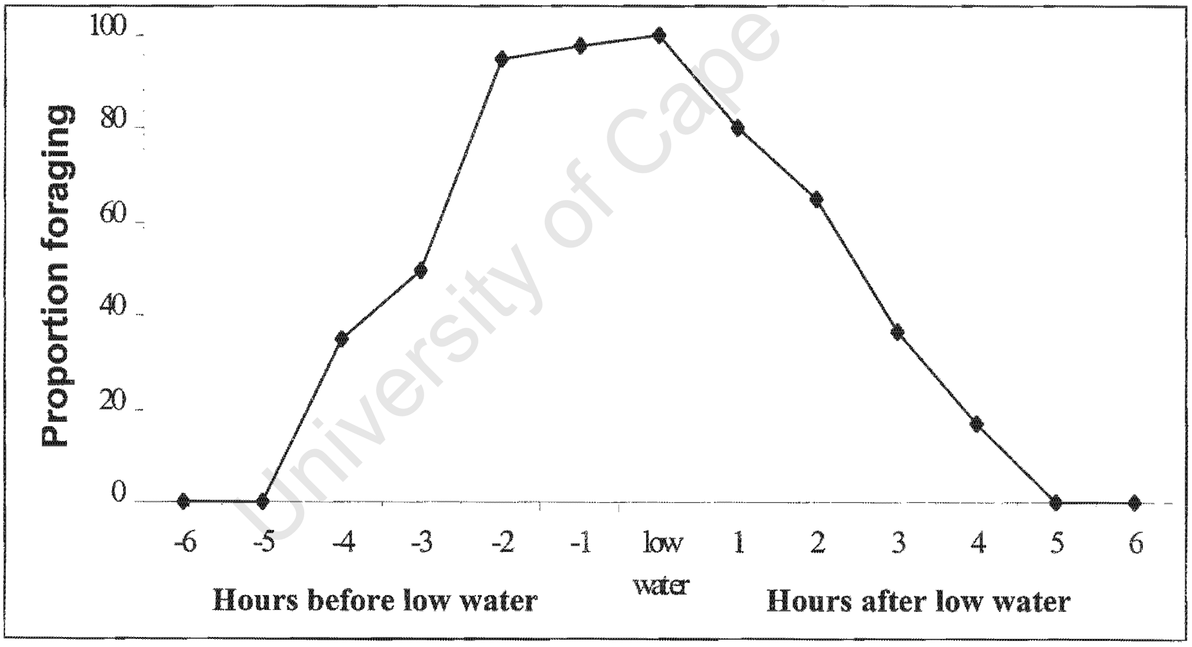


Figure 3.3. The foraging activity of African Black Oystercatchers at Swakopmund related to time before or after low water.

Few nocturnal activity studies of the African Black Oystercatcher have been made thus far. Ryan (1983) calculated nocturnal foraging time of breeding adult oystercatchers on an island off the west coast of South Africa as 94% of the daytime value, and Hockey (1984), at the same site, calculated a ratio of 59% during the nonbreeding season. Sitters (2000) found diurnal and nocturnal foraging times in mussel-feeding Eurasian Oystercatchers to be similar. None of these studies included juveniles however, and, for the purpose of estimating daily energy intake (DEI), it was assumed that nocturnal and diurnal foraging times and rates were equal. Based on this assumption, a foraging time of 446 ± 90 minutes.24hrs^{-1} was estimated for juvenile oystercatchers at Swakopmund.

Energy intake rates

The energy content of the flesh of different prey species varied little – both across seasons and among species (Table 3.1). For the calculations of intake rates, however, the seasonal values were used (Appendix 1). A summary of the seasonal length–dry weight regression equations for all prey species is given in Appendix 2.

Table 3.1. The average energy content (± S.D.) of prey species sampled at Walvis Bay and Swakopmund during the study.

Prey species	Energy content (kJ.g dry mass^{-1})
Discinisca tenuis	17.9 ± 0.17
Dosinia lupinus	17.8 ± 0.59
Mytilus galloprovincialis	16.9 ± 1.95
Perna perna (from rocks)	16.5 ± 1.78
Perna perna (washed up)	15.4 ± 0.22
Mussel species combined	16.7 ± 1.79
Cymbula granatina	17.0 ± 0.51
Cymbula miniata	15.0 ± 1.03
Scutellastra granularis	16.1 ± 0.63
Limpet species combined	16.2 ±1.03

Oystercatcher intake rates fluctuated seasonally in response to prey abundance (range 1.0–2.6 kJ.min^{-1}, Table 3.2). The intake rate of 4.4 kJ.min^{-1} recorded at Swakopmund in Aug/Sep was

70% higher than the next highest intake rate recorded (2.6 kJ.min^{-1}) and was almost certainly an overestimate because many of the prey eaten by the birds could not be sized accurately. *Discinisca* and *Dosinia* yield almost the same energetic reward per gram of dry flesh ingested (Table 3.1). However, while *Dosinia* abundance remained constant in the mudflat throughout the study (excepting Aug/Sep, Chapter 2), *Discinisca* was an unpredictable resource and wash-

Table 3.2. Seasonal energy intake rates (kJ.min^{-1} ± S.D.), foraging effort (steps.min^{-1} ± S.D.) and effort-reward ratios (steps.kJ^{-1} ± S.D.) of African Black Oystercatchers (juveniles and immatures combined) feeding in different habitats at Walvis Bay and Swakopmund. Sample sizes are given in brackets. N/B = no birds present in habitat.

		Walvis Bay feeding habitats			Swakopmund
		Mudflat (*Dosinia*)	North Shore (*Discinisca*)	Bird Rock (mussels/limpets)	(mussels/limpets)
Aug/Sep	kJ.min^{-1}	**(17)** 1.9 ± 1.6*	**(41)** 2.4 ± 0.9	N/B	**(30)** 4.4 ± 3.8
	Steps.min^{-1}	59.1 ± 12.4*	36.0 ± 9.9		43.8 ± 17.3
	Steps.kJ^{-1}	38.6 ± 25.3*	18.1 ± 11.8		27.4 ± 47.7
Nov/Dec	kJ.min^{-1}	**(50)** 2.0 ± 1.5	**(25)** 1.5 ± 1.0	N/B	**(42)** 1.5 ± 1.3
	Steps.min^{-1}	67.9 ± 16.9	39.3 ± 15.0		43.5 ± 14.3
	Steps.kJ^{-1}	84.3 ± 142.2	41.6 ± 48.9		58.0 ± 92.6
Feb/Mar	kJ.min^{-1}	**(39)** 2.4 ± 1.9	**(35)** 1.0 ± 1.5	N/B	**(37)** 1.9 ± 0.7
	Steps.min^{-1}	69.9 ± 15.6	57.1 ± 19.5		32.6 ± 12.8
	Steps.kJ^{-1}	50.1 ± 48.3	95.8 ± 114.5		20.2 ± 12.0
May/Jun	kJ.min^{-1}	**(6)** 1.1 ± 1.13	**(22)** 2.5 ± 1.5	**(26)** 2.6 ± 1.3	**(30)** 2.3 ± 1.7
	Steps.min^{-1}	62.2 ± 16.6	57.0 ± 18.3	36.9 ± 9.6	42.8 ± 15.0
	Steps.kJ^{-1}	85.3 ± 64.0	34.5 ± 40.1	18.1 ± 10.9	23.6 ± 19.8

* intake rates and foraging effort while foraging opportunistically on *Dosinia* in the drained evaporation pan.

up events varied in their duration and intensity. Intake rates of birds foraging on *Discinisca* were lowest in Feb/Mar, when very few *Discinisca* were available to oystercatchers (Chapter 2, Table 2.1), and they were significantly lower than intake rates in the other foraging habitats in this season (Kruskal-Wallis test $H_2 = 20.76$, $p < 0.001$). Specifically, there were significant differences in intake rate between the north shore and both the mudflat and Swakopmund (Mann-Whitney tests, both $p < 0.001$), but there was no significant difference between intake rates on the mudflat and at Swakopmund in Feb/Mar ($p = 0.503$). In Aug/Sep intake rates were significantly different between foraging habitats (Kruskal-Wallis test $H_2 = 11.61$, $p = 0.003$). Specifically, intake rates were significantly higher at Swakopmund than on either the north shore or in the pan (Mann-Whitney tests, both $p < 0.01$), probably due to intake rates at Swakopmund being overestimated (see above). However, during both Nov/Dec and May/Jun,

Table 3.3. Daytime foraging duration and intake rates (* ± S.E. or ** ± S.D., as reported) of African Black Oystercatchers in different habitats and seasons.

Study	Breeding/non-breeding adults	Habitat type	Average daytime foraging minutes	Average intake rate (kJ.min^{-1})
Hockey (1984b)	nonbreeding	rocky shore	210 (± 28.8) – 225 (± 11.0)**	Not recorded
Wilhelm (1999)	nonbreeding	rocky shore	128 (± 24.9) – 176 (± 30.3)*	2.4 (± 0.5) – 3.2 (± 0.6)*
	nonbreeding	sandy beach	197 (± 27.0) – 353 (± 61.6)*	2.5 (± 0.7) – 6.6 (± 2.0)*
Leseberg *et al.* (2000)	nonbreeding	rocky shore	129 (± 34.0) – 273 (± 67.0)**	Not recorded
Turpie Unpubl. data	breeding	rocky shore	214 ± 60.0**	Not recorded
This study	Juveniles	rocky shore	234 ± 65.0**	1.5 (± 1.3) – 4.4 (± 3.8)**
	Juveniles	Mudflat	not recorded	1.1 (± 1.1) – 2.4 (± 1.9)**
	Juveniles	sandy beach/ wash-up	not recorded	1.0 (± 1.5) – 2.5 (± 1.5)**

there was no significant difference in intake rates across habitats (Kruskal-Wallis tests, $p = 0.207$ & $p = 0.099$, n.s).

Foraging effort differed significantly across habitats in all seasons (Kruskal-Wallis tests, all $p < 0.001$). Oystercatchers foraging on the *Dosinia* mudflat consistently showed the highest level of foraging effort (Table 3.2). On the north shore, foraging effort was highest in Feb/Mar and May/June (Table 3.2), when oystercatchers were frequently chased by kleptoparasitic Cape Gulls *Larus vetula*. The effort-reward ratios (steps.kJ^{-1}) are a reflection of the effects that seasonal prey abundance and foraging effort have on intake rate. In Feb/Mar oystercatchers travelled further due to a combination of low *Discinisca* abundance and aggressive encounters with gulls. The low energetic yield, together with a high step rate resulted in the highest effort-reward ratio calculated for the study period (95.8 steps.kJ^{-1}, Table 3.2).

The daytime foraging times of juvenile oystercatchers at Swakopmund were similar to those of adult birds in the breeding range to the south (Table 3.3), and no significant difference between juvenile and adult foraging times was found (Mann-Whitney test $U_{4,7} = 8.00$, $p = 0.257$). Wilhlem (1999) recorded intake rates at spring and neap tide of 2.4–3.2 kJ.min^{-1} on rocky shores and 2.5–6.6 kJ.min^{-1} on sandy shores in False Bay, South Africa. However, given the relative foraging times of Wilhelm's birds (Table 3.3), it seems likely that her calculation of an average intake rate of 4.6 kJ.min^{-1} for birds on sandy shores is an overestimate.

No significant difference was found between the intake rates of 1-year old and older oystercatchers foraging on *Discinisca* on the north shore in Aug/Sep (Mann-Whitney test $U_{7,31} = 82$, $p = 0.318$) or in Nov/Dec ($U_{6,16} = 45.5$, $p = 0.854$), nor was there any significant difference ($U_{6,39} = 60$, $p = 0.174$) in performance of the two age classes on the mudflat in Nov/Dec (Fig. 3.4a-c). Older birds did, however, achieve higher average intake rates on the north shore in Aug/Sep and on the mudflat in Nov/Dec (Fig. 3.4a, c), and a greater sample size (i.e. a greater number of ringed birds) may have a yielded a significant difference between age classes.

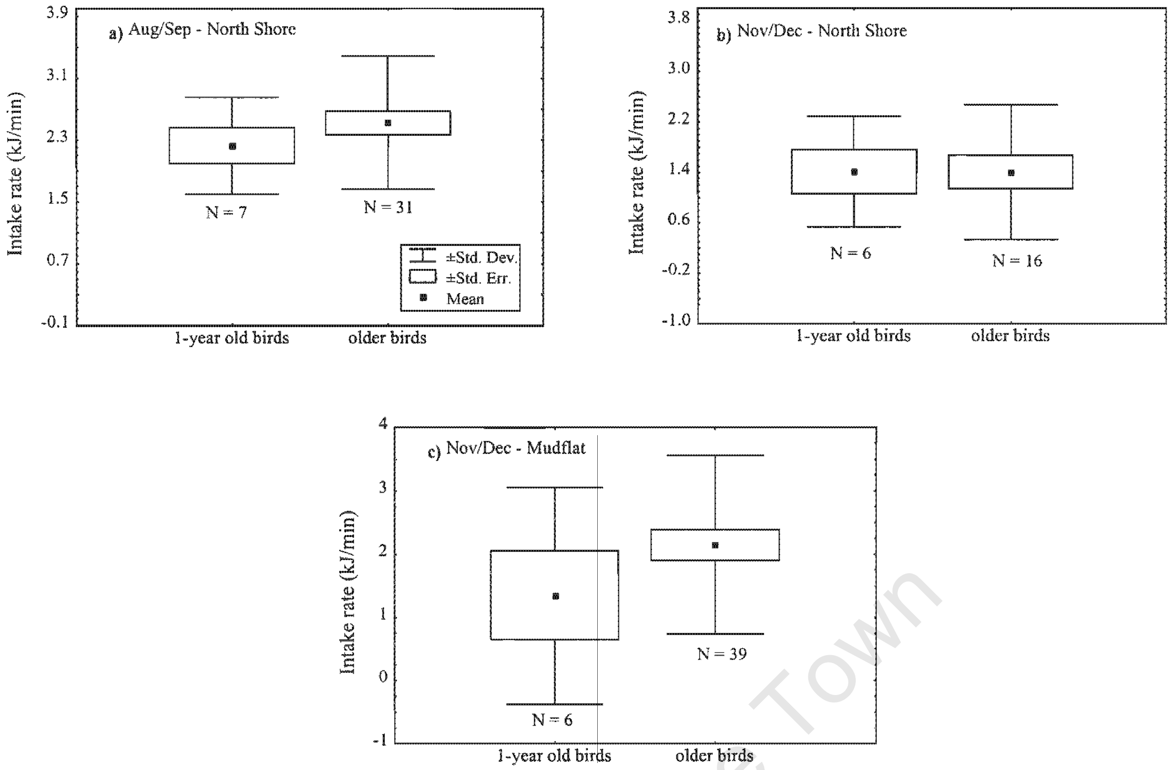


Figure 3.4. Average (± S.E. & S.D.) intake rates of 1-year old and older African Black Oystercatchers on the north shore and mudflat at Walvis Bay.

Prey size choice

The sizes of *Dosinia* eaten by oystercatchers (empty shells collected from the mudflat surface) compared well with the sizes estimated during FAOs and ranged from 11–52 mm and 11–44 mm in Nov/Dec and Feb/Mar respectively (Fig. 3.5d, e). Within these ranges, clams of 20–38 mm in length were taken with greatest frequency. The sizes of *Dosinia* sampled in the mudflat during these two seasons ranged from 5–40 mm and 9–42 mm respectively (Fig. 3.5d, e) – significantly different to sizes eaten by the birds in both seasons (χ^2 tests, both $p < 0.0001$). Very few of the clams found on the mudflat surface exceeded the maximum size found during sampling (6 of 115 in Nov/Dec and 1 of 125 in Feb/Mar).

The frequency distributions of limpet sizes obtained during intertidal sampling (i.e. size range potentially available to oystercatchers) were compared to those recorded during FAOs (i.e. size range eaten by oystercatchers) and were significantly different in all seasons (χ^2 tests, all $p < 0.0001$). Aug/Sep was excluded from the analysis due to insufficient data. There was little shore that were larger than 45 mm were all *Cymbula granatina* and were not taken by the oystercatchers. Very small limpets (< 15 mm) were most abundant low on the shore, amongst the mussel beds, and were also never seen to be eaten during FAOs.

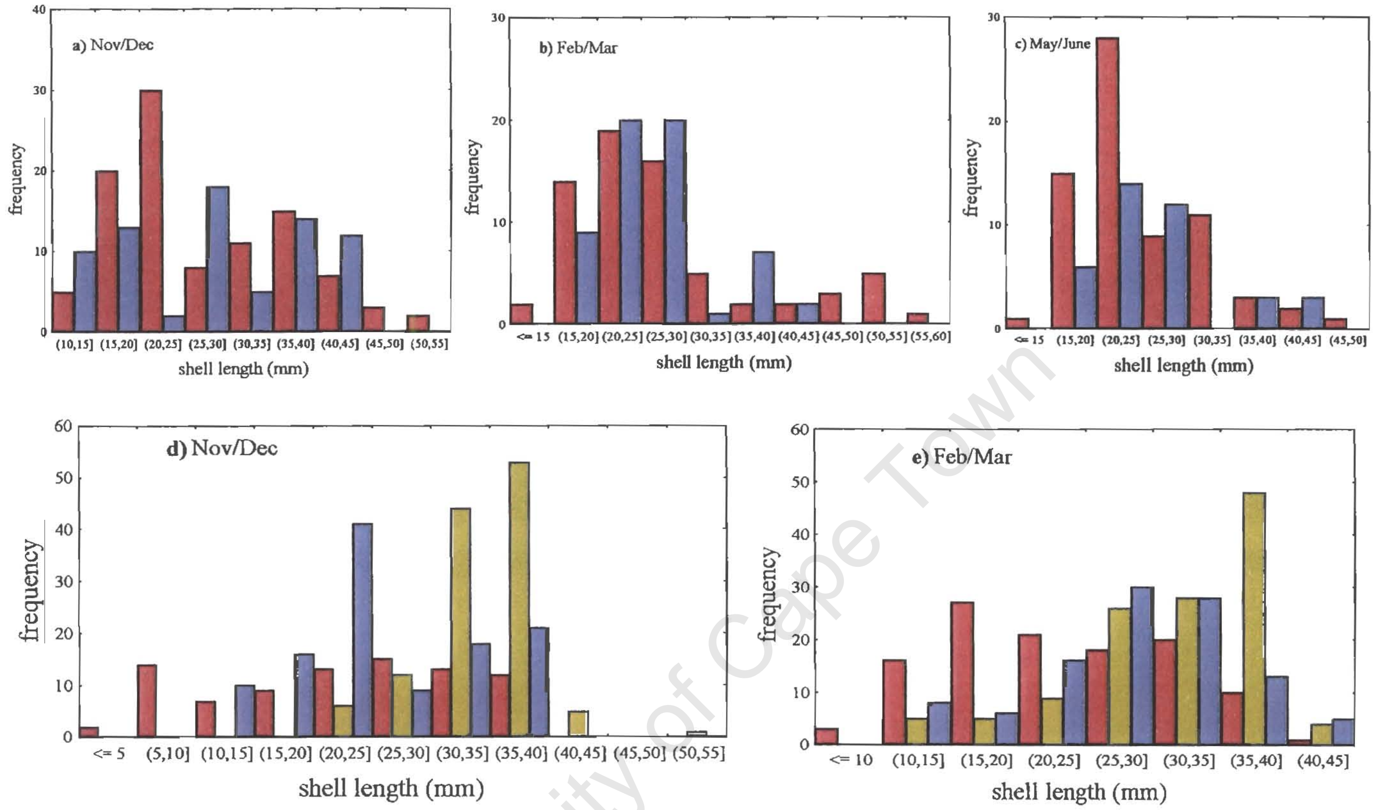


Figure 3.5. Size frequency distributions of limpets on the shore (red bars) and those eaten (FAOs-blue bars) by oystercatchers in a) Nov/Dec, b) Feb/Mar and c) May/Jun and distributions of sampled *Dosinia* (red bars), empty *Dosinia* collected from mudflat surface (yellow bars) and *Dosinia* eaten by oystercatchers (FAOs-blue bars) in d) Nov/Dec and e) Feb/Mar.

The effects of intra- and interspecific interactions on oystercatcher foraging behaviour

Interactions with other shorebird species in which oystercatchers were the aggressors were uncommon throughout the study, and were only observed at the pumphouse mudflat and on the *Discinisca* shore. On rare occasions oystercatchers chased Grey Plovers *Pluvialis squatarola* and Common Whimbrels *Numenius phaeopus* when feeding on *Dosinia,* although neither of these shorebird species consumed *Dosinia* (pers. obs.). North of the pumphouse, Sanderlings and Common Whimbrels *Numenius phaeopus* when feeding on *Dosinia,* although neither of these shorebird species consumed *Dosinia* (pers. obs.). North of the pumphouse, Sanderlings *Calidris alba* and Ruddy Turnstones *Arenaria interpres* regularly fed in large numbers on washed up *Discinisca* and were occasionally chased by the oystercatchers. Oystercatchers were however, never seen to steal prey from other shorebird species.

Aggressive encounters and intra-specific food stealing amongst foraging oystercatchers were less common than expected (cf. Eurasian Oystercatchers, Ens & Goss-Custard 1984, Sitters 2000). Encounter rate remained constant across seasons, averaging 0.43 ± 0.17 encounters.10-minute foraging observation^{-1} and prey items were rarely stolen during these encounters because oystercatchers took evasive action from nearby birds and did not relinquish items easily. In all foraging habitats and seasons, intra-specific encounters had no significant effect on oystercatchers intake rates (Mann-Whitney U tests, all $p > 0.1$). The most intense aggression was observed in the roost, where a sudden disturbance frequently triggered a wave of aggression amongst the oystercatchers, with birds pecking viciously at those nearest to them. Throughout the study there was no evidence of age-related patterns of intra-specific aggression. Behaviour amongst conspecifics, such as piping displays and 'pseudo-sleeping', normally associated with territorial adults (Baker & Hockey 1984), was recorded in the roost. Piping displays have not been previously observed in juvenile oystercatchers (Baker & Hockey 1984).

The Cape Gull was the only interspecific kleptoparasite on the oystercatchers. Kleptoparasitic pressure from gulls was low or absent at Swakopmund during the study period (Table 3.4), but gulls pursued foraging oystercatchers on the north shore and the mudflat at Walvis Bay, especially in Feb/Mar and May/June, when gull numbers were highest. Oystercatchers were extremely wary of nearby gulls and frequently abandoned their prey well before a physical encounter could occur. Abandoned items, especially on the north shore, were often not retrieved by the gulls, but nonetheless represented food lost to the oystercatcher. The energetic loss as a result of food stealing by gulls was insignificant during most of the study period, and in Aug/Sep and Nov/Dec, the rate of energy loss incurred by oystercatchers represented less than 1% of their average intake rates (Tables 3.2 & 3.4). However, when oystercatchers fed on large *Dosinia* in the drained evaporation pan in Aug/Sep, gull kleptoparasitism was the highest of the study and oystercatcher intake rates were reduced by 32% (Table 3.4). In Feb/Mar and May/Jun higher gull numbers at Walvis Bay increased the energetic loss experienced by the oystercatchers, and the highest losses recorded represented 7.25 and 12.5% of the birds' intake rates (north shore & mudflat in May/Jun respectively).

Table 3.4. The average number of kleptoparasitic encounters between oystercatchers and gulls and the corresponding energetic loss (in kJ) calculated per 10-minute foraging observation. Energetic loss expressed as a percentage of average oystercatcher intake rates is shown in brackets. N/B – no birds present in habitat.

	Walvis Bay North Shore		Walvis Bay Mudflat		Walvis Bay Bird Rock		Swakopmund	
	No. of Encounters	energetic loss	no. of encounters	energetic loss	no. of encounters	Energetic Loss	no. of encounters	energetic loss
Aug/Sep	0.09	0.18 (0.73)	0.53*	5.98* (32.0)	N/B		0.00	0.00
Nov/Dec	0.04	0.10 (0.71)	0.04	0.17 (0.86)	N/B		0.00	0.00
Feb/Mar	0.11	0.30 (2.99)	0.13	0.03 (0.13)	N/B		0.00	0.00
May/Jun	1.64	1.80 (7.25)	1.17	1.39 (12.50)	0.50	0.38 (1.44)	0.20	0.21 (0.92)

* losses experienced while foraging opportunistically on *Dosinia* in the drained evaporation pan.

Black-backed Jackals *Canis mesomelas*, common on the Namibian coast and regularly observed near the Walvis Bay and Swakopmund oystercatcher roosts during the study, were largely ignored by the oystercatchers and did not seem to pose a serious threat to the birds. On a few occasions jackals were observed as close as 10 m from the roost, and only then did the birds take flight. Whether predation risk increases significantly at night is not known. Although jackals had little effect on juvenile African Black Oystercatchers, high predation risk is thought to be one of the reasons why the birds do not breed in a habitat that offers such favourable foraging conditions. On two of the visits 1–2 juvenile Eurasian Oystercatchers were present at Walvis Bay. Although these vagrants foraged and roosted together with the black oystercatchers there was no evidence of aggressive interactions between the two species.

Discussion

Activity rhythms and energy budgets

At Swakopmund, activity rhythms were tidally controlled and the foraging time of the juvenile oystercatchers observed during the study was not significantly different from that of adults within the breeding range to the south. Indeed, adult African Black Oystercatchers studied in nature reserves along South Africa's south coast (Leseberg *et al.* 2000), as well as sandy beach foragers (Wilhelm 1999) foraged for longer than did juveniles at Swakopmund. Juvenile intake rates however, were, on average, lower than those reported for adult birds elsewhere. On average, older birds achieved higher energetic intake rates than first-year birds at Walvis Bay, but the results were not significant, probably due to the small sample size of colour-ringed ringed birds that could be accurately aged. Cadman (1980) recorded that second-year American Pied Oystercatchers *H. palliatus* consumed more oysters per unit time foraging than first-year birds but his results also lacked significance due to small sample sizes. Assuming that 446 $min.d^{-1}$ is an accurate estimate of overall foraging time at Swakopmund, and that birds gain 2.13 $kJ.min^{-1}$ on average, this would yield an daily energy intake (DEI) of 950 kJ. Corrected for an assimilation efficiency (AE) of 72.7%, an oystercatcher would thus gain 690 $kJ.d^{-1}$.

During three of the four visits to Walvis Bay, oystercatcher activity rhythms were independent of tidal fluctuations. Almost all oystercatchers roosted from mid-morning to early afternoon, regardless of tidal state. Birds foraged intensively for the first 3–4 hours after sunrise, whereupon they returned to the roost. Departure times varied between the seasons, but, on average, birds left the roost after five hours of roosting and continued foraging until sunset or close thereafter, when the majority of the birds returned to the roost. If, as suspected, oystercatchers at Walvis Bay perform little or no nocturnal foraging, the four hours of foraging in the morning together with a further four hours in the afternoon (480 minutes in total) must be sufficient to meet the daily energetic requirements of the birds. A bird that forages at the seasonal maximum intake rate (Table 3.2) for 480 minutes gains a DEI of 960–1152 $kJ.d^{-1}$, which relates to 698–872 $kJ.d^{-1}$ when corrected for AE. While it is unlikely that an individual forages continuously during the eight hour period (exact foraging times were not obtained for Walvis Bay – see methods), roosting and prolonged inactivity was seldom observed on the mudflat or north shore. This is in contrast to Swakopmund where only 57% of time on the shore was spent actively foraging (see results). Even, if oystercatchers foraged for only 75% of the 480 minutes they spent on the foraging habitats at Walvis Bay, they would still achieve a DEI of 720–864 kJ.d^{-1} (523–628 kJ.d^{-1} corrected for AE).

No empirical measurements of the energy requirements of African Black Oystercatchers are available. Nagy *et al.'s* (1999) allometric equation for Charadriiformes predicts a field metabolic rate (FMR) of 1214 kJ.d^{-1} when applied to juvenile oystercatchers with an average weight of 666 g. This translates to a DEI of 1670 kJ.d^{-1} (DEI = FMR / AE). However, by far the majority of the bird species (13 in total) included in Nagy *et al.'s* equation belong to groups that are taxonomically the least closely related to oystercatchers within the Charadriiformes (auks, terns and gulls). Groups closely related to oystercatchers such as stilts and avocets are not represented in the data set. Furthermore, the species included are not only distantly related to oystercatchers, but are predominantly taxa of small body mass and high energetic requirements due to their migrant status (terns) or their energetically costly flight mode (auks). Lastly, Nagy *et al.'s* measurements were taken during the breeding season, when the birds' energetic requirements may be maximal.

An earlier allometric equation based on 25 species of birds from across the taxonomic spectrum (Nagy 1987) predicts a FMR of 960 kJ.d^{-1}, equalling a DEI of 1320 kJ.d^{-1} for juvenile African Black Oystercatchers. The species comprising the data set are again very unrelated to oystercatchers. In Nagy *et al's* (1999) analysis, 70 bird species were added to the original data set, and while this will certainly increase the predictive power of his allometric equations, the majority of species added are characterised by small mass (< 100 g), and high energetic requirements, thereby further reducing the applicability of Nagy's predictions to oystercatchers.

Kersten (1996) measured the FMR of Eurasian Oystercatchers *H. ostralegus*, categorised as either resident or 'leap-frog' territory holders, using the doubly labeled water technique. The average value for resident territory holders was 682 kJ.d^{-1} (n = 4). When applying the average body mass (530 g) of Kersten's four birds to Nagy *et al's* (1999) allometric equation for Charadriiformes, the predicted FMR = 1018 kJ.d^{-1}, resulting in a ratio of observed to predicted FMR of 0.67. If this ratio is applied to Nagy *et al's* prediction for the FMR of *H. moquini* (1214 kJ.d^{-1}), the corrected value would be 813 kJ.d^{-1}. Corrected for the AE of *H. moquini* this yields a DEI of 1118 kJ.d^{-1}, considerably less than 1670 kJ.d^{-1} predicted from Nagy *et al's* (1999) equation, but only 168 kJ.d^{-1} more than the DEI calculated for Swakopmund (950 kJ.d^{-1})

and 34 kJ.d^{-1} less than the maximum estimate for Walvis Bay (1152 kJ.d^{-1}). Even if oystercatchers fed for only 75% of the time they spent away from the roost, their predicted DEI values would be only 254–398 kJ.d^{-1} lower. There is probably little significance in these differences given that Kersten's (1996) measurements were made on breeding birds.

Daytime foraging – linked to digestion rates?

If juvenile oystercatchers at Walvis Bay can meet their daily energy demands by foraging only during daylight hours – and the results outlined above suggest this to be possible – it could be predicted that they will time their afternoon departure from the roost in such a way as to ensure that their oesophagus is full when they cease foraging shortly after sunset.

Intake rates of captive Eurasian Oystercatchers can be up to four times their food processing rate (Kersten & Visser 1996) and this can quickly lead to a digestive bottleneck. The oesophagus of an Eurasian Oystercatcher was estimated to hold 12 g dry flesh and the food processing rate was 0.0396 g ash-free-dry-weight (AFDW) min^{-1} (Kersten & Visser 1996). Oystercatchers with a full oesophagus required five hours of processing time. African Black Oystercatchers are larger birds than Eurasian Oystercatchers and are probably able to store more food in their oesophagus. Assuming that oesophagus volume scales linearly with body mass, and based on the average mass of 666 g for juvenile oystercatchers at Walvis Bay and an average body mass of 468 g for Eurasian Oystercatchers held in captivity in summer (cf. Zwarts *et al.* 1996b), African Black Oystercatchers are predicted to be able to store 17.1 g dry flesh in their oesophagus. Kersten and Visser's (1996) digestion rate (based on captive Eurasian Oystercatchers fed on mussels) predicts a processing time of seven hours for 17.1 g dry flesh. While African Black Oystercatchers may be able to digest partially decomposed *Discinisca* at a faster rate, this may be offset by reduced digestion rates due to a smaller surface area to volume ratio in the larger oesophagus.

To test whether birds leave the foraging grounds at sunset with a full oesophagus, the time it took to fill a 17.1 g oesophagus was calculated, based on the maximum seasonal intake rates (corrected for AFDW) observed at Walvis Bay (Table 3.2), and the digestion rate of Kersten and Visser (1996). Results fluctuated seasonally in response to intake rates: In Aug/Sep a bird was predicted to take just over four hours to fill its oesophagus, while in Nov/Dec and Feb/Mar it would take eight and five hours respectively. These predictions only partially explain the observed seasonal activity rhythms:

In Aug/Sep, oystercatchers lose up to two hours of foraging time due to a later sunrise and earlier sunset and this can, at least partially, explain the extended foraging activity observed in this season. According to the prediction, they can fill their oesophagus in four hours of foraging and are therefore able to return to the roost at sunset with a full oesophagus. The lower intake rates in Nov/Dec are predicted to double oesophagus filling time to eight hours and, assuming this is accurate, it is surprising that birds return to the roost at 10:00, considering that only 50% (8.6 g) of their oesophagus would have been filled if they began foraging at sunrise. By the time the birds leave the roost at 14:00 (one hour earlier than in Feb/Mar), their oesophagus would be empty (3.5 hours needed to empty 8.6 g) but it would not be full once more by sunset. In Feb/Mar, birds are predicted to require five hours to fill their oesophagus and results indicate that they can return to the roost at sunset with a full oesophagus. In all seasons, however, it would not have been possible for birds to fully digest the contents of the oesophagus in the five hour roosting period.

While the hypothesis of limited nocturnal foraging at Walvis Bay is supported by the daily energy intake rates (DEI) obtained at the site, daytime activity rhythms and movements to and from the roost could not be fully explained by the oesophagus filling and digestion rates used in the above calculations. Digestive bottlenecks will certainly be the underlying factor, but whether the parameters used (based largely on studies of *H. ostralegus*) adequately describe digestion rates in *H. moquini* are uncertain.

Adult and immature American Pied Oystercatchers *H. palliatus* display a strong diurnal foraging rhythm when feeding on commercial oyster beds, moving to and from the beds at sunrise and sunset each day (Cadman 1980). Although birds were tidally constrained, only being able to feed on the oyster beds at low tide, the entire night roost left for the oyster beds in small groups at sunrise. If the beds were covered by the tide at this time, the birds rested at a nearby high tide roost until the beds became available. At sunset all the birds returned to the night roost. This activity pattern led Cadman (1980) to conclude that no nocturnal foraging was taking place and visits to the oyster beds at night never recorded any nocturnal activity. Although foraging itself is tidally controlled, the activity pattern of these American Pied

Oystercatchers is very similar to the activity rhythms observed at Walvis Bay, where observations and energy budgets suggest that nocturnal foraging is not taking place.

The significance of kleptoparasitism at the nursery

Intra-specific kleptoparasitism is known to have a significant impact on the foraging performance of mussel-eating Eurasian Oystercatchers *H. ostralegus* (Ens & Goss-Custard 1984): Intra-specific interference increases significantly above a threshold bird density and intake rates are depressed (Goss-Custard & Durell 1987c, Stillman *et al.* 1996). Furthermore, an oystercatcher's dominance status can directly affect the frequency with which it will experience aggression and food stealing from conspecifics (Ens & Goss-Custard 1984, Goss-Custard & Durell 1987b, Sitters 2000). Kleptoparasitism is costly, not only in terms of time and energy lost by the victim, but a high incidence of food stealing requires increased vigilance amongst foraging birds to reduce the chances of losing prey (Goss-Custard *et al.* 1999). When young inexperienced Eurasian Oystercatchers first join adults on the wintering grounds, they frequently steal food items from conspecifics instead of searching for mussels independently. However, as their foraging efficiency improves stealing mussels becomes energetically less profitable and birds search for their own prey (Goss-Custard *et al.* 1998). At the same time they become increasingly susceptible to interference from older or adult birds (Goss-Custard & Durell 1987b). Kleptoparasitism is also a common occurrence amongst American Pied Oystercatchers *H. palliatus* foraging on oyster beds (Cadman 1980). Immature birds had lower energetic intake rates than adults and stole more prey items than adult birds, which are able to acquire energy more efficiently by searching for oysters themselves than by stealing from conspecifics.

Kleptoparasitism is only a profitable foraging strategy when a) there are many, generally more experienced hosts to choose from in a foraging habitat and b) when the hosts' handling times are long. The absence of competition and interference from adult conspecifics at both Walvis Bay and Swakopmund does not make foraging conditions conducive to kleptoparasitism. Although the age of juveniles at the nurseries can span 2–3 years, no age-linked dominance hierarchy could be detected during this study. Furthermore, handling times, although not measured in this study, were short and oystercatchers required little time to open the soft and often partially decayed *Discinisca* shells. While handling times for *Dosinia* and mussels and limpets at Swakopmund were longer, the rarity of suitable hosts resulted in equally low levels of kleptoparasitism in these habitats. Whilst intra-specific encounters were observed in all foraging habitats, they generally only consisted of a short, aggressive pursuit and no genuine attempt at stealing a prey item, i.e. they appeared to be conflicts over foraging space rather than over food *per se*. Intra-specific encounters had no significant effect on intake rates.

Oystercatchers were more threatened by kleptoparasitic Cape Gulls than by conspecifics, and quickly abandoned prey items on the north shore when approached by a gull. Because *Discinisca* was readily available to the birds it was probably energetically more profitable to give up the prey item than to risk a fight, even though prey abandoned by the oystercatchers was often not retrieved by the gulls. However, levels of gull kleptoparasitism were low for most of the study, with energetic loss to oystercatchers representing less than 1% of intake rates. Only in May/Jun when gull pressure was highest did energetic loss increase to around 10% of intake rates. In Aug/Sep, the oystercatchers fed opportunistically in the drained evaporation pan, and kleptoparasitism was profitable for the gulls because host availability was high – for several days, virtually the entire oystercatcher roost fed on *Dosinia* in the pan and intake rates were reduced by 32%.

Conclusions

1. Juvenile oystercatchers at Walvis Bay and Swakopmund have very different foraging strategies. At Swakopmund, birds follow a tidal foraging regime, while at Walvis Bay, they forage independently of the tides for most of the time. Foraging activity peaked in the early morning and late afternoon and evening and daily energy intake rate supported the hypothesis that limited, or no, nocturnal foraging occurs at Walvis Bay. Daytime foraging rhythms were, however, only partially explained by predicted oesophagus filling and digestion rates.

2. Daily foraging time at Swakopmund was comparable to the upper range of adult foraging times obtained in previous studies. Whilst juvenile foraging efficiency recorded during this study is not directly comparable with that of adults in other regions and seasons, results do suggest that foraging conditions at Swakopmund are sufficiently good for juveniles to achieve intake rates comparable to adults. At Walvis Bay, foraging efficiency did increase

with age, although differences in intake rates between first-year and older birds were not significant.

3. No information is available on the Field Metabolic Rate (FMR) of African Black Oystercatchers. Nagy *et al.'s* (1999) allometric equation for the Charadriiformes did not adequately predict the FMR of juvenile African Black Oystercatchers. However, by using measured values of FMR of breeding *H. ostralegus* (Kersten 1996) and comparing them to predicted values according to Nagy *et al.* (1999), a ratio of measured to predicted FMR was used to determine the FMR of African Black Oystercatchers, corrected for body mass differences. Once corrected for assimilation efficiency (AE), the daily energy intake (DEI) of 1118 kJ.d^{-1} was calculated for *H. moquini* at Walvis Bay, well below Nagy *et al.'s* DEI value (1670 kJ.d^{-1}), but only 168 kJ.d^{-1} higher than the DEI calculated for Swakopmund birds (950 kJ) and 34 kJ.d^{-1} lower than the maximum estimate for Walvis Bay (1152 kJ.d^{-1}).

4. In strong contrast to other oystercatcher species, where kleptoparasitism can have a significant effect on foraging performance, intra-specific food stealing was infrequent at both Walvis Bay and Swakopmund. Foraging conditions at Walvis Bay were not conducive to profitable kleptoparasitism because a) experienced conspecifics (adults) were absent from the foraging habitat and b) prey items were easy to process, reducing handling times.

5. Kleptoparasitism by gulls was highly seasonal at Walvis Bay and virtually absent from Swakopmund. Only in May/Jun, and while foraging in the drained evaporation pan in Aug/Sep, was gull pressure high and oystercatchers lost food in aggressive encounters. During the remainder of the study energetic loss to oystercatchers from kleptoparasitism represented less than 1% of their intake rates.

Chapter 4

CHAPTER 4

Dichotomous dispersal strategies of juvenile African Black Oystercatchers – possible explanations and conservation implications

The Oystercatcher Conservation Programme's chick ringing efforts, initiated in the 1997/98 breeding season, have shed much light on juvenile dispersal in the African Black Oystercatcher. Two contrasting strategies have been identified – juvenile oystercatchers either disperse over short distances (usually < 150 km) and in a random direction from their natal site, or they migrate up to 3000 km and target specific nurseries on the coasts of Namibia and southern Angola. Whilst juvenile dispersal and the subsequent return to natal breeding sites is a common trait amongst many bird species, two such divergent strategies within the same species do not appear to have been reported for any other bird species, let alone shorebird. Amongst fish and insects there are numerous examples of dispersal way from the natal site and subsequent return to breeding areas (e.g. salmon, Monarch Butterfly) but none of these examples are comparable to the patterns observed in African Black Oystercatchers (Dingle 1996).

The African Penguin *Spheniscus demersus* breeds on islands and a few mainland colonies from Namibia to Algoa Bay in South Africa and is another southern African species that displays a migratory juvenile phase and a sedentary adult phase (Randall *et al.* 1987). The exact routes followed and the areas visited by young penguins during their 3–4 year migration are not yet clearly understood, but there is strong evidence for a clockwise movement around the coast of South Africa (Randall *et al.* 1987, Randall 1989). Juveniles from the Eastern Cape Province move westward, while those from the southwestern Cape move both in a northerly and easterly direction – long distance movements, however, tend to follow the west coast of South Africa, reaching as far north as Namibia (Randall 1989, P. Whittington pers. comm.). Penguins have been recorded visiting other colonies more than 1000 km from their natal island (Randall 1989). Returning juveniles generally settle and breed in their natal colonies to breed. However, while the duration and direction of juvenile African Penguin movements may be comparable to those of African Black Oystercatchers, penguins do not display two highly dichotomous dispersal strategies, nor do they target specific nursery areas.

Oystercatchers are essentially a non-migratory group of waders. Of the world's 11 species only the American Black Oystercatcher *H. bachmani* and the four races of the Eurasian

Oystercatcher *H. o. ostralegus, longipes, osculans* and *finschi* are truly migratory (Hockey 1996a,b). The races *ostralegus* and *longipes* move over approximately 32° of latitude between their breeding and nonbreeding grounds (Hockey 1996a). The remainder of the species are either sedentary year-round or undertake small-scale seasonal movements between habitats. Juveniles of migratory species generally join the adults at traditional nonbreeding sites but little is known about the extent of juvenile dispersal amongst sedentary oystercatcher species. Ring resightings of juvenile Variable Oystercatchers *H. unicolor* indicate an average juvenile dispersal distance of *ca.* 30 km from natal sites – 483 km was the maximum distance recorded (Baker 1974), while juvenile Chatham Island Oystercatchers *H. chathamensis* are known to disperse *ca.* 40 km between islands (Marchant & Higgins 1993).

After having identified five oystercatcher nurseries, predicted to support > 40% of South Africa's juvenile oystercatchers (Chapter 1), the question how a dispersal strategy is 'chosen' still begs to be answered. Juveniles that migrate to a nursery must be physically able to meet the energetic costs of the journey, which presumably exceed those of being a short-distance disperser. Once a nursery is reached, however, important benefits come into play – foraging conditions are favourable, both in terms of food abundance and availability, and juveniles experience no competition from more proficient conspecifics (adults). Juveniles that disperse over short distances and remain relatively close to natal sites do not incur the same energetic costs of long-distance travel, but have the potential to be exposed to high levels of interference by territorial adults. No comparative data on the foraging performance of short-distance dispersers exist.

Juvenile African Black Oystercatchers are known to remain at the Walvis Bay/Swakopmund nursery for a minimum of two years (Chapter 1). Deferred return migration to the breeding grounds is a common trait amongst young Holarctic-breeding waders (Hockey *et al.* 1998), where juveniles of species that undergo long-distance migration often spend one or more boreal summers on their nonbreeding grounds. Lower foraging proficiencies of juveniles are thought to have driven the evolution of deferred migration, with juveniles being unable to accumulate enough reserves to undergo a non-stop migration nor to provide the energy needed for breeding. Their migration would require one or more refuelling stops, thereby delaying the arrival at the breeding grounds and sharply increasing the risk of breeding failure (Hockey *et al.* 1998). African Black Oystercatchers, however, only become sexually mature at three to four years of age (Hockey 1996a) and therefore do not forfeit reproductive output by remaining in nurseries for two to three years – but they do benefit from favourable foraging conditions and the opportunity of improving their foraging proficiency in the absence of adult competition (Chapters 2, 3).

While juvenile oystercatchers from all seven South African ringing regions have been recorded at the Walvis Bay/Swakopmund nursery during the course of the study (August 1999 to June 2000), oystercatchers ringed on the Saldanha Bay islands dominated the resightings of colour-ringed birds (Fig. 4.1). However, ringed oystercatchers from the Cape Peninsula and the south coast regions were represented at the nursery in the highest proportions (17% and 22% respectively – Fig. 4.1), indicating that juvenile oystercatchers from all these South African regions target the Walvis Bay/Swakopmund nursery. Only two Eastern Cape oystercatchers had been resighted at the nursery by the end of July 2001. A significant number of chicks was ringed in the Eastern Cape Province between the 1997/98 and 2000/01 breeding seasons (145) but resightings have primarily been from the Cape Town area or of short-distance dispersers remaining within the Eastern Cape (Chapter 1, Fig. 1.3).

Oystercatchers ringed on Possession Island have the shortest distance to travel to reach the Walvis Bay/Swakopmund nursery (*ca.* 460 km) and yet very few of them (two) were resighted at the nursery during the study. Although there is seasonal and regional variation in the onset of breeding (Table 4.1), Namibian juveniles will, on average, reach a nursery before the first South African arrivals and it is hypothesised that they would target the nurseries closest to their natal sites. This would imply that the two Lüderitz roosts would be dominated by juveniles from islands in the vicinity of Lüderitz. South African juveniles, having to cover a much greater migratory distance, would arrive in Namibia later in the year, when nurseries such as the Lüderitz roosts may already be filled with Namibian birds. They would consequently continue their migration, performing essentially a leap-frog migration (Rappole 1995), and reach the Walvis Bay/Swakopmund nursery or nurseries further north. To confirm this hypothesis may prove difficult, however, because the vast majority of Namibian juveniles are unringed and impossible to identify as such. A much closer inspection of the two Lüderitz nurseries is required to assess the arrival times of first-year juveniles and thereby decide on the origin of these birds.

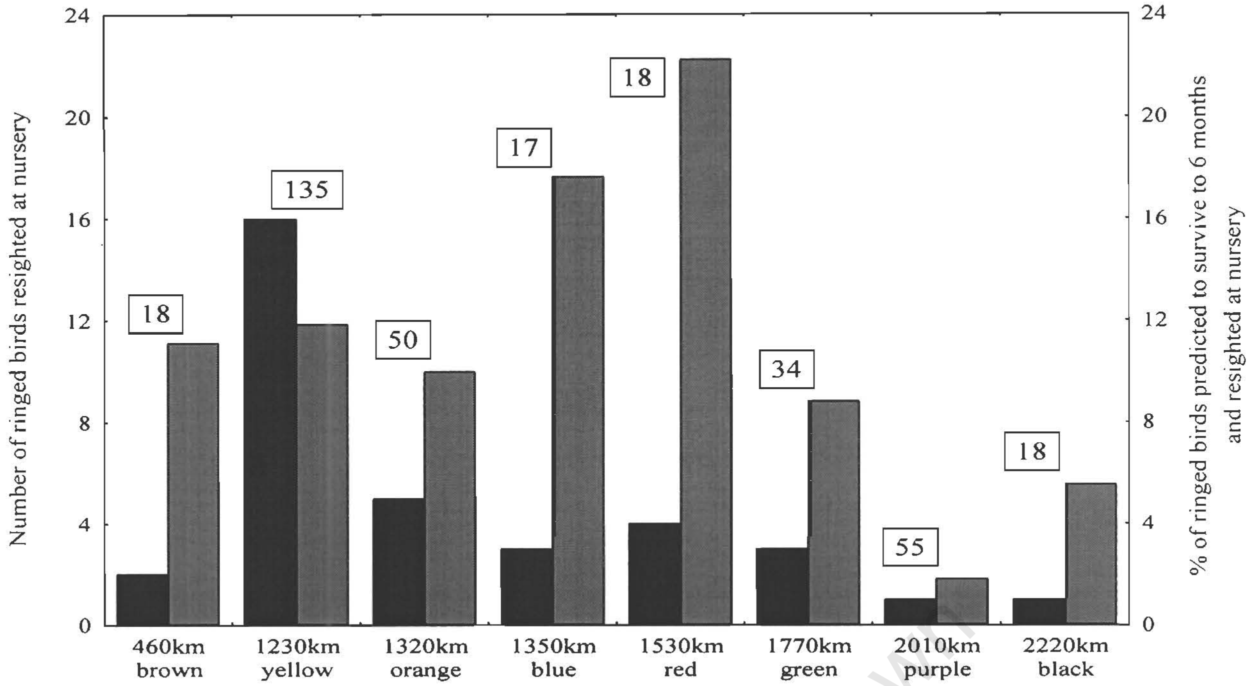


Figure 4.1 The number (black bars) of ringed oystercatchers resighted at the Walvis Bay/ Swakopmund nursery between August 1999 and June 2000 in relation to distance from ringing region (see Chapter 1, Fig. 1.1 for ringing regions), and the proportion of ringed oystercatchers, predicted to have survived to 6 months, resighted at the nursery (grey bars). (Numbered boxes indicate the number of oystercatchers ringed in the 1997/98 and 98/99 seasons and predicted to have survived to 6 months).

In trying to explain the dichotomous patterns of juvenile dispersal, body condition (used as a surrogate for physiological state) of resighted juveniles (at the time of ringing), as well as extrinsic factors such as the regional variation in the onset of breeding were considered as possible triggers for a specific dispersal strategy.

Trigger 1: Body condition?

Juvenile oystercatchers vary considerably in body mass and size at time of fledging due to different levels of parental provisioning (Groves 1984, Kersten & Brenninkmeijer 1995). Such differences could be further intensified during the average one month period when juveniles forage for themselves but still remain close to natal sites (Hockey 1983b). To test whether body condition determines dispersal pattern, body mass and tarsus measurements (tarsus length varies the least with age – Hockey 1984b) of individually identifiable juveniles resighted at a nursery were compared with measurements of birds repeatedly seen close to natal sites in South Africa.

Any juvenile resighted close to natal sites more than six months after being ringed was assumed not to migrate to a nursery. Furthermore, two years was taken as the minimum time away from natal sites (based on juveniles sighted at Walvis Bay and back near natal sites – Chapter 1) and any juvenile resighted back at its natal site in less time was also assumed not to have been to a nursery. The measurements used for the analysis were taken during chick ringing, and while ages of chicks ringed vary, a substantial proportion of chicks were close to fledging (> 400 g) when ringed.

Results

There was no significant difference in the ratio of body mass to tarsus length between long-distance and short-distance dispersers (Fig. 4.2) – both slopes ($t = 0.567$, $p > 0.5$) and intercepts ($t = -1.984$, $p > 0.05$) were statistically indistinguishable. These results suggest that condition during chick development and/or close to fledging does not play a role in determining the dispersal strategy chosen.

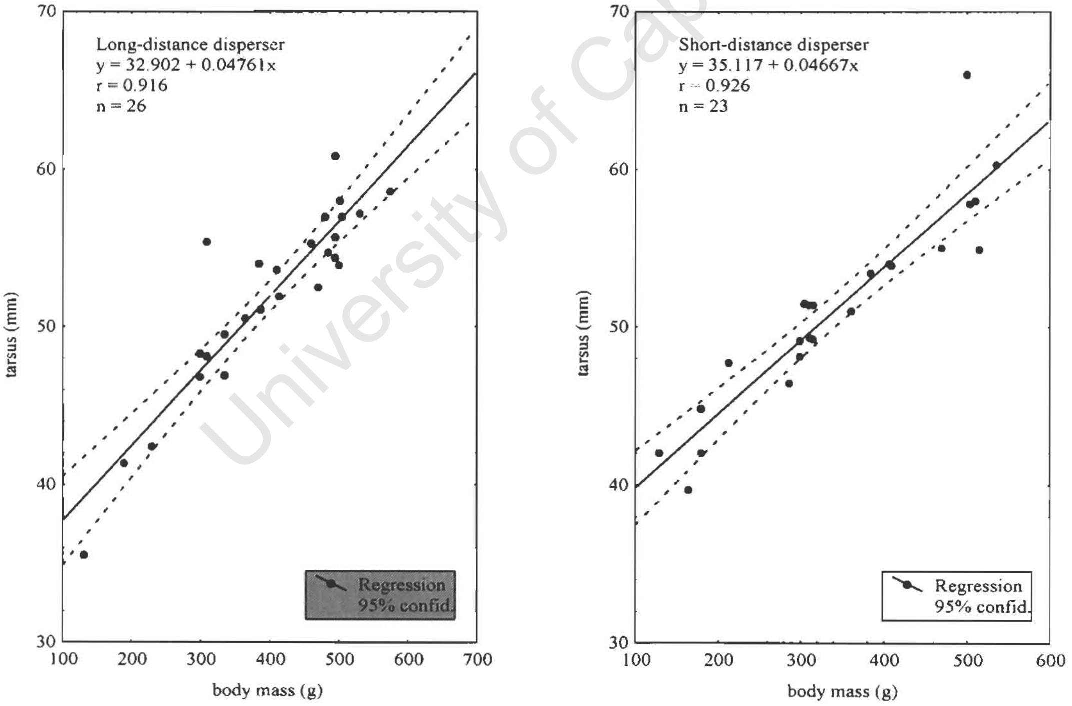


Figure 4.2. Regression analysis comparing body mass and tarsus length of long- and short-distance dispersers.

Studies of American Black Oystercatchers *H. bachmani* and Eurasian Oystercatchers *H. ostralegus* have shown that body mass at fledging had no effect on juvenile survival to one or two years of age or on the probability of returning to natal sites (Groves 1984, Kersten & Brenninkmeijer 1995).

Trigger 2: Extrinsic factors – hatching date?

If patterns of juvenile movements are not linked to body condition, this raises the possibility that extrinsic/environmental factors activate one or the other dispersal strategy. There is some evidence that dispersal has a density dependent component. All young oystercatchers move away from South African islands where adult density is high, but small numbers remain on islands with lower adult densities, e.g. Dassen Island (Hockey 1983b, A. Wolfaardt *in litt*). Similarly, juveniles tend to be more common in sites at the fringes of high density adult areas than within them (Hockey 1983b). But the demonstration of short-distance movements along a density gradient cannot be extrapolated to interpretation of movements in excess of 2000 km, which must have required birds to have bypassed areas of suitable resources – one of the key definitions of true migration (Dingle 1996).

If there is a significant cost to long-distance movement, juveniles that hatch, and consequently fledge, early in the season may occupy suitable habitats near their natal sites and, by the time that chicks hatched later in the season fledge, such areas may already be saturated with older juveniles. Late-fledged birds may be forced to migrate to a nursery.

The hypothesis that hatching date triggers dispersal strategy was tested by calculating the hatching dates for all ringed and resighted juveniles (both confirmed short- and long-distance dispersers) based on their age at ringing (obtained from mass and tarsus measurements – Hockey 1984b). Birds were grouped according to ringing region and year and the hatching dates were scored against the earliest hatching date (day 1) of any ringed bird in each group in each year (Table 4.1). This ensured that regional or inter-annual differences in the onset of the breeding season were accounted for.

Results

Hatching dates of birds resighted at a nursery were compared with those that remained close to their natal sites using a Mann-Whiney test: although there was no significant difference between the two dispersal strategies ($U_{21,21} = 153$, $p = 0.09$), the result does suggest that hatching date may become a dispersal trigger once sample sizes (no. of resightings) increase.

Table 4.1 The earliest hatching dates for oystercatcher chicks ringed in seven ringing regions and across four breeding seasons.

Ringing Region	1997/98	1998/99	1999/00	2000/01
Yellow	24 Nov	29 Oct	3 Dec	16 Dec
Orange	No ringing	1 Nov	9 Nov	13 Nov
Blue	6 Jan	13 Dec	1 Jan	16 Dec
Red	29 Dec	2 Jan	2 Jan	22 Dec
Green	26 Nov	1 Dec	23 Nov	25 Nov
Purple	1 Jan	22 Dec	27 Nov	10 Dec
Black	29 Dec	27 Dec	27 Nov	No ringing

Neither the physiological state of young oystercatchers, nor variations in the timing of breeding, explains what triggers a juvenile to undertake either a short- or long-distance dispersal strategy. The conditions juvenile oystercatchers experience at the time of independence do not seem to influence dispersal behaviour, although with the constant increase in juvenile resightings, a density dependent effect may still emerge as the determining factor. If however, there is a genetic basis to the dichotomous dispersal behaviour of the African Black Oystercatcher, it would have to be in the form of a balanced polymorphism for it to be maintained in the population. Whether such a polymorphism exists within broods is not known as siblings displaying opposing dispersal strategies have not yet been observed. A sibling pair where both partners have chosen long-distance dispersal to a nursery has been observed at Walvis Bay (July 2001).

Conservation implications based on the dispersal strategies and activity rhythms of juvenile African Black Oystercatchers

With the discovery of large oystercatcher nurseries north of the adults' breeding range, the conservation requirements of the African Black Oystercatcher have become more complex than previously anticipated. A large proportion of the global annual production is concentrated in a few, very specific localities: ensuring the survival of juveniles at these sites is as important as any conservation measures implemented in South Africa aimed at enhancing the population's productivity. If such measures are successful in increasing the annual productivity it can be predicted that more juvenile oystercatchers will move to Namibian nurseries, thereby further increasing these areas' contribution to oystercatchers' conservation. Since the outset of this study, and with the realisation of the importance of Namibian nurseries, the status of the African Black Oystercatcher in Namibia has been elevated and the species is now included in the "specially protected vertebrates" listing in the new Parks and Wildlife Management Bill (2001).

Because nurseries need to meet specific ecological requirements of juvenile oystercatchers (abundant food and an absence of adult competition – Chapter 1), the number of suitable sites is limited. Five nurseries have been identified thus far, and it unlikely that large, as yet unknown, nurseries exist. The Walvis Bay/Swakopmund nursery is the largest, followed by the two nurseries north of Lüderitz. Together, these contain approximately 300 young oystercatchers. Walvis Bay not only accommodates the largest number of juvenile oystercatchers, but it is also Namibia's only large port and fishing harbour north of Lüderitz and is facing increasing pressure from human activities. The other nurseries are all situated in very remote areas (Hoanib River and Baia dos Tigres) or sites where human access is restricted (the Lüderitz nurseries are located within diamond mining areas). Should Walvis Bay deteriorate and no longer be suitable for juvenile oystercatchers in the future, it is questionable whether all the birds could be absorbed into other existing nurseries or whether suitable sites exist where new nurseries might form. Low oystercatcher counts from Sandwich Harbour over the last decade (Chapter 2) suggest that the wetland is no longer an adequate alternative site and geomorphological changes have reduced the suitable foraging habitats (mudflat areas) for juvenile oystercatchers.

This study has highlighted the diversity of foraging habitats utilised by oystercatchers at Walvis Bay. Birds displayed a highly opportunistic foraging behaviour and moved over large distances as new food resources became available (Chapter 2). These movements make conservation planning for the area difficult. Oystercatchers clearly require access to several spatially distinct foraging habitats in the greater Walvis Bay area to meet their year-round energetic requirements and the loss of any one of these habitats could have negative implications for the birds.

The Walvis Bay Lagoon faces serious threats to its future sustainability. Concerns have been raised that sedimentation, a natural process in coastal inlets but accelerated by human activities and development, is destroying much tidal habitat and it has been identified as the primary threat to one of southern Africa's most important wetlands (Appendix 3 gives an overview of the threats faced by the Walvis Bay wetlands, as well as their current conservation status and the management plans for the future). Large-scale geomorphological changes to the lagoon, in terms of reduced tidal inundation and scouring of the bay could lead to the drying out of tidal areas such as the pumphouse mudflat, as well as the cessation of *Discinisca* and *Semimytilus* wash-ups along the Pelican Point shoreline. However, while *Dosinia* and *Discinisca* are the primary prey species of oystercatchers at Walvis Bay (Chapter 2), the mussel beds at Bird Rock and at Swakopmund are a consistently available food resource and could be utilised by the birds if food shortages occur elsewhere within the Bay. Temporarily high numbers of oystercatchers recorded at Swakopmund in the winter months may be a result of such shortages, when overall numbers at the Walvis Bay/Swakopmund nursery are at their maximum (Chapter 1). Furthermore, mussel abundance may increase on the rocky shores at both Bird Rock and Swakopmund in years to come with the rapid spread of the invasive Mediterranean Mussel *Mytilus galloprovincialis* (Hockey & van Erkom Schurink 1992).

A further threat to the Walvis Bay/Swakopmund nursery is coastal development, especially near Bird Rock where any increase in disturbance would result in oystercatchers avoiding the area and the loss of a potentially important foraging habitat. High-density mussel beds near existing coastal resorts were completely ignored by the birds during this study: juvenile oystercatchers seem to be more prone to disturbance than are adults and are certainly less approachable on their foraging areas. Mariculture initiatives, such as the harvesting and drying of the alga *Gracilaria* (for the extraction of agar) along the *Discinisca* shore, have been proposed for Walvis Bay in recent years but this particular proposal was turned down. Whilst mariculture *per se* poses no threat to oystercatchers, the proposed site for the *Gracilaria* plant would have not only destroyed the *Discinisca* resource but the resulting human activity would have caused constant disturbance to the oystercatcher roost.

It is important to stress that the apparently low intensity of intra-specific competition, as well as the seasonal variation in the number of birds at the Walvis Bay/Swakopmund nursery, suggest that the African Black Oystercatcher population at this nursery is not currently at carrying capacity. The foraging habitats and resources in the area (especially the under-utilised mussel beds) could support greater numbers of oystercatchers than they do at present and any negative impacts on these habitats may not inevitably lead to a reduction in oystercatchers numbers at Walvis Bay. Walvis Bay does, however, face a conservation crisis and management plans need to be put in place immediately (Appendix 3).

Chapter 5

SYNTHESIS

Background

- In the 1980s, much research was carried out on the biology of the African Black Oystercatcher and aspects concerning breeding biology, size and distribution of the adult population, morphometrics and behavioural affinities of the species, as well as diet and foraging behaviour were investigated. Knowledge of juvenile dispersal was limited at the time and the maximum dispersal distance was thought to be a few hundred kilometres. Only with the launch of a country-wide chick colour-ringing operation in 1998 (part of the Oystercatcher Conservation Programme) did a markedly different picture emerge when a South African juvenile ringed on the south coast was mist-netted at Swakopmund, Namibia. Surveys of the area revealed several South African-ringed oystercatchers, especially from the west coast islands. It quickly became apparent that the puzzling absence of any large groups of juvenile oystercatchers within the breeding range was due to an inadequate search radius and that Swakopmund and nearby Walvis Bay were supporting large numbers of South African juveniles.

- As the focus was redirected to the Namibian coast four further oystercatcher nurseries were discovered: two < 100 km north of Lüderitz, one at the mouth of the Hoanib River in northern Namibia and the fifth as far north as Baia dos Tigres in southern Angola. Together with the Walvis Bay/Swakopmund nursery these five sites, all located outside the adult breeding range, are known to support about 400 juvenile and immature oystercatchers. Furthermore, it is highly probable that these nurseries, particularly Walvis Bay/ Swakopmund, are traditional sites. In the 1850s mention was made in the literature of large flocks of oystercatchers at Walvis Bay that were difficult to approach – most certainly a roost of juvenile birds.

- Multiple resightings of individually identifiable juveniles in close proximity to their natal sites in South Africa have, however, revealed a second dispersal strategy. These repeated resightings indicate that some juveniles are short-distance dispersers that never migrate to a nursery but remain close to natal sites. Their dispersal distances are short (usually < 150 km, sometimes < 10 km) and they do not aggregate in discrete nurseries within the breeding range but are scattered around the coast. During the nonbreeding season they join adults at high tide roosts. Both strategies are employed throughout the breeding range and no equivalent dichotomous post-fledging dispersal pattern has yet been found in any other bird species.

- The discovery of these nurseries, and the large numbers of young oystercatchers within them, holds major conservation implications for the African Black Oystercatcher. This prompted the Walvis Bay/Swakopmund nursery to be studied in greater detail during four separate visits to the area in Aug/Sep and Nov/Dec 1999 and Feb/Mar and May/Jun 2000.

Findings of this study

- An average number of 135 oystercatchers was present at the Walvis Bay/Swakopmund nursery during this study and juveniles from the entire South African breeding range were represented, some from breeding sites > 2500km distant. Juveniles from the west coast islands dominated in number amongst ringed birds, while Eastern Cape oystercatchers were significantly under-represented. Only two juveniles ringed on Possession Island near Lüderitz were resighted at Walvis Bay during this study. While this indicates that Namibian juveniles do utilise the nursery, it is surprising that not more Possession birds were recorded, considering that they have a much shorter distance to cover to reach Walvis Bay than do South African birds. However, the two Lüderitz nurseries are located much closer to the natal sites of Namibian juveniles and it is predicted that these may be dominated by Namibian birds. However, only once the Lüderitz sites are surveyed in detail can this be determined.

- Juveniles first arrived at the nursery in May–June and are thought to spend a minimum of two years there before returning south. Numbers at Walvis Bay decreased in early summer when many of the oldest birds returned to natal sites. Four individuals seen at the nursery during the study have since been resighted near their natal sites in South Africa (May 2001). Transient birds that remained at the nursery for < six weeks (i.e. the duration of one visit) appear to be using the nursery as a stop-over point on their journey to other nurseries or on their return to natal sites. At the Swakopmund roost, seasonal fluctuations in bird numbers (significantly higher in winter) were a reflection of the arrival and departure of birds from the nursery and could not be explained by seasonal variation in food abundance at either Walvis Bay or Swakopmund.

- Primary moult has been identified as an ageing tool for immature African Black Oystercatchers up to their third year (after which their moult cycles are synchronous with adults'). Based on observed moult ratios amongst small groups of oystercatchers, as well as the position of the wing-gap in birds of known age (ringed) it was determined that in the second half of the year, when all long-distance dispersers had arrived at the nursery, 50% of the Walvis Bay/Swakopmund nursery population comprises first-year birds (the previous season's production). If this ratio applies to all nurseries, up to 200 recently fledged juveniles (50% of a total of 400) arrive at nurseries each year. These birds originate from both South African and Namibia.

- Of 327 oystercatchers ringed in the 1997/98 and 1998/99 seasons and predicted to still be alive at 6 months, 41 (12.5%) were resighted at the Walvis Bay/Swakopmund nursery during this study. Assuming that all nurseries support the same proportion of South African-ringed oystercatchers (an assumption that may be flawed if the Lüderitz roosts are dominated by Namibian birds), and considering that Walvis Bay holds 30% of all long-distance dispersers, 42% of oystercatchers ringed in the two seasons will have dispersed to nurseries. Furthermore, because unringed oystercatchers are just as likely to undertake a long-distance migration as ringed birds, 42% can be considered the representative proportion of South African juveniles that employ a long-distance dispersal strategy.

- The diet of juvenile oystercatchers at Walvis Bay is diverse and dominated by washed up prey. Species such *Dosinia lupinus, Discinisca tenuis* and *Semimytilus algosus* have not previously been recorded in the prey spectrum of the African Black Oystercatcher. *Dosinia* and *Discinisca* were the dominant prey species, but foraging dispersion was highly opportunistic in response to seasonal variations in prey availability and abundance. As more profitable, albeit temporary, resources became available elsewhere, primary foraging habitats were temporarily abandoned. Opportunistic scavenging on kelp lice, jellyfish and barnacles was observed on several occasions. At Swakopmund, habitat diversity was low and movements in response to prey availability few. The oystercatchers fed exclusively on mussels and limpets, and except for occasional foraging on washed up mussels along the high water mark, foraging rhythms followed a strict tidal regime.

- At the outset of this study it was hypothesised that inexperienced juvenile oystercatchers target specific nursery sites because these provide them with important ecological requirements, namely the absence of adult competition and the availability of food resources that are abundant, easy to process and available at all stages of the tidal cycle. Both these requirements are met at the Walvis Bay/Swakopmund nursery, making it an ideal foraging environment for young birds while they improve their foraging and prey handling skills.

- Foraging strategies and activity rhythms differed markedly between Walvis Bay and Swakopmund. At Walvis Bay, foraging activity was tidally independent, except in May/Jun, when the majority of the oystercatchers foraged on mussels and limpets at Bird Rock. During the summer visits (Nov/Dec and Feb/Mar) birds foraged for four hours in the morning (sunrise–10:00) and a further four hours, on average, in the late afternoon and evening (14:00–sunset). No foraging activity was consistently observed between 10:00 and 14–15:00 when birds roosted. In winter (Aug/Sep), shorter day-length caused small numbers to continue foraging during the midday period. Throughout the study, the majority of the birds returned to the roost at sunset and no nocturnal foraging activity could be detected at Walvis Bay. This finding was supported by calculations of their daily energy intake (DEI), suggesting that juveniles at Walvis Bay do not need to forage at night to meet daily energetic demands. The DEI ranged seasonally from 960–1152 $kJ.d^{-1}$, and compares well with a predicted DEI of 1118 $kJ.d^{-1}$ for African Black Oystercatchers.

- Once the hypothesis of limited nocturnal foraging at Walvis Bay was substantiated by juvenile energetics, it was tested whether birds time their afternoon departure from the roost so as to fill their oesophagus during the afternoon's foraging bout and return to the roost at sunset with the maximum amount of stored food in their oesophagus. Daytime activity patterns and movements to and from the roost were, however, only partially explained by digestion and oesophagus filling rates (based on data from captive Eurasian Oystercatchers). In Aug/Sep and Feb/Mar, birds are predicted to require 4–5 hours to fill their oesophagus and could therefore return to the roost at sunset with it filled to capacity. Due to lower intake rates in Nov/Dec, birds are predicted to require eight hours to fill their oesophagus and this could not be accomplished during their daytime foraging time.

- At Swakopmund, birds actively foraged for 57% of the time spent on the shore, resulting in 234 minutes of daytime foraging. This value is comparable with the upper range of adult foraging times obtained within the breeding range. Foraging efficiency cannot be compared with that of adults in other regions and seasons, but the results do suggest that conditions at Swakopmund are sufficiently good for juveniles to achieve intake rates similar to those of adults. Nocturnal foraging was confirmed at this site, but due to lack of suitable night-vision equipment exact foraging times could not be determined. These were assumed to equal diurnal foraging minutes and based on this assumption, a foraging time of 446 minutes.d^{-1} was estimated for juvenile oystercatchers at Swakopmund. This relates to a DEI of 950 kJ.d^{-1}, close to the lower limit of performance at Walvis Bay, as well as to the predicted DEI for African Black Oystercatchers.

- The oystercatchers at the Walvis Bay/Swakopmund nursery displayed no evidence of an age-related dominance hierarchy. In strong contrast to other oystercatcher species, only very infrequent instances of intra-specific aggression and food stealing could be observed during this study and encounters had no significant negative effect on intake rates. Kleptoparasitism is most productive for the parasite if there are numerous more experienced conspecifics to steal from and when handling times are long, leaving greater opportunity for successful food stealing. Neither of these conditions, however, apply at Walvis Bay. Experienced foragers (adults) are absent and there were no differences between the foraging performance of different juvenile age classes. Furthermore, when feeding on washed up prey, handling times were short due to the ease with which items could be opened and eaten.

- Oystercatchers were far more wary of kleptoparasitic Cape Gulls than of conspecifics and abandoned prey rather than risking a fight. Gull pressure was seasonal at Walvis Bay and effectively absent from Swakopmund. In May/Jun, kleptoparasitism was intense enough for oystercatchers to lose food items in aggressive encounters and, when the majority of the Walvis Bay oystercatchers foraged opportunistically for a short period in a drained evaporation pan in Aug/Sep, intake rates were reduced by up to 32% by gulls. During the remainder of the study energetic loss to oystercatchers from kleptoparasitism represented less than 1% of their intake rates.

- Black-backed Jackals, common in the Walvis Bay area, were largely ignored by the oystercatchers, and an animal had to move in close proximity of the roost (< 20 m) for the oystercatchers to take flight. Although jackals had little effect on juvenile African Black Oystercatchers, high predation risk is thought to be one of the reasons why the birds do not breed in a habitat that offers such favourable foraging conditions.

Towards an explanation for dichotomous juvenile dispersal

- Both long- and short-distance dispersal holds benefits and costs for the dispersing juvenile. Oystercatchers that migrate to a nursery must be able to meet the energetic costs of the journey but, once there, they benefit from favourable foraging conditions that result in intake rates comparable to those of adults in the breeding range. Furthermore, competition with territorial adults is absent and the incidence of interference by conspecifics is low. Short-distance dispersers that remain within the adults' range do not incur the same energetic costs of long-distance travel but are likely to experience higher levels of aggression and interference from adults.

- The choice of dispersal strategy was hypothesised to be triggered either by body condition at time of fledging or by hatching date. Body condition was determined for all resighted juveniles (i.e. confirmed short- or long-distance dispersers) from body mass and tarsus measurements obtained at the time of ringing. Heavier and larger juveniles were predicted to select the long-distance dispersal strategy (because of their greater energetic "cushion") but analyses revealed no significant difference in condition between juveniles employing the two strategies. Similarly, hatching dates for all resighted juveniles (based on the age at ringing) were scored against the first hatching date of the season (day 1), but were not significantly different between short- and long-distance dispersers.

- Neither body condition at fledging nor hatching date can explain the dispersal strategy chosen by a juvenile. If there is a genetic basis to the dispersal behaviour of the African Black Oystercatcher it must be in the form of a balanced polymorphism to be maintained in the population.

What does the future hold for these nurseries?

- The discovery of large numbers of South African juveniles in nurseries outside the adult breeding range has increased the spectrum of conservation considerations for African Black Oystercatchers. Conserving nursery sites and ensuring the survival of the juveniles within them has become as important as the conservation measures implemented in South Africa to enhance the productivity of the population. Conservation successes in South Africa may lead to even greater numbers of juveniles migrating to nurseries in the future.

- Because nurseries need to fulfil specific ecological requirements of juvenile oystercatchers (plentiful food resources and no adult competition), the number of suitable nursery sites is finite. In the event of a nursery such as Walvis Bay/Swakopmund no longer being able to support large numbers of juveniles, it is unlikely that all the birds could be absorbed into other existing nurseries or that new nurseries will form. The continued spread of the alien Mediterranean Mussel may, however, enhance the food resources at Walvis Bay and other nurseries in the future. Walvis Bay is a large and important port and fishing harbour and is increasingly under threat by growing human pressure. Concerns have been raised that increasing rates of sedimentation in the lagoon and reduced tidal flow is destroying tidal habitat. Sedimentation is a natural process in coastal inlets – Sandwich Harbour, an undisturbed wetland 50 km south of Walvis Bay, used to support large numbers of juvenile oystercatchers in the 1970s but large-scale geomorphological changes in the area have significantly reduced suitable foraging habitats for oystercatchers. Counts over the last decade at Sandwich Harbour have reported far fewer oystercatchers and numbers frequently fall below ten individuals. These natural geomorphological processes can, however, be accelerated by human activities.

- The other four oystercatcher nurseries are located in very remote areas or where human access is restricted and face no immediate threats.

- Opportunistic juveniles utilise a wide range of foraging habitats in Walvis Bay and move between spatially disjunct areas to meet their year-round energetic requirements. This makes conservation planning for the area difficult. Large-scale changes to the Walvis Bay Lagoon could lead to the drying out of tidal habitats such as the *Dosinia* mudflat, as well as the cessation of *Discinisca* and *Semimytilus* wash-up events. While such changes will influence the distribution and activity rhythms of the oystercatchers, it is not certain that it will lead to a reduction in numbers *per se*. The apparent low incidence of intra-specific competition, as well as the seasonal variation in numbers at the Walvis Bay/Swakopmund nursery, suggests that the juvenile population at the nursery is not currently at carrying capacity. Furthermore, Bird Rock is a rich food resource that was under-utilised by the birds for the majority of this study. It represents a resource that birds can fall back on, should primary habitats suffer food shortages or disappear entirely. Here too, the alien mussel should serve to increase the abundance of mussels on rocky shores between Bird Rock and Swakopmund.

REFERENCES

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* **49**: 227-265.

Baker, A.J. 1974. Ecological and behavioural evidence for the systematic status of New Zealand Oystercatchers (Charadriiformes: Haematopodidae). *Life Sciences Contributions 96,* Royal Ontario Museum pp. 1-34.

Baker, A.J. 1975. Morphological variation, hybridisation and systematics of New Zealand oystercatchers (Charadriiformes: Haematopodidae). *J. Zool.* **175**: 357-390.

Baker, A.J. & Hockey, P.A.R. 1984. Behavioural and vocal affinities of the African Black Oystercatcher (*Haematopus moquini*). *Wilson Bull.* **96**: 656-671.

Berry, H.H. & Berry, C.U. 1975. A check list and notes on the birds of Sandvis, South West Africa. *Madoqua* **9**: 5-18.

BirdLife International 2000. *Threatened birds of the world.* Lynx Edicions and BirdLife, Barcelona and Cambridge, UK.

Braine, S. 1987. Extension of the breeding range of the African Black Oystercatcher *Haematopus moquini. Madoqua* **15**: 87-88.

Branch, G.M. & Branch, M.L. 1981. *The living shores of Southern Africa.* Struik, Cape Town.

Branch, G.M., Griffiths, C.L., Branch, M.L. & Beckley, L.E. 1994. *Two Oceans. A guide to the marine life of Southern Africa.* David Philip, Cape Town.

Burger, L. & Seely, M.K. 1998. Walvis Bay Lagoon Integrated Environmental Management Plan. Environmental Evaluation Unit, University of Cape Town and Desert Research Foundation of Namibia.

Cadman, M.D. 1980. Age-related foraging efficiency of the American Oystercatcher (*Haematopus palliatus*). Unpubl. M.Sc. thesis, University of Toronto.

De Boer, W.F. & Bento, C.M. 1999. Birds of Inhaca Island, Mozambique. *Mondi BLSA Guide* 22. BirdLife South Africa, Johannesburg.

Dingle, H. 1996. *Migration: The biology of life on the move.* Oxford University Press, New York and Oxford.

Ens, B.J. & Goss-Custard, J.D. 1984. Interference among oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe Estuary. *J. Anim. Ecol.* **53**: 217-231.

Goss-Custard, J.D., & Durell, S.E.A. le V. dit 1983. Individual and age differences in the feeding ecology of oystercatchers *Haematopus ostralegus* wintering on the Exe Estuary, Devon. *Ibis* **125**: 155-171.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit 1987a. Age-related effects in oystercatchers *Haematopus ostralegus,* feeding on mussels, *Mytilus edulis.* I. Foraging efficiency and interference. *J. Anim. Ecol.* **56**: 521-536.

Goss-Custard, J.D., & Durell, S.E.A. le V. dit 1987b. Age-related effects in oystercatchers *Haematopus ostralegus,* feeding on mussels, *Mytilus edulis.* II. Aggression. *J. Anim. Ecol.* **56**: 537-548.

Goss-Custard, J.D, & Durell, S.E.A. le V. dit 1987c. Age-related effects in oystercatchers *Haematopus ostralegus,* feeding on mussels, *Mytilus edulis.* III. The effect of interference on overall intake rate. *J. Anim. Ecol.* **56**: 549-558.

Goss-Custard, J.D., Cayford, J.T. & Lea, S.G. 1998. The changing trade-off between food finding and food stealing in juvenile oystercatchers. *Anim. Behav.* **55**: 745-760.

Goss-Custard, J.D., Cayford, J.T. & Lea, S.G. 1999. Vigilance during food handling by oystercatchers *Haematopus ostralegus* reduces the chances of losing prey to kleptoparasites. *Ibis* **141**: 368-376.

Goss-Custard, J.D. & Sutherland, W.J. 1984. Feeding specializations in oystercatchers *Haematopus ostralegus*. *Anim. Behav.* **32**: 299-301.

Groves, S. 1984. Chick growth, sibling rivalry, and chick production in American Black Oystercatchers. *The Auk* **101**: 525-531.

Gurney, J.H. 1872. *Notes on the birds of Damaraland and the adjacent countries of South-West Africa*. John van Voorst, London.

Hale, W.G. 1980. *Waders.* Collins, London.

Heather-Clark, S. 1996. An environmental overview of the Walvis Bay 'bay area', Namibia. Unpubl. M. Phil. thesis, University of Cape Town.

Hines, C., & Kolberg, H. 1996. Importance of wetland management in arid regions. pp. 75-77 in: Tarr, P. (ed.). *Namibia Environment Volume 1.* Ministry of Environment and Tourism, Namibia.

Hockey, P.A.R. 1981a. Morphometrics and sexing of the African Black Oystercatcher. *Ostrich* **52**: 244-247.

Hockey, P.A.R. 1981b. Feeding techniques of the African Black Oystercatcher *Haematopus moquini.* pp. 99-115 in: Cooper, J. (ed.). *Birds of the Sea Shore.* African Seabird Group, Cape Town.

Hockey, P.A.R. 1983a. The distribution, population size, movements and conservation of the African Black Oystercatcher *Haematopus moquini. Biol. Conserv.* **25**: 233-262.

Hockey, P.A.R. 1983b. Aspects of the breeding biology of the African Black Oystercatcher. *Ostrich* **54**: 26-35.

Hockey, P.A.R. 1984a. Behaviour patterns of non-breeding African Black Oystercatchers *Haematopus moquini* at offshore islands. pp. 707-727 in: Ledger, J.A. (ed.). *Proceedings of the 5th Pan-African Ornithological Congress, Lilongwe Malawi.* Southern African Ornithological Society, Johannesburg.

Hockey, P.A.R. 1984b. Growth and energetics of the African Black Oystercatcher *Haematopus moquini. Ardea* **72**: 111-117.

Hockey, P.A.R. 1986. Family Haematopodidae. pp 190-193 in: Urban, E.K., Fry, C.H. & Keith, S. (eds.). *The Birds of Africa, Vol. II.* Academic Press, London.

Hockey, P.A.R. 1987. The influence of coastal utilisation by man on the presumed extinction of the Canarian Black Oystercatcher *Haematopus meadewaldoi* Bannerman. *Biol. Conserv.* **39**: 49-62.

Hockey, P.A.R. 1996a. Family Haematopodidae. pp 308-325 in: del Hoyo, J., Elliott, A. & Sargatal, J. (eds.). *Handbook of the Birds of the World, Vol 3.* Lynx Edicions, Barcelona.

Hockey, P.A.R. 1996b. *Haematopus ostralegus* in perspective: comparisons with other Oystercatchers. pp. 251-285 in: Goss-Custard, J.D. (ed.). *The Oystercatcher. From individuals to populations.* Oxford University Press.

Hockey, P.A.R. & Bosman, A.L. 1983. Conservation-management of the Walvis Bay Lagoon with special reference to its importance as a bird habitat. Percy FitzPatrick Institute Report, Association of Round Tables of South Africa, Walvis Bay Section.

Hockey, P.A.R., Navarro, R.A., Kalejta B. & Velasquez, C.R. 1992. The riddle of the sands: why are shorebird densities so high in southern estuaries? *Am. Nat.* **140**: 961-979.

Hockey, P.A.R., Turpie, J.K., & Velásquez, C.R. 1998. What selective pressures have driven the evolution of deferred northward migration by juvenile waders? *J. Avian Biol.* **29**: 325-330.

Hockey, P.A.R. & Underhill, L.G. 1984. Diet of the African Black oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related variation. *S. Afr. J. Zool.* **19**: 1-11.

Hockey, P.A.R. & van Erkom Schurink, C. 1992. The invasive biology of the mussel *Mytilus galloprovincialis* on the southern African coast. *Trans. Roy. Soc. S. Afr.* **48**: 123-139.

Hulscher, J.B. 1976. Localisation of cockles (*Cardium edule* L.) by the oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. *Ardea* **64**: 292-310.

Kensley, B.F. & Penrith, M.J. 1977. Biological survey of Sandvis 1, introduction and faunal list. *Madoqua* **10**: 181-190.

Kersten, M. 1996. Time and energy budgets of oystercatchers *Haematopus ostralegus* occupying territories of different quality. *Ardea* **84A**: 291-310.

Kersten, M. & Brenninkmeijer, A. 1995. Growth, fledging success and post-fledging survival of juvenile Oystercatchers *Haematopus ostralegus. Ibis* **137**: 396-404.

Kersten, M. & Visser, W. 1996. The rate of food processing in the oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. *Funct. Ecol.* **10**: 440-448.

Leseberg, A., Hockey, P.A.R. & Loewenthal, D. 2000. Human disturbance and the chick-rearing ability of African Black Oystercatchers (*Haematopus moquini*): a geographical perspective. *Biol. Conserv.* **96**: 379-385.

Loewenthal, D. 1998. Population dynamics and conservation of the African Black Oystercatcher, *Haematopus moquini.* Unpubl. M.Sc. thesis, University of Cape Town.

Marchant, S. & Higgins, P.J. 1993. *Handbook of Australian, New Zealand and Antarctic Birds. Volume 2 Raptors to Lapwings*. Oxford University Press, Melbourne.

McLachlan, A., Wooldridge, T., Schramm, M. & Kühn, M. 1980. Seasonal abundance, biomass and feeding of shore birds on sandy beaches in the east Cape, South Africa. *Ostrich* **51**: 44-52.

Nagy, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* **57**: 111-128.

Nagy, K.A., Girard, I.A. & Brown, T.K. 1999. Energetics of free-ranging mammals, reptiles, and birds. *Ann. Rev. Nutr.* **19**: 247-277.

Noli-Peard, K.R. & Williams, A.J. 1991. Wetlands of the Namib Coast. *Madoqua* **17**: 147-153.

Norton-Griffiths, M.N. 1969. The organisation, control and development of parental feeding in the Oystercatcher (*Haematopus ostralegus*). *Behaviour* **34**: 55-114.

Randall, R.M. 1989. Jackass Penguins. pp. 244-256 in: Payne, A.I.L. & Crawford, R.J.M. (eds.). *Oceans of Life off Southern Africa.* Vlaeberg, Cape Town.

Randall, R.M., Randall, B.M., Cooper, J., La Cock, G.D. & Ross, J.B. 1987. Jackass Penguin *Spheniscus demersus* movements, inter-island visits, and settlement. *J. Field Ornithol.* **58**: 445-455.

Rappole, J.H. 1995. The ecology of migrant birds: A neotropical perspective. Smithsonian Institution Press, Washington & London.

Ryan, P.G. 1983. The feeding ecology of multispecies flocks of waders (Charadrii) on an island rocky shore: competition or coexistence? Unpubl. B.Sc. (Hons) thesis, University of Cape Town.

Simmons, R.E. 1997. Ecological factors promoting large bird populations at Walvis Bay. in: Environmental Management Committee (eds.). *Towards an integrated management and development plan for the Walvis Bay Lagoon and environs.* Paper delivered at a Workshop, 22 July 1997, Walvis Bay.

Simmons, R.E. 2000. What is the world population of the Chestnutbanded Plover? *Bird Numbers* **9**: 45.

Simmons, R.E., Boix-Hinzen, C., Barnes, K.N., Jarvis, A.M. & Roberton, A. 1998. Important bird areas of Namibia. pp 319-324 in: Barnes, K.N. (ed.). *The important bird areas of Southern Africa.* BirdLife South Africa, Johannesburg.

Sitters, H.P. 2000. The role of night-feeding in shorebirds in an estuarine environment with specific reference to mussel-feeding oystercatchers. Unpubl. Ph.D. thesis, University of Oxford.

South African Weather Bureau (SAWB) – All temperature variables for Cape Town (1999 & 2000). Weather@iafrica.com

Stillman, R.A., Goss-Custard, J.D., Clarke, R.T. & Durell, S.E.A. Le V. dit 1996. Shape of interference function in a foraging vertebrate. *J. Anim. Ecol.* **65**: 813-824.

Summers, R.W. & Cooper, J. 1977. The population, ecology and conservation of the African Black Oystercatcher *Haematopus moquini. Ostrich* **48**: 28-40.

Tree, A.J. 1998. Highlights of a seven-week visit to Namibia in early 1998. *Lanioturdus* **31**: 21-27.

Turpie, J.K. & Hockey, P.A.R. 1993. Comparative diurnal and nocturnal foraging behaviour and energy intake of premigratory Grey Plovers *Pluvialis squatarola* and Whimbrel *Numenius phaeopus* in South Africa. *Ibis* **135**: 156-165.

Underhill, L.G. 2000. Chestnutbanded Plover *Charadrius pallidus*. p.45 in: Barnes. K.N. (ed.). *The Eskom Red Data Book of birds of South Africa and Swaziland.* BirdLife South Africa, Johannesburg.

Ward, D. 1990. The demography, diet and reproductive success of African Black Oystercatchers on a sandy beach. *Ostrich* **61**: 125-133.

Ward, J.D. 1997. Sedimentation of the Walvis Bay Lagoon. in: Environmental Management Committee (eds.). *Towards an integrated management and development plan for the Walvis Bay Lagoon and environs.* Paper delivered at a Workshop, 22 July 1997, Walvis Bay.

Webb, S.C. & Korrûbel, J.L. 1994. Shell weakening in marine mytilids attributable to Blue-Green Alga *Mastigocoleus* Sp. (*Nostochopsidaceae*). *J. Shell. Res.* **13**: 11-17.

Wilhelm, M. 1999. Comparative foraging performance of African Black Oystercatchers *Haematopus moquini* on sandy beaches and artificial rocky shores. Unpubl. B.Sc. (Hons) thesis, University of Cape Town.

Williams, A.J. 1991. Wetland birds and conservation in Namibia: an overview. *Madoqua* **17**: 245-248.

Wunderle, J.M. 1991. Age-specific foraging proficiency in birds. pp. 273-324 in: Power, D.M. (ed.). *Current Ornithology Volume 8.* Plenum Press, New York.

Zar, J.H. 1996. *Biostatistical analysis*. Prentice-Hall, New Jersey.

Zwarts, L., Cayford, J.T., Hulscher, J.B., Kersten, M., Meire, P.M. & Triplet, P. 1996a. Prey size selection and intake rate. pp. 30-55 in: Goss-Custard, J.D. (ed.). *The Oystercatcher. From individuals to populations.* Oxford University Press.

Zwarts, L., Ens, B.J., Goss-Custard, J.D., Hulscher, J.B. & Kersten, M. 1996b. Why oystercatchers *Haematopus ostralegus* cannot meet their daily energy requirements in a single low water period. *Ardea* **84A**: 269-290.

Appendices

Appendix 1. The seasonal energy content (kJ.g dry mass^{-1}) of prey species collected during the study.

N/C – not collected.

Prey species	Aug/Sep 99	Nov/Dec 99	Feb/Mar 00	May/Jun 00
Dosinia lupinus	18.21	18.17	17.26	17.69
Discinisca tenuis	17.91	17.99	N/C	17.94
Mytilus galloprovincialis	18.68	N/C	15.11	16.89
Perna perna	18.45	16.82	14.37	16.41
Cymbula granatina	16.43	17.40	17.43	16.86
Cymbula miniata	N/C	15.95	14.09	15.02
Scutellastra granularis	16.96	15.47	15.96	16.39
all limpets combined	16.66	16.27	15.84	16.14
all mussels combined	18.56	16.82	14.70	16.65

Appendix 2. The seasonal length–dry weight regression equations for the prey species collected during the study. Given in $W = aL^b$ format, where W = dry flesh weight (g) and L = shell length (mm). N/C – not collected.

Prey species	Aug/Sep 99	Nov/Dec 99	Feb/Mar 00	May/Jun 00
Dosinia lupinus	$W = 1.80^{-5} L^{2.9938}$	$W = 1.87^{-5} L^{3.0043}$	$W = 4.57^{-5} L^{2.7114}$	$W = 3.21^{-5} L^{2.8119}$
Dosinia lupinus (pan)	$W = 5.11^{-6} L^{3.2984}$	N/C	N/C	N/C
Discinisca tenuis	$W = 1.19^{-5} L^{3.0084}$	$W = 4.92^{-5} L^{2.6884}$	N/C	$W = 1.53^{-5} L^{3.0625}$
Mytilus galloprovincialis	$W = 1.17^{-5} L^{2.9334}$	N/C	$W = 2.13^{-5} L^{2.5511}$	N/C
Perna perna (rocks)	$W = 9.46^{-6} L^{2.8266}$	$W = 4.11^{-5} L^{2.3343}$	$W = 2.61^{-5} L^{2.4437}$	$W = 4.32^{-5} L^{2.3142}$
Perna perna (washed up)	N/C	N/C	$W = 2.15^{-5} L^{2.3662}$	N/C
Cymbula granatina	$W = 4.41^{-6} L^{3.2320}$	$W = 8.51^{-7} L^{3.7435}$	$W = 9.66^{-7} L^{3.6751}$	$W = 2.92^{-6} L^{3.3420}$
Cymbula miniata	N/C	$W = 2.78^{-6} L^{3.3908}$	$W = 1.75^{-5} L^{2.8410}$	$W = 7.16^{-5} L^{2.4637}$
Scutellastra granularis	$W = 4.42^{-6} L^{3.3492}$	$W = 1.56^{-6} L^{3.7084}$	$W = 2.90^{-6} L^{3.4363}$	$W = 1.17^{-4} L^{2.3576}$
all limpets combined	$W = 8.71^{-6} L^{3.1097}$	$W = 3.60^{-6} L^{3.3608}$	$W = 4.13^{-6} L^{3.2793}$	$W = 5.33^{-5} L^{2.5675}$
all mussels combined	$W = 1.78^{-5} L^{2.7207}$	$W = 4.11^{-5} L^{2.3343}$	$W = 7.71^{-5} L^{2.2008}$	$W = 4.32^{-5} L^{2.3142}$

The importance of the Walvis Bay wetlands to waterbirds and the threats to its future ecological integrity.

Walvis Bay with its lagoon and tidal mudflats is rated as one of the most important wetlands for waterbirds in Africa and certainly supports more waterbirds than any other wetland in southern Africa (Simmons *et al.* 1998). In the austral summer, Walvis Bay Lagoon may hold 90 000 birds (peak counts estimate use by up to 150 000 wetland birds). Of these, 50% are non-breeding intra-African migrants, 45% are nonbreeding Palearctic migrants and the remaining 5% are resident coastal species (Noli-Peard & Williams 1991, Hines & Kolberg 1996). Furthermore, with up to 18 species regularly occurring in numbers > 1% of their global population, the Walvis Bay wetlands are internationally important (Simmons 1997). Together with Sandwich Harbour, 80-90% of the southern African subcontinent's flamingo population winters at these two coastal wetlands (Simmons 1997). Furthermore, Walvis Bay holds 60% and Sandwich Harbour holds a further 39% of the Namibian population of the *pallidus* race of the Chestnut-banded Plover, a species that breeds primarily in Namibia and Botswana (Simmons 2000, Underhill 2000).

These large bird populations present in the coastal wetlands at Walvis Bay and Sandwich Harbour are a response to an upwelling system that begins at Lüderitz, bringing deep nutrient rich water to the surface and transporting it northwards in the Benguela Current. Only once in the warmer waters of the central Namibian coast, where onshore winds push nutrients ashore, do primary and secondary productivity in the form of algal and zooplankton blooms form the basis of the food chain leading to birds (delayed blooming effect – Simmons 1997). This coastline supports an abundance of invertebrates both on rocky and sandy shores. Shorebird surveys undertaken along these shores reflect this pattern of nutrient transport and in some years shorebird densities are an order of magnitude higher along the central Namibian coast, especially between Swakopmund and Walvis Bay (450 birds.km^{-1}), than anywhere else in southern Africa (Simmons 1997, Simmons *et al.* 1998). Hockey *et al.* (1992) analysed migratory wader densities at 31 coastal wetlands in the western Palearctic and Ethiopian regions during the nonbreeding season and concluded that wader densities are higher in southern latitudes due to a higher carrying capacity of wetlands further south.

Damara Terns *Sterna balaenarum*, a globally near-threatened species, rely heavily on the northern section of the 30 km stretch of coastline between Swakopmund and Walvis Bay and their densest breeding colony (60 pairs.km^{-2}) is found here (Simmons *et al.* 1998).

Threats to the Walvis Bay Lagoon and wetlands

These can be grouped into the following broad categories:

- Pollution associated with the harbour, fish processing factories and the salt works;
- Sedimentation of the lagoon and a reduced tidal sweep in the bay; and
- Uncontrolled recreational activities and further coastal development.

Pollution

Walvis Bay is Namibia's only large commercial harbour and is used by a variety of shipping interests including container vessels, tankers, cargo ships and fishing vessels (Burger & Seely 1998). Sources of pollution include solid waste and bilge water released from ships and the use of marine and antifouling paints containing lead and tributyl compounds that are highly toxic to marine organisms (Burger & Seely 1998). Recent upgrading of the harbour involved dredging of the sea floor, thereby risking the release of toxic contaminants from the sediments and their circulation throughout the lagoon. Furthermore, there is the constant threat of accidental crude oil or petrochemical spills that would quickly filter into the lagoon and directly affect foraging birds. The effluent from the fish processing factories (fish waste and oils) affects an already eutrophic system and could lead to anoxic conditions in the lagoon (Heather-Clark 1996). Independently of exogenous sources of toxins, Walvis Bay experiences regular natural sulphur eruptions that lead to marine die-offs (and may explain the abundance of washed up *Discinisca tenuis* and *Semimytilus algosus* – Chapter 2).

The Walvis Bay salt works, covering a surface area of 40 km^2 (K. Wearne, pers. comm.), do not contribute significantly to a pollution problem in the lagoon and bay. Water is pumped from the outer lagoon into a gravity-fed system of evaporation pans from which various crystallised minerals as well as the salt are extracted. If the hypersaline brine water should leak into the adjacent lagoon it could have negative effects on lagoon functioning and lead to osmotic shock amongst marine organisms. However, the evaporation pans are well maintained and such pollution is unlikely.

Sedimentation

Over the years much concern has been expressed about the possible loss of the Walvis Bay Lagoon because of sedimentation (Hockey & Bosman 1983, Heather-Clark 1996, Ward 1997, Simmons *et al.* 1998). Natural processes in the region (wind-blown dune sand) cause sedimentation and geomorphic changes to occur in coastal inlets over time, but anthropogenic influences can accelerate such changes (Ward 1997). The Walvis Bay system has been shaped by two major processes for millennia – prevailing southerly winds drive a strong longshore drift that transports and deposits sediments to form northward-directed sand spits such as Pelican Point. Pelican Point is estimated to grow by 17.4 m per year (Burger & Seely 1998) and increasingly prevents Atlantic swells from reaching and scouring the bay. These same winds promote the aeolian transport of large amounts of dune sand from the Kuiseb River delta into the lagoon (Hockey & Bosman 1983, Ward 1997). In the past, siltation was slow however, because flooding of the Kuiseb River and fast-flowing tidal water was responsible for large-scale sand removal from the lagoon (Hockey & Bosman 1983). Dredging is also thought to have augmented the water-borne sediment load in the lagoon (Burger & Seely 1998).

Development over the past 30 years has greatly reduced the extent of tidally flooded areas, decreasing tidal flushing and thereby accelerating siltation processes in the lagoon. The construction of an access road to the Salt Works truncated the southern section of the lagoon and dried out adjacent intertidal areas, although recent attempts, using culverts running under road, have been made to allow water to once again flood these areas (Burger & Seely 1998). Urban expansion in the north-east corner of the lagoon in the early 1980s further reduced the flooding area within Walvis Bay. The Salt Works destroyed large areas of naturally flooded salt pans when first developed but at the same time provide an array of shallow water feeding habitats utilised by a large proportion of the birds in the wetland (Noli-Peard & Williams 1997).

These developments have all contributed in reducing the volume of water entering the lagoon at high tide and have significantly reduced the scouring effect so important in keeping the bay and lagoon clear of suspended sediments.

Uncontrolled recreational use

Walvis Bay and the surrounding coastline (including the Mile 4 coast at Swakopmund) experience intense pressure from recreational fishermen and most of these areas are accessible to off-road vehicles (ORVs). ORVs can cause considerable disturbance to roosting birds and, more importantly, nests and chicks of resident breeding species such as Damara Terns *Sterna balaenarum*, White-fronted Plovers *Charadrius marginatus* and Chestnut-banded Plovers *C. pallidus* are easily destroyed (pers. obs). The Damara Tern breeding colony between Walvis Bay and Swakopmund has recently been cordoned off with a fence. Uncontrolled off-road driving damages dune vegetation and contributes to dune erosion and the further sedimentation of wetland habitats.

Numerous tour operators fly over the Walvis Bay Lagoon on a daily basis and height restrictions are regularly violated. These 'planes cause large scale disturbance of waterbirds, especially flamingos and oystercatchers that take to the air in large flocks each time a 'plane flies over them (pers obs.). Water sports such as wind surfing and kayaking have increased over the years but pose little disturbance to birds and motorised boats are only allowed into the lagoon during fishing competitions (Burger & Seely 1998).

Any further urban development that encroaches on the lagoon and on important bird foraging habitats would seriously impact on the ecological sustainability of the Walvis Bay wetlands: rather, efforts to restore dried up tidal areas and to reduce sources of sedimentation should be treated as a priority.

The current conservation status of the wetlands and management plans for the future

Whilst still an enclave of South Africa, Walvis Bay was declared a nature reserve in 1991 under the Cape Nature and Environmental Conservation Ordinance. However, when the town was ceded to Namibia in 1994, the reserve was not re-promulgated and, besides its Ramsar status (proclaimed a Wetland of International Importance in 1995), the area is not formally protected (Burger & Seely 1998, Simmons *et al.* 1998). Concern over the future of Walvis Bay has been expressed for many years (Hockey & Bosman 1983, Noli-Peard & Williams 1991, Williams 1991), but only very recently, with the formation of the Coastal Environmental Trust of

Namibia (CETN), has progress been made to ensure the future survival of the Walvis Bay Lagoon and wetlands. A CETN workshop in 1997 brought major role players together (CETN, Namibian Ministry of Environment and Tourism – MET, Walvis Bay Municipality and the Namibian Ports Authority –NAMPORT) and the key conservation issues and management plans were identified. The Danish Co-operation for Environment and Development (DANCED) has recently become involved, offering financial assistance in the formulation of an integrated coastal zone management plan for Namibia's Erongo region (which includes the Walvis Bay area). Baseline reports were compiled (Heather-Clark 1996) to aid in an overall management plan for the region and, in 1998, an integrated environmental management plan was drafted for the Walvis Bay Municipality (Burger & Seely 1998), providing recommendations (not detailed here) on how to restore and conserve the ecological integrity of the Walvis Bay Lagoon. Hopefully these recommendations will be set in motion soon – rectifying some of the development mistakes of the past, as well as ensuring the future sustainability of the Walvis Bay Lagoon and surrounding coastal areas.

References

Burger, L. & Seely, M.K. 1998. Walvis Bay Lagoon Integrated Environmental Management Plan. Environmental Evaluation Unit, University of Cape Town and Desert Research Foundation of Namibia.

Heather-Clark, S. 1996. An environmental overview of the Walvis Bay 'bay area', Namibia. Unpubl. M. Phil thesis, University of Cape Town.

Hines, C., & Kolberg, H. 1996. Importance of wetland management in arid regions. pp. 75-77 in: Tarr, P. (ed.). *Namibia Environment Volume 1.* Ministry of Environment and Tourism, Namibia.

Hockey, P.A.R. & Bosman, A.L. 1983. Conservation-management of the Walvis Bay Lagoon with special reference to its importance as a bird habitat. Percy FitzPatrick Institute Report, Association of Round Tables of South Africa, Walvis Bay Section.

Hockey, P.A.R., Navarro, R.A., Kalejta B. & Velasquez, C.R. 1992. The riddle of the sands: why are shorebird densities so high in southern estuaries? *Am. Nat.* **140**: 961-979.

Noli-Peard, K.R. & Williams, A.J. 1991. Wetlands of the Namib Coast. *Madoqua* **17**: 147-153.

Simmons, R.E. 1997. Ecological factors promoting large bird populations at Walvis Bay. in: Environmental Management Committee (eds.). *Towards an integrated management and development plan for the Walvis Bay Lagoon and environs.* Paper delivered at a Workshop, 22 July 1997, Walvis Bay.

Simmons, R.E. 2000. What is the world population of the Chestnutbanded Plover? *Bird Numbers* **9**: 45.

Simmons, R.E., Boix-Hinzen, C., Barnes, K.N., Jarvis, A.M. & Roberton, A. 1998. Important bird areas of Namibia. pp 319-324 in: Barnes, K.N. (ed.). *The important bird areas of Southern Africa.* BirdLife South Africa, Johannesburg.

Underhill, L.G. 2000. Chestnutbanded Plover *Charadrius pallidus.* p.45 in: Barnes. K.N. (ed.). *The Eskom Red Data Book of birds of South Africa and Swaziland.* BirdLife South Africa, Johannesburg.

Ward, J.D. 1997. Sedimentation of the Walvis Bay Lagoon. in: Environmental Management Committee (eds.). *Towards an integrated management and development plan for the Walvis Bay Lagoon and environs.* Paper delivered at a Workshop, 22 July 1997, Walvis Bay.

Williams, A.J. 1991. Wetland birds and conservation in Namibia: an overview. *Madoqua* **17**: 245-248.