DIET AND HABITAT USE BY THE AFRICAN BLACK OYSTERCATCHER *HAEMATOPUS MOQUINI* IN DE HOOP NATURE RESERVE, SOUTH AFRICA

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SUMMARY

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A study of the diet and habitat used by African Black Oystercatchers *Haematopus moquini* at De Hoop Nature Reserve, Western Cape Province, South Africa, showed that the area is important as a mainland habitat for the birds. Within the study site, the central sector, with rocky/mixed habitat and extensive wave-cut platforms, was a particularly important oystercatcher habitat, even though human use of this area was high. This positive association was apparently linked to the diversity of potential food items and the abundance of large brown mussel *Perna perna*, the major prey. In contrast, the diversity of prey species was lower in mixed/sandy habitat where the dominant prey was white mussel *Donax serra*. The diversity of prey (28 species) for the combined study area is higher than that recorded at any one site for the African Black Oystercatcher previously. This total includes several food items not previously recorded for the species (relatively large numbers of Cape false limpets *Siphonaria* spp. and low numbers of African periwinkle *Nodilittorina africana*, smooth turban shell *Turbo cidaris*, abalone *Haliotis midae*, spiral-ridged siffie *H. parva* and oblique arkshell *Barbatia obliquata*). The study shows that the establishment of the marine reserve was associated with increases in the modal sizes of the main prey species consumed.

Key words: African Black Oystercatcher, *Haematopus moquini*, diet, South Africa, numbers, territories, habitat, *Donax serra, Perna perna, Siphonaria* spp.

INTRODUCTION

Oystercatchers *Haematopus* spp. are a highly specialized group of birds adapted to foraging along the shores of oceans, large lakes and large rivers, but their main foraging areas are rocky intertidal zones and sandy beaches (Hockey 1996). In southern Africa, the endemic African Black Oystercatcher *Haematopus moquini* forages almost exclusively in the intertidal zones of rocky islands and rocky mainland shores (Randall & Randall 1982, Hockey & Underhill 1984) and mainland sandy habitats (McLachlan *et al*. 1980, Ward 1990).

Both these habitats are influenced to varying degrees by human activities, and research in the Sundays River dunefield in the Eastern Cape Province of South Africa (Watson & Kerley 1995) has demonstrated that humans and oystercatchers overlap in their use of sandy beaches. Some of these human activities reduce food availability (Siegfried *et al*. 1985, Hockey & Bosman 1986, Hockey 1987, Hockey *et al*. 1988). On the south coast of southern Africa, intake rates of African Black Oystercatchers are considered to be relatively lower than on the west coast where food is more abundant (Kopler *et al*. 2009), and the birds' ability to rear even a single chick could be compromised by relatively low levels of disturbance (Leseberg *et al*. 2000). Other human impacts, for example the introduction of alien invasive marine invertebrate species, may lead to increased food availability for oystercatchers and the exploitation of new foraging niches (Hockey & Van Erkom Schurinck 1992).

The benefits of protected areas for African Black Oystercatchers were demonstrated in a national survey of the species in March 1997 (Loewenthal 1998), which showed substantial increases in protected areas such as the Cape of Good Hope Nature Reserve since the initial survey in 1980. A significant increase (57%) in numbers of oystercatchers was also recorded at Goukamma Nature Reserve after its designation as a marine reserve in 1990 (Leseberg *et al*. 2000).

The food of African Black Oystercatchers is fairly well known (Hockey 1996). Studies include lists of hard-shelled prey items in middens (chick feeding piles) on the Eastern Cape mainland coast (McLachlan *et al*. 1980) and on St Croix Island (Randall & Randall 1982), and in other areas within their distribution range (Hockey & Underhill 1984). The main prey items of chicks on rocky shores include brown mussel *Perna perna*, black mussel *Choromytilus meridionalis* and ribbed mussel *Aulacomya ater*, limpets such as *Scutellastra* (formerly *Patella*) *granularis* and *S. argenvillei,* and alikreukel *Turbo sarmaticus* (Randall & Randall 1982, Hockey & Underhill 1984). A recent study using traditional diet analysis coupled with carbon and nitrogen stable isotope analysis, conducted on rocky shores on the southeast coast of South Africa (Kohler *et al*. 2009), has confirmed dietary partitioning between genders in breeding pairs of African Black Oystercatchers (noted by Hockey & Underhill 1984), and the preferential feeding of chicks with the limpet *S. cochlear* and the alien invasive Mediterranean mussel *Mytilus galloprovincialis*. In sandy habitats in the Eastern Cape, prey items such as white mussel *Donax* spp. and plough shells *Bullia* spp. have also been found in their diet (McLachlan *et al*. 1980, Ward 1990). These prey items include species eaten by humans (e.g., *P. perna*, white mussel *Donax serra* and *T.*

sarmaticus). No quantitative data on African Black Oystercatcher diet are available for the area from Saldanha Bay on the west coast to Robberg, near Plettenberg Bay, on the south coast. This includes De Hoop Nature Reserve (DHNR), which lies within a transition area between two marine biogeographical provinces (Emanuel *et al*. 1992). This paper presents quantitative data on the diet of African Black Oystercatchers within the reserve, and examines the relationship between diet and habitat.

STUDY SITE

DHNR (30°26'S 20°37'E) lies in the Western Cape Province of South Africa (Fig. 1). The reserve was proclaimed in 1957 and administered by the provincial agency Cape Nature Conservation (now a statutory board, CapeNature). Before 1986 the entire coast was open to the public, and vehicles were allowed to drive on the sandy beach. The reserve was a popular traditional venue for angling and the collection of intertidal organisms for bait and human use, all resulting in high levels of disturbance to shorebirds. Much of this human activity took place in the central part of the reserve coastline, at the end of the main access road to the coast. In March 1986, the entire coastline was included in the new proclaimed marine reserve. Although only day visitors were permitted within the reserve up to 1990, and their numbers remained low (<2500 per year) and fairly stable (DHNR records), the prohibition of angling and of collecting intertidal organisms by visitors to the coast is likely to have influenced the diet of the oystercatchers. In 1988 the reserve size was increased to 36 000 ha, and the coastline extended eastwards to a total of 43.1 km.

The study took place from 1984/85 to 1989/90, over the entire reserve coastline as demarcated in August 1984 (10.7 km). The study area was divided into three sectors on the basis of physical/ topographical characteristics: the eastern (3.1 km), central (2.0 km) and western (5.6 km) sectors. Three habitat types were identified in each sector: rocky habitat consisting of continuous stretches of rock of more than 200 m along the shore line; sandy habitat comprising continuous stretches of sand of more than 200 m along the

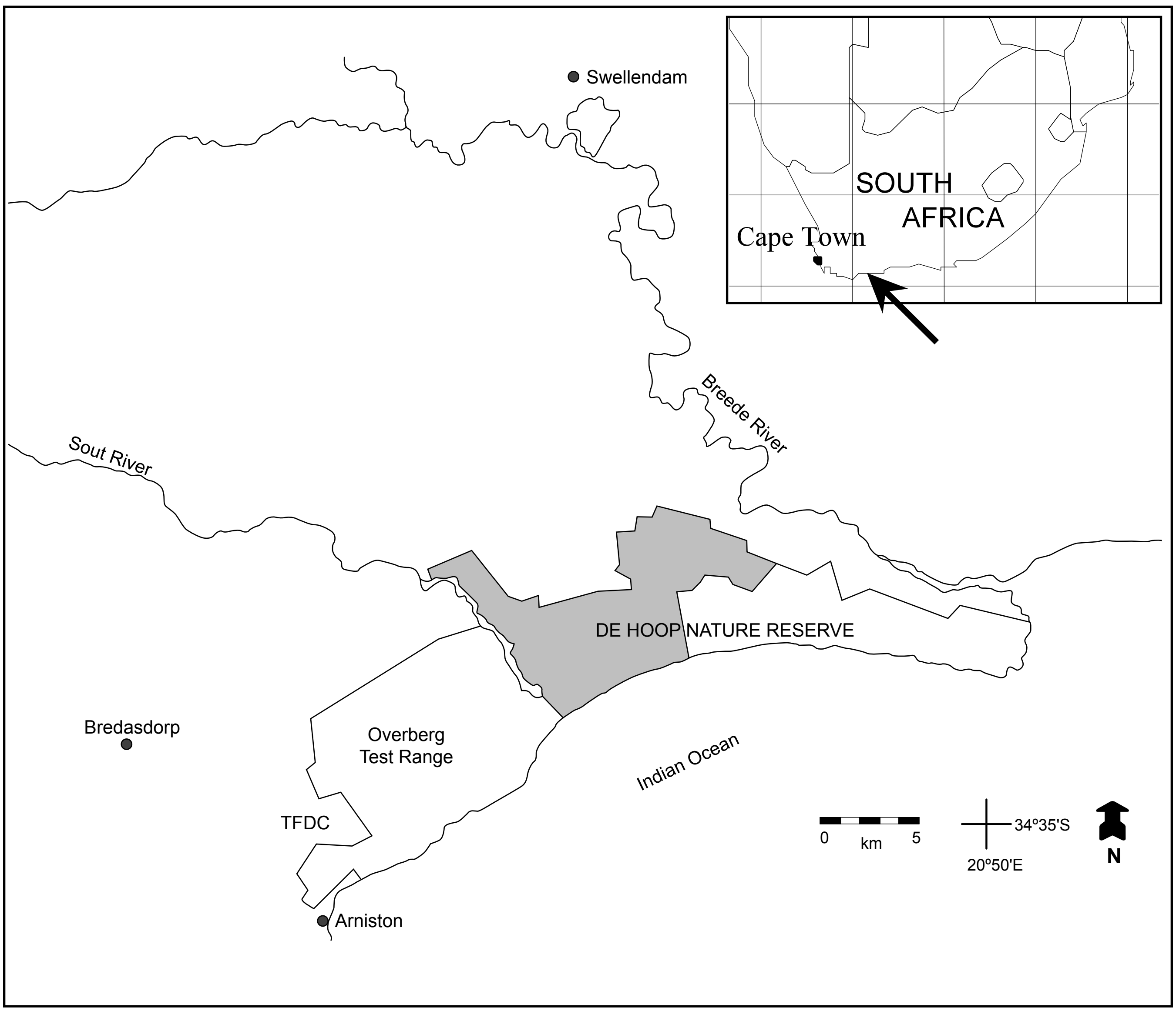

Fig. 1. The study area, De Hoop Nature Reserve, in relation to South Africa (inset). Shading indicates the size of the reserve and length of the coastline at the start of the present study (August 1984).

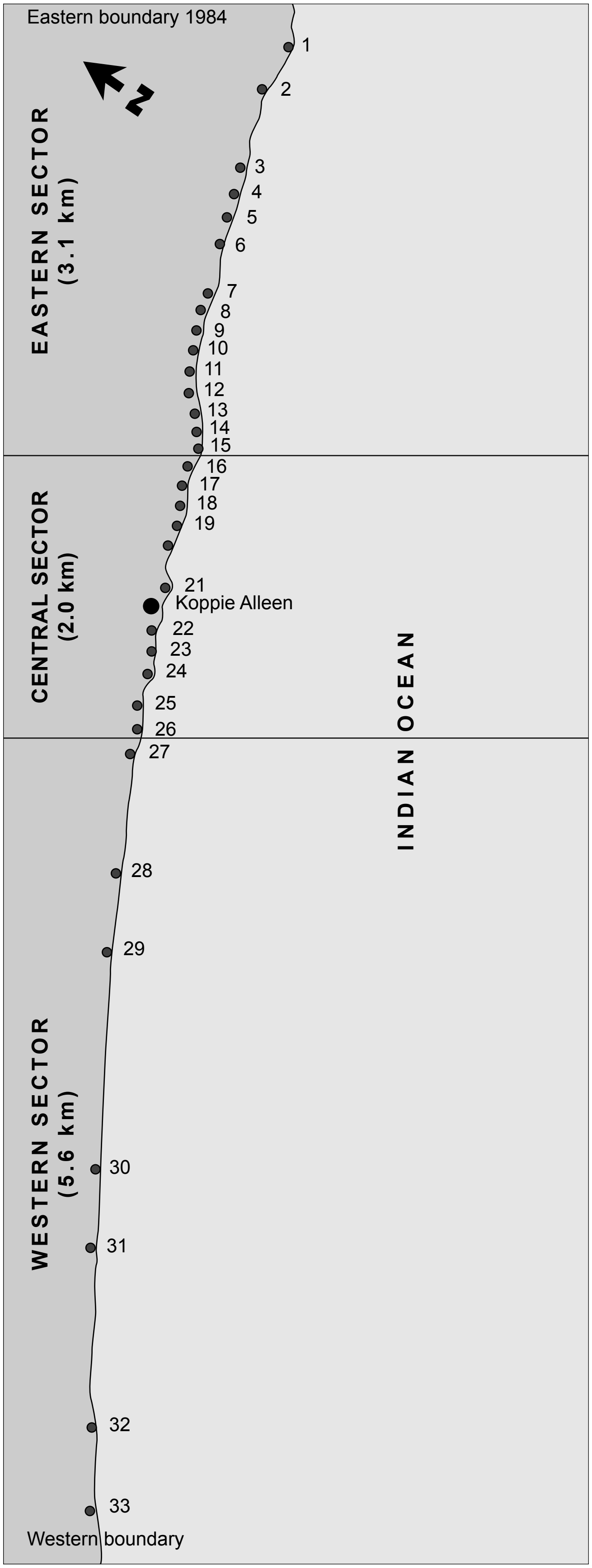

Fig. 2. Territories of African Black Oystercatchers in the eastern, central and western sectors within the study area in De Hoop Nature Reserve, 1984/85 to 1989/90.

shoreline; and mixed habitat consisting of rocky and sandy stretches interspersed over shore lengths of less than 200 m. Although the eastern and central sectors were both characterized by rocky and mixed habitat, the central sector differed in that the wave-cut platforms below the spring high-water mark were more continuous than those in the eastern sector. This aspect was investigated in relation to food availability and foraging of oystercatchers.

METHODS

Habitat use

Habitat composition was analysed on 1:10 000 ortho-photographs to determine the relative proportions of the three habitat types above the spring high-water mark. The estimated total length of each habitat type identified from the photographs was converted to the actual distance and calculated as a percentage of the total length of each sector. The relative proportion of rocky intertidal or wave-cut platforms (Hockey 1983) below the spring high-water mark was determined for each sector from the photographs.

Each month during the study, individuals and pairs of adult oystercatchers were counted along the coast of the study area, and the habitat for each was noted. Oystercatcher territories were numbered linearly from east to west (1–33; Fig. 2). Up to March 1986, counts in the western sector were done by vehicle; all other counts were done on foot. The number of adults per kilometre was calculated for each sector at the end of each breeding season (March; Loewenthal 1998). A single-factor ANOVA and Tukey multiple comparison test (Zar 1999) was used to test whether the mean annual number of adults per kilometre was equal between sectors. The mean number of pairs (territories) per kilometre was calculated for each sector during the breeding season (November to February) and non-breeding season (March to October). A two-factor ANOVA and Tukey test (Zar 1999) was used to test whether the mean number of pairs per kilometre was equal between sectors and seasons.

The maximum number of territories in each sector was recorded during the study, and the mean number per kilometre of territories calculated for each sector. The mean inter-territory distance (distance between the centres of adjacent territories) was calculated for each sector. A Kruskal–Wallis test (Zar 1999) was used to test whether the mean inter-territory distances were equal among sectors. For each year, the presence or absence of oystercatchers was recorded at each territory, and the annual mean percentage occupancy per territory calculated for each sector. A Kruskal–Wallis test (Zar 1999) was used to test whether the mean percentage occupancy was equal among sectors. Percentages were arcsine-transformed for analysis.

Diet

The remains of hard-shelled prey items for chicks were collected from middens during monthly surveys within the study area. Middens are the piles of empty mollusc shells where oystercatchers feed their chicks, usually at exposed sites above the high-water mark (Randall & Randall 1982, Hockey & Underhill 1984). Samples were collected at 17 middens from 10 territories in the eastern sector, 18 middens from nine territories in the central sector, and 13 middens from three territories in the western sector, together representing 67% of all the territories and most of the middens observed. Each prey item was identified, to species level where possible. Smaller items found among the prey remains that could have been attached to larger prey (e.g., considered probable bycatch owing to their small size) were excluded from the analysis.

The mean prey species composition (as percentages of the total number of prey items collected) for each territory sampled over six years was examined by means of a Bray–Curtis Similarities analysis, using unweighted group-pair averaging with the programme PRIMER (Clarke & Warwick 1994). The analysis was done in three different sets. The first set compared among years within sites, the second among sites within years, and the third combined all data for each site (across years) and compared averages. As the first two sets of analyses provided no conclusive result because of low numbers of samples for some individual territories, only the third set was used for the final analysis.

Because of the large variations in individual sample (midden) sizes, the proportions of prey items in all samples were combined for each sector and calculated for each year. As the diet composition in the eastern and central sectors showed the same trends in the above analysis, samples from these two sectors, termed the "eastern/central sector," were combined in the final analysis. The total proportion (percentage) of each prey item over six years in the eastern/central and western sectors was then calculated. The frequencies of the two main prey items, *P. perna* and *D. serra*, in relation to the total number of prey items were compared between the eastern/central sector and the western sector using a contingency table (Zar 1999).

Within the eastern/central sector and the western sector, prey items were classed as "dominant" (including species collected by humans during the period 1984 to 1986) or "minor." The annual proportions of items in these categories were calculated for each sector. To test whether the proportions of major prey items remained the same over time, the numbers of dominant mussels, limpets and whelks were compared using contingency tables (Zar 1999). Two prey items in the western sector showed strong trends in annual proportions and were therefore tested for constancy over time by linear regression analysis (Zar 1999).

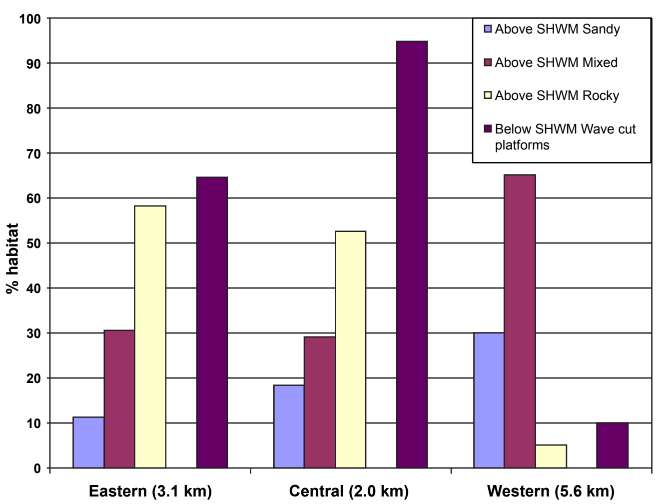

Fig. 3. The proportion of sandy, mixed and rocky habitat and of wave-cut platforms in the eastern, central and western sectors of the study area. SHWM = spring high-water mark.

The maximum lengths of the dominant prey species fed to the oystercatcher chicks were measured to the nearest 1 mm with calipers, and placed in 5 mm size classes (from 31–35 mm to 56–60 mm). The annual modal size classes were determined for the eastern/central sector and the western sector to determine changes over time.

RESULTS

Habitat use

The eastern and central sectors were characterized by rocky (≥53%) and mixed habitat (≥29%), whereas the western sector consisted predominantly of mixed (65%) and sandy habitat (30%; Fig. 3). The central sector differed from the eastern and western sectors in the almost continuous wave-cut platforms below the spring high-water mark (central = 95%; eastern = 65%; western sector = 10%; Fig. 3).

The mean number of adults per kilometre differed significantly among sectors ($F = 58.508$, $P < 0.001$; Table 1). The central sector had the highest mean number of adults (9.0 adults/km), followed by the eastern (6.5 adults/km) and western sectors (1.6 adults/km). The mean number of pairs in the central sector increased significantly during the breeding season, when it was also significantly higher (3.9 pairs/km) than elsewhere (ANOVA sector: $F = 101.403$, $P < 0.001$; season: $F = 21.641$, $P < 0.001$; interaction: $F = 3.840$, $P < 0.05$; Table 1). In contrast, the mean number of pairs in the eastern and western sectors did not differ according to season, and the mean number of pairs in the western sector remained significantly lower at all times.

Thirty-three territories were identified within the study area during the six-year study period: 15 in the eastern sector, 11 in the central sector and seven in the western sector (Fig. 2). The mean number of territories per kilometre was highest in the central sector (5.5), followed by the eastern (4.8) and the western sectors (1.3; Table 2). There was no difference between mean inter-territory distances in the eastern sector (206.2 m) and the central sector (193.7 m), but those in the western sector (924.7 m) were significantly greater

TABLE 1
Adult oystercatchers at the end of the breeding season (March) and pairs of adult birds during the breeding and non-breeding seasons in the eastern, central and western sectors, for six annual counts

	Mean number per kilometre ± SD (range)		
Oystercatchers	**Eastern sector**	**Central sector**	**Western sector**
Adults	6.5 ± 0.9^a (5.5–7.7)	9.0 ± 2.0^b (6.5–11.5)	1.6 ± 0.5^c (0.9–2.3)
Pairs			
Breeding season	2.8 ± 0.3^a (2.3–3.1)	3.9 ± 0.7^b (3.2–5.2)	1.0 ± 0.2^c (0.6–1.3)
Non-breeding season	2.5 ± 0.2^a (2.2–2.6)	2.6 ± 0.7^a (1.6–3.3)	0.5 ± 0.2^c (0.3–0.6)

$^{a, b, c}$Single factor ANOVA (adults), and 2-factor ANOVA (pairs); means with the same symbols do not differ significantly than those in other sectors (Kruskal–Wallis test: H = 13.049, P < 0.001). The percentage occupancy of territories in the central sector (92%) (Kruskal–Wallis test: H = 8.867, P < 0.05; Table 2) was significantly higher than those in the eastern (67%) and western sector (62%), which did not differ from each other.

Diet

A total of 28 prey items were recorded for the study area, predominantly molluscs (Table 3). In the eastern/central sector, 26 taxa were recorded, with most items (23) identified to species level. *P. perna* (51%, Table 3) accounted for the majority of the items recorded in this sector, followed by a variety of limpets (mainly *Scutellastra* spp., 37%). Among the more unusual prey items were more than 70 shells of Cape false limpets *Siphonaria* spp.; low numbers of crushed shells of African periwinkle *Nodilittorina africana*; and smooth turban shell *Turbo cidaris*, abalone *Haliotis midae*, spiral-ridged siffie *H. parva* and oblique arkshell *Barbatia obliquata*.

Eight prey species were identified in the western sector (Table 3). *D. serra* (56%) was the dominant species, followed by brown mussel (25%). *Bullia* (15%, possibly more than one species) and smaller proportions of other species made up the balance. The frequencies of *P. perna* and of *D. serra* in relation to the total number of prey items differed significantly between the eastern/central and western sectors (χ^2 = 5597.169, P < 0.001).

There was a division (<15% similarity) between the prey species composition of territories sampled in the western sector (Territory 29, 30 and 32) and the remaining territories in the eastern and central sectors (Fig. 4). The apparent discrepancy between Territory 7 and 14, in the eastern sector, and the other territories is ascribed to small sample sizes, rather than to any real difference. As there was no further division between territories sampled in the eastern (Territory 1 to 14) and central sectors (Territory 16 to 26), the proportions of prey items for territories in these sectors were lumped together.

The annual frequencies of dominant prey items in middens within the eastern/central sector differed significantly (χ^2 = 1266.828, P < 0.001), with no clear pattern except that frequencies of *P. perna* were higher than expected during the sixth year, whereas those of limpets were lower than expected for the same year, and those of *T. sarmaticus* were very low during the first year (Table 4). In the western sector there were significant differences in the annual frequencies of dominant prey items (χ^2 = 1964.837, P < 0.001), with lower than expected frequencies of *D. serra* during the second and

TABLE 2
Territories, inter-territory distances and percentage occupancy of territories in the eastern, central and western sectors, 1984/85 to 1989/90

Parameter	Eastern sector	Central sector	Western sector
Total number of territories	15	11	7
Mean number of territories per kilometre	4.8	5.5	1.3
Inter-territory distance, m (mean ± SD)	206.2[a] ± 107.6	193.7[a] ± 131.7	924.7[b] ± 640.9
% occupancy (mean ± SD)	66.7[a] ± 26.0	92.4[b] ± 11.5	61.9[a] ± 30.0

[a,b] Kruskal–Wallis test; means with the same symbols do not differ significantly

TABLE 3
Proportions of prey items in middens in the eastern/central sector and the western sector for the period 1984/85 to 1989/90 (n_1 = number of samples, n_2 = number of prey items).

Class	Item	Sector	
		Eastern/ central (n_1 = 35, n_2 = 9214)	Western (n_1 = 13, n_2 = 1724)
Bivalvia	*Perna perna*	50.5	25.1
Gastropoda	*Scutellastra (= Patella) cochlear*	14.3	-
Gastropoda	*Scutellastra granularis*	10.1	-
Gastropoda	*Turbo sarmati*cus	6.6	-
Gastropoda	*Scutellastra longicosta*	5.8	-
Gastropoda	*Scutellastra argenvillei*	3.9	-
Gastropoda	*Scutellastra barbara*	3.1	0.4
Polyplacophora	Chiton (2 spp.)	1.2	-
Gastropoda	*Siphonaria* spp.	0.8	-
Gastropoda	*Oxystele sinensis*	0.6	-
Malacostraca	Brachyura (crab)	0.4	-
Gastropoda	*Cymbula (= Patella) oculus*	0.4	-
Gastropoda	*Nodilittorina africana*	0.4	-
Gastropoda	*Oxystele variegata*	0.4	-
Gastropoda	*Thais capensis*	0.4	-
Gastropoda	*Burnupena* sp.	0.2	-
Gastropoda	*Haliotis spadicea*	0.2	0.4
Gastropoda	*Scutellastra miniata*	0.2	-
Cirripedia	*Tetraclita serrata*	0.2	1.4
Bivalvia	*Donax serra*	0.1	56.0
Gastropoda	*Turbo cidaris*	0.1	-
Gastropoda	*Bullia* spp.	<0.1	15.1
Gastropoda	*Fisurella mutabilis*	<0.1	-
Gastropoda	*Haliotis midae*	<0.1	-
Gastropoda	*Haliotis parva*	<0.1	-
Bivalvia	*Donax sordidus*	-	1.4
Bivalvia	*Barbatia obliquata*	-	0.2
	Subtotal prey items	26.0	8.0
	Total prey items	28.0	

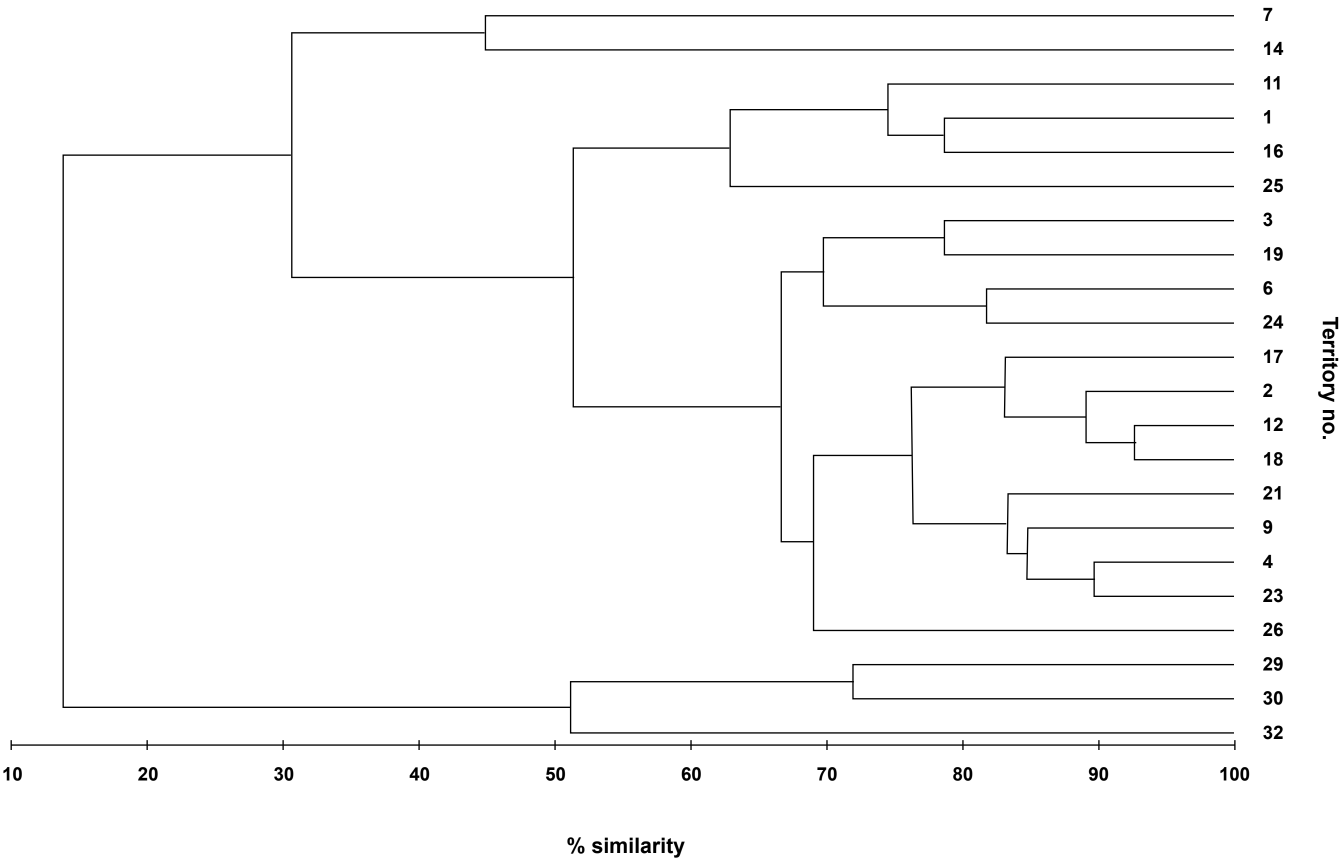

Fig. 4. Bray–Curtis Similarities analysis of oystercatcher prey items in the study area, 1984/85 to 1989/90 (n = 48 samples/middens and 10 938 prey items).

TABLE 4
Annual number of dominant hard-shelled prey items of oystercatchers for the period 1984/85 to 1989/90, and of species subject to human collection for the period 1984/85 to 1985/86, in the eastern/central and western sectors

	Number (and % of middens containing evidence of species consumed)					
Prey item	**1984/85**	**1985/86**	**1986/87**	**1987/88**	**1988/89**	**1989/90**
Eastern/central sector						
Number of middens with evidence of species eaten	470	1646	437	2217	3356	1405
P. perna	296 (63.0)	866 (52.6)	287 (65.7)	1264 (57.0)	2903 (86.5)	914 (65.1)
Limpets	160 (34.0)	603 (36.6)	102 (23.3)	795 (35.9)	116 (3.4)	333 (23.7)
T. sarmaticus	4 (0.9)	168 (10.2)	23 (5.3)	115 (5.2)	1 67 (5.0)	125 (8.9)
Other	10 (2.1)	9 (0.6)	25 (5.7)	43 (1.9)	170 (5.1)	33 (2.3)
Western sector						
Number of middens with evidence of species eaten	–	122	261	642	630	69
D. serra	–	40 (32.8)	63 (24.1)	437 (68.1)	553 (87.8)	55 (79.7)
P. perna	–	44 (36.1)	157 (60.2)	123 (19.1)	10 (1.6)	14 (20.3)
Bullia spp.[a]	–	35 (28.7)	39 (14.9)	81 (12.6)	57 (9.0)	0 (0)
Other	–	3 (2.4)	2 (0.8)	1 (0.2)	10 (1.6)	0

[a] Linear regression analysis; all means differ significantly

third year, but higher frequencies of *P. perna* for the same period (Table 4). The increase in frequencies of *D. serra* (R^2 = 0.765, F = 9.749, P > 0.05) was not statistically significant, but frequencies of *Bullia* decreased significantly over the study period (R^2 = 0.921, F = 34.779, P < 0.05; Table 4).

In the eastern/central sector, modal size classes of *P. perna* increased steadily from 31–35 mm in 1984/85 to 51–55 mm in 1987/88, then remained constant (Fig. 5). In the western sector, modal size classes of *D. serra* also increased from 41–45 mm in 1985/86 to 51–55 mm in 1987/88, then remained constant. Modal size classes of *P. perna* in this sector increased from 26–30 mm in 1985/86 to 50–60 mm in 1989/90.

DISCUSSION

Habitat use

This study showed clear habitat differences among sectors within the study area. The western sector consisted predominantly of mixed and sandy habitat. In contrast, the eastern and central sectors were both characterized by rocky habitat and mixed habitat. The relatively high proportion of rocky habitat (>50%) within these two sectors more closely approximates the habitat of the west coast islands, where densities of these oystercatchers are highest (Hockey 2000, 2005; see below). Within this rocky/mixed habitat, the central sector also differed strikingly from the eastern sector in the almost continuous and extensive wave-cut platforms below the spring high-water mark, whereas in the western sector the proportion of wave-cut platforms was very low.

These habitat differences were associated with significant differences in the distribution of adult African Black Oystercatchers, with the highest mean number in the central sector, followed by the eastern sector, and the lowest mean number in the western sector. As in the Eastern Cape dunefield study (Watson & Kerley 1995), this distribution pattern also appears to correspond to the level of human disturbance, with concentrations of oystercatchers and observed numbers of humans both being highest in the central sector.

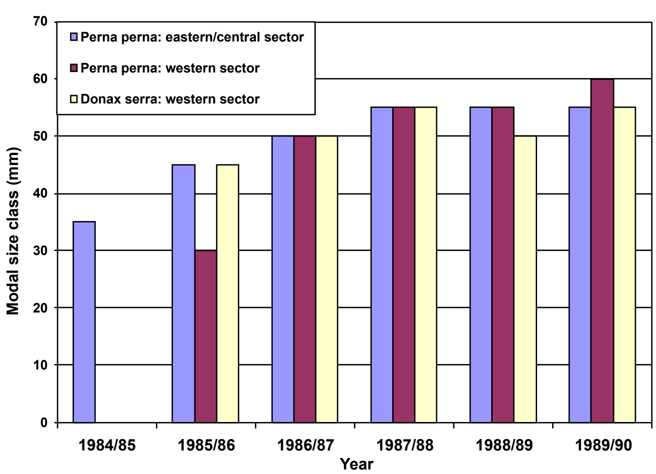

Fig. 5. Annual modal size classes (5 mm) of dominant hard-shelled prey items of oystercatchers for the period 1984/85 to 1989/90, and of species collected by humans for the period 1984/85 to 1985/86, in the eastern/central and western sectors (see Table 4 for total number of prey items in each sample).

Mixed habitat is normally regarded as one of the more frequently used habitats for oystercatchers on the mainland, possibly because it provides rocky sites for feeding as well as sandy sites for breeding (Summers & Cooper 1977, Hockey 1983). At DHNR, although the proportion of mixed habitat was higher in the western sector, the mean number of territories per kilometre was higher in the rockier habitats of the central sector and the eastern sector, with significantly smaller mean inter-territory distances in both than in the western sector. These differences could reflect the relative paucity of the "preferred" dominant prey species, *D. serra*, on this section of coastline compared with other areas (Hockey 1981, 1983). This is corroborated by a study in the Eastern Cape, where the abundance of oystercatchers has been positively correlated with the biomass of *D. serra* (Ward 1990). The relative absence of wave-cut platforms in the western sector of DHNR would also result in low proportions of the other dominant prey species, *P. perna* (25%), in the diet of oystercatchers in this habitat.

Territory quality appeared to differ among habitats within the DHNR study area, and the significantly higher percentage occupancy of territories in the central sector suggested that food availability was higher there, perhaps because there are more wave-cut platforms in this sector. This geomorphological feature is relatively uncommon within the distribution range of the African Black Oystercatcher (Hockey 1983), which also highlights the importance of DHNR for the species.

Recorded numbers of these oystercatchers are highest on the west coast islands (a mean of 75.0 adults/km) but lower on the mainland (a mean of 2.5–4.0 adults/km; Loewenthal 1998, Hockey 2000, 2005), although higher mean numbers have been recorded more recently on the Cape Peninsula (17.8 adults/km; Hockey 2000). On the mainland, oystercatchers show a positive association with rocky shores (1.8 adults/km) above sandy shores (1.2 adults/km), especially with mixed habitat (4.1 adults/km) and wave-cut platforms (2.4 adults/km; Hockey 1983). The relatively high mean numbers of both adult oystercatchers and pairs at DHNR, particularly in the central sector, thus appear to be related to habitat composition.

At DHNR, the trend in all sectors was towards higher numbers of pairs per kilometre during the breeding season than during the non-breeding season, and this increase was significant in the central sector, where the mean number of pairs per kilometre was also significantly higher than elsewhere. This does not correspond with the norm in other locations, where adult African Black Oystercatchers have been observed to move away from sheltered islands and rocky mainland shores towards exposed islands and sandy shores on the mainland during the breeding season (Summers & Cooper 1977, McLachlan *et al*. 1980, Hockey 1983), a pattern thought to reflect predator avoidance, rather than superior food supply or weather conditions (Hockey 1996). Conversely, the abundance of these oystercatchers is thought to remain constant on mixed shores throughout the year but, at DHNR, roughly half of the territories in the western sector were occupied during the breeding season only.

Diet

African Black Oystercatchers feed on a variety of prey items at DHNR, with *P. perna* the dominant species in rocky/mixed habitat and *D. serra* dominant in mixed/sandy habitat, as expected. Several items collected in rocky/mixed habitat in our study have not previously been recorded as prey items for the species. There is some doubt as to whether *Siphonaria* spp. are eaten by oystercatchers, as the tissues of these limpets are laden with a toxic mucus known to repel predators (Hockey & Underhill 1984, Branch *et al*. 1994), but the large proportion of empty shells of this species collected in the present study suggests that they may have been eaten, and this warrants further study. Shell fragments of *Littorina* sp. have been found in the faeces of Eurasian Oystercatchers (Hulscher 1996). The related African periwinkle *Nodilittorina africana* may be a new prey item for African Black Oystercatchers, as crushed shells of this species were found in the fresh droppings of a chick when feeding was interrupted, as well as in several other samples. Crabs (Brachyura) have also not previously been recorded as a prey species, but we found the fresh remains of small (unidentified) crabs in one midden. Other new items that we recorded for the African Black Oystercatcher were *T. cidaris*, *H. midae*, *H. parva* and *B. obliquata*. One chiton species *Acanthochiton garnoti* (Polyplacophora) had already been recorded as a prey species for the African Black Oystercatcher elsewhere (Hockey & Underhill 1984), but at least two (unidentified) chiton prey species were recorded at DHNR. At least seven (or possibly eight) items recorded in the eastern/central sector at DHNR during the present study could thus be added to the total list of prey species, although the total may be inflated due to bycatch of smaller organisms.

Differences in habitats and territory quality at DHNR (suggested by relative abundances of major prey items taken) appear important. *P. perna* was the most dominant organism in a baseline intertidal study in DHMR in January 1988, and its biomass at this site appears to be substantially higher than the average (Coetzee & Zoutendyk 1993). This finding appears to be directly related to the high occurrence of intertidal wave-cut platforms and, within the central/eastern sector, *P. perna* was by far the most dominant prey item (50%). It was also the numerically dominant item (35%) in oystercatcher middens sampled at Robberg, on the south coast, although values recorded in the Eastern Cape (71% at Cove Rock and 91% at St Croix Island) were higher (Randall & Randall 1982, Hockey & Underhill 1984). The relatively lower proportions of this species at DHNR were offset by a high diversity of 25 other prey species. As in the study on the rocky shores of the southeast coast (Kohler *et al*. 2009), the second most dominant prey item was *S. cochlear*, a large limpet that lives in high densities on the very low shore of the wave-cut platforms.

D. serra was one of the main species used by the oystercatchers in the western sector. Although the macrofauna of this sandy beach have been classified as "poor," with only moderate species diversity (De Ruyck & McLachlan 1992), adult *D. serra* occur at mid-tide level on the south and southeast coast (De Ruyck & McLachlan 1992, Branch *et al*. 1994), and are therefore available to oystercatchers for a longer period of the tidal cycle than those on the west coast, where the species is subtidal. Within the western sector at DHNR, the diet of the oystercatcher chicks is supplemented by *P. perna*, which probably originates from the few small rocky outcrops that characterize this sector.

Unusual prey items in the western sector were 261 *Bullia* specimens, collected high above the spring high-water mark and within discrete feeding piles. This genus is not listed in the species' diet study by Hockey and Underhill (1984). However, three species of *Bullia* have been identified on the DHNR sandy beach, with a combined abundance and a biomass higher than those of *D. serra* at this site (De Ruyck & McLachlan 1992), which may explain the relatively high frequency of *Bullia* items (15%) in this study. The possible use of *Bullia* spp. as a prey item corresponds with the findings of Ward (1990) in the Eastern Cape, although, both there and at DHNR, the oystercatchers were not directly observed feeding items of this genus to chicks. This aspect also requires further investigation.

The total number of prey species for the African Black Oystercatcher is among the highest known for the genus (for which a total of 52 prey species have been recorded in rocky/mixed habitat and three species in sandy habitat, including a total of 31 mollusc species; Hockey 1996). In contrast, only 30 items have been recorded for the American Oystercatcher *H. palliatus*, and 24 each for the South Island Oystercatcher *H. ostralegus finschi* and Variable Oystercatcher *H. unicolor* in New Zealand, and for the Sooty Oystercatcher *H. fulginosus* in Australia (Hockey 1996). During the present study, the recorded total of 28 items for the combined study area, with 26 prey items in the eastern/central sector (compared with eight in the western sector), appears to be relatively higher than those recorded in the literature for the species at any other specific site. On the west coast islands a total of 17 prey species were recorded, including a maximum of 14 species at Jutten Island (Hockey & Underhill 1984). On St Croix Island in the Eastern Cape, maxima of 11 and 12 species were recorded (Randall & Randall 1982, Hockey & Underhill 1984). On the mainland, 15 prey species were recorded at Cove Rock and seven at Robberg (Hockey & Underhill 1984). As few other comparable data are available for the diet of African Black Oystercatcher chicks between Vondeling Island on the west coast and Robberg on the south coast, the present study contributes to the available knowledge of the species' diet and emphasizes the importance of DHNR.

The large proportion of molluscs in the diet of African Black Oystercatchers corresponds with that for other oystercatcher taxa elsewhere in the world. In the northern hemisphere, Eurasian Oystercatchers are well known as predators of mussels and other bivalves, especially the cockle *Cerastoderma edule* and mussel *Mytilus edulis*, in estuaries, and their feeding behaviour has been intensively studied (e.g. Durell & Goss-Custard 1984, Goss-Custard & Durell 1987, Ens *et al*. 1996). On rocky shores these oystercatchers take mainly molluscs (mussels and gastropods such as whelks and periwinkles; Hulscher 1996) as well as limpets (gastropods; Wootton 1992; Coleman *et al*. 1999). The diet of the North American Oystercatcher *H. bachmani* also includes limpets (Wootton 1992). Eurasian Oystercatchers foraging on beaches feed on sandhoppers and polychaete worms, but they also forage inland, on fields, where they feed on several earthworm species, caterpillars and leatherjackets (Hulscher 1996).

Breeding oystercatchers tend to select large prey (and large sizes) for feeding their chicks (Randall & Randall 1982, Hockey & Underhill, 1984, Kohler *et al*. 2009). The maximum modal sizes for *P. perna* (55–60 mm in the western sector, and 51–55 mm in the eastern/central sector) noted during the present study appear to be among the largest on record for the African Black Oystercatcher, and possibly for any other oystercatcher species. Recorded modal size classes of *P. perna* in African Black Oystercatcher chick feeding piles include 35–45 mm at St Croix Island (Randall & Randall 1982) and 40–45 mm on the southeast coast (Hockey & Underhill 1984). The American Black Oystercatcher feeds on *M. edulis* of 45–50 mm in length (Webster 1941, Hartwick & Blaylock 1979), whereas the Eurasian Oystercatcher feeds on smaller specimens of the same species (20–35 mm; Norton-Griffiths 1967, Heppleston 1972). The maximum modal sizes of *D. serra* (50–60 mm) at DHNR correspond with those recorded for the African Black Oystercatcher in the Eastern Cape (Ward 1990).

On the west coast of southern Africa, the initial proportions of the two dominant intertidal prey species for African Black Oystercatchers (*C. meridionalis* and *A. ater*; Hockey & Underhill 1984) have changed because of the rapid invasion of alien Mediterranean mussel *Mytilus galloprovincialis*, which improved the food supply for the oystercatchers (Hockey & Van Erkom Schurink 1992; Hockey 2005). This change in diet has been implicated, at least in part, in an increase in breeding success and an increase in the overall population estimate of 4800 to 6700 (Hockey 2005, 2006).

At DHNR, *M. galloprovincialis* was not recorded at the time of the study. Indications of changes in prey species composition in the eastern/central sector (where human use was higher) appear to be linked to the proclamation of the marine reserve in March 1986 and subsequent recovery from human exploitation and competition for intertidal prey species. Only four specimens of *T. sarmaticus* were recorded in oystercatcher middens in this sector during the first year of the study, compared with up to 167 in the fifth year. In the western sector, proportions of *D. serra* showed an increasing trend, whereas those of *Bullia* spp. decreased significantly over time. Polychaete worms were also extensively collected by anglers before the proclamation, although changes in the abundance of the worms were not recorded during the present study. The increase in the annual modal sizes of *P. perna* in the eastern/central sector from 31–35 mm to 51–55 mm in 1987/88, and in the western sector from 26–30 mm in 1985/86 to 50–60 mm in 1989/90, followed the prohibition of mollusc collecting in the area. Likewise, modal sizes of *D. serra* in the western sector increased from 26–30 mm in 1985/86 to 50–60 mm in 1989/90.

The effects of sustained, long-term disturbance upon intertidal community structure have been investigated in the former Transkei on the east coast of South Africa (Siegfried *et al*. 1985, Hockey & Bosman 1986). In a short-term study at DHNR in 1985, marked differences were also found between the intertidal community in the more disturbed central sector at Koppie Alleen and at a similar, less disturbed site 3 km to the east (within the eastern sector of the present study area); these differences were ascribed to continual disturbance by bait collectors (Davies 1985).

The positive changes in prey species composition and the increases in the modal sizes of *P. perna* and *D. serra* after the proclamation of the marine reserve would be expected to be beneficial to the diet and breeding success of the African Black Oystercatcher within the DHNR study site. However, visitor numbers also increased after proclamation, and the expected benefits are likely to have been offset by increased disturbance at the site. The breeding success of the oystercatchers at DHNR is discussed in Scott, Dean & Watson (2011).

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