# Effects of an alien invertebrate species and wave action on prey selection by African black oystercatchers (*Haematopus moquini*)

# R. A. COLEMAN<sup>1\*</sup> AND P. A. R. HOCKEY<sup>2</sup>

<sup>1</sup>School of Biological Sciences, University of Southampton, Southampton SO16 7PX, UK; and <sup>2</sup>DST-NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa

Abstract Shorebirds foraging in the intertidal have been shown to exert a significant effect on assemblage level processes; this is particularly true of the ovstercatcher-limpet-algae system. The African black ovstercatcher (Haematopus moquini) is endemic to the southern African coastline, where it plays a significant role in ecosystem processes as a rocky-shore predator, especially of mussels and limpets. This understanding was based on studies of a rocky shore environment that has since been considerably modified following invasion of an alien mussel (Mytilus galloprovincialis). This invasion has not only changed the relative proportions of different food types on the shore, but has also greatly increased overall food biomass. We tested the previous model that food selection by oystercatchers reflected prey abundance and that intake by male and female ovstercatchers differed owing to bill morphology. We predicted that this difference would persist despite the changed nature of the food base. We also predicted that wave action would modify prey selection as a result of both its influence on prey behaviour and its impact on searching and handling times of the birds. Overall, both sexes consumed more limpets than expected by encounter rate alone, but contrary to prediction, the relative proportions of different prey types taken post invasion did not differ between the sexes. Dietary convergence is interpreted as a result of greatly increased food biomass on the shore, which is also reflected in increased ovstercatcher densities since the invasion. Also contrary to prediction there was no evidence that waves acted as indirect modifiers of the interaction between oystercatchers and their prey. The results of this study indicate that models of trophic cascades will need to be altered in the event of a significant change in a trophic level, which then effects behavioural changes in the key predator.

Key words: feeding behaviour, limpet, mussel, rocky shore, shorebird.

## INTRODUCTION

Much of our understanding of how trophic interactions influence assemblage level processes comes from studies carried out on rocky shore systems (Wootton 1993; Menge 2000), including some of the most cited works in ecology (for example Paine 1974). This understanding of the role of predators led to the trophic cascade debate in the early 1990s (e.g. Strong 1992), which is still ongoing. The key context of this debate is the relative strengths of the often opposing forces of predation removing grazers and/or space occupiers which then releases algae or other space occupiers, leading to a shift in community state. The alternative force derives from the ability of primary producers to outgrow, reduce or tolerate grazers. The

\*Corresponding author. Present address: Centre for Research on Ecological Impacts of Coastal Cities, Marine Ecology Laboratories (A11), The University of Sydney, NSW 2006, Australia (Email: ross.coleman@bio.usyd.edu.au)

Accepted for publication March 2007.

problem with this model of opposing predation and productivity forces is that there is the assumption of the players being drawn from a pool of species local to the system under investigation. This is not always the case. In some systems changes in prey and/or predators, often owing to invasions, can seriously disrupt trophic structures (Strayer *et al.* 2006) with concomitant effects on putative cascades. Here we examine the effect of the establishment of an invasive species on what has been held up as one of the key examples of trophic cascades (Bosman & Hockey 1988; Wootton 1993; Menge 2000; Thompson *et al.* 2002).

Birds are significant predators on rocky shores (e.g. Hockey *et al.* 1983; Marsh 1986; Wootton 1992) and understanding how prey populations interact with the ecology of their bird predators is fundamental to understanding ecosystems in which birds are important predators. Studies of wading birds in general and oystercatchers (Haematopodidae) in particular have contributed much to our understanding of foraging theory (e.g. Sutherland 1996) and of how predators modify their foraging behaviour in response to adverse

weather. Most of these studies, however, have been carried out in estuarine habitats, characterized by soft sediments and a lack of wave action.

The African black oystercatcher Haematopus moquini Bonaparte 1856 is southern Africa's second rarest coastal bird, with approximately 3000 breeding pairs distributed around the coast of southern Africa from Lüderitz, Namibia to southern KwaZulu-Natal, South Africa (Hockey et al. 2005). Foraging by H. moquini has been well studied (Hockey 1981a,b; 1984a; Hockey & Branch 1984; Bosman et al. 1989), as has their ecological role as predators on rocky shores (Bosman & Hockey 1988; Bosman et al. 1989). However, at the time of these studies, the rocky shore invertebrate communities of western South Africa (where the studies were carried out) were different to those of today. Since the early 1980s, southern Africa's rocky shores have been invaded, and many are now dominated, by the alien Mediterranean mussel Mytilus galloprovincialis (Lamarck) (Branch & Steffani 2004).

In recent years, African black oystercatchers have undergone a dietary shift as a result of this invasion. The alien mussel now dominates their diet, and additionally has altered the spatial distribution of the limpet Scutellastra granularis (L) - another important prey item (Hockey & Underhill 1984) - by direct competition for primary space (Hockey & Van Erkom Schurink 1992). In the late 1970s and early 1980s, S. granularis made up about 35% of the ovstercatchers' diet. As the M. galloprovincialis invasion progressed, this proportion decreased substantially and the indigenous mussel Aulacomya ater (Mollina), which was a significant preinvasion prey item (Hockey & Underhill 1984; Hockey & Van Erkom Schurink 1992), all but disappeared from the diet (Hockey & Van Erkom Schurink 1992). For about 8 years (mid 1980s to mid 1990s) ovstercatcher diet remained constant (60-65% M. galloprovincialis) (Hockey & Van Erkom Schurink 1992). Although M. galloprovincialis alters the demography of the S. granularis population, high recruitment success (limpets settling on the shells of M. galloprovincialis) increases both the biomass and reproductive output of S. granularis providing mussel cover of the shore does not exceed about 75% (Griffiths et al. 1992).

Shorebird predators may forage differently when facing extremes of wind, rain and/or cold (see Goss-Custard *et al.* 1996 for review). This is due to the interactive effects of changing prey abundance and/or availability in response to cold or rain (Hulscher 1996) and increased demands on the birds to maintain a sufficiently high daily energy intake (Goss-Custard *et al.* 1996). In respect of oystercatchers on rocky shores, however, patterns are less clear. Most oystercatchers utilizing rocky shore habitats primarily consume molluscs (mostly limpets and/or mussels), with some polychaetes and other unshelled items

(Hockey & Underhill 1984; Hulscher 1996). Cold, rain and strong winds can influence the physiology and hence the behaviour of prey, thus changing their availability to oystercatcher predators independently of their abundance. For example, during rainy periods when salinity is lowered, mussels close their valves (Shumway 1977; Davenport 1979). Under similar conditions, limpets clamp down on the rock to reduce osmotic shock from fresh water (Arnold 1957) thus are much harder to remove (Coleman et al. 2004). Similarly, extreme cold depresses prey metabolic levels leading to lowered respiration rates, necessitating reduced gas exchange and leading in turn to a smaller gap between the valves of mussels and between the shell and the substratum in limpets. This will again reduce availability.

The role of waves in modifying prev availability to wading birds is understudied. As wave amplitude increases, so the extent of wave wash over the shore increases (Helmuth & Denny 2003). A foraging bird can no longer see its potential prey and may risk being washed away. The interaction of wave period and wave amplitude will determine how much of the foraging area is accessible and for how long. Thus, in periods of strong wave action, emersions at low tide will be reduced and it would be expected that foraging oystercatchers would take fewer limpets, which potentially require a long in situ attack phase (Coleman et al. 1999), and take more mussels, which, once the posterior adductor muscle has been severed (Hockey 1981a), can be rapidly removed from the mussel bed for handling in a safer location (Hulscher 1996).

The aim of this study was to assess how the diet spectrum of ovstercatchers reflects prev abundance on the shore after successful dominance by an alien invertebrate invader. Specifically, we tested the hypothesis that diet directly reflects prey abundance (Krebs 1978). A second aim was to assess whether prey choice would be further modified by the effect of the most significant environmental hazard during the nonbreeding season, that of high waves. We predicted that choices would be modified by wave action as foraging oystercatchers would have less time to handle prey when attempting to feed in between waves breaking on the shore. Relative to the prey spectrum taken under calm conditions, reduction in search time was anticipated to force selection of an increased proportion of common, smaller but less profitable items.

#### METHODS

The study was carried out at Marcus Island  $(33^{\circ}3'S, 17^{\circ}58'E - Fig. 1)$  during the austral winter of 1997, during the non-breeding period for *H. moquini*. Marcus Island is a small (11 ha) granitic island, with a predominantly rocky coastline representative of



**Fig. 1.** Location of Marcus Island, Saldanha Bay within Southern Africa and positions of observation sites. The dotted line indicates the extent of the intertidal. The wave recorder is located in the entrance to Saldanha Bay some 2 km south-west of Marcus Island. The prevailing swell direction is from the south-west.

Benguela rocky coastlines (Bustamante & Branch 1996). Coastal exposure to wave action ranges from moderate to severe (Hockey & Underhill 1984). At the time of the study, the island supported a population of approximately 35–40 pairs of African Black Oyster-catchers, with small numbers of non-breeding birds present. The African Black Oystercatcher differs from the European Oystercatcher (*H. ostralegus*), in being territorial year-round (Hockey 1996), hence it was relatively easy to fix the numbers of birds observed. As each study site on the island was occupied by one or two territorial pairs of birds, it was possible to sex individuals based on bill morphology (Hockey 1981b).

The amount of time the birds spent foraging was assessed by instantaneous scans (Altman 1974) at 15-min intervals from dawn to dusk for each of the four designated sites (Fig. 1) on four separate occasions (two when high tide occurred at mid-day, and two when low tide occurred at mid-day, all tides intermediate between neap and spring), interspersed with the focal animal observations detailed below.

Focal animal (Altman 1974) observations were conducted for 10 min immediately following a predation event (Coleman *et al.* 1999). Oystercatchers foraging in the four sites where the distribution of prey was known were observed from a vantage point (far enough away to avoid disturbing the birds) through a  $60\times$  telescope. Prey choice data were described in real time into a dictaphone, which was then later transcribed into a computer using The Observer behavioural recording software (Noldus Technology, Wageningen, the Netherlands) for analysis. The 60× telescope allowed visual determination of prev choice even when oystercatchers were foraging in mussel beds where the prey may not be lifted clear of the substratum. The sizes of prey (mussel or limpet) taken were estimated relative to bill lengths of males and females (Hockey 1981b), and observations were calibrated by comparison with shells from observed predation events. The concern of Ens (1982) that shell collection underestimates the proportion of small prey taken is not valid here because the use of a powerful telescope allowed precise locations of shells from predation events to be identified; furthermore, the immediacy of recovery meant nearly all shells were collected. These and size estimates for the same prey in the field at the time of capture were used to calculate energy yield from the regressions of prey size versus energy yield.

Prey distributions in each of the study sites were mapped and described. Forty  $0.5 \times 0.5$  m quadrats were randomly placed on the rock at each site (Fig. 1), but at site 4, the smallest site, only 25 quadrats were used. Within each quadrat, the percentage cover of mussels and bare rock was determined from a  $7 \times 7$ intersection grid, and the numbers, sizes and species of all limpets present in the quadrat were recorded. Differences in prey density (number of limpets per square metre and percentage cover of mussels) were assessed using ANOVA with sample size randomly adjusted to 25 to give a balanced dataset and homogeneity of variances checked by Cochran's test, where appropriate separation of significant factors was achieved by SNK tests (Underwood 1997). The size structure of mussel populations at each site was obtained by taking five random  $0.1 \times 0.1$  m samples of mussel bed, removed using a paint scraper. All mussels present (>16 mm) were measured using vernier callipers. As mussels less than 16 mm long are not eaten by oystercatchers (Hockey & Underhill 1984), these were simply counted. The energy values for all available sizes of each prey species were obtained by collecting specimens of all sizes for each prey type (78 mussels and 88 limpets) and drying to a constant weight at 60°C for 48 h. This was then converted to energetic values by determining the energetic value of known amounts of mussel or limpet flesh using bomb calorimetry (DDS CP 500 Digital Oxygen Bomb Calorimeter, Digital Data Systems Ltd, Northcliff, South Africa). Previous work (R. Coleman, unpubl. data 1997) had shown that the best regression for explaining the relationship between limpet length and energy yield was a power function, hence this was used here.

While it was relatively easy to observe species consumed by oystercatchers, it was not always possible to determine sizes of mussels because, in some cases, the birds did not detach the shells and consumed the contents in situ. In order to estimate energy intake, these mussels of unknown sizes were allocated to the most frequent mussel size (20-24 mm, Fig. 4) and allocated an energy value accordingly. This was supported by observations that the birds only removed large mussels from the bed. This allowed a realistic estimate of energy intake, which was compared with energy available from prey present on the shore and tested using a log-likelihood (G) test (Sokal & Rohlf 1995). In order to test the strength of this relationship, a second analysis was carried out whereby the mussels of unknown size were allocated to the largest possible size class and the intake compared with the potential energy available on the shore using the same test structure. Prey other than mussels and limpets, including polychaetes, worms and whelks (mainly Nucella dubia) were also taken occasionally. These events were noted but no shells collected. In the few cases where prey identification was not possible, prey were classified as unknown. Formal statistical comparison with prey records from an earlier study (Hockey & Underhill 1984) was not logical as the data in that study were not obtained in a comparable manner.

It was hypothesized that wave action may modify prey choice. The prevailing swell direction is from the south-west. The small size of the island and wave

refraction meant we could assume, and was confirmed on site (R. Coleman, pers. obs. 1997), that at the scale which could influence ovstercatchers, all sites were more or less equally exposed. Data on maximal wave height and period during focal bird observations were obtained from a nearby wave recorder (approx. 2 km seaward of Marcus Island). This gave us a single figure for wave height comparable across all sites. First, the hypothesis that maximal wave height and period were correlated was checked from three wave heights and periods at three randomly chosen times for all the observation days. Wave height usually has greater variation than periodicity and thus a major effect on exposing and covering of the ovstercatcher's foraging arena, so this was regressed against the proportion of mussel prey in the diet (arcsin transformed). In the event of wave height explaining prev selection for each sex, the relationship between regression lines would be tested using homogeneity of slope tests and ANCOVA procedures based on samples which were randomly adjusted to give a balanced set (Underwood 1997).

#### RESULTS

Sites 3 (72.0 per square metre, SEM = 6.77, n = 40) and 4 (3.28.6 per square metre, SEM = 4.26, n = 25) had significantly fewer limpets than sites 1 (93.6 per square metre, SEM = 4.26, n = 40) and 2 (95.4 per square metre, SEM = 7.8, n = 40) (ANOVA, square-root transformed data to correct for homogeneity of variances;  $F_{3,96} = 21.30$ , P < 0.001), and all sites differed in percentage cover of mussels ( $F_{3,96} = 2.77, P < 0.05$ ) (Site 1: 38.8, SEM = 2.84, n = 40; Site 2: 59.9, SEM = 3.97, *n* = 40; Site 3: 59.4, SEM = 4.75, *n* = 40; Site 4: 48.5, SEM = 6.82, n = 25). Power functions of prey size significantly explained 87% of the variation in energy yield of limpets (Fig. 2a) and 92% of the variation in energy yield of mussels (Fig. 2b) with limpets yielding more energy for a given prey size than mussels.

In total, 43 focal bird observations were made of females and 31 of males across all sites. The number of observations for each sex was independent of site  $(G = 2.29, \chi^2_{(3, 0.05)} = 7.82, \text{ not significant})$  which indicated no sex-site bias. Over the period of the study, the birds foraged actively for 35% of the time available (there was no difference between the sexes, data discussed in Leseberg et al. 2000). During this period mussels constituted about 65% of all the prey items consumed which represented an increase of about 14% relative to the period 1979-1980 (Table 1, Hockey & Underhill 1984). For female taking limpets (15 observed events) the prey size taken closely matched that on the shore, whereas males took limpets of sizes from the smaller end of the distribution: when they did take larger (>30 mm) limpets these were



**Fig. 2.** Energy yield from prey as a function of maximum length (mm). (a) Length (mm) – energy (kJ) regression for limpets *Scutellastra granularis* at Marcus Island (Energy = 0.0001 length<sup>3.0956</sup>,  $r^2 = 0.868$ ,  $F_{1,86} = 597.80$ , P < 0.0001). (b) Length (mm) – energy (kJ) regression for mussels *Mytlius galloprovincialis* at Marcus Island (Energy = 0.0002 length<sup>2.9235</sup>,  $r^2 = 0.910$ ,  $F_{1,86} = 774.85$ , P < 0.0001).

taken at a size frequency similar to that present on the shore (Fig. 3). When feeding on mussels, both sexes took mainly medium-sized mussels (24-36 mm), despite the fact that these were relatively scarce (Fig. 4). Historically, when foraging on the larger Choromytilus meridionalis, the sizes of mussels selected by oystercatchers closely mirrored availability, with a modal size of 35-40 mm (Hockey 1981a). Eighty-one per cent of females' energy intake was derived from mussels and 19% from limpets. Mussels contributed 79% of males' energy intake and limpets 21%. These values were significantly different from the energy intake expected if oystercatchers matched intake to availability (males' G = 621.8, d.f. = 40, P < 0.001; females' G = 600.5, d.f. = 40, P < 0.001). The proportion of energy obtained from limpets was greater (males' G = 92.2, d.f. = 40, P < 0.001; females'

G = 200.5, d.f. = 40, P < 0.001) than would be expected on the basis of available energy alone. This difference in energy intake remained significant even if the mussels of unknown size were allocated to the largest, rather than the average size class.

Wave height was weakly correlated with period (r = 0.32, d.f. = 76, P < 0.05). From three randomly selected times on 15 randomly selected days, the average maximal wave height was 1.92 m (n = 45, SD = 0.83) and the period was 12.58 s (n = 45, SD = 2.22). The standard deviations represented 43% of the mean for wave height and 17.6% of the mean for wave period, respectively; hence the use of wave height instead of period as the independent variable for examining prev choice was justified. Wave action had no effect on prey choice (Fig. 5). The proportion of mussels consumed in any one foraging bout was not affected by wave height. Neither of the regressions significantly explained any variation with respect to wave height in the proportion of mussels taken by males or females (males: proportion of mussels in the diet =  $-0.829 \times$  wave height + 65.83,  $r^2 = 0.027$ ,  $F_{1,29} = 0.023$ , not significant; for females: proportion of mussels in the diet =  $-1.476 \times$  wave height + 75.176,  $r^2 = 0.015$ ,  $F_{1,29} = 0.006$ , not significant). Tests for homogeneity of slopes or analyses of covariance were therefore not applicable.

#### DISCUSSION

In all branches of biology, samples are taken from a population (in a statistical sense) to be representative of that population (Underwood 1997). Sample size is then a limit of resources, complexity of work involved and primarily the needs of any hypotheses under test. Here, while the sample size was small – six males and six females, the sample was representative of oyster-catchers on Marcus Island in terms of behaviour and of food supply. Studies have shown the birds on Marcus Island to be representative of the population as a whole (Hockey 1981b,a; 1983; 1984a,b,), hence there is no reason to regard the data from this study as unrepresentative on the basis of small sample sizes.

This study aimed to assess patterns of food selection by oystercatchers following establishment of a successful invertebrate invader that changed the absolute and relative abundance of food types on the shore. Additionally, the hypothesis that increased wave action would reduce the proportion of limpets taken by foraging oystercatchers was tested. Mussels were the most frequent prey item in the diet, although limpets were taken more often than would be expected on the basis of encounter frequency alone. The results did not support the hypothesis of an effect of wave height on prey selection by oystercatchers.

Prey	1979/80		1997	
	Males	Females	Males	Females
Limpet	23.7 (6.9)	3.1 (2.1)	15.8 (0.9)	6.5 (0.3)
Mussel (all)	50.5 (17.5)	62.9 (24.5)	68.4 (1.1)	63.4 (0.7)
Mytilus galloprovincialis	Not present	Not present	68.4 (1.1)	63.4 (0.7)
Aulacomyer auter	8.7 (8.2)	10.9 (10.9)	0 (0)	0 (0)
Chroromytilus meridionalis	41.9 (25.7)	51.9 (35.4)	0 (0)	0 (0)
Others	25.8 (24.4)	34.1 (26.5)	15.8 (0.7)	30.1 (0.6)

 Table 1. Proportions of prey items in foraging bouts of adult prebreeding Haematopus moquini (authority) observed on Marcus

 Island, South Africa

Data (means with standard errors in parentheses) for 1979/80 were calculated from Hockey and Underhill (1984) from 2 m f<sup>-1</sup> pairs of birds. Data for 1997 are means, with standard errors in parentheses, for six males (31 observations) and six females (43 observations) observed over a month period for 10 min each.



**Fig. 3.** Relative abundance of limpets (*Scutellastra granularis*) of different sizes compared with the size-frequency of prey items eaten by adult non-breeding African black oystercatchers. The bars refer to limpet abundance and are from  $145 \times 0.25 \text{ m}^2$  quadrats across four sites. The lines are from observed predation events.

On rocky shores, oystercatchers are presented with a choice of prey items and prey on a wide diversity of species (Hulscher 1996). They are known predators of limpets and mussels on rocky shores in South Africa (e.g. Hockey & Underhill 1984; Hockey & Van Erkom Schurink 1992), NW Pacific coasts (e.g. Wootton 1992), the UK (e.g. Harris 1967; Lewis & Bowman 1975; Coleman et al. 1999), Australia (Lane & Davies 1987) and New Zealand (Baker 1974). On many rocky shores, limpets and mussels are direct competitors for space, hence understanding the role of predator and prey selection becomes important in predicting changes in assemblage structure in response to predator behaviour or changes in prey abundance (Wootton 1993). It has previously been argued (Hockey 1981b) that female H. moquini favour mussels (Table 1, Hockey & Underhill 1984) because their bill mor-

phology is finer and more suited to stabbing (sensu Tinbergen & Norton-Griffiths 1964). By contrast, male H. moquini favour limpets because their blunterended bill is more suited to removal of limpets from the substratum. The evidence from this study does not support this model for individuals - no one bird was faithful to any one prey type. On occasions, individuals would take all mussels on one day and all limpets the following day. Across all observations there was a difference of 9.3% in the proportion of limpets in the diets between males and females. This is a substantial reduction in difference from 20% in 1979/80 (Table 1, Hockey & Underhill 1984) which suggests that the current superabundance of food (especially of M. galloprovincialis) has resulted in intersexual dietary convergence, regardless of intersexual differences in bill morphology.





**Fig. 4.** Relative abundance of mussels *Mytilus galloprovincialis* of different sizes compared with the size-frequency of prey items eaten by adult non-breeding African black oystercatchers. The bars refer to limpet abundance and are from  $145 \times 0.25$  m<sup>2</sup> quadrats across four sites. The lines are from observed predation events across the whole investigation.



**Fig. 5.** Proportion of mussels in foraging bouts of adult non-breeding *Haematopus moquini as* affected by wave action based on observed known predation events. Numbers of birds and observations are given in Table 1. As regression lines are non-significant, they are not shown.

In this study, oystercatchers took far more limpets than would be expected on the basis of either their relative biomass on the shore or their encounter frequency by oystercatchers. The levels of mussel removal (by *H. moquini*) are highly unlikely to affect mussel numbers on the shore at Marcus Island because of the high level of natural mortality due to crowding effects as the mussels grow (Griffiths *et al.* 1992), but the substantial numbers of limpets eaten may deplete their numbers significantly (Hockey & Branch 1984; Bosman & Hockey 1988) facilitating the spread of mussels. It has been suggested that oystercatchers in this system may affect the competitive interaction between *M. galloprovincialis* and *S. granularis* by differential removal of either prey species (Steffani & Branch 2005). Hockey and Van Erkom Schurink (1992) proposed that there was an oscillation between peaks of abundance of the different prey species, a pattern that has persisted in the 15 years since that study was published (P. A. R. Hockey, unpubl. data 2007).

Wave action is a significant abiotic influence on rocky shore ecosystems. Classical studies have shown that assemblages on exposed sites differ markedly from those at more sheltered locations (see Hawkins & Hartnoll 1983 for review). More recently, the impact of waves have been shown to modify species' biologies via phenotypic plasticity such as modifying the shape of algae (Fowler-Walker et al. 2006), influencing the shape of limpets (Denny 2000) or even the morphology of barnacle cirri (Arsenault et al. 2001). In a parallel development, ecologists have come to understand that indirect interactions whereby predators influence assemblages by modifying the behaviour of animals from lower trophic levels can be as important as direct predation effects in modifying assemblage processes (Wootton 1993). For example, the presence of a feeding crab can modify the behaviour of nearby snails such that grazing effects are changed (Trussell et al. 2002). Here, we tested whether wave action modifies the foraging behaviour of oystercatchers, such that strong wave action would change the relative abundance of the two prey species in the diet. If this were true and representative of areas where oystercatchers are significant predators of grazers (Hockey et al. 1983; Wootton 1992), then there would be new insight into the interaction between waves and the functioning of rocky shores. However, this was not the case: while periods of greater wave action modified the frequency of foraging bouts, they did not modify prey choice. Thus the consequences of the noted trophic cascade of oystercatchers–limpets–algae (Bosman & Hockey 1988; Wootton 1992) are unlikely to be modified by wave action in this system.

In conclusion, this study has shown that despite the very high biomass of *M. galloprovincialis* on the shore and the numerical dominance of this species in the diets of oystercatchers there is a greater proportion of limpets in the diet of *H. moquini* than would be expected by encounter rates alone, which may facilitate colonization of open rock areas by *M. galloprovincialis*. Contrary to prediction, we found no evidence for wave-induced modification of prey choice. Finally, although prior to the *M. galloprovincialis* invasion there was evidence for sexual differentiation in the diet of oystercatchers, subsequent to the invasion this difference is much smaller.

The trophic cascade of oystercatchers eating limpets which then releases algae from grazing pressure is a much discussed phenomenon. This work has demonstrated that invasive species can disrupt existing foodwebs, consistent with other work (Strayer et al. 2006). The novelty here is that the invasive prey has proved beneficial for a threatened bird species whose numbers are now increasing probably as a result of the invasion by M. galloprovinicalis. It is highly likely that the trophic cascade noted in earlier work (Bosman & Hockey 1988) is not now working on shores on the west coast of South Africa. Instead there is a situation where ovstercatcher predation may interact with interspecific competition between limpets and mussels, the outcome of which is expressed not in changes in primary productivity (the accepted opposing force to predation) but in changes in space occupancy. More work on the nature of this predation mediated competition is needed if we are to really understand trophic interactions and assemblage structuring.

### **ACKNOWLEDGEMENTS**

This work was supported by a British Ecological Society Travel Grant (97/14) to RAC and the Oystercatcher Conservation Programme to PARH. The South African National Parks Board granted access to Marcus Island. Portnet Saldanha provided the wave data. RAC is grateful to Kim Prochazka and Chris Tobler for assistance. Analysis was supported while RAC was employed at the University of Plymouth, UK. The manuscript was much improved by thoughtful comments by Michael Bull, Kris French and two anonymous referees.

#### REFERENCES

- Altman J. (1974) Observational study of behaviour: sampling methods. Anim. Behav. 49, 227–67.
- Arnold D. C. (1957) The response of the limpet Patella vulgata L. to water of different salinities. J. Mar. Biol. Assoc. UK 36, 121–8.
- Arsenault D. J., Marchinko K. B. & Palmer A. R. (2001) Precise tuning of barnacle leg length to coastal wave action. *Proc. R. Soc. Lond. B Biol. Sci.* 268, 2149–54.
- Baker A. J. (1974) Prey-specific feeding methods of New Zealand oystercatchers. *Notornis* 21, 219–33.
- Bosman A. L. & Hockey P. A. R. (1988) Life history patterns of populations of the limpet *Patella granularis*: the dominant roles of food supply and mortality. *Oecologia* 75, 412–9.
- Bosman A. L., Hockey P. A. R. & Underhill L. G. (1989) Oystercatcher predation and limpet mortality: the importance of refuges in enhancing the reproductive output of prey populations. *Veliger* 32, 120–9.
- Branch G. M. & Steffani C. N. (2004) Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *J. Exp. Mar. Biol. Ecol.* **300**, 189–215.
- Bustamante R. H. & Branch G. M. (1996) Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. *J. Biogeogr.* 23, 339–51.
- Coleman R. A., Goss-Custard J. D., Le V., Dit Durell S. E. A. & Hawkins S. J. (1999) Limpet *Patella* spp. consumption by oystercatchers *Haematopus ostralegus*: a preference for solitary prey items. *Mar. Ecol. Prog. Ser.* 183, 253–61.
- Coleman R. A., Browne M. & Theobalds T. (2004) Prey aggregation functioning as a group defense via vibrationvigilance: limpet tenacity changes in response to simulated predator attack. *Ecology* 85, 1153–9.
- Davenport J. (1979) The isolation response of mussels (Mytilus edulis L.) exposed to falling sea-water concentrations. J. Mar. Biol. Assoc. UK 59, 123–32.
- Denny M. W. (2000) Limits to optimization: fluid dynamics, adhesive strength and the evolution of shape in limpet shells. *J. Exp. Biol.* 203, 2603–22.
- Ens B. (1982) Size selection in mussel feeding oystercatchers. *Wader Stud. Group Bull.* **34**, 16–20.
- Fowler-Walker M. J., Wernberg T. & Connell S. D. (2006) Differences in kelp morphology between wave sheltered and exposed localities: morphologically plastic or fixed traits? *Mar. Biol.* 148, 755–67.
- Goss-Custard J. D., Le V., dit Durell S. E. A. et al. (1996) How oystercatchers survive the winter. In: The Oystercatcher: From Individuals to Populations (ed. J. D. Goss-Custard) pp. 133– 54. Oxford University Press, Oxford.
- Griffiths C. L., Hockey P. A. R., Van Erkom Schurink C. & Le Roux P. J. (1992) Marine Invasive Aliens on South African shores: implications for community structure and trophic functioning. S. Afr. J. Mar. Sci. 12, 713–22.
- Harris M. P. (1967) The biology of oystercatchers (Haematopus ostralegus) on Skokholm Island, S. Wales. *Ibis* 109, 180–93.
- Hawkins S. J. & Hartnoll R. G. (1983) Grazing of intertidal algae by marine invertebrates. Oceanogr. Mar. Biol. Annu. Rev. 21, 195–282.
- Helmuth B. & Denny M. W. (2003) Predicting wave exposure in the rocky intertidal zone: do bigger waves always lead to larger forces? *Limnol. Oceanogr.* **48**, 1338–45.
- Hockey P. A. R. (1981a) Feeding techniques of the African Black Oystercatcher Haematopus moquini. In: Proceedings of the

#### doi:10.1111/j.1442-9993.2008.01864.x

#### © 2008 The Authors

Journal compilation © 2008 Ecological Society of Australia

*Symposium on Birds of the Sea and Shore 1979* (ed. J. Cooper) pp. 99–115. African Seabird Group, Cape Town.

- Hockey P. A. R. (1981b) Morphometrics and sexing of the African Black Oystercatcher. *Ostrich* **52**, 244–7.
- Hockey P. A. R. (1983) The distribution, population size, movements and conservation of the African Black Oystercatcher *Haematopus moquini. Biol. Conserv.* 25, 233–62.
- Hockey P. A. R. (1984a) Behaviour patterns of non-breeding African Black Oystercatchers *Haematopus moquini* at offshore islands. In: *Proceedings of the Pan-African Ornithological Congress* (ed. J. A. Ledger) pp. 707–29. Southern Africa Ornithological Society, Johannesburg, Lilongwe.
- Hockey P. A. R. (1984b) Observations on the communal roosting of African Black Oystercatchers. Ostrich 56, 52–7.
- Hockey P. A. R. (1996) Haematopus ostralegus in perspective: comparisons with other oystercatchers. In: The Oystercatcher: from Individuals to Populations (ed. J. D. Goss-Custard) pp. 251–8. Oxford University Press, Oxford.
- Hockey P. A. R. & Branch G. M. (1984) Oystercatchers and limpets: impact and implications, a preliminary assessment. *Ardea* 72, 199–206.
- 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. R. Soc. S. Afr.* 48, 123–39.
- Hockey P. A. R., Cooper J. & Duffy D. C. (1983) The roles of coastal birds in the functioning of marine ecosystems in South Africa. S. Afr. J. Sci. 79, 130–4.
- Hockey P. A. R., Dean W. R. J. & Ryan P. G. (2005) *Roberts Birds of Southern Africa.* The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Hulscher J. B. (1996) Food and feeding behaviour. In: *The Oystercatcher: From Individuals to Populations* (ed. J. D. Goss-Custard) pp. 7–29. Oxford University Press, Oxford.
- Krebs J. R. (1978) Optimal foraging: decision rules for predators. In: *Behavioural Ecology: An Evolutionary Approach* (eds J. R. Krebs & N. B. Davies) pp. 23–63. Blackwell Scientific Publications, Oxford.
- Lane B. & Davies J. (1987) Shorebirds in Australia. Nelson, Melbourne.
- 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, 379–85.

- Lewis J. R. & Bowman R. S. (1975) Local habitat induced variations in population dynamics of Patella vulgata L. J. Exp. Mar. Biol. Ecol. 104, 185–201.
- Marsh C. P. (1986) Impact of avian predators on high intertidal limpet populations. J. Exp. Mar. Biol. Ecol. 104, 185–201.
- Menge B. A. (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. J. Exp. Mar. Biol. Ecol. 250, 257–89.
- Paine R. T. (1974) Intertidal community structure, experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15, 93–120.
- Shumway S. E. (1977) Effect of salinity fluctuation on the osmotic pressure and Na+, Ca2+ and Mg2+ ion concentrations in the hemolymph of bivalve molluscs. *Mar. Biol.* 41, 153–77.
- Sokal R. R. & Rohlf F. J. (1995) *Biometry*. W.H. Freeman, New York.
- Steffani C. N. & Branch G. M. (2005) Mechanisms and consequences of competition between an alien mussel, Mytilus galloprovincialis, and an indigenous limpet, Scutellastra argenvillei. J. Exp. Mar. Biol. Ecol. 317, 127–42.
- Strayer D. L., Eviner V. T., Jeschke J. M. & Pace M. L. (2006) Understanding the long-term effects of species invasions. *Trends Ecol. Evol.* 21, 645–51.
- Strong D. R. (1992) Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. *Ecology* 73, 747– 54.
- Sutherland W. J. (1996) From Individual Behaviour to Population Ecology. Oxford University Press, Oxford.
- Thompson R. C., Crowe T. P. & Hawkins S. J. (2002) Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environ. Conserv.* 29, 168–91.
- Tinbergen N. & Norton-Griffiths M. (1964) Oystercatchers and mussels. Br. Birds 57, 64–70.
- Trussell G. C., Ewanchuk P. J. & Bertness M. D. (2002) Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. *Ecol. Lett.* 5, 241–5.
- Underwood A. J. (1997) Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.
- Wootton J. T. (1992) Indirect effects, prey susceptibility, and habitat selection: impact of birds on limpets and algae. *Ecology* **73**, 981–91.
- Wootton J. T. (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. Am. Nat. 141, 71–89.

Copyright of Austral Ecology is the property of Blackwell Publishing Limited and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.