Austral ECOLOGY A Journal of ecology in the Southern Hemisphere

Austral Ecology (2014) **39**, 567–578

Trophic overlap between sexes in the dimorphic African black oystercatcher foraging on an alien mussel

SOPHIE A. KOHLER,[1,2,3]* MAËLLE CONNAN,[3,4] JOANNA KOLASINSKI,[2,5] YVES CHEREL,[6] CHRISTOPHER D. MCQUAID[3] AND SÉBASTIEN JAQUEMET[2,5]

[1]*Animal Demography Unit, Department of Biological Sciences, University of Cape Town, Rondebosch 7701, South Africa (Email: kohler84@gmail.com),* [4]*DST-NRF Centre of Excellence at the Percy Fitzpatrick Institute of African Ornithology, University of Cape Town, Rondebosch, Departments of* [3]*Zoology* and *Entomology and* [5]*Botany, Rhodes University, Grahamstown, South Africa; and* [2]*Laboratoire ECOMAR, Université de La Réunion, Saint Denis, La Réunion, and* [6]*Centre d'Etudes Biologiques de Chizé, Villiers-en-Bois, France*

Abstract Sex-specific feeding segregation related to sexual bill dimorphism has been described in several oystercatcher species, including the African black oystercatcher. For the latter, studies concerned only a small number of breeding pairs and were done prior the invasion of the South African rocky shores by the Mediterranean mussel, which is believed to have benefited oystercatchers by increasing overall biomass. Here, we investigated geographic variability in the segregation of diet, biometrics and body condition between sexes in the African species, in relation to changes in foraging habitats along the South African coastline, using stable isotope analyses. Males and females and their potential prey (mussels, limpets, polychaetes and ascidians) were sampled on the southern African west, south-west and south-east coasts for stable isotope analyses and biometrics and body conditions of birds were measured. Bill dimorphism occurred throughout the study area and south-west males had lower body conditions than other males and females in general. Sexes displayed little differences in their $\delta^{13}C$ ratios and in the relative consumption of the different prey throughout the study area, except on the south-east coast where males were slightly depleted in ^{13}C relative to females and the most abundant prey elsewhere (the Mediterranean mussel) is rare. Females were slightly but significantly enriched in ^{15}N by 0.3‰ compared to their breeding partners and this did not link clearly to differences in diet. We argue that the combined effect of biogeographic variations in rocky shores diversity and biomass, heterogeneous invasion by the Mediterranean mussel on the South African coastline and bill dimorphism may have altered the sex-specific feeding behaviour of oystercatchers differently between coastal regions and possibly had an additional cost for male oystercatchers faced with lower prey biomass and diversity on the south-west coast.

Key words: *Haematopus moquini*, *Mytilus galloprovincialis*, sexual differences, South Africa, stable isotopes, trophic ecology.

INTRODUCTION

Physiological stress and behavioural constraints induced by breeding can often trigger food partitioning between sexual partners, which is seen as a way of reducing intra-pair competition and optimizing food intake (Andersson & Norberg 1981). Moreover, energetic requirements are believed to be unbalanced between breeding males and females (e.g. egg formation; Meijer & Drent 1999), and can further segregate feeding habits between breeding partners. Among birds, ecological niche divergence between sexes can involve the targeting of food items of different sizes or species, the use of different foraging methods or the use of different foraging areas (Selander 1966) and these segregation mechanisms are often associated with sexual dimorphism. In seabirds, sexual dimorphism is often expressed as differential body size (González-Solıs *et al.* 2000; Székely *et al.* 2000) and sexes are known to differ in their foraging ranges and depth (Weimerskirch *et al.* 2009), in the trophic level at which they feed (Bearhop *et al.* 2006) or in their prey size (Mariano-Jelicich *et al.* 2008). In shorebirds, ecological niche divergence is often expressed as different feeding substrates, prey types or tidal preferences, and this has been closely related to sex-related differences in bill morphology (reviewed in Durell 2000).

The Eurasian oystercatcher (*Haematopus ostralegus*) is one of the best studied shorebirds and particular attention has been paid to its feeding specialization, related to both prey types and handling techniques, and how these relate to bill morphology (Hulscher 1996; Sutherland *et al.* 1996). The shape of bill-tips in

*Corresponding author.
Accepted for publication December 2013.

doi:10.1111/aec.12117

oystercatchers is the combined result of continuous growth (average of 0.44 mm per day in European oystercatchers) and abrasion rate (Hulscher 1996). Individuals with pointed bills typically specialize on polychaetes, while birds with chisel-shaped and blunt bills specialize in stabbing and hammering shellfish. Beside the Eurasian oystercatcher, 10 other oystercatcher species exist, spread out between Australasia, the American continent and southern Africa, and share many ecological and morphological similarities: they are highly territorial during the breeding season, monogamous, form long-term pair bonds and provide full bi-parental care. Interestingly, consistent sexual dimorphism occurs with females being heavier and having longer and more pointed bills than males in all species (Hockey 1996). Evidence of sex-specific segregation in food exploitation in relation to bill morphology has been reported on the basis of direct observations for Eurasian oystercatchers (Durell *et al.* 1993; Van De Pol *et al.* 2009) and for the two species occurring in Australia (Lauro & Nol 1995; Aplin & Cockburn 2012). In the case of the African black oystercatcher, *Haematopus moquini*, a non-migrating species breeding exclusively in southern and south-western Africa, Hockey and Underhill (1984) also reported sex-specific dietary differences, but in two breeding pairs only.

African black oystercatchers can encounter a wide range of potential prey on the southern African rocky shores, including mussels, limpets, polychaetes, chitons, isopods, barnacles and ascidians (Hockey & Underhill 1984). The structure of these rocky shore communities is however strongly influenced by the two contrasting large marine ecosystems that dominate South African nearshore waters: the Benguela upwelling system on the west coast, and the Agulhas current along the east and south coasts (Shannon 1985; Lutjeharms 2006). Overall this gives rise to broad differences in seawater nutrient concentration and intertidal biomass, which are greater on the west coast, while species richness is greater on the east coast (Bustamante & Branch 1996). The invasion of the southern African coastline by the Mediterranean mussel *Mytilus galloprovincialis* has profoundly altered rocky intertidal communities since its accidental introduction in the late 1970s on the South African west coast (Robinson *et al.* 2007). There, the invasive mussel has replaced the indigenous species as the dominant mussel in the low- and mid-shore and outcompetes adult limpets for rocky space (Steffani & Branch 2005; Robinson *et al.* 2007). On the south-west coast, *M. galloprovincialis* and the indigenous brown mussel *Perna perna* exhibit partial spatial segregation within the mussel zone. Finally on the south-east coast, abundances of the alien mussel are low, except for certain locations (von der Meden *et al.* 2008). The invasion of *M. galloprovincialis* is also believed to have positively influenced African black oystercatcher population dynamics on the west coast by increasing the overall food biomass available to this species (Hockey & Van Erkom Schurink 1992). The natural variability of coastal habitats in southern Africa and their recent alteration by the invasive mussel constitute a unique opportunity to investigate sex-specific foraging strategies in the African black oystercatcher.

Until now, studies on the feeding ecology of shorebirds have relied on conventional methods, such as collection of droppings and food remains, and mostly on direct visual observations (Goss-Custard 1977; Backwell *et al.* 1998; Kuwae *et al.* 2010), because shorebirds are relatively large, easily recognizable and occupy open and accessible habitats. Although they have provided an enormous amount of knowledge and understanding on the feeding ecology of shorebirds, these methods are time-consuming and give only a snapshot of the diet for a limited number of individuals. In the study of oceanic birds however, in addition to conventional stomach content analyses, researchers have embraced the use of chemical dietary tracers such as stable isotopes for the past 15 years, as they provide integrated dietary information at different population, temporal and spatial scales (Dalerum & Angerbjörn 2005; Cherel & Hobson 2007; Jaeger *et al.* 2009). The use of carbon and nitrogen stable isotopes relies on the fact that their ratios ($\delta^{13}C$ and $\delta^{15}N$) in consumer tissues reflect those of their prey in a predictable manner (DeNiro & Epstein 1978, 1981). The $\delta^{13}C$ varies little along the food chain, about 0.5‰ (McCutchan *et al.* 2003), and is a good indicator of sources of primary productivity. This is particularly relevant in coastal habitats where there are clear $\delta^{13}C$ gradients between benthic and pelagic organisms (France 1995) and grazing and filter-feeding invertebrates (Vander Zanden & Rasmussen 1999). Conversely, the shift in $\delta^{15}N$ between a prey and its consumer varies between 2‰ and 5‰ (DeNiro & Epstein 1981; Bearhop *et al.* 2002; McCutchan *et al.* 2003) and is often used to infer the trophic position of organisms within a food web (Cherel *et al.* 2008).

In this study, we investigated between-sex trophic segregation in breeding African black oystercatchers living in three contiguous coastal regions characterized by contrasting oceanographic conditions, intertidal invertebrate assemblages and biomasses and finally different degrees of alien invasion by the Mediterranean mussel. Our aim can be summarized in three questions. First, does trophic segregation between male and female African black oystercatchers occur on South African rocky shores? Second, does this degree of trophic segregation vary geographically? Third, if geographic variations occur in sexual segregation of food exploitation, is it also associated with variability in the degree of sexual dimorphism? To answer these questions, we combined biometric measurements to

doi:10.1111/aec.12117

assess the degree of sexual dimorphism and the analysis of food segregation between male and female oystercatchers breeding in three South African coastal regions (west, south-west and south-east) by employing stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) analysis in their tissues and potential prey.

METHODS

Study areas

Fieldwork was carried out in South Africa during three consecutive breeding seasons (December 2007 to February 2010) in the rocky shore habitats of African black oystercatchers. Birds and their potential prey were sampled in three distinct regions and during the same breeding season for any of the nine study sites: the south-east coast (East London, Kenton and Port Elizabeth), the south-west coast (Plettenberg Bay, Goukamma, de Hoop and Arniston) and the west coast (Koeberg and Langebaan, Fig. 1). At each site, birds and their potential prey (apart from polychaetes, see below), were sampled during the same month.

Sampling of oystercatchers and potential prey

Breeding males and females were captured during incubation on nests using walk-in traps. Efforts were made to capture as many complete pairs as possible. For each bird, 0.5 mL of blood was taken and preserved in 70% alcohol and five cover feathers were cut on each adult to measure their $\delta^{13}C$ and $\delta^{15}N$ ratios. A few drops of blood were spared for molecular sexing (Griffiths & Tiwari 1996, Griffiths *et al.* 1998, see Appendix S1). Tarsus and bill lengths were measured to the nearest 0.1 mm using callipers and wing length was measured to the nearest 1 mm with a ruler. Birds were weighed to the nearest 1 g. A lateral headshot photo was taken of each bird to estimate the bill depth (halfway down) and bill-tip depth *a posteriori* on digital photograph. Birds were ringed and released after handling. Each photograph was scaled using CPCe software (Kohler & Gill 2006, available at http://www.nova.edu/ocean/cpce), with the bill length measured in the field as the scaling parameter. Bill depth and bill-tip depth were measured to the nearest 0.1 mm at 50% and 5% respectively from the bill-tip on the scaled photograph (Fig. 2). Selection of prey categories to sample was based on the literature (Randall & Randall 1982; Hockey & Underhill 1984; Kohler *et al.* 2009) as well as opportunistic and informal observations of the feeding behaviour of African black oystercatchers at several of the study sites. Mussels and limpets compose the bulk of oystercatcher's diets, but polychaetes are also considered in the literature to be occasional prey (Hockey & Underhill 1984; Hockey & Van Erkom Schurink 1992; Kohler *et al.* 2009). In East London, Kenton, Goukamma, Koeberg and Langebaan, direct observations of feeding activities of a total 16 breeding pairs with binoculars (8x40L) confirmed the consumption of either mussels, limpets or polychaetes in mussel beds (S. Kohler, unpubl. data, 2010). In Port Elizabeth, two breeding pairs were also seen regularly scavenging on beached ascidians on the high shore. Five specimens per species of mussels (*Perna perna* and *Mytilus galloprovincialis*) and limpets (*Cymbula oculus*, *Scutellastra argenvillei*, *S. cochlear*, *S. granularis* and *S. longicosta*) were collected at each site when present on feeding grounds. We also included the stable isotope ratios of the suspension-feeding polychaete *Gunnarea capensis* that were collected by Hill and McQuaid (2008) in the three studied coastal regions (see Fig. 1). In Port Elizabeth, three specimens of the ascidian *Pyura stolonifera* were additionally collected.

Stable isotope analysis

Whole blood of birds has a rapid turnover (Bearhop *et al.* 2002) and represents the diet integrated over a period of a few weeks prior to sampling. Feathers are grown during moult, which occurs during the non-breeding season for most shorebirds (Hulscher 1977; Klaassen *et al.* 2001) and

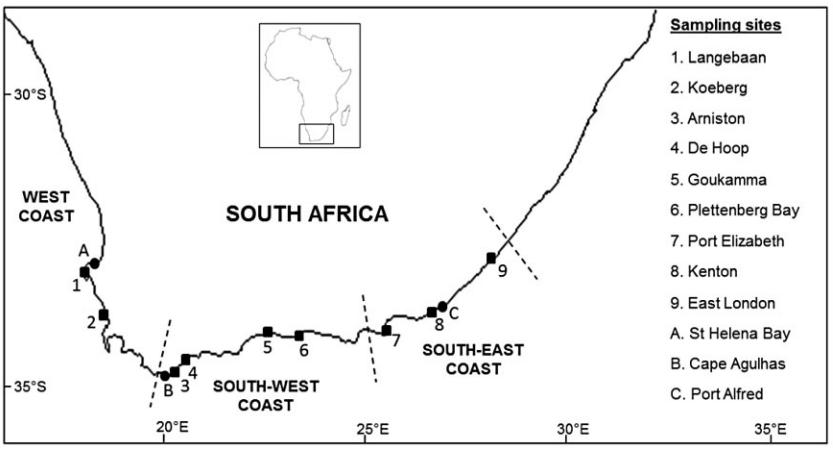

Fig. 1. Location of the nine sampling sites for African black oystercatchers and their prey on the South African coastline. A, B and C indicate the sampling sites for the polychaete *Gunnarea capensis* (Hill & McQuaid 2008).

doi:10.1111/aec.12117

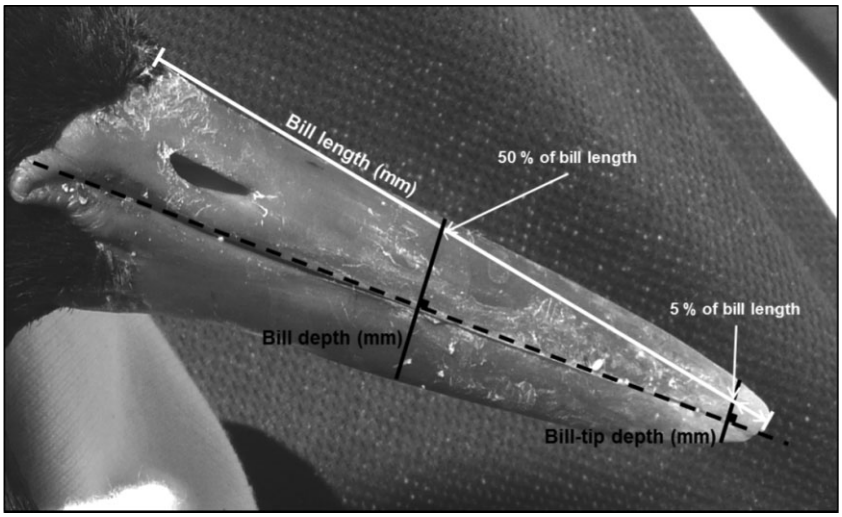

Fig. 2. Lateral photo of an African black oystercatcher's bill. Bill length was measured in the field and used to scale the picture with CPCe (Kohler & Gill 2006). A mark was made at 5% and 50% of the bill length, from the bill-tip, to estimate the bill depth halfway down and the bill-tip depth respectively, perpendicular to the slit between the maxilla and mandibule (dashed line) (Photo: S.A. Kohler).

remain isotopically inert once fully grown (Mizutani *et al.* 1990). Feathers can be therefore used as proxy of the diet during the non-breeding season (Jaeger *et al.* 2009). Pooled feathers were cleaned of surface organic contaminants by immersion in a chloroform/methanol solution (2:1) placed in an ultrasound bath for 2 min and then rinsed with deionized water and dried (60°C, 24 h). In marine invertebrates, muscle tissues have a slow turnover rate and are unlikely to be affected by temporal changes in environmental conditions (Gorokhova & Hansson 1999). Adductor and foot tissue were collected from mussels and limpets respectively. Ascidian body was extracted from the discarded tunic and the buccal siphon tissue was sampled for analysis. All samples were rinsed, dried in an oven (60°C, 24 h) and individually ground into a fine homogenous powder. Relative isotope abundances of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) were determined from approximately 1 mg sub-samples of the homogenous powder with a continuous flow isotope ratio mass spectrometer interfaced to an elemental analyser (EA-IRMS). Results were expressed relative to the levels of ^{13}C in Vienna Pee Dee Belemnite and ^{15}N in atmospheric air. Samples were analysed at the Stable Light Isotope Unit (University of Cape Town, South Africa). Precision of replicate determinations was <0.2‰ for both carbon and nitrogen.

Data analysis

Statistical analyses were performed using R statistical Software (available at http://www.r-project.org). Our datasets did not meet normality (Shapiro test, $\alpha = 0.05$) or homoscedasticity (Levene's test, $\alpha = 0.05$) assumptions therefore we proceeded with non-parametrical analyses and were precluded from analysing directly sex and region interactions on variables using two-way analyses of variance (see below). Kruskal–Wallis tests (H, $\alpha = 0.05$) and multiple comparison post-hoc tests (Student–Newman–Keuls, SNK, $\alpha = 0.05$) were used to test whether $\delta^{13}C$ and $\delta^{15}N$ ratios in prey (mussels, limpets, polychaetes and ascidians) differed within each coastal region (south-east, south-west and west coasts, Hill & McQuaid 2008). A Mann–Whitney test (U, $\alpha = 0.05$) was used to test sex-specific differences in morphology and stable isotope ratios within each region. We also investigated whether each sex differed in its morphology and stable isotopic composition among regions using a Kruskal–Wallis test and post-hoc SNK procedure ($\alpha = 0.05$). For paired birds, we used Wilcoxon tests (W, $\alpha = 0.05$) to investigate whether $\delta^{13}C$ and $\delta^{15}N$ differed between the tissues of breeding partners.

Body condition index (BCI) was calculated for each bird according to the following equation: $BCI = 1 - \frac{mass_{expected} - mass_{observed}}{mass_{expected}}$, where the expected mass was calculated from the linear relationship between wing length (mm) and mass (g), established separately for each sex and from a sample of 47 males and 42 females captured on southern African shores between 2007 and 2010 (Kohler 2011):

$$mass_{expected-males} = 1.87 \times wing\ length + 163.55$$

$$mass_{expected-females} = 3.98 \times wing\ lenth - 369.08$$

A BCI of 1 is the expected mass predicted from the wing length. A BCI < 1 suggests that the individual has a lower body condition that it should have for its size, and a BCI > 1 indicates a higher body condition than expected. Student t tests and one-way ANOVAs (F, $\alpha = 0.05$, $n = 63$) were performed on BCI data for differences between sexes within regions and between males and females of different regions, respectively. Finally, linear regressions (F, $\alpha = 0.05$) were performed on the bill-tip depth/bill length ratios of males and females along the coast.

Prey types contributions to the diet of birds at each site were estimated using the IsoSource stable isotope mixing

doi:10.1111/aec.12117

model software (Phillips & Gregg 2003, available at http://www.epa.gov/wed/pages/models.htm). We used mean carbon and nitrogen stable isotope values of males and females and their potential prey species and trophic enrichment factors (TEFs) of +0.2‰ for $\delta^{13}C$ and +2.7‰ for $\delta^{15}N$ (Kohler *et al.* 2011). Potential contributions of prey to the diet were estimated for males and females at each site and outputs were aggregated *a posteriori* by prey types (Phillips *et al.* 2005).

RESULTS

Sixty-three breeding African black oystercatchers and 20 breeding pairs were sampled from nine breeding sites grouped into the three coastal regions (Fig. 1). The molecular sexing technique identified 30 females and 33 males (see Appendix S1 for details on the molecular sexing method).

Biometrics and body conditions

Females were larger than males and had longer tarsi and wings than males in all regions but the sexual dimorphism was not significant at all locations (Table 1a, Appendix S2). Within all three study regions, females displayed significant longer bills than males, however their bill-tips were only significantly thinner than males on the south-east coast and bill-tip depth/bill length ratios were not significantly different between sexes on the west coast (Table 1a, Appendix S2). Non-parametric tests and post-hoc comparisons of biometrics between males or females of different regions did not show significant geographical differences, either for females or males (Table 1b, Appendix S2). BCIs varied between 0.87 and 1.11 among sexes and coastal regions, and displayed high variability within each considered group, as shown by the standard deviations in Figure 3. BCIs did not differ significantly between sexes in any of the three regions (west: $t = -1.04$, $P = 0.33$; south-west: $t = 1.42$, $P = 0.17$; south-east: $t = 0.77$, $P = 0.45$). However males tended to display lower BCIs than females in the west and south-east regions, while the opposite was observed in the south-west (Fig. 3). Between regions, males differed significantly in body conditions (ANOVA: $F = 4.12$, $P = 0.02$), with south-west males being in

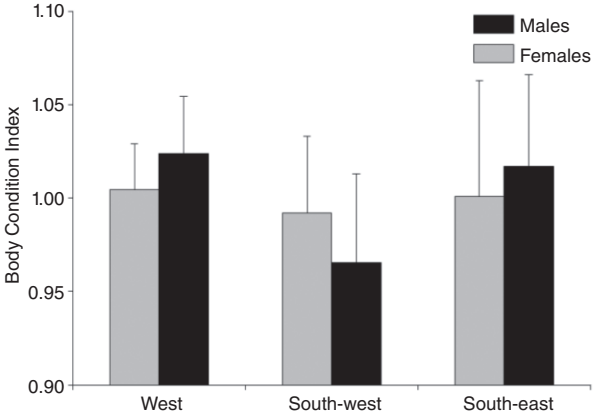

Fig. 3. Body condition index (BCI) of male and female African black oystercatchers on the west, south-west and south-east coasts.

Table 1. (a) Mean (±SD) values of $\delta^{13}C$, $\delta^{15}N$ and biometric measurements of male and female African black oystercatchers in the three study regions. Values in bold indicate significant differences between sexes (Mann–Whitney tests, U, $\alpha = 0.05$), (b) Kruskal–Wallis test results and Student–Newman–Keuls post-hoc comparisons (H, $\alpha = 0.05$) of the stable isotopic compositions and biometric parameters of males and females between regions (SE = south-east; SW = south-west; W = west). Significant differences are indicated in bold

	(a) Mean (±SD) values and differences between sexes within each region						(b) Differences among regions for each sex	
	South-east		South-west		West			
	Females ($n = 13$)	Males ($n = 16$)	Females ($n = 12$)	Males ($n = 11$)	Females ($n = 4$)	Males ($n = 5$)	Females	Males
Mass (g)	706 ± 51	673 ± 36	**691 ± 26**	**635 ± 31**	**711 ± 15**	**675 ± 18**	SE = SW = W	SE = SW = W
Wing (mm)	269 ± 4	267 ± 7	268 ± 3	264 ± 4	271 ± 4	265 ± 4	SE = SW = W	SE = SW = W
Tarsus (mm)	**58 ± 2**	**56 ± 3**	59 ± 2	57 ± 2	59 ± 2	57 ± 1	SE = SW = W	SE = SW = W
Bill length (mm)	**73.0 ± 2.7**	**64.8 ± 2.3**	**73.4 ± 3.0**	**63.7 ± 3.0**	**70.0 ± 4.1**	**63.2 ± 1.4**	SE = SW = W	SE = SW = W
Bill depth 50% (mm)	12.0 ± 0.8	12.2 ± 0.7	12.5 ± 0.8	12.5 ± 3.3	11.8 ± 0.4	13.1 ± 1.1	SE = SW = W	SE = SW = W
Bill depth 5% (mm)	**5.6 ± 0.6**	**6.2 ± 0.7**	5.5 ± 0.5	6.0 ± 0.8	5.0 ± 0.9	5.5 ± 0.7	SE = SW = W	SE = SW = W
Bill ratio	**0.076 ± 0.001**	**0.096 ± 0.010**	**0.075 ± 0.006**	**0.093 ± 0.006**	0.069 ± 0.013	0.088 ± 0.009	SE = SW = W	**SE = SW = W**
Blood $\delta^{13}C$ (‰)	−13.6 ± 1.7	−13.1 ± 1.2	−15.4 ± 0.5	−15.2 ± 0.5	−15.0 ± 0.4	−14.8 ± 0.4	**SE ≠ (SW = W)**	**SE ≠ (SW = W)**
Blood $\delta^{15}N$ (‰)	11.7 ± 0.8	11.5 ± 0.6	11.7 ± 0.4	11.3 ± 0.6	12.3 ± 0.8	12.2 ± 0.9	SE = SW = W	**(SE = SW) ≠ W**
Feathers $\delta^{13}C$ (‰)	−12.8 ± 1.6	−12.6 ± 1.6	−14.9 ± 0.6	−14.7 ± 0.6	−14.3 ± 1.1	−14.3 ± 0.5	**SE ≠ (SW = W)**	**SE ≠ (SW = W)**
Feathers $\delta^{15}N$ (‰)	13.2 ± 0.7	13.0 ± 0.7	13.1 ± 0.4	12.9 ± 0.3	14.0 ± 1.3	13.8 ± 0.8	SE = SW = W	**(SE = SW) ≠ W**

For details of the statistical results, report to Appendix S2.

doi:10.1111/aec.12117

lesser condition than south-east individuals (post-hoc Tukey tests: $SW_{males} - SE_{males}$, $P = 0.02$). No similar pattern was observed for females ($F = 0.14$, $P = 0.87$).

Stable isotope ratios in prey

Overall, the four prey types could be segregated by their mean (±SD) $\delta^{13}C$ and/or $\delta^{15}N$ values (Fig. 4). Limpets were significantly ^{13}C-enriched compared to mussels in all three regions ($SNK_{limpets\text{-}mussels}$: south-east: $U = 18.3$, $P < 0.001$; south-west: $U = 23.8$, $P < 0.001$; west: $U = 20.4$, $P < 0.001$) and polychaete worms ($SNK_{limpets\text{-}polychaetes}$: south-east: $U = 9.6$, $P < 0.001$; south-west: $U = 11.3$, $P < 0.001$; west: $U = 18.8$, $P < 0.001$), while for the two latter prey types, $\delta^{13}C$ ratios were not significantly different ($SNK_{polychates\text{-}mussels}$: south-east: $U = 1.21$, $P = 0.39$; $U = 1.09$, $P = 0.45$) except on the west coast ($SNK_{polychates\text{-}mussels}$: $U = 2.99$, $P = 0.04$). The polychaete *Gunnarea capensis* was significantly enriched in ^{15}N compared to mussels ($SNK_{polychates\text{-}mussels}$, south-east: $U = 10.56$, $P < 0.001$; south-west: $U = 12.13$, $P < 0.01$; west: $U = 6.53$, $P < 0.01$) and limpets ($SNK_{polychaetes\text{-}limpets}$: south-east: $U = 10.05$, $P < 0.001$; south-west: $U = 9.38$, $P < 0.001$; west: $U = 3.06$,

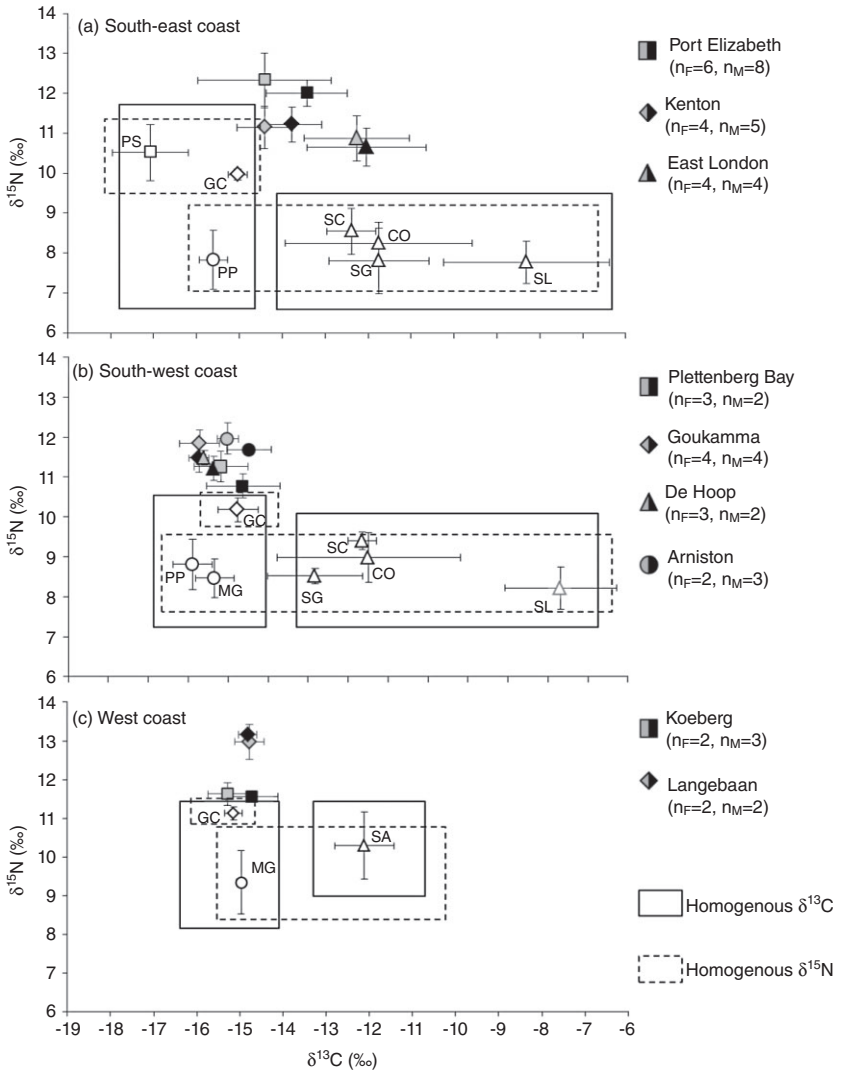

Fig. 4. Carbon and nitrogen stable isotope values from blood of male (black symbols) and female (grey symbols) oystercatchers, mussels (open circles – PP = *Perna perna*, MG = *Mytilus galloprovincialis*), limpets (open triangles – CO = *Cymbula oculus*, SA = *Scutellastra argenvillei*, SC = *S. cochlear*, SG = *S. granularis*, SL = *S. longicosta*), polychaetes (open diamonds – GC = *Gunnarea capensis*), and ascidians (open square – PS = *Pyura stolonifera*) in the south east (a), south-west (b) and west coast (c). Values are mean ± SD per site for oystercatchers and mean ± SD per region for prey species. Continuous and dotted rectangles group prey species with similar $\delta^{13}C$ or $\delta^{15}N$ ratios based on Kruskal–Wallis test and Student–Newman–Keuls post-hoc comparison ($\alpha = 0.05$).

doi:10.1111/aec.12117

$P = 0.04$), while the two molluscs had similar $\delta^{15}N$ ratios on the south-east coast ($SNK_{limpets\text{-}mussels}$: $U = 1.98$, $P = 0.17$) but not on the south-west ($SNK_{limpets\text{-}mussels}$: $U = 3.37$, $P = 0.02$) nor the west coast ($t = 4.01$, $P = 0.01$). Ascidians only occurred on the south-east coast where they were ^{13}C-depleted compared to limpets ($SNK_{ascidians\text{-}limpets}$: $U = 9.53$, $P < 0.001$), but only marginally compared to polychaetes ($SNK_{ascidians\text{-}polychaetes}$: $U = 3.34$, $P = 0.05$) and mussels ($SNK_{ascidians\text{-}mussels}$: $U = 2.94$, $P = 0.05$). Ascidians displayed significantly higher $\delta^{15}N$ ratios than mussels ($SNK_{ascidians\text{-}mussels}$: $U = 5.95$, $P < 0.001$) and limpets ($SNK_{ascidians\text{-}limpets}$: $U = 5.39$, $P < 0.001$), but similar to those of polychaetes ($SNK_{ascidians\text{-}polychaetes}$: $U = 0.57$, $P = 0.69$). Prey species are grouped in Figure 4 according to their $\delta^{13}C$ or $\delta^{15}N$ statistical similarity.

Geographic and sex-specific differences in stable isotope ratios of oystercatchers

Blood of females and males from the south-east coast were significantly enriched in ^{13}C compared to their counterparts in the two western regions (Table 1a,b, Appendix S2). Male blood on the west coast was significantly enriched in ^{15}N compared to males from the south-west and south-east coasts while females displayed similar $\delta^{15}N$ ratios in all three regions (Table 1a,b, Appendix S2). The same patterns of stable isotope variations between males or females of the different regions were observed in feathers (Table 1a,b, Appendix S2).

On the south-east coast, oystercatchers' blood $\delta^{13}C$ ratios ranged from −17.1‰ to −10.8‰, and from 10.4‰ to 13.4‰ for $\delta^{15}N$. High intra-site variation was observed in both isotope ratios, and male and female value ranges overlapped greatly (Fig. 4a). Nonetheless, higher mean $\delta^{13}C$ values were observed for males in Kenton and Port Elizabeth ($\Delta\delta^{13}C = +0.6$ and +1.0 respectively, with $\Delta = \delta_{males} - \delta_{females}$), and slightly higher mean $\delta^{15}N$ values were measured for females in East London and Port Elizabeth ($\Delta\delta^{15}N = +0.3$ for both sites; Fig. 4a). On the south-west coast, $\delta^{13}C$ values of oystercatchers ranged from −16.1‰ to −14.0‰ and $\delta^{15}N$ values ranged from 10.6‰ to 12.3‰ (Fig. 4b). On the west coast, individuals from Koeberg and Langebaan had similar $\delta^{13}C$ values (from −15.6‰ to − 14.2‰) but differed by approximately 2‰ in their $\delta^{15}N$ values (from 11.4‰ to 13.3‰, Fig. 4c). In the two western regions, stable isotope differences between sexes were less obvious: the global pattern of ^{13}C-enrichement in males was however observed at four out of six sites, with $\Delta\delta^{13}C$ varying between 0.0‰ and +0.6‰, and ^{15}N-enriched females at five sites, with $\Delta\delta^{15}N$ varying between +0.2‰ and +0.5‰ (Fig. 4b,c). Overall, blood and feathers of males were ^{13}C-enriched and ^{15}N-depleted compared to females at all sites except Langebaan (west coast, Fig. 4a), however these isotope differences were not significant in any of the three regions (Appendix S2).

Breeding pairs

At a finer scale, consistent pattern of inter-sexual partition in $\delta^{13}C$ and $\delta^{15}N$ ratios could be observed between paired birds, but varied with the tissues and sites considered (Fig. 5). There were significant $\delta^{13}C$ differences between breeding partners for both blood (Fig. 5a) and feathers (Fig. 5c). However, one female caught in Port Elizabeth was particularly depleted in ^{13}C (blood: $\delta^{13}C = -17.1$‰, feathers: $\delta^{13}C = -15.3$‰) compared to her mate (blood: $\delta^{13}C = -12.6$‰, feathers: $\delta^{13}C = -12.9$‰; Fig. 5, pair indicated with an arrow). When this pair was excluded from the analysis, the differences between paired birds were only marginally significant (Fig. 5a,c). Finally, the $\delta^{13}C$ ratios of breeding pairs sampled on the south-east coast also varied greatly between one another as opposed to the western birds which showed little between-pair $\delta^{13}C$ variability (Fig. 5a,c). Breeding partners displayed significant differences in their $\delta^{15}N$ ratios (Fig. 5b) measured in blood with an overall enrichment in ^{15}N in females (average +0.3‰), while their feather $\delta^{15}N$ ratios were not significantly different (Fig. 5d). The trend persisted even when the pair from Port Elizabeth was excluded from the analysis (Fig. 5b,d).

Diet

The IsoSource model outputs indicated that mussels and limpets composed the bulk of the diet of African black oystercatchers, and that their relative contributions varied mostly among sites and regions rather than between sexes (Fig. 6). On the south-west and west coasts, mussels dominated the diet (39–100%; Fig. 6, Appendix S3) while on the south-east the contribution of limpets was substantial though variable (0–100%; Fig. 6, Appendix S3). With the exceptions of Port Elizabeth (0–75%) and Langebaan (43–60%), the contribution of polychaetes was low (0–39% and 0–31% at all the other sites combined; Fig. 6, Appendix S3). There was much overlap in the range of feasible contributions of males and females from the same site (Appendix S3). However in Kenton, females seemed to feed more on mussels (mean value of 66%; range of 59–70%) than did males (mean value of 47%, range of 41–52%), which fed more on limpets (males: mean value of 27%; range of 25–29%; females: mean value of 15%, range of 13–19%). One female ('F4') in Port Elizabeth had a different isotope composition from other females in the area, and was not pooled

doi:10.1111/aec.12117

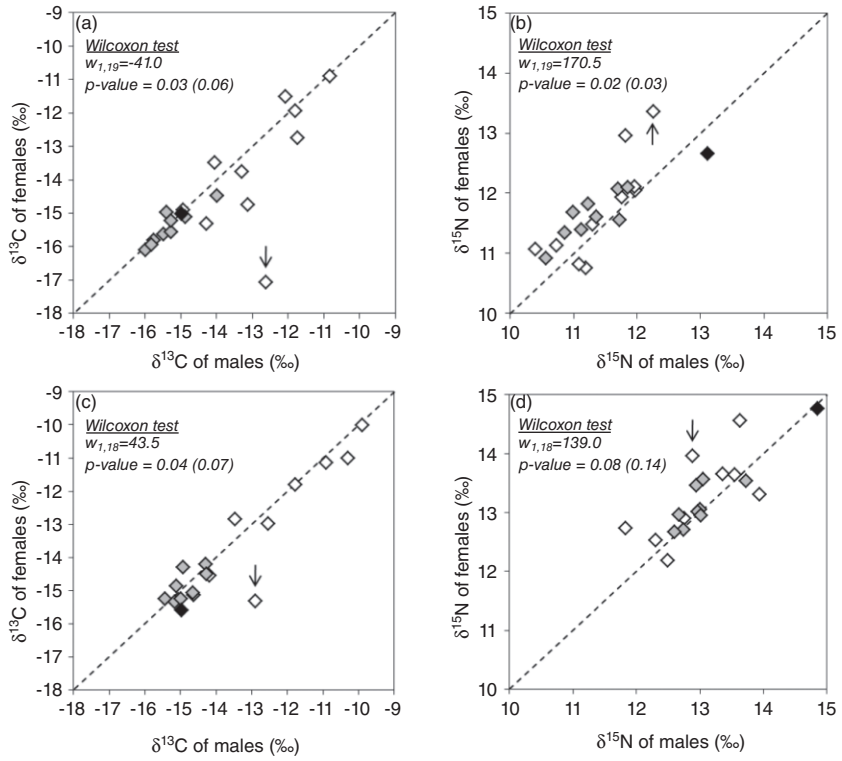

Fig. 5. Blood carbon (a) and nitrogen (b) and feather carbon (c) and nitrogen (d) stable isotope signatures of breeding pairs from the south-east (open diamonds), south-west (grey diamonds) and west (black diamond) coasts. The arrows indicate an outlier pair sampled in Port Elizabeth with contrasted stable isotope compositions (Female 'F4'). A Wilcoxon matched-pairs signed rank test (W, $\alpha = 0.05$) was used to test for differences in $\delta^{13}C$ and $\delta^{15}N$ between breeding partners. Values between brackets indicate the p-value when the pair indicated by an arrow was removed from the analysis.

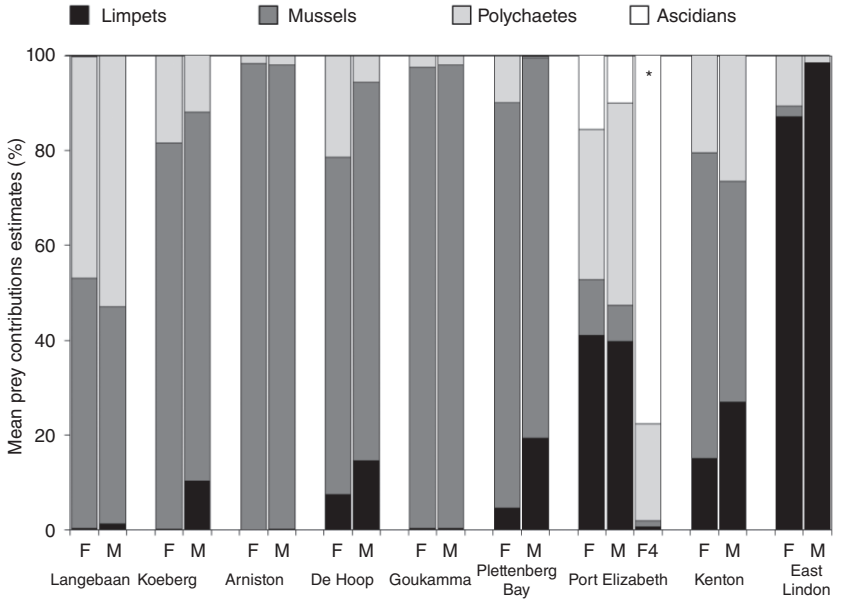

Fig. 6. Mean potential contribution (%) of limpets (black), mussels (dark grey), polychaetes (light grey) and ascidians (white) to the diet of male and female oystercatchers at the 9 study sites (east to west, see Fig. 1), calculated with IsoSource software. ⋆ indicates contributions estimated individually for the female (F4) with contrasting stable isotopic compositions sampled at Port Elizabeth (see Fig. 5).

doi:10.1111/aec.12117

with them in the mixing model (Fig. 6, individual indicated with an asterisk). The IsoSource model outputs revealed a much higher consumption of ascidians for this female (66–100%) than for other birds (0–59%) from Port Elizabeth (Fig. 6, Appendix S3). Finally, the polychaete consumption was balanced between sexes, with females having a higher consumption than males at five sites, but intersexual differences only ranged between 1% (Goukamma) and 16% (De Hoop; Fig. 6, Appendix S3).

DISCUSSION

Carbon and nitrogen stable isotopes have been used to successfully demonstrate sex-specific food partitioning in a wide variety of seabird taxa, including penguins, cormorants, procellariiformes and skimmers (Forero *et al.* 2005; Bearhop *et al.* 2006; Mariano-Jelicich *et al.* 2008) but have rarely been used for this purpose in shorebirds. Variations in stable isotope ratios in marine predator tissues can result from: (i) environmental changes affecting the isotopic composition of the base of the food web (Cherel & Hobson 2007), (ii) differences in the relative consumption of isotopically distinct prey (Gannes *et al.* 1998), and/or (iii) physiological status and diet-tissue fractionation (McCutchan *et al.* 2003).

At large scales, differences in carbon and nitrogen stable isotope ratios and dietary composition estimated from stable isotope mixing models, were observed between oystercatchers from different regions (Table 1b, Figs 4–6). First, an overall increase in $\delta^{15}N$, although only significant in males, could be observed between south-eastern, south-western and western birds. Second, African black oystercatchers from the two western regions displayed depleted ^{13}C ratios and less variability among individuals and breeding sites compared to birds from the south-east (Fig. 4, Table 1b). Third, birds displayed a higher consumption of limpets towards the east (Fig. 6). These geographic variations in the trophic ecology of African black oystercatchers have been previously reported by Kohler *et al.* (2011) in adults and chicks between the southern Namibian coast and East London (Eastern Cape, South Africa). The authors hypothesized that those were related to the broad differences in primary production, the structure of rocky intertidal communities and abundance of prey (including the uneven distribution and abundance of *M. galloprovincialis*) between the two large marine ecosystems surrounding the South African coastline, the Benguela upwelling system (west coast) and the Agulhas current on the south and east coasts of southern Africa (Bustamante & Branch 1996). Indeed, these large-scale patterns have been shown to affect the stable isotopic composition of nearshore primary producers, rocky shore invertebrates (Hill *et al.* 2006; Hill & McQuaid 2008) and their common predator, the African black oystercatcher (Kohler *et al.* 2011).

The potential food sources considered in this study displayed clear and consistent differences in their $\delta^{13}C$ and/or $\delta^{15}N$ values across the study area, making this an ideal system for the investigation of feeding preferences in a rocky shore predator. Limpets were ^{13}C-enriched compared to mussels and polychaetes and this $\delta^{13}C$ segregation is typically observed between inshore grazing and filtering organisms feeding on ^{13}C depleted particulate organic matter (France 1995; Vander Zanden & Rasmussen 1999). Furthermore, the suspension-feeder polychaete *Gunnarea capensis* was consistently ^{15}N-enriched by about 2‰ compared to mussels. Finally, the filter-feeder ascidians, additionally sampled in Port Elizabeth, significantly differed in their $\delta^{13}C$ and $\delta^{15}N$ ratios from other prey. Nevertheless, males and females displayed locally little differences in their stable carbon isotope ratios or in the relative contribution of prey types to their diet as shown by the IsoSource model outputs (Fig. 6). This suggested that sex-specific diet segregation in African black oystercatchers is not as clear-cut as in other oystercatcher species (Durell *et al.* 1993; Lauro & Nol 1995; Aplin & Cockburn 2012). Two exceptions were observed on the south-east coast. In Kenton, the stable isotope mixing model outputs suggested that females, with their longer and more pointed bills, were feeding more on mussels while males, with their blunted bills, focused more on limpets. This corroborated previous findings on the feeding ecology of this species on the south-east coast of South Africa (Kohler *et al.* 2009). In addition, beached ascidians seemed to be an important alternative prey for females in Port Elizabeth, Similar feeding behaviour has been described for American pied oystercatchers (*Haematopus palliatus*) in Chile (Pacheco & Castilla 2001) and female sooty oystercatchers (*H. fuliginosus fuliginosus*) in Australia (Aplin & Cockburn 2012). In both studies, authors interpreted this uncommon behaviour as a local adaptation to the unusual abundance of Tunicidae and pointed out the niche flexibility of these birds, especially in the case of female sooty oystercatchers. A similar hypothesis can be postulated for African black oystercatchers in Port Elizabeth. Finally, south-east breeding birds had larger between-pair variability which may reflect the larger prey choice available there compared to the two western regions where rocky shores are largely dominated by mussels and by the invasive *M. galloprovincialis* in particular (Robinson *et al.* 2007).

Records of sex-specific feeding behaviour in African black oystercatchers prior to the invasion of South African rocky shores by the Mediterranean mussel *Mytilus galloprovincialis* are limited to observations made on two breeding pairs on Marcus Island on the

doi:10.1111/aec.12117

west coast in 1979/1980 (Hockey & Underhill 1984). Hence, it is difficult to extrapolate this pattern to the rest of the breeding population at that time. In that study, the authors reported that both sexes fed similarly on mussels, the indigenous *Choromytilus meridionalis* and *Aulocomya ater*, but that males consumed more limpets and whelks, and females more polychaetes. It was suggested that the longer and more pointed bills of females were more adapted for probing polychaetes in mussel beds, while males with their more robust bills were better equipped for removing limpets from rocks. Feeding specializations in oystercatchers are not only prey-type related (soft-bodied polychaetes *versus* hard-shelled prey), but also characterized by different handling techniques (stabbing, ventral or dorsal hammering of bivalves, Sutherland *et al.* 1996). There is however no evidence of different prey-handling techniques among African black oystercatchers. In the piles of shells left by oystercatchers, mussel and limpet shells are mostly found intact (S. Kohler, pers. obs., 2007), suggesting the use of only stabbing to open mussels and prying to dislodge limpets. In the present study, bill dimorphism occurred throughout the study area, however the degree of this dimorphism increased eastwards, with males having higher bill-tip depth and bill ratios than females on the east coast but not in the west. Concordantly, on one hand the only evidence of sex-related trophic segregation could be observed at two eastern sites, Kenton and Port Elizabeth, with males feeding more on limpets and females more on mussels and/or ascidians (Fig. 6), and where males displayed significantly more blunted bills than females. On the other hand, both sexes seemed to have converged to a diet essentially composed of the invasive mussel in the two western regions, as recently reported on Marcus Island, off the west coast by Coleman and Hockey (2008), and the bill dimorphism observed in this region was only related to bill length.

Sex-related feeding differences associated with bill dimorphism in oystercatchers have mostly been attributed to the need for diet segregation to reduce competition within pairs (Hockey & Underhill 1984; Lauro & Nol 1995) and to increase winter survival and fitness (Durell *et al.* 1993), under the assumptions of limited food resources. In the present study, minimal and location-specific trophic segregation between male and female African black oystercatchers, along with discrepancies in the BCI of males across regions and only limited regional differences in bill dimorphism, were consistent with several factors unique to the southern African coastline. Food availability may not be a limiting factor for the species on the west coast as a result of the invasion of rocky shores by the Mediterranean mussel (Hockey & Van Erkom Schurink 1992), which greatly increased the biomass of mussels, a group historically favoured by African black oystercatchers (Randall & Randall 1982; Hockey & Underhill 1984). This hypothesis was firstly supported by the opposite pattern on the south-east coast where some degree of food partitioning was observed and where the invasive mussel is virtually absent and overall prey biomass is lower than on the west coast (Bustamante & Branch 1996). Secondly, the body condition of birds was not significantly different between regions (Fig. 3), suggesting that the access to food is no more limiting in a region invaded by *M. galloprovincialis* than in a non-invaded one. In the south-west region on the other hand, prey biomass was relatively low, comparable to that of the south-east coast due to the influence of the oligotrophic Agulhas current, but the oystercatchers' feeding areas there were dominated by mussels (both *P. perna* and *M. galloprovincialis*; Robinson *et al.* 2007) and lacked the high diversity of the south-east coast. There, the combined effects of lacking an alternative prey (limpets) and the relatively low mussel biomass (compared with the west coast) resulted in limited bill dimorphism and food partitioning but also lower BCI in males (Fig. 3).

Long-term consequences of biological invasions in aquatic habitats can be difficult to ascertain, especially when considering their effects on a long-lived predator. Moreover phenotypic variability in feeding apparatus within a population can have significant consequences on the ability of each individual to efficiently exploit available food sources and face shifts in prey communities (Durell 2000; Van De Pol *et al.* 2010). Overall African black oystercatchers demonstrated great plasticity in their feeding behaviour, as shown by the variety of their diet under contrasting conditions and their positive response to an invasive mussel species. Nonetheless our study raises questions regarding the cost of this dietary shift may have on male oystercatchers on South African rocky shores.

ACKNOWLEDGEMENTS

We wish to thank CapeNature and Koeberg Nature Reserve for granting access to conservation area and providing human and logistic support. We are also very grateful to B. Bonnevie, B. Dubillot, K. Ludynia, C. Mablouké, N. Parsons, P. Pinet, N. Richoux, A. Valery, C. Vernon, the Animal Demography Unit and the Lakes Bird Club. Isotope samples were analysed by I. Newton and J. Lanham at the Stable Light Isotope Laboratory (University of Cape Town). Molecular sexing was done by S. Dano at the CEBC-CNRS (2007–2008 samples) and by L. Humeau at the UMR-PVBMT (Université de La Réunion, 2008–2009 and 2009–2010 samples). This manuscript greatly benefited from the constructive comments of J.P. Roux, R. Sherley, two anonymous reviewers and the editor of

doi:10.1111/aec.12117

Austral Ecology M. Bull. This research was financially supported by a WIOMSA MARG I, a research grant from Région Réunion and Rhodes University. This work is based upon research supported by the South African Research Chairs Initiative of the Department of Science and Technology and the National Research Foundation. S. Kohler was funded by a PhD grant awarded by the French Ministry of Higher Education and Research via the Université de La Réunion.

REFERENCES

Andersson M. & Norberg R. Å. (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15,** 105–30.

Aplin L. M. & Cockburn A. (2012) Ecological selection and sexual dimorphism in the sooty oystercatcher, *Haematopus fuliginosus*. *Austral Ecol.* **37,** 248–57.

Backwell P. R. Y., O'Hara P. D. & Christy J. H. (1998) Prey availability and selective foraging in shorebirds. *Anim. Behav.* **55,** 1659–67.

Bearhop S., Phillips R. A., McGill R., Cherel Y., Dawson D. A. & Croxall J. P. (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Mar. Ecol. Prog. Ser.* **311,** 157–64.

Bearhop S., Waldron S., Votier S. C. & Furness R. W. (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiol. Biochem. Zool.* **75,** 451–8.

Bustamante R. & Branch G. (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.

Cherel Y., Ducatez S., Fontaine C., Richard P. & Guinet C. (2008) Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. *Mar. Ecol. Prog. Ser.* **370,** 239–47.

Cherel Y. & Hobson K. A. (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar. Ecol. Prog. Ser.* **329,** 281–7.

Coleman R. A. & Hockey P. A. R. (2008) Effects of an alien invertebrate species and wave action on prey selection by African black oystercatchers (*Haematopus moquini*). *Austral Ecol.* **33,** 232–40.

Dalerum F. & Angerbjörn A. (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia* **144,** 647–58.

DeNiro M. J. & Epstein S. (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* **42,** 495–506.

DeNiro M. J. & Epstein S. (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. Cosmochim. Acta* **45,** 341–51.

Durell S. E. A. L. V. D. (2000) Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biol. Rev.* **75,** 503–18.

Durell S. E. A. L. V. D., Goss-Custard J. D. & Caldow R. W. G. (1993) Sex-Related Differences in Diet and Feeding Method in the Oystercatcher *Haematopus ostralegus*. *J. Anim. Ecol.* **62,** 205–15.

Forero M. G., González-Solis J., Hobson K. A. *et al.* (2005) Stable isotopes reveal trophic segregation by sex and age in the southern giant petrel in two different food webs. *Mar. Ecol. Prog. Ser.* **296,** 107–13.

France R. L. (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar. Ecol. Prog. Ser.* **124,** 307–12.

Gannes L. Z., Martínez del Rio C. & Koch P. (1998) Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. *Comp. Biochem. Physiol., Part A Mol. Integr. Physiol.* **119,** 725–37.

González-Solıs J., Croxall J. P. & Wood A. G. (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos* **90,** 390–8.

Gorokhova E. & Hansson S. (1999) An experimental study on variations in stable carbon and nitrogen isotope fractionation during growth of *Mysis mixta* and *Neomysis integer*. *Can. J. Fish. Aquat. Sci.* **56,** 2203–10.

Goss-Custard J. D. (1977) Optimal foraging and the size selection of worms by redshank, *Tringa totanus*, in the field. *Anim. Behav.* **25,** 10–29.

Griffiths R., Double M. C., Orr K. & Dawson R. J. G. (1998) A DNA test to sex most birds. *Mol. Ecol.* **7,** 1071–5.

Griffiths R. & Tiwari B. (1996) Avian Ghd genes and their use in methods for sex identification in birds. International patent publication no W09639505, published 12 December 1996, Isis Innovation Oxford.

Hill J. M. & McQuaid C. D. (2008) $\delta^{13}C$ and $\delta^{15}N$ biogeographic trends in rocky intertidal communities along the coast of South Africa: evidence of strong environmental signatures. *Estuar. Coast. Shelf Sci.* **80,** 261–8.

Hill J. M., McQuaid C. D. & Kaehler S. (2006) Biogeographic and nearshore–offshore trends in isotope ratios of intertidal mussels and their food sources around the coast of southern Africa. *Mar. Ecol. Prog. Ser.* **318,** 63–76.

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. & 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.

Hulscher J. B. (1977) The progress of wing-moult of Oystercatchers *Haematopus ostralegus* at Drachten, Netherlands. *Ibis* **119,** 507–12.

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.

Jaeger A., Blanchard P., Richard P. & Cherel Y. (2009) Using carbon and nitrogen isotopic values of body feathers to infer inter- and intra-individual variations of seabird feeding ecology during moult. *Mar. Biol.* **156,** 1233–40.

Klaassen M., Lindström Å., Meltofte H. & Piersma T. (2001) Arctic waders are not capital breeders. *Nature* **413,** 794.

Kohler K. E. & Gill S. M. (2006) Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. *Comput. Geosci.* **32,** 1259–69.

doi:10.1111/aec.12117

Kohler S. (2011) *Ecologie trophique de l'Huîtrier Noir Africain (*Haematopus moquini*) sur les littoraux rocheux de l'Afrique Australe en relation avec la variabilité de son habitat* (Thèse de Doctorat). Université de La Réunion, Saint-Denis.

Kohler S. A., Connan M., Hill J. M. *et al*. (2011) Geographic variation in the trophic ecology of an avian rocky shore predator, the African Black Oystercatcher, along the southern African coastline. *Mar. Ecol. Prog. Ser.* **435,** 235–49.

Kohler S., Bonnevie B., McQuaid C. & Jaquemet S. (2009) Foraging ecology of an endemic shorebird, the African Black Oystercatcher (*Haematopus moquini*) on the south-east coast of South Africa. *Estuar. Coast. Shelf Sci.* **84,** 361–6.

Kuwae T., Miyoshi E., Sassa S. & Watabe Y. (2010) Foraging mode shift in varying environmental conditions by dunlin *Calidris alpina*. *Mar. Ecol. Prog. Ser.* **406,** 281–9.

Lauro B. & Nol E. (1995) Feeding behavior, prey selection, and bill size of pied and sooty oystercatchers in Australia. *Wilson Bull.* **107,** 629–40.

Lutjeharms J. R. E. (2006) The coastal ocean of south-eastern Africa. In: *The Sea* (eds A. R. Robinson & K. H. Brink) pp. 783–834. Harvard University Press, Cambridge.

McCutchan J. H., Lewis W. M. Jr., Kendall C. & McGrath C. C. (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* **102,** 378–90.

Mariano-Jelicich R., Botto F., Martinetto P., Iribarne O. & Favero M. (2008) Trophic segregation between sexes in the Black Skimmer revealed through the analysis of stables isotopes. *Mar. Biol.* **155,** 443–50.

Meijer T. & Drent R. (1999) Re-examination of the capital and income dichotomy in breeding birds. *Ibis* **141,** 399–414.

Mizutani H., Fukuda M., Kabaya Y. & Wada E. (1990) Carbon Isotope Ratio of Feathers Reveals Feeding Behavior of Cormorants. *Auk* **107,** 400–3.

Pacheco C. J. & Castilla J. C. (2001) Foraging behavior of the American oystercatcher Haematopus palliatus pitanay (Murphy 1925) on the intertidal ascidian *Pyura praeputialis* (Heller 1878) in the Bay of Antofagasta, Chile. *J. Ethol.* **19,** 23–6.

Phillips D. L. & Gregg J. W. (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* **136,** 261–9.

Phillips D. L., Newsome S. D. & Gregg J. W. (2005) Combining sources in stable isotope mixing models: alternative methods. *Oecologia* **144,** 520–7.

Randall R. M. & Randall B. M. (1982) The hard-shelled diet of African Black Oystercatcher chicks at St-Croix Island, South Africa. *Ostrich* **53,** 157–63.

Robinson T. B., Branch G. M., Griffiths C. L., Govender A. & Hockey P. A. R. (2007) Changes in South African rocky intertidal invertebrate community structure associated with the invasion of the mussel *Mytilus galloprovincialis*. *Mar. Ecol. Prog. Ser.* **340,** 163–71.

Selander R. K. (1966) Sexual Dimorphism and Differential Niche Utilization in Birds. *Condor* **68,** 113–51.

Shannon L. V. (1985) The Benguela ecosystem. Part 1: Evolution of the Benguela physical features and processes. *Oceanogr. Mar. Biol. Annu. Rev.* **23,** 105–82.

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. Bio. Ecol.* **317,** 127–42.

Sutherland W. J., Ens B. J., Goss-Custard J. D. & Hulscher J. B. (1996) Specialization. In: *The Oystercatcher: From Individuals to Populations* (ed. J. D. Goss-Custard) pp. 56–76. Oxford University Press, Oxford.

Székely T., Reynolds J. D. & Figuerola J. (2000) Sexual size dimorphism in shorebirds, gulls and alcids: the influence of sexual and natural selection. *Evolution* **54,** 1404–13.

von der Meden C. E. O., Porri F., Erlandsson J. & McQuaid C. D. (2008) Coastline topography affects the distribution of indigenous and invasive mussels. *Mar. Ecol. Prog. Ser.* **372,** 135–45.

Van De Pol M., Brouwer L., Ens B. J., Oosterbeek K. & Tinbergen J. M. (2010) Fluctuating selection and the maintenance of individual and sex-specific diet specialization in free-living oystercatchers. *Evolution* **64,** 836–51.

Van De Pol M., Oosterbeek K., Rutten A. L., Ens B. J., Tinbergen J. M. & Verhulst S. (2009) Biometric sex discrimination is unreliable when sexual dimorphism varies within and between years: an example in Eurasian oystercatchers *Haematopus ostralegus*. *Ibis* **151,** 171–80.

Vander Zanden M. J. & Rasmussen J. B. (1999) Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. *Ecology* **80,** 1395–404.

Weimerskirch H., Shaffer S. A., Tremblay Y. *et al*. (2009) Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Mar. Ecol. Prog. Ser.* **391,** 267–78.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Example of DNA sex identification results for 10 individuals.

Appendix S2. Comparisons between sexes and regions of morphometric measurements and stable isotope ratios of oystercatchers.

Appendix S3. Dietary data for male and female oystercatchers at the 9 study sites.

doi:10.1111/aec.12117