Trophic ecology of the African Black Oystercatcher (haematopus-moquini) on the Southern African rocky shores, in relation with it's habitat variability

Sophie Kohler

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ECOLOGIE TROPHIQUE DE L'HUITRIER NOIR AFRICAIN *(HAEMATOPUS MOQUINI)* SUR LES LITTORAUX ROCHEUX DE L'AFRIQUE AUSTRALE EN RELATION AVEC LA VARIABILITE DE SON HABITAT

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Sophie KOHLER

Devant le jury composé de

Pr. Dominique DAVOULT	Université Paris VI – Roscoff	Rapporteur
Dr Pierrick BOCHER (HDR)	Université de La Rochelle	Rapporteur
Dr Yves CHEREL (HDR)	CNRS – CEBC	Directeur
Dr Sébastien JAQUEMET	Université de La Réunion	Co-directeur
Pr. Matthieu LE CORRE	Université de La Réunion	Examinateur
Pr. Christopher McQUAID	Rhodes University (Afrique du Sud)	Examinateur

Il vaut mieux mobiliser son intelligence sur des conneries

que mobiliser sa connerie sur des choses intelligentes

(Proverbe Shadock)

AVANT-PROPOS

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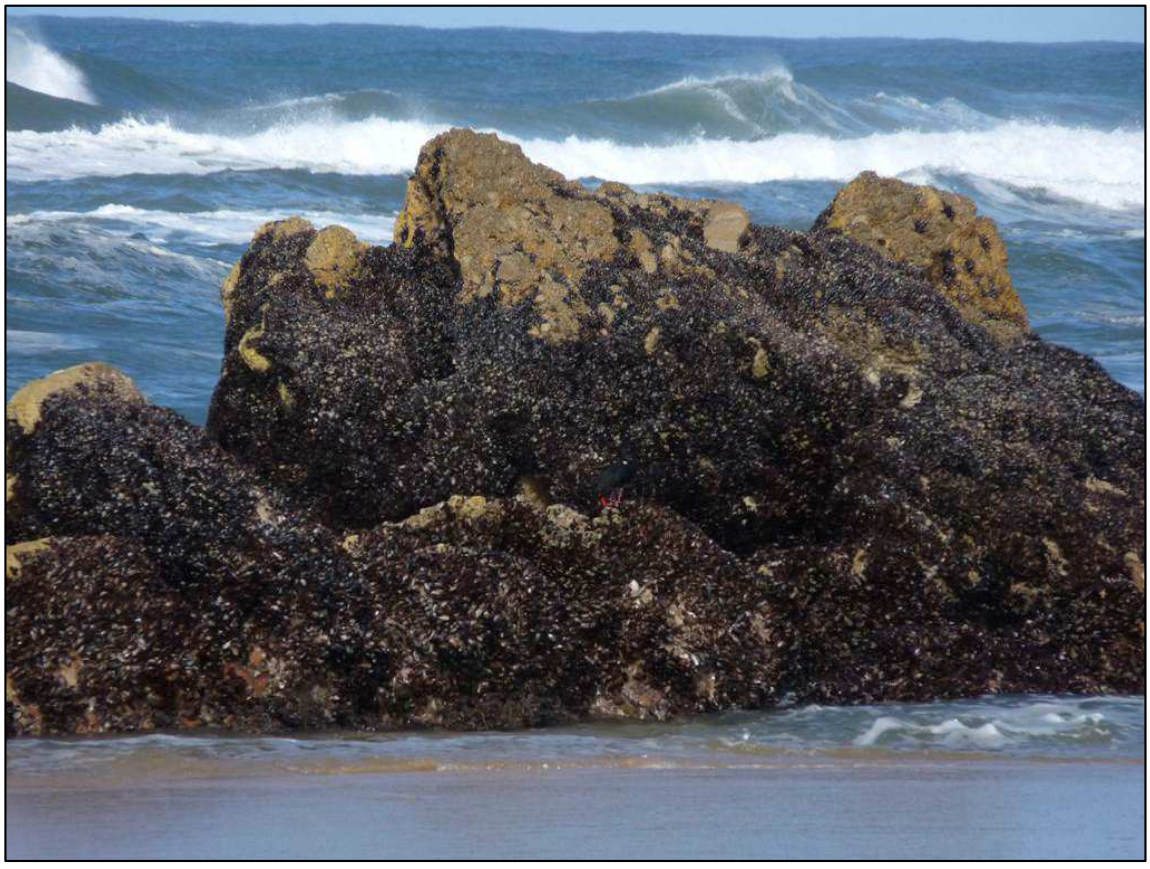
SOMMAIRE

INTRODUCTION GENERALE



(Photo: . S. Kohler)

I. Cadre théorique de l'étude

Les milieux intertidaux se situent entre les lignes de basse mer et pleine mer et ne représentent de ce fait qu'une infime partie des terres émergées mais aussi des écosystèmes marins (Menge & Branch 2001). Ils sont en revanche parmi les plus diversifiés et productifs du monde et la production primaire côtière peut représenter jusqu'à plus de 20% de la production marine globale (Wollast 1998). Par ailleurs, les milieux côtiers sont constitués d'un grand nombre d'habitats (herbiers, forêts de kelps, milieux rocheux, mangroves, récifs coralliens) qui accueillent une importante diversité biologique en invertébrés et en algues (McRoy & Lloyd 1981, Dayton 1985, Birkeland 1997, Le Hir & Hily 2005). Ils peuvent également héberger de nombreux prédateurs marins, dont de fortes diversités en oiseaux limicoles, à la fois sur leurs sites de reproduction et d'hivernage (Baker & Baker 1973, Gandini et al. 1998, Henningsson & Alerstam 2005). Par ailleurs, environ 70% de la population mondiale vit sur les côtes ou à proximité et la densité de population littorale connaît un fort accroissement (Norse 1995). Ainsi, les écosystèmes côtiers sont soumis à de fortes pressions liées aux activités humaines et sont de ce fait particulièrement sensibles aux impacts de la pollution, de la surexploitation des ressources côtières, de l'altération ou la destruction d'habitats, aux activités touristiques et à l'introduction, volontaire ou non, d'espèces invasives qui constituent une menace majeure pour la biodiversité marine (Gray 1997).

Face aux perturbations engendrées par les activités humaines et par le changement global, il est maintenant préconisé d'avoir une approche écosystémique dans la gestion et la conservation des milieux naturels (Hughes et al. 2005). Ainsi un aspect majeur en écologie aujourd'hui tend à comprendre le fonctionnement des réseaux trophique c'est-à-dire les flux d'énergie et de matière au sein des différents voies de transfert trophique composant les différentes communautés (Frontier et al. 2008). Dans les écosystèmes intertidaux, la distribution spatiale des espèces benthiques ainsi que les relations trophiques entre espèces sont particulièrement influencées par les facteurs physiques de l'environnement océanique (Menge et al. 2003, Blanchette et al. 2006). De plus, la distribution des ressources (nutriments) va avoir un impact fort sur la dynamique des producteurs primaires, qui a leur tour peuvent exercer un contrôle sur les consommateurs primaires et les autres niveaux trophiques. L'effet de ces facteurs ascendants (« Bottom-up ») a été abondamment étudié sur les niveaux trophiques inférieurs (Menge & Olson 1990, Frederiksen et al.

2006). En effet, les zones intertidales constituent de formidables laboratoires *in situ* qui ont suscité très tôt l'intérêt des scientifiques (Raffaelli & Hawkins 1999), en raison de leur accessibilité et des larges populations de petits animaux aisément manipulables qu'ils hébergent. De plus, les écosystèmes intertidaux ont la particularité de présenter de forts gradients de paramètres physiques (exposition à la houle et à l'air, température, salinité, lumière) sur un espace vertical réduit, produisant une gamme de stress pour les espèces qui les occupent (Raffaelli & Hawkins 1999). Ainsi la zonation des espèces benthiques le long de gradients abiotiques a été mise en évidence dès la première moitié du vingtième siècle (Baker 1909, Fisher-Piette 1931, Stephenson & Stephenson 1949), alors que les concepts de compétition inter-spécifique, de régulation des communautés intertidales par les facteurs descendants (« Top-down ») et de cascades trophiques trouvent également leurs racines dans les études sur les milieux intertidaux (Dayton 1971, Connell 1972, Paine 1974, 1980).

L'effet des facteurs environnementaux sur les niveaux trophiques supérieurs, notamment sur les oiseaux côtiers, reste en revanche peu étudié, alors qu'un déclin global des oiseaux limicoles est observé depuis les années 1980 (Howe et al. 1989, Gratto-Trevor et al. 1998, Stroud et al. 2006), en grande partie dû à l'altération de leurs habitats d'alimentation en reproduction et/ou en hivernage (Piersma et al. 2001, Baker et al. 2004, Van Gills et al. 2006, Bocher et al. 2011). Inversement, l'impact des fluctuations de l'environnement océanographique, notamment climatiques, sur les populations de prédateurs marins, a été montré par exemple chez de nombreux oiseaux océaniques (Barber & Chavez 1983, Guinet et al. 1998, Barbraud et al. 2008). Les effets sur les prédateurs marins sont en réalité essentiellement indirects, passant par l'intermédiaire de fluctuations de la disponibilité ou des assemblages de proies répondant aux variations des facteurs abiotiques. De telles variations dans les liens trophiques entre les ressources alimentaires et les prédateurs marins ont pu être mis en évidence notamment par l'utilisation des isotopes stables (Hilton et al. 2006, Newsome et al. 2007, Jaeger & Cherel 2011). La compréhension des réponses des prédateurs marins en termes trophiques aux conditions environnementales peut permettre d'anticiper les effets de perturbations actuelles et futures de leur habitat à l'échelle de leur répartition. Cependant, le lien entre conditions environnementales côtières et écologie trophique des oiseaux côtiers

reste à démontrer. En effet, les oiseaux limicoles démontrent une grande variabilité individuelle, d'une part morphologique et d'autre part comportementale, souvent associée au statut social. Dès lors, au sein d'une population, les individus peuvent varier dans leur façon d'exploiter leurs ressources alimentaires (Baker 1979) et cela peut affecter leur valeur sélective (Durell 2000), sans que la variation des forçages environnementaux en soit la cause ultime.

Les littoraux du sud de l'Afrique sont essentiellement constitués d'estrans rocheux et caractérisés par des conditions hydrologiques et physico-chimiques contrastées entre les façades indiennes et atlantiques (Shannon 1985, Lutjeharms et al. 2000, Lutjeharms 2004). En accord avec ce contexte océanographique, Hill et al. (2006) et Hill et McQuaid (2008) ont également montré récemment des tendances biogéographiques de fonctionnement trophique au sein des estrans rocheux, à l'aide de l'outil isotopique, sur les niveaux trophiques inférieurs. Enfin, les littoraux sud-africains ont connu plusieurs introductions d'espèces exotiques, mais la moule de Méditerranée (*Mytilus galloprovincialis*) est de loin celle qui a engendré jusqu'à maintenant le plus de perturbations sur les communautés intertidales des côtes rocheuses de la région (Robinson et al. 2005, 2007). Les conditions océanographiques contrastées et la présence de perturbations biologiques constituent un contexte intéressant pour étudier les effets des fluctuations des paramètres abiotiques et biotiques sur l'écologie trophique d'un prédateur supérieur. Un oiseau limicole en particulier, l'huîtrier noir africain (*Haematopus moquini*) présente des caractéristiques écologiques idéales pour une telle étude. D'une part il se distribue sur la majeur partie des côtes sud de l'Afrique (Afrique du Sud et Namibie), et d'autre part il est inféodé aux estrans, rocheux en particulier, et présente une affinité particulière pour la moule invasive (Hockey & Van Erkom Shurink 1992, Hockey 2005). Enfin, chez cette espèce endémique et menacée, une bonne compréhension des facteurs influençant son écologie alimentaire permettrait à terme de cibler les mesures de protection nécessaire pour sa préservation.

II. Objectifs de l'étude et structure du manuscrit de thèse

Ces travaux de thèse s'inscrivent dans la continuité des travaux de recherche menés par le Coastal Research Group de l'Université de Rhodes (Afrique du Sud) sur les estrans rocheux d'Afrique Australe, notamment dans le cadre des interactions

entre l'environnement océanographique côtier et les communautés littorales (Hill et al. 2006, Jaquemet & McQuaid 2008, Von der Meden et al. 2008) et des interactions au sein des communautés intertidales (McQuaid et al. 1999, Bownes & McQuaid 2006, Plass-Johnson et al. 2010).

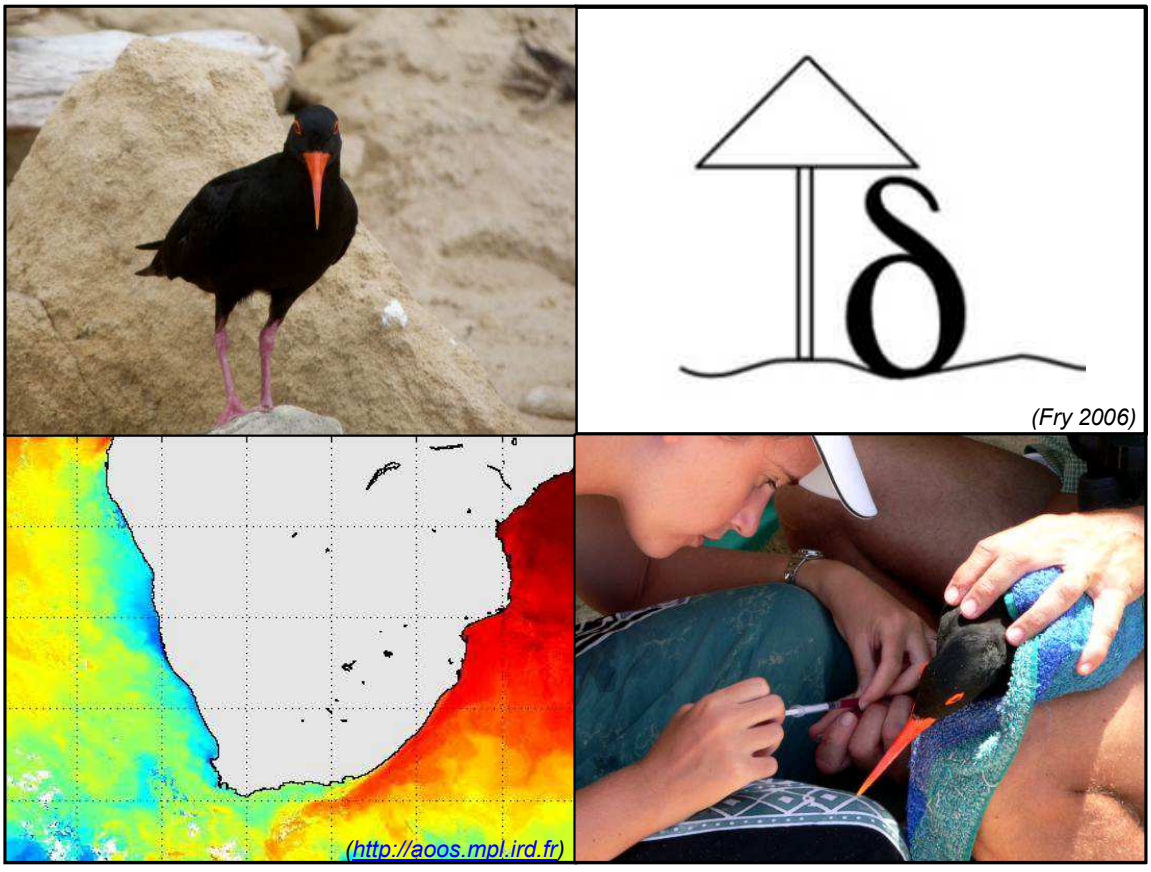
L'objectif premier de cette étude est d'examiner l'influence des conditions océanographiques côtières et des assemblages de proies sur l'écologie alimentaire de l'huîtrier noir africain à l'échelle locale et à l'échelle de sa répartition géographique, par l'utilisation des isotopes stables du carbone et de l'azote. L'intérêt est en particulier de comprendre si le signal isotopique enregistré à la base de la chaîne alimentaire se répercute de façon constante et prévisible jusqu'au niveau du prédateur qu'est l'huîtrier noir africain. Le deuxième objectif est d'étudier l'interaction des caractéristiques morphologiques et comportementales individuelles qui sont spécialement marquées chez les espèces limicoles, du genre *Haematopus* en particulier (Hockey 1996), et les assemblages locaux de proies en particulier pendant la saison de reproduction.

Ce manuscrit se décline en six chapitres. Le premier présente le contexte biogéographique de l'étude de façon détaillée, fait l'état des connaissances sur le modèle biologique étudié, l'huîtrier noir africain et décrit les propriétés de l'outil principal utilisé pour cette étude, les isotopes stables. Enfin les méthodes de collecte de données sont également présentées et reprennent notamment les résultats de deux courts articles méthodologiques portant sur le baguage et le sexage sur le terrain des huîtriers noirs africains (Bonnevie & Kohler 2007, Appendix 2 ; Kohler et al. 2009a, Appendix 3). Les Chapitres 2 et 3 constituent un travail préliminaire décrivant la structure des réseaux trophiques et établissant les sources de variabilité locale et intrinsèque de la composition isotopique des invertébrés benthiques et des tissus du prédateur étudiés. Ils s'appuient sur un article publié au début de cette thèse (Kohler et al. 2009b, Appendix 4) et les données récoltées par la suite. Les résultats présentés dans ce chapitre serviront de base dans un deuxième temps pour interpréter les variations des ratios isotopiques du carbone et de l'azote chez l'huîtrier noir africain et ses proies à plus grande échelle. Le chapitre 4 est tiré d'un article soumis (Appendix 6) et aborde la ségrégation alimentaire entre les mâles et femelles d'huîtrier noir africain, présentant un dimorphisme sexuel marqué, dans un contexte de contraste géographique des communautés intertidales. Le chapitre 5 reprend les

résultats présentés dans un article sous presse (Appendix 5) et décrit l'effet des variations géographiques de conditions océanographiques côtières et des assemblages d'espèces benthiques sur l'écologie trophique d'un prédateur aviaire des estrans rocheux à l'échelle de sa répartition mondiale. Enfin le sixième et dernier chapitre s'appuie sur une approche plus traditionnelle d'étude du comportement alimentaire et examine le partage des rôles parentaux et des stratégies d'alimentation pendant les périodes d'incubation et de nourrissage des poussins. Enfin la discussion générale synthétise l'ensemble des résultats présentés dans les chapitre 2 à 6 et discute de leurs implications pour la conservation de l'espèce.

CHAPITRE 1

Contexte géographique, modèle biologique, isotopes stables et méthodes d'échantillonnage



(Photos: S. Kohler & B. Bonnevie)

I – Contexte géographique : Les littoraux rocheux d'Afrique du Sud et de Namibie

Les littoraux d'Afrique Australe (ici définie comme le pourtour littoral de la Namibie, de l'Afrique du Sud et du Mozambique), sont entourés de deux écosystèmes marins majeurs: Le courant froid du Benguela sur la côte ouest, constitué de plusieurs cellules d'upwellings côtiers riches en nitrates (5 à 8 µg $N.L^{-1}$, Verheye-Dua & Lucas 1988), déplace des eaux froides (11-16°C, Demarcq et al. 2003) d'origine antarctique vers le nord (Shannon 1985). Sur les côtes sud et est de l'Afrique du sud, le courant des Aiguilles transporte des eaux chaudes (22-26°C) et oligotrophiques (0.62 µg $N.L^{-1}$, Machu et al. 2005) du canal du Mozambique vers le sud-ouest (Fig 1.1, Lutjeharms 2004). Ce contraste de conditions océaniques a pour conséquences de larges différences géographiques en termes de concentrations de nutriments, de production intertidale et de biomasse le long des côtes (Bustamante et al. 1995a,b). Trois provinces biogéographiques majeures, basées sur des analyses quantitatives et qualitatives des communautés des estrans rocheux de cette région d'Afrique, ont ainsi été identifiées : la province du *Namaqua* (côte ouest atlantique), la province des *Aiguilles* (la côte sud chaude et tempérée) et la province du *Natal* (la côte est subtropicale) (Fig 1.1). La biomasse est plus importante sur la côte ouest que sur les côtes sud et est, qui en revanche présentent une plus grande richesse spécifique (Stephenson & Stephenson 1972, Emmanuel et al. 1992, Bustamante & Branch 1996b).

A une échelle plus locale, les facteurs abiotiques tels que le type de substrat rocheux, la topographie, l'hydrodynamisme ou encore la température de surface ont une forte influence sur la structure des réseaux trophiques, le recrutement des organismes sessiles et les flux d'énergie au sein de communautés intertidales (McQuaid & Branch 1984, 1985, Erlandsson et al. 2005, McQuaid & Lindsay 2007). En particulier, plusieurs études ont montré que l'action de la houle avait un rôle prépondérant dans la structure des communautés benthiques sur les estrans rocheux sud-africains (McQuaid & Branch 1985, Bustamante & Branch 1996b). Ainsi, sur les estrans fortement exposés, l'importation de nutriments et de matière organique en suspension favorisera les producteurs primaires ainsi que les organismes filtreurs (Bustamante & Branch 1996a,b). Inversement, un fort hydrodynamisme constitue un stress physique qui dicte les chances de survie des

espèces benthiques, mais limite également le temps de recherche et les mouvements des prédateurs (Goss-Custard et al. 2006, Coleman & Hockey 2008). Ainsi, les conditions physico-chimiques locales des estrans rocheux sud-africains contrôlent la survie des organismes et les interactions entre les différents groupes trophiques les habitant, producteurs primaires, brouteurs, filtreurs et prédateurs, et par conséquent la structure des communautés intertidales (Menge & Olson 1990).

Ces 30 dernières années, les communautés des estrans rocheux du sud de l'Afrique ont également été influencées par la présence de la moule de Méditerranée *Mytilus galloprovincialis*, introduite accidentellement sur la côte ouest sud-africaine (Fig 1.1) dans les années 1970 et qui s'est dispersée vers le nord, jusqu'en Namibie, et le sud depuis ce point d'introduction (Branch & Steffani 2004). En raison de performances physiologiques supérieurs à celles des espèces indigènes, cette espèce invasive a profondément altéré le fonctionnement des écosystèmes intertidaux rocheux des côtes sud-africaines (Robinson et al. 2007). Sur la côte ouest, *M. galloprovincialis* a remplacé les espèces de moules indigènes *Aulacomya ater* et *Choromytilus meridionalis* dans les zones médiolittorales moyennes et inférieures, en raison de ses capacités supérieures de croissance et de dispersion et sa résistance aux parasites indigènes (Branch & Steffani 2004). L'espèce invasive prévaut également sur les adultes des espèces de patelles dominantes de la région, *Scutellastra granularis* et *S. argenvillei,* pour l'occupation des substrats rocheux (Hockey & Van Erkom Schurink 1992, Steffani & Branch 2003). D'autre part, la moule de Méditerranée a été introduite à Port-Elizabeth (Fig. 1.1) sur la côte sud pour des essais de conchyliculture en 1988. Depuis cette zone, l'espèce s'est répandue vers l'ouest, tandis qu'à l'est de Port Elizabeth l'abondance de la moule invasive reste faible (Bownes & McQuaid 2006, Von der Meden et al. 2008). Ainsi *M. galloprovincialis* chevauche également l'aire de répartition de la moule indigène dominante des estrans rocheux de la côte sud, *Perna perna*. Les deux espèces se ségrègent dans la zone médiolittorale, avec *P. perna* plus présente dans la partie inférieure et *M. galloprovincialis* dans la partie supérieure tandis que les deux se chevauchent dans une zone intermédiaire et ce, en raison d'une efficacité de recrutement différente des deux espèces selon la hauteur de l'estran (Bownes & McQuaid 2006). Ainsi, de nos jours, *M. galloprovincialis* couvre environ 2000 kilomètres de côtes sud-africaines et namibiennes et constitue l'essentielle de la

biomasse intertidale des littoraux rocheux de l'ouest de l'Afrique du Sud (Robinson et al. 2005).

II – Modèle d'Etude : l'huîtrier noir africain (Haematopus moquini)

Le genre *Haematopus.* Les huîtriers sont un groupe d'oiseaux limicoles réunissant 11 espèces actuelles ainsi qu'une espèce présumée éteinte, l'huîtrier noir des Canaries (*Haematopus meadewaldoi*) (Hockey 1987, 1996). Malgré leur répartition éparpillée à travers le monde (Eurasie, Océanie, continents américains, Afrique australe), ces espèces partagent un grand nombre de similarités, en premier lieu leur apparence. Deux morphes existent, les espèces « pie » (noir et blanc), dont l'exemple le plus connu est l'huîtrier-pie d'Europe *H. ostralegus,* et les espèces noires ou brunes (Fig 1.2). Une espèce vivant sur les côtes australiennes, *H. unicolor,* fait exception puisqu'elle présente les 2 morphes ainsi qu'un morphe intermédiaire (Fig 1.2c, Hockey 1996). De manière générale mais non absolue, les espèces dites « pie » se nourrissent sur les substrats mous comme les vasières ou estrans sableux, alors que les espèces sombres se nourrissent principalement sur des substrats durs tels que les littoraux rocheux. Ceci est particulièrement visible dans les régions où les 2 morphes vivent en sympatrie, comme en Amérique centrale, en Australie et en Nouvelle-Zélande. Les huîtriers habitent essentiellement les milieux côtiers, à l'exception d'*H. ostralegus, H. longirostris (*Amerique du Sud*)* et *H finschi* (Nouvelle-Zélande) qui se reproduisent aussi à l'intérieur de terres (Hockey 1996). Comme l'ensemble des limicoles, les huîtriers ont un bec particulièrement adapté à la recherche et capture de petits invertébrés benthiques, mais la particularité du genre *Haematopus* tient à la robustesse du bec, latéralement compressé, qui leur permet notamment d'ouvrir les bivalves (Hulscher 1996). Ainsi les huîtriers ne consomment que la chair des mollusques, ce qui leur permet de cibler de plus grosses proies que les autres espèces de limicoles occupant les mêmes habitats, qui consomment les mollusques avec leur coquille (Hulscher 1996).

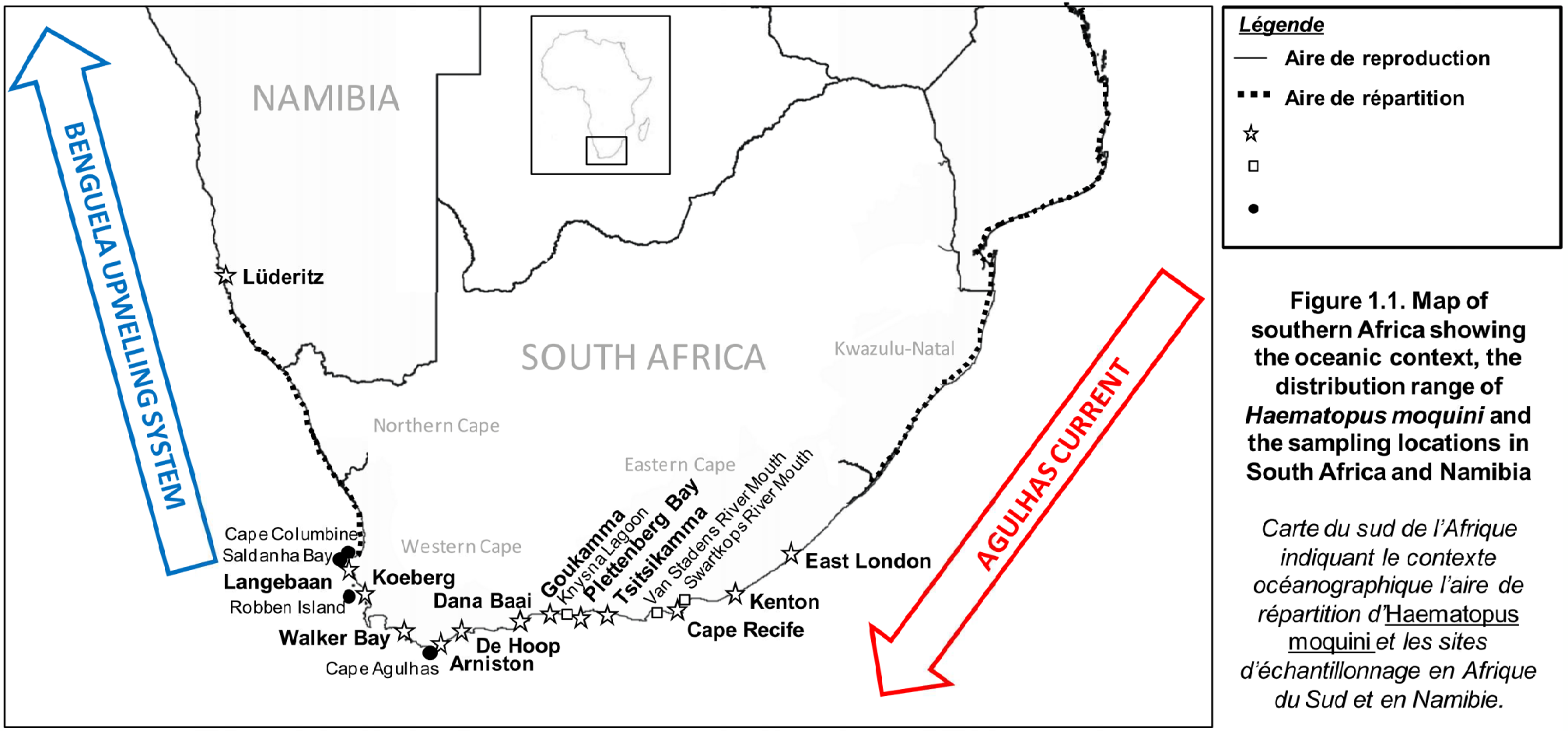


Figure 1.1. Map of southern Africa showing the oceanic context, the distribution range of *Haematopus moquini* and the sampling locations in South Africa and Namibia

Carte du sud de l'Afrique indiquant le contexte océanographique l'aire de répartition d'Haematopus moquini et les sites d'échantillonnage en Afrique du Sud et en Namibie.

Figure 1.2. Examples of oystercatchers species a) *Haematopus ostralegus* living on the eurasian continent, b) *H. ater* inhabiting the coasts of Chile and Argentina, c) *H. unicolor*, endemic of New-Zealand and showing different morphs d) *H. moquini*, sole species breeding on the African continent.
Exemples d'espèces d'huîtrier a) Haematopus ostralegus *vivant sur le continent eurasiatique, b)* H. ater *habitant sur les côtes du Chili et de l'Argentine c)* H. unicolor *endémique de Nouvelle-Zélande et présentant différents morphes d)* H. moquini*, seule espèce se reproduisant sur le continent africain*.

Répartition géographique et reproduction. L'huîtrier noir africain (Fig 1.2d) est endémique des côtes sud-africaines et namibiennes et le seul représentant du genre *Haematopus* à se reproduire sur le continent africain. Son aire de répartition s'étend des côtes sud de l'Angola jusqu'au Mozambique. Cependant, lors la saison de reproduction, les couples sont restreints à la région de Lüderitz en Namibie et aux littoraux sud-africains situés entre Cape Columbine et le sud la province du Kwazulu Natal (Hockey 2005, Brown & Hockey 2007, Kemper 2007, Fig 1.1). Cet oiseau se reproduit pendant l'été austral et plus précisément entre octobre et mars sur les côtes sud-africaines (Hockey 2005), et de janvier à juin en Namibie (J. Kemper, *pers. com.*). L'huîtrier noir africain habite les littoraux rocheux et sableux et les estuaires des côtes continentales et il se reproduit également sur de nombreuses îles au large des côtes sud-africaines et namibiennes (Hockey 1983b, Ward 1990). *H. moquini* est une espèce sédentaire et donc non-migratrice au sens strict. Cependant, des

mouvements complexes de dispersion et migration ont été mis en évidence chez les juvéniles (Hockey et al. 2003). Ces derniers peuvent parcourir entre une centaine et plusieurs milliers de kilomètres pour rejoindre des « nurseries », notamment sur les côtes namibiennes, avant de retourner sur leur site de naissance à l'âge de première reproduction (environ 3 ou 4 ans). Les huîtriers noirs africains sont monogames et montrent une forte fidélité vis-à-vis de leur partenaire sexuel et de leur site de reproduction, période durant laquelle ils sont très territoriaux (Hockey 2005). Cette espèce longévive (longévité estimée à au moins 25 ans, d'après une recapture en février 2009 d'un individu bagué adulte en 1987, SAFRING, *obs. pers*.) a un taux de reproduction naturellement faible, avec moins d'un poussin à l'envol par saison en moyenne (Vernon 2004, Jeffrey & Scott 2005, Hockey 2005, Parsons 2006). Les femelles pondent 1 à 3 œufs (2 le plus souvent) dans un nid souvent constitué d'une simple cavité creusée dans le sable au-dessus de la ligne de marée haute, ou aménagés au milieu de rochers ou de végétation littorale (Fig 1.3). L'incubation dure une trentaine de jours (Hockey 1983a, Parsons 2006), et est assurée par les deux parents (Chapitre 6). Les poussins sont mobiles quelques heures après l'éclosion, mais sont nourris par les deux parents pendant plusieurs semaines après l'âge d'envol (6 à 7 semaines) jusqu'à leur départ du site de naissance (~3 mois), ils sont donc par définition semi-nidifuges (Chapitre 6, Safriel et al. 1996).

Figure 1.3. Examples of African Black Oystercatchers nests.

Exemples de nids d'huîtriers noir africains.

Population et Conservation. Au début des années 1980, le faible succès reproducteur et la petite taille de la population (à l'époque estimée à 4800 individus,

Hockey 1983) laissaient présager une possible extinction à court terme pour l'huîtrier noir africain. Cependant, sa population s'est sensiblement accrue ces 30 dernières années en réponse à plusieurs facteurs. D'une part grâce à la mise en place de mesures de conservation qui ont permis d'interdire l'accès des plages aux véhicules tout-terrain (Williams & Underhill, 2004), et de sensibiliser le public quant au statut précaire de cette espèce endémique (Hockey 1997, Tjørve & Underhill 2006). D'autre part, l'invasion des estrans rocheux sud-africains par la moule de Méditerranée *Mytilus galloprovincialis,* introduite accidentellement sur la côte ouest dans les années 1970, semble avoir contribué de manière positive au succès reproducteur d'*H. moquini,* en augmentant de manière significative la biomasse totale de nourriture disponible pour cet oiseau (Hockey & Van Erkom Schurink 1992). Aujourd'hui, les dernières estimations évaluent la population mondiale de l'huîtrier noir africain à environ 6000 individus (Hockey 2005), et l'espèce est toujours considérée comme menacée (« near-threatened ») en Afrique du Sud ainsi qu'à l'échelle internationale (Underhill 2000). Cependant il a été recommandé récemment que son statut de conservation soit révisé de « near-theratened » à « least concern » (Kemper 2007). Aujourd'hui les principales menaces pesant sur l'huîtrier noir africain sont d'une part les prédateurs mammaliens indigènes et introduits, et d'autre part les activités humaines. Notamment, la saison de reproduction de l'espèce coïncide avec le pic d'activité touristique sur les littoraux sud-africains pendant les vacances de fin d'année (Leseberg et al. 2000, Jeffrey & Scott 2005, Tjørve & Underhill 2008).

Ecologie alimentaire. Peu d'études ont été menées sur l'écologie alimentaire de l'espèce, ou ces dernières étaient restreintes dans le temps, l'espace ou par la taille de l'échantillonnage. Les recherches ont mis en évidence que les huîtriers noirs africains se nourrissent quasi-exclusivement dans la zone de balancement des marées (ou zone intertidale). Sur les estrans sableux, ils se nourrissent essentiellement de bivalves *Donax*, de polychètes et de petits crustacés (McLachlan et al. 1980, Ward 1990, Parsons 2006). Sur les estrans rocheux de l'Afrique australe, les huîtriers disposent d'une grande variété de proies potentielles parmi les invertébrés benthiques qui les peuplent, dont les polychètes, les chitons, les isopodes, les balanes, les gastéropodes, les ascidies, les moules et les patelles. Cependant ces deux derniers types de proies constituent l'essentiel de leur régime

alimentaire (Randall & Randall 1982, Hockey & Underhill 1984, Coleman & Hockey 2008, Kohler et al. 2009b).

III – Les isotopes stables du carbone et de l'azote comme traceurs alimentaires des réseaux trophiques

Les méthodes dites traditionnelles d'étude de l'écologie alimentaire de prédateurs marins impliquent les observations directes, l'analyse de contenus stomacaux et de fèces, et la collecte de restes alimentaires sur les sites de reproduction (Backwell et al. 1998, Dekinga & Piersma 1993, Kojadinovic et al. 2008a, Farrell et al. 2000, Rogers et al. 1990). Ces méthodes ont notamment l'avantage de permettre d'identifier de manière taxonomique les espèces et taille de proies ingérées. Cependant, ces outils sont également sujets à de nombreux biais. Ils ne fournissent des informations que sur le régime alimentaire à court terme et dans le cas des contenus stomacaux, reposent uniquement sur l'identification de proies possédant des parties dures (os, otolithes de poissons, éléments chitineux). Ainsi, l'importance des proies à corps mous, donc rapidement digérées, est souvent sous-estimée. D'autre part les observations directes demandent beaucoup de temps, informent sur le comportement alimentaire sur une période de temps restreinte et ne peuvent être accomplies que sur un nombre limité d'individus (Barret et al. 2007).

Ainsi, les méthodes indirectes des traceurs alimentaires comme les isotopes stables et acides gras présents naturellement dans les tissus ont été proposées comme alternatives pour pallier à ces obstacles (Hobson et al. 1994, Connan et al. 2007). Ces méthodes reposent sur le précepte « Tu es ce que tu manges » (« You are what you eat », Lindlahr, 1942) et permettent d'avoir une information intégrative à une plus grande échelle spatio-temporelle de l'écologie alimentaire de l'organisme étudié. A l'origine privilégiée dans d'autres domaines scientifiques tels que la paléontologie, l'archéologie ou la géochimie, l'utilisation des isotopes stables naturels s'est peu à peu démocratisée en écologie et ce, en raison des progrès en matière de spectrométrie de masse depuis les années 1970 (Kelly 2000, McKechnie 2004). L'analyse des isotopes stables est ainsi devenue depuis quelques années un outil prisé en écologie animale, en particulier pour élucider les relations de type prédateurs-proies au sein des réseaux trophiques. Les isotopes stables constituent un outil puissant pour mettre en évidence les processus, les relations et les flux d'énergies au sein des écosystèmes, aquatiques en particulier (Michener &

Schell, 1994). Leur utilisation en écologie repose sur le principe que la composition en isotope stable des tissus d'un consommateur reflète celle de sa nourriture et ce, de manière relativement prévisible (DeNiro & Epstein 1978, 1981). En effet les variations des ratios isotopiques chez les animaux vont dépendre de processus physiologiques, physiques et biologiques qui interviennent à différentes échelles de temps et d'espace et à différents niveaux des chaînes alimentaires (Dalerum & Angerbjörn 2005, Cherel and Hobson 2007, Jaeger et al. 2009).

Ci-dessous sont revues les principales propriétés biochimiques, physiologiques et environnementales des isotopes stables du carbone et de l'azote qui font des analyses isotopiques un outil particulièrement puissant pour l'étude de l'écologie trophique des prédateurs marins.

Propriétés biochimiques des isotopes stables. Les isotopes dits « stables » sont les différentes formes d'un même élément chimique (hydrogène-H, azote-N, carbone-C, soufre-S, Oxygène-O par exemple) et, à l'opposé des isotopes dits « instables », n'émettent pas de radioactivité (Fry 2006). Les isotopes stables du carbone (^{12}C, ^{13}C) et de l'azote (^{14}N, ^{15}N) existent naturellement dans de nombreux réservoirs environnementaux comme l'eau et les sols et dans toutes les matrices biologiques. Les éléments lourds (^{13}C et ^{15}N) existent naturellement en faible concentration, et possèdent un neutron de plus dans leur noyau que les isotopes légers (^{12}C et ^{14}N), qui sont les formes les plus communes dans la nature. A titre d'exemple, les abondances naturelles de ^{12}C et ^{13}C dans l'environnement sont respectivement de 98,9% et 1,1%, ce qui donne un rapport de 0,011 pour $^{13}C/^{12}C$ (Fry 2006). La différence dans le nombre de neutrons leur confère peu de différences en termes de propriétés chimiques car ils possèdent le même nombre d'électrons et de protons. En revanche la différence de masse entre les 2 types d'isotopes a pour conséquence des différences de vitesse de réaction chimique et de manière générale, les isotopes légers sont mobilisés plus rapidement que les isotopes lourds dans les réactions biochimiques dans lesquelles ils interviennent (Fry 2006). Ceci mène à une accumulation préférentielle des isotopes lourds dans les substrats par rapport aux isotopes légers qui sont plus abondants dans les produits de réaction. Ainsi, lors des différents processus biochimiques impliqués dans l'assimilation, les synthèses protéiques et l'excrétion des composants alimentaires chez les organismes vivants, il s'opère une ségrégation des isotopes d'un élément chimique

entre les sources et les produits des réactions (Ponsard & Averbuch 1999, Vanderklift & Ponsard 2003). Ce processus appelé « fractionnement isotopique » a pour résultat un enrichissement des tissus d'un consommateur en isotopes lourds, alors qu'en comparaison, les produits d'excrétion (tel que l'acide urique chez les oiseaux) ou de respiration (CO_2) sont relativement enrichis en isotopes légers (Kelly 2000). Ainsi en termes de composition isotopique, ce qui est mesuré dans les tissus des organismes sont les ratios entre les concentrations de l'isotope lourd (^{13}C ou ^{15}N) et de l'isotope léger (^{12}C ou ^{14}N). Ces ratios sont notés $\delta^{13}C$ et $\delta^{15}N$ pour le carbone et l'azote respectivement et exprimé en ‰. Ces ratios étant très faibles (puisque les isotopes lourds n'existent naturellement qu'en faibles concentrations), leur valeur est exprimée de façon relative à des standards internationaux qui sont le Pee-Dee Belemite pour le carbone et le diazote atmosphérique pour l'azote et est déterminée selon l'équation suivante :

$$\delta \mathrm{X} = \left(\left[\frac{R_{sample}}{R_{standard}} \right] - 1 \right) \times 1000$$

avec X l'élément considéré (C ou N) et R le ratio de l'isotope lourd sur l'isotope léger.

Variations des isotopes stables du carbone dans l'environnement. Au cours des transferts trophiques, le fractionnement isotopique (défini comme la modification isotopique intervenant entre une source de nourriture et son consommateur) du carbone est généralement faible (de l'ordre de 0 à 2 ‰, McCutchan et al. 2003) et dès lors, les valeurs de $\delta^{13}C$ varient peu d'une source de nourriture à son consommateur (DeNiro & Epstein 1978). En réalité la plus grande source de variations de $\delta^{13}C$ intervient à la base des chaînes trophiques, lors du fractionnement se produisant au cours de la photosynthèse et qui diffère parmi les producteurs primaires. Ainsi les plantes terrestres fixant le carbone via le mécanisme photosynthétique dit en « C_3 » sont appauvries en ^{13}C (de – 35 à –21 ‰) par rapport au plantes en « C_4 » (valeurs de $\delta^{13}C$ de –14 à –10‰). De même, les organismes végétaux marins qui réalisent une photosynthèse similaire aux plantes en C_3 sont généralement appauvris par rapport à leurs homologues terrestres. Enfin, dans les milieux aquatiques, les algues planctoniques sont généralement appauvries en ^{13}C par rapport aux algues benthiques et ce également en réponse à un taux de fractionnement différent, mais lié à une diffusion différentielle du carbone à travers

les membranes (Peterson & Fry 1987, France 1995, Kelly 2000). A plus grande échelle, les masses d'eaux océaniques peuvent présenter des contrastes d'enrichissement en ^{13}C dus aux propriétés physico-chimiques des eaux (Trull & Armand 2001, Hill et al. 2006) et des gradients latitudinaux de $\delta^{13}C$ dans le plancton ont également été mis en évidence (Rau et al.1982, François et al. 1993). En raison de toutes ces propriétés, les isotopes stables du carbone constituent d'excellents indicateurs de sources d'énergie à la base des chaînes trophiques (Fig 1.4, Kelly 2000, McCutchan et al. 2003) mais permettent aussi d'identifier les zones d'alimentation de prédateurs marins (Bearhop et al. 1999, Quillfeldt et al. 2005, Cherel & Hobson 2007, Graham et al. 2010)

Variations des isotopes stables de l'azote dans l'environnement. Comme pour le carbone, l'utilisation des isotopes stables de l'azote en écologie repose sur leur distribution dans l'environnement et la manière par laquelle ils sont intégrés dans les chaînes alimentaires (Kelly 2000). Le $\delta^{15}N$ augmente typiquement de 2 à 5 ‰ (DeNiro & Epstein 1981, Bearhop et al. 2002, McCutchan et al. 2003) entre une source de nourriture et son consommateur, en réponse au fractionnement isotopique intervenant lors des différentes étapes de désamination et transamination des acides aminés. Ainsi les ratios isotopiques de l'azote sont souvent utilisés comme indicateur de position trophique d'un organisme au sein d'un réseau trophique (Fig 1.4).

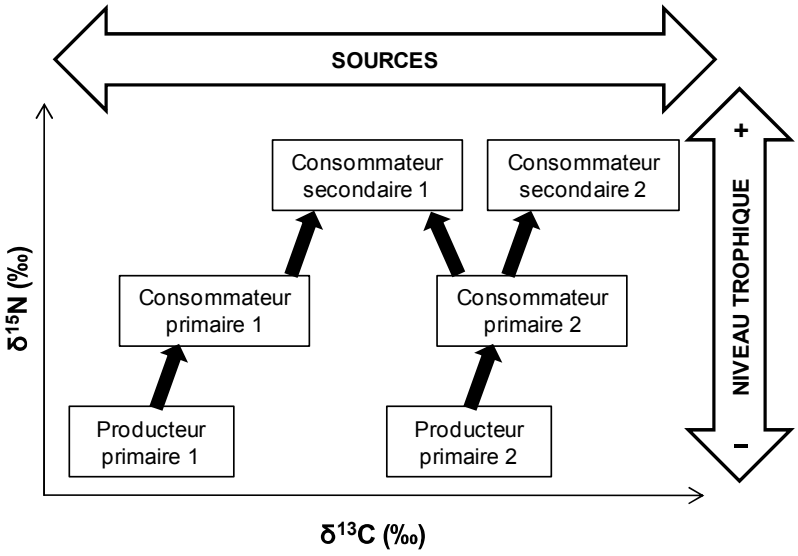


Figure 1.4. Traditionnal bi-plot representation of a trophic food web using stable isotope ratios of carbon and nitrogen

Représentation traditionnelle d'un réseau trophique en deux dimensions par les ratios isotopiques du carbone et de l'azote

Cependant, l'azote fixé par les producteurs primaires existe sous différentes formes, le diazote atmosphérique (N_2), les nitrates (NO_3^-), l'ammonium ($NH4^+$) et ces formes diffèrent par leur composition en ^{15}N en réponse au fractionnement intervenant pendant les processus de nitrification et dénitrification. Ainsi, les nitrates sont typiquement enrichis en ^{15}N par rapport à l'ammonium, un produit d'excrétion (Miyake & Wada 1967). Dès lors, le $\delta^{15}N$ peut également être utilisé comme indicateur de qualité et d'origine des nutriments utilisés par les producteurs primaires à la base des chaînes trophiques (Cabana & Rasmussen 1996, Bode et al. 2006, Hill et al. 2006). Il peut en particulier indiquer des enrichissements en azote de synthèse d'origine anthropique, qui constituent souvent des pollutions (Heaton 1986, Constanzo et al. 2005)

Taux de renouvellement isotopique des tissus. Comme montrée précédemment, l'utilisation des isotopes stables en écologie repose d'abord sur le fait que la composition isotopique d'un consommateur reflète celle de sa nourriture. Mais l'intérêt de la méthode des isotopes stables en écologie tient également au fait que les tissus des consommateurs se renouvellent à des vitesses différentes et, de ce fait, intègrent les informations sur leur régime alimentaire à des échelles de temps différentes (Hobson & Clark 1992a, Bearhop et al. 2002). La période pendant laquelle la composition isotopique d'un tissu reflètera celle d'une alimentation particulière dépendra de l'activité métabolique de ce tissu et en particulier de sa vitesse de renouvellement protéique (Tieszen et al. 1983). Ainsi le foie et le plasma sanguin présentent une activité métabolique rapide et leur composition isotopique renseigne sur les aliments assimilés à très court terme, de l'ordre de la semaine (Hobson & Clark 1992a, 1993). La fraction entière du sang présente un renouvellement isotopique de l'ordre de quelques semaines, ainsi sa composition isotopique donnera des informations sur l'activité alimentaire de l'organisme pendant les quelques semaines précédant l'échantillonnage (Hobson & Clark 1992, 1993, Bearhop et al. 2002, Haramis et al. 2001). Pour les périodes d'intégration plus longue, les muscles sont souvent utilisés car ils ont un renouvellement protéique de l'ordre de plusieurs mois (Gorokhova & Hansson 1999, Lorrain et al. 2002). Enfin, les tissus à base de kératine comme les plumes des oiseaux ou les ongles des mammifères restent métaboliquement inertes une fois leur croissance terminée (Hobson & Clark 1992b, Mizutani et al 1990). Ainsi, leur composition isotopique

informera sur l'activité alimentaire du consommateur pendant la période de croissance du tissu (Jaeger et al. 2010a). L'utilisation combinée de plusieurs tissus collectés simultanément sur un organisme présente donc l'avantage d'informer sur de possibles variations spatiales et temporelles de son régime alimentaire (Dalerum & Angerbjörn 2005, Jaeger et al. 2009, Morrissey et al. 2010).

Influence du fractionnement et des lipides sur la composition isotopique des tissus. Différents tissus collectés simultanément sur un organisme peuvent donc présenter des compositions isotopiques contrastées, en relation avec les vitesses de renouvellement isotopiques dans les tissus. Mais ces différences peuvent également résulter de différences de fractionnement isotopique dans les tissus (Hobson & Clark 1992, Lorrain et al. 2002, Quillfeldt et al. 2008) liées à leur activité métabolique. C'est pourquoi de nombreuses études expérimentales ont porté sur l'estimation de valeurs de fractionnement isotopique spécifique à certains tissus (muscle, sang, plumes) et ce, sur une grande variété d'organismes (Burkhardt et al. 1999, Evans-Ogden et al. 2004, Caut et al. 2008,2009, Hill & McQuaid 2009). Enfin, en dehors du renouvellement protéique et du fractionnement isotopique, la composition en isotopes stables du carbone peut être affectée par la teneur en lipides des tissus car les lipides sont naturellement appauvris en ^{13}C par rapport aux tissus individuels dans leur ensemble (DeNiro and Epstein 1977, Post et al. 2007). Dès lors, pour éviter les interprétations erronées quant aux relations trophiques entre des consommateurs et leurs sources de nourriture, l'échantillonnage de tissus avec la même teneur en lipides sera privilégié, et le cas échant, des traitements de délipidation peuvent être utilisés (Bearhop et al. 1999, Cherel et al. 2005b).

IV – Sites d'étude, échantillonnage et analyses en laboratoire

Sites d'étude. Pendant les 3 saisons de terrain nécessaires pour couvrir l'ensemble de la zone d'étude (environ 2000 km de côtes), les huîtriers noirs africains et leurs proies potentielles ont été échantillonnés sur 13 sites dispersés sur les côtes du sud de l'Afrique (Fig 1.1), essentiellement pendant l'été austral, d'octobre à avril de l'année suivante. Ces 3 saisons de terrain seront par la suite appelées les saisons 2007-2008, 2008-2009 et 2009-2010. Les sites d'étude échantillonnés sont caractérisés par la présence de plusieurs couples d'huîtriers reproducteurs ayant pour habitat d'alimentation principal des estrans rocheux, et, à l'exception de Lüderitz

(Namibie), où deux îlots ont été échantillonnés, se situent sur le continent. Le site d'échantillonnage de Kenton a reçu une attention particulière (voir chapitre 2) car il se situe à proximité de l'Université de Rhodes et constitue par conséquent un des sites privilégiés du Coastal Research Group (Department of Zoology and Entomology, Université de Rhodes) qui mène des études sur l'écologie des estrans rocheux (McQuaid & Lindsay 2007, Hill & McQuaid 2008, Hill et al. 2008). Des huîtriers et leurs proies ont également été échantillonnés sur des sites présentant des habitats d'alimentation différents (vasières, estuaires, estrans sableux) afin d'augmenter le nombre d'échantillons dans le cadre d'analyses à vocations plus méthodologiques (Fig 1.1, voir « sexage des huîtriers noirs africains dans ce Chapitre et le Chapitre 3). Enfin, en raison de la faible densité des huîtriers en générale (Hockey 2005) et des contraintes liées à leur capture, il était parfois nécessaire de les échantillonner dans différentes zones séparées de plusieurs kilomètres sur la côte afin d'échantillonner un nombre d'oiseaux suffisant par site d'étude. Le tableau 1.1 présente l'ensemble des caractéristiques d'échantillonnage de chaque site d'étude.

Echantillonnage des huîtriers. Les échantillons biologiques ont d'une part été récoltés sur les huîtriers noirs africains adultes en incubation. Les oiseaux étaient capturés à l'aide d'un piège posés sur le nid (Fig 1.5), alors que leurs œufs étaient remplacés par des faux afin de ne pas les endommager involontairement lors de la capture et d'éviter tout stress thermique qui pourrait nuire au développement du poussin. D'autre part, les poussins âgés d'une à sept semaines (âge moyen pour l'envol) sont le plus souvent cachés dans les dunes, les rochers ou végétation situés au-dessus de la ligne de marée haute, ou sur les estrans lorsqu'ils sont nourris par les adultes pendant les phases de basse mer. Ils pouvaient donc être capturés à la main jusqu'à l'âge d'envol. Un échantillon de sang (0.5 ml) était prélevé dans le tarse de chaque oiseau à l'aide d'une seringue à insuline à usage unique, et conservé dans un eppendorf contenant 1 ml d'éthanol jusqu'à son traitement en laboratoire. Cinq à huit plumes de couvertures étaient coupées à la base sur le cou ou le haut du dos sur les adultes et les poussins âgés de 2 semaines et plus, et préservées dans des sachets en plastiques dûment étiquetés et scellés jusqu'à leur traitement en laboratoire.

Table 1.1. Summary of sites characteristics and birds numbers

Résumé des caractéristiques des zones d'études et des effectifs d'échantillonnage

Sites d'études	Localisation		Habitat d'alimentation	Proies		Effectifs d'oiseaux échantillonnés (Adultes/Poussins)	Saisons de terrain	Statut de conservation	Nombre total de nids sur le site	Etendue du site d'étude**
	Régime océanique	Régions biogeographiques côtières *		Type échantillonnés	Présence de *Mytilus galloprovincialis*					
East London	Courant des Aiguilles Chaud et oligotrophique	SUD-EST	Estran rocheux	Moules Patelles	NON	12/13	2007-2008 2008-2009	Pas de statut	26	2 zones < 40 km
Kenton			Estran rocheux	Moules Patelles Polychaetes	NON	12/7	2007-2008 2008-2009 2009-2010	Pas de Statut	16	3 zones < 20 km
Swartkops River Mouth			Estuaire avec estran rocheux	Moules	OUI	5/5	2007-2008	Pas de Statut	4	1 zone < 1 km
Cape Recife			Estran rocheux	Moules Patelles Ascidies	NON	14/6	2007-2008 2008-2009 2009-2010	Réserve municipale	9	1 zone < 1 km
Van Stadens River Mouth			Estran sableux	Moules des sables	NON	4/1	2007-2008 2008-2009	Pas de Statut	12	1 zone < 10 km
Tsitsikamma		SUD-OUEST	Estran rocheux	Moules Patelles	OUI	1/1	2009-2010	Parc National (SANParks)	3	1 zone < 1 km
Plettenberg Bay			Estran rocheux	Moules Patelles Moules des sables	OUI	5/4	2008-2009 2009-2010	Réserve régionale (CapeNature)	18	2 zones < 5 km
Knysna lagoon			Estuaire avec vasières	Aucune	NON	0/6	2009-2010	Parc National (SANParks)	11	1 zone < 1 km
Goukamma			Estran rocheux	Moules Patelles Moules des sables	OUI	8/10	2008-2009 2009-2010	Réserve régionale (Cape Nature)	27	3 zones < 30 km
DanaBaai			Estran rocheux	Moules	OUI	2/8	2008-2009	Pas de statut	8	1 zone < 10 km
De Hoop			Estran rocheux	Moules	OUI	5/7	2008-2009	Réserve régionale (CapeNature)	11	1 zone < 5 km
Arniston			Estran rocheux	Moules Patelles	OUI	7/1	2008-2009	Réserve régionale (CapeNature)	6	1 zone < 1 km
Walker Bay	Courant du Benguela Froid et eutrophique	OUEST	Estran rocheux	Moules Patelles	OUI	1/3	2008-2009 2009-2010	Réserve régionale (CapeNature)	8	1 zone < 10 km
Koeberg			Estran rocheux artificiel	Moules Patelles	OUI	1/3	2007-2008 2008-2009	Centrale nucléaire de Koeberg	15	1 zone < 1km
Langebaan			Estran rocheux	Moules Patelles	OUI	4/2	2008-2009 2009-2010	Pas de statut	6	1 zone < 1 km
Lüderitz			Estrans rocheux sur îlots	Moules Patelles	OUI	3/1	2009-2010	Aire Marine Protégée (NIMPA)	67	2 zones < 5 km

** Régions biogéographiques définies par les compositions isotopiques de producteurs primaires et invertébrés benthiques d'estrans rocheux des côtes de l'Afrique australe (Hill et al. 2006) et (Hill & McQuaid 2008)*

*** Distance estimée d'après les coordonnées GPS des 2 nids ou poussins échantillonnés les plus éloignés sur un site d'étude*

Sur tous les oiseaux, la longueur du bec (à partir des plumes du crâne) et du tarse étaient mesurés au 0.1 mm près avec un pied à coulisse. L'aile pliée était mesurée au 1 mm près avec une règle à butée. Les oiseaux étaient ensuite pesés au 1 g près avec un peson. Enfin tous les oiseaux échantillonnés étaient bagués avec une bague métallique de 8 ou 10 mm gravée d'un code unique (SAFRING) et une combinaison de 2 ou 3 bagues en plastique de couleurs a été ajoutée sur les adultes capturés pendant les saisons 2007-2008 et 2008-2009 (voir Chapitre 6). Le choix de la taille des bagues a fait l'objet d'une évolution au cours de l'étude, suite à l'observation que les bagues de 8 mm (recommandées jusque-là par SAFRING pour les huîtriers) étaient trop étroites pour certaines femelles et pouvaient provoquer une déformation du tarse, voire une perte du membre (Bonnevie & Kohler 2007, Appendix 1). Ainsi à partir de la saison 2008-2009, des bagues de 10 mm uniquement ont été utilisées sur tous les huîtriers, adultes et poussins.

Figure 1.5. Trap set on an Africain Black Oystercatcher's nest.
Piège posé sur un nid d'huîtrier noir africain.

Echantillonnage des proies potentielles. La collecte d'invertébrés benthiques des estrans rocheux s'est concentrée sur les moules et patelles puisqu'elles constituent l'essentiel du régime alimentaire des huîtriers noirs africains sur les estrans rocheux du sud de l'Afrique (Randall & Randall 1982, Hockey & Underhill 1984, Hockey 2005). Sur l'ensemble de la zone d'étude (Fig 1.1), les espèces collectées comprennent les moules *Perna perna, Mytilus galloprovincialis, Choromytilus*

meridionalis, Aulacomya ater et les patelles *Cymbula oculus, Scutellastra argenvillei, S. cochlear, S. granatina, S. granularis and S. longicosta* (Fig 1.6). Toutes ces espèces ne se rencontrent pas sur l'ensemble des sites d'étude car leurs aires de répartition sont spécifiques de provinces biogéographiques caractéristiques des littoraux sud-africains (Bustamante & Branch 1996b).

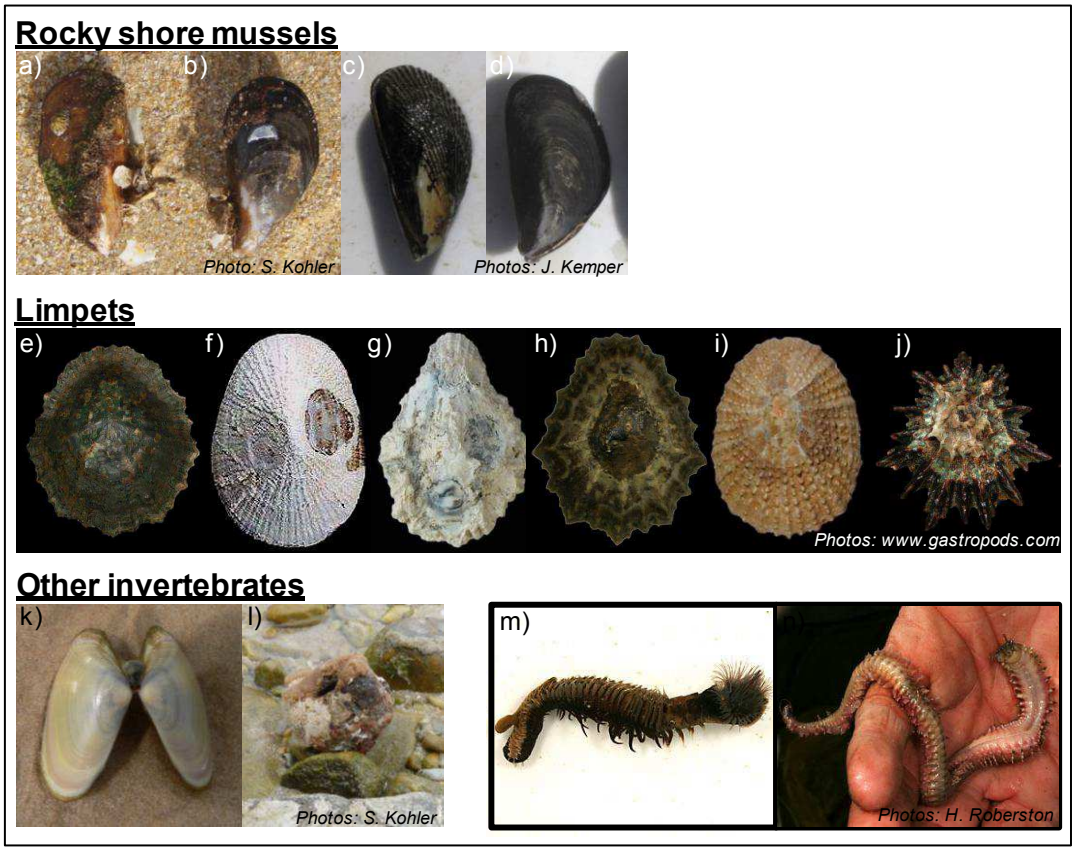


Figure 1.6. Prey species sampled through the study area a) *Perna perna*, b) b) *Mytilus galloprovincialis*, c) *Aulacomya ater*, d) *Choromytilus meridionalis*, e) *Cymbula oculus*, f) *Scutellastra argenvillei*, g) *S. cochlear,* h) *S. granatina*, i) *S. granularis*, j) *S. longicosta*, k) *Donax serra,* l) *Pyura stolonifera*, m) *Gunnarea capensis*, n) *Pseudonereis variegata.*

Espèces de proie échantillonnées à travers la zone d'étude a) Perna perna*, b)* Mytilus galloprovincialis*, c)* Aulacomya ater*, d)* Choromytilus meridionalis*, e)* Cymbula oculus*, f)* Scutellastra argenvillei*, g)* S. cochlear*, h)* S. granatina*, i)* S. granularis*, j)* S. longicosta*, k)* Donax serra*, l)* Pyura stolonifera*, m)* Gunnarea capensis*, n)* Pseudonereis variegata.

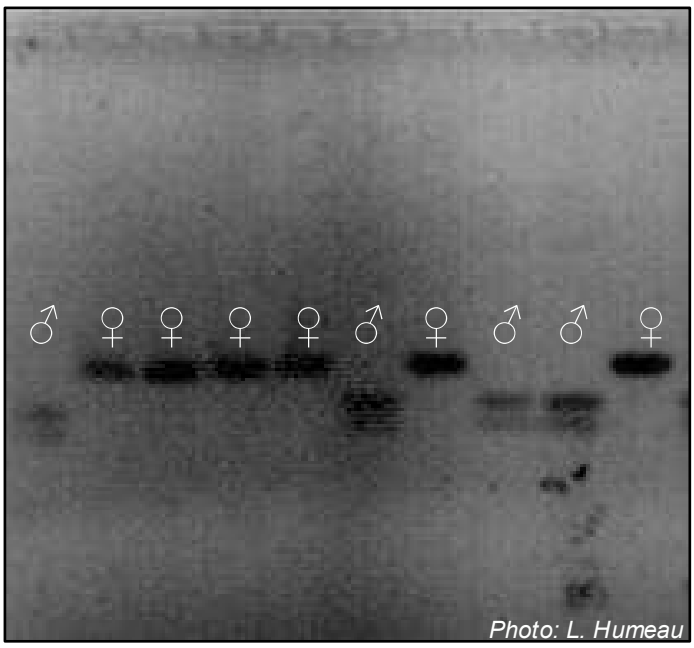
D'autres types de proies potentielles ont été échantillonnées de manière ponctuelle et sur certains sites uniquement. Le bivalve *Donax serra* a été échantillonné sur l'estran sableux à Van Stadens River Mouth et sur des bancs de sable à Goukamma et Plettenberg Bay. Les ascidies échouées *Pyura stolonifera* ont été collectées à

Cape Recife. Enfin les polychètes *Gunnarea capensis* et *Pseudonereis variegata* ont également été échantillonnés à Kenton (Fig 1.1 et 1.5). Cinq spécimens par espèce de proie étaient collectés sur chaque site où elles étaient présentes et gardées à –20°C jusqu'à leur traitement en laboratoire. Les données récoltées à partir de producteurs primaires échantillonnés par Jackie Hill pendant ses travaux de thèse à Port Alfred (environ 20 km à l'est de Kenton) et présentées dans Hill & McQuaid (2008) seront également utilisés, mais uniquement dans le Chapitre 2.

Sexage des huîtriers noirs africains. Toutes les espèces d'huîtriers présentent un dimorphisme sexuel, particulièrement marqué au niveau de la morphologie du bec. Typiquement, les femelles sont plus grosses, ont un bec plus long et plus pointu que les mâles et, au sein des couples, les femelles ont un bec invariablement plus long que leur partenaire sexuel (Hockey 1996). Par le passé, le sexage d'*H. moquini* s'est basé uniquement sur l'observation de caractères morphologiques, en particulier ceux du bec, ou d'analyses discriminantes utilisant plusieurs paramètres biométriques (Hockey 1981, Coleman & Hockey 2008). Une autre technique consiste à palper le cloaque des oiseaux, typiquement distendu chez les femelles qui viennent de pondre (Hockey 1981), mais difficilement discernable plusieurs jours après la ponte. Au niveau de la population, il existe un certain degré de chevauchement des paramètres morphométriques des mâles et femelles (voir Chapitre 5) et le sexage sur le terrain peut être problématique si un seul individu du couple est capturé et qu'il est impossible de comparer la longueur du bec avec son partenaire. De plus, les poussins huîtriers ne présentent pas de dimorphisme sexuel et il est donc impossible de les sexer sur des critères strictement morphométriques (Hockey 1981). Ainsi le sexage par les outils moléculaires reste le moyen le plus fiable de sexer les huîtriers. La méthode de sexage moléculaire développé pour les oiseaux par Fridolfsson & Ellegren (1999) repose sur les différences de taille entre les introns CHD1W et CHD1Z situés sur les chromosomes sexuels W et Z respectivement (les femelles étant ZW et les mâles ZZ). Ainsi, quelques gouttes de sang prélevées sur chaque huîtrier ont été utilisées pour le sexage moléculaire. L'ADN était extrait et les introns CHD1W et CHD1Z (110 pb) amplifiés avec le couple de primers P2-P3. L'enzyme de restriction *Hae III* ajoutée par la suite coupe les produits au niveau d'une séquence nucléique spécifique uniquement présente sur l'intron CHD1Z. Ainsi, chez les mâles, la bande de 110 pb est fragmentée en 2 morceaux de 65 et 45 pb, alors que les

femelles gardent la bande de 110 pb de l'intron CHD1W qui ne possède pas de site de restriction pour l'enzyme *Hae III* (Fig 1.7, Baker & Piersma 1999). Le sexage moléculaire a été réalisé par S. Dano au Centre d'Etudes Biologique de Chizé (CNRS) pour les adultes capturés pendant la saison 2007-2008, tandis que l'ensemble des autres individus a été sexé sous la supervision du Dr L. Humeau au laboratoire de biologie moléculaire de l'UMR-PVBMT (Université de La Réunion).

Figure 1.7. Results of molecular sexing done on 10 *Haematopus moquini*'s juveniles. Females (ZW) have one large band (CHD1W intron of 110 pb) and males (ZZ) have 2 smaller bands (CHD1Z intron cut into 2 bits by Hae III). *Résultats de sexage moléculaire réalisé sur 10 poussins d'*Haematopus moquini*. Les femelles (ZW) présentent une bande plus grosse (l'intron CHD1W de 110 pb) et les mâles (ZZ) 2 bandes plus petites (l'intron CHD1Z coupés en 2 par l'enzyme Hae III).*



Guzzetti et al. (2008) ont mis en évidence une nouvelle méthode de sexage *in situ* chez l'huîtrier noir américain (*H. bachmani*), basée notamment sur la présence de tâches oculaires sombres (« eyeflecks ») sous la pupille des femelles, alors que les mâles en présentent rarement ou de faible intensité. L'utilisation des tâches oculaires comme moyen de sexage a donc été testé chez les adultes d*'H. moquini* capturés pendant la saison 2007-2008 et couplé avec l'outil moléculaire (Fig.1.8). Cette étude a fait l'objet d'une publication (Kohler et al. 2009a, Appendix 2). Les poussins ont un iris brun, à l'opposé du rouge des adultes, et aucun tâche n'a été détecté chez eux (Fig.1.8), ils n'ont donc pas été pris en compte dans l'étude. Le sexage par les tâches oculaires a pu être confirmé par l'outil moléculaire avec une précision de 93.5 % pour les femelles adultes (n = 17) et de 100% pour les mâles (n = 17) (Kohler et al. 2009a, Appendix 2). Cette méthode présente donc une alternative

intéressante au sexage moléculaire, qui est coûteux et pour lequel les résultats ne sont pas immédiatement disponibles, ainsi qu'au sexage morphométrique traditionnel. Enfin avec un bon équipement optique, les tâches oculaires peuvent permettre de sexer les huîtriers adultes à distance et sans nécessité de capture.

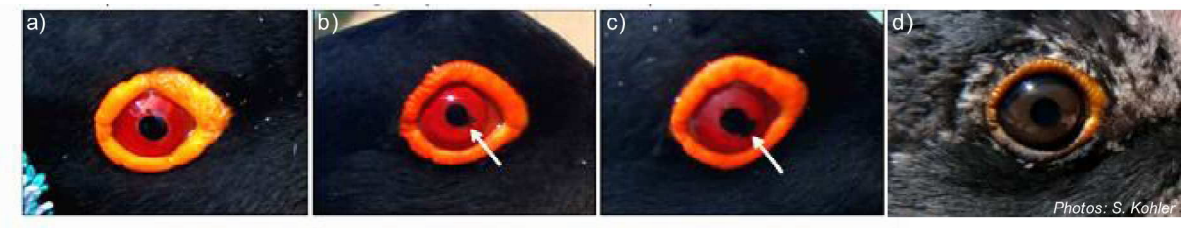


Figure 1.8. Categories of eyeflecks (indicated with a white arrow) in African Black Oystercatchers. (a) No eyefleck, (b) slight eyefleck, (c) eyefleck, (d) No eyeflecks visible in juveniles. Males display (a) and (b) eyeflecks and females (c) eyeflecks.

Catégories de tâches oculaires chez l'huîtrier noir africain (indiquées par une flèche). a) absence de tâche, b) tâche légère, c) tâche marquée, d) absence de tâche chez les poussins. Les mâles présentent des tâches de type (a) et (b) et les femelles de type (c).

Préparation des échantillons en laboratoire. Les échantillons de sang ont été séchés à 60°C pendant 24h dans un four et réduits en poudre homogène à l'aide d'un pilon et d'un mortier. Les plumes d'un individu ont été mises en commun et nettoyées de contaminants de surface par immersion dans une solution de chloroforme/méthanol (2:1) placée dans une cuve à ultrasons pendant 2 minutes (Hobson & Clark 1992), puis rincées avec des bains successifs d'éthanol et d'eau distillée, séchées (60°C, 24h) et réduites en fragments de petite taille et homogènes avec des ciseaux fins et propres. Sur les échantillons de proies, les tissus de muscle ont été choisis car ils ont un renouvellement protéique lent, leur composition en isotopes stable est donc peu affectée par les fluctuations environnementale à court terme (Gorokhova & Hansson 1999, Hill & McQuaid 2009). De plus, comme le sang et les plumes des oiseaux, les muscles sont typiquement pauvres en lipides (DeNiro & Epstein 1977, Cherel et al. 2005b, Kojadinovic et al. 2008b, Post et al. 2007). Le muscle adducteur a été extrait des moules d'estrans rocheux et sableux pour mesurer leur composition en isotopes stables alors que sur les patelles, une portion du pied était analysée. Les polychètes ont été conservés entier du fait de leur petite taille. Aucune référence bibliographique n'a été trouvée sur la méthode à utiliser pour les ascidies, en conséquence, l'animal a été extrait de sa tunique et une portion du siphon buccal a été utilisée pour les analyses isotopiques. Les échantillons de proies ont été rincés avec de l'eau distillée, séchés (60°C, 24h) et broyés individuellement

en une poudre homogène. L'abondance isotopique relative du carbone ($^{13}C/^{12}C$) et de l'azote ($^{15}N/^{14}N$) était déterminée pour chaque échantillon à partir d'1 mg de poudre dans un spectromètre de masse de ratio isotopique à flux continue (IRMS) après la combustion des échantillons dans une unité de préparation Carlo-Erba et exprimée en ‰. La précision des réplicats (de l'ordre de 0.1 ‰ pour le carbone et l'azote) varie d'un laboratoire à l'autre (Stable Light Isotope Unit de l'Université du Cap ou IsoEnvironmental cc de l'Université de Rhodes) et d'une série d'échantillons à l'autre et sera donc indiquée pour chaque chapitre.

CHAPITRE 2

Local variations in the carbon and nitrogen stable isotope composition of African Black Oystercatcher's potential prey

(Photos : B. Dubillot)

RESUME

Les milieux côtiers sont particulièrement propices pour l'utilisation des isotopes stables dans le cadre d'études trophiques en raison de la ségrégation des principales voies de production primaires, benthiques et pélagiques par leurs valeurs de $\delta^{13}C$. Cependant un grand nombre d'incertitudes existe quant aux valeurs de fractionnement isotopique entre producteurs primaires et consommateurs primaires. Il est donc préférable de s'attacher à la composition isotopique d'invertébrés benthiques plutôt qu'à la ligne de base isotopique des producteurs primaires lorsqu'on s'intéresse à l'écologie alimentaire d'un prédateur. Dans une première section, je décris la structure trophique des habitats rocheux dans lesquels les huîtriers noirs africains se nourrissent, en portant une attention particulière à la relation trophique entre les deux principales proies des huîtriers, les moules et patelles. De manière générale, une ségrégation claire des ratios isotopiques de carbone s'opère sur l'ensemble de la zone d'étude entre d'une part les patelles se nourrissant sur les algues benthiques et, enrichis en ^{13}C, et d'autre part les moules qui filtrent la matière particulaire pélagique, appauvries en ^{13}C. Les invertébrés benthiques montrent un enrichissement de ^{15}N relatif aux producteurs primaires, mais ne présentent pas de différences significatives entre brouteurs et filtreurs. Les brouteurs montrent des différences persistantes de ratio de $\delta^{13}C$ au sein de leurs guildes trophiques, reflétant une diversité spécifique de leur écologie alimentaire. Inversement les deux espèces de moules principalement échantillonnées, *Perna perna* et *Mytilus galloprovincialis* ont montré très peu de variabilité intra- et interspécifique dans leur composition isotopique car elles dépendent localement du même mélange de débris de macroalgues et de phytoplancton présents dans la colonne d'eau. Les valeurs isotopiques de $\delta^{15}N$ des huîtriers noirs africains étaient strictement enrichies par rapport aux invertébrés benthiques, et leurs valeurs de $\delta^{13}C$ étaient intermédiaires entre celles des moules et des patelles. Finalement la stabilité des relations trophiques entre les niveaux trophiques inférieurs des estrans rocheux sud-africains met clairement en évidence les relations prédateurs-proies et la structure de la chaîne trophique de ce milieu.

Dans une deuxième section je m'intéresse à deux sources potentielles de variations isotopiques dans les proies, ontogénétiques et temporelles, qui peuvent intervenir à l'échelle intra-spécifique et pourraient amener à des interprétations erronées des

ratios isotopiques des huîtriers. Cela peut être notamment problématique dans le cas de déterminations contributions alimentaires des sources, ou de comparaison de tissus de consommateurs ayant des temps d'intégration différents (ex : sang et plumes). Le muscle est souvent privilégié pour les analyses isotopiques d'invertébrés ; cependant, le muscle adducteur des moules et le pied des patelles ne représentent pas la même proportion de l'animal entier pour les deux types de proies. Ainsi l'utilisation des signatures isotopiques du muscle comme proxy des proies entières nécessite d'être validée. Pour deux espèces de patelles (*Scutellastra cochlear* et *Cymbula oculus*) et la moule *P. perna*, trois classes de taille, correspondant aux longueurs de coquilles minimales, modales et maximales mesurées dans des restes alimentaires laissés par des huîtriers, ont été collectées pour analyses isotopiques. En complément, un échantillonnage mensuel de *P. perna* et *S. cochlear* a été effectué sur 13 mois pour examiner les variations temporelles des ratios isotopiques du muscle et des proies entières. Aucune différence concrète de composition isotopique n'a été observé dans les 3 classes de taille de moules et de *S.cochlear.* Chez *C. oculus* les individus de petite taille étaient significativement appauvris en ^{15}N par rapport aux spécimens de moyenne et grande taille. Cependant les huîtriers sont connus pour éviter les proies les plus petites. La taille des proies ingérées ne devrait donc pas influencer les ratios de $\delta^{13}C$ et de $\delta^{15}N$ des huîtriers noirs africains. Les ratios de $\delta^{13}C$ et de $\delta^{15}N$ des tissus de moules ont varié de moins de 1 ‰ et de 1.5 ‰ respectivement au cours des 13 mois, bien qu'un léger appauvrissement en ^{13}C soit observé pendant l'été et un enrichissement en ^{15}N soit observé pendant l'hiver. Les valeurs de $\delta^{15}N$ ont varié de 1.5 ‰ au cours des 13 mois d'étude. Le muscle adducteur était appauvri de 0.5 ‰ en ^{13}C par rapport à l'animal entier mais les deux types de tissus n'ont pas montré de différence dans leur composition en ^{15}N. Les compositions isotopiques moyennes des tissus des patelles ont en revanche montré une forte variabilité pour chaque mois, mais ne présentaient pas de tendance saisonnière particulière. Enfin, les ratios isotopiques du carbone et de l'azote n'étaient pas significativement différents entre le pied et les patelles entières. Ces résultats indiquent que les variations saisonnières des compositions isotopiques des moules et patelles sont minimes et ne devraient pas affecter l'interprétation des ratios isotopiques du sang et des plumes des oiseaux qui renseignent sur le régime alimentaire de oiseaux pendant les saisons de reproduction et d'hivernage respectivement. Enfin les signatures isotopiques des

muscles étaient représentatives de celles des animaux entiers sur l'ensemble de la période d'étude et indiquent que ce tissu est un bon proxy pour les ratios de $\delta^{13}C$ et de $\delta^{15}C$ des proies entières.

I – Trophic structure of the feeding habitat of African Black Oystercatchers on South African rocky shores.

1. INTRODUCTION

In-situ trophic ecology studies of marine predators using stable isotopes of carbon and nitrogen have encompassed particular development in the past 20 years thanks to progresses in mass spectrometry (Kelly 2000) and because of their practical application that provide integrated dietary information at different population, spatial and temporal scales (Hobson & Clark 1992a, b, 1993) on marine species otherwise difficult to study. The utility of $\delta^{13}C$ for the study of trophic ecology derives from the fact that on one hand, sources of dietary carbon may have distinct ^{13}C signatures and on the other hand that the carbon-isotope signature of food sources is incorporated into consumers tissues (DeNiro & Epstein 1978). $\delta^{15}N$ increases in a relatively predictable step-wise manner (+ 2 to 5 ‰, McCutchan et al. 2003) between one source and its consumer, and is therefore particularly informative on the trophic position of an organism within a food chain.

In the case of far-ranging foraging seabirds and migratory birds, the properties of naturally occurring stable isotopes and their spatial distributions in the environment have been used to identify their foraging areas and migration strategies (Atkinson et al. 2005, Jaeger et al. 2010b). However for non-migrating and territorial intertidal feeders like African Black Oystercatchers (ABOs), the question is not whether individuals feed in one area or the other. Instead the interest is in gathering information on the composition of their diet, in term of prey size, species etc ... found on their feeding ground, and its significance in respect to the social or breeding status of individuals, their foraging strategies or location.

Because many uncertainties exist regarding trophic enrichment factors and assimilation between primary producers and primary consumers (Vander Zanden & Rasmussen 2001, Vanderklift & Ponsard 2003), it is preferable to know the stable isotope composition of a predator's potential prey, rather than the baseline isotopic signature of primary producers, which undergo short-term temporal variations in their specific composition and nutrient quality, affecting their stable isotope ratios (Hill et al. 2008, Hill & McQuaid 2009). Among primary consumers, large organisms, such as intertidal limpets and mussels, are characterized by relatively long tissue turnover

time, making them less likely to undergo strong isotopic variation in response to primary producers short term temporal fluctuations. (Cabana & Rasmussen 1996, Post 2002). Those organisms are therefore ideal biological models to study intertidal predators' trophic ecology. Nevertheless, a good knowledge of the natural variability of $\delta^{13}C$ and $\delta^{15}N$ in the potential food sources at a local scale is fundamental to interpret variations in the stable isotope composition of an intertidal predator.

Coastal ecosystems are particularly suitable for trophic studies using stable isotope analyses because $\delta^{13}C$ can be used to discriminate between the two main sources of organic carbon: phytoplankton (from pelagic habitats) and macrophytes (from inshore benthic habitats) (Cabana & Rasmussen 1996). The $\delta^{13}C$ differences between the two originate from differential fractionation of dissolved inorganic carbon during carbon fixation by primary producers (France 1995). As a consequence, pelagic primary production and organisms that depend on it are depleted in ^{13}C compared to littoral primary producers and consumers (France 1995, Post 2002).

This first section of Chapter 2 is a preamble that aims at establishing the trophic structure of the rocky shore habitats of African Black Oystercatchers, with a particular attention on the trophic relationships involving the main prey of ABOs, mussels and limpets.

2. MATERIALS & METHODS

Prey (mussels and limpets) and ABOs samples presented in this section were collected at the 13 main sampling sites (Fig 1.1) throughout the 3 breeding seasons (Table 1.1). Furthermore, polychaetes (*Gunnarea capensis* and *Pseudonereis variegata*) were sampled in Kenton during the 2009-2010 season. For a detailed description of the sampling methods, laboratory processing and stable isotope analysis of animal samples, see Chapter 1, Section IV ("Sites d'étude, échantillonnage et analyses en laboratoire"). Additionally, in the present section we included carbon and nitrogen stable isotope ratios of primary producers collected in Port Alfred in 2006 and presented in Hill & McQuaid (2008). Nearshore suspended particular matter (SPM) was obtained from 5 litres of surface waters collected from the shore. Macroalgae (*Sargassum heterophyllum*, *Ralfsia verrucosa*, *Ulva sp*, and *Gelidium sp)* were collected on rocky substrates. All primary producers were

collected in 3 replicates in February-March 2006, except for *R. verrucosa* that was sampled in September 2006.

3. RESULTATS

The $\delta^{13}C$ and $\delta^{15}N$ values of primary producers, rocky shore invertebrates and blood and feathers of ABOs sampled in the Kenton area are presented in Fig 2.1. Primary producers displayed the lowest $\delta^{15}N$ values, between 5.7 and 7.2 ‰. Benthic algae had $\delta^{13}C$ values ranging from –15.2 and – 7.8 ‰ and were enriched in ^{13}C compared to the suspended particular matter (SPM) collected in the water column that had $\delta^{13}C$ values of – 15.8 (± 0.4) ‰.

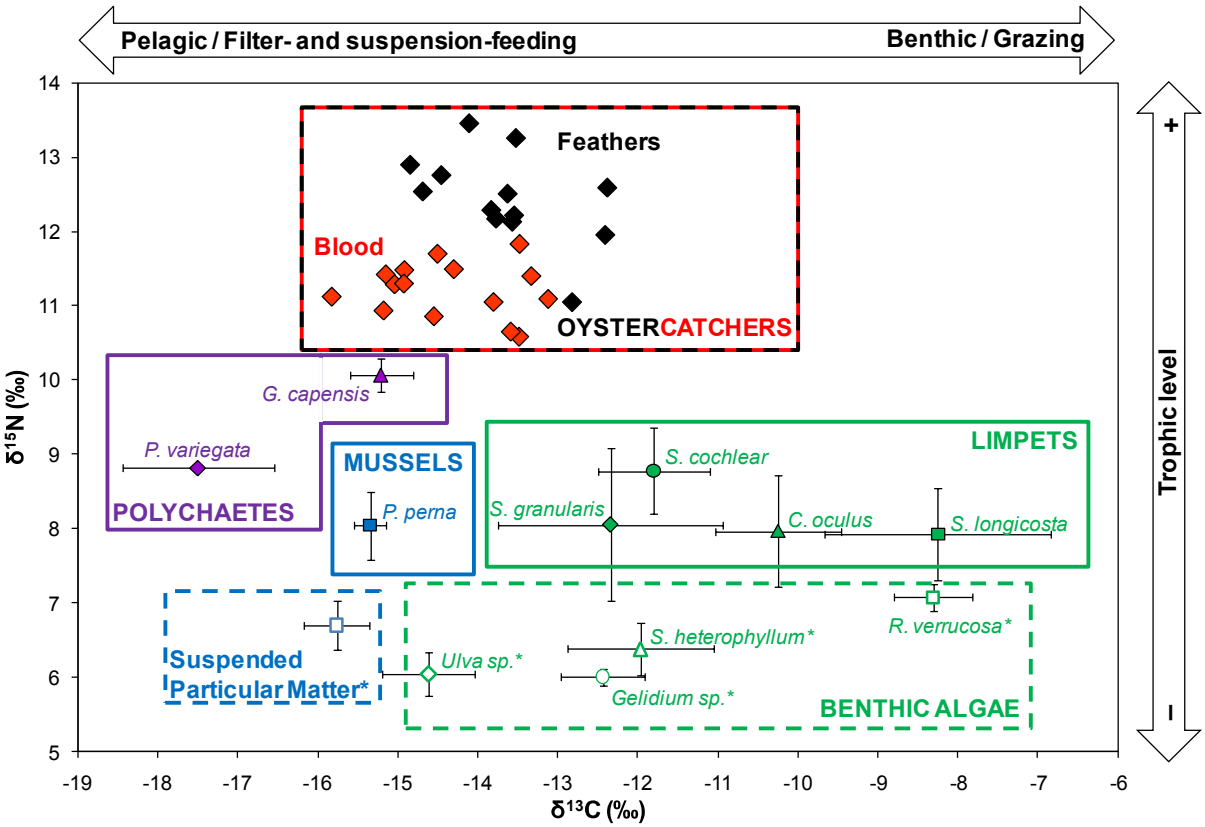


Figure 2.1. Individual $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) of African Black Oystercatchers tissues and mean (± SD) ratios of primary producers and benthic invertebrates in the Kenton area. *Data collected in Port Alfred (Hill & McQuaid 2008)

*$\delta^{13}C$ et $\delta^{15}N$ individuels (‰) des tissus d'huîtriers noirs africains et ratios moyens (± écart-types) des producteurs primaires et invertébrés benthiques échantillonnés dans la région de Kenton. *Données collectées à Port Alfred (Hill & McQuaid 2008)*

Limpets, mussels and polychaetes were globally enriched in ^{15}N compared to primary producers, with $\delta^{15}N$ values ranging from 6.9 to 10.4 ‰. Limpets species displayed

important intra-specific $\delta^{13}C$ variations, as shown by large standard deviations but also between species and their overall $\delta^{13}C$ values ranged from – 13.8 and – 6.8 ‰. They were however strictly enriched in ^{13}C compared to the brown mussel *Perna perna* (– 15.2 ± 0.2 ‰). The suspension-feeding polychaete *Gunnarea capensis* had $\delta^{13}C$ values similar to mussels (– 15.2 ± 0.4 ‰) but was enriched in ^{15}N by 2.0 ‰.The carnivorous polychaete *Pseudonereis variegata* was the most ^{13}C-depleted invertebrate organisms (– 17.5 ± 0.9 ‰) and displayed intermediate $\delta^{15}N$ value between *P. perna* and *G. capensis* (8.8 ± 0.1 ‰). At the other rocky shore locations (Fig 2.2), similar segregation between ^{13}C-depleted mussels and ^{13}C-enriched limpets was observed when both types of invertebrates were collected. One exception was Lüderitz where *M. galloprovincialis* and *S. granatina* had similar $\delta^{13}C$ ratios (–15.7 ‰). On the other hand, as observed in the Kenton area, no consistent separation in the $\delta^{15}N$ ratios of mussels and limpets could be observed.

Across all rocky shore locations sampled, the $\delta^{13}C$ values of ABOs blood varied between – 16.5 and – 10.0 ‰. One individual sampled at Cape Recife (Fig 2.2) departed from this range with a $\delta^{13}C$ value of -17.1 ‰ (see Chapter III). Birds were globally enriched in ^{15}N compared to benthic invertebrates with $\delta^{15}N$ values ranging from 9.3 and 13.8 ‰. Feathers were enriched in ^{13}C and ^{15}N compared to blood (see this Chapter, section II)

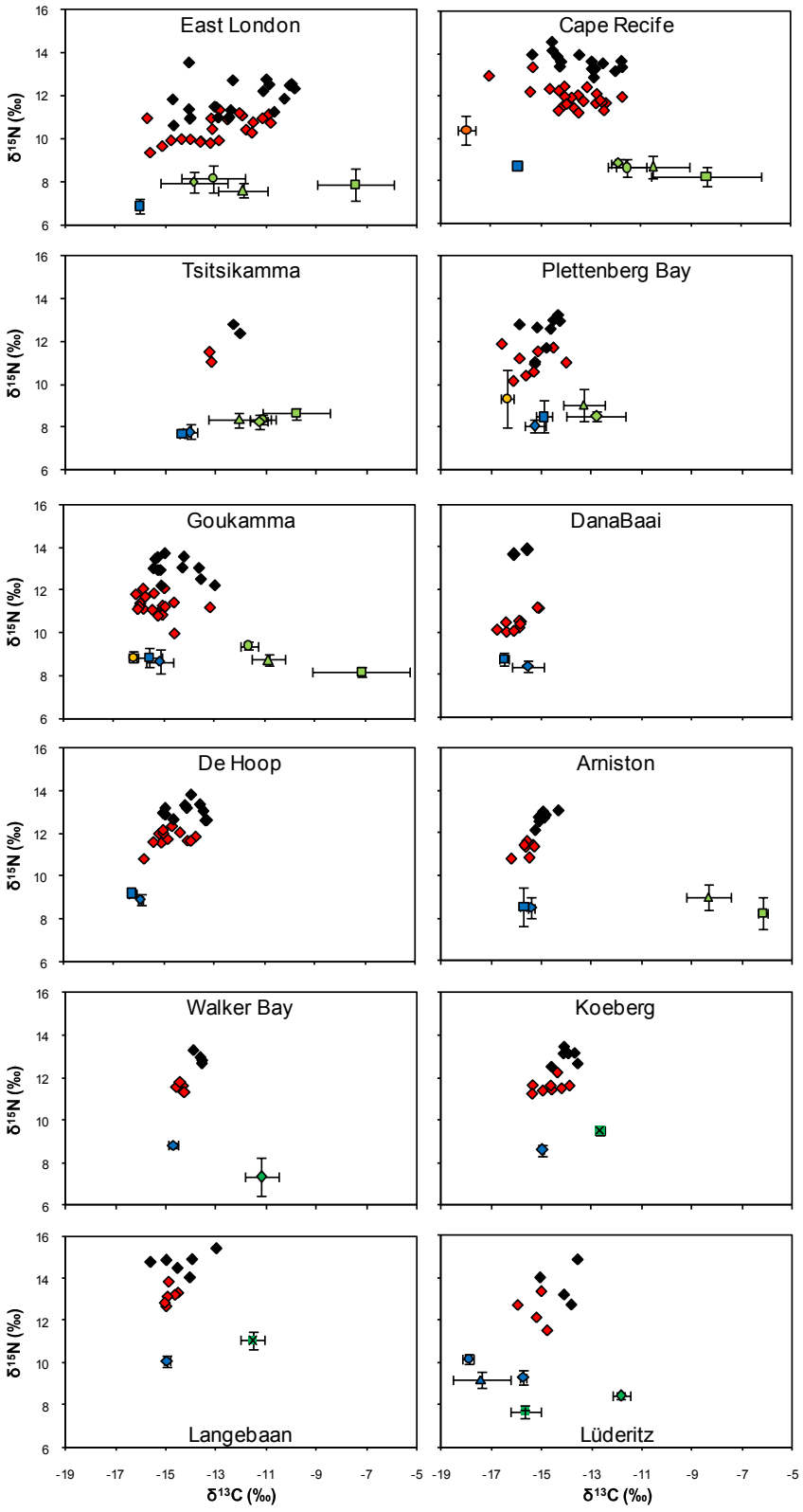


Figure 2.2. $\delta^{13}C$ et $\delta^{15}N$ individuels (‰) des tissus d'huîtriers noirs africains et ratios moyens (± écart-types) des proies potentielles collectés aux sites d'études principaux (Fig 1.1), excepté Kenton (Fig 2.1)

Individual $\delta^{13}C$ and $\delta^{15}N$ (‰) of African Black Oystercatchers tissues and mean (± sd) ratios of potential prey sampled at all main study sites (Fig 1.1) but the Kenton area (Fig 2.1).

4. DISCUSSION

$\delta^{13}C$ segregation was visible between benthic algae and grazing invertebrates on one hand and pelagic primary producers and filter-feeding organisms on the other hand. In addition grazing and filter-feeding invertebrates were enriched in ^{15}N by 1 to 3 ‰ compared to suspended particular matter and seaweeds characterizing the direct trophic link between coastal primary producers and benthic primary consumers.

There was very little intra- and inter-specific variability in the stable isotope ratios of mussels sampled on the South African coast (*P. perna* and *M. galloprovinicialis*). Rocky shore mussels rely on a mixture of pelagic phytoplankton and organic and organic debris, mostly macroalgae detritus, present in the nearshore water column (Bustamante & Branch 1996a). At large scale, the prevalence of ^{13}C-depleted phytoplankton or ^{13}C-enriched macroalgae detritus in nearshore waters can vary geographically (and temporally) on the South African coastline, in relation to biogeographical gradients of nutrients quality and the offshore position of the oligotrophic Agulhas current on the south-coast (Hill et al. 2006, Hill & McQuaid 2008). Locally however, mussels filter suspended-particular matter almost non-selectively, leading to little small-scale variability in their stable isotope ratios (Hill & McQuaid 2008).

Limpets displayed important intra- and inter-specific variations in their stable isotope ratios, especially in $\delta^{13}C$. The four limpet species sampled during this study, *C. oculus*, *S. cochlear*, *S. granularis* and *S. longicosta* constitute the large majority of the limpets consumed by ABOs (Randall & Randall. 1982, Hockey & Underhill 1984, Kohler et al. 2009b). They have different territorial and feeding regimes and occupy different zones on the rocky intertidal area. *S. cochlear* occurs at high densities in seclusion of shallow depressions on the low shore where it feeds exclusively on encrusted coralline algae. *C. oculus* and *S. granularis* occurs throughout the intertidal range, however displaying a spatial segregation between juveniles occupying the low shore and adults occurring mostly on the high shore. Theses limpets are generalist grazers, feeding on any available food (Branch 1975). Adult *P. longicosta* are territorial and occupy gardens of the crustose brown algae *Ralfsia verrucosa* (McQuaid & Froneman 1993), where they exclude other types of algae by grazing them, as well as other limpet competitors (Branch 1975). Therefore the large array of

$\delta^{13}C$ values observed for individuals of *S. longicosta* at all sites is somewhat surprising, while wider range of stable isotope ratios would be expected for the two generalist limpet species. Nonetheless, the 4 limpet species displayed a remarquably consistent isotopic pattern across sites, and more particularly on the south-east where they all co-occur sympatrically: *S. longicosta* was enriched in ^{13}C compared to the other species while no consistent differences in their $\delta^{15}N$ ratios were observed.

ABOs presented $\delta^{13}C$ ratios that were intermediate and varied between those of the ^{13}C-depleted mussels and ^{13}C-enriched limpets at the different study sites. Conversely, the $\delta^{15}N$ difference between ABOs and their potential prey remained stable, between 2 and 3 ‰ (See Chapter 3) which is characteristic of the $\delta^{15}N$ increase between marine avian predators and their prey (Hobson et al. 1994, Evans-Ogden et al. 2004, Cherel et al. 2005c). Overall $\delta^{13}C$ and $\delta^{15}N$ ratios of nearshore and intertidal primary producers, mussels, limpets and ABOs tissues presented in this chapter give a clear picture of the trophic structure of rocky-shore ecosystems across the study area. There are two distinct trophic pathways leading to ABOs on rocky shores: a ^{13}C-depleted “pelagic” pathway with mussels relying on water-column suspended particular matter and a ^{13}C-enriched “benthic pathway” with limpet species relying on a wide range of benthic seaweeds and crustose algae. The relative stability in the trophic relationships between the different lower trophic levels compartments observed on the South African rocky shores and more specifically between filter-feeding mussels and grazing limpets makes it an ideal trophic system to investigate the intra-specific variations in the dietary composition of rocky shore predator such as the African Black Oystercatcher. The lack of inter-site variability in the trophic structure of ABOs feeding habitats, makes it particular suitable for large-scale comparison of the trophic ecology of ABOs in relation with geographic changes in intertidal communities and sex-specific foraging strategies of breeding birds, which will be presented in Chapter 4 and 5.

II – Ontogenetic and temporal variability in the $\delta^{13}C$ and $\delta^{15}N$ ratios of mussels and limpets in the Kenton area

1. INTRODUCTION

The use of stable isotope analyses in animal ecology relies essentially on the fact that the stable isotope composition of consumer's tissues reflects those of their food source in a predictable manner (Chapter 1). Thus sampling of potential prey seems essential for interpreting $\delta^{13}C$ and $\delta^{15}N$ ratios of marine predators and understanding predator-prey relationships. While this can be problematic in the study of large pelagic fish, seabirds and marine mammals foraging over offshore oceanic waters, this is not the case for coastal predators like the African Black Oystercatcher (ABO) feeding in land-based accessible area and restricted feeding territory. At each rocky shore where African Black Oystercatchers were sampled for their blood and feathers, potential prey species, essentially mussels and limpets, were concomitantly sampled for stable isotope analyses. An accurate assessment of the proportion represented by mussels and limpets in the diet of ABOs requires prior thorough characterization of the isotopic variability occurring within each prey species. Since isotopic ratios of prey are reflected in their predators, any variability occurring in the prey will also be reflected in the stable isotope ratios of its consumer, hence affecting the determination of sources' contribution. Here, I identified two intra-specific sources of variability in prey species that could have consequence regarding dietary habits of ABOs: size-related and temporal variability of stable isotope ratios

Ontogenetic shifts in diet can occur over a benthic invertebrate's life as a way to overcome physiological constraints (Rossi et al. 2004). Furthermore assimilation efficiency of diet components and the allocation of nutrients to tissues differ between growing and adult animal (Gannes et al. 1997). This can lead to substantial differences of the carbon and nitrogen stable isotope composition between organisms of different age classes. Mechanisms of food segregation in birds can involve the targeting of different size of prey (Selander 1966, Davis & Smith 2001) especially in sexually dimorphic birds (Favero et al. 1998, Mariano-Jelicich et al. 2008). Moreover in ABOs, it has been shown that breeding adults select particularly large prey to feed their chicks (Randall & Randall 1982, Hockey & Underhill 1984). Therefore consumption of mussels and limpets of various sizes by ABOs could add

variability to their $\delta^{13}C$ and $\delta^{15}N$ ratios and further complicate interpretation of the isotopic results.

Temporal variations in the isotopic ratios of marine producers and consumers have been demonstrated in pelagic and coastal ecosystems, at the scale of months (Kreeger & Newell 2001), seasons (Schaal et al. 2010) or years (Rolff 2000). On the South African coast, Hill et al. (2008) showed contrasts in the $\delta^{13}C$ and $\delta^{15}N$ ratios of suspended particular matter (SPM) and mussels between summer and winter. The authors related this phenomenon to local hydrographic processes and seasonality in the composition of nearshore primary production (Fig 2.3).

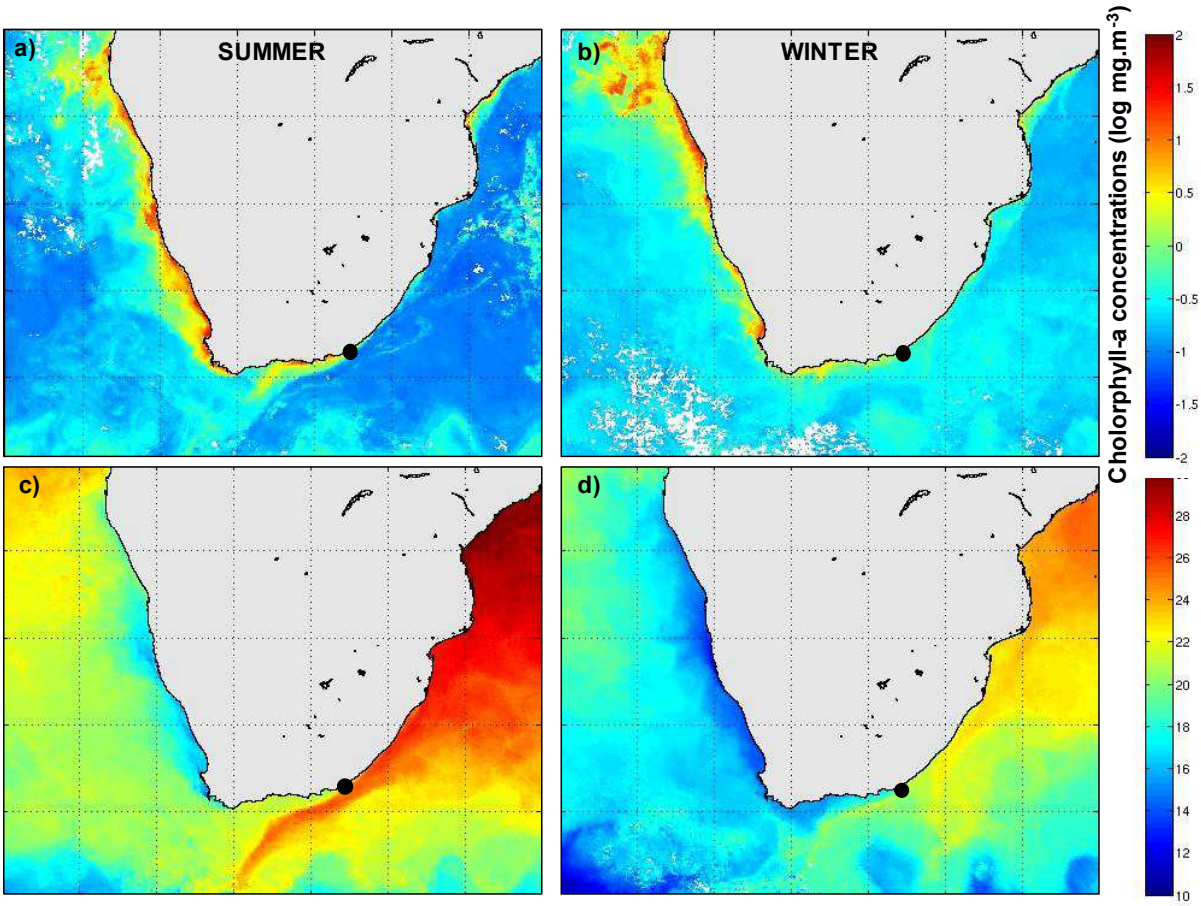


Figure 2.3. Satellite views (http://aoos.mpl.ird.fr) of cholorphyll-a and sea surface temperature respectively during austral summer (a and c – January 2008) and winter (b and d – July 2009), on the coasts of Southern Africa. Black circles indicate Kenton.

Vues satellites (http://aoos.mpl.ird.fr) des concentrations en chlorophylle-a et des température de surface pendant l'été austral (a et c – Janvier 2008) et l'hiver austral (b et d – Juillet 2008) sur les côtes de l'Afrique Austral. Les cercles noirs indique la position de Kenton

In consumers, different tissues provide dietary information integrated over different time-scales (Kelly 2000), and this property makes stable isotope analyses particularly attractive to investigate temporal changes in the feeding ecology of marine predators. However, it is important to clarify whether temporal changes observed in consumers tissues are strictly related to changes in dietary habits, or whether they are also influenced by monthly or seasonal variability in the stable isotope signatures of prey related to temporal changes in environmental conditions, and physiological state of the invertebrates. Tissues usually selected for stable isotope analysis on mussels and limpets are adductor muscles and feet respectively. The choice of muscle tissues is practical because it is easier to process single protein-rich tissues rather than whole animals, including lipid-rich organs (Post et al. 2007). Muscle tissues in addition have slow isotopic turnover rates; therefore their stable isotope composition represent long-term integrated diet and are unlikely to be affected by short-term environmental variations (Gorokhova & Hansson 1999). However while a limpet's foot represents the majority of its body mass, mussel adductor tissue is only a small part of the whole animal. Since ABOs eat entire prey, the validity of using stable isotope ratios of single-tissue as proxy for whole bodies should be investigated.

The aim of this chapter section is to investigate two potential sources of variations in the stable isotope ratios of mussels and limpets that might be relevant for the interpretation of stable isotope ratios of ABOs blood and feathers: 1) ontogenetic variations in *P. perna*, *S. cochlear* and the generalist limpet *Cymbula oculus* and 2) monthly variations in muscle tissues and whole bodies of brown mussel *P. perna* and the limpet *S. cochlear* and tissue-specific differences.

2. MATERIALS & METHODS

Sampling of mussels and limpets. Field sampling was carried out at Middle Beach (33° 41.699'S, 26° 40.119'E), a rocky shore in Kenton (Fig 1.1). For the ontogenetic variations experiment, five *P. perna* of 3 size classes (25, 45 mm and 65 mm in shell length), five specimens of three size-classes of the generalist limpet *C. oculus* (25, 45 and 65 mm) and five specimens of three size classes of *S. cochlear* (20, 40 and 55 mm) were collected at Middle Beach in March 2010. The 3 size groups are hereafter called small, medium and large for the 3 species and were chosen based on the literature (Randall & Randall 1982, Hockey & Underhill 1984) and after measuring the

shell size of middens collected at two ABO's breeding site at Middle Beach (Fig. 2.4) and presented in Kohler et al. 2009a. For the monthly variations experiment, ten specimens of the brown mussel *P. perna* (40-50 mm shell length) and five specimens of the limpet *S. cochlear* (~30-40 mm shell length) were collected monthly at spring low tide between March 2009 and March 2010. *S. cochlear* was chosen as opposed to the other limpets present in the area (*S. longicosta*, *C. oculus* and *S. granularis*), and only 5 specimens were collected monthly as opposed to ten for mussels for the sustainability of the experiments spanning over 13 months. Samples were kept in a cooler box filled with sea water for the trip back to the laboratory, and then kept frozen (–80°C) until further processing.

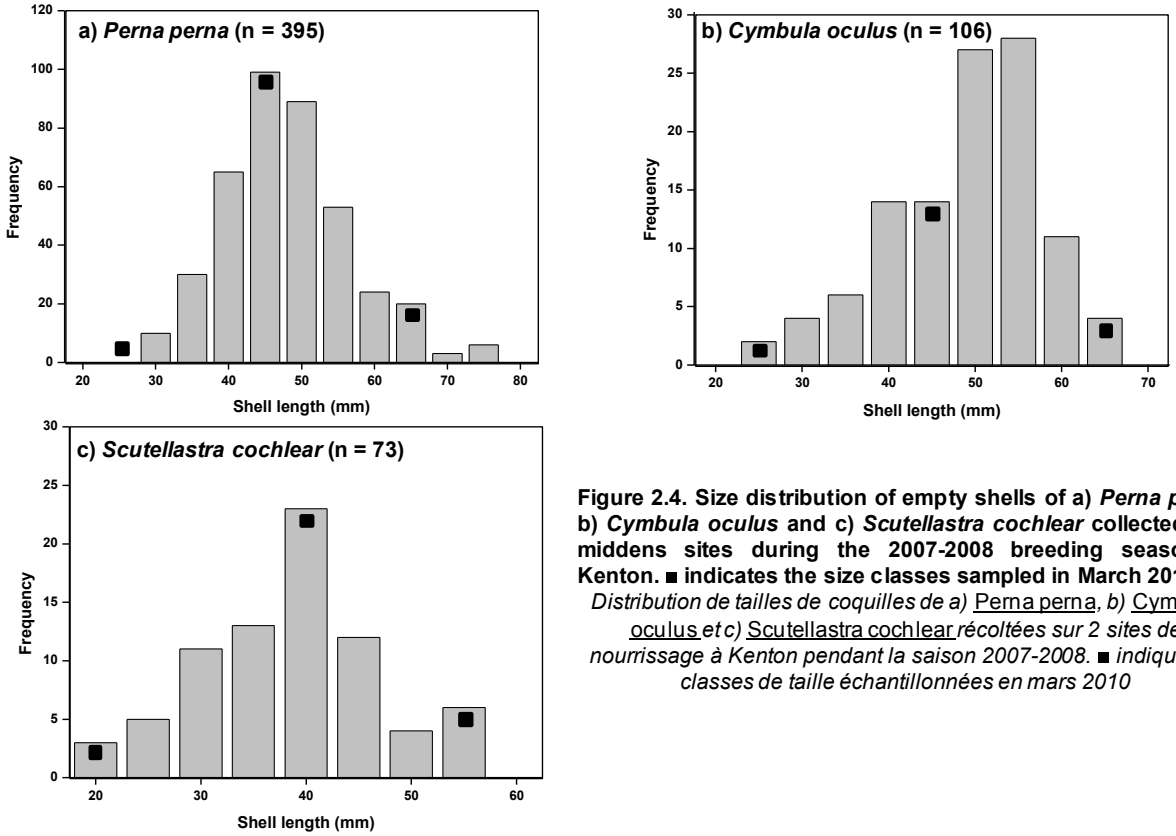


Figure 2.4. Size distribution of empty shells of a) *Perna perna*, b) *Cymbula oculus* and c) *Scutellastra cochlear* collected at 2 middens sites during the 2007-2008 breeding season at Kenton. ■ indicates the size classes sampled in March 2010.
Distribution de tailles de coquilles de a) Perna perna*, b)* Cymbula oculus *et c)* Scutellastra cochlear *récoltées sur 2 sites de nourrissage à Kenton pendant la saison 2007-2008. ■ indique les classes de taille échantillonnées en mars 2010*

Samples preparation and stable isotope analysis. For the size class samples collected in March 2010, analyses were done on muscle tissues, i.e. adductor muscle of mussels and foot of limpets. For the monthly sampling spanning over 13 months, the adductor muscle was removed from five mussels for stable isotope analysis and the rest of the body discarded. On the five remaining mussels, the whole body was removed from the shell for stable isotope analysis. On limpets, a small tissue piece was cut out from the foot and the rest of the body preserved, and both were used for analysis of their stable isotope composition. This procedure was done for each

monthly sampling. All samples, muscle tissues and whole bodies, were dried in a freeze-drier (- 40°C, 12hr) and ground individually into a fine homogenous powder. Lipids were extracted from whole bodies of mussels and limpets using 4 ml of cyclohexane for 100g of homogenous powder (Lorrain et al. 2002, Cherel et al. 2005a, Kojadinovic et al. 2008b). Size class samples were analyzed at the Stable Light Isotope Unit of the University of Cape Town. Monthly collected samples were analyzed at IsoEnvironmental cc (Botany Department, Rhodes University). Relative isotopic abundances of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) were determined from ~1 mg sub-samples of the homogenous powder with a continuous flow isotope ratio mass spectrometer (IRMS). Results are expressed relative to the international standards of ^{13}C in Pee Dee Belemnite and ^{15}N in atmospheric air. Precision of replicate determinations was < 0.17 ‰ for carbon and < 0.20 ‰ for nitrogen for both laboratories.

Data Analysis. All statistical analyses were performed using R statistical software (available at http://www.r-project.org/). Normality (Shapiro test, $\alpha = 0.05$) and homogeneity of variances (Levene's test) were tested for all datasets and in case they did not meet these assumptions, non-parametrical procedures were applied.

Paired t-tests and Pearson's correlation were used to look at differences and correlations in the $\delta^{13}C$ and $\delta^{15}N$ values between muscle tissues and delipidated bodies. One-Way ANOVAs (F, $\alpha = 0.05$) or Kruskal-Wallis tests (H, $\alpha = 0.05$) were used to test for significant monthly changes of the $\delta^{13}C$ and $\delta^{15}N$ in muscle tissues and whole bodies of *P. perna* and *S. cochlear.* In case of significant differences between months, a post-hoc Tukey Honest Significant Differences test (Tukey HSD, $\alpha = 0.05$) was performed to determine which size class differs from each other.

3. RESULTS

Ontogenetic variations of $\delta^{13}C$ and $\delta^{15}N$ in mussels and limpets. Small, medium and large mussels had very similar $\delta^{13}C$ and $\delta^{15}N$ values and did not differ significantly (Table 2.1, Fig 2.5). Although small and medium-sized specimens of the limpet *S. cochlear* displayed a wide range of $\delta^{13}C$ values (- 13.5 ± 2.5‰ and – 12.7 ± 2.2‰ respectively), they were not significantly different from large specimens and all size classes had very consistent nitrogen stable isotope composition (Table 2.1, Fig 2.5).

Table 2.1. Kruskal-Wallis test (*H, df = 2, α = 0.05*) on the $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) of the 3 size classes of *Perna perna, Cymbula oculus* and *Scutellastra cochlear.* In case of significant differences, a multiple comparison pos-hoc test was used.

Test de Kruskal-Wallis (H, ddl = 2, α = 0.05) sur les valeurs de $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) des 3 classes de tailles de Perna perna*,* Cymbula oculus *et* Scutellastra cochlear*. En cas de différences significatives, un test post-hoc de comparisons multiples a été utilisé.*

	$\delta^{13}C$		$\delta^{15}N$	
	H	*p-value*	*H*	*p-value*
Perna perna	2.27	n.s.	2.90	n.s.
Cymbula oculus	5.11	n.s.	8.66	* Small ≠ medium = large
Scutellastra cochlear	1.52	n.s.	1.34	n.s.

** p < 0.05 ; n.s. non-significant p > 0.05*

Finally small individuals of the limpet *C. oculus* were significantly depleted in ^{15}N (7.2 ± 0.5 ‰) compared to both medium and large specimens (8.1 ± 0.3 and 8.2 ± 0.5 ‰ respectively; H = 8.66, p = 0.01) but the $\delta^{13}C$ ratios of the 3 size classes were similar (small = -11.4 ± 0.8 ‰, medium = - 10.3 ± 0.8 ‰ and large = - 10.1 ± 0.7 ‰; H = 5.11, p> 0.05) (Table 2.1, Fig 2.5).

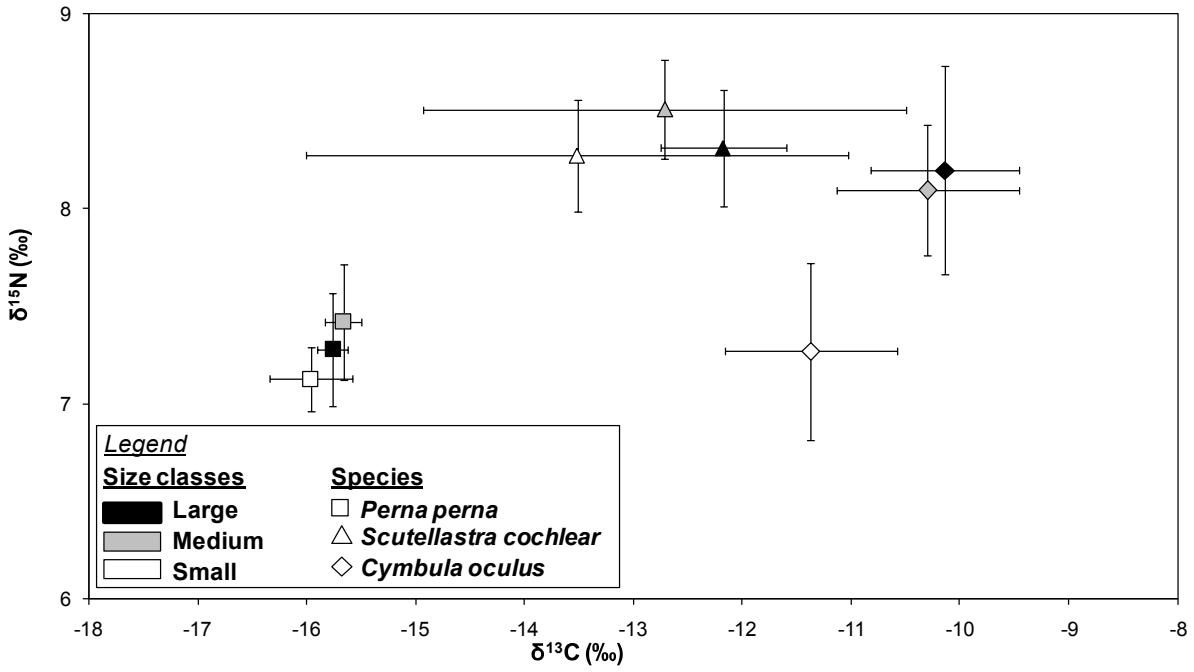


Figure 2.5. Carbon and nitrogen stable isotope ratios (mean ± SD) of small, medium and large specimens of the brown mussel *Perna perna*, the pear limpet *Scutellastra cochlear* and the goat's eye limpet *Cymbula oculus.*

Ratios isotopiques moyens (± écart-type) du carbone et de l'azote des spécimens de petite, moyenne et grande taille des moules Perna perna *et des patelles* Scutellastra cochlear *et* Cymbula oculus

Monthly $\delta^{13}C$ and $\delta^{15}N$ variations in mussels. Between March 2009 and 2010 the mean $\delta^{13}C$ of *P. perna* muscle tissues varied between a minimum of -16.2 ‰ and a maximum of -15.2 ‰ and whole bodies varied between -16.9 and -15.6 ‰ (Fig 2.6a).

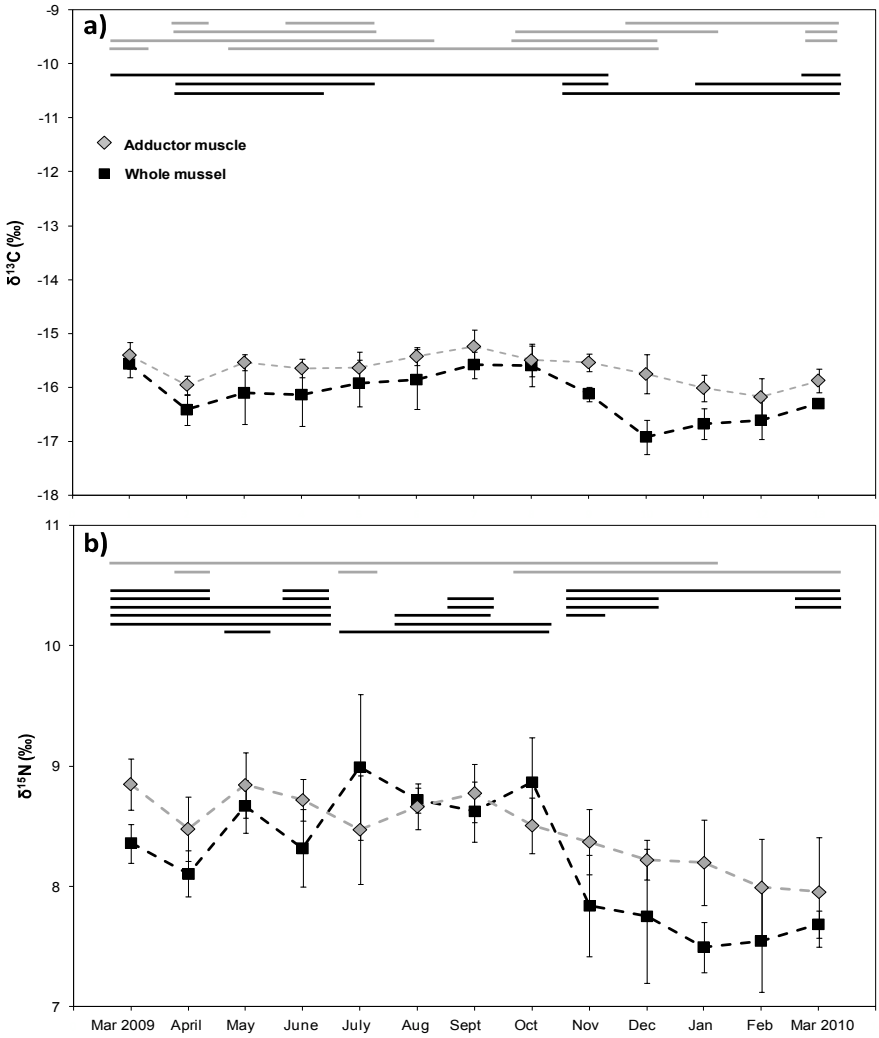


Figure 2.6. Monthly variations of a) $\delta^{13}C$ (‰) and b) $\delta^{15}N$ (‰) in adductor muscles and whole bodies of the mussel *Perna perna*. Lines above the graph indicate homogenous months (Tukey post-hoc test, α = 0.05).

Variations mensuelles des ratios de a) $\delta^{13}C$ (‰) et b) $\delta^{15}N$ (‰) dans le muscle et le corps entier des moules Perna perna*. Les lignes continues indiquent les mois homogènes (Test post-hoc de Tukey, α = 0.05).*

Muscle adductor tissues and delipidated bodies showed significant temporal differences in their $\delta^{13}C$ values (One Way ANOVA, F = 5.72 and 5.61 for muscles and bodies respectively, $p < 0.001$ for both), with an average enrichment of +0.5 ‰ in muscles compared to whole delipidated animals (Fig 2.6a). For 9 out of 13 months adductor muscles had similar $\delta^{13}C$ ratios, and samples collected in April 2009 and January, February and March 2010 were depleted in ^{13}C compared to the other months. For whole bodies, samples collected between March and November 2009

had similar $\delta^{13}C$ ratios but were enriched in ^{13}C compared to samples collected between December 2009 and March 2010. $\delta^{13}C$ values of adductor muscles were consistently and significantly enriched by average 0.5 ‰ compared to whole bodies (Paired t-test, $t = -6.42$, $p < 0.001$) and the two were monthly correlated (Pearson's correlation, $t = 4.72$, $p < 0.001$, $R^2 = 0.82$).

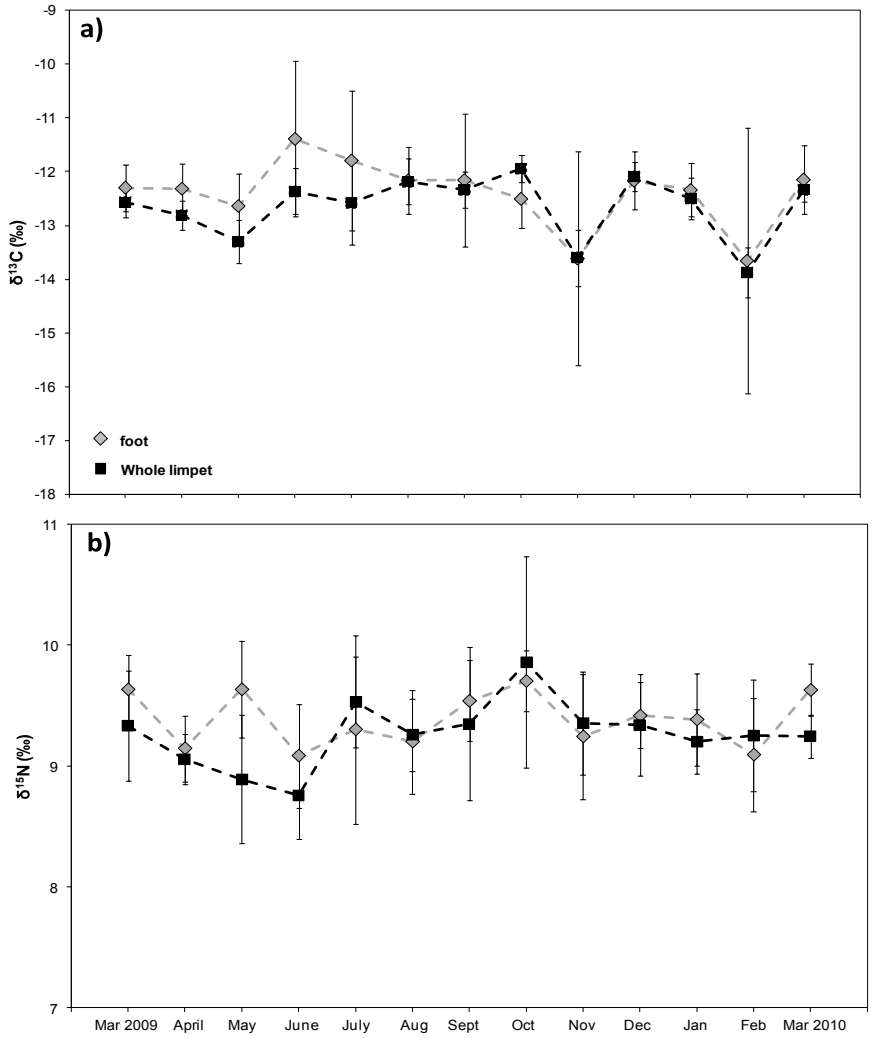


Figure 2.7. Monthly variations of a) $\delta^{13}C$ (‰) and b) $\delta^{15}N$ (‰) in foot tissues and whole bodies of the limpet *Scutellastra cochlear*.

Variations mensuelles des ratios a) $\delta^{13}C$ (‰) et b) $\delta^{15}N$ (‰) dans le pied et le corps entier des patelles Scutellastra cochlear.

The mean $\delta^{15}N$ varied between 8.0 and 8.8 ‰ for adductor muscles and between 7.5 and 9.0‰ for delipidated bodies (Fig 2.6b). There were significant temporal variations in the $\delta^{15}N$ values of both adductor muscles and whole bodies ($F = 5.18$ and 5.61 for muscles and bodies respectively, $p < 0.001$ for both). $\delta^{15}N$ values of adductor muscles were similar between March 2009 and January 2010 but enriched compared to samples collected in February and March 2010. For delipidated bodies, $\delta^{15}N$ values were segregated in 3 continuous periods: March to June 2009 with intermediate $\delta^{15}N$ values, July to October 2009 displaying the highest $\delta^{15}N$ values and November 2009 to March 2010 with the lowest values. The monthly variations in $\delta^{15}N$ ratios of adductor muscles and whole bodies were significantly correlated (Spearman's correlation, $S = 120$, $p = 0.01$, $R^2 = 0.67$) and did not significantly differ (Wilcoxon paired-test, $V = 19$, $p = 0.07$).

Monthly $\delta^{13}C$ and $\delta^{15}N$ variations in limpets. The mean $\delta^{13}C$ ratios in the foot tissue of limpets varied between –13.7 and –11.4‰ and between –13.9 and –11.9 ‰ for delipidated bodies over the 13 months study period (Fig. 2.7a). For some months, however, mean $\delta^{13}C$ displayed high standard variations in foot tissues or whole bodies or both (e.g. June, July, September, November 2009 and February 2010). $\delta^{13}C$ ratios of both foot tissues and delipidated bodies did not show significant temporal variations (Kruskal-Wallis test, $H = 9.65$ and 12.66 for foot and body respectively, $p > 0.05$ for both) and were not correlated (Spearman's correlation, $S = 188$, $p = 0.09$). Overall foot tissues were significantly enriched in ^{13}C by average 0.3 ‰ compared to whole bodies (Wilcoxon paired-test, $V = 14$, $p = 0.03$).

Between March 2009 and 2010, mean $\delta^{15}N$ ratios varied between 9.1 and 9.7 ‰ for foot tissue and between 8.8 and 9.9 ‰ for delipidated bodies, but again mean $\delta^{15}N$ ratios displayed high standard deviations for a majority of months (Fig 2.7b). There was no significant pattern of temporal variations in either foot tissues or delipidated bodies (One-way ANOVAs, $F = 1.37$ and 1.78 for foot tissue and delipidated body respectively, $p > 0.05$ for both) and monthly $\delta^{15}N$ ratios of foot tissues and whole bodies were not significantly correlated (Pearson's correlation, $t = 1.46$, $p > 0.05$). Finally, at the monthly scale, the $\delta^{15}N$ values of the samples were not significantly different (Paired t-test, $t = -1.59$, $p > 0.05$).

4. DISCUSSION

Ontogenic shifts in the stable isotope ratios of mussels and limpets. There were no clear differences observed between the $\delta^{13}C$ and $\delta^{15}N$ ratios of the sizes of specimens of the brown mussel *P. perna.* This suggests that small, medium-sized and large mussels feed in a similar way in the water column, on a mixture of macroalgae detritus and phytoplankton (Hill et al. 2006, 2008). A similar pattern was observed for the limpet *S. cochlear,* with however large variations in the $\delta^{13}C$ of small and medium-sized animals. *S. cochlear* is a specialist limpet restricted to the appropriately-named "cochlear zone" on the lower eulittoral zone. It feeds exclusively on encrusting coralline algae, and excludes no only other herbivores but also seaweeds (Maneveldt et al. 2006). Therefore in such a poorly diversified habitat, dietary shifts between age classes are unlikely, and the variability is probably related to the physiology of young limpets or to small-scale variability of their food source. Conversely in *C. oculus,* small specimens were clearly depleted in ^{15}N compared to medium-sized and large animals. Branch (1971) observed that larger specimens of *C. oculus* occupied the high shore in a greater extent than juveniles and this could account for the size-related difference in $\delta^{15}N$ observed for this generalist species. As for *S. cochlear*, physiological mechanisms related to young stages may also contribute to explain the lower nitrogen ratios in small individuals. Previous studies have shown that the mean size of prey selected by ABOs is significantly larger than the mean size of prey available to them, especially when they feed their chicks, whether they feed on rocky shore mussels and limpets in rocky area (Randall & Randall 1982, Hockey & Underhill 1984), or on the sand mussel *D. serra* on sandy beaches (Ward 1991). On the other hand Sutherland (1982) showed that European oystercatchers avoided the largest prey because they were less likely to be successful in opening them, but also because of the risk of damage when handling them. Therefore, when balancing the energetic benefit of consuming large prey and the risks of handling them, ABOs, like European oystercatchers, are restricted to a limited range of optimal prey size (Zwarts et al. 1996), most likely toward medium-sized individuals that show the most of consistencies in their isotopic signatures.

Temporal variations in muscle tissues and whole bodies of *P. perna*. The $\delta^{13}C$ ratios of adductor muscles and whole bodies of *P. perna* varied only within 1 ‰ over 13 months. However a ^{13}C-depletion pattern was observed between November 2009

and March 2010, which corresponds to the austral summer. In a previous study, Hill et al. 2008 reported similar decrease in $\delta^{13}C$ in nearshore suspended particular matter (SPM) and mussels' adductors during the 2004-2005 austral summer. The authors could not link these seasonal variations to estuarine inputs, temperature or the position of the Agulhas current (Fig 2.3). Instead it was suggested that this temporal pattern of $\delta^{13}C$ variations in SPM and mussels was related to changes in the pool of nearshore macroalgal detritus. In the present study, an enrichment in ^{15}N was also observed in whole bodies of mussels over the winter months (July to October 2009), and a depletion during summer, with a difference of ~ 1.5 ‰ between the two months showing the most extreme values (July 2009 and January 2010). A slight decrease in $\delta^{13}C$ was also visible in adductor muscles over the summer months. This correlated with findings of Hill et al. (2008), which showed an increase of $\delta^{15}N$ ratios in nearshore SPM over winter, though the origin of this temporal pattern was unclear. Inshore-offshore patterns of $\delta^{15}N$ are not as well understood as the $\delta^{13}C$ gradient that exists between the ^{13}C- enriched coastal waters and the ^{13}C-depleted offshore waters (Hill et al. 2006) and require further investigation. Overall monthly variations of stable isotope ratios in both muscles and whole bodies could be linked to seasons (winter vs summer), but remain small. Finally muscle tissues and whole bodies displayed little differences in their $\delta^{13}C$ ratios (0.5 ‰) and no significant differences in $\delta^{15}N$.

Temporal variations in foot tissues and whole bodies of *S. cochlear.* The $\delta^{13}C$ and $\delta^{15}N$ ratios variations in foot tissues and whole bodies of *S. cochlear* displayed no clear temporal pattern. Instead limpets displayed high monthly variability in their stable isotope ratios. Limpets rely on fixed benthic primary production, which isotopic composition can vary at a very small-scale, depending on local micro-conditions (pH, temperature, irradiance etc ...). This micro-scale variability will have buffer-effect on additional temporal variability. Finally, despite large standard variations, foot tissues and whole limpets displayed very similar $\delta^{13}C$ and $\delta^{15}N$ ratios for all months.

Conclusion. I found no clear isotopic differences between the medium-sized and large mussels and limpets, for which shell length is comprised within the range of prey size typically targeted by ABOs, suggest that the prey size factor should not significantly influence $\delta^{13}C$ and $\delta^{15}N$ ratios of ABOs. Mussels displayed a small seasonal trend in their $\delta^{13}C$ ratios and $\delta^{15}N$, while there was no temporal trends in

limpets tissues. Additionally limpets foot and mussels adductors muscle were representative of whole individual isotope signatures through time. This suggests that 1) muscle tissues sampled once during the year can be considered as good proxies for the $\delta^{13}C$ and $\delta^{15}N$ of whole bodies and 2) comparison between ABOs tissues with different temporal integration of the diet (blood and feathers), based on a single sampling of prey, should not lead to misinterpretation regarding the potential seasonal change in their feeding habits.

CHAPITRE 3

Trophic enrichments factors and tissue-specific variations of $\delta^{13}C$ and $\delta^{15}N$ in adults and chicks of African Black Oystercatchers

(Photos: S. Kohler)

RESUME

Une connaissance de valeurs fiables de fractionnement isotopique, qui peuvent varier d'une espèce animale à l'autre, est essentielle pour comprendre les relations trophiques entre sources et consommateurs et pour l'utilisation de modèles de mélange isotopiques. Dans de nombreuses études, les chercheurs se basent sur des valeurs estimées pour des espèces proches de leur modèle biologique, cependant celles-ci sont rares et peu précises pour les oiseaux limicoles. L'utilisation des modèles de mélange sur les valeurs isotopiques de l'huîtrier noir africain et ses proies nécessite donc une estimation du fractionnement isotopique pour cette espèce. De plus dans les études isotopiques sur les oiseaux, l'utilisation du sang et des plumes sont de plus en plus privilégiées car leur prélèvement est non destructif et ils procurent des informations alimentaires sur des périodes de temps différentes (période de reproduction et repos). Cependant, la comparaison de signatures isotopiques de différents tissus ayant des temps d'intégration différents prélevés chez des adultes peut être problématique car ceux-ci présentent également des fractionnements isotopiques différents. Chez des poussins en revanche, ces deux tissus prélevés simultanément informent sur des périodes d'intégration alimentaires similaires. Ainsi, un autre aspect important à éclaircir est la différence isotopique d'origine physiologique observée entre le sang et les plumes des huîtriers afin de pouvoir exploiter leurs valeurs dans le cadre de variations saisonnières des habitudes alimentaires. Pour estimer le fractionnement isotopique entre les sources de nourriture et le sang des huîtriers, j'ai considéré 4 zones géographiques sur lesquels les oiseaux ne se nourrissaient que sur un type de proie (moule, patelle ou moule des sables). Pour les différences isotopiques du sang et des plumes, notées $\Delta\delta^{13}C_{blood\text{-}feathers}$ et $\Delta\delta^{15}N_{blood\text{-}feathers}$, j'ai examiné en particulier les signatures isotopiques de ces deux tissus chez des poussins âgés de plus 10 jours, chez qui ils représentent une intégration temporelle équivalente de l'alimentation, mais également celles des adultes. Les valeurs de fractionnement isotopique pour le sang des huîtriers sont de + 0.2 (± 0.4) % pour le $\delta^{13}C$ et de + 2.7 (± 0.4) pour le $\delta^{15}N$. Les plumes étaient strictement enrichies en ^{13}C et ^{15}N par rapport au sang chez les deux classes d'âge. Les valeurs isotopiques du carbone et de l'azote étaient également fortement corrélés à la fois chez les poussins ($R^2_{carbone}$= 0.92, R^2_{azote} = 0.79) et chez les adultes ($R^2_{carbone}$ = 0.86, R^2_{azote} = 0.75). Les pas isotopiques sang-plumes pour le carbone et l'azote ($\Delta\delta^{13}C_{blood\text{-}feathers}$ et $\Delta\delta^{15}N_{blood\text{-}feathers}$) étaient toutefois légèrement différents entre poussins et adultes et pourraient résulter de différences

physiologiques intrinsèques entre les deux classes d'âge, notamment la croissance chez des poussins qui peut altérer le fractionnement isotopique dans leurs tissus. De manière générale l'existence de différences isotopiques sang-plumes constantes chez les poussins peut aider à interpréter les différences de $\delta^{13}C$ et $\delta^{15}N$ observées chez les tissus des adultes. Notamment de larges déviations des valeurs individuelles $\Delta\delta^{13}C_{blood\text{-}feathers}$ et $\Delta\delta^{15}N_{blood\text{-}feathers}$ par rapport à celles des poussins peuvent indiquer des changements de régime alimentaires ou d'habitats d'alimentation entre les saisons de reproduction et d'hivernage.

1. INTRODUCTION

As introduced in Chapter 1, the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope composition of consumer tissues depends on both the isotopic composition of their food sources (DeNiro & Epstein, 1978, 1981) and diet-consumer fractionation processes occurring during the metabolic assimilation and excretion (Ponsard & Averbuch 1999). This diet-consumer isotopic fractionation, also called the trophic shift or trophic enrichment factor (TEF), varies among species or taxa but also according to the type of nitrogen excretion, trophic guild (herbivores vs. carnivores) and the consumer tissues into which the material is incorporated. TEF values have been extensively reviewed in Vander Zanden & Rasmussen (2001) and McCutchan et al. (2003) and it is generally accepted that they range from 0 to 2 ‰ and from 2 to 5 ‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively. Knowledge of the TEF values is particularly relevant to investigate trophic positions (Post 2002) and the evaluation of food source contributions derived using stable isotope mixing models. To run these models, for example in the IsoSource visual basic program (Phillips & Gregg 2003), it is necessary to provide stable isotope ratios of potential sources and consumers and TEFs for each isotope element used (C, N, S …). In the more recently developed stable isotope mixing model running on R Statistical Software (SIAR, Parnell et al. 2010), it is also possible to include uncertainty regarding mean sources and consumer isotopic ratios as well as TEFs in the form of standard deviations.

TEF values have been estimated for several terrestrial and aquatic bird species (see summary in Table 3.1). The wide ranges of $\delta^{13}C$ and $\delta^{15}N$ TEF values found among species in the earliest studies (Mizutani et al. 1992, Hobson et al. 1993,) have encouraged further investigation, mainly through experimental studies using controlled diet and environmental conditions (but see Thompson & Furness 1995). These studies have provided fundamental understandings of the effect of food quality and origin (e.g. terrestrial vs marine) (Hobson & Clark 1992, Bearhop et al. 2002, Pearson et al. 2003) on diet-consumer fractionation processes and have raised awareness about appropriate methodological approaches, especially regarding prey tissues (e.g. whole prey vs muscle tissues, Cherel et al. 2005c) and the need for delipidation (Bearhop et al. 2002). Investigations of TEFs in seabirds have received particular attention in the past 20 years (Table 3.1), but to my knowledge, diet-blood fractionation values in shorebirds has been estimated for only one species, the Dunlin *Calidris alpina pacifica* (Evans-Ogden et al. 2004). This work, however, only concerned 4 birds that were fed on an artificial terrestrial-based diet. In addition, no

information was provided on variance in the mean TEF values. Considering the wide range of TEF values found for the many seabird species studied (Table 3.1), it is imprudent to extrapolate the values found for dunlins to other shorebird species.

Nowadays, researchers investigating the trophic ecology of marine birds with stable isotopes favour the combined use of blood and feathers, for two reasons. Firstly, sampling these tissues is non-destructive and relatively easy to perform (Hobson & Clark 1993, Thompson et al. 2005, Bearhop et al. 2002, Cherel et al. 2005b). Secondly, sampled simultaneously, their stable isotope compositions represent diets integrated during different time-periods and can be equivalent to a recapture (Bearhop et al. 2002, Dalerum & Angerbjörn 2005). Blood proteins have a half-life of 10 to 30 days, depending on the size of the bird, therefore the whole blood stable isotope composition provides information on the diet of the bird during the few weeks prior the sampling (Hobson & Clark 1992a, Evans-Ogden et al. 2004). Conversely, feathers remain isotopically inert once they are fully grown (Mizutani et al. 1990), their isotopic composition therefore reflects the diet assimilated over their formation period, usually during the moulting season. For most marine adult birds (seabirds and shorebirds), moult occurs during the non-breeding period, when birds are not bound to their breeding colony or territory, and are not as accessible as when they reproduce (Cherel et al. 2000, Quillfeldt et al. 2005, 2008, Jaquemet et al. 2008). This is also true for African Black Oystercatchers, as breeding adults moult (Dare & Mercer 1974, Pienkowski & Knight 1975, Hulscher 1977, L.G. Underhill, pers. com.) and tend to relax their territorial behaviour outside the breeding season (Hockey 2005, pers. obs.). Little is known about their movements and feeding habits when wintering, therefore feathers collected during their breeding season and used as dietary proxies, can be an interesting method of investigating the feeding ecology of ABOs outside their breeding season when their capture on the nest is not feasible.

The comparison of different tissues sampled from one organism is, however, complicated by the fact that isotopic diet-consumer enrichment can differ among consumer tissues (Hobson & Clark 1992, Evans-Ogden et al. 2004). Indeed the stable isotope composition of tissues depends on their lipid and protein constitution and the metabolic processes involved in tissues synthesis, all of which can vary among tissues (DeNiro and Epstein 1978, 1981, Hobson & Clark 1993, Cherel et al. 2005b). In contrast to adults, whole blood and newly grown feathers of juvenile birds both reflect the diet integrated over the same period, i.e. the few weeks between

hatching and sampling. Thus, theoretically, differences in the stable isotope ratios of whole blood and feathers of chicks will only reflect differences between the diet-blood and diet-feather enrichment factors. Thus, blood-feather isotopic differences in chicks can theoretically subsequently be used as a basis for interpreting tissue differences in adults (Cherel et al. 2000).

The aims of this chapter are 1) to estimate TEF values for $\delta^{13}C$ and $\delta^{15}N$ for African Black Oystercatchers, which will subsequently be used in stable isotope mixing models (see Chapters 4 and 5) and 2) to investigate differences between the $\delta^{13}C$ and $\delta^{15}N$ of blood and feathers in chicks and adults.

Table 3.1. Estimates of blood and feathers trophic enrichment factors (‰) for $\delta^{13}C$ and $\delta^{15}N$ in seabirds (dark grey), shorebirds (grey), freshwater (light grey) and terrestrial birds (white) in the literature

Estimation de facteurs d'enrichissement trophique de $\delta^{13}C$ et $\delta^{15}N$ (‰) pour le sang et les plumes espèces d'oiseaux marins (gris foncé), limicoles (gris), aquatiques (gris clair) et terrestres (blanc) dans la littérature

Species	Feeding treatment (analyzed tissue)	Whole blood		Feathers			Reference
		$\delta^{13}C$	$\delta^{15}N$	Type	$\delta^{13}C$	$\delta^{15}N$	
Seabirds							
Humboldt's Penguin (*Sphenicus humboldti*)	Anchovy (whole fish)	-	-	Body	+2.9 ± 0.2	+4.8 ± 0.5	Mizutani et al. (1992)
Great Cormorant (*Phalacrocorax carbo*)	Mackerel (whole fish)	-	-	Primary	+3.8 ± 0.5	+3.7 ± 0.6	
Black-tailed Gull (*Larus crassirostris*)	Saurel (whole fish)	-	-	Primary	+3.6 ± 0.5	+5.3 ± 0.8	
Ringed-billed Gull (*L. delawarensis*)	Perch (gutted body)	−0.3 ± 0.8	+3.1 ± 0.2	Not specified	+0.2 ± 1.3	+3.0 ± 0.2	Hobson & Clark (1992)
Common Murre* (*Uria aalge*)	Sandeels† (homogenized & delipidated)	-	-	Body	+1.0	+3.3	Thompson & Furness (1995)
Arctic Tern* (*Sterna paradisaea*)		-	-		+2.1	+3.4	
Broad-billed Prion* (*Pachyptila vittata*)	zooplancton† (homogenized & delipidated)	-	-		+2.5	+4.3	
Subantarctic Skua* (*Catharacta lönnbergi*)	Broad-billed Prion† (body feathers)	-	-		+0.4	+3.0	
Goosanders*,Shags* & Great cormorants (*Mergus merganser, P. aristotelis* & *P. carbo*)	Salmon parr, sandeel & sprat (delipidated whole fish)	-	-	Primary	+2.3 (averages for the 3 species)	+4.2 (averages for the 3 species)	Bearhop et al. (1999)
Great Skuas (*Catharacta skua*)	Sprat (whole fish)	+4.3	+2.6	Primary	+5.3	+4.4	Bearhop et al. (2002)
	Sprat (delipidated whole fish)	+1.1	+2.8		+2.1	+4.6	
	Beef (homogenized)	+7.1	+4.0		+7.0	+4.8	
	Beef (homogenized & delipidated)	+2.3	+4.2		+2.2	+5.0	
King Penguins (*Aptenodytes patagonicus*)	Herring (delipidated whole fish)	−0.8	+2.1	Back	+0.1	+3.5	Cherel et al. (2005)
	Herring (muscle)	−0.6	+1.2		+0.3	+2.7	
Rockhopper Penguins (*Eudyptes chrysocome*)	Capelin (delipidated whole fish)	+0.0	+2.7		+0.1	+4.4	
	Capelin (muscle)	+0.5	+1.9		+0.6	+3.5	
Common Murre (*U. aalge*)	Capelin (delipidated muscle)	-	-	Breast	+2.5 ± 0.2	+3.6 ± 0.2	Becker et al. (2007)
		-	-	Primary	+1.9 ± 0.3	+3.7 ± 0.2	
Shorebirds							
Dunlin (*Calidris alpina pacifica*)	Terrestrial-based diet (homogenized)	+1.3	+2.9	Body	−1.6 ± 1.3	−2.8 ± 2.1	Evans-Ogden et al. (2004)
Freshwater birds							
Scarlet Ibis (*Eudocimus ruber*)	Krill & pellets (homogenized)	-	-	Primary	+3.8 ± 0.3	+4.5 ± 0.4	Mizutani et al. (1992)
White Ibis (E. albus)		-	-	Primary	+2.5 ± 0.5	+1.7 ± 3.3	
3 Flamingo species (*Phoenicopterus sp*)		-	-	Primary	+3.6 ± 0.6	+5.6 ± 0.4	
Night Heron (*Nycticorax caledonicus*)		-	-	Primary	+3.2 ± 0.4	+4.2 ± 0.3	
Great White Egret (*Egretta alba*)	Saurel (whole fish)	-	-	Nuptial	+3.1 ± 0.4	+3.9 ± 0.2	
Grey Heron (*Ardea cinerea*)		-	-	Primary	+3.4 ± 0.6	+4.3 ± 0.4	
Canvasback (*Aythya valisineria*)	Commercial diet (homogenized)	+1.5	+3.0	-	-	-	Haramis et al. (2001)

Table 3.1 (suite)

Terrestrial birds							
Chicken (*Gallus gallus*)	Grain-based diet (homogenized)	-	-		- 0.4 ± 0.0	+ 1.1 ± 0.1	
Quail (*Coturnix japonica*)		+ 1.2 ± 0.6	+ 2.2 ± 0.2		+ 1.4 ± 0.6	+ 1.6 ± 0.1	
Peregrine Falcon (*Falco peregrinus*)	Quails (pectoral muscle)	+ 0.2 ± 0.0	+ 3.3 ± 0.4	Not specified	+ 2.1 ± 0.1	+ 2.7 ± 0.5	Hobson & Clark (1992)
American Crows (*Corvus brachyrhynchos*)	Plant-based diet (homogenized)	− 1.2 ± 1.5	+ 3.9 ± 2.5		+ 0.3 ± 4.0	+ 3.7 ± 0.5	
	Perch (gutted body)	+ 2.9 ± 3.0	+ 1.8 ± 1.0		+ 1.2 ± 0.8	+ 2.0 ± 1.0	
Yellow-rumped Warbler (*Dendroica coronata*)	20% insect (homogenized)	− 1.2	+ 1.7	Tail	+ 1.9 ± 0.1	'+ 3.2 ± 0.1	Pearson et al. (2003)
	49% insect (homogenized)	+ 1.5	+ 1.8		+ 3.5 ± 0.1	+ 3.3 ± 0.0	
	73% insect (homogenized)	+ 1.8	-		+ 3.8 ± 0.1	+ 3.6 ± 0.0	
	97% insect (homogenized)	+ 2.2	+ 2.7		+ 4.3 ± 0.1	+ 3.5 ± 0.1	
Garden Warbler (*Sylvia borin*)	Semi-synthetic control diet (homogenized)	+ 1.7	+ 2.4	Primary	+ 2.7	+ 4.0	Hobson & Bairlein (2003)

* *Bird tissues collected on wild specimens*

† *Prey tissues collected in the wild*

2. MATERIAL & METHODS

Sampling. To estimate the TEFs for $\delta^{13}C$ and $\delta^{15}N$, I compared the isotopic composition of ABO blood (adults and chicks together) and their food sources at four sites where only one type of prey (either mussels or limpets) was available and where prior feeding observations confirmed that this prey was the main food ingested by those individuals. The selected sites were Goukamma, where birds fed primarily on the rocky shore mussels *Mytilus galloprovincialis* and *Perna perna*, Bonza Bay, where birds fed mainly on limpets, and two additional sites, the sandy beach of Van Stadens and the Swartkops River Mouth where ABOs fed respectively on the sand mussel *Donax serra* and the rocky shore mussels *P. perna* and *M. galloprovincialis* (Fig 1.1, Table 1.1). Finally, to investigate the differences between the stable isotope composition of blood and feathers (denoted as $\Delta\delta^{13}C_{blood\text{-}feathers}$ and $\Delta\delta^{15}N_{blood\text{-}feathers}$), adult ABOs (n = 89) and their chicks (10 days and older, n = 51) from throughout the study area (including the additional sites, Fig. 1.1) and for which both blood and feathers were collected on the same individual, were used. For a detailed description of the sampling and processing of prey tissues, blood and feathers of ABOs for carbon and nitrogen stable isotope analyses, refer to Chapter 1, section IV. All samples used in this chapter were analysed at the Stable Light Isotope Unit of the

University of Cape Town and precision of isotopic measurements was < 0.1 ‰ for $\delta^{13}C$ and < 0.2 ‰ for $\delta^{15}N$, based on internal laboratory standards.

Data Analyses. Paired t-tests or Wilcoxon paired-tests (α = 0.05) were used to test for significant differences between the stable isotope composition of blood and feathers at the individual level and were carried out separately for adults and chicks. A Wilcoxon test was used to compare the blood-feather isotopic shift of adults and chicks.

3. RESULTS

Trophic enrichment factors (TEFs). The estimated mean TEF between main prey and blood of ABOs was +0.2 (± 0.4) for $\delta^{13}C$, with a minimum of – 0.3‰ observed between sand mussels and ABOs (Van Staden's River Mouth) and a maximum of + 0.4‰ observed at Swartkops River Mouth and Bonza Bay with rocky shore mussels and limpets as main prey respectively. TEFs values for $\delta^{15}N$ ranged from + 2.3 between sand mussels and ABOs blood and + 3.1‰ between rocky shore mussels and ABOs at Swartkops River Mouth and the mean (± sd) value for the four sites was + 2.7 (±0.4) ‰ (Table 3.2).

Table 3.2. Mean carbon and nitrogen stable isotope composition (‰) of blood in African Black Oystercatchers and their unique prey type present at 4 study sites and estimated Trophic Enrichment Factor (TEF).

Composition isotopique du carbone et de l'azote (‰) du sang d'huîtriers noirs africains et leur proie unique aux 4 sites d'études et facteur d'enrichissement trophique

	Van Staden's River mouth		Swartkops River Mouth		Goukamma		Bonza Bay		Mean (± sd) TEF estimated	
Prey type	Sand mussels		Rocky shore mussels		Rocky shore mussels		Limpets		$\delta^{13}C$	δ15N
***n* ABOs**	13		14		11		13			
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$		
Prey	-15.3	9.8	-17.3	9.0	-15.7	9.0	-12.5	8.0	**0.2 ± 0.4**	**2.7 ± 0.4**
Blood	-15.6	12.1	-17.0	12.1	-15.5	11.5	-12.1	10.9		
Mean TEF	-0.3	2.3	0.4	3.1	0.3	2.5	0.4	3.0		

Stable isotope differences between blood and feather tissues. Feathers were significantly enriched in ^{13}C and ^{15}N compared to whole blood, although the difference between the two tissues was variable at the individual level for both adults (from – 1.4 to + 1.8 for $\delta^{13}C$ and from + 1.4 to + 3.0 for $\delta^{15}N$) and chicks (from – 0.5 to + 3.7 for $\delta^{13}C$ and from -0.12 to 3.7 for $\delta^{15}N$). The stable isotope compositions of the two tissues were significantly correlated in individuals, for both chicks and adults

(Fig 3.1 and 3.2, Table 3.3). $\Delta\delta^{13}C_{blood\text{-}feathers}$ and $\Delta\delta^{15}N_{blood\text{-}feathers}$ were slightly but significantly different between age groups (Table 3.3).

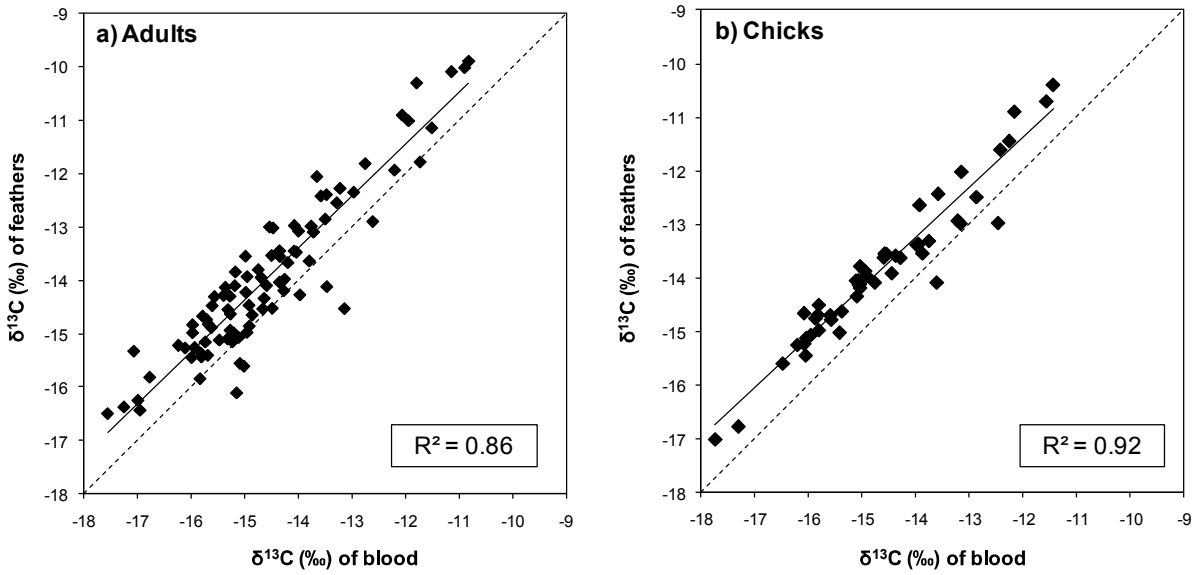


Figure 3.1. $\delta^{13}C$ (‰) of blood and feathers in a) adults and b) chicks of African Black Oystercatchers. R^2 indicate significant associations (Spearman's rho and Pearson's correlation coefficient for adults and juveniles respectively, α = 0.05) between blood and feathers of individuals.

$\delta^{13}C$ (‰) du sang et des plumes a) des adultes et b) des poussins d'huîtriers noirs africains. Les valeurs de R^2 indiquent des associations significatives entre tissus (rho de Spearman et coefficient de corrélation de Pearson utilisés respectivement pour les adultes et les poussins, α = 0.05)

4. DISCUSSION

Trophic enrichment factors (TEFs). The $\delta^{13}C$ and $\delta^{15}N$ trophic enrichment factors found for ABOs blood (mean values + 0.2 ± 0.4 ‰ and + 2.7 ± 0.4 ‰ respectively) were well within the range of values found experimentally for other bird species (Table 3.1 and 3.2). The TEF value found for $\delta^{13}C$ however was appreciably different from the one found for the taxonomically closest species previously investigated the Dunlin (+ 1.3 ‰, Evans-Ogden et al. 2004). This finding reinforces the need to estimate TEFs values that are specific to the animal under study, even if non-experimentally. Indeed, discrepancies between TEFs values of closely related species have been found between studies, for example the $\delta^{13}C$ TEFs values for feathers of penguin species (Mizutani et al 1992, Cherel et al. 2005b, see Table 3.1).

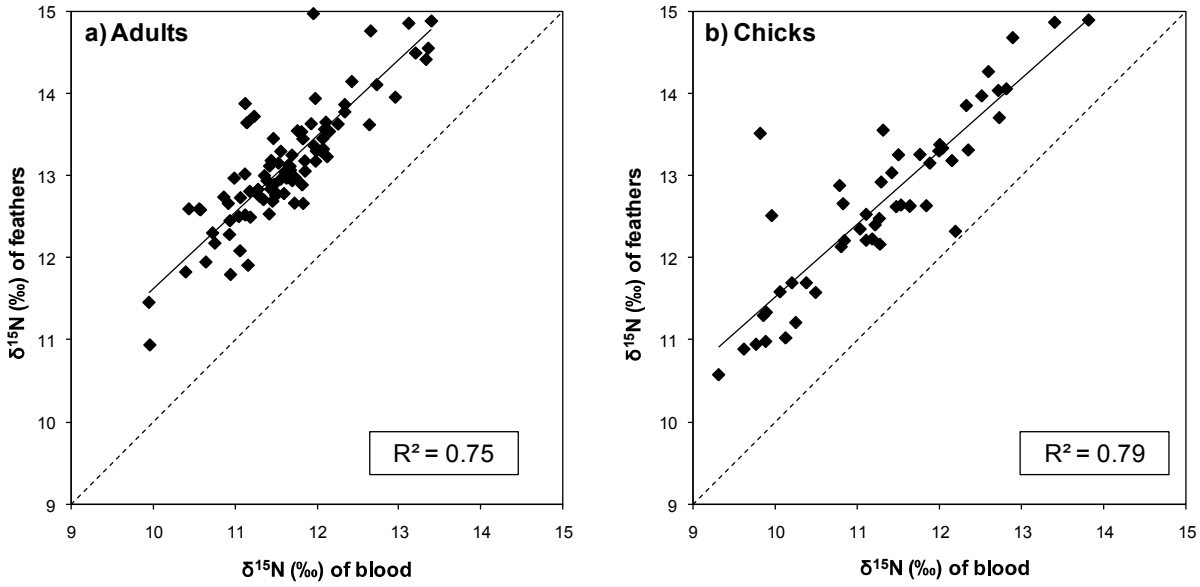


Figure 3.2. $\delta^{15}N$ (‰) of blood and feathers in a) adults and b) chicks of African Black Oystercatchers. R^2 indicate significant associations (Pearson's correlation coefficient, $\alpha = 0.05$) between blood and feathers of individuals.

$\delta^{15}N$ (‰) du sang et des plumes a) d'adultes et b) de poussins d'huîtriers noirs africains. Les valeurs de R^2 indiquent des associations significatives entre kes deux tissus (coefficient de corrélation de Pearson, $\alpha = 0.05$).

The main potential prey of ABOs, mussels and limpets, are mostly segregated by their $\delta^{13}C$ values, with the filter-feeding mussels being significantly depleted in ^{13}C compared to grazing limpets (see Chapter 2). In such trophic systems, the use of the $\delta^{13}C$ TEF value found for dunlins (+ 1.3 ‰, Evans-Ogden et al. 2004) in stable isotope mixing models would increase the estimated relative contributions of mussels to the diet of ABOs compared to those of limpets, leading to inaccurate conclusions about the feeding preferences of ABOs, regardless of the location (Chapter 4) or the individual status (Chapter 5).

Table 3.3. Pair-wise differences of the $\delta^{13}C$ and $\delta^{15}N$ between blood and feathers in adults and chicks of African Black Oystercatchers.

Différences par paires des ratios $\delta^{13}C$ et $\delta^{15}N$ entre le sang et les plumes chez les adultes et poussins d'huîtriers noirs africains.

		Pair-wise test Blood vs Feathers	Mean (± sd) blood-feathers isotopic shift (‰)	Statistical differences Adults vs Chicks
$\delta^{13}C$	Adults	W = 272, p < 0.001	**+ 0.6 ± 0.6**	W = 1856.5, p = 0.034
	Chicks	t = - 11.3, p < 0.001	**+ 0.9 ± 0.6**	
$\delta^{15}N$	Adults	t = -35.9, p < 0.001	**+ 1.5 ± 0.4**	W = 3071.5, p = 0.002
	Chicks	t = -17.7, p < 0.001	**+ 1.3 ± 0.5**	

The TEF values of 0.2 (± 0.4) ‰ and 2.7 (0.4) ‰ respectively estimated for $\delta^{13}C$ and $\delta^{15}N$ from wild ABOs and their main prey type at 4 different sites should however be

treated with caution when applied to other shorebird species. I recommend further experimental studies on different shorebirds species, using muscle tissues of prey (or delipidated whole prey) and blood and feather tissues for birds, as has been done to a greater extent for seabirds (Cherel et al. 2005b, Becker et al. 2007).

Blood-feather isotopic shifts. In adults and chicks, feathers were enriched in both ^{13}C and ^{15}N compared to blood. To my knowledge, Quillfeldt et al. (2008) are the only authors that have directly compared carbon and nitrogen stable isotope compositions of blood and feathers in wild birds. In their study, blood and feathers were collected on five different Procellariiformes species inhabiting offshore islands near the Brazilian Atlantic coast, during their moult. Therefore, as for ABO chicks, the stable isotope composition of both tissues collected simultaneously on these birds recorded dietary information integrated over the same period of time. The results of that study showed consistent enrichment in ^{13}C (between 0.9 and 1.6 ‰) and ^{15}N (between 0.4 and 1.5 ‰) in feathers compared to blood in the 5 studied species. Similarly, Cherel et al. (2005b) investigated the diet-tissues isotopic discrimination in captive King and Rockhopper Penguins (*Aptenodytes patagonicus and Eudyptes Chrysocome*) and found blood-feather discrimination of + 0.9 ‰ and for + 0.1 ‰ for $\delta^{13}C$ and + 1.5 and +1.7 ‰ for $\delta^{15}N$, for the two species respectively. Overall, between these two previous studies and my results, the values of $\Delta\delta^{13}C_{blood\text{-}feathers}$ and $\Delta\delta^{15}N_{blood\text{-}feathers}$ seem to remain very consistent across marine bird species.

In controlled studies, the difference in the $\delta^{15}N$ ratios between blood and feathers has been mostly attributed to the difference in their biochemical composition (Hobson et al. 1992), feathers being mainly made of keratin, while whole blood is constituted of several proteins like hormones, globulins and albumins (Wolf et al. 1985). Bearhop et al. (2000) also suggested that the presence of variable concentrations of ^{15}N-depleted uric acid, one of the excretion products of protein catabolism present in blood plasma, could be a meaningful source of variation in blood $\delta^{15}N$ ratios. Juvenile birds tend to have higher plasma concentrations of uric acids than adults because of faster metabolic activity during growth (Swick 1982, Wolf et al. 1985). In our study the $\Delta\delta^{15}N_{blood\text{-}feathers}$ for chicks was slightly but significantly higher than for adults (Table 3.3). Higher concentrations of ^{15}N-depleted uric acid in chick's blood could result in slightly lower $\delta^{15}N$ ratios and increase their $\Delta\delta^{15}N_{blood\text{-}feathers}$. However it is important to notice also that this difference between age groups for their $\Delta\delta^{15}N_{blood\text{-}feathers}$ value

was only 0.3‰, close to the precision of isotopic measurement (< 0.2 ‰) for this batch of samples, and could therefore be an artefact.

The main biochemical source of variation in the $\delta^{13}C$ values among tissues is lipid content, naturally depleted in ^{13}C compared to proteins. As previous authors have demonstrated for birds (Bearhop et al. 2000, Cherel et al. 2005b) however, the low lipid content of blood (less than 1% of total wet mass, Rosa et al. 1993) affects $\delta^{13}C$ ratios only marginally. Conversely, it is believed that juvenile birds have larger energy storage in the form of lipids than adults (Blem 1990, Cherel et al. 2005c). $\Delta\delta^{13}C_{blood\text{-}feathers}$ value for chicks was 0.2 ‰ lower than for adults and could result from a slight ^{13}C-depletion of chicks blood because of higher lipid content. On the other hand, this could again bear little significance, as precision for $\delta^{13}C$ measurements was < 0.1 ‰ for the samples used in this study.

Finally, individual $\delta^{13}C$ and $\delta^{15}N$ values of blood and feathers were highly correlated for both age groups, though there was a wide range of individual $\Delta\delta^{13}C_{blood\text{-}feathers}$ and $\Delta\delta^{15}N_{blood\text{-}feathers}$ values. In an experimental study of fasting King Penguins, Cherel et al (2005a) suggested that the use of endogenous (stored) or exogenous (dietary) reserves for the precursors of protein synthesis could differ between tissues and lead to differences in the isotopic ratios of tissues. This is unlikely to be the case for sedentary shorebirds like ABOs that store very little reserves (Meijer & Drent 1999). The isotopic composition of their tissues can thus be directly linked to their dietary habits, during the synthesis of these tissues. For ABOs, large deviations of individual $\Delta\delta^{13}C_{blood\text{-}feathers}$ and $\Delta\delta^{15}N_{blood\text{-}feathers}$ based on the mean (± sd) values presented in Table 3.3, are most likely related to changes in diet composition or foraging locations between summer and winter for adults, and dietary shifts during their first few weeks for chicks. Combined used of blood and feathers for both chick and adult ABOs, can therefore give information on temporal changes of their feeding ecology.

Knowledge of TEFs values and tissue-specific isotopic shifts can be especially useful in the investigations of migratory connectivity, feeding habits at stop-over sites, moulting strategies and use of endogenous vs. exogenous resources in migrating shorebirds (Hobson 1999a,b, Klaassen et al. 2001, Atkinson et al. 2005, Hobson 2006), for which stable isotope analysis has become a powerful tool. Despite apparent stability in $\Delta\delta^{13}C_{blood\text{-}feathers}$ and $\Delta\delta^{15}N_{blood\text{-}feathers}$ across marine bird species, determination of precise and reliable values remain an essential methodological step in the use of stable isotope analysis for these biological models.

CHAPITRE 4

Sex-specific trophic segregation in the African Black Oystercatcher, in relation with sexual dimorphism

(based on an article submitted to Journal of Avian Biology, Annexe 6)

(Photo: J. Kemper)

RESUME

Le dimorphisme sexuel se rencontre chez toutes les espèces d'huîtriers et se caractérise essentiellement par le fait que les femelles sont légèrement plus grosses et ont un bec plus long et plus pointu que les mâles. Ce dimorphisme sexuel de la forme du bec a été mis en relation avec des différences d'habitudes alimentaires entre les sexes chez plusieurs espèces du genre *Haematopus,* dont l'huîtrier noir africain. Pour cette dernière espèce en revanche, les études étaient limitées à un petit nombre de couples reproducteurs et/ou ont été effectuées avant l'invasion des littoraux rocheux sud-africains par la moule de Méditerranée. Dans le chapitre présent, j'ai examiné les ségrégations alimentaires entre les mâles et femelles chez l'huitrier noir africain à l'aide des isotopes stables du carbone et de l'azote, en mettant cela en relation avec les changements de son habitat d'alimentation sur les côtes rocheuses sud-africaines et le degré de dimorphisme sexuel, en particulier celui du bec. Du sang et des plumes ont été collectés pour analyses isotopiques chez les mâles et femelles pendant l'incubation sur 9 sites répartis sur les côtes ouest, sud-ouest et sud-est de l'Afrique dus Sud. Les proies potentielles (moules, patelles, polychaetes, ascidies) ont été collectés en parallèle sur chaque site où elles étaient présentes, pour mesurer leurs ratios isotopiques du carbone et de l'azote.

Le dimorphisme sexuel du bec était visible sur l'ensemble de la zone d'étude et similaire au patron précédemment décrit, à savoir un bec plus long et pointu chez les femelles. Les mâles et les femelles montraient peu de différences au niveau de leurs valeurs en $\delta^{13}C$ et des contributions relatives des différentes types proies à leur régime alimentaire, sauf sur la côte sud-est où la proie la plus abondante sur le reste de la côte (la moule de Méditerranée) est rare et où les mâles étaient légèrement enrichis en ^{13}C par rapport aux femelles. Les femelles présentaient un enrichissement léger mais significatif en ^{15}N par rapport à leurs partenaires sexuels, mais cette différence ne pouvait être clairement liée à des différences de régime alimentaire. Cette divergence en $\delta^{15}N$ entre les mâles et femelles huîtriers reproducteurs pourrait être liée à des différences d'exigences physiologiques pendant les périodes de pré-ponte et d'incubation. De manière générale, les faibles différences de régime alimentaire entre mâles et femelles pourraient résulter d'un manque de limitation de nourriture induit par l'invasion de la moule de Méditerranée sur les côtes ouest et sud-ouest. Dès lors le lien entre la forme des extrémités du bec et le régime alimentaire et/ou les techniques d'alimentation montré de manière répétée chez l'huîtrier européen semble moins clair chez l'huîtrier noir africain. La

persistance du dimorphisme sexuel du bec chez l'espèce africaine pourrait être fixé génétiquement, déterminé par la sélection sexuelle ou induit par des comportements encore non-identifié affectant l'abrasion du bec de manière différentes entre les sexes.

1. INTRODUCTION

Food partitioning as a way of reducing competition in a limited resource environment, and optimizing energy intake and fitness is widespread in animals (Stephens & Charnov 1982), particularly in both terrestrial and aquatic birds (Donald et al. 2007, Masello et al. 2010). Mechanisms of food segregation among birds involve the targeting of food items of different sizes or species, the use of different foraging methods and behaviour or the use of different foraging areas or strata (Selander 1966). These mechanisms are often related to phenotypic differences in morphology, skills and social status especially in shorebirds (Durell 2000). During the breeding season, energy demand is high for parents and physiological and behavioural constraints often differ between males and females (Drent & Daan 1980, Meijer & Drent 1999). As a consequence, sex-related differences in diet and foraging strategies frequently occur (Andersson & Nordberg 1981, Forero et al. 2005). In this situation sexual dimorphism can be a way of reducing intersexual food competition. In seabirds, sexual dimorphism is mostly related to differential body size (Székely et al. 2000, Gonzales-Solis et al. 2000) and in colony-based species, males and females are known to differ in their foraging ranges (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, males and females can also differ in their body sizes, but most sex-specific diet and feeding techniques have been related to differences in the bill morphology (reviewed in Durell 2000).

The Eurasian Oystercatcher (*Haematopus ostraleg*us) is one of the best studied shorebirds and particular attention has been paid to its feeding specialization, in terms of both diet and handling techniques, and how these relate to bill morphology (Hulscher 1996, Sutherland et al. 1996): individuals with pointed bills typically specialize on polychaetes, while birds with chisel-shaped and blunt bills specialize on stabbing and hammering shellfish respectively. Beside *H. ostralegus,* there are 10 oystercatcher species throughout the world and one presumed to be extinct. Despite their scattered distribution (Eurasia, Australasia, North and South America, Southern Africa), oystercatcher species share many ecological and morphological similarities (Hockey 1996). They are highly territorial during the breeding season, monogamous, form long-term pair bonds and provide full biparental care (Hockey 1996). 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 with bill morphology has been reported on the basis of direct observations for Eurasian oystercatchers (Durell et al. 1993, Van de Pol et al. 2010) and for the two species occurring in Australia (Lauro & Nol 1995). In the case of the African Black Oystercatcher (ABO), which is a non-migrating species that breeds exclusively along the coastlines of Namibia and South Africa, Hockey & Underhill (1984) also reported sex-specific dietary differences, but in two breeding pairs only.

On southern African rocky shores, ABOs can encounter a wide range of potential prey and this includes mussels, limpets, polychaetes, chitons, isopods, amphipods, barnacles and ascidians (Hockey & Underhill 1984). The structure of these rocky shore communities is however mediated by wave action at local scale (McQuaid & Branch 1985) and strongly influenced at larger scale 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 that flows along the east and south coasts (Shannon 1985, Lutjeharms 2004). Overall this gives rise to broad differences in nutrient concentration and intertidal biomass, which are greater on the West coast, while species richness is greater on the east coast (Bustamante & Branch 1996b). 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). On the West coast, the invasive mussel has replaced the indigenous species as the dominant mussel in the low- and mid-shore where it also outcompetes adult limpets for primary rocky space (Hockey & Van Erkom Schurink 1992, 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 (Bownes & McQuaid 2006). 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 ABO population dynamics on the west coast by increasing the overall food biomass available to this bird (Hockey & Van Erkom Schurink 1992). The natural variability of coastal habitats in southern Africa and their recent perturbation by the invasive mussel constitute a unique opportunity to investigate sex-specific foraging strategies in the ABO. More precisely, variations in abundance and diversity of food sources across the breeding range of ABOs could

result in geographic variation in the prevalence of food limitation, so that optimal foraging theory would predict consequences for the degree of dietary segregation between males and females.

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 have the disadvantage of being very time-consuming and can only give a snapshot of the diet for a limited number of individuals of the population. On the other hand in the study of oceanic birds, 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 at al. 2009). The use of carbon and nitrogen stable isotopes relies on the fact that their ratios (denoted as $\delta^{13}C$ and $\delta^{15}N$) in consumer tissues reflect those of their prey in a relatively predictable manner (DeNiro & Epstein 1978, 1981). $\delta^{13}C$ varies little along the food chain and is therefore a good indicator of baseline sources. This is especially interesting in coastal habitats where there are clear $\delta^{13}C$ gradients between benthic and pelagic organisms (France 1995) and grazing and filter-feeding invertebrates (Chapitre 2, Vander Zanden & Rasmussen 1999). On the other hand 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 chain (Cherel et al. 2008).

Our primarily aim in this study was to investigate the segregation of resources between sexes and within pairs of the ABO, and its possible variation in relation to changes in their foraging habitats. For this purpose we combined the analysis of biometric measurements to assess the degree of sexual dimorphism in this species and the analysis of food segregation between male and female oystercatchers breeding on the South African coastline using carbon and nitrogen stable isotope ratios in their tissues and their potential prey.

2. MATERIALS & METHODS

Study areas. Fieldwork was carried out during 3 consecutive breeding seasons (December 2007 to February 2010) in the rocky shore habitats of ABOs in South Africa. Birds and their potential prey were sampled in 3 distinct regions in South Africa: the south-east coast (from East London to Port Elizabeth), the south-west coast (from Plettenberg Bay to Arniston) and the west coast (Koeberg and Langebaan) (Fig. 4.1).

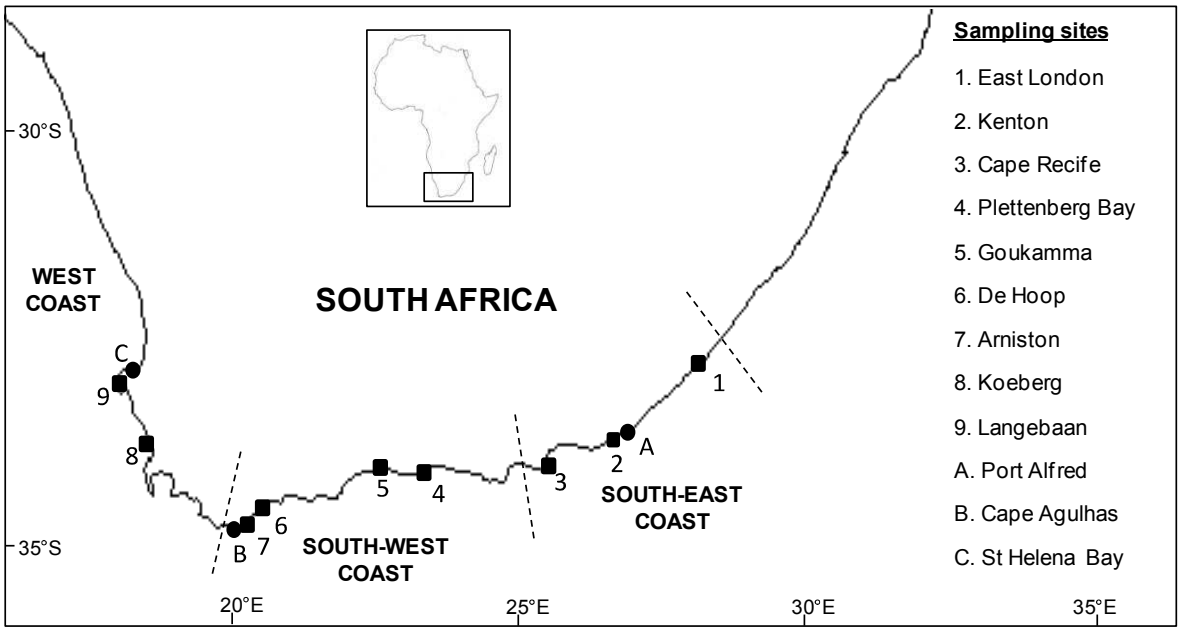


Figure. 4.1 Location of the sampling sites for African Black Oystercatchers and their prey (1 to 9) on the South African coastline. A, B and C indicate the sampling sites for the polychaete *Gunnarea capensis* (Hill and McQuaid 2008)

*Sites d'échantillonnage des huîtriers noirs africains (*Haematopus moquini*) et leur proies (sites 1 à 9) sur les côtes sud-africaines. A, B et C indiquent les sites où le polychète Gunnarea capensis a été échantilloné en 2006 (Hill & McQuaid 2008)*

Sampling of oystercatchers and potential prey. Breeding males and females were captured during incubation and efforts were made to capture as many complete breeding pairs as possible. For a detailed description of the sampling of blood and feathers on adults, refer to Chapter 1, section IV. The tarsus and bill (from the feather line) lengths were measured to the nearest 0.1 mm using callipers and the wing length was measured to the nearest 1 mm with a ruler. Birds were weighted 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 photos. Each photo 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 photo (Fig. 4.2). Although most oystercatchers can be sexed in the field according to morphological features, such as bill morphology and eyeflecks (Hockey 1981; Kohler et al. 2009a), we used molecular sexing based on the CHD1W and CHD1Z introns located on the sex chromosomes (Chapitre 1, section IV, Fridolfsson & Ellegren 1999) to confirm the sex of birds.

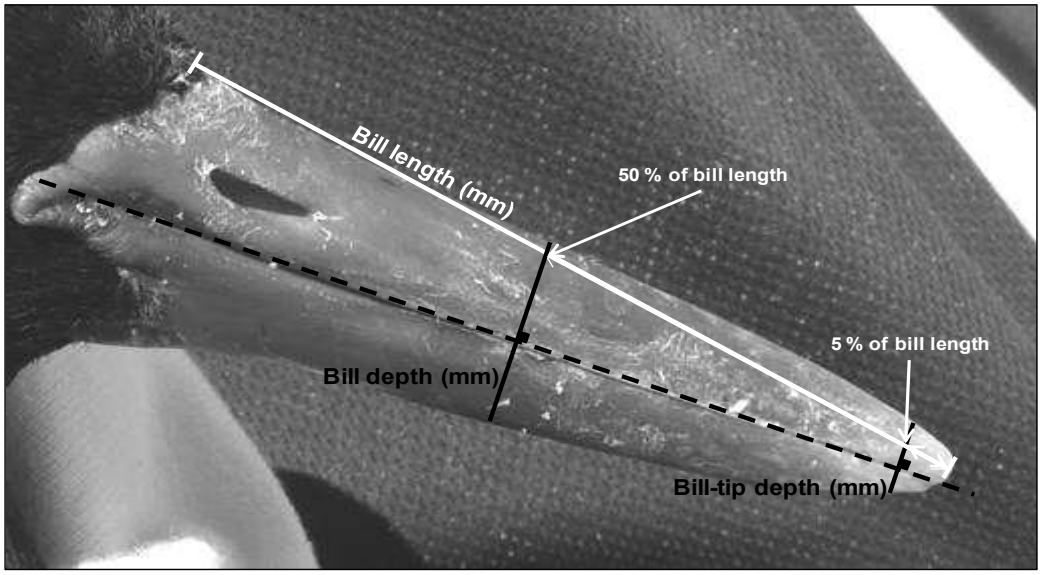


Figure. 4.2 Lateral photo of an African Black Oystercatcher's bill. Bill length was measured in the field and used to scale the picture with CPCe (Kohler and McGill 2006). A mark was made at 5% and 50% of the bill length, from the bill-tip, to estimate the bill depth halfway down and the bill-tip depth respectively, perpendicular to the slit between the maxilla and mandibule (dashed line). (Photo: S. Kohler)

Photo latérale d'un bec d'huîtrier noir africain. La longueur du bec était mesurée sur le terrain et utilisée pour calibrer la photographie avec le logiciel CPCe (Kohler & McGill 2006). Sur la photo, une marque était faite à 5% et 50% de la longueur du bec, depuis son extrémité, pour estimer les hauteurs respectivement à la moitié et à l'extrémité du bec, perpendiculaire à la fente dessinée par les mandibules supérieures et inférieures (ligne pointillé).

Collection of the potential prey to sample was based on the literature (Randall & Randall 1982, Hockey & Underhill 1984) but also on prior visual observations of the feeding behaviour of ABOs at the different study sites. Five specimens per species of mussels (*Perna perna* and *Mytilus galloprovincialis*) and limpets (*Cymbula oculus, Scutellastra argenvillei, S. cochlear, S. granularis* and *S. longicosta,* Fig. 1.6) were collected when present on feeding grounds. Mussels and limpets compose the bulk of oystercatcher's diets (Hockey & Underhill 1984, Hockey & Van Erkom Schurink 1992, Kohler et al. 2009b); polychaetes however are also considered in the literature to be an occasional prey (Hockey & Underhill 1984). In Port Elizabeth, oystercatchers were regularly observed scavenging on beached ascidians, *Pyura stolonifera*; hence, 3 specimens were collected at this site and body was sorted from the thick tunic. In

addition, stable isotope ratios of the suspension-feeding polychaete worm *Gunnarea capensis* were taken from Hill & McQuaid (2008), who collected specimens from three sites between the west and south-east coasts of South Africa (see Fig. 4.1).

Body Condition Index (BCI). Body condition indexes were calculated for each bird,

$$BCI = 1 - \frac{mass_{expected} - mass_{observed}}{mass_{expected}}$$

where the expected mass was calculated for each bird from the linear relationship between wing length (mm) and mass (g), established separately for each sex because of the sexual size dimorphism (see results) and from all birds sampled over the course of the thesis (n_{males} = 47 and $n_{females}$ = 42):

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

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

A BCI of 1 is the expected mass predicted with the length wing. If BCI is <1, it suggests that the individual has a worst body condition that it should have for its size, and a BCI >1 indicates a better body condition that the excepted values for its size.

Stable isotope analysis. Whole blood of birds has a rapid turnover (Hobson & Clark 1992, 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 remain isotopically inert once fully grown (Mizutani et al. 1990). Feathers can be therefore used as proxy for the diet during the non-breeding season (Jaeger et al. 2009). In marine invertebrates, muscle tissues have a slow turnover rate and are unlikely to be affected by short-term changes in environmental conditions (Gorokhova & Hansson 1999). For a description of the processing and stable isotope analyses of birds and prey tissues see Chapter I, section IV. Ascidian samples were analyzed at IsoEnvironmental cc at Rhodes University, Grahamstown (South Africa) while all other samples were analyzed at the Stable Light Isotope Unit of the University of Cape Town (South Africa). Precision of replicate determinations for the samples analysed in this chapter was < 0.17 ‰ for carbon and < 0.20 ‰ for nitrogen for both laboratories.

Data analysis. All statistical analyses were performed using R statistical Software (available at www.r-project.org). When datasets did not meet the required

assumptions of normality (Shapiro-Wilk's test, $p > 0.05$) and homoscedasticity (Levene's test), we performed non-parametrical tests. A two-way ANOVA (F, $\alpha = 0.05$, $n = 63$) was performed on BCI data with sex and regions as fixed factors. Two-way ANOVAs were also used with $\delta^{13}C$ (‰) or $\delta^{15}N$ (‰) ratios as response variables and sex and breeding site as fixed factors to test for significant differences in the blood stable isotope compositions of males and females. In cases of significant differences, we used Tukey's Honest Significant Difference test (Tukey HSD) for post-hoc multiple comparison. The Wilcoxon test was used to investigate $\delta^{13}C$ and $\delta^{15}N$ differences between the blood and feather tissues of paired individuals. We used two-way ANOVAs to investigate variations in morphometric parameters of oystercatchers, related to gender and location, except for bill length, for which the non-parametric Scheirer-Ray-Hare procedure, a two-way extension of the Kruskall-Wallis test, was used. To estimate the relative contribution of the different types of prey (mussels, limpets, polychaetes and ascidians) to the diet of males and females, the IsoSource stable isotope mixing model software was used (Phillips & Gregg 2003, available at http://www.epa.gov/wed/pages/models.htm.). We used mean blood signatures of males and females, mean signatures of potential prey species at each site and trophic enrichment factors (TEFs) of + 0.2‰ for $\delta^{13}C$ and + 2.7‰ for $\delta^{15}N$ (Chapter 3) to run the model for each sex at each study site. The outputs were aggregated *a posteriori* to pool mussel species together and limpet species together (Phillips et al. 2005).

3. RESULTS

A total of 63 breeding ABOs, including 30 females, 33 males and 20 breeding pairs, were sampled from 9 different breeding sites grouped into 3 coastal regions along the South African coastline (Fig. 4.1).

Table 4.1. Biometric measurements of male and female African Black Oystercatchers. A two-way ANOVA (*F*, α=0.05) was used on all biometric measurements, except bill length, with sex and sites as co-factors. For bill length, the non-parametric Sheirer-Ray-Hare procedure (*H*, α=0.05) was used.

Mesures biométriques prises sur les mâles et femelles d'huîtrier noir africain. Une ANOVA avec le sexe et le site comme facteurs (F, α = 0.05) a été utilisée sur tous les paramètres biométriques, sauf pour la longueur du bec, avec. Pour cette dernière, la procédure non-paramétrique de Sheirer-Ray-Hare (H, α = 0.05) a été utilisée.

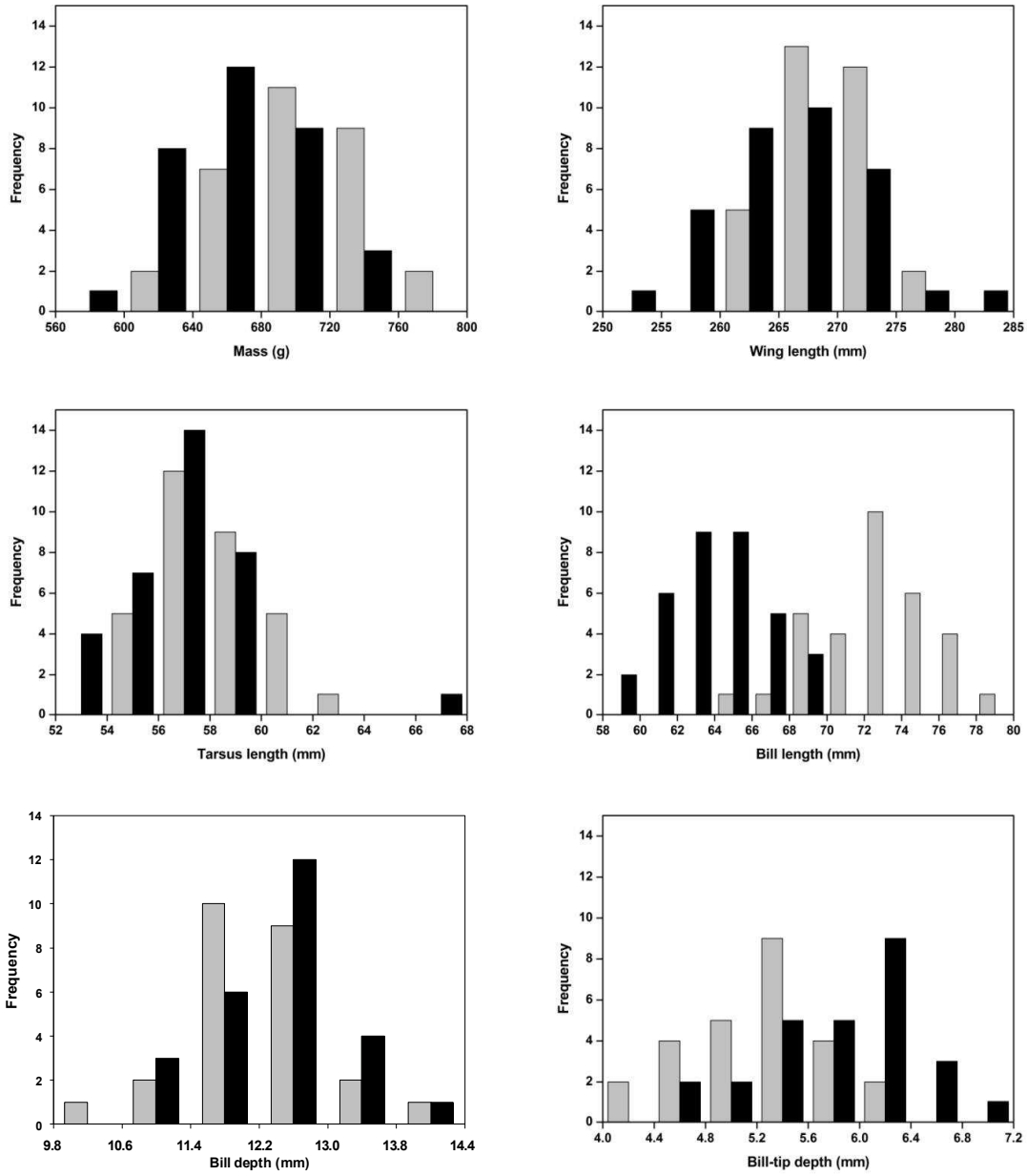
	Females		Males		Statistical outputs								
	Mean ± SD (range)	*n*	Mean ± SD (range)	*n*	Sex			Sites			Sex X Sites		
					Df	*F/H*	*p-value*	*Df*	*F/H*	*p-value*	*Df*	*F/H*	*p-value*
Mass (g)	701 ± 39 (630 – 775)	29	660 ± 36 (580 – 730)	32	1	16.7	***	8	1.07	n.s.	8	0.50	n.s.
Wing (mm)	269 ± 4 (260 – 277)	30	265 ± 6 (253 - 282)	33	1	9.81	**	8	1.16	n.s.	8	0.72	n.s.
Tarsus (mm)	58.2 ± 2.1 (54.5 - 62.2)	30	56.7 ± 2.5 (52.7 - 66.3)	33	1	6.67	*	8	1.06	n.s.	8	0.53	n.s.
Bill length (mm)	72.6 ± 3.2 (64 - 78)	30	64.1 ± 2.6 (58.7 - 69.8)	33	1	51.70	***	8	5.27	n.s.	8	− 6.49	n.s.
Bill depth (mm)	12.3 ± 0.7 (11.1 – 14.1)	25	12.3 ± 0.9 (10.0 – 14.4)	26	1	0.76	n.s.	8	1.96	n.s.	8	0.83	n.s.
Bill-tip depth (mm)	5.6 ± 0.5 (4.6 - 6.8)	25	6.0 ± 0.7 (4.5 - 7.2)	26	1	7.88	**	8	1.48	n.s.	8	0.59	n.s.
Bill-tip depth / Bill length	0.08 ± 0.01 (0.06 - 0.09)	25	0.09 ± 0.01 (0.07 - 0.11)	26	1	51.12	***	8	1.18	n.s.	8	0.51	n.s.

** p < 0.05 ; ** p< 0.01 ; *** p < 0.001 ; n.s. non-significant differences*

Biometrics & Body Condition Index. Males and females displayed significantly high levels of dimorphism for all biometric parameters except for the bill depth (Fig 4.3, Table 4.1). Females were about 40 g heavier than males and had longer tarsi, wings and bills than males (Table 4.1). On the other hand males had significantly deeper bill-tips and higher bill-tip depth / bill length ratios than females (Table 4.1, Fig. 4.3 & 4.5). There was no evidence of geographic changes in the morphology of either sex (Table 4.1, Fig. 4.5). BCIs varied between 0.87 and 1.11 (1.0 being the expected value) between genders and coastal regions, but also within the considered groups, as shown for the high standard deviations for the mean values in Fig. 4.4. BCIs of males and females were not significantly different, nor they differ between regions (F_{sex} = 0.04, p = 0.85; F_{region} = 3.04, p = 0.06, $F_{sex:region}$ = 1.41, p = 0.25, Fig.

4.4). Nonetheless, males had higher BCIs in the west and south-east regions, while the opposite situation was observed on the south-west. Moreover in the latter, birds had overall lower BCIs than in the other regions. (Fig. 4.4).

Figure. 4.3 Distributions of a) mass, b) wing length, c) tarsus length, d) bill length e) bill depth (half-way down) and f) bill-tip depth in male and female African Black Oystercatchers.



Distributions des a) masses et des tailles b) d'ailes, c) de tarses et d) de longueurs de becs et des hauteurs de becs à e) 50% de la longueur et f) à l'extrémité, chez les males et femelles d'huîtrier noir africain.

Stable isotope composition of prey. Mean (±SD) carbon and nitrogen stable isotope values of potential prey in each coastal regions are presented in Fig. 4.6 a, b and c. On the three coastlines, limpet species (from – 16.8 to – 5.3‰) were enriched

in ^{13}C compared to mussels (from – 16.7 to – 14.3‰) and polychaete worms (from – 15.4 to – 14.2‰). Conversely the polychaete *Gunnarea capensis* was enriched in ^{15}N (from 9.9 to 11.2‰) compared to mussels (6.4 to 10.9‰) and limpets (from 5.8 to 11.5‰). On the south-east coast, ascidians were ^{13}C-depleted (mean = - 17.1 ± 0.9‰) and ^{15}N-enriched (mean = 10.5 ± 0.7‰) compared to other benthic invertebrates.

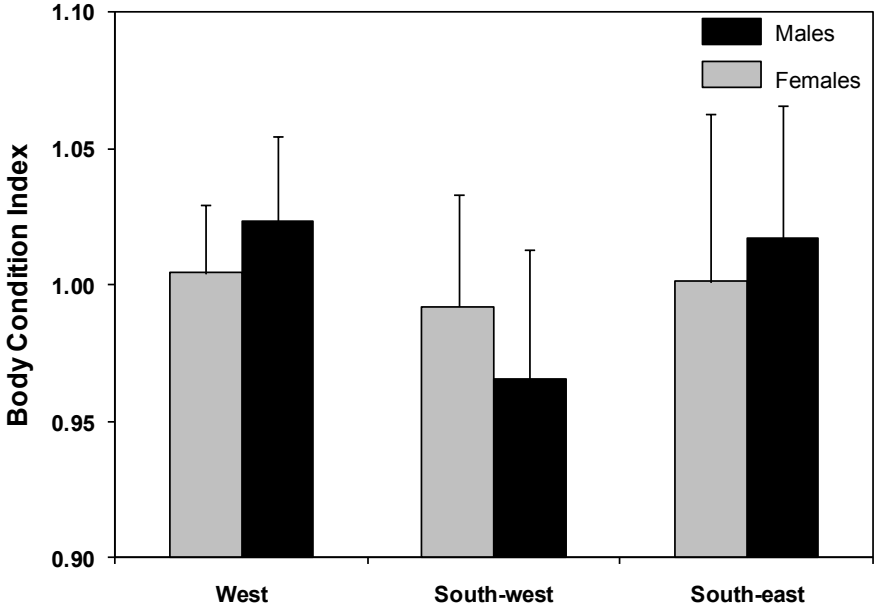


Figure 4.4. Body Condition Index (BCI) of male and female African Black Oystercatchers on the west, south-west and south-east coasts.

Indices de condition corporelle des mâles et femelles d'huîtrier noir africain sur les côtes ouest, sud-ouest et sud-est.

Stable isotope composition of birds. Mean (±SD) blood $\delta^{13}C$ and $\delta^{15}N$ ratios of males and females from the nine study sites are also presented by regions in Fig 4.6. On the south-east coast (Fig 4.7a), birds from East London, Kenton and Port Elizabeth displayed different $\delta^{13}C$ ratios (from – 17.1 to – 10.8 ‰) with East London birds being significantly enriched in ^{13}C compared to those from Kenton and Port Elizabeth (Tukey HSD, $p < 0.001$) (Table 2). On this coastline, $\delta^{15}N$ ratios of birds ranged from 10.4 to 13.4 ‰ and individuals from Port Elizabeth had significantly higher $\delta^{15}N$ values than individuals from both Kenton and East London (Tukey HSD, $p < 0.001$). Females were depleted in ^{13}C at the 3 breeding sites and enriched in ^{15}N compared to males in Port Elizabeth and East London (Fig. 4.6a), though not significantly so (Table 4.2).

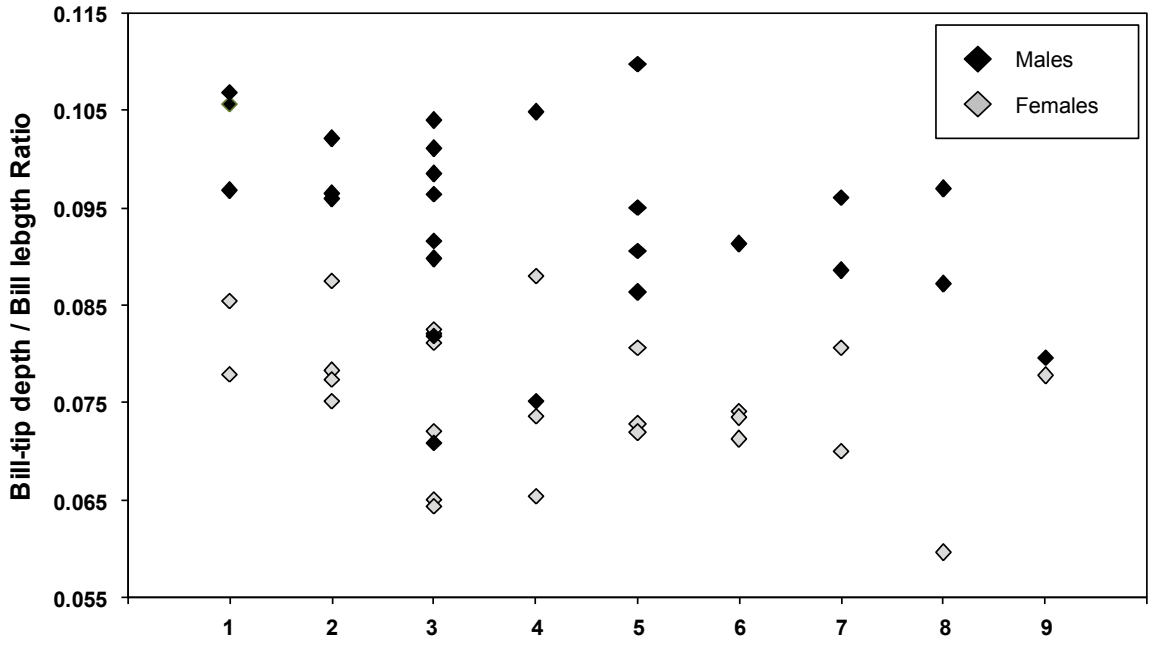
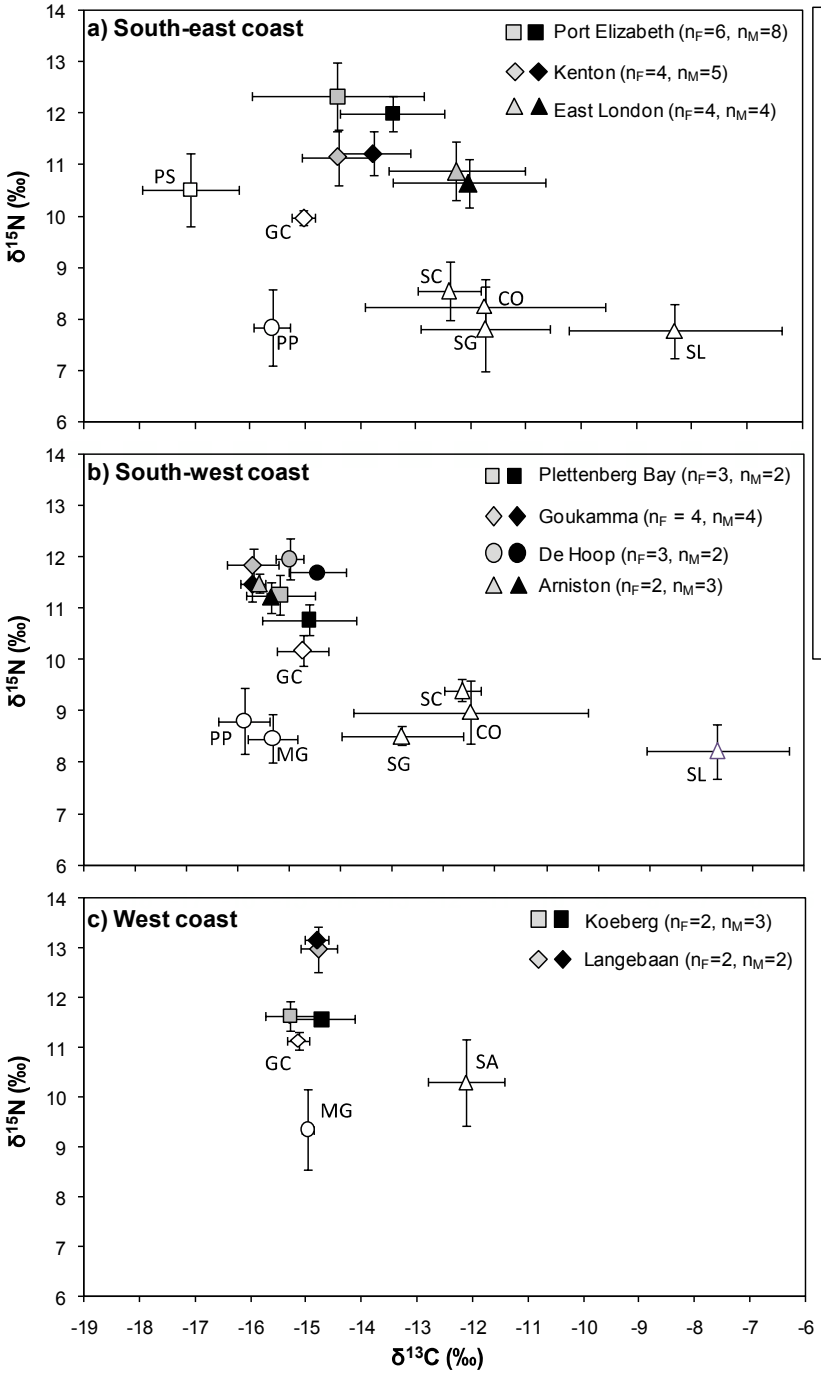


Fig. 4.5 Bill-tip depth/ bill length ratios of male (black diamonds) and female (grey diamonds) African Black Oystercatchers at the 9 study sites (from east to west, as coded in Fig. 4.1)

Ratios de la hauteur du bec à son extrémité sur la longueur chez les mâles et femelles d'huîtrier noir africain aux 9 sites d'étude (d'ouest en est et codé selonla Fig. 4.1)

On the south-west coast, $\delta^{13}C$ values of oystercatchers ranged from -16.1 to -14.0‰ and individuals from Goukamma were significantly depleted in ^{13}C compared to De Hoop (Tukey HSD, $p = 0.01$) and Plettenberg Bay (Tukey HSD, $p = 0.04$). The $\delta^{15}N$ values ranged from 10.6 to 12.3‰ with values of $\delta^{15}N$ for birds from Plettenberg Bay being significantly depleted compared to De Hoop (Tukey HSD, $p < 0.01$) and Goukamma ($p = 0.02$). At the same sites no sex-related differences in $\delta^{13}C$ values were recorded (Fig. 4.6b, Table 4.2). Conversely, females displayed slightly but significantly higher $\delta^{15}N$ ratios than males (Fig. 4.6b, Table 4.2). Post-doc Tukey HSDs, however, revealed that this was due to significant differences between males from Plettenberg Bay and females from De Hoop ($p = 0.02$) and Goukamma ($p = 0.03$), rather than a clear sex-related trend in $\delta^{15}N$ values from a same site.



Prey Legend

Mussels
PP = *Perna perna*
MG = *Mytilus galloprovincialis*

Polychaetes
GC = *Gunnarea capensis*
PS = *Pseudonereis variegata*

Limpets
CO = Cymbula oculus
SA = *Scutellastra argenvillei*
SC = *Scutellastra cochlear*
SG = *Scutellastra granularis*
SL = *Scutellastra longicosta*

Ascidians
PS = *Pyura stolonifera*

Figure. 4.6. Carbon and Nitrogen stable isotope values (mean ± SD) for male (black symbols) and female (grey symbols) oystercatchers, mussels (open circles), limpets (open triangles), polychaetes (open diamonds) and ascidians (open square)

Valeurs moyennes (± écart-types) d'isotopes stables du carbone et de l'azote des mâles (diamants noirs) et des femelles (diamants gris) d'huîtrier noir africain, des moules (cercles vides), des patelles (vides), des polychètes (diamants vides) et des ascidies (carré vide) triangles

On the west coast, individuals from Koeberg and Langebaan had similar $\delta^{13}C$ values (from –15.6 to – 14.2 ‰, Fig. 4.6c, Table 4.2) and differed significantly in their $\delta^{15}N$ values (from 11.4 to 13.3‰, Table 4.2), with birds from Langebaan being relatively enriched in ^{15}N. At Langebaan males and females had similar values of both $\delta^{13}C$ and $\delta^{15}N$ (Fig. 4.6c, Table 4.2) and at Koeberg females were slightly (but not significantly) depleted in ^{13}C compared to males (Table 4.2).

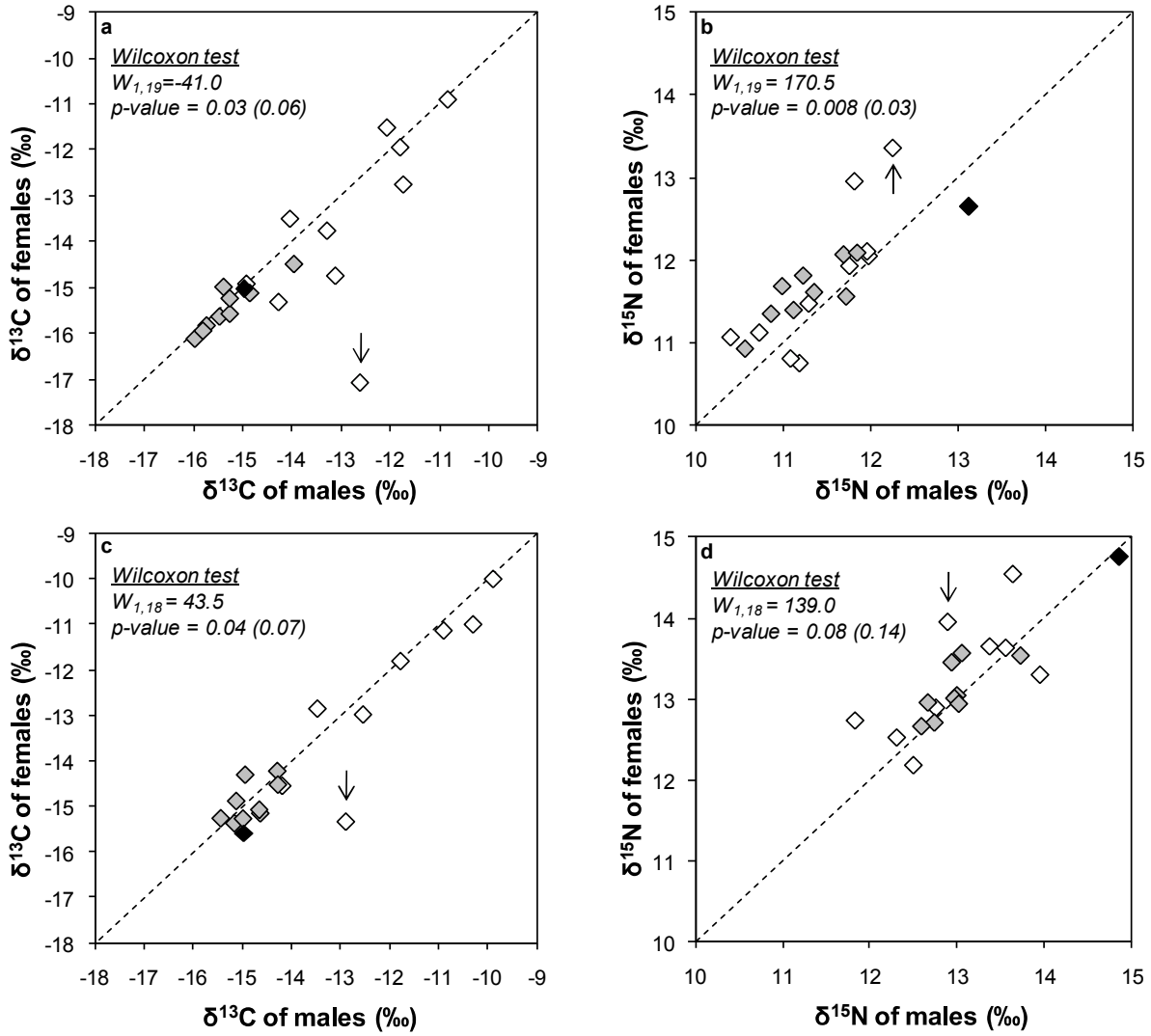


Figure 4.7 Blood carbon (a) and nitrogen (b) and feather carbon (c) and nitrogen (d) stable isotope signatures of African Black Oystercatcher's breeding pairs from the south-east (open diamonds), south-west (grey diamonds) and west (black diamond) coast. The arrows indicate a pair sampled in Cape Recife with contrasted stable isotope compositions. A Wilcoxon rank-sum test (*W*, α = 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.

Signatures isotopiques du carbone et de l'azote du sang (a et b) et des plumes (c et d) des couples reproducteurs d'huîtrier noir africain sur les côtes sud-est (diamants vides), sud-ouest (diamant gris) et ouest (diamant noirs). Les flèches indiquent le couple échantillonné à Cape Recife et présentant des signatures isotopiques contrastées. Un test de Wilcoxon (W, α = 0.05) a été utilisé pour tester les différences de $\delta^{13}C$ and $\delta^{15}N$ entre les partenaires sexuels. Les valeurs entre parenthèses indiquent les p-values lorsque le couple à Cape Recife indiqué par une flèche était retiré de l'analyse.

Breeding pairs. There were significant differences in the $\delta^{13}C$ ratios of males and females from the same breeding pair for both blood (Fig. 4.7a) and feathers (Fig. 4.7c). 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 its mate (blood: $\delta^{13}C$ = - 12.6 ‰, feathers: $\delta^{13}C$ = - 12.9‰) (Fig. 4.7, pair indicated by an arrow). When this pair was excluded from the analysis, significant differences between paired birds disappeared (Fig. 4.7a and c). Breeding partners displayed significant differences in

their $\delta^{15}N$ ratios (Fig. 5.6b) for blood with an overall enrichment in ^{15}N (average + 0.3‰) in females, while their feather $\delta^{15}N$ were not significantly different (Fig. 4.7d). The trend persisted even when the pair from Port Elizabeth was excluded from the analysis (Fig. 4.7b and d).

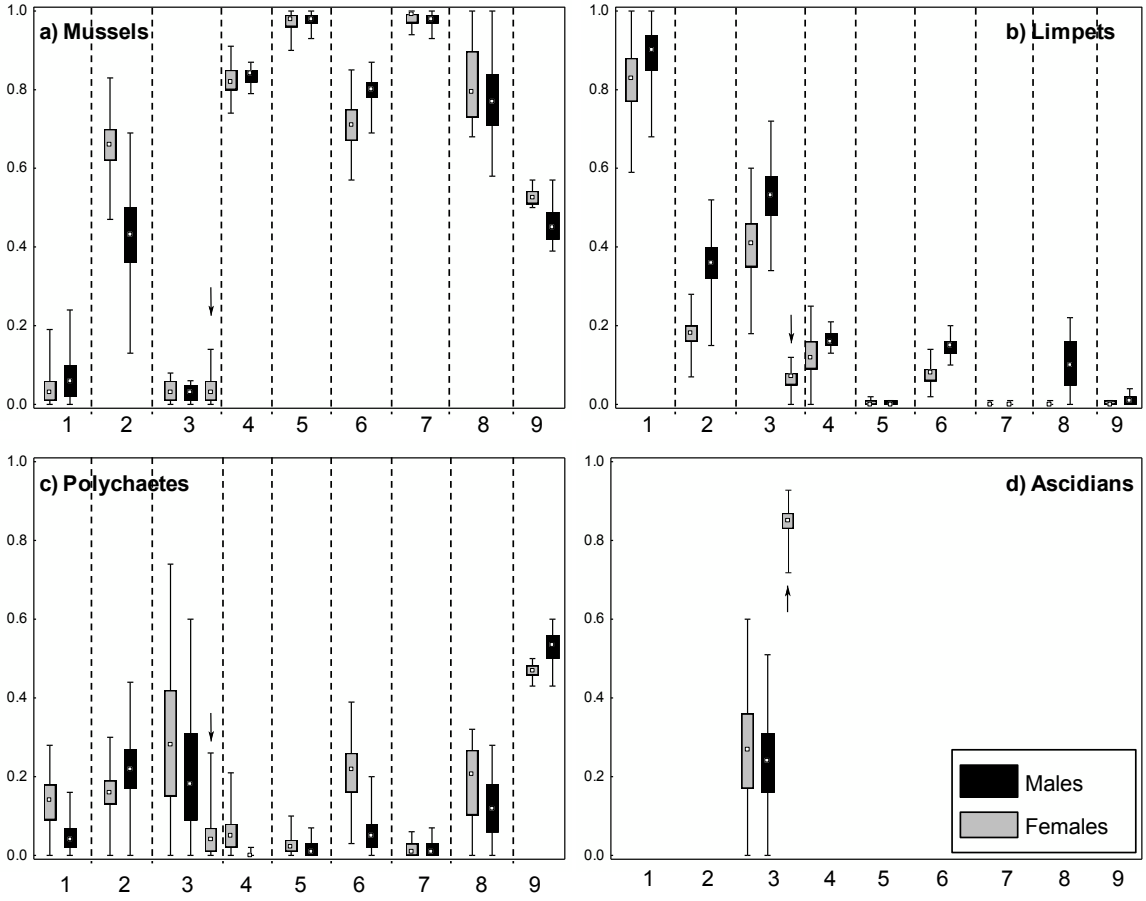


Figure 4.8 Relative Contribution of a) mussels, b) limpets, c) polychaetes and d) ascidians to the diet of male and female African Black Oystercatchers at the 9 study sites (as coded from east to west in Fig. 4.1), estimated from IsoSource. Boxes represent interquartile ranges and white squares within represent median values. Whiskers represent ranges of feasible contributions. The arrows indicate contributions estimated individually for the female with contrasting stable isotope signatures sampled at Port Elizabeth (see Fig. 4.7).

Contributions relatives des a) moules, b) patelles, c) polychaetes et d) ascidies au régime alimentaire des males et des femelles d'huîtrier noir africain aux 9 sites d'études (codé d'est en ouest selon la Fig. 4.1) et estimées avec IsoSource. Les boîtes indiquent l'écart interquartile et les carrés blancs les valeurs de médiane. Les moustaches indiquent les valeurs minimum et maximum de contributions possibles. Les flèches indiquent les contributions estimées individuellement pour la femelles présentant des ratios isotopiques différent des autres oiseaux échantillonnés à Cape Recife (voir Fig. 4.7)

Diet. The IsoSource outputs indicated that mussels and limpets contributed the bulk of the diet of ABOs, and that their relative contributions varied mostly between sites and regions rather than between sexes (Fig. 4.8). On the south-west and west coasts, mussels dominated the diet (range = 40 – 100%; Fig. 4.8a) while on the

south-east the contribution of limpets was substantial though variable (range = 7 - 100%; Fig. 4.8b). With the exceptions of Port Elizabeth (range = 0-74%) and Langebaan (range = 43-60%), the contribution of polychaetes was low (range = 0 - 44%, Fig. 4.8c). There was much overlap in the range of feasible contributions (represented by whiskers in Fig. 4.8) and in the interquartile ranges (represented by boxes in Fig. 4.8) of males and females from the same sites. However in Kenton, females seem to feed more on mussels (median = 66%; range = 47 - 83%) than males (median = 43%, range = 13 – 69%), which fed more on limpets (Males: median = 36%; range = 15 – 52%; Females: median = 18%, range = 7 – 28%). One female sampled in Port Elizabeth had very different stable isotope signatures compared to other females from the same area, and was not pooled with them in the stable isotope mixing model (Fig. 4.8, individual indicated with an arrow). The IsoSource outputs revealed a much higher consumption of ascidians (*Pyura stolonifera*) for this female (range = 75 – 95%) than for other birds (range = 0 – 61%) from Port Elizabeth (Fig. 4.8d).

4. DISCUSSION

The main result emerging from this study is that despite clear sexual dimorphism, especially in bill morphology, male and female ABOs displayed very little differences in their stable isotope signatures during either the breeding and non-breeding periods. Although the pattern was not significant, at most locations, males tended to be enriched in ^{13}C compared to females, which in turn were slightly ^{15}N-enriched compared to males. Between breeding mates, $\delta^{13}C$ segregation was only observed on the south-east coast in blood and to a lesser extent in feather tissues. In addition, one breeding pair from Port Elizabeth displayed extreme sex-related $\delta^{13}C$ differences (+ 4.5‰ in the female) but this seems to have reflected individual idiosyncrasy in feeding preference of the female. Finally, mild ^{15}N enrichment in females compared to their breeding partners was visible, and only concerned blood tissues. Sexual dimorphism has already been described in several oystercatcher species including the ABO (Hockey 1996). This has mostly been attributed to the need for diet segregation to reduce competition within pairs (Hockey and Underhill 1984, Lauro & Nol 1995) and to increase winter survival and fitness (Durell et al. 1993). The fact that we found only slight sex-related differences in stable isotope signatures raises the question of whether sexual dimorphism in ABOs is really driven by food partitioning between partners.

Carbon and nitrogen stable isotopes have successfully demonstrated sex-specific food partitioning in a wide variety of seabird taxa, including alcids, penguins, procellariforms, and skimmers (Forero et al. 2005, Bearhop et al. 2006, Paredes et al. 2008, Mariano-Jelicich et al. 2008), but has rarely been used for this purpose for shorebirds. Variations in stable isotope ratios of marine predators can result from: 1) environmental changes affecting the isotopic composition of the basis of the food web (Cherel & Hobson 2007), 2) differences in the relative consumption of isotopically distinct prey (Gannes et al. 1998) or 3) physiological status and diet-tissue fractionation (McCutchan et al. 2003). At one level we can eliminate the first possibility as we compared territorial males and females feeding on territories or on the scale of 0-1 km of coastline. Persistent environmental changes in food web baseline stable isotope ratios at such a small scale are unlikely. At larger scales on the other hand significant differences in carbon- and nitrogen-stable isotope ratios were observed between ABOs from different sites and regions. Those are related to the broad differences in primary production and structure of rocky intertidal communities between the two large marine ecosystems surrounding the South African coastline, the Benguela Upwelling System on the west coast and the Agulhas Current on the south and east coasts of southern Africa (Bustamante & Branch 1996b). These large-scale patterns have already been shown to affect the stable isotope composition of nearshore primary producers and benthic invertebrates (Hill & McQuaid 2008) as well as oceanic (Jaquemet & McQuaid 2008) and are further discussed for ABOs in Chapter 5 (Kohler et al. *in press*)

In term of dietary preferences, potential food sources 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 enriched in ^{13}C compared to mussels and polychaetes and this $\delta^{13}C$ segregation is typically observed between inshore grazing and filtering organisms (France 1995, Vander Zanden & Rasmussen 1999). Furthermore, the suspension-feeding polychaete *Gunnarea capensis* was consistently enriched by ~ 2‰ in ^{15}N compared to mussels. Finally the filter-feeding ascidian *Pyura stolonifera*, additionally sampled in Port Elizabeth, clearly differed from mussels, polychaetes and limpets in their $\delta^{13}C$ and $\delta^{15}N$ values. Conversely, the lack of clear differences in stable-carbon isotope composition of males and females or in the relative contribution

of the different types of prey to their diet as shown by the mixing models (Fig 4.8) suggest that sex-specific diet segregation in ABOs is not as widespread as in other oystercatchers species (Durell et al. 1993; Lauro & Nol 1995). Two exceptions were observed on the south-east coast: the stable isotope mixing model outputs suggested that females in Kenton were feeding more on mussels and males on limpets. This correlates with previous findings on the feeding ecology of ABOs on the south-east coast of South Africa (Kohler et al. 2009b). In addition, one female from Port Elizabeth fed almost exclusively on ascidians, while other males and females from this area seemed to feed on a mixed diet of polychaetes, limpets and ascidians. The solitary ascidian *P. stolonifera* forms dense beds from the low littoral to a depth of about 10 m on rocky reefs (Fielding & Weerts 1994), which can be dislodged locally by wave action and brought high on the shore by the tide where they become accessible for oystercatchers (Fig 4.9a). Pacheco & Castilla (2001) described similar feeding behaviour in American Pied Oystercatchers (*Haematopus palliatus*) exploiting ascidians *Pyura praeputialis* in Chile. This requires a combination of feeding techniques to perforate the tunic and then to extract the animal: striking, hammering, prying, cavity food searching and swallowing (Pacheco & Castilla 2001). Direct observations of similar sequence of feeding techniques were made on African Black Oystercatchers foraging on ascidians in Cape Recife (Fig 4.9a & b, *pers. obs.).*

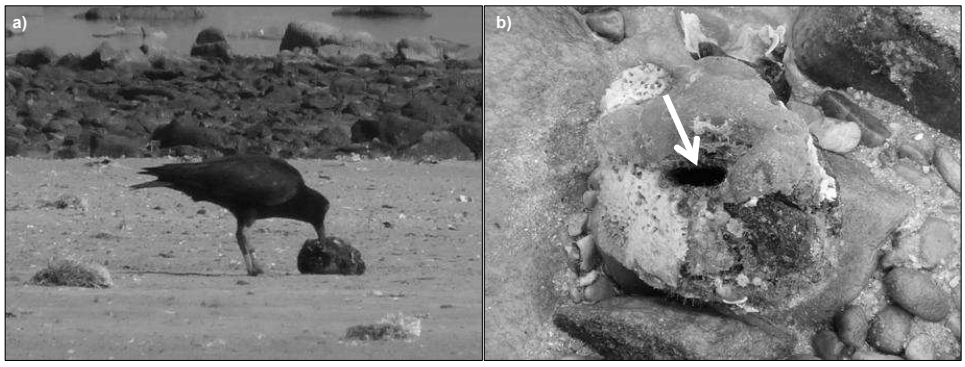


Figure 4.9. a) African Black Oystercatcher piercing the tunic of a beached ascidian at cape Recife, b) Ascidian tunic left by an African Black Oystercatcher at Cape Recife., after extracting and the animal inside. The arrow points the scar left by the bill of the bird (*Photos: S. Kohler).*

a) Huîtrier noir africain perçant la tunique d'une ascidie échouée à Cape Recife, b) Tunique d'ascidie laissé epar un huîtrier noir africain, après après avoir extrait et consommé le corps de l'animal. La flèche indique la cicatrice laissée par le bec de l'oiseau.

Female oystercatchers were slightly enriched in ^{15}N by an average + 0.3 ‰ compared to their breeding partners and this could indicate that females feed on prey at higher trophic levels than males, and more specifically feed differentially on larger prey size classes or on different species (Bearhop et al. 2006). Eurasian

oystercatchers are known to select against small bivalves (Zwarts et al. 1996) for their own diets and the American oystercatcher (*Haematopus bachmani*) and ABOs select larger prey when feeding their chicks than the modal size available on the feeding grounds (Randall & Randall 1982, Hockey & Underhill 1984). Ontogenetic shifts in $\delta^{15}N$ related to changes in diet, feeding habitats and trophic levels have been observed in several marine consumers such as fish (Kolasinski et al. 2009), shrimps (Pakhomov et al. 2004) and squids (Cherel et al. 2009). In Chapter 3, however, I showed that were no obvious isotopic differences between the size classes of mussels and limpets typically targeted by ABOs, i.e. > 30 mm (Randall & Randall 1982, Hockey & Underhill 1984), which correspond to our medium and large prey-size classes. Hence if female ABOs were eating larger mussels or limpets, this would not be reflected in their $\delta^{15}N$ ratios. The different types of prey sampled in this study displayed different $\delta^{15}N$ ratios. Specifically polychaete worms were enriched by ~2 ‰ compared to mussels and limpets. Outputs from the stable isotope mixing model did not however detect any consistent differences in the relative consumption of *G. capensis* by males and females. This suggests that $\delta^{15}N$ differences between partners are not strongly linked to dietary differences. On the other hand, variations in $\delta^{15}N$ between sexes could result from differential ^{15}N diet-tissue fractionation, related to their physiological status (Gannes et al. 1997). Food deprivation has been shown to induce ^{15}N increases in fasting breeding King penguins (Cherel et al. 2005a) and Ross' Geese (Hobson et al. 1993), which literally "feed on themselves" during this period. Conversely, other studies have demonstrated that moderate nutritional stress can result in decreased diet-consumer ^{15}N fractionation in seabirds (Williams et al. 2007, Sears et al. 2009). However the overall good body condition observed in females in all 3 regions indicates that they are unlikely to suffer from food-related stress. More generally, the level of nitrogen-use efficiency, in other words the ratio between the ^{15}N depleted nitrogenous waste excreted (uric acid in the case of birds) and the dietary ^{15}N assimilated through protein catabolism, affects the nitrogen fractionation in consumer's tissues (Vanderklift & Ponsard 2003). In this study, individuals were caught during incubation, which lasts for about 30 days in this species (Parsons 2006). Whole blood has a turnover of 4 to 5 weeks in aquatic birds (Bearhop et al. 2002), therefore, the stable isotope composition of blood tissue in oystercatchers reflects the diet integrated over the pre-laying, laying and incubation periods. Male and female oystercatchers have different energy allocation and requirements during the breeding season, specifically regarding the production of

eggs (Meijer & Drent 1999, Morissey et al. 2010) and this could result in differences in nitrogen fractionation between genders. A relation between nitrogen fractionation and sex in breeding oystercatchers is further suggested by the lack of consistent sex-specific differences in $\delta^{15}N$ in feathers, which are grown during the non-breeding season. The difference in $\delta^{15}N$ between breeding partners was small (0.3‰) and not significant at the scale of the whole study, and so may not be biologically meaningful. Nevertheless, it may be precisely because breeding partners displayed little diet segregation that we were able to observe this $\delta^{15}N$ variation. In Kenton where females seemed to prefer mussels and males limpets, there was no such observed sex-specific difference in $\delta^{15}N$. While many studies have focused on the energy allocation to the egg-production in different organisms (Hendry et al. 1999, Klaassen et al. 2004) to our knowledge, no study has demonstrated the effect of egg-production on female nitrogen stable isotope composition and fractionation in their own tissues. These findings emphasize the need for more experimental and field studies on the allocation of stable isotopes in non-fasting and resident breeding birds.

Records of sex-specific feeding behaviour in ABOs prior to the invasion of South African rocky shores by the Mediterranean mussel *Mytilus galloprovincialis* are limited to observations made on 2 breeding pairs on Marcus Island in 1979/1980 (Hockey and Underhill 1984). Hence, it is difficult to extrapolate this pattern to the rest of the ABO 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* (47.3% vs. 62.9% for males and females respectively), but males consumed more limpets and whelks (50.1 vs. 6.2% for females) and females more polychaetes (0.9 and 19.3% for males and females respectively). 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 would be better equipped for removing limpets from rocks. Since then, numerous studies have been published on the close association between individual or sex-related diet specialization and bill shape in Eurasian Oystercatchers (*Haematopus ostralegus*) (Goss-Custard & Sutherland 1984, Durell et al. 1993, Van de Pol et al. 2010). Feeding specializations in this species are not only prey-type related (polychaetes vs hard-shelled prey), but also characterized by different handling techniques (stabbing, ventral hammering or dorsal-hammering of bivalves, Sutherland et al. 1996). Conversely there is no evidence of different prey-handling techniques among ABOs. In middens (piles of empty shells left by oystercatchers while feeding their chicks)

collected to quantitatively study the diet of African Black Oystercatcher (Randall & Randall 1982, Hockey & Underhill 1984, Kohler et al. 2009b), mussels and limpets shells are mostly found intact (*pers. obs.*), which suggests the use of only stabbing to open mussels and prying to dislodged limpets. Recently, in a study of the feeding ecology of ABOs breeding on sandy shores on the West coast, Parsons (2006) observed that all birds, males and females, mostly ate polychaetes and small crustaceans and that overall bill morphology and sex did not seem to play an important role in the feeding behaviour of breeding oystercatchers, which fed opportunistically on the most abundant prey (the polychaete *Scololepsis* sp). Similarly the lack of association between sex (and bill-shape) with one type of prey in African Black Oystercatcher was recently suggested by Coleman & Hockey (2008) on Marcus Island off the west coast, where males and females seem to have converged towards a diet almost exclusively composed of the invasive mussel.

All these lines of evidence lead to the conclusion that breeding ABOs display very little sex-specific food segregation, despite the potential for feeding specialization in such a species. This could result from the lack of food limitation in their foraging habitat possibly caused by the invasion of rocky shores by the Mediterranean mussel (Hockey & Van Erkom Schurink 1992), which greatly increased the biomass of mussels, a food item historically favoured by African Black Oystercatchers (Randall & Randall 1982, Hockey & Underhill 1984). Such hypothesis is supported by the slight food segregation observed on the south-east coast where the invasive mussel is virtually absent, and where overall prey biomass is lower than further west (Bustamante & Branch 1996b). The body condition of birds was not drastically different between regions (Fig. 4.4), suggesting that the access to food is no more limiting in a region invaded by *M. galloprovincialis* than a region where it is virtually absent. One singular difference was however observed between males from the south-west coast and all other groups. In this region, we sampled at sites where feeding areas had very little limpets and were dominated by mussels (both *P. perna* and *M. galloprovincialis*), but with overall lower biomass than on the west coast (Robinson et al. 2005). The combined effects of lacking an alternative prey (limpets) and relative low mussel biomass (compared to the west coast) might actually induce food limitation for males on the south-west coast. These findings suggest that male and female oystercatchers may not be equal when it comes to the efficiency in

exploitation rocky shores, and this might very well be related to the sexual dimorphism displayed by the bill of ABOs.

Nonetheless, the ABOs population has been increasing for the past 20 years and extended its breeding range further east (Vernon 2004, Tjørve & Underhill 2006, Brown & Hockey 2007, Kemper 2007), presumably as a result of this mussel invasion. However the breeding population as a whole may not have reached the carrying capacity of their rocky shore habitats and therefore intra-specific competition and need for food partitioning could be relaxed, although evidences presented here suggest that males are less efficient in their assimilation of mussels. Thus sexual dimorphism in ABOs, especially bill dimorphism, could be maintained genetically or by other ultimate factors than food partitioning.

The relative influence of sexual selection and/or ecological processes in sexual dimorphism especially in Charadrii (gulls, shorebirds and alcids) remains controversial (Hedrick & Temeles 1989, Shine 1989, Székely et al. 2000, Van de Pol et al. 2010). There was overlap in the distribution of bill length between the two sexes (Fig 4.3 and Table 4.1), however within breeding pairs, females always had longer bills than their breeding partners, with differences ranging from + 2.6 to +18.3 mm. The same observations were made by Hockey & Underhill (1984) for ABOs and by Baker (1974) for New Zealand oystercatchers. These authors suggested that sex recognition and pair formation could be the ultimate causes. If females had longer bills than males, the bill-depth (halfway down) however was similar between sexes. Therefore, intuitively, males had deeper bill-tips than females. The shape of bill-tips in oystercatchers is the combined result of continuous growth (average of 0.44 mm per day) and abrasion rate (Hulscher 1996). Behaviours, other than strictly feeding-related, such as territory defence, differing between males and females could result in differential abrasion rate, but are yet to be identified.

CHAPITRE 5

Geographic variations in the trophic ecology of African Black Oystercatchers along the southern African coastline

(based on an article published in Marine Ecology Progress Series, Annexe 5)

(Photo: B. Dubillot)

RESUME

Le principe de transmission des signatures isotopiques de la base des réseaux trophiques le long des chaînes alimentaires jusqu'aux niveaux trophiques supérieurs a été largement utilisés dans l'étude des prédateurs supérieures en milieux océaniques, mais rarement dans le cas de prédateurs intertidaux. Dans ce chapitre, j'ai étudié les variations des ratios isotopiques du carbone et de l'azote chez un prédateur sédentaire des littoraux rocheux d'Afrique Australe, l'huîtrier noir africain (*Haematopus moquini*) sur environ 2000 km de côtes s'étendant du sud de la Namibie au sud-est de l'Afrique du Sud. Ces littoraux sont caractérisés par de forts gradients biogéographiques de productivité primaire côtière et de communautés intertidales, largement influencés par les deux courants majeurs et contrastés du Benguela à l'Ouest et des Aiguilles à l'est et au sud. De plus, cette région connaît une invasion biologique conséquente de la moule de Méditerranée (*Mytilus galloprovincialis*) depuis la fin des années 1970, qui a fortement altéré la structure des communautés intertidales sur les littoraux rocheux sud-africains et namibiens. Cependant l'huîtrier noir africain, auparavant menacé d'extinction, semble avoir tiré profit de cette invasion et de l'accroissement de la biomasse de moules, en particulier sur les côtes ouest sud-africaines. Dès lors, les conditions environnementales uniques de cette région littorale, les perturbations liées à l'invasion par la moule de Méditerranée ainsi que caractéristiques propres à l'huîtrier noir africain (sa distribution géographique, sa sédentarité, sa dépendance aux estrans pour se nourrir et sa relation particulière avec *M. galloprovincialis*) font des littoraux du Sud de l'Afrique un terrain particulièrement propice pour étudier les effets des variations géographiques de conditions océanographiques littorales et d'assemblages d'espèces benthiques sur l'écologie trophique d'un prédateur intertidale. Pour ce faire, du sang et des plumes d'adultes reproducteurs et poussins d'huîtriers ainsi que ses principales proies (moules et patelles) ont été collectés entre les littoraux du sud de la Namibie et le sud-est de l'Afrique du Sud. Un enrichissement en ^{15}N a été observé entre les côtes sud-est et ouest dans les tissus d'huîtriers et ses proies, reflétant un shift isotopique entre le courant oligotrophe des Aiguilles sur la côte est et le système d'upwelling du Benguela à l'ouest. Le sang des huîtriers montrait des valeurs de $\delta^{13}C$ variant entre celles de moules et des patelles, respectivement appauvries et enrichies en ^{13}C, et reflétant un changement dans les proportions de filtreurs et de brouteurs dans le régime alimentaire des huîtriers à travers la région d'étude. Ce changement géographique dans le régime alimentaire

des huîtriers, dominés à l'ouest par les moules et composés de proportions mixtes de brouteurs et filtreurs sur les côtes sud-est, reflétait fortement les abondances géographiques relatives de la moule invasive. Enfin, les signatures isotopiques du sang et des plumes des huîtriers montraient de fortes corrélations à travers l'ensemble de la zone d'étude, indiquant soit une forte stabilité des conditions environnementales, soit des habitudes alimentaires des adultes huîtriers au cours du cycle annuel. Des disparités entre les tissus étaient toutefois visibles pour certains sites de la côte sud, suggérant des mouvements de la part des adultes ou des modifications de leurs habitudes alimentaires en dehors de la saison de reproduction. Ce pourrait constituer une réponse des oiseaux aux abondances de nourriture plus faible dans la région. En conclusion cette étude indique que les conditions océaniques régionales ont une influence sur réseaux trophiques côtiers depuis leur base jusqu'à un prédateur supérieur, mais que des effets plus locaux peuvent aussi fortement affecter l'écologie trophique de ce prédateur.

1. INTRODUCTION

Spatial distributions of carbon and nitrogen stable isotopes at the base of marine food webs are affected by oceanic parameters such as sea surface temperature and CO_2 concentration (Rau et al. 1982, Goericke & Fry 1984), biochemical processes and the composition of primary producers (Saino & Hattori 1980). This baseline signal is then transmitted along the food chain in a predictable manner and is ultimately reflected in organisms at higher trophic levels (Cherel & Hobson 2007). This effect has been widely used to investigate spatial and temporal aspects of the feeding ecology of oceanic predators (Burton & Koch 1999, Quillfeldt et al. 2005, Cherel & Hobson 2007), but rarely in large-scale studies involving higher trophic level organisms of intertidal ecosystems (but see Atkinson et al. 2005). $\delta^{13}C$ has been particularly exploited at the lower trophic levels to distinguish between the two main potential sources of carbon in intertidal habitats: nearshore benthic and offshore pelagic primary production (Fry & Sherr 1984, France 1995, Post 2002). Recently, based on the ^{13}C and ^{15}N signatures of rocky shore primary producers and consumers, Hill et al. (2006) and Hill & McQuaid (2008) described four isotopic regions and continuous gradients of $\delta^{13}C$ and $\delta^{15}N$ ratios between the Mozambican and Namibian coasts (Fig. 5.1 & 5.2). These reflected variations in coastal hydrographic features along the coastline and the shift between oligotrophic and eutrophic conditions set respectively by the Agulhas Current bringing warm waters from the Mozambique Channel along the east and south coasts (Lutjeharms 2004) and the nutrient-rich Benguela Upwelling system that flows northwards along the west coast (Shannon 1985).

The trophic structure of southern African rocky shores has also been profoundly influenced by the accidental introduction of the Mediterranean mussel *Mytilus galloprovincialis* to the west coast of South Africa in the 1970s (Grant and Cherry 1985). The arrival of this invasive species has caused major changes in the structure and functioning of intertidal communities on these rocky shores (Robinson et al. 2007).

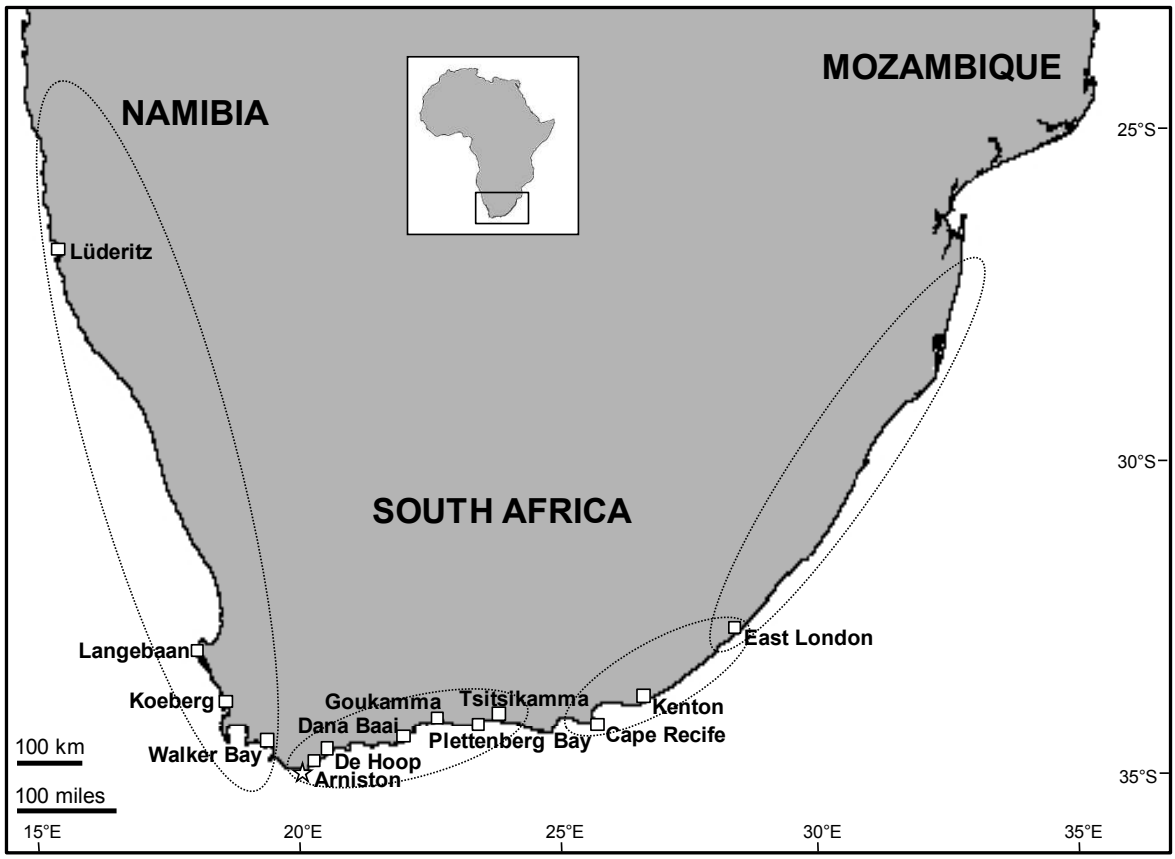


Figure 5.1. Location of the breeding sites where African Black Oystercatchers and prey were sampled. Isotopic regions described in Hill et al. (2006) and Hill & McQuaid (2008) are delineated by dotted circles.
Localisation des sites de reproduction où les huîtriers noirs africains et leurs proies ont été échantillonnés. Les régions isotopiques décrites dans Hill et al. (2006) et Hill & McQuaid (2008) sont délimités par des cercles pointillés.

Because of its higher physiological performances, dispersal rates and ability to colonize free space (Branch & Steffani 2004, Erlandsson et al. 2006), the invasive species has replaced the indigenous mussels *Aulocomya ater* and *Choromytilus meridionalis* as the dominant mussel on the mid- and low-shore on the west coast (Robinson et al. 2007). Moreover *M. galloprovincialis* outcompetes adult limpets (*Scutellastra argenvillei* and *S. granularis*) for primary space on exposed rocky shores on the west coast (Hockey & Von Erkom Schurink 1992, Steffani & Branch 2003). The Mediterranean mussel was also introduced for aquaculture in Port Elizabeth on the south coast in 1988 (McQuaid & Phillips 2000). The distributions of the indigenous *Perna perna* and *M. galloprovincialis* now overlap in this region but where they co-occur, they exhibit partial spatial segregation, with *M. galloprovincialis* dominating the upper mussel zone, *P. perna* the lower zone and a mix of the two species in the mid-mussel zone (Bownes & McQuaid 2006). At the start of the 21st century, *M. galloprovincialis* occurred along 2000 km of shoreline from Namibia to

South Africa, and dominated intertidal biomass on the west coast (Robinson et al. 2005).

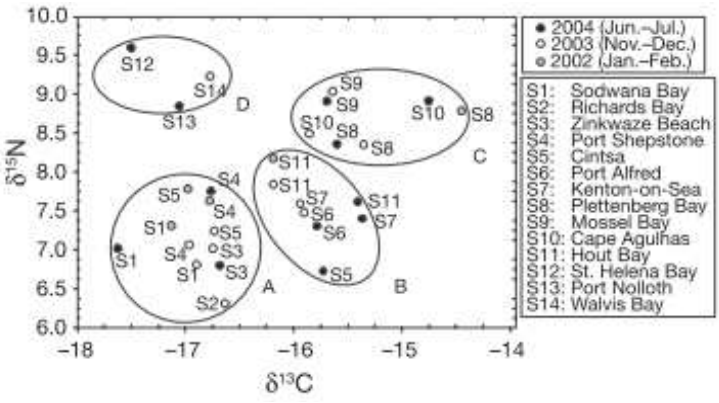


Figure 5.2. ^{13}C and ^{15}N signatures of intertidal mussels. Groupings according to k-means cluster analysis: (A) east coast, (B) south-east coast, (C) south-west coast, (D) west coast (from Hill et al. 2006). *Signatures de ^{13}C and ^{15}N de moules intertidales. Groupements définis d'après une analyse de cluster(k-mean): (A) côte est, (B) côte sud-est, (C) côte sud-ouest, (D) côte ouest (d'après Hill et al. 2006)*

Although the arrival of *M. galloprovincialis* on the Southern African coasts had mostly negative effects for the rocky shore communities, it has benefited a near-threatened endemic shorebird species, the African Black Oystercatcher (*Haematopus moquini*, ABO). Since the 1980s the reproductive output of ABOs has increased in response to a combination of conservation measures and enhanced mussel biomass due to the invasive species on the west coast (Hockey & Van Erkom Schurink 1992, Hockey 1997, Williams et al. 2004, Tjørve & Underhill 2006). As a consequence, in the past 30 years, the overall population has increased from 4,800 (Hockey 1983b) to approximately 6,000 birds (Hockey 2005), which might be an underestimation of the present population size. The breeding range of this shorebird has also expanded eastwards (Vernon 2004, Brown & Hockey 2007). This seems to reflect a spill-over effect, with vagrant individuals from the burgeoning west coast populations spreading farther east (Vernon 2004), rather than a direct consequence of the eastward spread of *M. galloprovincialis* as this mussel is present at only low abundances at most sites on the south-east coast (von der Meden et al. 2008). The breeding range of ABOs now extends from the Lüderitz region of southern Namibia to the south-east coast of South Africa, with a gap between the Lüderitz region and Cape Columbine on the west coast (Hockey 2005, Fig. 5.1). ABOs are non-migratory and are territorial during the breeding season, which extends from October to March in South Africa (Hockey 2005) and from January to June in Namibia (*J. Kemper*, *pers. com.*). Finally they depend exclusively on intertidal invertebrates, mostly mussels and limpets for their food (Hockey & Underhill 1984). This set of features makes them excellent biological model organisms to study the influence of physical processes and biological perturbation on intertidal communities. In particular it makes them ideal for the study

of how conditions at the base of the intertidal food web are transmitted to higher trophic levels under different environmental conditions.

Here we investigate the trophic ecology of this rocky shore predator across the full extent of its breeding range, relating this to spatial changes in the local assemblages of prey species in its habitat and to larger oceanic processes. Analysis of stable carbon and nitrogen isotope signatures allows us to examine the balance between biogeographic and local effects and to test whether the ABO responds more strongly to large-scale oceanic characteristics, conforming to previously defined isotopic provinces (Hill et al. 2006), or whether local physical and biological conditions have a more powerful influence.

2. MATERIALS & METHODS

Sample collection. Breeding oystercatchers and their chicks were sampled during three consecutive breeding seasons (from December 2007 to April 2010), at 13 sites from Lüderitz (26°38.8' S, 15°9.2 'E) on the south coast of Namibia to East London (33°3.2' S, 27°52.4' E) on the south-east coast of South Africa (Fig. 1). For a detailed description of the sampling of prey, blood and feathers of ABOs for carbon and nitrogen stable isotope analyses, refer to Chapter 1, section IV. Collection focused on mussel and limpet species as they are known to form the bulk of oystercatcher diet on rocky shores (Hockey Underhill 1984, Hockey & Van Erkom Schurink 1992, Kohler et al. 2009b). Across the whole study area, the prey species collected comprised the mussels *Perna perna, Mytilus galloprovincialis, Choromytilus meridionalis, Aulocomya ater* and the limpets *Cymbula oculus, Scutellastra argenvillei, S. cochlear, S. granatina, S. granularis and S. longicosta* (see Fig 1.6). Not all of these species occur throughout the study region which comprises two major biogeographic provinces. In addition, the Benguela system and the Agulhas Current give rise to broad geographic differences in nutrient concentration, intertidal primary production and ultimately species assemblages and biomass along the coastline (Emanuel et al. 1992; Bustamante & Branch 1996b): Intertidal biomass is greater on the west coast than on the south and east coasts which are in turn characterized by higher species richness. Local hydrography plays an important role in the ecosystem dynamics of rocky shore communities (Menge et al. 2003). On the South African coastline in particular, it has been suggested that temporal variability in hydrographic processes may profoundly affect the composition and distribution of nearshore suspended particular matter (SPM) and subsequently its ^{13}C signatures (Hill et al.

2008). Consequently, prey species and oystercatchers at a given site were sampled during the same breeding season as far as possible to limit temporal effects on isotope signatures. However in order to cover the entire study area (~2000km) and sample sufficient numbers of birds, it was logistically necessary to sample over 3 breeding seasons (see Table 5.1).

Table 5.1. Carbon and nitrogen stable isotope values of blood (adults and chicks) and body feathers (adults only) of African Black Oystercatchers. Values are mean ± SD.

Valeurs des isotopes stables du carbone et de l'azote du sang (adultes et poussins) et des plumes (adultes seulement) des huîtriers noirs africains. Les valeurs indiquées sont les moyennes (± écart-types).

Sites	Blood (Adults + chicks)		Feathers (Adults only)		N			Sampling seasons*
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Adults	Chicks	Total	
Lüderitz	-15.2 ± 0.5	12.4 ± 0.7	-13.8 ± 0.2	13.6 ± 0.9	3	1	4	2010
Langebaan	-14.9 ± 0.2	13.2 ± 0.4	-14.5 ± 1.0	14.9 ± 0.3	4	2	6	2009
Koeberg	-14.6 ± 0.6	11.6 ± 0.3	-13.8 ± 0.4	13.2 ± 0.1	4	4	8	2008 and 2009
Walker Bay	-14.4 ± 0.1	11.6 ± 0.2	-13.5	12.8	1	3	4	2009 and 2010
Arniston	-15.6 ± 0.3	11.3 ± 03	-14.9 ± 0.3	12.8 ± 0.2	6	1	7	2009
De Hoop	-14.8 ± 0.6	11.8 ± 0.4	-14.9 ± 0.3	12.8 ± 0.2	5	7	12	2009
Dana Baai	-15.9 ± 0.5	10.5 ± 0.4	-15.8 ± 0.3	13.8 ± 0.1	2	8	10	2009
Goukamma	-15.5 ± 0.5	11.4 ± 0.4	-15.0 ± 0.4	13.3 ± 0.3	8	9	17	2009
Plettenberg Bay	-15.3 ± 0.8	11.0 ± 0.6	-14.9 ± 0.6	12.8 ± 0.2	5	2	7	2009
Tsitsikamma	-13.2 ± 0.0	11.3 ± 0.2	-12.3	12.8	1	1	2	2010
Cape Recife	-13.6 ± 0.8	11.9 ± 0.4	-13.1 ± 1.0	13.5 ± 0.4	12	6	18	2008 and 2009
Kenton	-14.4 ± 0.9	11.2 ± 0.4	-13.7 ± 0.9	12.7 ± 0.4	10	7	17	2008 and 2009
East London	-13.0 ± 1.4	10.5 ± 0.6	-11.6 ± 1.6	11.4 ± 0.5	11	13	24	2008

Sample preparation and isotope analysis. Whole blood has a rapid turnover rate and for birds, gives information on the diet integrated over a few weeks prior to sampling (Hobson & Clark 1992a, Bearhop et al. 2002). Isotopic signatures of blood collected in summer were therefore used as a proxy for the diet of adults and chicks during the breeding season. Adult feathers are produced during moult and remain metabolically inert once fully grown (Mizutani et al. 1990). No published data exist on the moult of ABOs, however, it is believed that this takes place from March to September, i.e. during the non-breeding season (*L.G. Underhill, pers. com.*). Moreover, other shorebirds (Klaassen et al. 2001, Atkinson et al. 2005) and oystercatcher species (Dare & Mercer 1974, Hulscher 1977) are known to moult

during the wintering/non-breeding season. Therefore we assume that the isotopic composition of adult body feathers reflects their diet during the non-breeding season (Jaeger et al. 2009). Different tissues have different protein turnover rates and routings. Consequently, $\delta^{13}C$ and $\delta^{15}N$ signatures vary from one tissue to the other and this must be taken into consideration when comparing isotopic signatures of different tissues (Tieszen et al. 1983, Vanderklift & Ponsard 2003, Cherel et al. 2005b). Prey species were analysed using muscle tissues because of their slow isotopic turnover rate and the fact that they are unlikely to be affected by short-term environmental fluctuations (Gorokhova & Hansson 1999). Consequently, the adductor muscle of mussels and the foot muscle of limpets were analysed for their isotopic composition, to provide an isotopic signal integrated over a period of months (Hill & McQuaid 2009). For a detailed description of the processing of prey, blood and feathers for stable isotope analyses, refer to Chapter 1, section IV Precision of replicate determinations for the samples analyzed in this chapter was < 0.10 ‰ for carbon and < 0.13 ‰ for nitrogen. All samples were analyzed at the Stable Light Isotope Unit of the University of Cape Town, South Africa.

Prey contributions. To investigate variations in the relative contribution of mussels and limpets to the diet of oystercatchers along the coastline, we used the Bayesian stable isotope mixing model SIAR. The SIAR package (Parnell et al. 2010; available at http://cran.r-project.org/web/packages/siar/index.html), running on the statistical software R (R Development Core Team 2009), allows the incorporation of standard deviations of mean sources and consumers signatures as well as uncertainty regarding diet-consumer discrimination. We used mean (± SD) signatures of oystercatcher blood (Table 5.1) and prey (Table 5.2) and the TEFs estimated in Chapter 3, i.e. +2.7‰ (±0.4) for $\delta^{13}C$ and +0.2‰ (±0.4) for $\delta^{15}N$, to calculate prey contributions at each location. No limpets were present on the feeding grounds at De Hoop, DanaBaai and Goukamma but for reasons of comparison, limpet signatures from nearby areas (less than 50km away) were included to run the model for these sites (see footnotes in Table 5.2). With the SIAR outputs, an *a-posteriori* aggregation (Phillips et al. 2005) was carried out to pool results for limpet species on one side and for mussel species on the other side.

Statistical analyses. All statistical analyses were performed using R Statistical software (R Development Team Core 2009). When data sets did not meet the assumptions of normal distribution (Shapiro-Wilk test, $p < 0.05$) or homoscedasticity

(Bartlett test, $p < 0.05$), non-parametric procedures were used. Although the purpose of this study was not to investigate differences between individuals at a local scale, we tested local differences between age groups to see whether adults and chicks from the same site could be considered as a homogenous local population. A two-way ANOVA ($\alpha = 0.05$) was performed with sites (n = 13) and age (chicks or adults) as factors and $\delta^{13}C$ or $\delta^{15}N$ as response variables for each site. There was a significant effect of site on individuals for both $\delta^{13}C$ ($F_{12,123} = 13.66$, $p < 0.01$) and $\delta^{15}N$ ($F_{12,123} = 24.57$, $p < 0.01$) values. Chicks were slightly but significantly depleted by – 0.4 ‰ in ^{13}C ($F_{1,122} = 5.85$, $p=0.02$) and by – 0.3 ‰ in ^{15}N ($F_{1,122} = 30$, $p < 0.01$) compared to adults. There was no interaction between site and age ($\delta^{13}C$: $F_{11, 122} = 1.27$, $p = 0.25$; $\delta^{15}N$: $F_{11,122} = 1.46$, $p = 0.15$) and adult and chick isotope signatures showed very strong correlations ($\delta^{13}C$: $R^2_{adults\text{-}chicks} = 0.85$, $p < 0.01$; $\delta^{15}N$: $R^2_{adults\text{-}chicks} = 0.93$, $p < 0.01$), meaning that adult and chick signatures co-varied along the coastline. Geographic variations of chick and adult blood signatures are represented separately and correlation tests were performed for each age group. We pooled chicks and adults for the estimation of the contributions of limpet and mussel to the diet of ABOs along the coastline (see “prey contributions” in Material & Methods) because the SIAR model incorporates individual variability in the output. Geographic grouping of $\delta^{13}C$ and $\delta^{15}N$ values of adult tissues were analyzed using a K-means cluster analysis, subsequently tested with a discriminant function analysis (DFA). We also tested if the presence of *M. galloprovincialis* and/or limpets on the feeding grounds had an effect on the overall contribution of mussels (estimated from SIAR) to the ABO diet, using a two-way ANOVA ($\alpha = 0.05$).

Table 5.2. Carbon (a) and nitrogen (b) stable isotope values of mussels and limpets along the southern African coastline. Values are mean ± SD (‰). ^{a,b,c} indicate homogenous groups of species with non-significant differences in their $\delta^{13}C$ or $\delta^{15}N$ values (Kruskal-Wallis *H* test, Dunn post-hoc test and Bonferroni corrections, *p > 0.05*).

Valeurs des isotopes stables du carbone (a) et de l'azote (b) des moules et des patelles sur les côtes de l'Afrique australe. Les valeurs indiquées sont les moyennes (± écartypes) eexprimées en ‰. ^{a,b,c} indiquent les groupes d'espèces homogènes ne présentant pas de différences significatives dans leurs ratios isotopiques (test H de Kruskal-Wallis, test post-hoc de Dunn et corrections de Bonferroni, p > 0.05)

a. $\delta^{13}C$ Sites	Mussels				Limpets					
	A. ater	*C. meridionalis*	*M. galloprovincialis*	*P. perna*	*C. oculus*	*S. argenvillei*	*S. cochlear*	*S. granatina*	*S. granularis*	*S. longicosta*
Lüderitz	-17.9 ± 0.2^{a}	-17.4± 1.0^{a}	-15.7± 0.1^{a,b}	-	-	-	-	-15.7± 0.6^{a}	-11.8± 0.3^{b}	-
Langebaan	-	-	-15.0± 0.1^{a}	-	-	-11.6± 0.4^{b}	-	-	-	-
Koeberg	-	-	-15.0± 0.1^{a}	-	-	-12.7± 0.2^{b}	-	-	-	-
Walker Bay	-	-	-14.7± 0.2^{a}	-	-	-	-	-	-11.2± 0.6^{b}	-
Arniston	-	-	-15.4± 0.1^{a}	-15.6± 0.1^{a}	-8.3± 0.8^{a,b} **	-	-	-	-	-6.2± 0.2^{b} **
De Hoop	-	-	-15.9± 0.1^{a}	-16.3± 0.1^{a}	-	-	-	-	-	-
Dana Baai	-	-	-15.5± 0.6^{a}	-16.5± 0.2^{a}	-	-		-	-	-
Goukamma	-	-	-15.2± 0.5^{a,b}	-15.6± 0.5^{a}	-10.9± 0.6^{b,c} *	-	-11.6± 0.3^{b,c} *	-	-	-7.2± 1.7^{c} *
Plettenberg Bay	-	-	-15.2± 0.4^{a}	-15.9± 0.3^{a}	-13.1± 0.7^{b}	-	-	-	-13.4± 1.1^{b}	-
Tsitsikamma	-	-	-14.0± 0.3^{a,b}	-14.3± 0.1^{a}	-12.1± 1.1^{a,b,c}	-	-11.1± 0.5^{b,c}	-	-11.3± 0.3^{a,b,c}	-9.8± 1.2^{c}
Cape Recife	-	-	-	-15.9± 0.1^{a}	-10.5± 1.3^{a,b}	-	-11.6± 0.7^{a,b}	-	-11.9± 0.2^{a,b}	-8.4± 1.9^{b}
Kenton	-	-	-	-15.2± 0.1^{a}	-12.8± 0.7^{b,c}	-	-11.8± 0.6^{b}	-	-12.4± 1.6^{b,c}	-8.2± 1.0^{c}
East London	-	-	-	-15.8± 0.1^{a}	-13.2± 1.1^{a,b}	-	-13.0± 0.1^{b,c}	-	-11.9± 0.6^{b,c}	-8.2± 0.6^{c}

b. $\delta^{15}N$ Sites	Mussels				Limpets					
	A. ater	*C. meridionalis*	*M. galloprovincialis*	*P. perna*	*C. oculus*	*S. argenvillei*	*S. cochlear*	*S. granatina*	*S. granularis*	*S. longicosta*
Lüderitz	10.2± 0.2^{b}	9.2± 0.3^{a,b}	9.3± 0.3^{a,b}	-	-	-	-	7.7^{a,b}± 0.3	8.5± 0.1^{a}	-
Langebaan	-	-	10.1± 0.2^{a}	-	-	11.1± 0.4^{b}	-	-	-	-
Koeberg	-	-	8.6± 0.3^{a}	-	-	9.5± 0.2^{b}	-	-	-	-
Walker Bay	-	-	8.8± 0.1^{a}	-	-	-	-	-	7.4± 0.8^{b}	-
Arniston	-	-	8.5± 0.5^{a}	9.0± 1.2^{a}	9.0± 0.6^{a} **	-	-	-	-	8.3± 0.7^{a} **
De Hoop	-	-	8.9± 0.2^{a}	9.2± 0.2^{a}	-	-	-	-	-	-
Dana Baai	-	-	8.4± 0.2^{a}	8.7± 0.3^{a}	-	-	-	-	-	-
Goukamma	-	-	8.6± 0.5^{a,b}	8.8± 0.5^{a,b}	8.7± 0.2^{a,b} *	-	9.4± 0.2^{b} *	-	-	8.2± 0.2^{a} *
Plettenberg Bay	-	-	8.1± 0.3^{a}	8.6± 0.6^{a,b}	8.8± 0.4^{b}	-	-	-	8.2± 0.2^{a,b}	-
Tsitsikamma	-	-	7.8± 0.3^{a}	7.7± 0.1^{a}	8.4± 0.3^{a,b}	-	8.4± 0.2^{a,b}	-	8.3± 0.3^{a,b}	8.6± 0.2^{b}
Cape Recife	-	-	-	8.7± 0.1^{a}	8.7± 0.5^{a}	-	8.6± 0.4^{a}	-	8.9± 0.2^{a}	8.2± 0.4^{a}
Kenton	-	-	-	8.1± 0.2^{a}	8.0± 0.0^{a,b}	-	9.2± 0.3^{b}	-	7.3± 0.9^{a}	7.7± 0.3^{a}
East London	-	-	-	7.1± 0.1^{a}	8.1± 0.4^{b}	-	8.2^{b}± 0.0	-	7.6±0.1^{a,b}	8.0± 0.3^{b}

**Not present on the feeding grounds and collected ~10km eastwards. Limpet data used to run SIAR for Goukamma and Dana Baai*
***Limpet data used to run SIAR for De Hoop*

3. RESULTS

Isotopic variation among sites, trophic groups and species of benthic invertebrates. Across the study region, individual carbon isotope signatures ranged from – 18.9 ‰ (*Choromytilus meridonalis*, Lüderitz) to – 13.7 ‰ (*Mytilus galloprovincialis*, Tsitsikamma) for mussels and from – 16.1‰ (*Scutellastra granatina*, Lüderitz) to – 5.3 ‰ (*S. longicosta*, East London) for limpets. Filter-feeders and grazers were separated by their $\delta^{13}C$ values with mussels being depleted in carbon at all sites compared to limpets. Differences in their carbon isotope signatures, however, were not always significant (Table 5.2) and in Lüderitz, *M. galloprovincialis* and the limpet *S. granatina* had both a mean $\delta^{13}C$ ratio of – 15.7 ‰. Overall no consistent separation in the $\delta^{15}N$ values of mussels and limpets was observed (Table 5.2). However, west of Cape Agulhas (Namibia excluded), the only mussel present, *M. galloprovincialis*, was significantly depleted in ^{15}N compared to the dominant limpets, *S. argenvillei* or *S. granularis* (Table 5.2).

The invasive mussel *M. galloprovincialis* and the indigenous brown mussel *Perna perna* co-occurred at six locations (Table 5.2). No significant differences in carbon or nitrogen isotope ratios were recorded between the two species at a local scale (Table 5.2). In Namibia, *M. galloprovincialis* was significantly enriched in ^{13}C compared to the indigenous mussels *C. meridionalis* and *Aulocomya ater* (Table 5.2). When *S. longicosta* was present, this limpet was always enriched in ^{13}C compared to other limpets (Table 5.2). Overall, the different limpet species had similar $\delta^{15}N$ values throughout the sampling area (Table 5.2).

Muscle $\delta^{13}C$ values of mussels and limpets did not show any geographic trends along the coastline. The lowest mean ^{13}C signatures for both mussels and limpets were observed in Lüderitz, while the highest signatures were in Tsitsikamma for mussels and Arniston, near Cape Agulhas for limpets. However it is worth noting that the mean $\delta^{13}C$ signatures of limpets presented in Fig. 5.3a were affected by the presence or absence of *S. longicosta,* which was particularly enriched in ^{13}C.

Unlike carbon signatures, nitrogen-isotope signatures showed a clear geographic pattern. The $\delta^{15}N$ values of mussels varied from 9.6‰ in Lüderitz (West coast, Namibia) to 7.1 ‰ in East London (south-east) and they displayed a significant depletion (Pearson's correlation test, $R^2_{mussels\text{-}longitude} = 0.80$, $p < 0.01$) from the west to the south-east coast (Fig 5.3b). Geographic patterns in limpets $\delta^{15}N$ signatures were not as clear and a marginally significant depletion was only observed from Arniston (close to Cape Agulhas) eastwards (Pearson's correlation test, $R^2_{limpets\text{-}}$

$_{longitude}$ = 0.76, p = 0.05). Particularly high ^{15}N signatures were observed for both mussels and limpets at Langebaan on the west coast compared to neighbouring sites and to a lesser extent, this was also the case on the south coast for Cape Recife compared to Kenton and Tsitsikamma (Fig. 5.3b). In Walker Bay, limpets displayed depletion in ^{15}N compared to those sampled at the nearest sites, Koeberg to the west and and Arniston to the east (Fig 5.3b).

Geographic and tissue-specific variations in the stable isotope ratios of African Black Oystercatchers. Altogether 136 oystercatchers (53 % adults and 47 % chicks) were sampled for this study. Oystercatcher blood showed $\delta^{13}C$ values (from – 16.7 ‰ in Dana Baai to – 10.8 ‰ in East London) that were intermediate between those of mussels and limpets (Tables 5.1 & 5.2). $\delta^{15}N$ values ranged from 9.3 ‰ (East London) to 13.8 ‰ (Langebaan) and on average were enriched by + 2.7 ‰ (± 0.4) compared to benthic invertebrates (Tables 5.1). Blood-feather discrimination in adults was + 0.5 ‰ (± 0.5) for $\delta^{13}C$ and + 1.6 ‰ (± 0.4) for $\delta^{15}N$. (n = 71).

No significant correlation existed between the geographic variations of $\delta^{13}C$ values of mussels or limpets and the blood of ABOs (Spearman's rank correlation test; Adults: $R^2_{blood\text{-}mussels}$ = 0.41, p = 0.16, $R^2_{blood\text{-}limpets}$ = 0.01, p = 0.98; Chicks: $R^2_{blood\text{-}mussels}$ = 0.47, p = 0.10, $R^2_{blood\text{-}limpets}$ = 0.20, p = 0.55), nor did blood display clear geographic patterns in ^{13}C signatures. However, an increase in the ^{13}C signatures in blood was visible between Plettenberg Bay and the more easterly sites. Overall, blood $\delta^{13}C$ values varied between the mean values of mussels and limpets along the coastline, suggesting that the ^{13}C signatures of ABOs were dependent on the relative consumption of filter-feeders or grazers. Blood and feather carbon-isotope signatures of adults displayed identical patterns across the ABO breeding range (Fig. 5.3a) and showed a strong correlation (Pearson's correlation test, $R^2_{blood\text{-}feathers}$ = 0.92; p < 0.01).

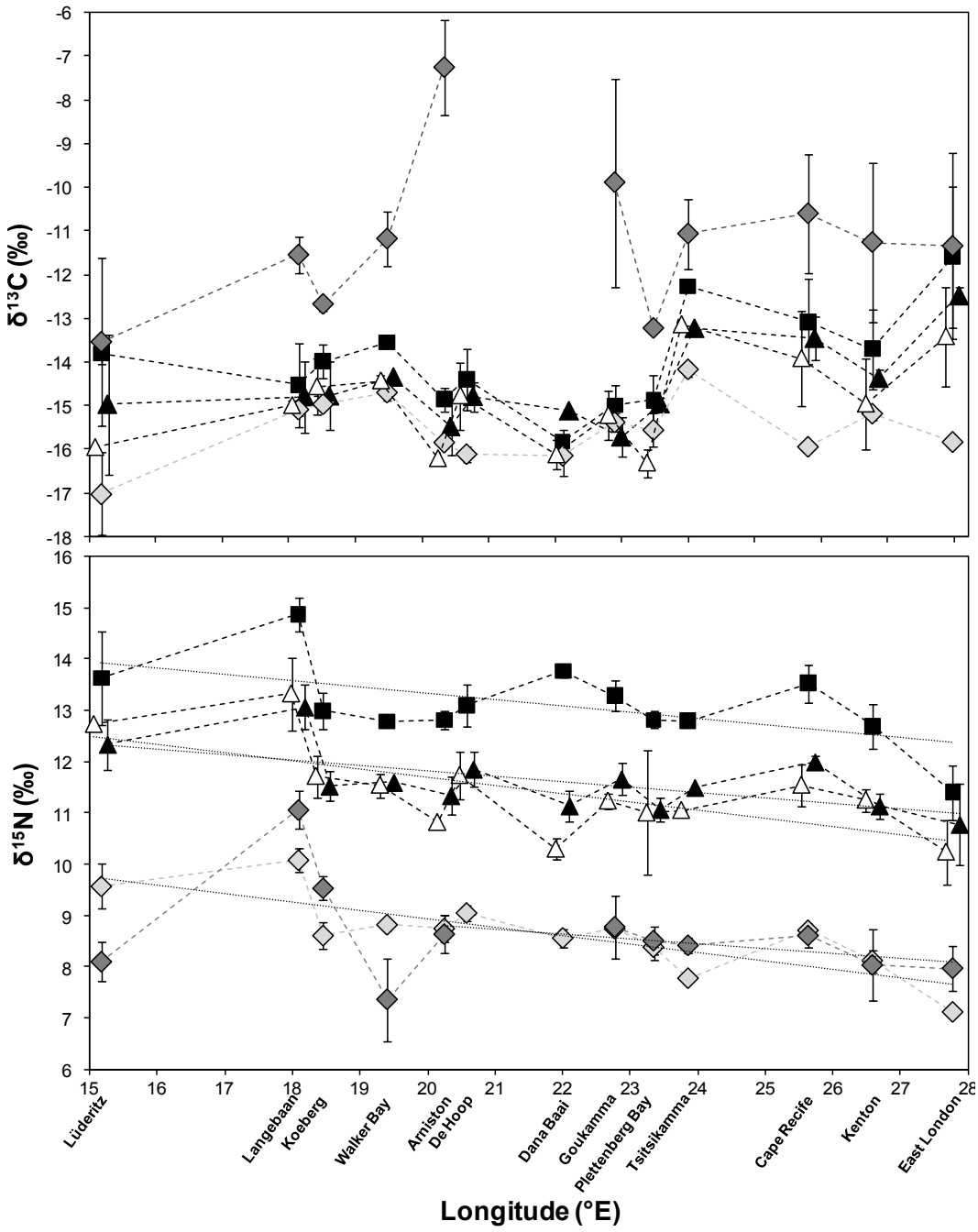


Figure 5.3. Stable carbon (a) and nitrogen (b) isotope ratios (‰) of blood (dark triangle) and feathers (dark square) of adult oystercatchers, blood of chicks (empty trinagle), mussels (light grey diamonds) and limpets (dark grey diamonds) along the coastline. Values are mean ± SD. Dotted lines indicated significant correlation with longitude. Adults and chicks mean ratios are voluntarily shifted for more clarity

Ratios d'isotopes stables du carbon (a) et de l'azote (b) (‰) du sang (triangle noir) et des plumes (carré noir) des adultes huîtriers, du sang des poussins (triangle vide), des moules (diamant gris clair) et des patelles (diamant gris foncé) sur les côtes de l'Afrique australe. Les valeurs représentées sont les moyennes (± écart-types). Les lignes en pointillés indiquent des corrélations significatives avec la longitude. Les ratios moyens des adultes et poussins sont volntairement décalés pour des raisons de lisibilités.

The $\delta^{15}N$ variations of ABO tissues along the coastline showed very similar patterns to mussels (Pearson's correlation test, Adults: $R^2_{blood\text{-}mussels} = 0.86$, $p < 0.01$; Chicks: $R^2_{blood\text{-}mussels} = 0.85$, $p < 0.01$). Significant depletion was observed from Lüderitz to East London in the blood of adults and chicks (Pearson's correlation test, Adults: $R^2_{blood\text{-}longitude} = 0.61$, $p = 0.03$; Chicks: $R^2_{blood\text{-}longitude} = 0.69$, $p < 0.01$) and in adult feathers (Pearson's correlation test, $R^2_{feathers\text{-}longitude} = 0.57$, $p = 0.04$). Blood and feathers of adults displayed very significant correlations along the coastline (Pearson's correlation test, $R^2_{blood\text{-}feathers} = 0.81$, $p < 0.01$) between Namibia and the south-east coast of South Africa (Fig. 5.3b).

K-means classifications based on the $\delta^{13}C$ and $\delta^{15}N$ ratios of blood and feathers of adults showed a similar biogeographic pattern between tissues (Fig 5.4a & b). Classifications were subsequently confirmed by a DFA with 100% accuracy. Group A was characterized by enriched ^{13}C signatures in blood (Group A centroids: $\delta^{13}C = -13.1$ ‰, $\delta^{15}N = 11.4$ ‰) and grouped 3 of the 4 most eastern sites together (Tsitsikamma being at the eastern limit of the south-west coast) (Fig. 5.4a). Group B had intermediate ^{13}C signatures and enriched ^{15}N signatures (Group B centroids: $\delta^{13}C = -14.7$‰, $\delta^{15}N = 11.9$‰) compared to other groups and was composed of all the western sites but also Kenton (south-east coast) and De Hoop (south-west coast). Group C was exclusively composed of south-west coast sites and was defined by depleted ^{13}C signatures and ^{15}N signatures similar to those of Group B (Group C centroids: $\delta^{13}C = -15.3$‰, $\delta^{15}N = 11.3$‰). Feather classification displayed a similar pattern, with the exception of Cape Recife that fell into Group B with the western sites, De Hoop and Kenton.

Trophic relationships between benthic invertebrates and African Black Oystercatchers along the coastline. The relative contributions of mussels and limpets to the diet of ABOs varied greatly across the sampling area, with a contrast between the west/south-west coasts and the south-east coast (Fig. 5.5). ABOs relied almost exclusively on mussels between Langebaan (95.0 %) and Goukamma (91.7 %) while the contributions of mussels and limpets were more balanced in Namibia (60.1 and 39.9 % respectively) and at the eastern sites, between Plettenberg Bay and Kenton ($Min_{mussels} = 38.2 \pm 14.8$ %; $Max_{mussels} = 72.1 \pm 7.4$ %). In East London, 74.1 % of the overall diet of ABOs was composed of limpets.

The presence/absence of limpets on feeding grounds (see Fig. 5.5) had no effect on the overall dietary composition of birds (ANOVA; $F_{1,11} = 2.20$, $p = 0.17$). The

presence of *M. galloprovincialis* however had a significant effect expressed as an increase in the relative contribution of mussels to ABOs diets (ANOVA, $F_{1,11} = 5.54$, $p = 0.04$). Additionally there was no significant interaction between the effects of *M. galloprovincialis* and whether limpets were present (ANOVA, $F_{2,10} = 3.27$, $p = 0.08$).

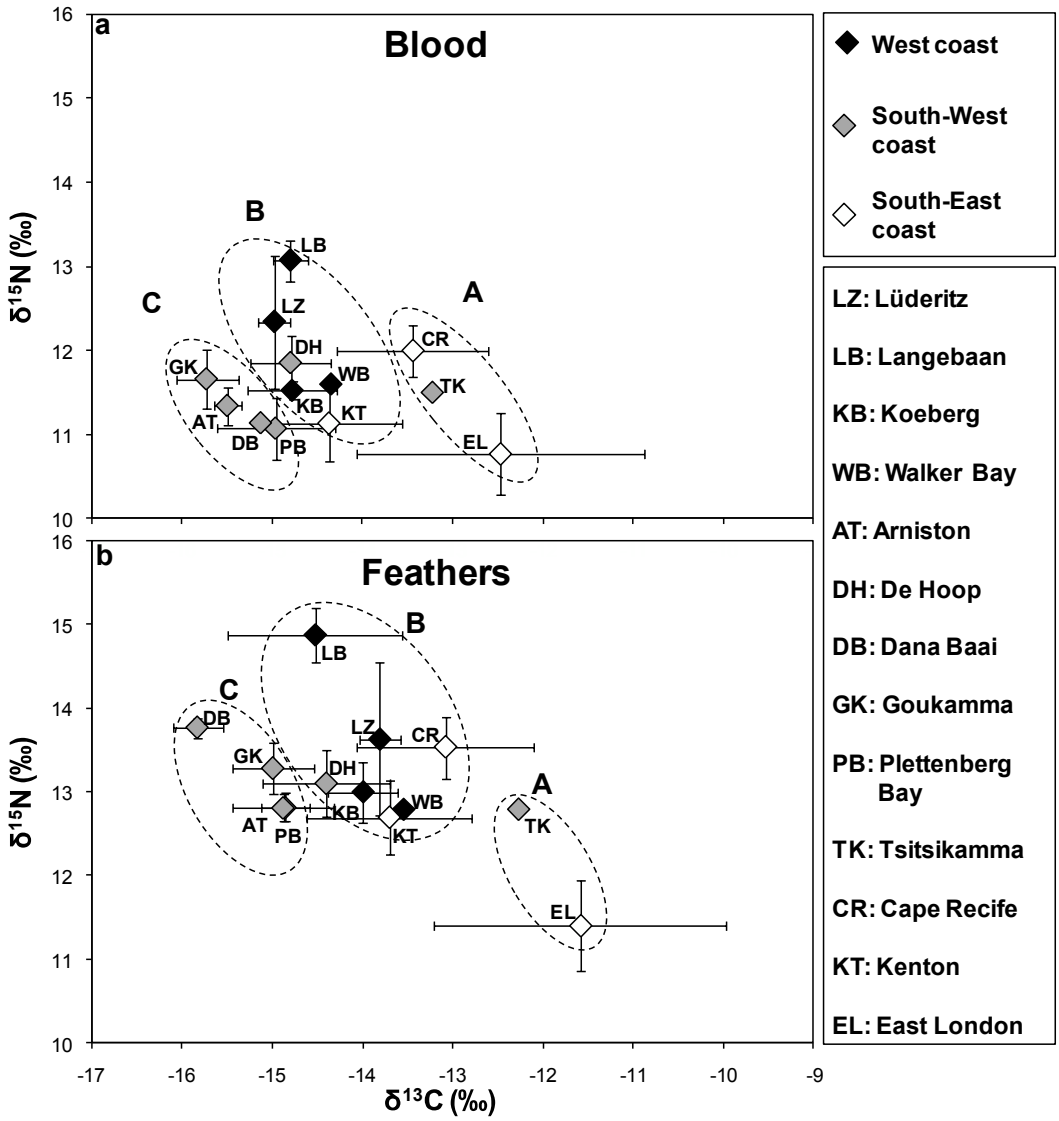


Figure 5.4. $\delta^{13}C$ and $\delta^{15}N$ ratios in blood (a) and feathers (b) of adult birds. Dotted circles indicate grouping of sites accroding to k-means cluster analysis and confirmed by a discriminant function analysis. Shading of diamonds shows the isotopic regions described by Hill et al. (2006).

Ratios de $\delta^{13}C$ et $\delta^{15}N$ dans le sang (a) et les plumes (b) des huîtriers adultes. Les cercles pointillés indiquent les groupes définies par l'analyse de cluster (k-means) et confirmés par une analyse fonctionnelle dsciminante. La coloration des symboles montrent les régions isotopiques décrites par Hill et al. (2006).

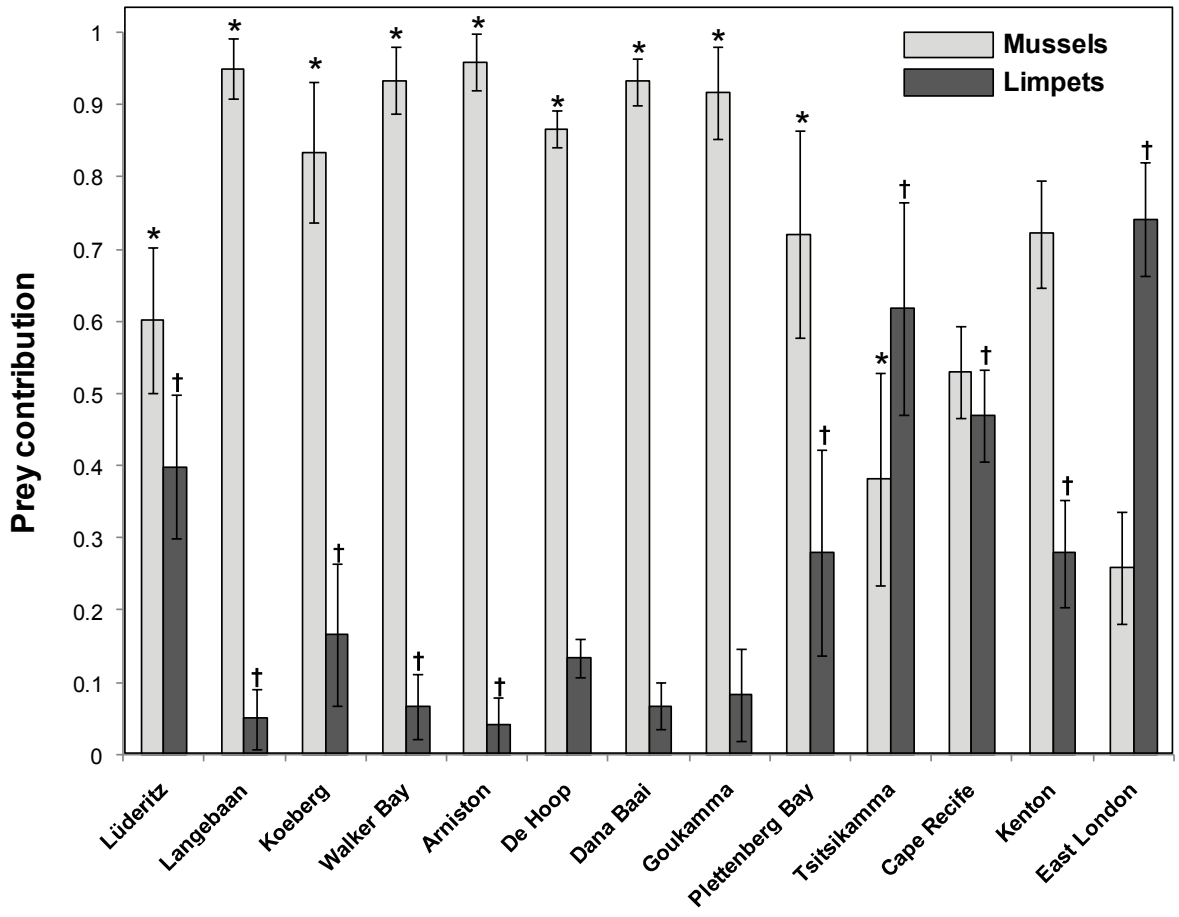


Figure 5.5. Contributions of mussels and limpets to the African Black Oystercatchers diet along the coastline. Values are mean ± SD estimated from Bayesian mixing models (SIAR). Results for mussels species and limpet species were pooled for each site according to Phillips et al. (2005) a posteriori aggregation. *indicates sites where Mytilus galloprovincialis was present. †indicates sites where limpets were present on the feeding grounds.

*Contributions des moules et des patelles dans le régime alimentaires des huîtriers noirs africains sur l'ensemble de la zone d'étude. Les valeurs indiquées sont les moyennes (± écart-types) estimées par le modèle de mélange isotopique baysien (SIAR). Les résultats pour les espèces de moules et de patelles ont été regroupés a posteriori pour chaque site selon Phillips et al. (2005). *indique les sites où Mytilus galloprovincialis était présente. † indique les sites où les patelles étaient présente sur les territoires d'alimentation*

4. DISCUSSION

The $\delta^{13}C$ and $\delta^{15}N$ signatures of ABOs in this study discriminated between birds from different biogeographic locations, grouping them together in three distinct clusters. Birds from the west coast were enriched in ^{15}N, birds from the south-east coast were enriched in ^{13}C and birds from the south-west coast had depleted $\delta^{13}C$ ratios (see Fig 5.4). This clear isotopic pattern in biogeography is similar to previous studies conducted from lower trophic levels to top predators in the region (Hill et al. 2006, Hill & McQuaid 2008, Fig 5.2, Jaquemet & McQuaid 2008), where organisms from the Agulhas and Benguela systems could be segregated by their carbon and nitrogen signatures. Furthermore, differences in $\delta^{13}C$ signatures of oystercatchers among sites reflected variations in the relative consumption of mussels and limpets associated with changes in prey community structure (Hockey & Von Erkom Schurink 1992, Bustamante & Branch 1996b).

Oligotrophic versus productive systems. Clear ^{15}N enrichment was observed between the south-east and west coasts in oystercatchers and mussels, and to a lesser extent in limpets. This westwards enrichment was previously described for rocky shore mussels and other benthic filter-feeders on the South African coastline (Hill et al. 2006, Hill & McQuaid 2008, Fig 5.2) and for Cape Gannets (*Morus capensis*) on offshore islands (Jaquemet & McQuaid 2008). Presumably the $\delta^{15}N$ gradient between organisms from the regions dominated by the Agulhas current and the Benguela upwelling system mirrors the isotope shift described by Saino & Hattori (1980) between waters that are oligotrophic (reliance on recycled nitrogen – ^{15}N depleted) to those that are eutrophic (rich in nitrates – ^{15}N enriched). Surprisingly, however, the southeast – west coast increase in $\delta^{15}N$ was disjointed and samples collected in Cape Recife, just outside Port Elizabeth, and Langebaan located within Saldanha Bay displayed high nitrogen-isotope ratios compared to adjacent sampling sites. This may be the result of increased nitrogen-loading through anthropogenic inputs (Heaton 1986, Schaal et al. 2010) associated with urban, industrial and tourist activities in these areas. Another discrepancy was observed in Walker Bay where the limpet *S. granularis* displayed ^{15}N-depleted signatures. We do not have a clear explanation for this pattern other than possible local depletion in de $\delta^{15}N$ ratios of the benthic algae on which this limpet grazes. Overall local and large-scale patterns of nitrogen-isotope ratios in benthic invertebrates and oystercatchers confirm that large scale physical processes affecting patterns of primary productivity are transmitted up through the intertidal food web to a rocky shore predator.

Carbon signatures of ABOs and their prey showed clear differences from biogeographic patterns of ^{13}C enrichment in SPM and mussels from the east coast to Cape Agulhas, which were suggested to mirror changes in the overall composition of nearshore SPM (phytoplankton vs. macroalgae detritus; Hill et al. 2006, see also Bode et al. 2006). Our mussel data showed consistent $\delta^{13}C$ ratios across the board of approximately – 15.7 ‰ (± 0.5) between Arniston and East London, with one exception (Tsitsikamma = – 14.2 ± 0.2 ‰). This difference from previous studies probably reflects the type of local and inter-annual changes in coastal hydrography described by Hill et al. (2008). In contrast, the $\delta^{13}C$ depletion in mussels, limpets and oystercatchers sampled off the Namibian coast conformed to expected biogeographic patterns (Hill et al. 2006) and thus appears to be consistent through time and visible at multiple levels of the intertidal food web. The mechanisms behind this depletion are not well understood and further isotopic investigations into nutrient dynamics and upwelling processes of the Benguela ecosystem are needed. With the exception of Lüderitz, the geographic variations of limpet $\delta^{13}C$ ratios (Fig. 5.3a) appeared to be linked to the species pool rather than environmental conditions. For example, the territorial limpet *Scutellastra longicosta* displayed particularly ^{13}C-enriched signatures, which confirmed its reliance on gardens of *Ralfsia verrucosa* (See Chapter 2, McQuaid & Froneman 1993, Hill & McQuaid 2008) and clearly departed from the $\delta^{13}C$ displayed by other species. This obviously increased the mean $\delta^{13}C$ values for limpets on the south west and south east coast when *S. longicosta* was present (see Table 5.2). Some significant localized variations and large standard deviations in limpets (see Table 5.2) also suggested local and micro-scale variability, either in the composition of the benthic algae and/or the conditions (e.g. carbon source, light intensity, temperature) affecting photosynthesis and therefore isotopic fractionation of the benthic primary producers on which the limpets graze (Wong & Sackett 1978, Burkhardt et al. 1999).

Large scale $\delta^{13}C$ patterns at the base of marine food webs in relation to spatial variability of CO_2 concentration, water temperature and growth rates of primary producers (Rau et al. 1982, Goericke & Fry 1994) have been widely used to investigate animal migration patterns (see review in Hobson 1999b) and foraging movements in marine predators (Burton & Koch 1999, Quillfeldt et al. 2005). $\delta^{13}C$ ratios can also be used to identify the ultimate sources of carbon for consumers when the ^{13}C signatures of food sources differ (Post 2002), and in the case of higher level predators, can help to determine the main component of the diet. This latter aspect

was clearly shown in this study, with the blood $\delta^{13}C$ variations in ABOs not correlating with the geographic variations displayed by either mussels or limpets, but instead oscillating between the contrasting ^{13}C signatures of the two main prey items. This confirms the fact that although primary/secondary consumer ratios may reflect geographic differences in nutrient/primary productivity regimes, variations in the $\delta^{13}C$ signatures of ABOs are primarily due to the proportion of grazers and filter-feeders in their diet across the sampling range.

Impact of prey assemblages on the diet of African Black Oystercatchers. The blood $\delta^{13}C$ signatures of oystercatchers varied significantly along the coastline, ranging between approximately – 11.0 ‰ and – 17.0 ‰, with maximum $\delta^{13}C$ values observed between Tsitsikamma and East London, and lowest value on the south-west coast. Limpets were enriched in ^{13}C compared to mussels throughout the study area, which is an isotopic segregation typically observed between grazers and filter-feeders (Post 2002, Schaal et al. 2008). In contrast, the ^{15}N signatures of mussels and limpets were very similar at a local scale, with the exception of the west coast, and varied mostly in relation to changes in primary production processes associated with the Benguela and Agulhas ecosystems.

Broadly contrasting $\delta^{13}C$ ratios and local differences in $\delta^{15}N$ ratios between prey allowed the application of the stable isotope mixing model SIAR to relate geographic variations in ABO isotope signatures to potential changes in the assimilation of mussels or limpets in their diet along the coastline. The SIAR model revealed a biogeographic pattern in the contribution of different prey to the diet of ABOs with the diet largely dominated by mussels on the west and south-west coasts of South Africa and a mixed diet of mussels and limpets in Namibia and on the south-east coast of South Africa. Finally, on the eastern boundary of the study area, limpets made up nearly 75 % of the prey items assimilated by ABOs (Fig. 5). This shift in diet along the coastline indicates that ABO prey selection is influenced by prey availability, which reflects biogeographic trends in species composition and abundances along the coastline (Bustamante & Branch 1996b). The extremely high abundances of the invasive Mediterranean mussel on the west coast have a particularly clear effect on bird diets (see results).

The west coast supports a higher intertidal invertebrate biomass than the south and east coasts, reflecting the higher productivity of the Benguela upwelling system as opposed to the oligotrophic Agulhas current. Following the arrival of the

invasive Mediterranean mussel on the west coast in the 1980's (Grant & Cherry 1985), the benthic biomass on rocky shores in this region became largely dominated by this species (Robinson et al. 2007). In Saldanha Bay, a change in the feeding habits of ABOs following the invasion by *M. galloprovincialis* in the 1980's has been described for three offshore Islands, based on direct observations or collection of emptied molluscs shells left by adults feeding their chicks (Hockey & Van Erkom Schurink 1992, Coleman & Hockey 2008). ABOs had shifted from a mixed diet of mussels (the ribbed mussel *Aulocomya ater* and the black mussel *Choromytilus meridionalis*) and limpets (mainly S*. granularis* on these islands) prior to the invasion, to a diet dominated by *M. galloprovincialis* in the late 1980s and 1990s. Our results show an even more extreme scenario in Langebaan in 2009 (also situated in Saldanha Bay, but on the mainland), where *M. galloprovincialis* accounts for 95% of the prey versus 5% for the limpet *S. argenvillei*. In Walker Bay and Koeberg, similar preference of the invasive mussel was observed (Fig. 5.5), despite the presence of the limpets *S. granularis* or *S. argenvillei* previously favoured by ABOs (Hockey & Underhill 1984). During the 1979/1980 breeding season in the Lüderitz region (Namibia), the diet of ABOs was almost exclusively composed of limpets (average 96.8%; Hockey & Underhill 1984). *M. galloprovincialis* is now well established on the southern Namibian coast and dominates rocky shores in the Lüderitz region (*B. Currie, pers. com.*). Results from this study show that mussels have become the predominant source of food for ABOs here, although limpets still contribute significantly (39.9% ±0.6). Although the diet of oystercatchers remains more balanced in Namibia than on the South African west coast, the increasing reliance on the Mediterranean mussel reflects a clear dietary shift in response to changes in prey availability. On the south-west coast, mussels also dominated the diet of ABOs (between 72% and 95%), except at the eastern boundary of the region (only 40%), in Tsitsikamma (see Fig. 5.5). This is not surprising as limpets were scarce or even absent from oystercatchers feeding grounds between De Hoop and Goukamma. The inverse proportions of filter-feeders and grazers in the diet of ABOs between Plettenberg Bay (Mussels = 72 %; Limpets = 28 %) and Tsitsikamma (Mussels = 38 %; Limpets = 62 %) is however surprising considering that the two sites are separated by only ~ 50 km (see Fig. 5.1). Bownes & McQuaid (2006) investigated the potential for *M. galloprovincialis* to replace the indigenous mussel *P. perna* on the south coast, in Plettenberg Bay and Tsitsikamma. They observed that mussel abundance was significantly lower in Tsitsikamma than in Plettenberg Bay, which

forms a focal point of high *M. galloprovincialis* abundance along this coast (von der Meden et al. 2008) and mixing model outputs from our study support these finding. *P. perna* and *M. galloprovincialis* co-occurred at six sites, but were sometimes the only prey available. Based on empty shell and feeding area analysis, Kohler et al. (2009b) reported active selection of the invasive mussel by ABOs feeding their chicks rather than the indigenous mussel at Port Elizabeth, probably because *M. galloprovincialis* has weaker attachment strength than *P. perna* (Zardi et al. 2007). Unfortunately, the lack of differences in $\delta^{13}C$ and $\delta^{15}N$ signatures between these two mussel species prevented confirmation of this selective behaviour further west where they often co-occur. This emphasizes the need to combine stable isotope analyses with more conventional techniques (e.g. feeding behaviour observations, collection of food remains) in the study of marine predators when possible.

The diet of ABOs on the south-east coast was characterized by a significant contribution of limpets; however the brown mussel *P. perna* was also well represented, specifically in Kenton (72 %). This is consistent with a previous study (Kohler et al. 2009b), where *P. perna* represented between 84 and 97 % of the relative prey abundance on three of the feeding grounds sampled in this area for the present study. Indeed mussel dominance on rocky shores is driven by wave exposure (Bustamante & Branch 1996b), which is strong in Kenton (McQuaid & Lindsay 2007). *M. galloprovincialis* remains scarce and site-specific on this part of the coastline (Bownes & McQuaid 2006) and no invasive mussel >16 mm (minimum shell size for consumption by ABOs, see Hockey & Underhill 1984) were found on feeding grounds sampled at Cape Recife, Kenton or East London. Thus, as opposed to the south-west and west coasts sites, breeding sites sampled on the south-east coast have so far effectively been unaffected by the *M. galloprovincialis* invasion. Thus the feeding behaviour of ABOs on the south-east coast can also be regarded as "unaltered", but will be mediated by extrinsic factors such as wave action and sex-specific or individual specialization (see Chapter 4), as documented for other oystercatcher species (Baker 1974, Goss-Custard & Sutherland 1984, Lauro & Nol 1995).

Seasonal variation in the trophic ecology of the African Black Oystercatcher. Variations in stable isotope ratios of blood and feathers, displayed very strong correlations along the coastline for both $\delta^{13}C$ and $\delta^{15}N$. Since adult ABOs are known to be territorial year-round (Hockey 1996), this suggests an overall seasonal stability

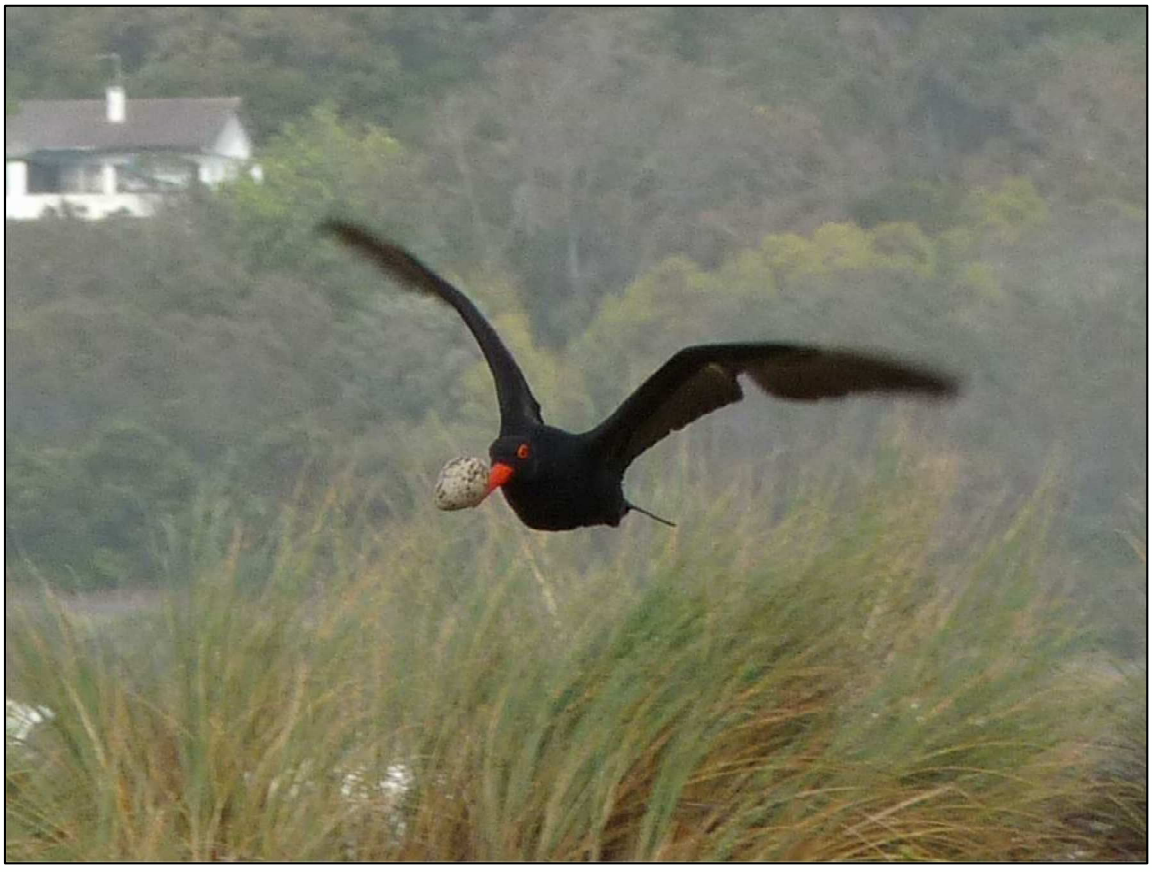
in the environmental conditions influencing rocky shore food webs along the coastline and a consistency in the feeding behavior of adults throughout the year. However, some local discrepancies were observed between the blood and feather ratios. In East London for example, the blood-feather $\delta^{15}N$ discrimination factor was + 0.6 ‰ (as opposed to + 1.6 ‰ (± 0.4) for adults throughout the study area and + 1.3 ‰ (± 0.5) for chicks in Chapter 3). This indicates either a seasonal shift in feeding behaviour, or that outside the breeding season, ABOs from East London feed in areas with lower $\delta^{15}N$ ratios at the base of the food web than in their breeding site. Another clear blood-feather shift was in DanaBaai (+ 2.6‰) which indicated that adults there seem to feed in a wintering habitat with a higher basal $\delta^{15}N$ than the breeding habitat.

Climate variations between seasons are mild in the study region compared to the north hemisphere, where oystercatchers have to endure harsh winters and often migrate southwards (Goss-Custard et al. 1996). Consequently, like the other southern hemisphere oystercatcher species, breeding ABOs do not migrate after reproduction, but remain territorial year-round and, especially those birds that breed on offshore islands on the west coast of South Africa, (Hockey 1996, Tjørve & Underhill 2006, Coleman & Hockey 2008). However color-ringed birds have been resighted in flocks over 10 km east from their breeding site during the non-breeding season in the East London region (SAFRING), while in Kenton, color-ringed pairs are rarely spotted on their breeding site outside the breeding season (*pers. obs.*). Similarly in Goukamma and Plettenberg Bay, breeding pairs do no stay on their breeding site, instead large flocks of birds gather around river mouths and on beaches during winter (*J. Huisamen & C.D. McQuaid, pers. com.*). Therefore it seems that on the south-west and south-east coasts, adults move around substantially outside the breeding season. This again reflects a contrast between the west coast and the rest of the ABOs breeding range. One potential explanation may be that breeders are not bound to their feeding territory and their confines during winter and may choose to move to more advantageous feeding areas. Conversely, on the west coast, feeding territories may be profitable for year-round occupation, because of high food biomass (Hockey & Van Erkom Schurink 1992, Bustamante et al. 1995b, Bustamante & Branch 1996b). Further investigation of the wintering movement strategies of ABOs would require complementary techniques such as radio-telemetry (Warnock & Takekawa 2003, Wilson et al. 2009)

Conclusion. Overall we show that carbon and nitrogen stable isotope ratios in a rocky shore avian predator, the African Black Oystercatcher, were able to integrate a balance of large scale patterns of oceanic productivity and local-scale prey assemblages. This indicates that the influence of major large-scale current systems penetrates to the top of the food web, but that local-scale effects embedded within this framework can be important. The $\delta^{15}N$ variations of the tissues of ABOs were indicative of changes in intertidal nutrient quality in relation to major oceanic influences along the southern African coastline and local anthropogenic perturbations. $\delta^{13}C$ ratios and stable isotope mixing models revealed geographic changes in the main diet of ABOs that were strongly influenced by the presence of the invasive mussel, *M. galloprovincialis*. ABOs demonstrated plasticity in their trophic ecology in connection with biogeographic provinces, changes in prey communities and seasonality. In the context of global changes and overexploitation of marine resources, this could help them face future changes in their trophic environment.

CHAPITRE 6

Parental roles and feeding strategies of African Black Oystercatchers during incubation and chick-rearing periods



(Photo : S. Kohler, Africa Birds & Birding, Annexe 7)

RESUME

Le compromis entre la reproduction actuelle et les perspectives de survie et de reproductions futures constitue la base des théories actuelles sur les traits d'histoire de vie et l'évolution. La reproduction a un coût énergétique et immunitaire important pour les oiseaux mais limite également le temps alloué à la recherche de nourriture pour leur propre maintien. Chez les huîtriers, le coût de la reproduction est partagé également entre les deux sexes notamment pendant l'incubation et l'élevage des poussins. Par ailleurs, chez le genre *Haematopus*, les poussins sont nidifuges mais requierent le nourrissage par les parents jusqu'à plusieurs mois après d'envol. La saison de reproduction de l'huîtrier noir africain coïncide avec la saison touristique estivale en Afrique du sud. Les couples reproducteurs sont donc soumis à une perturbation accrue des activités humaines sur les côtes à la période de leur cycle annuel où leur coûts énergétiques et leurs enjeux à long terme sont les plus forts. Les oiseaux limicoles qui se nourrissent sur les estrans devraient être capables d'organiser leurs activités journalières autour du cycle diurne des marées en fonction de leurs propres besoin énergétiques et ceux de leur progéniture mais aussi des caractéristiques de leur environnement. Dans ce chapitre, j'ai donc examiné le partage des rôles parentaux des huîtriers noirs africains pendant les périodes d'incubation et de nourrissage des poussins ainsi que les stratégies de nourrissage et de reproduction leur permettant de maximiser leur apports de nourriture et leur chances de succès reproducteur. Douze couples ont été suivis sur les côtes sud-est et sud-ouest pendant la période d'incubation et deux pendant la période d'élevage des poussins. Des sessions d'observations continues de 6 à 8 heures, concentrées autour de la basse mer diurne, ont été accomplies sur les couples, et les activités (nourrissage, incubation, repos, soins, agressions etc...) de chaque individu suivi ont été enregistrées toutes les 5 minutes. De plus, les événements tels que les interactions avec d'autres huîtriers ou d'autres espèces indigènes et les perturbations occasionnées par les activités humaines ont été notées. Les femelles passaient plus de temps à incuber et les mâles plus de temps à se nourrir pendant la journée lors de la période de reproduction. De plus, dans la région sud-est, les mâles semblaient accentuer leurs efforts de nourrissage autour de la basse mer. Les différences de tendances temporelles observées dans le comportement alimentaire des mâles entre le sud-est et le sud-ouest restent difficiles à interpréter, mais pourraient être liées aux différences de structure de communautés des proies entre les deux régions, aux préférences alimentaires des mâles ainsi qu'au comportement des proies,

notamment des moules. Les femelles en contrepartie pourraient accentuer leur apport de nourriture pendant la nuit, pendant laquelle les mâles pourraient incuber pendant de plus longues périodes. A plusieurs reprises, les oiseaux ont montré des comportements alimentaires peu référencés tels que la nécrophagie sur des organismes échoués en haut d'estran et le nourrissage sur des zones hors des limites du territoire sur des dunes. Les interactions des individus étudiés avec d'autres couples établis étaient rares et rapidement résolues. Inversement, les perturbations occasionnées par des non-reproducteurs et les activités humaines (pêche récréative et utilisation des plages par les vacanciers) ont été observées de manière récurrente et parfois sur de longues périodes et pourraient constituer une perte de temps de nourrissage significative et un risque de prédation accru sur les nids. Pendant le nourrissage des poussins, les mâles et femelles ont montré peu de différences dans leurs rôles respectifs vis-à-vis du poussin. les deux sites de reproduction suvis montraient des différences dans la configuration territoire de reproduction-zone d'alimentation, menant à des strétagies d'alimentation différentes des couples pour survenir à leurs besoins et à ceux de leurs poussin, similaires à celles décrites pour l'huîtrier européen (« leap-frog » et « resident »).

Cette étude, d'une part souligne la flexibilité du comportement alimentaire des huîtriers noirs africains vis-à-vis de leurs conditions environnementales pendant la reproduction et, d'autre part suggère qu'une part des limites du succès reproducteur des huîtriers noirs africains pourrait être liée à l'intensité des interactions agonistiques avec les huîtriers non-résidents et les activités humaines estivales sur les littoraux sud-africains.

1. INTRODUCTION

The assumption that future reproductive outputs and survival decrease with allocation of resources to current reproduction, otherwise known as the “cost of reproduction”, is central to life-history theory and evolutionary biology (Williams 1966, Reid 1987). Limited internal resources have typically been viewed as the main constrain causing allocation trade-offs during the breeding period. Reproduction also reduces the time with opportunities of foraging and compromises immune functions and defenses against parasitism, stress and diseases (Hanssen et al. 2005, Harshman & Zera 2006). Thus long-lived birds in particular should minimized the risk of adult mortality during reproduction and maximize the chance of future breeding success (Williams 1966). The male and female of a breeding pair have a shared interest in successfully raising their common young, although each parent would do better if the other one was doing most of the hard work. This opposite interest of the sexes leads to sexual conflict over care (Kosztolányi & Székely 2002). However in monogamous and long-lived species such as oystercatchers, paired males and females fully share current and future interests, therefore, breeding partners should divide their parental effort more or less equally (Bergstrom 1986, Kosztolányi 2003).

Shorebirds (Charadrii) exhibits one of the highest diversity of parental care, here defined as any parental behaviour that increases the survival prospects of the offspring (Clutton-Brock 1991), compared to other bird taxa (Székely & Reynolds 1995). It varies along a gradient from the two extreme mode of uniparental care provided by the male (e.g. jacanas and curlews) or the female (mainly represented in plover species), to full biparental care (e.g. oystercatchers and avocets). The length of care may also vary, from a few days to several years and the different forms of parental care in birds include territorial defense, incubation of eggs, feeding and protection of chicks (Kosztolányi & Székely 2002).

There are two main opposite strategies related to brood rearing in birds, namely the altrical and the precocial strategies, that have evolved in relation with variable food availability and predation risks (Ar & Yom-Tov 1978). Altrical chicks have closed eyes, little or no down, are secluded to the nest and entirely dependent on their parents for food until they fledge. It is the situation of all passerine species. Precocial chicks on the other hand are fully mobile at hatching and capable of feeding on their own early on. There are however many intermediary modes of parental care along this precocial-altrical gradient (O’Connor 1984) that are

preponderant in shorebird species. Categories of chick's precociality in shorebirds range from the semi-altrical mode (incapable of leaving the nest, open eyes and covered with down), solely represented by the crab-plover (*Dromas ardeola*), to full-precocial chicks (ex: plovers) that follow their parents but find their own food. Chicks of the *Haematopus* genera are however unique in that they are fully mobile, but are fed entirely by their parents, sometimes up to half a year old (Safriel et al. 1996).

African Black Oystercatchers (ABOs) display modest sexual body size dimorphism, with female being larger than males while the longer and more pointed bills of females compared to their mates is a pronounced dimorphic feature that has been described in all oystercatcher species (Hockey 1996, Chapter 5). The difference in reproductive roles of males and females is one of the three selective forces (along with resource partitioning and sexual selection) that have been proposed to explain sexual dimorphism (Hedrick & Temeless 1989, Székely et al. 2000). Jönsson & Alerstam (1990) reviewed the adaptive significance of parental role division and sexual size dimorphism in shorebirds and suggested that sexual size body and bill length dimorphism in monogamous species should be associated with sexual role division during the reproduction, as an adaptation to make possible successful breeding under narrow resource conditions.

The breeding range of ABO is restricted to the coasts of Namibia and South Africa (25 and 75% of the breeding population respectively, Hockey 1983b) and the species breeds on the open coast and at offshore islands. ABOs feed in the intertidal zone almost exclusively therefore feeding constrains arise from tidal cycles that periodically limit access to feeding grounds and affect food availability for ABOs. Their breeding season on the South African coastline (November to March), coincides with the holiday season and make them particularly vulnerable to direct effects of human disturbances, at a period of intense and natural stress related to the cost of reproduction (Adams et al. 1999, Leseberg et al. 2000). These include the destruction of nests by walkers, predation of nest and chicks by unleashed dogs. Additionally, interruption of incubation and chick-attendance can lead to overheating off eggs, increase of predation risk and drowning of chicks. Finally recreational fishing can induce loss of parent foraging time (Lambeck et al. 1996).

Breeding shorebirds should be able to structure their daily activities to maximize the difference between costs and benefits in respect to tidal cycles, perturbations, incubation and chick-rearing obligations, weather conditions and prey

availability. In this context, the aims of this chapter are 1) to investigate the partitioning of parental care between male and female African Black Oystercatchers during the incubation and chick-rearing period and 2) to see whether ABOs adopt particular strategies in their incubation and chick-rearing behaviours to optimize their energy inputs and breeding success in respect to the natural and anthropogenic confines of their environment.

2. MATERIALS & METHODS

Study sites and breeding pairs. Fieldwork was carried out during the 2009-2010 breeding season at 4 study sites, Goukamma, Plettenberg Bay, Cape Recife and Kenton (See Chapter 1, Fig 1.1). A total of 12 pairs were followed during daytime incubation. These pairs were chosen for this particular study following 3 criteria 1) at least one of the breeding partner had been color-ringed during the 2007-2008 or 2008-2009 fieldwork seasons (Fig 6.1), 2) the configuration of the nesting/feeding area was suitable for observations with binoculars (8 x 40) from a hiding spot, 3) relatively good breeding success, based on the nest monitoring over the past two breeding seasons (carried out by myself, conservation authorities or bird clubs volunteers).

Figure 6.1. Color-rings put on *Haematopus moquini* during the 2007-2008 and 2008-2009 fieldwork seasons and used for the incubation and chick-rearing study in 2009-2010.

Bagues de couleurs posées sur Haematopus moquini *pendant les saisons 2007-2008 et 2008-2009 et utilisées pour le suivi des incubations et le nourrissage des poussins pendant la saison 2009-2010.*

Hatching success and chick survival were however particularly low during the 2009-2010 breeding season, therefore, not all the initial objectives were filled and only two pairs could be studied during the chick rearing period (see Material & Methods and Results below). Satellite views and descriptions of breeding pair territories are presented in Appendix 1 and Table 6.1 respectively. Schematic descriptions of the feeding areas are presented in Fig 6.2.

Table 6.1. Environmental characteristics of the 12 breeding territories

Caractéristiques environnementales des 12 territoires de reproduction

Study site	Breeding site	Pair number	Type of nest	Feeding area	Observations of chick rearing	Human activities
Kenton	High Rocks (Annexe 1a)	P1	Scrape in the sand	Mixed shore with wave-cut sandstone platforms. Mussels, limpets and worms present	No	Fishing area
		P2			No	
	Shelley Beach (Annexe 1b)	P1	Higher ground, on a rocky ledge		No	Touristic area
		P2			No	
Cape Recife (Annexe 1c)		P1	Scrape in the sand	Mixed shore with boulders field on the high shore and large sandstone rocks on the low shore. Mussels, limpets, worms and ascidians present	No	Touristic and fishing area
		P2			Yes	
		P3			No	
		P4			No	
		P5			No	
Plettenberg Bay	Robberg (Annexe 1d)	P0	Higher ground, in a rocky recess	Narrow rocky wave-cut platform, situated at the bottom of a cliff. Mussels and limpets present	No	Hiking trail
Goukamma	"River Mouth" (Annexe 1e)	P1	Scrape in the sand	Mixed shore with large sandstone rocks situated 500 meters from the nesting area. Mussels and worms present.	On hatching day	Touristic and fishing area
	Gericke's Point (Annexe 1f)	P2	Higher ground, in a rocky rift	Mixed shore with wave-cut sand	No	Touristic and fishing area

Observations during incubation. Observations of focal pairs were done either on one pair at the time by two observers or on two pairs simultaneously with one observer following each pair, depending on the configuration of the nesting/feeding areas (Appendix 1), using 8x40 binoculars. Initially, two observation sessions were supposed to be done on each focal pair. However 4 pairs lost their clutch before the second session and logistical constraints or weather conditions prevented us from doing a second session. Finally, the two pairs nesting at "Shelley Beach" in Kenton were additionally followed for 3 days in a row. Pairs were observed over daytime for 5 to 8 continuous hours (hereafter referred as "sessions"), starting 2 to 3 hours before low tide. A scan was made every 5 minutes (triggered by a stopwatch carried by each observer set to go off every 5 minutes) on each breeding partner and "activity" and location were recorded within 1 minute (Altmann 1974). Description of standardized activities is presented in Table 6.2.

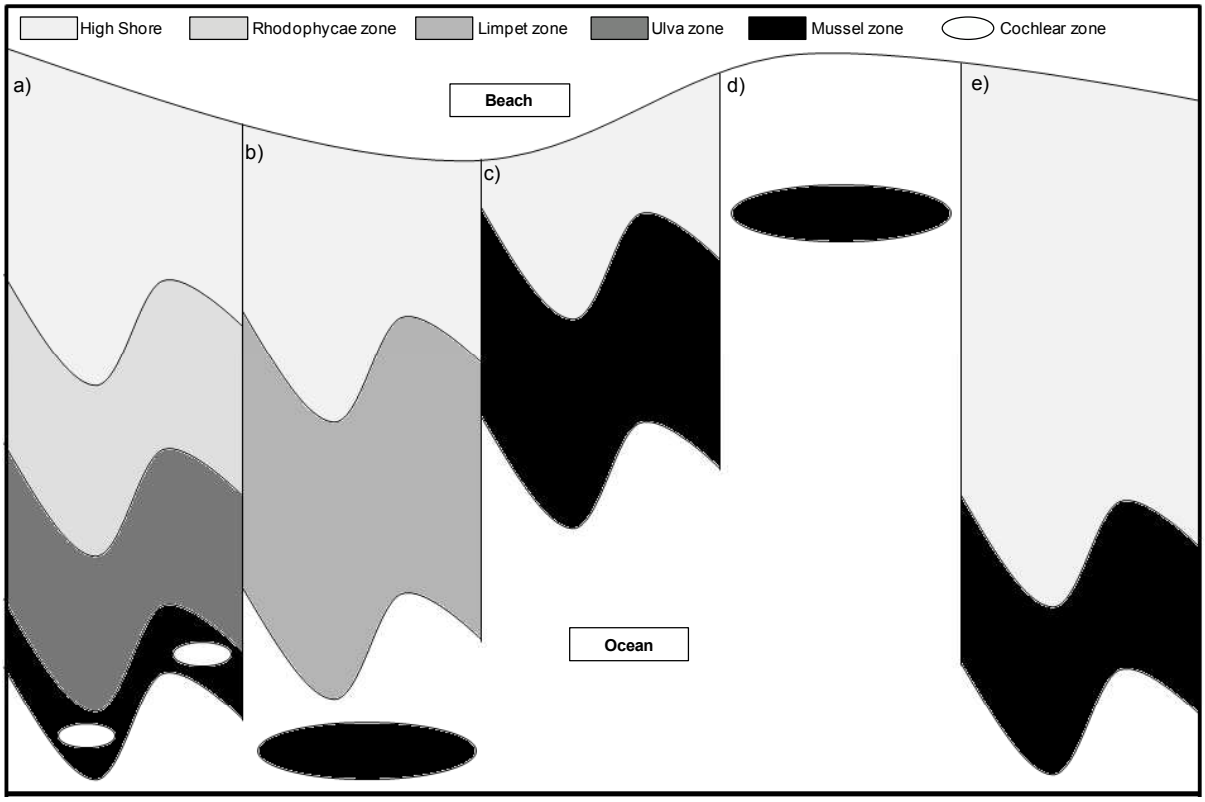


Figure 6.2. Schematic representation of the intertidal area zonations at a) Kenton , b) Cape Recife and c) Plettenberg Bay, d) Goukamma "Rivermouth" and e) Goukamma's "Gericke's Point"

Représentation schématique des zones intertidales à a) Kenton, b) Cape Recife, c) Plettenberg Bay, d) Goukamma "Rivermouth" et e) Goukamma's "Gericke's Point"

Observations during chick rearing. Two focal pairs managed to bring their eggs to hatching were followed during chick rearing, one in Cape Recife and one in Goukamma. Initially, we had planned on doing 1 session a week per pair for 4 weeks in a row; however the two chicks disappeared within 3 weeks after hatching. Therefore only two sessions were performed on each pair, the first when the chicks were ~3 days old and the second at 1~10 days old. Parents and their chick were followed for 4 hours by two observers, starting 2 hours before maximum low tide. Observations and recording of "activities" of parents were done in the same fashion as during incubation. There was however a distinction made with the "Standing up" activity. When the adult was standing up, alert and in proximity of the chick, it was considered "guarding the chick". The activity "feeding" also concerned bringing food to the chick (Table 6.2). For each scan, the parent accompanying the chick (male, female, neither or both) was recorded, to evaluate "chick" attendance by each breeding partner. This informs on the sex-related parental investment during chick-rearing period. Perturbation events (with conspecifics, other avian species or humans) were recorded similarly as during incubation. Finally, "chick feeding" event

by each parent and the type of food that was brought (e.g. mussel, limpet, worm etc …) were also recorded.

Table 6.2. Descriptions of categories of activity recorded during scans

Description des catégories d'activité notées lors des scans

Activities	Description
Feeding	Foraging, handling and consumption of prey, bringing food to ayhechick
Incubating	Seating or standing above the nest
Standing Up	Standing up still (outside the nest), alert or not
Preening	Bathing and preening of feathers
Resting	Seating (outside the nest) or sleeping, up with the head tucked under plumage
Territorial display	Piping, aggressions towards other oystercatchers or chasing
Locomotion	Walking, running or flying not associated with foraging
Out of territory	The bird is outside of is territory range and not visible to the observer
Out of sight	The bird is within tits territory but not visible to the observer
Chick caring	Feeding or preening of chicks (on hatching day only)
Chick guarding	Standing up, alert in proximity of the chick

Data Analyses. Several behavioural variables were calculated from the regular collection of activities and location of incubating and chick-rearing oystercatchers. Time and activity unit used for data analyses was the scan (1 scan = 5 minutes) and was converted into minutes when necessary. A Generalized Linear model (GLM, quasi-poisson distribution, $\alpha = 0.05$) was used to test whether males and females spent different amount of time in the different activities. Scan counts were used as the data unit.

- Time-activity budgets: To measure the relative importance of the time devoted to each type of activity by breeding partners during incubation and chick rearing, I calculated a time-activity index (TAI) per session and per sex (Morrier & McNeil 1991):

$$TAI\ (\%) = \frac{TSA\ \times 100}{TNS}$$

where *TSA* is the total number of scan recording a type of activity during the session and *TNS* is the total number of scan for the session.

- Duration of incubation shifts and nest attendance (%)**:** Duration of incubation shifts is defined as the time elapsed between the beginning of the incubation by a

given parent and the end when its breeding partner relieves the incubating parent. Incubation shifts that were on-going at the beginning or the end of the session are not taken into account.

The nest attendance (%) per bird per session was calculated as following:

$$\%\ nest\ attendance = \frac{(S_i + S_d)\ \times 100}{TNS}$$

where S_i is the number of scan with incubation activity, S_d is the number of scans during an incubation shift for which the bird was off the nest because of disturbances and *TNS* the total number of scans of the session. Sessions during which a great amount of disturbances occurred (see Appendix 1) and focal birds were off the nest for prolonged periods were not taken into account for the data analysis. This was the case for two sessions in Kenton, on Pair 1 in “High Rocks” and Pair 2 at “Shelley Beach” (see Appendix 1). Finally egg hatching occurred during the second session at Gericke’s Point (see Appendix 1), disrupting the feeding and incubation routines of the parent. This session was not used to calculate duration of incubation and nest attendance (%) either.

- Feeding-activity during incubation over the tidal cycle: Each session was divided into 1 hour (= 12 scans) intervals, relative to the time of maximal low tide (e.g. - 3h, -2h, -1h, +1h, +2h, +3h) and only full hour intervals were used. For example if the session started 1h35 before and ended 4h45 after low tide, then only the one hour before and the four hours after low tide would be used. Time of maximal low tide and tidal height variations for each session were taken from standard tide tables which provide hourly heights above chart datum *(www.sanho.co.za)*. Cumulated time devoted to feeding activities was calculated for each hourly interval for males and females and for each study site (Kenton, Cape Recife, Plettenberg Bay and Goukamma). Breeding partners of pair n°1 in Kenton “Shelley Beach” see Appendix 1b & 2b), spent a lot of time outside their breeding territory and no activity could be recorded for a significant number of scans. Therefore this pair and the session performed on hatching day in Goukamma “Gericke’s Point were not taken into account to calculate the time devoted to feeding.

- Chick attendance (%): the % of chick attendance by each of the parent was calculated as followed:

$$\%\ chick\ attendance = \frac{S_p \times 100}{TS}$$

where S_p is the number of scans during which the chick was accompanied by each parent and *TNS* is the total number of scans for the session.

3. RESULTS

Activities during incubation. Egg incubation was the most time-consuming activity for both males and females during the incubation period, however, there was a great variability regarding the amount of time spent incubating between days, even successive days (Fig 6.3b) and between pairs. Male and female incubation time-budget varied between 25 and 61% and 28 and 70% respectively and nest attendance was slightly but significantly greater for female than males (Fig 6.4). The "incubation" activity mostly consisted in the bird sitting on the nest. However on very hot days (> 35°C), incubating birds could be seen standing over and shading the eggs and/or keeping their bill open, most probably to prevent over-heating of their eggs and themselves (Downs & Ward 1997).

Feeding was the second most time-consuming activity and occupied about one-quarter of their time (Fig 6.3 and 6.5). During all sessions, males spent more time feeding (10 to 50% of their time budget) than their respective breeding partners, (1 to 30 %), except at High rocks where 2 breeding partners spent equivalent amount of time to feed (Fig 6.3a). Overall males spent significantly more time feeding than females during the incubation period (Fig 6.5). One pair in Kenton (Pair 1 at "Shelley Beach", Appendixs 1b and 2b) spent a large amount of time outside their breeding territory (10 ± 8 % and 27 ± 8 % of the time on average for the male and the female respectively, Fig 6.3b), therefore their time-budget activities, beside nest duties, could not be assessed properly. The female was usually seen taking off westwards, flying over the neighbouring pair's territory (noticed by the observer of Pair 2), up to the Bushman's River (Appendix 2b). This was recorded for each of the 5 sessions performed on this breeding pair.

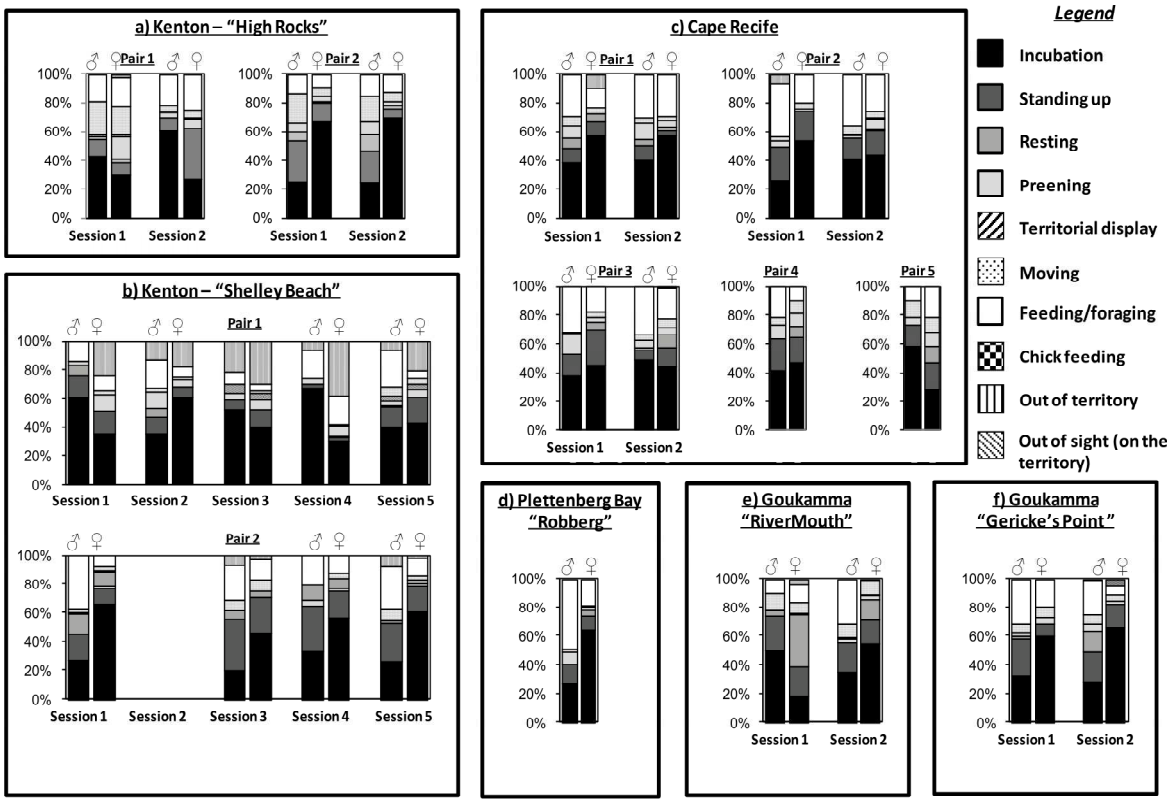


Figure 6.3. Time-activity budget of the 12 breeding pairs of African Black Oystercatchers during incubation

Budget-temps des activités des 12 couples reproducteurs d'huîrirers noir africains pendant la période d'incubation

The male on the other hand was usually seen flying eastwards towards Middle Beach, where another oystercatcher pair breeds (Appendix 1b), and this occurred at 4 sessions. During one session, 3 observers were present, allowing me to investigate the whereabouts of the female while off its territory. On that occasion the female was observed about 700 meters up the river, probing the sand and feeding on unidentified buried prey, preening and resting on a sandbank in the middle of the river (Appendix 1b). The male was assumed to spend its time off territory on Middle Beach, but this could not be visually confirmed. These temporary "desertions" lasted up to 55 minutes for the male and 70 minutes for the female (Appendix 2b). An alternative feeding area was also identified at Goukamma Rivermouth (Appendix 1e): both the male and the female were seen foraging in the dune vegetation around the nesting area, along with white-fronted plovers.

"Standing up" occupied breeding oystercatchers significantly during incubation. Males and females were standing up for a similar amount of time, 19 ± 8 % and 16 ± 8% of their time respectively (GLM with quasi-poisson distribution, t = 1.304, p = 0.20, n= 20). Standing up activities were recorded while non-incubating birds were around the

nest area, however, long periods of this activity were also observed on the feeding grounds, in between feeding sessions and without obvious presence of disturbances.

Figure 6.4. Mean (± SD) nest attendance (%) of African Black Oystercatchers during incubation. * indicates significant difference between the % nest attendance of males and females (Generalized linear mode, quasi-poisson distribution, t = – 2.08, p = 0.05, n= 20).**

*Présence au nid moyenne (± écart-type, %) des huîtriers noirs africains pendant l'incubation. *** indique une différence significative ente le % de présence des males et des femelles (modèle linéaire généralisé, distribution de quasi-poisson, t = – 2.08, p < 0.01, n = 20)*

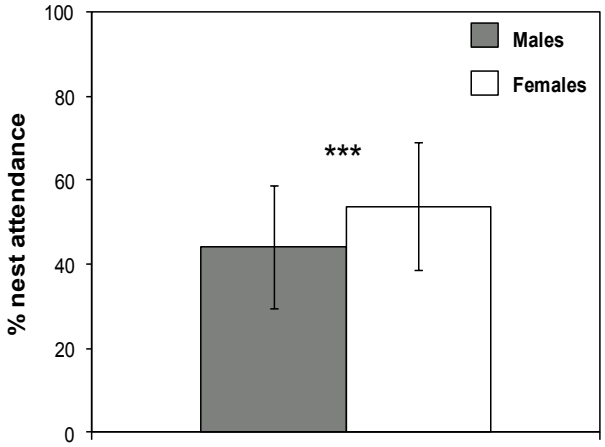
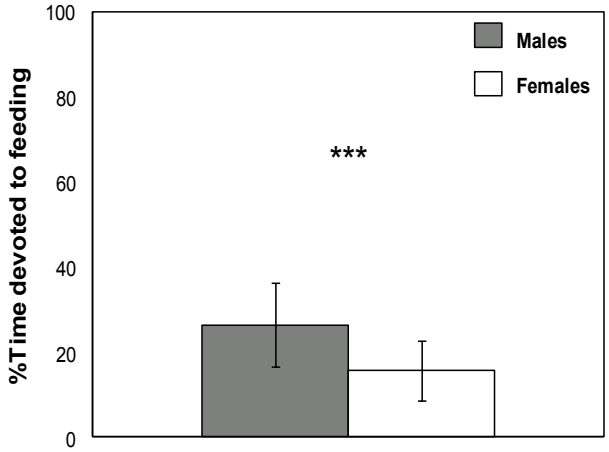


Figure 6.5. Mean (± SD) of feeding time of African Black Oystercatchers during incubation. * indicates significant difference between the % of feeding time of males and females (Generalized lineal mode, quasi-poisson distribution, t = – 3.78, p < 0.01, n= 20).**

*Temps de nourissage moyen (± écart-type, %) des huîtriers noirs africains pendant l'incubation. *** indicate une différence significative entre le % de temps de nourrissage des mâles et des femelles (modèle linéaire généralisé, distribution de quasi-poisson, t = – 3.78, p < 0.01, n= 20).*



Preening activities occurred for each focal bird and at each session, however, sometimes too briefly to be recorded during a scan. Preening occurred either between feeding scans or at the end of feeding sessions. For the later the preening activity could consist of a simple and short preening of feathers or long bathing/preening sessions taking place in pools on the high shore and lasting up to 20 minutes.

Resting activities (sitting or standing up with the head tucked under the wing) occurred very scarcely (2 ± 3% and 5 ± 8 % on average for males and females respectively).

Territorial displays were rarely recorded during scans (Fig 6.3) because of their brief duration. We noted territorial display during scans as obvious territorial behaviour consisting of "piping", performed by either the male or the female or both together (Fig 6.6a), fights (Fig 6.6b) or the chasing of intruders by one member of the focal

pair. However agonistic interactions with other oystercatchers often consisted in little "action", with birds standing up, in alert posture nearby each other or pseudo-sleeping (Fig 6.6c). Perturbation events induced by conspecifics shown in Appendix 2 give a better appreciation of the occurrence of territorial displays during sessions.

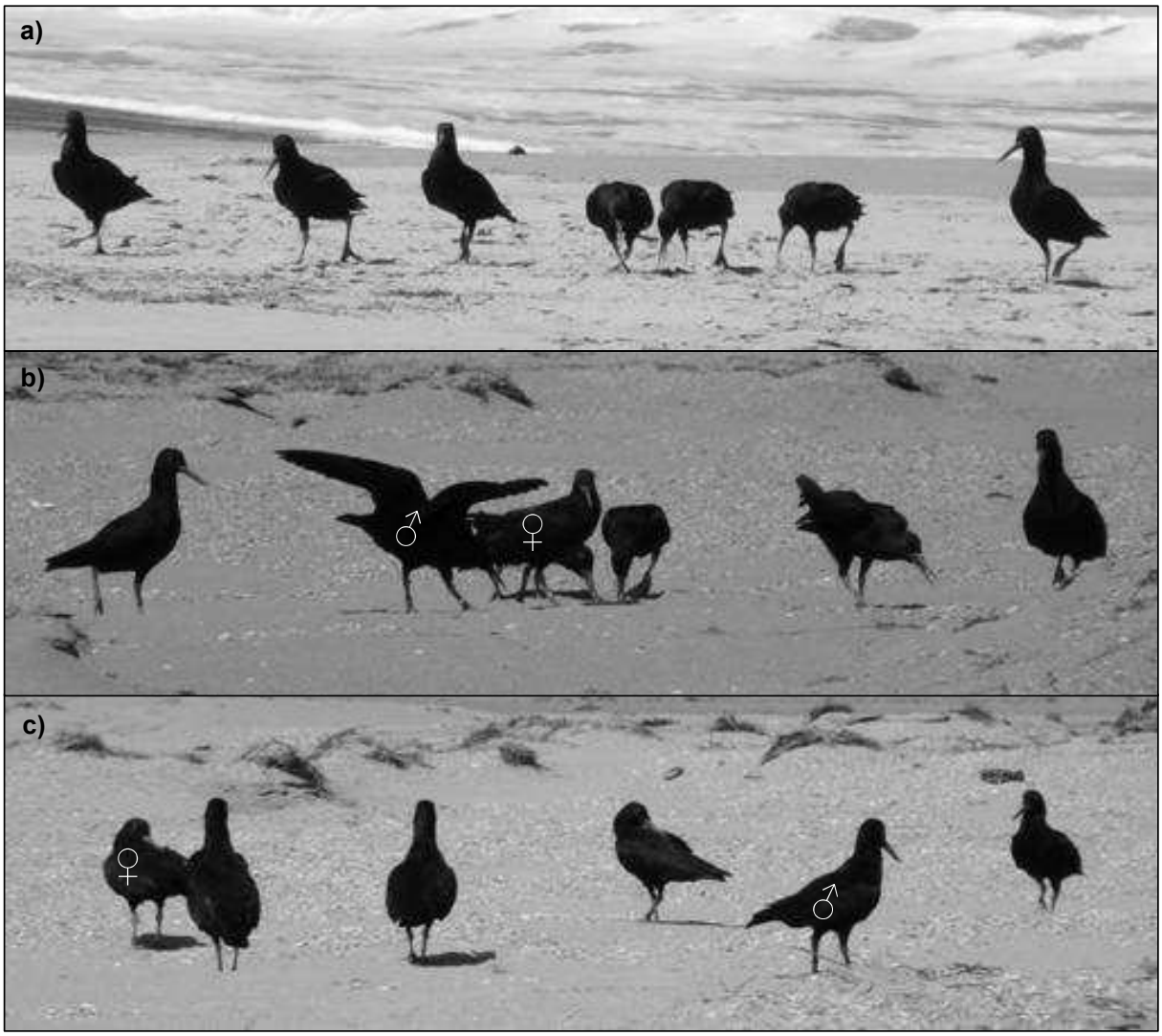


Figure 6.6. Examples of territorial display with conspecifics at "Robberg "(Plettenberg Bay): a) piping b) aggressive dominant display by the male and c) pseudo-sleeping. When present, members of the studied and color-ringed pair are indicated with ♂ and ♀ (*Photos: S. Kohler*)

Exemples de comportement territorial envers d'autres huîtriers à "Robberg" (Plettenberg Bay): a) démonstration aggressive par le male, b) "Piping", c) Pseudo-sommeil. Les membres du couple étudié et bagué sont indiqués par ♂et ♀ lorqsu'ils sont présents.

Incubation shifts and changeovers. Incubation shifts were highly variable in length and ranged from 10 to 260 minutes for both sexes (Fig 6.7). Average durations of incubation duties were 67 ± 46 minutes and 77 ± 50 minutes for males and females respectively and did not differ significantly (Mann-Whitney test, W = 1234.5, p = 0.22, n = 53 and 54 shifts for males and females respectively). Modes in the distribution of the duration of incubation shifts however differ between sexes and were 40-60 minutes and 60-80 minutes for males and females respectively. Short incubation shifts (10-20 minutes) were only observed along with perturbation events (Appendix 2). Outside perturbation events, changeovers occurred mostly at the nest, with the non-incubating bird approaching the nest. Two sessions at Kenton occurred under very warm temperatures (> 35°C). During these sessions, on two occasions, the incubating bird left the nest and joining the breeding partner, which flew to the nest and took over incubation duties.

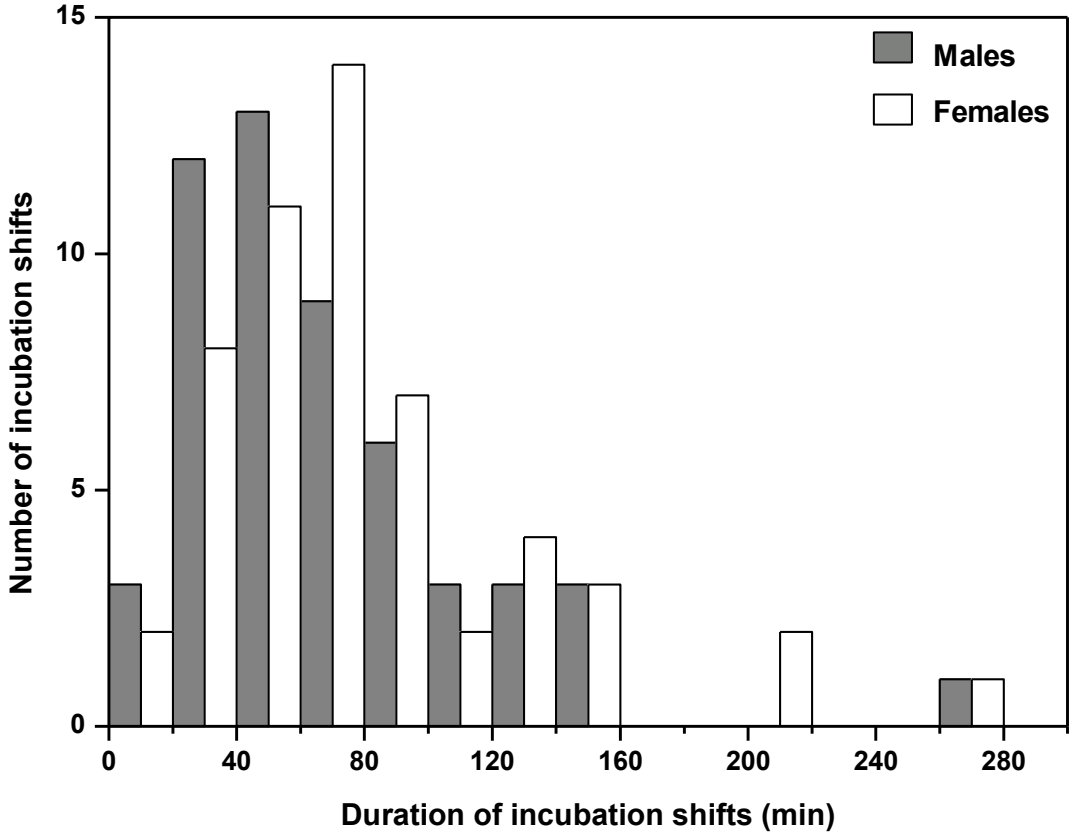


Figure 6.7. Durations of incubation shifts of African Black Oystercatchers. *Durées de période d'incubation chez les huîtriers noirs africains*

Feeding activities during incubation and tidal cycles. Cumulated feeding periods within hourly intervals relative to low tides were very variable between sessions (as

shown by large standard deviations in Fig 6.8). Different hour-related pattern of feeding activities however emerged between males and females and between study areas. In Kenton, males increased and decreased their feeding effort with the falling and rising tides respectively. Females on the other hand seemed to focus their feeding 3 hours before and after low tide. In Cape Recife, males took similar advantage of the low tide than in Kenton. For females, temporal distribution of feeding activities was bimodal, with increased feeding effort 1 hour before and 3 hours after low tide (Fig 6.8b). A different pattern was however observed at the western study sites (Plettenberg Bay and Goukamma): males spent a lot of time feeding 2 to 3 hours before low tide while females increased their feeding activity around low tide (Fig 6.8c)

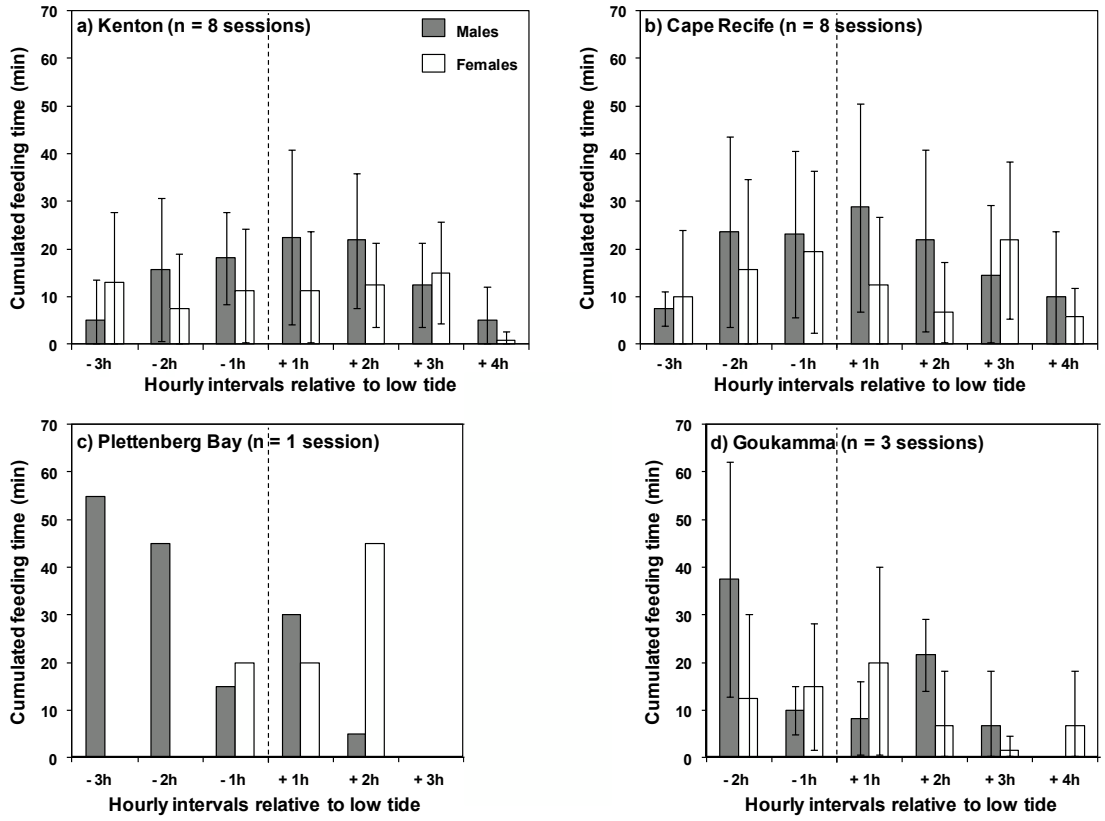


Figure 6.8. Mean (± SD) cumulated time (min) of feeding activities of African Black Oystercatchers over the tidal cycle during incubation. Dashed lines indicate maximal low tide.

Temps cumulé moyen (± écart-type) de nourrissage des huîtriers pendant le cycle de marée pendant l'incubation chez les huîtriers noirs africains. Les lignes en pointillés indiquent la basse-marée.

Chick-rearing activities at Cape Recife. At Cape Recife, the feeding ground was directly facing the nesting area (Pair 2, Appendix 1c). During feeding sessions, both parents were foraging simultaneously while the chick would hide or walk among rocks on the feeding ground, often in proximity of one or both parents. Total chick

attendance was 85% during the first session shared between the male (63 %) and the female (48 %), and lower, 65 % (35 and 46 % by the male and the female respectively, Fig 6.9) a week later.

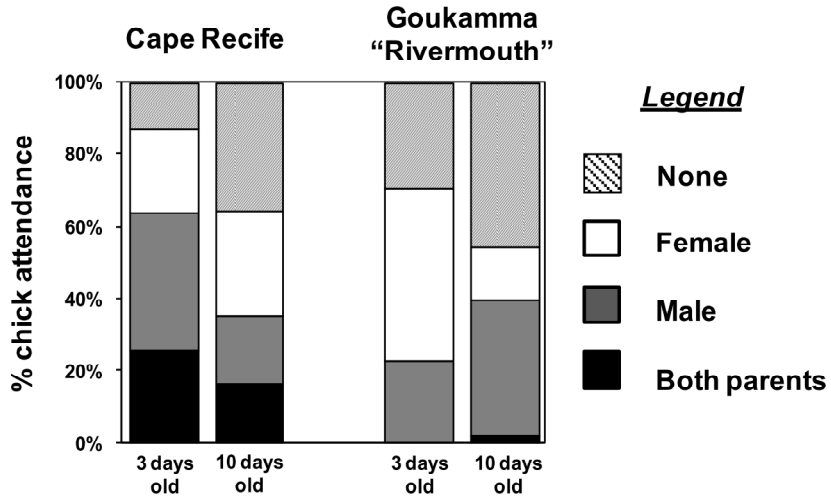


Figure 6.9. Chick attendance (%) of the 2 breeding pairs of African Black Oystercatchers during the chick rearing period, 3 days and 10 days after hatching at Cape Recife and Goukamma.

Présence au poussin (%) chez les 2 couples reproducteurs d'huîtrier noir africain pendant la période d'élevage, 3 et 10 jours après l'éclosion à Cape Recife et Goukamma.

Both parents were feeding about 50% of the time during both sessions (Fig 6.10a). Resting was the second most time-consuming activity (~ 20% of the time) during the first session while "Standing up", away from the chick, was the most significant activity after feeding during the second session (25 and 15 % for the male and the female respectively). The chick was hiding among rocks in a crouching posture or in cavities 81% of the time during both sessions. Other chick activities involved walking around its parents, preening and sitting on rocks. Parents brought a total of 24 prey to the chick over 4 hours during the first session (Fig 6.11a). The male fed the chick with limpets mostly (57% of the 14 items) while the female focused on feeding the chick with worms (40% out the 10 items, Fig 6.11a). On 4 occasions when the parent brought food, the chick remained hidden and did not respond to the parent's call therefore the parent ate the food item. However, a week later, the chick ate all prey brought to it. During this session, parents only brought a total of 16 items (9 from the male and 7 from the female).

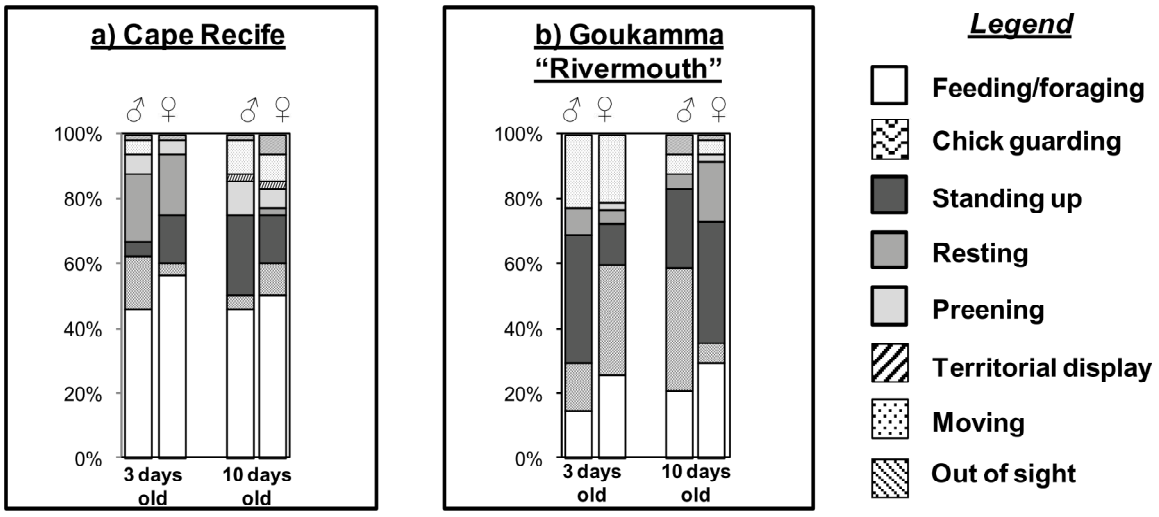


Figure 6.10. Time budget of 2 breeding pairs of African Black Oystercatchers during the chick rearing period, 3 days and 10 days after hatching at a) Cape Recife and b) Goukamma.

Budget-temps des 2 couples reproducteurs d'huitrier noir africain pendant la période d'élevage,, 3 et 10 jours après l'éclosion à a) Cape Recife et b) Goukamma.

Chick-rearing activities at Goukamma Rivermouth. At Goukamma Rivermouth, the feeding ground was 500 meters from the nesting area (a ~30 second flight) where parents kept their chick during the rearing period (Appendix 1e). Therefore parents alternated chick guarding and feeding duties in a very regular fashion, unless distracted by human-induced or conspecific disturbances. Short-term alternation of chick attendance and feeding duties between parents was also observed at Goukamma's "Gericke's Point" on hatching day (Appendix 2f), with the distinction that the attending parent was also incubating the remaining egg. While not feeding, the male kept a certain distance from the chick, that remained hidden under tree stumps most (91%) of the time, and would remain in an alert posture on the beach. The female on the other hand remained close to the chick when on "guarding duties (Fig 6.10.b). Feeding trips lasted 7 (± 3) minutes for both birds during the first session (range = 2 to 11 minutes), while during the second session, males did significantly longer trips on average (10 ± 6 minutes) than females (4 ± 2 minutes). While on the feeding ground, parents would systematically feed themselves until they picked a prey and flew back to the chick with it, regardless of the duration of the trip. As observed in Cape Recife, on 4 occasions, the chick in Goukamma did not respond to the parent's call when bringing food, and the adult ate the food intended to the chick instead.

During this first session, parents did 16 feeding trips within 4 hours and brought as many food items to their offspring (7 and 9 for the male and the female respectively), and in addition the male picked up a sand mussel for the chick to eat on one occasion (Fig 6.11b). A week later parents did 7 feeding trips and brought 7 prey each. Similarly to the parents in Cape Recife, chick attendance (54%) was lower during this second session (Fig 6.9).

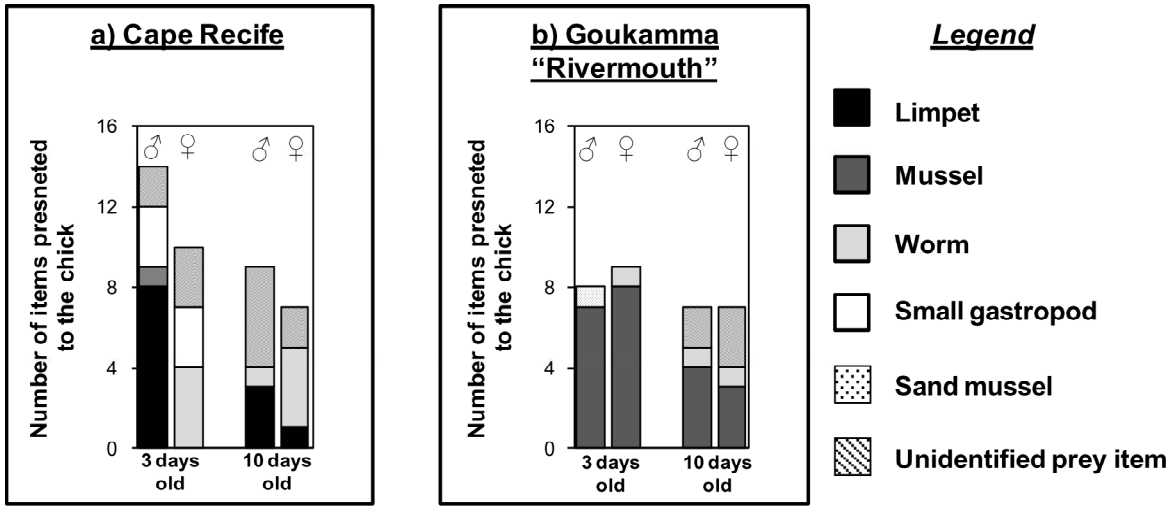


Figure 6.11. Food items presented by the 2 chick-rearing African Black Oystercatchers breeding pairs to the chick, 3 days and 10 days after hacthing at a) Cape Recife and b) Goukamma.

Proies présentées aux poussins pendant la période d'élevage par les 2 couples d'huîtriers noirs africains, 3 et 10 jours après l'éclosion à a) Cape Recife et b) Goukamma.

4. DISCUSSION

Nest attendance and feeding activities of African Black Oystercatchers during incubation. Males and females shared nest attendance, however female ABOs tended to incubate more often and performed longer incubation shifts than did males. There was also much variations associated with this pattern, and in some pairs, the roles were reversed. On the other hand males spent a significantly greater amount of time feeding. Males seemed to increase their feeding efforts around low tide, when much of the feeding area is uncovered. Therefore, it appears that males, as opposed to females, could take advantage of the apparent increase in prey availability brought by the tidal cycle, at least in Kenton and Cape Recife. However during low tide, most of the intertidal area is in the process of drying, and mussels, favored by ABOs (see Chapter 4 & 5), keep their valves closed to avoid desiccation. Mussels gap when they are washed by waves, at which time they are the most vulnerable to the stabbing of oystercatchers (Hulscher 1996). The time-window during which it is profitable to feed

on the low shore where mussels are the most abundant is even more restricted than the low-tide window and in the case of the American Black Oystercatcher *H. bachmani*, Hartwick (1976) noticed that low tide was usually accompanied by diminished feeding rates. This converges with observations of long period of non-feeding activities (standing up, resting, preening) by non-incubating ABOs around low tide, even in the absence of disturbances. The time-related pattern of feeding segregation between males and females and the variability within and between sites remain difficult to fully understand. Invertebrate distributions and complexity of intertidal zonations of the feeding areas differed greatly between study sites (see Table 6.1 and Fig 6.2). However Leseberg et al. (2000) pointed out that on South African rocky shores, correlation between food abundance and actual availability for ABOs was not predictable. Therefore prey distribution and abundance can hardly be used to predict oystercatcher feeding performance and choice of strategies. Nevertheless, in chapter 4, I showed that dietary segregation between breeding partners was minimal, except in Kenton and Cape Recife where males seemed to feed of limpets in higher proportions than females. Thus the different amount of time spent feeding by males and females around low tide at these sites could be very well related to gender specific dietary preferences. The longer foraging time periods recorded for males compared to their breeding partners may be explained by the fact that they forage outside the optimal foraging window. On the other hand, female often showed a bimodal foraging activity outside of the low tide. These shorter feeding events could better match with the period prior or after the highest risk of desiccation for mussels, when they are the most vulnerable. This suggests a strong complementarity among pairs in their foraging strategies, with female well-adapted to feed on mussels (Kohler et al 2009b) and optimizing food intakes during short time periods of highest prey vulnerability, and males foraging for longer period of time to compensate for their lower ability to stab mussels, and seek out their favorable prey more generally. This would explain the foraging patterns of males observed at Plettenberg Bay and Goukamma, sites known to be invaded by the Mediterranean mussel where their foraging success should be very low, and the fact that their foraging effort on the south-east coasts in higher around low tide to access to the small patches of limpets located on the lowest part of the shore. This would be in accordance with the poorer body conditions of males on the south-west coast observed in Chapter 4.

Disturbances either induced by conspecifics, humans or to a lesser extent, by other bird species (mainly Kelp Gulls) occurred at all sessions (Appendix 2). Disturbed incubating oystercatchers left their nest, which potentially increased the risk of predation and overheating of eggs (Adams et al. 1999). Once the situation resolved, however, birds on incubation duties quickly returned to their nests within 5 minutes. Human-induced perturbations also occurred on the feeding area and prevented non-incubating parent from feeding. Recreational fishing activities strained feeding ABOs to move away, sometimes repeatedly, and other times compelled the bird to leave the feeding area. Aggressions between breeding ABOs and kelp gulls occurred on the feeding area and were reciprocal, but rapidly resolved. Feeding oystercatchers were also aggressive toward smaller species such as turnstones and white-fronted plovers. Oddly enough, at Kenton "High Rocks", one male repeatedly chased off turnstones foraging nearby, while its female did not acknowledge their presence when feeding in close proximity to them. During one session at Goukamma "Rivermouth", I also witnessed the kleptoparasitism of the female on a white-fronted plover that had just caught a large flying insect (Fig 6.12).

Figure 6.12. Kleptoparasitism of a female African Black Oystercatcher on a white-fronted plover (*Charadrius marginatus)* at Goukamma "Rivermouth" *(Photo: S. Kohler)*

Kleptoparasitisme d'un femelle huîtrier noir africain sur un gravelot à front blanc (*Charadrius marginatus*) à Goukamma "Rivermouth"

Agonistic interactions with other oystercatchers were mostly observed between the focal pair and non-breeding individuals, rather than between established breeding pairs. Aggressions between neighbours were brief and restricted to the feeding area, and rarely involved both members of the focal pair. Intrusion by non-breeding oystercatchers on the other hand happened mostly outside the feeding area. It often resulted in resident birds stopping their activity (incubating, feeding, resting etc…), and proceeding with territorial display until the intruder(s) left for good. Such disturbance could last up to one hour and/ or be recurrent throughout several hours (Appendix 2). Overall, disturbances induced by human activities and non-breeders during the incubation period seem to have constituted a significant loss of

foraging time for breeding oystercatchers and increased the risks of eggs depredation.

Studies on European Oystercatchers have shown that under foraging time-stressed conditions, Eurasian Oystercatchers (*H. ostralegus*) were able to increase their prey intake rate (Swennen et al. 1989, Fitzpatrick & Bouchez 1998) or feed for longer period (Urfi et al. 1996). It is however unknown whether ABOs are capable of increasing their intake rates when stressed by human activities or disturbed by other oystercatchers. Nonetheless, females that seem to feed less during daytime could be able to compensate this limited daytime feeding, by increasing their foraging activity during night time to meet their energy requirements. Male nest attendance in return should be higher at night. Nocturnal feeding in shorebirds is well documented and constitutes a natural habit in response to regularly limited feeding space and time mainly induced by tide (Robert et al. 1989). Several studies on *Charadrius* species (plovers) have shown that nocturnal incubation is mainly carried out by males (Warnock & Oring 1996, Blanken & Nol 1998, Wallander 2003). Conversely females may benefit from nocturnal foraging to increase their food intake rate, when disturbance on the feeding ground are less intense and the activity of certain invertebrates such as polychaetes is greater (Robert & McNeil 1989, Blanken & Nol 1998). Moreover, incubation changeovers should also be less numerous and incubation shifts longer than during daytime, to avoid drawing attention from nocturnal mammalian predators such as spotted genets (*Genetta tigrina*) to the nest. The temperature being lower leads to more suitable conditions for long incubation shift. Data on the nocturnal feeding activities of ABOs are however very scarce (but see Ryan 1983, and Hockey & Underhill 1984 for night-feeding activities on islands). The main reason is that such investigations (on any coastal species) are difficult to carry out at most sites, particularly on the mainland, considering the problems of safety on South African beaches, especially at night. Additionally, the dark plumage of ABOs and the little obvious morphometric differences between sexes could be a problem for detailed nocturnal observations.

Recurrent off-territory feeding was observed for two breeding partners at Kenton “Shelley Beach” during incubation and happened regardless of the stage of the tidal cycle. This pair spent a lot of time defending their territory against intruders, and this territory included a large feeding area. Therefore it seems unusual for the birds to leave their territory, and their incubating partner, to search for food

elsewhere. Temporary territory desertion by breeding oystercatchers has been observed in at least two other species, the European Oystercatcher (Heppleston 1971) and the American Black Oystercatcher *H. bachmani* (Hartwick 1978). The two authors have linked this behaviour to the fact that these birds were unable to obtain sufficient food from their usual feeding area and had to supplement their diet with food from other feeding ground. The female of the aforementioned pair spent more time off-territory than its partner and the neighbouring pair's female (Pair N°2 at Kenton "Shelley Beach") also spent some time on sand banks in the Bushman's Rivermouth (Appendix 1b). Therefore off-territory feeding may be another way to pay off longer daytime incubation shifts by females.

Feeding activities outside the intertidal area were also frequent, especially in Cape Recife, where oystercatchers were observed scavenging on beached ascidians on repeated occasions (see Chapter 4). At Goukamma "Rivermouth", similarly, a significant amount of feeding scans was recorded while the birds were foraging in the dune vegetation around the nest area (55% and 10% of the scans for the male and the female respectively). ABOs were foraging there along with white-fronted plovers and several reciprocal aggressions occurred between the two species. The most common plant species on dunes along the Goukamma coastline are the indigenous *Arctotheca populifolia* and the introduced *Scaevola plumieri* (*J. Huisamen, pers. com.*). Plovers foraging in dunes mainly feed on isopods and amphipods (Hockey 2005), however such foraging behaviour has never been reported for ABOs, although these two groups of invertebrates were recorded as "uncommon prey" by Hockey & Underhill (1984).

Incubating shorebirds may adjust their incubation and feeding schedules daily to changes in environmental conditions (weather, disturbances, prey availability), to their own needs and those of their eggs but also in response to the previous night and day activities and events (Cartar & Montgomerie, 1987). Overall, during the incubation period, breeding ABOs showed a lot of flexibility in their feeding strategies as shown by the daily and pair-related variability in nest attendance and feeding efforts for both sexes, but also by the several alternative feeding behaviour demonstrated by the birds. This demonstrates the capacity of incubating African Black Oystercatchers to adapt their breeding and feeding behaviours to the natural and anthropogenic constrains of their environment.

Chick-rearing strategies in African Black Oystercatchers. As opposed to other shorebird species that raise true precocial chicks, the energy expenditure of rearing a dependant chick for oystercatchers is particularly high (Nol 1985, Safriel et al. 1996). Complementarity between mates, through coordinated provisioning and guarding of the young, was well developed at both sites. Both males and females participated equally to the feeding, although at Cape Recife the male provided more food items than the female. Otherwise, there was little distinction between parental roles of males and females. One basic condition for the evolution of cooperative parental care between breeding mates is that the offspring cannot be raised successfully by one parent alone (Trivers 1972), and in the case of oystercatchers, considering the high energetic cost of raising parent-fed chicks, this condition may very well be essential. Later in the chick-rearing period, Nol (1985) demonstrated divergence of sex role in American Pied Oystercatchers (*H. palliatus*), with males performing more territorial displays, while females were spending more time near the chicks. Presumably with fledglings, predation risks decreased and do not require both parents to remain close to the young(s). This converges with the decrease in chick attendance over time observed at two study sites in the present study. On the other hand the territorial defense against conspecifics by the male late in the breeding season may help in securing the territory for the next breeding season (Nol 1985). Unfortunately, the premature disappearance of the two chicks prevented any further investigation in the segregation of parental roles in ABOs later in the chick-rearing period.

The chick-rearing conditions were obviously different for the two pairs and are analogous to the contrasting situations of “resident” and “leapfrog” pairs abundantly studied in European Oystercatchers (reviewed in Ens et al. 1996, Safriel et al. 1996). Chicks of “residents” follow the foraging parents early in their development, conversely, “leapfrog” oystercatchers nest in one location and forage in another, transporting marine food to the chicks, which usually start following their parent only after fledging. At 3 days of age, the chick at Cape Recife was fed with a higher number prey than the one at Goukamma (24 vs. 17) but at 10 days old, the two chicks were fed with a similar number of items. Moreover at Goukamma “Rivermouth”, parents continuously alternated feeding trips and guarding duties, unless disturbed, while at Cape Recife, both parents were alternatively seen resting around low tide. The decreased rate of food provisioning between the two sessions at Cape Recife may have been counterbalanced by the capture of larger prey as the

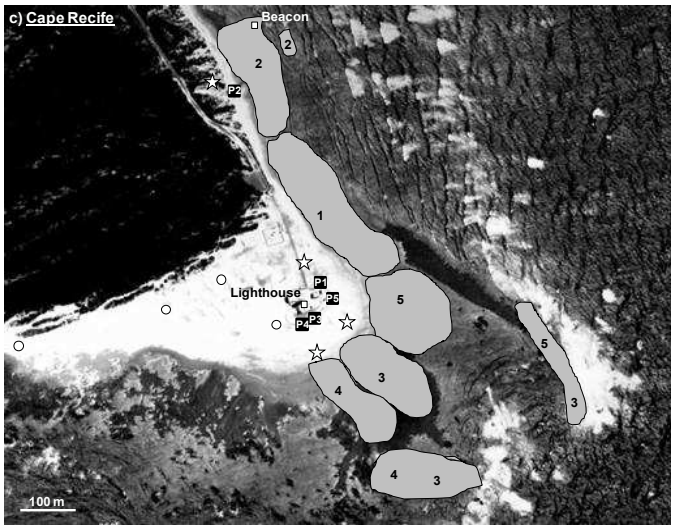
chick got older. Indeed a previous investigation on parental provisioning in American Black Oystercatchers show that provisioning rates of single chicks increased as the chicks got older (Hazlitt et al. 2002). If instead the pair at Cape Recife decreased the food provisioning of their young without compensating with the capture of larger prey, this would inevitably lead to decreased growth rate of the chick and possibly starvation (Hazlitt et al. 2002, Tjørve et al. 2007). The difference in food provisioning between the two pairs can be explained by two related phenomena. On one hand the parents at Goukamma, obliged to do 500 meters-foraging trips, could not reach the same food-provisioning rate than resident parents at Cape Recife. On the other hand, central-foraging theory (Orians & Pearson 1979) and predation-risks models developed in Safriel et al. (1996) predict that "leapfrogging" parents should therefore transport larger and more nutritious food items than resident parents. Overall comparison of the chick-provisioning strategies of these two pairs suggest that chick-rearing ABOs adopt different strategies to meet their own energetic requirements and those of their young to adapt to their feeding environment, as it has been shown for other oystercatcher species (Hartwick 1976, Nol 1985, Safriel et al. 1996).

Nevertheless, for both pairs, chick loss occurred before chicks reached 20 days of age. Three other pairs studied during incubation ("Robberg", "Gericke's Point and Pair 1 at "Shelley Beach") brought their eggs to hatching, but also lost their offspring within a week. The circumstances of their disappearance remain unclear. The pair at Goukamma "Rivermouth" fails in raising offspring until fledging every year (*CapeNature, pers. com.*). Considering the intense recreational activities in this area and the confines associated with their breeding territory, it is unclear whether their repeated breeding failure is food or human-related or a combination of both. The inexperience of the parents to raise chicks combined with an early deletion in the feeding investment by one of the parent has to be considered. These situations are common and have been shown to cause failure in the breeding success in many bird species (Nol & Smith 1987, Wooller et al. 1990, Van de Pol et al. 2006). The chick, ringed prior the first session, was found beached without external injuries by a holiday maker, who reported it to the conservation authorities two days after our second session. One likely scenario is that the chick was chased by an unleashed dog into the water and drowned, though this cannot be confirmed.

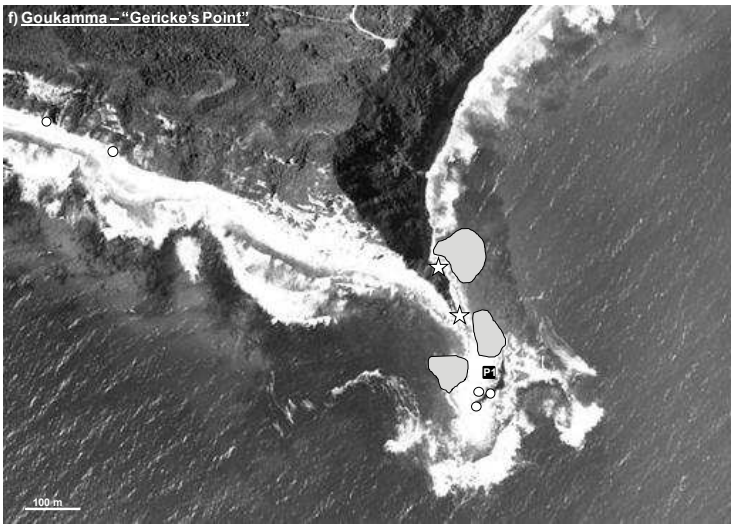
Conclusions. Decreasing intertidal productivity from west to east and local-scale variations in wave-exposure greatly influence rocky shore invertebrates biomass and the zonation of intertidal communities along the South African coastline (Bustamante et al. 1995a,b, Bustamante & Branch 1996b, Chapter 1 & 4). The invasion of the shores by the Mediterranean mussel also deeply impacts the assemblages and diversity of potential prey for oystercatchers. This logically results in geographic difference in food availability for ABO. Leseberg et al. (2000) however pointed out that the relation between food supply, intake rates and reproductive success of ABOs was difficult to establish. Nonetheless breeding productivity of ABOs on the west coast, especially on off-shore islands remains higher than on the south coast (Jeffery 1987, Leseberg et al. 2000, Calf 2002, Vernon 2004). The south coast (from Cape Agulhas to East London see Fig 1.1) has a warmer climate than the west coast that makes it more attractive to tourists during the summer holidays, which coincide with the peak of reproduction of ABOs (December-January). This suggests that breeding oystercatchers experience greater disturbance in this region. Overall, recurrent human-induced disturbances and agonistic interactions with conspecifics combined with the energetic constrains related to the feeding conditions of breeding oystercatchers seem to be the major cause of breeding failure in ABOs on the south coast, regardless of the adaptation of the species to its environment. The breeding population is known to have expanded eastwards these past 20 years as a consequence of an overall increase in the number of birds (Vernon 2004, Brown & Hockey 2007). As the species is highly territorial, this could mean that birds breeding in the Eastern Cape are most likely young individuals with little experience in reproduction. In well-established breeding sites, young individuals may mimicry older pairs as part of the learning process in successfully breeding. The combination of higher human disturbance with young and inexperienced breeders may explain this overall low breeding success.

5. APPENDIXES

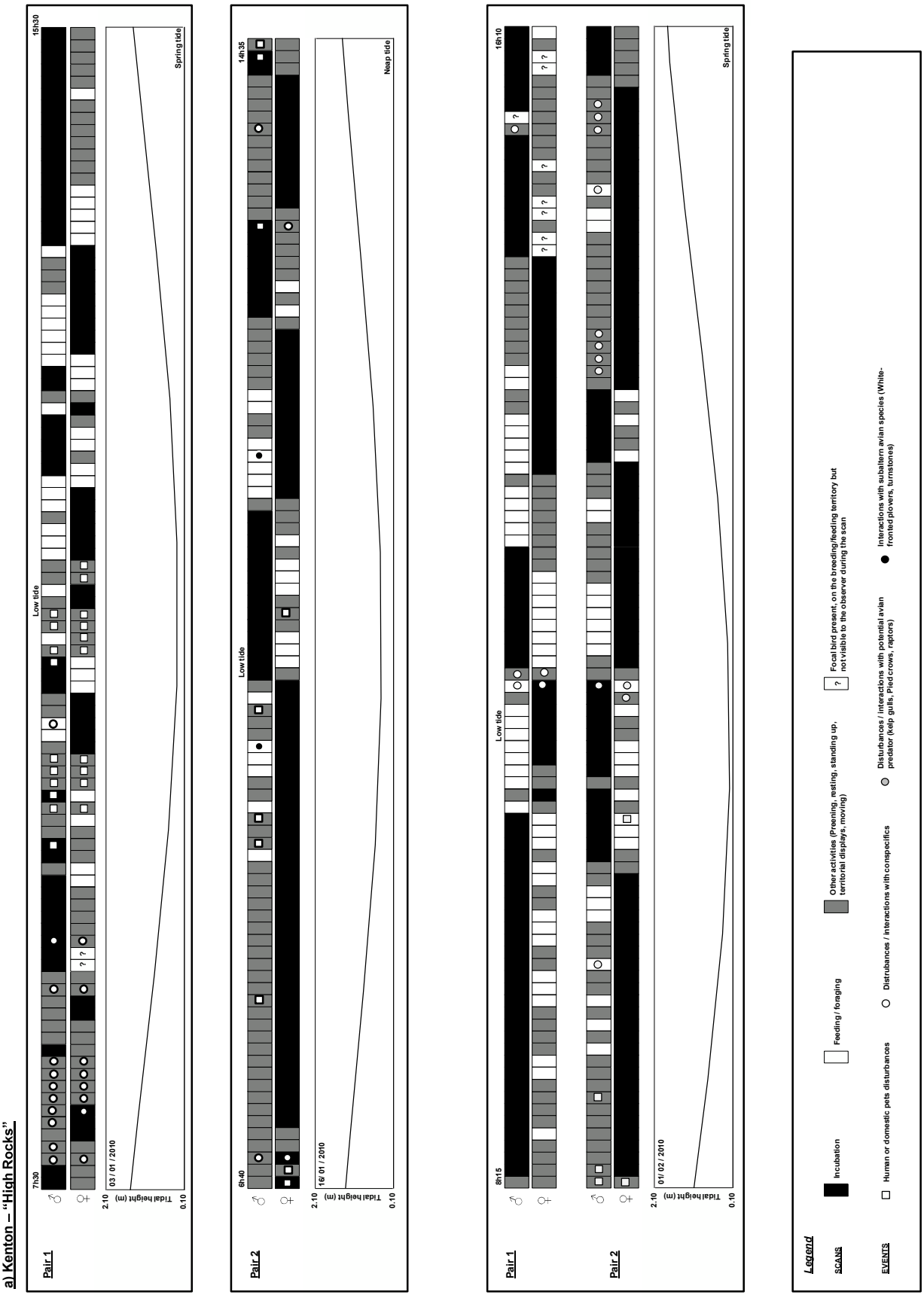
Appendix 1. Satellite views of the 12 breeding pairs territories in Kenton (a and b), Cape Recife (c), Plettenberg Bay (d) and Goukamma (e and f). P1, P2, P3, P4, P4 and P5 indicate the position of the studied nests. Grey-shaded areas indicate the main feeding areas for each pair (with pair-corresponding numbers). White shaded areas indicate alternative feeding grounds. ☆ indicates the position of the observers. ○ indicates other oystercatchers nests. □ indicates landmarks.



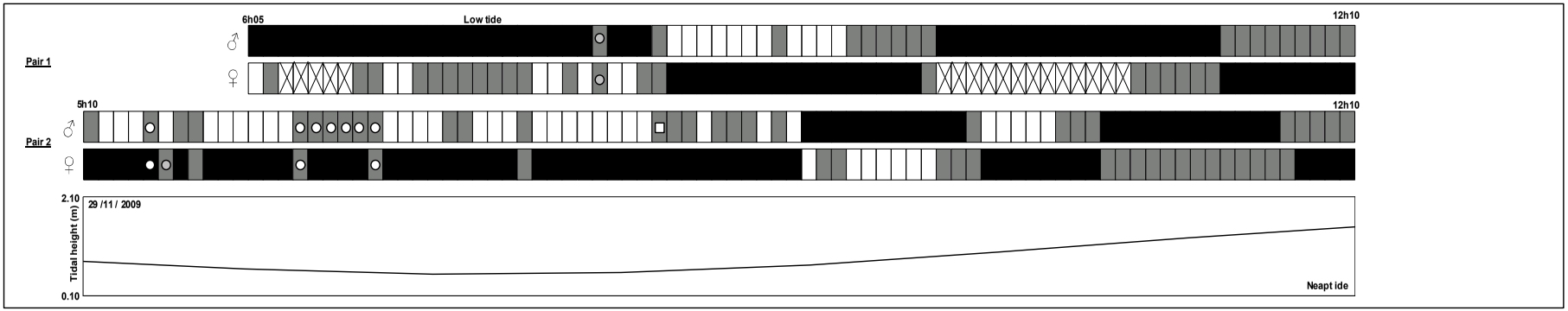

e) Goukamma – "River Mouth"
Goukamma River Mouth
P2
Buffel's Bay Backpackers
100 m

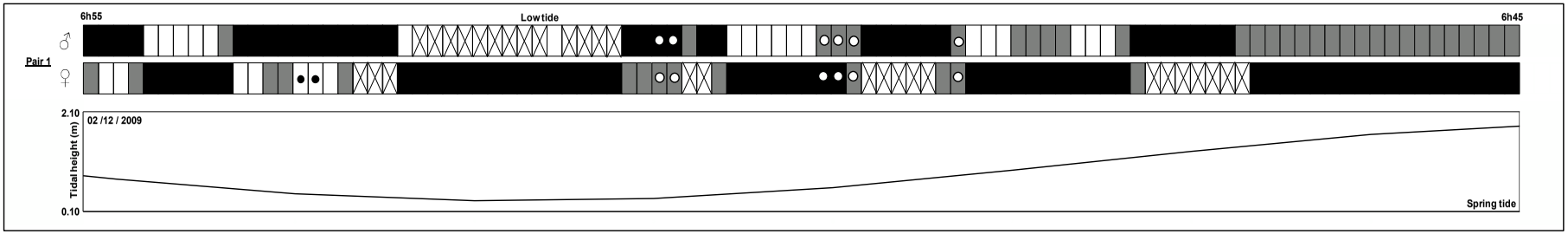

f) Goukamma – "Gericke's Point"
P1
100 m

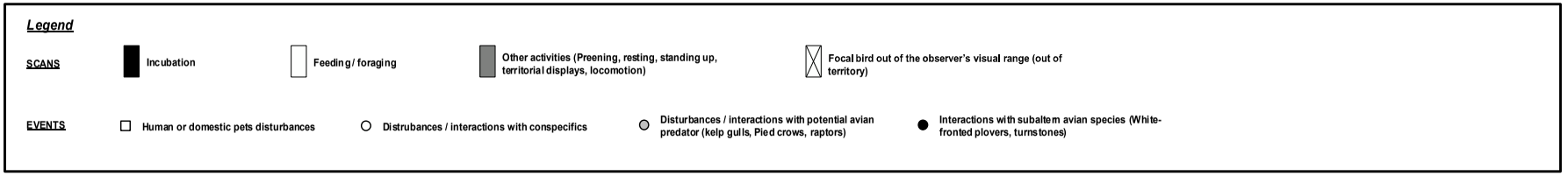
Appendix 2. Daily activity schedule of African Black Oystercatchers at a) Kenton "High Rocks", b) Kenton "Shelley Beach", c) Cape Recife, d) Plettenberg Bay "Robberg", e) Goukamma "RiverMouth", f) Goukamma "Gericke's Point".

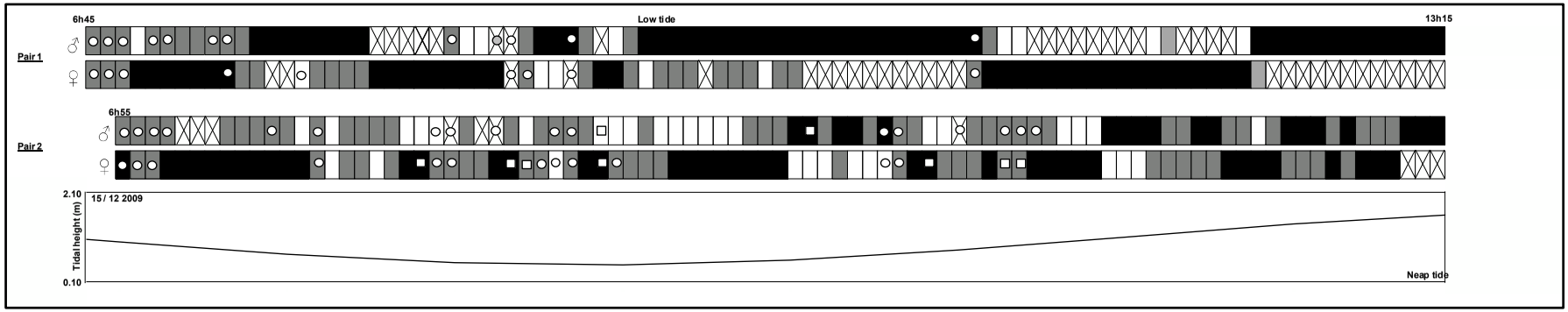


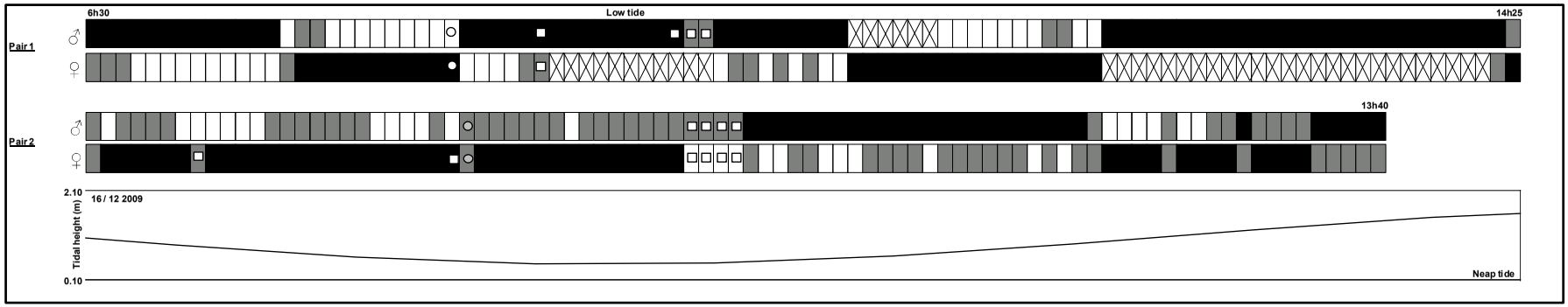
b) Kenton – "Shelley Beach"

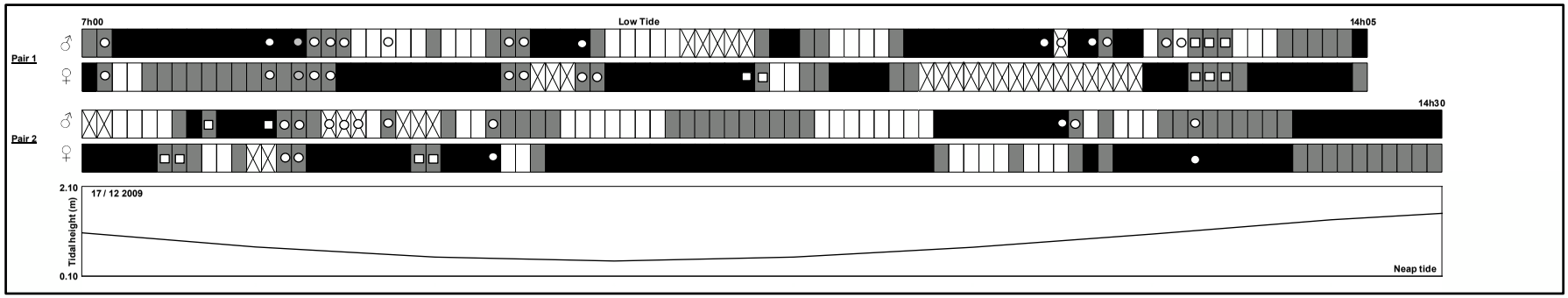


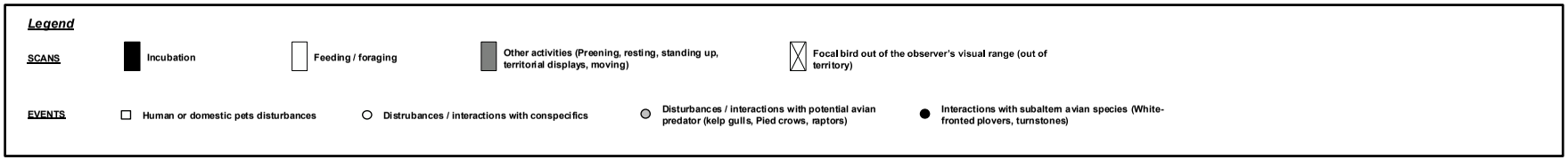




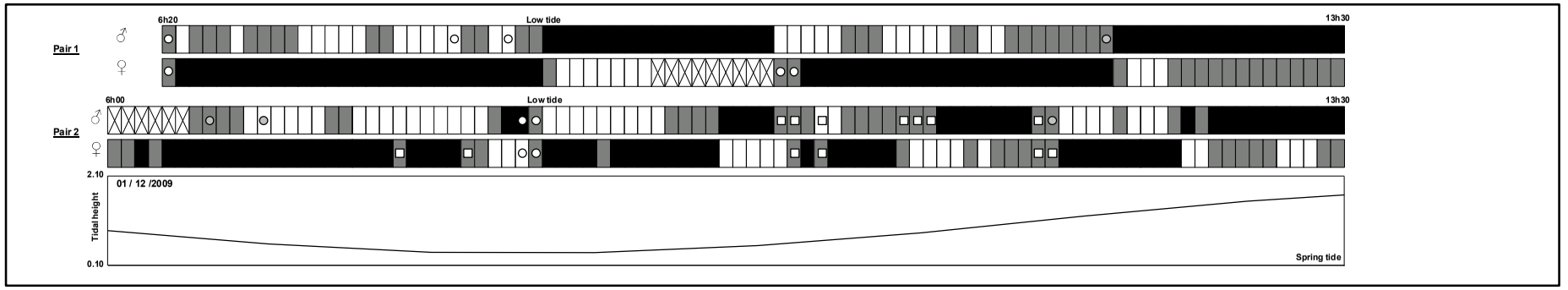

6h45
Low tide
13h15
Pair 1
♂
♀
6h55
Pair 2
♂
♀
2.10
15 / 12 2009
Tidal height (m)
0.10
Neap tide

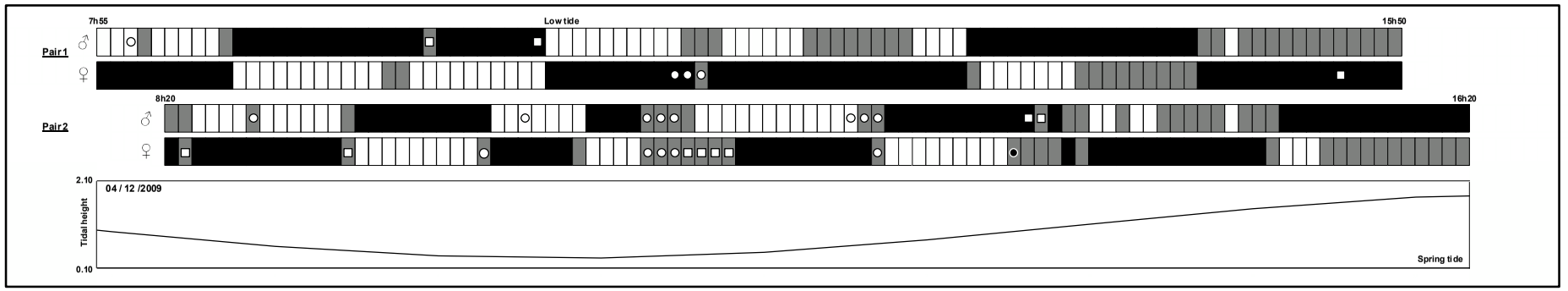

6h30
Low tide
14h25
Pair 1
♂
♀
13h40
Pair 2
♂
♀
2.10
16 / 12 2009
Tidal height (m)
0.10
Neap tide

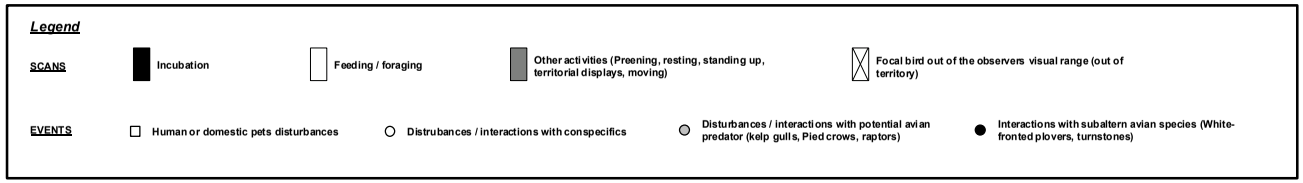

7h00
Low Tide
14h05
Pair 1
♂
♀
14h30
Pair 2
♂
♀
2.10
17 / 12 2009
Tidal height (m)
0.10
Neap tide

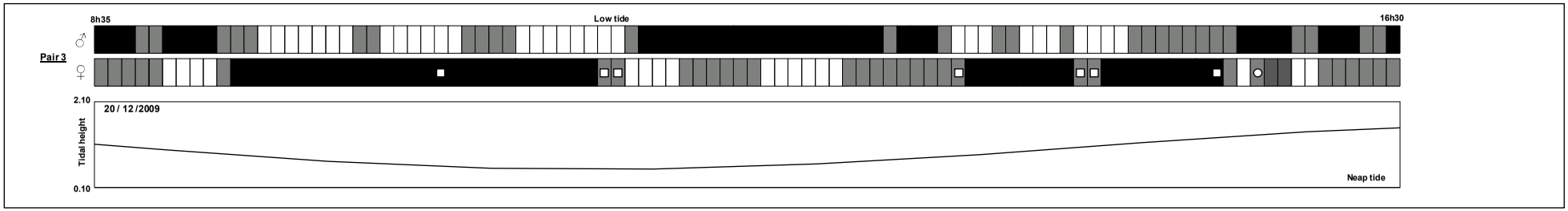

Legend
SCANS
Incubation
Feeding / foraging
Other activities (Preening, resting, standing up, territorial displays, moving)
Focal bird out of the observer's visual range (out of territory)
EVENTS
Human or domestic pets disturbances
Distrubances / interactions with conspecifics
Disturbances / interactions with potential avian predator (kelp gulls, Pied crows, raptors)
Interactions with subaltern avian species (White-fronted plovers, turnstones)

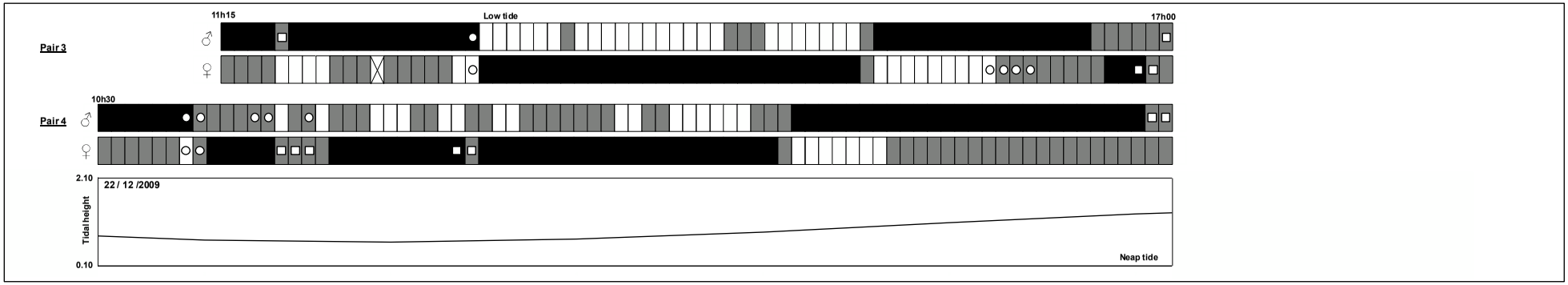
c) Cape Recife

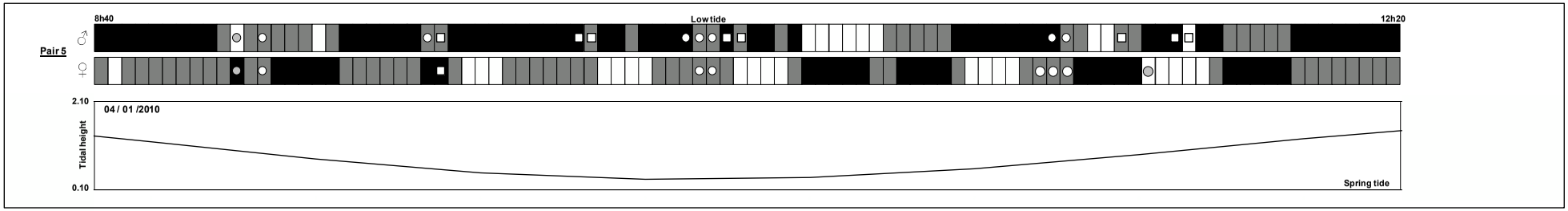


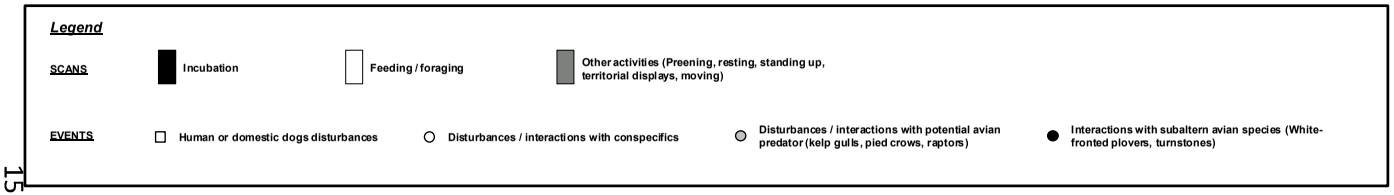




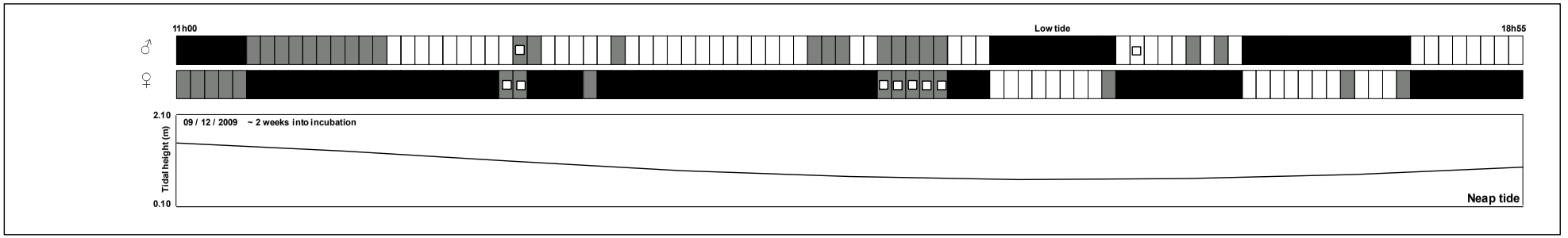

8h35
Low tide
16h30
Pair 3
♂
♀
2.10
20 / 12 /2009
Tidal height
0.10
Neap tide

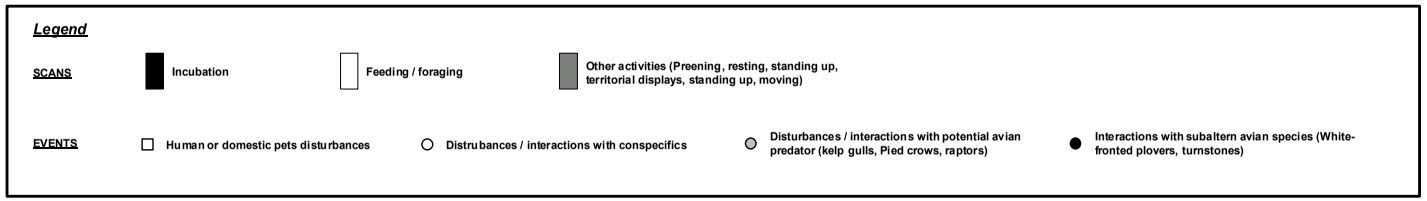

11h15
Low tide
17h00
Pair 3
♂
♀
10h30
Pair 4
♂
♀
2.10
22 / 12 /2009
Tidal height
0.10
Neap tide


8h40
Low tide
12h20
Pair 5
♂
♀
2.10
04 / 01 /2010
Tidal height
0.10
Spring tide

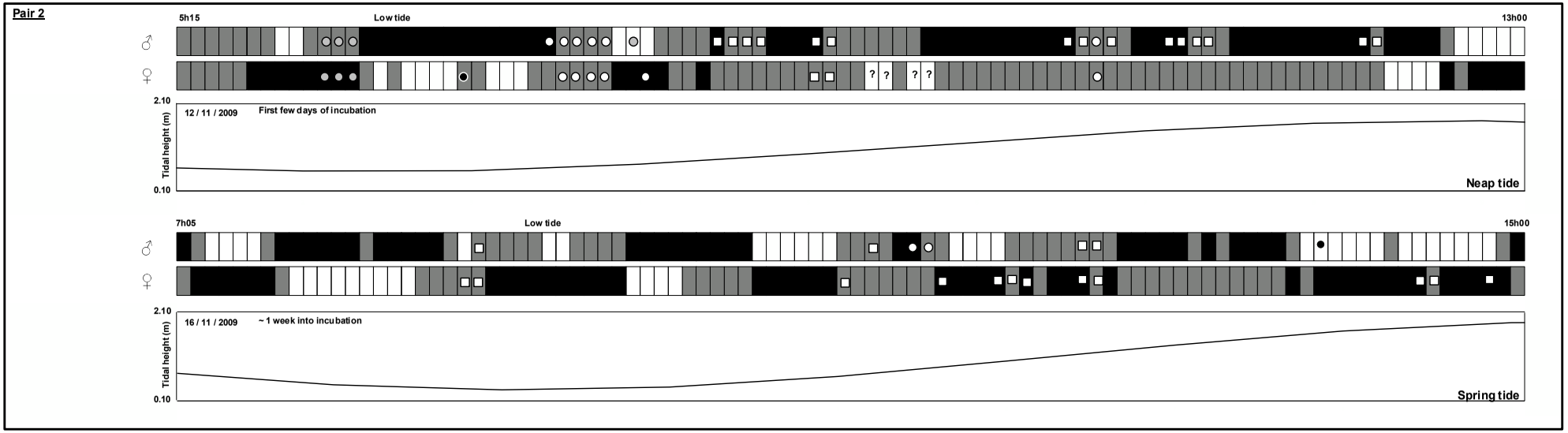

Legend
SCANS
Incubation
Feeding / foraging
Other activities (Preening, resting, standing up, territorial displays, moving)
EVENTS
Human or domestic dogs disturbances
Disturbances / interactions with conspecifics
Disturbances / interactions with potential avian predator (kelp gulls, pied crows, raptors)
Interactions with subaltern avian species (White-fronted plovers, turnstones)

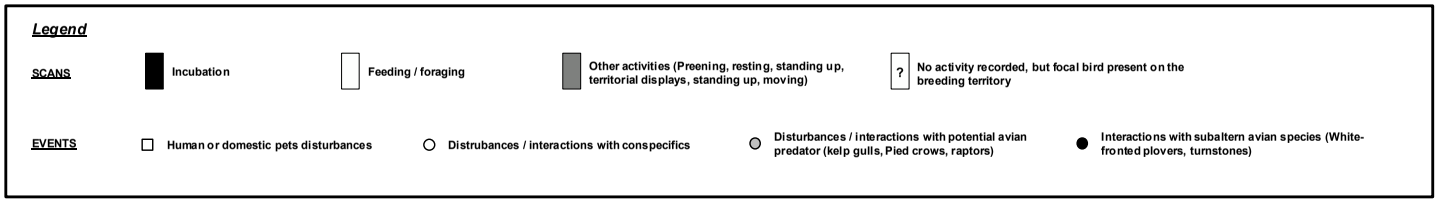
d) Plettenberg Bay – "Robberg Peninsula"



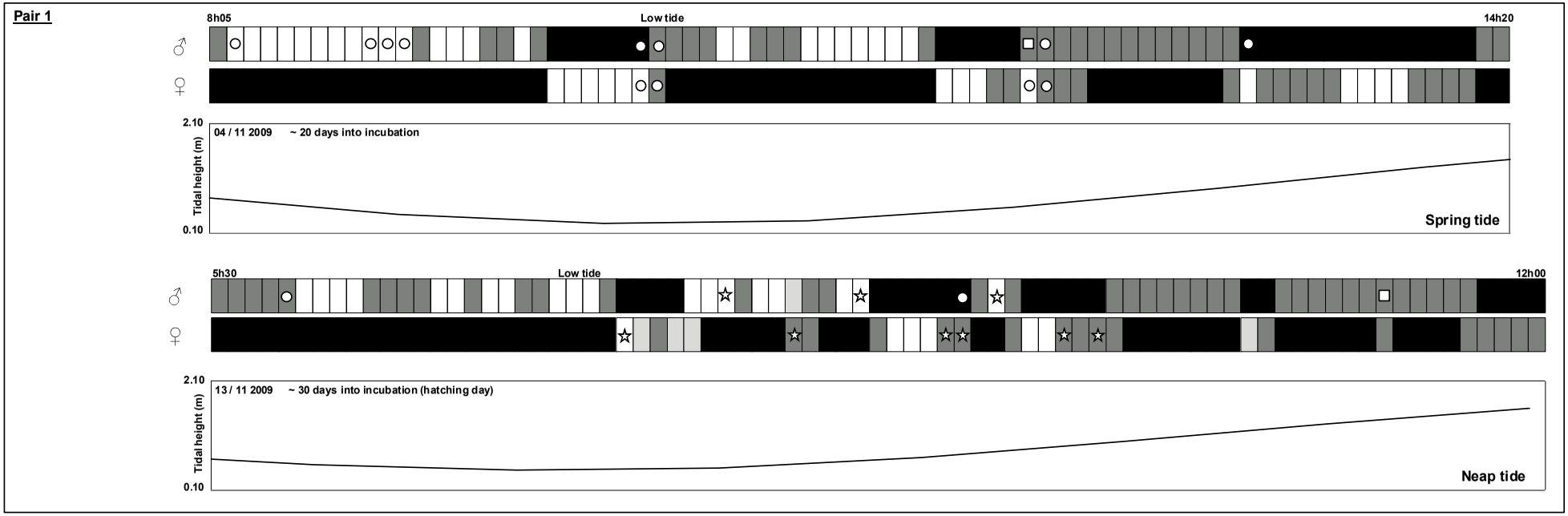


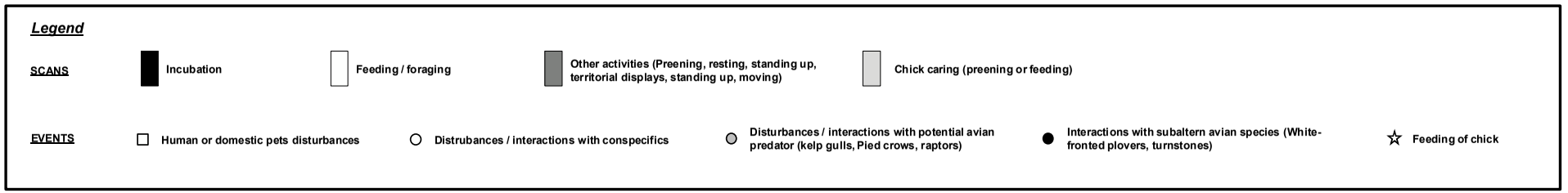
e) Goukamma – "Rivermouth"





f) Goukamma – "Gericke's Point"





DISCUSSION GENERALE

(Photo: B. Dubillot)

I. Structure des réseaux trophiques des estrans rocheux sud-africains: un système idéal pour l'étude de l'écologie d'un prédateur aviaire

Les estrans rocheux sud-africains sont largement dominés, en terme de biomasse, par deux types d'invertébrés benthiques (Bustamante & Branch 1996b): d'une part les bivalves de la famille des Mytilidés, représentés sur l'ensemble des côtes sud-africaines par plusieurs espèces indigènes et une espèce invasive, la moule de Méditerranée *Mytilus galloprovincialis,* introduite dans les années 1970 ; d'autre part les gastéropodes de la famille des Patellidés, qui comprend 11 espèces, dont 5 ont été prises en compte dans cette étude. Ainsi il est peu surprenant que les premières études menées sur l'huîtrier noir africain, principal prédateur aviaire des estrans rocheux sud-africains, se fondant sur des observations directes et la collecte de restes alimentaires, aient déterminé que moules et patelles constituaient l'essentiel de son régime alimentaire (Randall & Randall 1982, Hockey & Underhill 1984, Coleman & Hockey 2008). La dominance des estrans rocheux par ces deux groupes d'organismes est d'autant plus significative dans le cadre de cette étude qu'elle est associée à deux voies trophiques distinctes liées aux principales sources de carbone. La voie pélagique est caractérisée par des signatures appauvries en ^{13}C et peu variables au niveau local. Au sein de celle-ci les moules filtrent l'eau de mer pour se nourrir de la matière organique particulaire en suspension constituée d'un mélange de phytoplancton et de détritus de macroalgues côtières. L'autre voie trophique, benthique, est caractérisée par des signatures enrichies en ^{13}C, qui se répercutent dans les valeurs isotopiques des patelles broutant la production primaire benthique constituée par une large gamme de macroalgues, encroûtantes ou non, et de microalgues colonisant la surface des rochers (Chapitre 2). Encore plus remarquable est la persistance de cette dichotomie isotopique marquée pour l'ensemble des sites d'études, à l'exception de Lüderitz où la patelle *Scutellastra granatina* (échantillonnée exclusivement sur ce site) et *Mytilus galloprovincialis* ont montré des $\delta^{13}C$ similaires.

En revanche, pour la majorité des sites étudiés dans le cadre de cette thèse, les filtreurs et les brouteurs ne présentent pas de différence significative de leurs valeurs de $\delta^{15}N$. L'enrichissement relatif des uns par rapport aux autres entre les sites dépassant rarement les 1‰. Ces faibles différences semblent être relativement communes pour les communautés associées aux estrans rocheux en conditions préservées (Sara et al. 2007, Schaal et al. 2008, 2010). Elles semblent être liées aux faibles variations de $\delta^{15}N$ chez les producteurs primaires (à opposer à des fortes

variations de $\delta^{13}C$). Il semble en effet que le $\delta^{15}N$ des producteurs primaires dépend principalement de la signature isotopique de la source minérale azotée dominante (ammonium et/ou nitrates) alors que les processus métaboliques intrinsèques à chaque espèce y jouent un rôle moins important. A l'opposé, on constate fréquemment pour des producteurs primaires dépendant de la même source de carbone minéral des différences importantes de $\delta^{13}C$, associées à des fractionnements spécifiques à chaque espèce (Falkowski 1991, Raven et al. 2002)

Sur l'ensemble de la zone d'étude, les ratios isotopiques des huîtriers varient le long d'un gradient de $\delta^{13}C$, dont les extrêmes sont définis localement par les valeurs de $\delta^{13}C$ appauvries des moules et enrichies des patelles, avec cependant quelques exceptions notamment à Cape Recife (voir plus bas). Par ailleurs, les huîtriers sont systématiquement enrichis en ^{15}N par rapport aux invertébrés benthiques, en moyenne de +2.7 ± 0.4 ‰ (Chapitre 3), caractérisant clairement les relations prédateur-proies existant entre les deux. D'autres prédateurs existent sur les estrans rocheux sud-africains, notamment des organismes marins opérant à marée haute comme les céphalopodes (*Octopus vulgaris*) et des poissons de la famille des sparidés (*Sparodon durbanensis*, « musselcracker » en anglais), mais surtout parmi les organismes benthiques intertidaux, les gastéropodes carnivores *Nucella dubia* et *Burnupena sp*., l'étoile de mer *Marthasterias glacialis* et les crabes *Plagusia chabrus* et *Grapsus tenuicrustatus* (Branch & Branch 1981, Plass-Johnson et al. 2010). L'ensemble de ces carnivores consomme des moules et/ou des patelles en perçant ou brisant les coquilles de leurs proies. Ces prédateurs benthiques constituent également des proies potentielles pour l'huîtrier africain (Hockey & Underhill 1984). Cependant, l'enrichissement en ^{15}N observé chez les huîtriers par rapport aux consommateurs primaires (e.g. moules et patelles) indique un lien trophique direct, suggérant que les prédateurs intertidaux ne rentrent pas de manière significative dans leur alimentation. Enfin, les goélands (*Larus dominicanus*) sont des prédateurs (et charognards) opportunistes vis-à-vis des espèces intertidales (notamment les moules qu'ils lâchent en vol pour briser la coquille) mais également envers les œufs et les jeunes poussins d'huîtriers (Hockey 2005). En revanche la prédation sur les adultes huîtriers même par des mammifères carnivores (ex: la genette *Genetta tigrina*) est très rare. Dès lors on peut considérer l'huîtrier noir africain comme un prédateur apical des zones intertidales sud-africaines.

Ainsi la ségrégation entre les signatures isotopiques du carbone des deux principaux types de proies permet de lier le $\delta^{13}C$ de l'huîtrier noir africain aux contributions relatives des voies pélagiques et benthiques à son régime alimentaire. Inversement les valeurs de $\delta^{15}N$ similaires des moules et patelles et l'enrichissement en ^{15}N constant observé entre invertébrés benthiques et huîtriers permet d'apprécier les positions trophiques relatives des proies et de leur prédateur. Par ailleurs, le pas isotopique régulier observé entre le sang et les plumes d'huîtriers, qui représentent chez les adultes des périodes d'intégration alimentaire différentes (saison de reproduction vs. saison de repos, Chapitre 3) et la faible variabilité temporelle des ratios isotopiques dans les tissus des proies (Chapitre 2, Section II), permettent d'appréhender les questions de variations saisonnières de l'écologie alimentaire de l'huîtrier noir africain avec l'outil isotopique. L'ensemble des caractéristiques isotopiques du système décrites ci-dessus permet également l'utilisation des modèles isotopiques de mélange comme IsoSource (Phillips & Gregg 2003, Chapitre 4) ou SIAR (Parnell et al. 2010, Chapitre 5) qui nécessitent d'une part des sources de nourriture ayant des signatures isotopiques distinctes et d'autre part la connaissance de facteurs d'enrichissement trophique fiables pour estimer les contributions relatives des différentes sources le régime alimentaire de consommateurs.

II. Variations des ratios isotopiques du carbone et de l'azote de l'huîtrier noir africain le long des côtes sud-africaines en réponse aux conditions océanographiques côtières et aux communautés de proies

Un des objectifs principaux de ce travail de thèse était d'examiner l'influence des conditions océanographiques côtières et de la composition des communautés intertidales sur l'écologie trophique d'un prédateur aviaire des estrans rocheux du sud de l'Afrique par l'analyse des signatures en isotopes stables. Les huîtriers et leurs proies principales présentent un enrichissement en ^{15}N d'est en ouest, reflétant à l'échelle du sud de l'Afrique un changement de qualité des eaux littorales en termes de nutriments disponibles pour les producteurs primaires, entre le courant chaud des Aiguilles à l'est et le système d'upwellings du courant du Benguela à l'ouest. Ces différences font appel à la notion de production primaire nouvelle ou régénérée (Altabet & François 1994). Dans les milieux oligotrophes comme le courant des Aiguilles, l'azote existe essentiellement sous forme d'ammonium recyclé, typiquement appauvri en ^{15}N. C'est sous cette forme que les producteurs primaires marins l'assimilent majoritairement pour réaliser la photosynthèse, du fait de sa plus grande abondance dans ces milieux. Inversement dans un système eutrophe

typiquement alimenté par des upwellings, la forme dominante de l'azote est représentée par les nitrates qui sont enrichis en ^{15}N. Chaque injection de nitrates dans la couche euphotique contribue à une nouvelle efflorescence algale (i.e. bloom), dont l'enrichissement en ^{15}N va se transférer vers les niveaux supérieurs de l'écosystème pélagique (Jaquemet & McQuaid 2008). Plus localement, des incursions d'azote enrichi en ^{15}N, fort probablement d'origine anthropique, ont été clairement observées dans les signatures isotopiques des invertébrés benthiques et les tissus des oiseaux à Cape Recife et Langebaan (Fig 1.1). En effet, ces deux sites se situent respectivement à quelques kilomètres de la ville industrielle et portuaire de Port Elizabeth (4ème plus grande ville d'Afrique du Sud) et du port de la marine sud-africaine basée à Saldanha Bay, près du site de Langebaan (Fig 1.1). De précédentes études isotopiques ont montré que les rejets d'origine humaine dans le milieu littoral étaient souvent enrichis en azote présentant des $\delta^{15}N$ particulièrement élevés, et que cet enrichissement se retrouvait dans les ratios isotopiques de l'azote chez les producteurs primaires et les consommateurs (Riera et al. 2000, McClelland et al. 1997, Schaal et al 2010). De manière générale, les variations géographiques de $\delta^{15}N$ chez les huîtriers montrent une forte influence des conditions océanographiques, mais aussi des rejets en milieu côtier liés aux activités humaines, sur les réseaux trophiques rocheux de la région. En effet, la relative simplicité et la taille réduite (3 niveaux : producteurs primaires, invertébrés benthiques, huîtriers) du système trophique considéré favorisent une forte pénétration des facteurs influençant la base de la chaîne alimentaire jusqu'aux prédateurs apicaux via les processus ascendants, tels que les transferts de matière et d'énergie. De plus, la stabilité du décalage isotopique entre les ratios du sang et des plumes des adultes sur chacun des sites (+ 0.5 ‰ et + 1.6 ‰ pour le $\delta^{13}C$ et $\delta^{15}N$ respectivement) suggère une certaine stabilité saisonnière des conditions biotiques et abiotiques influençant l'écologie trophique de l'oiseau à la fois à l'échelle de sa population (Chapitre 5) et de l'individu (Chapitre 3 et 4) pendant ses saisons de reproduction et d'hivernage. Ces résultats sont conformes à ceux observés chez un prédateur aviaire océanique, le fou du Cap (*Morus capensis*) dans les provinces océaniques des Aiguilles et du Benguela (Jaquemet & McQuaid 2008).

Les ratios isotopiques du carbone des huîtriers ont pu être liés aux contributions relatives des invertébrés filtreurs et brouteurs, respectivement appauvris et enrichis en ^{13}C, dans l'alimentation des oiseaux. Ainsi, sur les côtes ouest et sud-ouest, les oiseaux présentent un régime alimentaire composé

principalement de moules, qui sont spécifiquement dominées par *Mytilus galloprovincialis* à l'ouest et constituées d'un mélange de moules invasives et de moules indigènes *Perna perna* sur la côte sud-ouest. Ceci contraste avec le régime alimentaire observé sur la côte est, caractérisée par l'absence de la moule invasive. Dans cette région, l'alimentation est constituée d'un mélange équilibré de moules et de patelles sur deux des sites d'étude, et dominée par les patelles sur le site le plus oriental (East London). Ainsi les variations géographiques de $\delta^{13}C$ des tissus d'huîtriers reflètent à la fois les compositions spécifiques des communautés littorales, les changements de biomasse associés aux fluctuations naturelles des conditions océanographiques côtières aux échelles locales et régionales, mais aussi la distribution de la moule invasive (Bustamante & Branch 1996b, Robinson et al. 2005).

III. *Haematopus moquini* et *Mytilus galloprovincialis*: une relation trophique complexe

En plus de ces processus abiotiques, locaux et régionaux, agissant sur la biomasse et la composition spécifique des invertébrés benthiques, l'écologie alimentaire de l'huîtrier noir africain est clairement influencée par l'invasion des estrans rocheux sud-africains par la moule méditerranéenne *M. galloprovincialis*. Les invasions biologiques sont généralement vues comme une menace majeure pour la biodiversité et le fonctionnement des écosystèmes indigènes (Sala et al. 2000, Mooney & Cleland 2001, Peck et al. 2007, Kurle et al. 2008). Les conséquences bénéfiques des invasions biologiques sont donc assez peu communes pour être, d'une part, soulignées, et d'autre part utilisées pour comprendre les interactions trophiques complexes entre espèces introduites et communautés indigènes, dont les organismes de niveau trophique supérieur. Le fait que l'huîtrier noir africain ait grandement profité de la prolifération de *M. galloprovincialis* sur les estrans de la côte ouest en raison de la surabondance de proies représentée par la moule invasive a été maintes fois rapporté (voir Griffith et al. 1992, Branch & Steffani 2004, Robinson et al. 2005). En effet au début des années 1990, Hockey & Van Erkom Shurink (1992) constataient une augmentation de production de poussins d'huîtrier noir africain à l'envol sur les îles de Saldanha Bay (Fig 1.1) parallèlement à la prolifération de la moule méditerranéenne dans la région. Cependant, un certain nombre d'études antérieures et de résultats collectés durant ces travaux de thèse soulèvent des questions quant à l'impact réel de la moule invasive sur la dynamique de populations de l'huîtrier noir africain à l'échelle de sa distribution actuelle.

Sur Robben Island, sur la côte ouest (Fig 1.1), la prolifération de *M. galloprovincialis* est loin d'avoir atteint les proportions observée dans le reste de la région, puisque la couverture de la moule exotique dans la zone médio-littorale inférieure n'atteint que 40% (Tjørve & Underhill 2006). Néanmoins la population d'huîtriers résidents a considérablement augmenté entre 1977 (40 individus comptés) et 2004 (225 individus, Tjørve & Underhill 2006) et semble avoir atteint la capacité de charge des estrans sur cette île (L.G. Underhill, com. pers.). Entre 2001 et 2004, le nombre moyen de poussins à l'envol par couple s'est abaissé de 0.74 à 0.35 (Tjørve & Underhill 2008), excédant tout juste le seuil nécessaire pour maintenir une population stable (0.33, Hockey 2001) et donc trop faible pour expliquer l'accroissement fulgurant de la population d'huîtriers sur cette île. Tjørve & Underhill (2006) suggèrent notamment l'afflux de jeunes huîtriers, originaires d'autres sites de la région ouest, et prospectant pour l'établissement d'un territoire de reproduction, comme explication possible de ce phénomène. Par ailleurs, un changement notable au cours des 30 dernières années a été la fermeture de la célèbre prison de cette île, qui a eu pour conséquence une diminution des activités humaines sur le littoral. Cette réduction des perturbations humaines auraient pu bénéficier aux oiseaux reproducteurs du site et permettre un meilleur recrutement des jeunes huîtriers au sein de la population reproductrice (Tjørve & Underhill 2006). Cependant, l'accroissement des activités touristiques ces dernières années, combinée à une augmentation du nombre de chats harets sur l'île pourraient contrebalancer cet effet (Tjørve & Underhill 2008). A l'extrémité orientale de la zone d'étude (East London), sur un site caractérisé par une large dominance de patelles sur les zones d'alimentation d'*H. moquini*, le nombre de couples reproducteurs est passé de 2 en 1988 à 14 en 2009, alors que le succès reproducteur reste particulièrement faible (1 poussin à l'envol pour 10 couples en moyenne par année, C. Vernon com. pers.). Parallèlement, de larges groupes de non-reproducteurs interagissant avec les couples établis sont fréquemment observés sur ce site, suggérant un fort potentiel de renouvellement des reproducteurs notamment en cas de décès des individus résidents (*obs. pers.).*

L'effet bénéfique de l'introduction de *M. galloprovincialis* sur la population d'*H. moquini*, jusqu'alors menacée d'extinction, et la forte relation trophique des deux espèces à l'échelle de leurs distributions respectives reste indéniable. Cependant, aux vues des éléments présentés ci-dessus, l'effet d'autres facteurs ne sauraient être ignoré. En particulier, les fluctuations cycliques à long terme de la population, (nécessitant des suivis à très long terme et à grande échelle pour être comprises),

associées à des flux migratoires de jeunes adultes permettant le recrutement de résidents dans des régions à faible succès reproducteur, ainsi que la mise en place simultanée de mesures de protection des sites de reproduction pourraient avoir eu en parallèle un impact majeur sur la dynamique de population d'*H. moquini* (Hockey 1997, 2001, Williams et al. 2004). Ainsi la moule invasive aurait pu avoir un effet bénéfique dans un premier temps, lorsque la population globale d'huîtriers était très diminuée, mais de nos jours, il semble que son impact soit moindre du fait d'autres facteurs densité-dépendants comme les sites favorables à l'établissement de nouveaux couples reproducteurs.

Inversement, l'effet potentiellement régulateur de la prédation d'*H. moquini* sur la population de *M. galloprovincialis* reste à ce jour non étudié. Les oiseaux peuvent avoir un impact important sur la dynamique de population de leurs proies (Otvos 1979, Tinbergen 1981, Zwarts & Drent 1981, Sanchez et al. 2006) parfois supérieur à celui des invertébrés carnivores (tels que *Nucella dubia* et *Burnupena sp*. sur les estrans sud-africains) en raison de leur besoins énergétiques plus conséquents (Marsh 1986). Hockey & Branch (1983) ont notamment montré qu'*H. moquini* avait un impact majeur sur les densités et structures de taille de *S. granularis* sur des îlots de la côte-ouest sud-africaine et qu'ainsi les populations de patelles étaient localement limitées par la prédation exercée par l'huîtrier noir africain.

Les résultats présentés dans Kohler et al. (2009b, Appendix 4) suggèrent une préférence de l'huîtrier pour l'espèce invasive par rapport à la moule brune indigène, et ce, potentiellement en raison de la force d'attachement au substrat plus faible de la moule invasive (Zardi et al. 2007). Par ailleurs *P. perna* est communément infectée par des trématodes parasites alors que *M. galloprovincialis* est largement épargnée (Calvo-Ugarteburu & McQuaid 1998, obs. pers.). Ainsi, la consommation de la moule indigène pourrait aussi présenter un avantage énergétique moindre. Ceci ne devrait en revanche affecter la sélection spécifique de l'oiseau seulement si celui-ci est capable de détecter les proies parasitées. Les huîtriers utilisent en effet à la fois la vue et le toucher pour détecter leurs proies et sont notamment capable d'utiliser des indices visuels pour exploiter les faiblesses de leurs proies et ne consommer que les plus intéressantes (Hulscher 1996, Nagarajan et al. 2002a,b). Inversement Zardi et al. (2009) ont mis en évidence un autre type de parasitisme affectant différemment les deux espèces de moules. En effet l'infection des moules par des cyanobactéries endolithes (exploitant le carbonate de calcium des coquilles) affecte notamment la

solidité des valves mais aussi la condition corporelle et la force d'attachement des moules de manière indirecte. Ce type de parasitisme a également pour effet de décolorer et déformer les coquilles des moules, laissant des indices visuels sur l'état de parasitisme des moules pour d'éventuels prédateurs. *M. galloprovincialis*, plus infectée par les endolithes que *P. perna* (Zardi et al. 2009) présenterait donc à la fois, pour un prédateur, l'avantage d'être facile à manipuler et le désavantage d'avoir un apport énergétique moindre. Une étude en cours d'élaboration par le Coastal Research Group, (Université de Rhodes, Afrique du Sud) en collaboration avec le CIMAR-Laboratorio Associado (Institut of Biotechnology & Bioenginnering, Portugal) a pour but d'examiner la sélection de *P. perna* et *M. galloprovincialis* par l'huîtrier noir africain en relation avec leur infection par les parasites endolithiques. Les résultats de cette étude pourraient fournir des informations supplémentaires sur la pression de prédation d'*H. moquini* sur la moule de Méditerranée. La compétition interspécifique, les traits d'histoire de vie (notamment le recrutement et la dispersion des larves McQuaid & Phillips 2000, 2006, McQuaid & Lindsay 2007) et le degré de résistance aux stress biotiques des deux espèces de Mytillidés coexistant sur la côte sud sont fortement régulées par les conditions abiotiques (exposition à la houle, intensité de la lumière, vents, topographie côtière, Calvo-Ugarbeturu & McQuaid 1998, Nicastro et al. 2007, Von der Meden 2008, Zardi et al. 2009). Celles-ci expliquent en partie la distribution géographique et la progression inégale de *M. galloprovincialis* sur le littoral sud (Bownes & McQuaid 2006). Cependant ces aspects pourraient également avoir des conséquences sur le comportement sélectif des huîtriers vis-à-vis des deux espèces de moule, et, à une échelle très locale, de fait limiter ou favoriser la prolifération de la moule de Méditerranée. Néanmoins, en raison de sa faible densité et de la fragmentation de sa population, il est fort probable qu'*H. moquini* n'ait qu'un impact minime sur la dynamique d'invasion de *M. galloprovincialis* à l'échelle de la côte sud.

IV. Comportements alimentaires et capacités d'adaptation aux conditions locales d'alimentation chez *Haematopus moquini*

Le long des côtes sud-africaines, les huîtriers noirs africains se nourrissent en grande majorité sur les invertébrés dominant localement les communautés benthiques des estrans rocheux, montrant de ce fait un comportement très opportuniste quant à la sélection de leurs proies. Avant la prolifération de la moule de Méditerranée sur la côte ouest, Hockey & Underhill (1984) remarquaient déjà que les huîtriers nourrissaient leurs poussins en prélevant les espèces de mollusques dans

des proportions comparables à celles observées sur l'estran, tandis que des observations similaires ont été faîtes sur la côte sud-est à la fois sur des îles (Randall & Randall 1982) et sur le continent (Kohler et al. 2009b, Appendix 4). Les huîtriers constituent de fait d'excellents échantillonneurs écologiques. Conjointement à ces observations faites à l'échelle de la population et de sa distribution, les deux sexes ont montré très peu de ségrégation alimentaire. En effet, à l'échelle locale, tous les oiseaux, mâles comme femelles se nourrissent globalement sur le même ensemble de proies, à l'exception toutefois de quelques cas sur les sites de l'extrémité est (Chapitre 4, Kohler et al 2009b). Les oiseaux du genre *Haematopus* sont connus pour leur spécialisation alimentaire individuelle liée, entre autre, à la morphologie de leur bec, qui présente aussi un dimorphisme sexuel marqué (Hockey 1996). Cette spécialisation alimentaire en relation avec la morphologie du bec ne semble cependant pas s'exprimer de manière significative chez *H. moquini*. Sur la côte ouest, le régime alimentaire d'*H. moquini* s'est mué en une consommation quasi-exclusive de la moule de Méditerranée surabondante en l'espace d'une vingtaine d'année (Hockey & Van Erkom Shurink 1992, Coleman & Hockey 2008, Chapitre 4 et 5). Pourtant, la relation particulière d'*H. moquini* et *M. galloprovincialis* n'est pas unique. En effet, son proche cousin européen *H. ostralegus* semble s'être accommodé de l'introduction volontaire de la palourde *Ruditapes philippinarum*, originaire du pacifique ouest, et qui pourrait jouer un rôle dans la réduction de la mortalité d'*H. ostralegus* pendant l'hiver, lorsque la compétition intra-spécifique pour l'accès à la ressource alimentaire est particulièrement forte (Caldow et al. 2007).

Pendant les périodes d'incubation et de nourrissage des poussins, les partenaires sexuels ont montré une capacité à moduler le temps dédié à leur propre alimentation et à celle de leurs poussins en fonction de leurs propres besoins énergétiques, mais aussi des caractéristiques des communautés de proies dans leurs habitats. De plus, des comportements alimentaires « alternatifs », jusqu'alors peu décrits chez *H. moquini*, ont également été observés pendant l'incubation, notamment l'exploitation de zones de nourrissage, soit éloignées de leur site d'incubation (à plus de 700 mètres comme par exemple à Kenton), soit fortement atypiques pour un huîtrier (par exemple les dunes à végétation à Goukamma). Enfin, la nécrophagie observée à Cape Recife, très importante pour certains individus (Chapitre 4) souligne leur capacité à exploiter des espèces qui n'entrent pas dans leur gamme typique de proies. Cependant, la consommation d'ascidies, échoués (*Pyura stolonifera*) et disponibles virtuellement à tout heure de la marée, requiert en

réalité un effort continu et un talent particulier alliant l'utilisation successive de plusieurs techniques pour percer la tunique des ascidies (Pacheco & Castilla 2001, *obs. pers*.). Enfin sur certains sites des côtes sud-est et sud-ouest, des disparités dans les pas isotopiques du sang et des plumes suggèrent des changements de résidence et/ou de régime alimentaire pendant la saison de repos, potentiellement dûs au relâchement du comportement territorial et à des limites associées à leurs territoires d'alimentation (Chapitre 5).

La variabilité individuelle, notamment morphologique, au sein d'une population, peut avoir de sérieuses conséquences sur les capacités de chacun à exploiter de manière optimale les ressources de nourriture à sa disposition (Durell 2000, Van de Pol et al. 2010). Contrairement aux prédictions tirées des études faites sur *H. ostralegus* sur le dimorphisme sexuel du bec et les différences alimentaires observées entre sexes chez *H. moquini* avant l'invasion (Hockey & Underhill 1984), il semblerait que les mâles et femelles d'huîtriers noirs africains puissent réagir de manière équivalente à la transformation de leur habitat d'alimentation par une nouvelle proie potentielle. L'estimation des conditions corporelles des huîtriers dans les différentes régions côtières (Chapitre 4) vient cependant nuancer ces observations. La condition corporelle des oiseaux sur la côte sud-ouest est en effet plus faible que dans les autres régions, à la fois chez les mâles et les femelles. La côte sud-ouest est caractérisée par une biomasse d'invertébrés benthiques comparable à la côte sud-est (Bustamante & Branch 1996b), mais sur les sites échantillonnés dans cette région, les brouteurs étaient particulièrement peu représentés sur les zones d'alimentation. En revanche les huîtriers se reproduisant dans des habitats dépourvus de moules invasives, mais présentant une diversité et des biomasses de patelles conséquentes (sud-est), avaient des conditions corporelles similaires à ceux vivant dans des habitats où la moule invasive est abondante et domine la biomasse de proies disponibles. On peut dès lors se demander si une biomasse relativement faible couplée à une pauvre diversité spécifique en proies n'aurait finalement pas plus d'impact que la présence ou l'absence de moules exotiques sur la capacité des huîtriers à se développer de façon optimale. Ceci suggèrerait qu'il pourrait exister une certain degré de ségrégation alimentaire entre les sexes comme cela a été mis en évidence sur les sites les orientaux (Kohler et al 2009b), quand les conditions d'alimentations deviennent plus limitantes. Ainsi, la moule de Méditerranée aurait pu provoquer un relâchement dans la sélection alimentaire sur les sites où elle est extrêmement abondante. Ce même

relâchement serait visible sur des sites non envahis mais présentant des biomasses en proies suffisantes par rapport au nombre d'huîtriers présents.

Enfin, les observations directes, parfois opportunistes, faites sur les huîtriers en reproduction ont montré la consommation d'une grande variété de types de proies autres que Mytillidés et Patellidés, comme les polychètes (*Gunnarea capensis*, *Pseudonereis variegata*, ainsi que des vers enfouis non-identifiés), les *Donax*, les ascidies échouées, les chitons géants (*Dinoplax gigas*), de petits gastéropodes (dont probablement *Oxystele variegata*), des insectes (via le kleptoparasitisme sur des pluviers) et de petits crustacés enfouis (isopodes et amphipodes). Cette liste est très certainement une sous-estimation de la gamme actuelle d'invertébrés qui peut être occasionnellement consommée par les huîtriers noirs africains, mais montre néanmoins la diversité des proies potentielles de l'oiseau.

Les espèces généralistes et spécialistes diffèrent par la largeur de leur niche écologique qui résulte d'un compromis entre la capacité à exploiter un large gradient de ressources et l'efficacité à exploiter chaque ressource (Roughgarden 1972, Futuyma & Moreno 1988). Le large éventail de proies consommées et le peu de variabilité isotopique individuelle à l'échelle locale, suggère qu'*H. moquini* est avant tout une espèce généraliste. En effet les espèces généralistes ont une niche écologique relativement large et sont capables d'exploiter un grand nombre de proies mais sont aussi théoriquement moins efficaces pour en tirer parti. Cependant, une espèce généraliste peut être composée soit strictement d'individus généralistes, soit d'une collection de spécialistes (exploitant chacun efficacement un sous-ensemble de proies disponibles), soit d'une combinaison d'individus spécialistes et généralistes (Bolnick et al. 2003). Il a été récemment suggéré que les espèces généralistes étaient en réalité principalement composées d'individus spécialistes capables de présenter une certaine plasticité selon le contexte (Bolnick et al. 2007). La plasticité est la capacité d'un organisme ayant un génotype donné d'exprimer différents phénotypes (ici le comportement alimentaire) selon l'environnement biotique ou abiotique dans lequel il se trouve (Agrawal 2001). Le type de transition alimentaire opérée par l'huîtrier en réponse à l'addition d'une proie plus favorable que les espèces natives témoigne en effet de la plasticité comportementale de cet oiseau et de sa capacité à s'adapter aux conditions changeantes de son habitat d'alimentation. Enfin, il est aussi prédit que les espèces généralistes sont plus à même de bénéficier des changements globaux et anthropogéniques affectant la biodiversité, notamment

en augmentant leur population ou en élargissant leur aire de répartition (Devictor et al. 2008, Clavel et al. 2011), ce qui est aujourd'hui le cas de l'huîtrier noir africain. Ces observations laissent penser qu'à long terme, les capacités d'adaptation de l'huîtrier peuvent lui permettre de faire face aux bouleversements qui pourraient perturber son habitat d'alimentation, en modifiant en particulier les assemblages de proies en réponse à l'augmentation de la température de l'eau de mer.

V. Atouts et limites des isotopes stables dans l'étude de l'écologie alimentaire d'*Haematopus moquini*

Les isotopes stables sont particulièrement appréciés pour étudier les différences interindividuelles du comportement alimentaire et sont aujourd'hui utilisés pour aborder des questions relatives aux dimensions de niche trophique des espèces (Bolnick et al. 2003, 2007, Bearhop et al. 2004, Cherel 2008). En effet, dans le cas de sources de nourriture (ou de zones d'alimentation) présentant des signatures isotopiques contrastées, les variations de $\delta^{13}C$ et $\delta^{15}N$ chez une population de consommateurs seront interprétées comme le reflet de variations de régime ou comportement alimentaire entre ses individus (Matthews & Mazumder 2004, Chapitre 2). Par exemple une large variance isotopique observée au sein d'une population peut suggérer une forte spécialisation individuelle (Bolnick et al. 2003). Paradoxalement, dans la présente étude, les conditions océanographiques contrastées de la région d'étude et les traits d'histoire de vie du modèle biologique, qui constituent à la fois l'originalité et la portée de ces travaux de thèse, représentent aussi d'importantes limites dans l'utilisation des isotopes stables. D'une part, la faible densité en huîtriers sur les sites de reproduction (Table 1.1) et une fragmentation inégale de leur population sur l'ensemble de leur aire de répartition compliquent la capture d'un nombre suffisant d'individus par unité géographique homogène. D'autre part, la ligne de base isotopique (matière organique particulaire et producteurs primaires) varie significativement le long des côtes du sud de l'Afrique. Pour cette raison, un échantillonnage le plus exhaustif possible des moules et des patelles a dû être réalisé, pour avoir une vision la plus claire possible de la ligne de base isotopique dans les différentes régions étudiées (Post 2002). Néanmoins il est difficile de comparer les signatures isotopiques d'individus échantillonnés sur différents sites ou régions pour étudier la variabilité trophique individuelle des consommateurs à l'échelle de la population, au risque de confondre la variabilité isotopique liée aux conditions environnementales avec la variabilité liée à des compositions de régime alimentaire différentes.

Un moyen de contourner ce problème est d'utiliser les modèles de mélange isotopiques de type IsoSource ou SIAR (Phillips & Gregg 2003, Parnell et al. 2010), qui intègrent à la fois la composition isotopique des proies et des consommateurs et l'enrichissement trophique entre les deux. Ainsi la variabilité spatiale isotopique existant à la base de la chaîne trophique est « lissée » entre les différentes unités géographiques considérées et les contributions relatives des différentes sources peuvent être comparées d'un site ou d'une région à l'autre (Chapitres 4 & 5).

L'application des isotopes stables du carbone et de l'azote dans le cadre de l'étude du régime alimentaire d'un organisme requiert au préalable de faire un choix sur les proies potentielles à considérer. En effet un trop grand nombre de proies limite d'une part les interprétations sur les relations trophiques entre proies et prédateurs et d'autre part la résolution des modèles de mélange. Les moules et les patelles dominent la biomasse d'invertébrés benthiques et occupent les deux extrémités du continuum de $\delta^{13}C$ qui existe sur les estrans rocheux sud-africains. De plus, leur importance dans le régime alimentaire d'*H. moquini* a été montré dans plusieurs études sur son écologie alimentaire (Randall & Randall 1982, Hockey & Underhill 1984, Coleman & Hockey 2008, Kohler et al. 2009b). Pour toutes ces raisons, ces deux taxons ont été largement privilégiés lors de l'échantillonnage de proies. Un biais majeur induit par cette approche est qu'on peut facilement passer à côte de proies potentiellement importantes, d'autant plus si elles ont des compositions isotopiques proches des proies échantillonnées. Par ailleurs, certains huîtriers ont présenté des signatures isotopiques ne pouvant s'expliquer sur la seule base des signatures isotopiques des moules et des patelles, suggérant une utilisation ponctuelle de proies non considérées en tant que sources potentielles dans les modèles de mélange. Par exemple, à Cape Recife, conjointement aux signatures isotopiques quelques peu inattendues de certains individus (Chapitre 4), j'avais observé à plusieurs reprises des huîtriers s'intéressant à des organismes marins échoués. L'échantillonnage additionnel des ascidies pour analyses d'isotopes stables sur ce site et l'observation des comportements alimentaires des huîtriers pendant l'incubation et le nourrissage des poussins ont permis de mettre en évidence l'importance de ces proies dans le régime alimentaire de certains huîtriers sur ce site en particulier. Ceci montre qu'il est essentiel, autant que possible, de coupler l'échantillonnage méthodique de proies avec des observations directes du comportement alimentaire des consommateurs, afin de limiter les interprétations erronées des sorties de modèles de mélange.

Dans les modèles de mélange, le problème du surplus de proies potentielles peut être partiellement résolu par l'agrégation *a posteriori* des sorties de modèles (Phillips et al. 2005) comme il a été fait séparément pour les moules et les patelles dans les Chapitre 4 & 5. Cela revient à considérer une guilde trophique (ex : brouteurs) ou un groupe taxonomique (ex : polychètes) agrégé comme un ensemble de proies homogène pour le consommateur. Cependant, cela ne prend pas en compte, par exemple, la zonation et l'activité des espèces de proies sur l'estran qui, dans un contexte de balancement des marées et d'exposition à la houle, peut avoir une très grande significativité sur la disponibilité des proies pour un prédateur terrestre comme l'huîtrier noir africain, qui doit donc adapter son comportement de recherche alimentaire (Coleman & Hockey 2008). Dans le chapitre 6 par exemple, l'observation des comportements alimentaires des oiseaux en incubation a mis en évidence une ségrégation temporelle de l'activité de nourrissage des mâles et de femelles autour de la basse mer et ce, différemment selon les sites et les communautés de proies.

Enfin, une question non clairement résolue dans ces travaux de thèse est le lien entre le dimorphisme sexuel du bec largement exprimé chez l'huîtrier noir africain et le peu de ségrégation trophique des mâles et femelles révélée par les isotopes stables du carbone et de l'azote. Chez l'huîtrier européen, la spécialisation alimentaire, soit sur un type de proie, soit par les techniques employées, a évolué parallèlement au polymorphisme continu de l'extrémité du bec, qui varie aussi entre classes d'âge et entre les sexes (Sutherland et al. 1996). Le fait que la forme de l'extrémité du bec soit avant tout dessinée par son abrasion, c'est-à-dire l'usage qu'en fait l'oiseau, limite les possibilités non liées à l'alimentation. D'autres hypothèses, telles que la reconnaissance sexuelle ou le partage des rôles parentaux (bien qu'apparemment peu prononcé chez l'huîtrier noir africain, voir Chapitre 6) peuvent être considérées pour expliquer, du moins partiellement, le maintien du dimorphisme sexuel du bec chez *Haematopus moquini.* Cependant il est hautement improbable que ce trait exprimé de façon similaire chez deux espèces, si proche écologiquement, morphologiquement et taxonomiquement ait des origines évolutives si différentes.

Finalement, tout un pan du comportement alimentaire des huîtriers, qui pourrait avoir une grande importance sur le caractère adaptatif et la dynamique de population d'*H. moquini*, semble être occulté par les limites intrinsèques des isotopes stables. En

effet, les ratios de $\delta^{13}C$ et de $\delta^{15}N$ donnent une résolution de l'écologie alimentaire à deux dimensions et ne peuvent rendre complètement compte de la complexité du comportement d'alimentation inhérent à ce type d'oiseau. Néanmoins, dans l'approche biogéographique et macro-écologique de ce travail, l'utilisation des isotopes stables a apporté des réponses sur les conséquences actuelles des perturbations biologiques couplées à des conditions océanographiques contrastées sur l'écologie d'un prédateur apical des estrans rocheux. L'efficacité de l'outil isotopique dans les approches régionales a déjà été mise en évidence dans de nombreux autres écosystèmes terrestres et aquatiques et pour de nombreux organismes animaux et végétaux (Ambrose & DeNiro 1986, Cerling et al. 1997, Rubenstein & Hobson 2004, Cherel & Hobson 2007, Newsome et al. 2007). Ce travail est à ma connaissance l'un des premiers à l'avoir vérifié sur un prédateur aviaire littoral, confirmant ainsi le potentiel des isotopes stables pour l'étude de l'écologie des limicoles dans d'autres milieux. Par exemple, un grand nombre de ces espèces, notamment en Europe, se distribuent sur des aires géographiques très grandes où les patrons de production primaire, les distributions spécifiques d'invertébrés benthiques et les perturbations humaines présentent de forts contrastes spatiaux et temporels multi-échelles, dont les impacts sur les populations de limicoles pourraient être renseignés à l'aide de l'outil isotopique. L'approche utilisée dans le cadre de cette thèse, couplant l'utilisation des isotopes stables à une perspective spatiale à grande échelle, représente dans ce cas une perspective particulièrement prometteuse pour l'étude de l'écologie trophique de ces espèces.

VI. Conclusions et perspectives

Dans ces travaux de thèse, je me suis à attachée principalement à comprendre l'influence des conditions environnementales sur l'écologie alimentaire d'un prédateur aviaire d'estrans rocheux endémique et menacé à l'échelle de sa répartition spatiale. Dans cette dernière partie, je mets les résultats obtenus en perspectives des caractéristiques démographiques actuelles et futures de l'espèce.

J'ai montré que les huîtriers noirs africains répondent d'un point de vue trophique aux fluctuations qualitatives et quantitatives des communautés de proies à plusieurs échelles. Ces fluctuations de biomasse et de diversité spécifique varient à l'échelle du sud de l'Afrique en réponse à la nature (origine des masses d'eau) et à la qualité des eaux littorales (nutriments et rejets anthropiques). De plus, à l'échelle de sa distribution spatiale, la composition du régime alimentaire d'*Haematopus moquini* est

étroitement liée à la distribution et à la dominance relative d'une espèce de moule invasive, *Mytilus galloprovincialis*, sur les côtes rocheuses du sud de l'Afrique. L'utilisation des isotopes stables du carbone et de l'azote, en combinaison avec des observations directes ont montré qu'*H. moquini* exploite avant tout les proies les plus abondantes dans son habitat d'alimentation, tout en présentant une diversité de comportements alimentaires lui permettant d'exploiter au mieux la variabilité locale de sont habitat et de faire ainsi face aux contraintes de son environnement. L'ensemble de ces résultats montre qu'avant tout *H. moquini* est une espèce avec une forte plasticité comportementale, s'adaptant localement et à l'échelle de sa distribution aux fluctuations de son environnement, tout en présentant une faible variabilité locale de son comportement alimentaire. Ces caractéristiques comportementales d'un point de vue de l'exploitation des ressources alimentaires suggèrent que dans le futur, les facteurs qui limiteraient sa croissance démographique ne seraient probablement pas d'ordre trophique. Néanmoins, pour renforcer ces résultats, il faudrait comprendre également les facteurs abiotiques et biotiques qui auraient pu modifier son régime alimentaire par le passé, notamment en réponse aux changements climatiques et aux perturbations humaines. Or, on connaît finalement peu de choses sur son écologie alimentaire avant les années 1980. L'outil isotopique utilisé sur des plumes de spécimens de musées et d'oiseaux contemporains pourrait notamment renseigner sur des variations de ligne de base isotopique sur les côtes sud-africaines au cours du siècle dernier, reflétant des changements temporels dans la qualité de la production primaire ou des modifications d'assemblage d'invertébrés benthiques comme cela a été mis en évidence chez d'autres oiseaux marins (Hilton et al. 2006, Jaeger & Cherel 2011). Un certain nombre d'échantillons historiques d'huîtrier noirs africains datant de 1870 jusqu'aux années 1980 a déjà été rassemblé et pourraient apporter des informations sur les changements d'habitats alimentaires qu'à connu *H. moquini* au cours des 100 dernières années.

Aujourd'hui, la population d'huîtriers noirs africains serait plutôt affectée par la capacité d'accueil de son environnement pour les reproducteurs à l'échelle locale et globale, elle-même influencée par des facteurs d'ordre climatique et surtout anthropique. Toutes les espèces d'huîtriers se reproduisent quasi-exclusivement dans des régions tempérées (Hockey 1996), et malgré son expansion récente vers l'est, la répartition géographique de reproduction d'*H. moquini* semble limitée par l'extension des provinces biogéographiques tempérées et subtropicales des côtes

africaines. Pourtant, la moule indigène *Perna perna*, proie privilégiée par les huîtriers sur la côte sud-est, est commune sur les côtes du Kwazulu-Natal (Fig 1.1). Par ailleurs, de Cape Columbine sur la côte ouest, jusqu'à la région de Lüderitz (Fig 1.1), les estrans rocheux supportent de fortes biomasses de moules, mais très peu de couples reproducteurs d'huîtriers. En revanche, de larges groupes de jeunes adultes non-reproducteurs et d'immatures, qui passent deux à trois ans à plusieurs centaines voire milliers de kilomètres de leurs sites d'origine après leur naissance, sont fréquemment observés dans ces régions. Ainsi, chez cet oiseau longévive, fidèle à son site de reproduction et présentant aussi une forte fidélité au partenaire sexuel, le choix de l'habitat pour s'établir ne serait pas dicté uniquement par la qualité des zones d'alimentation, mais aussi, chez cette espèce hautement territoriale, par le besoin d'un espace vital suffisant pour se reproduire.

Dès lors, on peut se poser des questions sur sa capacité à faire face aux perturbations futures liées au contexte du changement global qui influence la biodiversité et les stocks de ressources naturelles, en particulier en zone littorale (Gray 1997). *Haematopus moquini* présente une capacité à s'adapter aux changements de communautés de proies, donc les oiseaux devraient pouvoir absorber à « moindres frais » de possibles changements dans la composition spécifique des communautés d'invertébrés benthiques en conséquence de changements abiotiques ou anthropogéniques futurs, à condition que ces perturbations n'affectent pas drastiquement les biomasses disponibles. En revanche une réduction de la capacité d'accueil de son habitat pour la reproduction, notamment induite par les activités humaines en zones côtières, accentuerait la compétition intra-spécifique pour l'espace, ce qui pourrait avoir des conséquences plus négatives pour la santé démographique de l'espèce.

Il est donc essentiel aujourd'hui de focaliser les efforts de protection de l'espèce sur la préservation de son habitat de reproduction et de limiter le plus possible l'interférence des activités humaines sur ces sites, particulièrement importantes pendant la saison de reproduction. Ceci passe notamment par une information au public et par une application plus stricte des réglementations déjà en vigueur. Finalement l'observation que j'ai faite des interactions reproducteurs-prospecteurs reste anecdotique et n'est quasiment pas rapportée dans la littérature sur l'espèce. D'une part leurs effets potentiels sur le succès reproducteur des huîtriers résidents sont, à ce jour, ignorés. D'autre part, l'origine géographique exacte

de ces individus notamment sur la côte sud-est reste inconnue. Ces deux aspects pourraient avoir des conséquences importantes sur les capacités de l'espèce à faire face à des perturbations futures de son habitat de reproduction et d'alimentation. On pourrait donc envisager d'une part d'étudier la génétique des populations d'*H. moquini*, en se concentrant sur les sites connaissant une croissance importante des populations résidentes et supportant de fortes populations de non-reproducteurs et d'autre part d'étudier les interactions intra-spécifiques et leur impact sur la valeur sélective des populations locales.

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LISTE DES FIGURES

LISTE DES TABLEAUX

ANNEXES

Annexe 1. Liste des publications scientifiques, communications orales et posters

Annexe 2. Bonnevie, B. **Kohler, S.** (2007) What is the correct ring size for female African Black Oystercatchers (*Haematopus moquini*)? Afring News 36:13-14

Annexe 3. **Kohler S**, Bonnevie, B., Dano S (2009) Can eyeflecks be used to sex African Black Oystercatchers *Haematopus moquini* in the field? Ostrich 80:109-110

Annexe 4. **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. Estuarine, Coastal and Shelf Science 84:361-366.

Annexe 5. **Kohler SA**, Connan M, Hill JM, Mablouké C, Bonnevie B, Ludynia K, Kemper J, Huisamen J, Underhill LG, Cherel Y, McQuaid CD, Jaquemet S (*in press*). Geographic variation in the trophic ecology of an avian rocky shore predator, the African Black Oystercatcher along the southern African coastline. Marine Ecology Progress Series

Annexe 6. **Kohler SA**, Connan M, Kolasinski J, Cherel Y, McQuaid CD, Jaquemet S. (*submitted to Journal of Avian Biology*). Minimal sex-related trophic segregation in a sexually dimorphic shorebird, the African Black Oystercatcher (*Haematopus moquini*) revealed by stable isotope analyses.

Annexe 7. **Kohler SA**. (2010) Letters “Scrambling egg”. Africa Birds & Birding 15 (2): p4.

Annexe 1

Liste des publications scientifiques, communications orales et posters

Publications

- Bonnevie B, **Kohler S** (2007) What is the correct ring size for female African Black Oystercatchers (Haematopus moquini)? Afring News 36:13-14.

- Gaudron SM, **Kohler S**, Conand, C (2008) Reproduction of the sea cucumber *Holothuria leucospilota* in the western Indian Ocean: biological and ecological aspects. Invertebrate Reproduction and Development, 51 (1): 19-31.

- **Kohler S**, Gaudron SM, Conand C (2009) Reproductive Biology of Actinopyga echinites and Other Sea Cucumbers from La Réunion (Western Indian Ocean): Implications for Fishery Management. Western Indian Ocean Journal of Marine Science 8:97-111

- **Kohler S**, Bonnevie B, Dano S (2009) Can eyeflecks be used to sex African Black Oystercatchers Haematopus moquini in the field? Ostrich 80:109-110

- **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. Estuarine, Coastal and Shelf Science 84:361-366

- **Kohler SA**, Connan M, Hill JM, Mablouké C, Bonnevie B, Ludynia K, Kemper J, Huisamen J, Underhill LG, Cherel Y, McQuaid CD, Jaquemet S (in press) Geographic variation in the trophic ecology of an avian rocky shore predator, the African Black Oystercatcher, along the southern African coastline. Marine Ecology Progress Series

- **Kohler SA**, Connan M, Kolasinski J, Cherel Y, McQuaid CD, Jaquemet S (submitted) Minimal sex-related trophic segregation in a sexually dimorphic shorebird, the African Black Oystercatcher (Haematopus moquini) revealed by stable isotope analyses. Journal of Avian Biology

Communications orales et posters

- International Wader Study Group Conference 2007, La Rochelle, France, Septembre 2007. *Sex-specific foraging strategy of the African Black Oystercatcher (*Haematopus moquini*) in the Eastern Cape (South Africa* (ORAL)*)*.

- 5th Western Indian Ocean Marine Science Symposium, Durban, Afrique du Sud, Octobre 2007. **I)** *Foraging ecology of a near-threatened endemic shorebird: the African Black Oystercatcher (*Haematopus moquini*) on the southeast rocky coasts of South Africa* (ORAL). **II)** *Reproductive biology of sea cucumbers from La Réunion: a contribution for a regional management of the fishery* (ORAL).

- 13th Southern African Marine Science Symposium, Cape Town, Afrique du Sud, Juillet 2008. *Feeding ecology of the African Black Oystercatcher (*Haematopus moquini*) on the southeast rocky coasts of South Africa: Insights from an isotope analysis* (ORAL).

- 12th Pan African Ornithological Congress, Goudini Spa, Afrique du Sud, Septembre 2008. *Sex-specific foraging strategies of the African Black Oystercatcher (*Haematopus moquini*) on the south coast of South Africa: insights from stable isotope analysi* (ORAL).

- 6th Western Indian Ocean Marine Science Symposium, Saint-Denis, la Réunion, France, Août 2009. **I)** *New insight from stable isotope analysis in trophic segregation between male and female African Black Oystercatcher (*Haematopus moquini*)* (ORAL). **II)** *Biogeographic trends in stable isotope signatures in African Black Oystercatchers and their prey around the coast of South Africa* (POSTER – Awarded best student poster)

- 7th International Conference on Applications of Stable Isotope techniques to Ecological studies, Fairbanks, Alaska USA, Août 2010. **I)** Are African Black Oystercatchers good indicators of both local and large-scale trends in intertidal communities? (ORAL) **II)** Are muscle tissues a good proxy for whole body $\delta^{13}C$ and $\delta^{15}N$ signatures in intertidal invertebrate species throughout the year? Implications for top-predator studies (POSTER)

- International Wader Study Group Conference 2010. Lisbon, Portugal, Octobre 2010. Are African Black Oystercatchers good indicators of large-scale trends in intertidal communities? A stable isotope study (ORAL).

Annexe 2

What is the correct ring size for female African Black Oystercatchers (*Haematopus moquini*)?

Bo Bonnevie & Sophie Kohler (2007)

Afring News

Afring News online 36:13-14, 2007

What is the correct ring size for female African Black Oystercatchers *Haematopus moquini*?

***Bo Bonnevie*[1] *& Sophie Kohler*[2]**

1. Information Technology Division, Rhodes University, Grahamstown, South Africa, 6140; B.Bonnevie@ru.ac.za
2. Department of Zoology & Entomology, Rhodes University, Grahamstown, South Africa, 6140

Female African Black Oystercatchers *Haematopus moquini* are larger than the males (Hockey 1981, Maclean 1993). De Beer et al. (2000) recommend a size 8mm stainless steel (SS) ring for this species. During a study of blood and feather isotopes of African Black Oystercatchers in the Eastern Cape, South Africa, we have ringed both males (n = 9), females (n = 14) and chicks (n = 19) of this species, as well as 11 unsexed adults. We found that the 8mm ring was suitable for males, but that it was generally too small for females in this area.

We have re-trapped females with constricted tarsi clearly caused by rings that are too small (Fig. 1). The damaged tarsus is thinner than that of the other leg and discoloured because of reduced blood circulation (the colour of the tarsus under a loosely fitted ring is much darker). An additional problem is that when rings are fitted they are often closed into a round shape. The tarsi of African Black Oystercatchers are not round, so the rings should be flattened to fit the leg properly. This will also provide a looser fit for the same ring size. We flattened the ring on the female tarsus shown (Fig. 1) after which it could move up the leg, although it was still a tight fit.

SAFRING does not supply 9mm SS rings at present. We, therefore, started using 10mm SS rings on females as this is the next largest size available from SAFRING after the 8mm ring. Many African Black Oystercatchers are, however, ringed as chicks which cannot be sexed in the field. We, therefore, recommend that a 9mm SS ring should be sourced and used for both sexes of the African Black Oystercatcher in the Eastern Cape.

During this field work we have seen quite a number of oystercatchers with one foot missing and one was also caught (Fig. 2). It is possible that tightly fitted rings could cause this sort of injury. We have also caught birds with fishing line tangled around their feet and this also could possibly cause such injuries. It would be interesting to survey missing feet on oystercatchers: if there are more injuries on the right foot (where the ring is typically fitted) this could be an indication that too small a ring size contributes to these kinds of injuries.

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Fig. 1. Tarsus of a female oystercatcher damaged by a constricting ring (photo: Sophie Kohler)

Fig. 2. Dr Paul Martin holding an oystercatcher with a missing right foot (photo: Sophie Kohler)

Annexe 3

Can eyeflecks be used to sex African Black Oystercatchers *Haematopus moquini* in the field?

Sophie Kohler, Bo Bonnevie & Stéphanie Dano (2009)

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Short Note

Can eyeflecks be used to sex African Black Oystercatchers *Haematopus moquini* in the field?

Sophie Kohler[1,2]*, Bo Bonnevie[3] and Stéphanie Dano[4]
[1] *Laboratoire ECOMAR, Université de La Réunion, 97715 Saint-Denis Messag Cedex 09, France*
[2] *Coastal Research Group, Department of Zoology and Entomology, Rhodes University, PO Box 94, Grahamstown 6140, South Africa*
[3] *Information Technology Division, Rhodes University, PO Box 94, Grahamstown 6140, South Africa*
[4] *Centre d'Etudes Biologiques de Chizé, UPR 1934 – CNRS, 79360 Villiers-en-Bois, France*
* *Corresponding author, e-mail: kohler84@gmail.com*

Morphometric differences between males and females are a common feature among oystercatcher species (Hockey 1996), although breeding partners often appear similar when observed from a distance. Combinations of different biometric parameters such as bill size and shape, body mass, wing and tarsus lengths have been used to discriminate males and females in the field in European Oystercatchers *Haematopus ostralegus* (Zwarts et al. 1996), American Black Oystercatchers *Haematopus bachmani* (Guzzetti et al. 2008) and the three oystercatcher species present in New Zealand (Baker 1973). Sexual dimorphism also occurs in the African Black Oystercatcher *Haematopus moquini*, an endemic species living on the coasts of Namibia and South Africa. In this species, females tend to have longer and sharper bills than males (Hockey 1981, Hockey 2005). However, sex determination based solely on this parameter can be inaccurate because the ranges of bill size between males and females overlap. Variations in bill morphology between sites and/or regions may also occur in relation to feeding habits and prey assemblages (Hulscher 1996). Another way to sex oystercatchers is checking for cloacal distension in females during the period immediately after egg laying. Although molecular markers remain the most reliable tool for sexing non-ratite birds (Fridolfsson and Ellegren 1999), these techniques require capturing the birds, are relatively expensive and the results are not immediately available. A new field sexing technique for American Black Oystercatchers is based on the presence or absence of a black spot below the iris (Guzzetti et al. 2008). In this note, we investigated the potential use of this technique to sex African Black Oystercatchers in the field. Bill lengths and eyeflecks were used as discriminant factors to sex breeding individuals and we compared the accuracy of this technique with molecular sexing.

We captured breeding oystercatchers and chicks between December 2007 and February 2008 using walk-in traps on nests. Bill, wing, and tarsus lengths of adults were measured to the nearest 0.1 mm and birds were weighed to the nearest 1 g. As chicks were still growing, their biometric parameters were irrelevant for the purpose of this note. In addition, a high-resolution headshot of every bird was taken with a digital camera. A few drops of blood were drawn from the tarsus vein for molecular sexing based on size differences between the CHD1W and CHD1Z introns located on the sex chromosomes (Fridolfsson and Ellegren 1999).

A total of 34 breeding adults was captured, of which 17 were identified as female and 17 as male by molecular sexing. Twenty-nine chicks were caught by hand: 17 were later identified as females and 12 as males. Adult females had significantly longer bills than adult males (Student's *t*-test $P < 0.001$) with bill lengths ranging from 64.0 to 80.8 mm (mean 72.7 ± 3.8 mm) and 61.4 to 70.1 mm (65.2 ± 2.4 mm) for females and males, respectively (Figure 1). To test the accuracy of using bill length to discriminate between sexes, we assigned any bird with bill length >68.0 mm as female and <68.0 mm as male, 68.0 mm being the median of the bill length distribution. Using this technique, two females (bill length = 64.0 mm and 67.2 mm) were mistaken for males and two males (bill length = 68.2 mm and 70.1 mm) were incorrectly identified as females (Figure 1). In order to test the accuracy of eyeflecks in identifying males and females, we categorised eyeflecks as described in Guzzetti et al. (2008): a = no eyefleck, b = slight eyefleck and c = eyefleck (Figure 2). The following hypothesis was used: males have

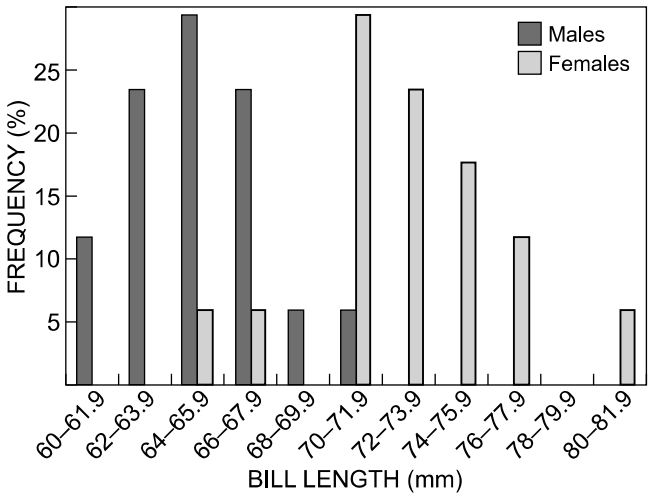

Figure 1: Distribution of bill sizes in males and females of adult African Black Oystercatchers

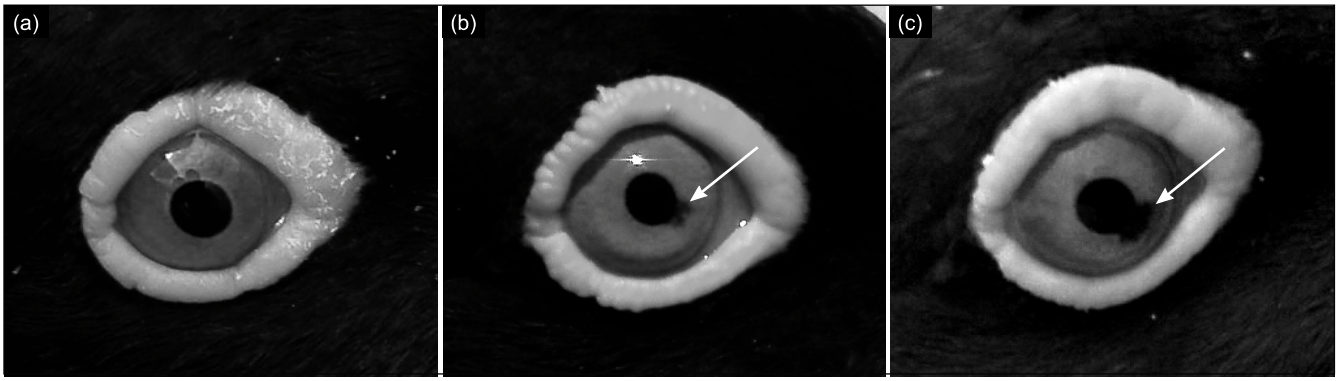

Figure 2: Categories of eyeflecks. (a) No eyefleck, (b) slight eyefleck and (c) eyefleck. When present, eyeflecks are indicated with a white arrow

no (Figure 2a) or slight eyeflecks (Figure 2b) and females have clear eyeflecks (Figure 2c). Out of 34 birds, only one female was misidentified as a male, based solely on this criterion (Figure 3) and no males were misidentified as females. No eyefleck was observed in any of the 29 chicks.

During bird sampling conducted between December 2007 and February 2008, we used bill length and eyeflecks to distinguish adult males from adult females after capture. A combination of these two factors allowed us accurately to sex each of the 34 sampled birds, as was later confirmed by molecular sexing. Except for one female with a slight eyefleck and a bill length of 70.4 mm, the absence or presence and intensity of eyeflecks in African Black Oystercatchers was a more reliable determinant of sex than bill length. Other morphometric factors, such as tarsus length and body mass, did not show any significant sex-related differences, although females displayed higher mean values for these parameters, as previously described in Hockey (1981). Using the same discriminating method as for bill length, sex determination using body mass and tarsus length were inaccurate for 32.4% and 41.2% of adults, respectively. Females had significantly longer wings (270.6 $\pm$ 7.7 mm) than males (266.1 $\pm$ 7.2 mm), but this was also a poor determinant of sex as 26.5% of adults were wrongly sexed based on this criterion.

Eyeflecks have been observed in at least 10 of the 11 oystercatcher species (Guzzetti et al. 2008), yet no explanation on the origin of these dark regions has been found. Hypotheses linking diet preferences, carotenoid allocation and health to eyeflecks have been proposed (B Guzzetti pers. comm.). Our conclusion is that eyeflecks are a reliable sex indicator for captured adult African Black Oystercatchers but not for chicks, thus sexing of juveniles in the field remains a problem. To increase the accuracy of sexing adults in the field, eyeflecks could be combined with other morphometric parameters, especially bill length. Finally, with proper optical equipment, using eyeflecks could provide a more objective method to assign sex from a distance than using other physical characteristics such as size and shape of bill.

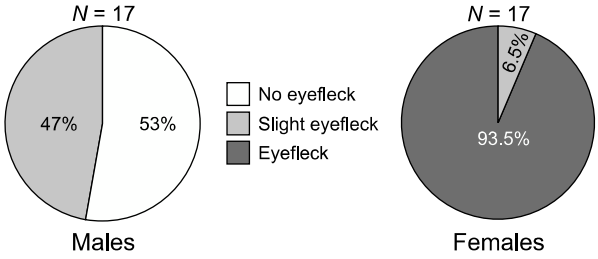

Figure 3: Proportions of eyefleck categories in males and females

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Annexe 4

Foraging ecology of an endemic shorebird, the African Black Oystercatcher (*Haematopus moquini*) on the south-east coast of South Africa

Sophie Kohler, Bo Bonnevie, Christopher D. McQuaid

& Sébastien Jaquemet (2009)

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Foraging ecology of an endemic shorebird, the African Black Oystercatcher (*Haematopus moquini*) on the south–east coast of South Africa

Sophie Kohler [a,b,*], Bo Bonnevie [c], Christopher McQuaid [b], Sébastien Jaquemet [a]

[a] Laboratoire ECOMAR, Université de La Réunion, 97715 Saint-Denis de La Réunion, France
[b] Coastal Research Group, Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa
[c] Information Technology Division, Rhodes University, Grahamstown 6140, South Africa

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ABSTRACT

We investigated small–medium (1–300 km) scale variation in the foraging ecology of the African Black Oystercatcher during its breeding season, using traditional diet analysis coupled with carbon and nitrogen stable isotope analysis. Fieldwork was conducted between January and March 2006 and 2007, on rocky shores on the south–east coast of South Africa at East London, Kenton and Port Elizabeth. Middens of shelled prey left by adults feeding their chicks were collected from five territories and the abundances of the collected prey on the foraging areas were estimated using quadrats. Blood samples from 45 birds (16 females, 10 males and 19 chicks) and tissues from the predominant prey species on the territory of each breeding pair were collected for isotope analysis. The Manly–Chesson selectivity index revealed that adults feed their chicks preferentially with the limpet *Scutellastra cochlear* and the Mediterranean mussel *Mytilus galloprovincialis*, if available. A slight enrichment in the ^{15}N stable-carbon isotope signature was observed towards the west in both prey and oystercatchers. Differences in isotope signatures between males and females from the same breeding pair indicate sex-related differences in the diet. Both had signatures indicating a mixed diet, but with males exhibiting a signature closer to that of limpets and females closer to that of mussels. In the single case where mussels were rare on the feeding territory, the two members of a pair showed carbon signatures which were identical and very similar to that of limpets. These results indicate dietary partitioning between genders in breeding pairs.

1. Introduction

The African Black Oystercatcher (ABO, *Haematopus moquini*) is an endemic shorebird of southern Africa with a limited population estimated at 6000 adults (Hockey et al., 2005). Until recently the species was threatened with extinction through perturbations in its habitat, as a consequence of increasing human activities and unsustainable practices on the shore (Hockey, 1983). The population size has, however, increased for the past 20 years (Hockey et al., 2005). Surprisingly this increase of population follows strong modifications of its foraging habitat. The invasion of the shore on the west coast of South Africa by the Mediterranean mussel (*Mytilus galloprovincialis*) has had a positive consequence on ABO population sizes (Hockey and Van Erkom Schurink, 1992). This invasion has led to the expansion of oystercatcher breeding ranges further eastwards along the coast of South Africa (Vernon, 2004; Hockey et al., 2005; Brown and Hockey, 2007), by enhancing the overall availability of food for this bird (Van Erkom Schurink and Griffiths, 1990; Branch and Steffani, 2004).

Shorebirds can exhibit various feeding strategies related to their social status, age, sex, individual skills and food availability (Durell, 2000). Several studies have demonstrated that breeding oystercatchers tend to select large prey to deliver to their chicks (Randall and Randall, 1982; Hockey and Underhill, 1984). In some cases, they are also able to detect the most energetically profitable prey using their bill (Nagarajan et al., 2002a,b). Moreover, sex-specific foraging strategies are common in oystercatchers (Durell et al., 1993) and allow optimization of the exploitation of the feeding territory by reducing intra-specific competition (Durell, 2000). Such differences in foraging strategy are associated with differences in bill shape between the sexes (Durell et al., 1993), allowing adaptation to particular prey (Sutherland, 1987).

Stable isotopes analyses are now widespread in ecology as a tool to investigate the diets of organisms over different time-integrated

* Corresponding author. Laboratoire ECOMAR, Université de La Réunion, 97715 Saint-Denis de La Réunion, France.
E-mail addresses: kohler84@gmail.com (S. Kohler), b.bonnevie@ru.ac.za (B. Bonnevie), c.mcquaid@ru.ac.za (C. McQuaid), sebastien.jaquemet@univ-reunion.fr (S. Jaquemet).

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periods. Stable-carbon and stable-nitrogen isotopes respectively provide information on the source of primary production at the base of the food chain and on the trophic level of the studied species (Hobson and Wassenaar, 1999). Predator-prey relationships and trophic segregation between individuals can be revealed through the isotopic signatures of their tissues and those of their prey. A recent study established biogeographic gradients in suspended particular matter (SPM) and of filter feeding mussels along the coast of southern Africa using ^{13}C and ^{15}N stable isotope analysis (Hill et al., 2006). This study also revealed mixed inshore–offshore sources of food for mussels. These geographic variations of isotope signatures at low trophic levels were related to contrasting oceanic conditions along the coastline (Hill et al., 2006).

The ecology of ABOs has already been well studied on the west coast of South Africa (Hockey, 1983; Hockey and Underhill, 1984; Hockey et al., 2005; Tjørve and Underhill, 2006). Less is known about the ABO ecology on the south–east coast, except that adults feed on mussels and limpets (Randall and Randall, 1982; Hockey and Underhill, 1984) and that the breeding population has increased in recent years (Vernon, 2004). In particular, the relationship of the ABO with the Mediterranean mussel has not been investigated on the south–east coast, though the invasive mussel has now spread to this region (Robinson et al., 2005). The increasing importance of *Mytilus galloprovincialis* in the diet of the ABO on the west coast has been related to its increasing availability rather than to an active selection by the birds (Hockey and Van Erkom Schurink, 1992). Similarly, differences in diet composition between adults of two pairs of oystercatcher have been described (Hockey and Underhill, 1984), but there has been no detailed investigation of sex-related feeding strategies. Finally, as high trophic level predators, shorebirds and seabirds are sensitive to changes at the lower levels of the ecosystems in which they live (Sandford, 1999). Hence differences in the assemblage of prey in their feeding habitats, or in the isotopic signatures at the base of the ecosystems are likely to propagate along the trophic chain to oystercatchers.

The main aim of this study was to investigate the foraging ecology of ABOs on rocky shores of the south–east coast of South Africa, through different and complementary approaches (i.e. collection of feeding remains and stable isotope analysis) and to ascertain:

(1) if the biogeographic trends in stable isotopes observed in SPM and mussels by Hill et al. (2006) could propagate at smaller scales to higher trophic levels;
(2) if breeding oystercatchers actively select particular prey when feeding their chicks;
(3) if males and females exhibit different foraging strategies during the breeding season.

2. Materials and methods

2.1. Study sites

The study was conducted along 300 km of coastline on the south coast of South Africa (Fig. 1) between January and March in 2006 and 2007. Birds and their prey were studied at 11 different localities, including 10 rocky shores and one estuary, in three main sampling areas: Port Elizabeth (Cape Recife and Swartkops River Mouth), Kenton (Cannon Rocks, Diaz Cross, Shelley Beach, High Rocks and Kleinemonde) and East London (Christmas Rock, Kidd's Beach, Cove Rock and Bonza Bay).

2.2. Oystercatchers sampling

Breeding adults were caught during incubation with a trap placed on their nest, and chicks were caught by hand when found

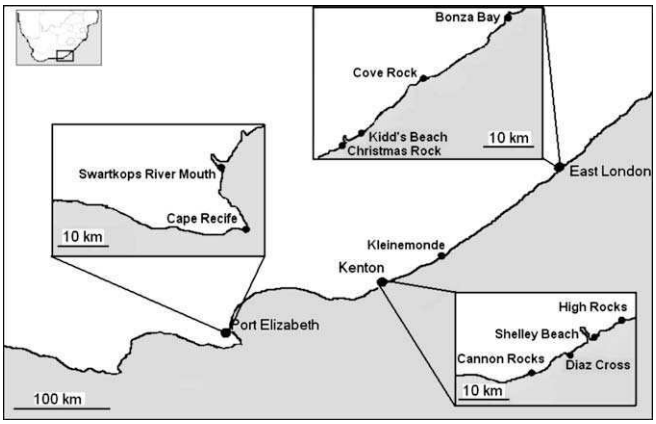

Fig. 1. Location of study sites in the Eastern Cape (South Africa).

on 10 rocky shores: Christmas Rock, Kidd's Beach, Cove, Bonza Bay (in the East London area), Cannon Rocks, Diaz Cross, Shelley Beach, High Rocks, Kleinemonde (in the Kenton area) and Cape Recife (Port Elizabeth) (Fig. 1). Blood samples (0.5 ml) were taken from the tarsus vein of chicks and adults and preserved in alcohol (70%) for stable isotope analysis. Body mass (g), culmen, tarsus, and wing length (mm) were taken according to the methods of De Beer et al. (2000) for each captured adult. When both breeding partners in a pair were captured, we could sex them without doubt according to the relative lengths of their bill as females have longer bills than their mates (Hockey, 1981; Hockey et al., 2005). All captured birds were marked with a unique engraved metal ring (SAFRING).

2.3. Prey sampling

Five specimens of the main known prey species (Randall and Randall, 1982; Hockey and Underhill, 1984; Hockey et al., 2005) were collected for stable isotope analysis on each of the 10 rocky shores where at least one chick or adult had been captured and sampled (see Section 2.2 and Fig. 1). When oystercatchers feed their chicks, they usually collect entire prey items on the territory and bring them to their chicks, which remain hidden above the high tide mark. As a result, feeding sites usually contain piles (middens) of empty mollusc shells, that we collected, identified and counted. When middens were found, the relative abundance of the main prey species was also estimated separately using quadrats (25×25 cm) on the foraging areas. Foraging areas were defined and delimited after observations of the movements and feeding behavior of both breeding partners during low tide. The intertidal area was then divided according to the rocky shore zonation established by Day (1969) and modified according to the specific composition (e.g. *Cochlear* zone, Mussel zone, *Granularis* zone). The approximate surface area of each zone was measured. The density of each species in each zone was estimated using 10 randomly placed quadrats. Abundance of each species on the entire territory was then estimated by weighting the density per zone by its size. This provided an estimate of the proportions of each prey species within the foraging area as a whole.

2.4. Stable isotope analysis

Blood samples were dried (60 °C, 24 h) and reduced to a homogeneous powder with a mortar and pestle cleaned with 70° alcohol and dried between samples to avoid contamination. For prey samples, muscle tissue was used, the adductor muscle tissue of mussels and the foot tissue of limpets. This material was removed, rinsed in distilled water (dH_20) and oven dried (60 °C, 48 h). As for

blood, samples were ground to a homogeneous powder for analysis. Adductor muscle and foot tissue were used in this study as they have low tissue turnover rates (Gorokhova and Hansson, 1999), and are therefore more representative of the isotopic signal of the diet as integrated over a period of months. In contrast, blood has a quicker turnover and provides information on the diet over the previous 4–5 weeks (Hobson and Clark, 1992).

$\delta^{13}C$ and $\delta^{15}N$ signatures of all samples were determined using a continuous flow isotope ratio mass spectrometer (IRMS), after sample combustion in on-line Carlo–Erba preparation units calibrated relative to the international standards of PDB for carbon and air for nitrogen. Results are expressed in standard notation, $\delta X = ([R_{sample}/R_{standard}] - 1) \times 1000$, where X is the element in question and R is the ratio of heavy to light isotope. Precision of replicate determinations was ±0.05‰ for both carbon and nitrogen.

2.5. Data analysis

To evaluate whether ABOs rearing their chicks are selective when foraging, we calculated the selectivity index of Manly–Chesson for the main prey (Chesson, 1983; see also Teixeira and Cortes, 2006). The index formula is:

$$\alpha_i = (r_i/p_i)/\sum (r_i/p_i), \quad i = 1, 2 \ldots m$$

where r_i = the proportion of the prey species i in the middens, p_i = the proportion of prey species i in the foraging area and m = the total number of prey species in the foraging area. If $\alpha_i > 1/m$, the prey species is selected. If $\alpha_i < 1/m$, the prey species is avoided and if $\alpha_i = 1/m$, the prey species is consumed in the same proportions as those on the foraging area. The selectivity index was calculated only for prey species found in both middens and on the foraging area during the prey density estimation using quadrats.

To test the significance of differences in stable isotope signatures between regions for the different organisms, we used a Kruskall–Wallis test and the Dunn post-hoc test.

3. Results

A total of 45 oystercatchers (16 females, 10 males and 19 chicks) were captured on 10 different rocky shores. Among the 26 captured adults, both the male and the female from a pair were captured on five occasions (Table 1). Three sets of middens were found and collected in Kenton (Shelley Beach, High Rocks and Diaz Cross) and a further two sets at the Swartkops River Mouth, in Port Elizabeth, though no birds were captured there.

3.1. Prey selectivity during the chick rearing period

Three sets of middens left by breeding oystercatchers were found at Kenton and two in Port Elizabeth at the Swartkops River Mouth. None were found in the East London area. Unlike the Kenton and Port Elizabeth areas, chicks in the East London area were always observed hidden on the feeding territory at low tide while their parents were foraging. As a result, middens were left in the intertidal zone and washed away with each high tide.

Table 1
Sampled oystercatchers during January–March 2006 and 2007, in the Eastern Cape.

	East London		Kenton		Port Elizabeth		Total
	2006	2007	2006	2007	2006	2007	
Females	6	4	0	5	0	1	16
Males	3	3	0	2	0	2	10
Chicks	3	7	3	5	1	0	19
Total	26		15		4		45

In the Kenton area, the indigenous Brown mussel *Perna perna* was the dominant prey in the middens as well as on the foraging areas (Table 2). The second most consumed prey species was the pear limpet *Scutellastra cochlear*. Other limpet species such as *Scutellastra longicosta*, *Cymbula oculus*, *Scutellastra granularis* and *Scutellastra barbara* were also regularly found in middens. Although present in high proportions in middens at High Rocks, Shelley Beach and Diaz Cross (24.6%, 65.2% and 54.6% of prey remains, respectively), the Brown mussel was in higher proportions on the feeding territories (97.0%, 84.4% and 95.5% respectively, Table 2). On these three breeding sites, the Manly–Chesson index (α) revealed a strong preference for *S. cochlear* compared to the other prey (Fig. 2).

At Port Elizabeth, two sets of middens were found at the Swartkops River Mouth, though the site generally supports four breeding pairs (P. Martin, pers. com.). Oystercatchers were observed crossing the river mouth and feeding on a small rocky shore located on the other side of the river. Mussel species (*Perna perna* and *Mytilus galloprovincialis*) formed the bulk of prey items in middens (60% and 84.5% in sets 1 and 2, respectively), whereas the sand mussel *Donax serra* also represented a significant proportion of chick diets (21.7% and 15.5% in sets 1 and 2, respectively). The Manly–Chesson Index (α) revealed strong selection of the Mediterranean mussel by oystercatchers rearing their chicks (Fig. 2), which was the less abundant mussel of the two mussel species on the shore (9.2%), but relatively more abundant in the two sets of middens (13.2% and 50.3%). In fact this species was the most abundant prey species in set 2 (see Table 2).

3.2. Isotope signatures in prey species and oystercatchers

Mussels and limpets showed an east–west enrichment in ^{15}N between East London and Port Elizabeth ($7.01‰ < \delta^{15}N < 9.45‰$ and $6.84‰ < \delta^{15}N < 8.97‰$ respectively) (Fig. 3). However, a Kruskall–Wallis test (K; $\alpha = 0.05$) revealed no significant differences between areas for limpets (*Cymbula oculus*: $K = 1.744$, df = 2, $n = 12$, $p = 0.418$; *Scutellastra cochlear*: $K = 0.327$, df = 1, $n = 13$, $p = 0.568$; *Scutellastra granularis*: $K = 4.151$, df = 2, $n = 13$, $p = 0.126$; *Scutellastra longicosta*: $K = 1.286$, df = 1, $n = 20$, $p = 0.257$; *Perna perna*: $K = 17.217$, df = 2, $n = 37$, $p < 0.001$). A significant east–west ^{13}C enrichment was also observed in mussels ($-15.74‰ < \delta^{13}C < -15.33‰$, $K = 12.596$, df = 2, $n = 37$, $p = 0.002$) ($p < 0.05$). The ^{13}C signatures segregated mussels and the different limpet species with mussels showing depleted $\delta^{13}C$ values compared to limpets ($-12.32‰ < \delta^{13}C < -7.96‰$ for limpets). Similarly to the prey species, oystercatchers showed a ^{15}N enrichment towards the West ($9.99‰ < \delta^{15}N < 11.82‰$; $K = 11.553$, df = 2, $n = 45$, $p = 0.003$). Moreover, the average $\delta^{15}N$ value for oystercatchers ($10.94 \pm 0.56‰$) was 3.04‰ higher than for the benthic species ($7.90 \pm 0.51‰$). No clear geographic gradient was observed for ^{13}C in oystercatchers, and individuals from Kenton (the middle region) showed depleted ^{13}C signatures compared to both East London to the east and Port Elizabeth to the west. Patterns of ^{13}C signatures among mussels, limpets and oystercatchers were the same in the three main localities with oystercatchers showing intermediate ^{13}C signatures ($-15.70‰ < \delta^{13}C < -11.84‰$) between minimum $\delta^{13}C$ values in mussels and maximum $\delta^{13}C$ values in limpets (Fig. 3).

In four of the five pairs in which both adults were captured, males showed enrichment of ^{13}C signatures compared to their female mate (Fig. 4). Both the absolute values for individual birds (−11.60 to −14.75‰) and the difference between genders (0.4–1.63‰) varied among sites (Cape Recife: ♀ = −12.78‰, ♂ = −12.38‰; Shelley Beach: ♀ = −14.74‰, ♂ = −13.11‰; High Rocks: ♀ = −14.63‰, ♂ = −13.75‰; Christmas Rock: ♀ = −13.09‰, ♀ = −11.82‰). On the other hand, the male and the female sampled at Bonza Bay had

Table 2
Prey species abundance (% in brackets) in middens left by breeding oystercatchers and estimated densities (m^{-2}) (% in brackets) on their foraging areas in the Kenton Region and at the Swartkops River Mouth (Port Elizabeth).

Prey species	High Rocks		Shelley Beach		Diaz Cross		Swartkops River Mouth		
	Middens	Foraging area	Middens	Foraging area	Middens	Foraging area	Middens 1	Middens 2	Foraging area
Mussels									
Donax Serra	–	–	–	–	1 (0.2)	0	41 (21.7)	24 (15.5)	–
Mytilus galloprovincialis	–	–	–	–	–	–	25 (13.2)	78 (50.3)	51.2 (9.2)
Perna perna	59 (24.6)	196.8 (97.0)	131 (65.2)	173.1 (84.4)	266 (54.6)	390.0 (95.5)	107 (56.6)	53 (40.5)	505.6 (98.8)
Limpets									
Cymbula oculus	10 (4.2)	0.5 (0.3)	3 (1.5)	2.2 (5.2)	3 (0.6)	1.0 (0.2)	–	–	–
Scutellastra argenvillei	2 (0.8)	0	–	–	–	–	–	–	–
Scutellastra Barbara	9 (3.8)	0.6 (0.3)	5 (2.5)	2.7 (1.4)	6 (1.2)	0	–	–	–
Scutellastra Cochlear	110 (45.8)	1.6 (0.8)	38 (18.9)	16.2 (7.9)	187 (38.4)	6.3 (1.5)	–	–	–
Scutellastra granularis	17 (7.1)	1.4 (0.7)	10 (5.2)	0	9 (1.8)	0	–	–	–
Scutellastra longicosta	29 (12.1)	1.9 (0.9)	4 (2.0)	10.7 (1.1)	14 (2.9)	11.3 (2.8)	–	–	–
"Keyhole limpets"	4 (1.7)	0	–	–	1 (0.2)	0	–	–	
Other prey	–	–	–	–	–	–	16 (8.5)	0	–

identical ^{13}C signatures ($\delta^{13}C = -11.60‰$ for both). No sex-related trend in ^{15}N signature was observed for the different breeding pairs.

4. Discussion

During reproduction, ABOs on rocky shores on the south–east coast rely on a reduced number of prey species for food and, as observed in other parts of the world (Hartwick, 1976; Goss-Custard and Sutherland, 1984), these are mostly mussels and limpets. The dominant prey were similar to those previously found on the south–east coast of South Africa (Randall and Randall, 1982; Hockey and Underhill, 1984). Stable isotope analyses and analysis of middens indicated that these prey formed the bulk of the diet. While proportions of prey varied between localities, the results of the Manly–Chesson index suggest active selection of particular prey species. Stable-carbon blood signatures also revealed segregation of prey within pairs, while stable-nitrogen signatures suggested enrichment in both prey and oystercatchers from east to west along the 300 km study area, as previously observed for the lower trophic levels by (Hill et al., 2006 and Hill and McQuaid (2008).

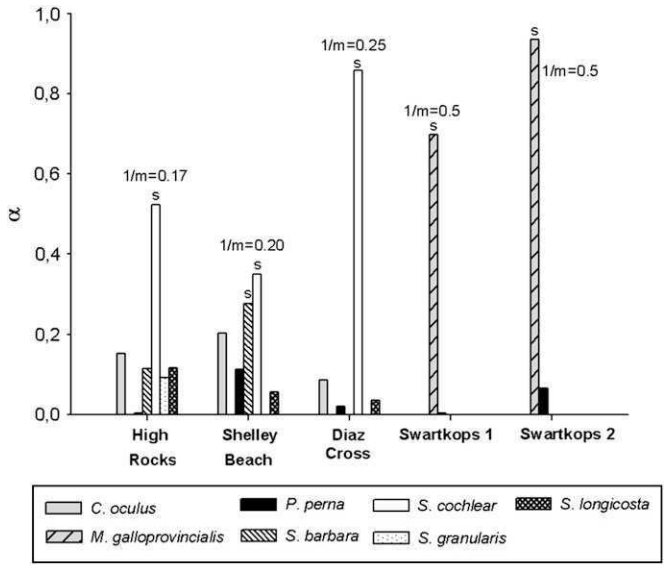

Fig. 2. Manly–Chesson index (α) for prey selectivity by breeding oystercatchers during the chick rearing period. Values >1/m indicate positive selection (specified by "S" when occurring). Values <1/m indicate avoidance.

4.1. Prey selection by breeding oystercatchers

The Brown mussel *Perna perna* was always less abundant in middens than in foraging areas. Thus, the fact that it formed the dominant prey in middens apparently reflects its abundance on rocky shores rather than active selection by oystercatchers, as confirmed by the Manly–Chesson selectivity index. This dominance of the brown mussel in the diet on the south and south–east coasts has previously been demonstrated for the African Black Oystercatcher (Randall and Randall, 1982; Hockey and Underhill, 1984). In contrast, limpets, especially *Scutellastra cochlear*, were always more abundant in middens than would be expected from their availability on feeding territories, indicating that the birds showed strong selection for them. The high proportions of *S. cochlear* in middens was unexpected, as it is a large limpet and lives at extremely high densities (100s per m^{-2}), but occurs only on the very low shore in the sublittoral fringe (Branch and Branch, 2005), where accessibility for shorebirds is low and wave action is especially strong. Given the brief period at low tide for which *S. cochlear* is accessible to oystercatchers, it must be heavily selected, presumably because of its high density, although individual skill at targeting this prey species is also possible. Hockey and Underhill (1984) also found that *S. cochlear* was a regular prey of oystercatchers, forming 55.2% of the diet of one chick. The other limpets

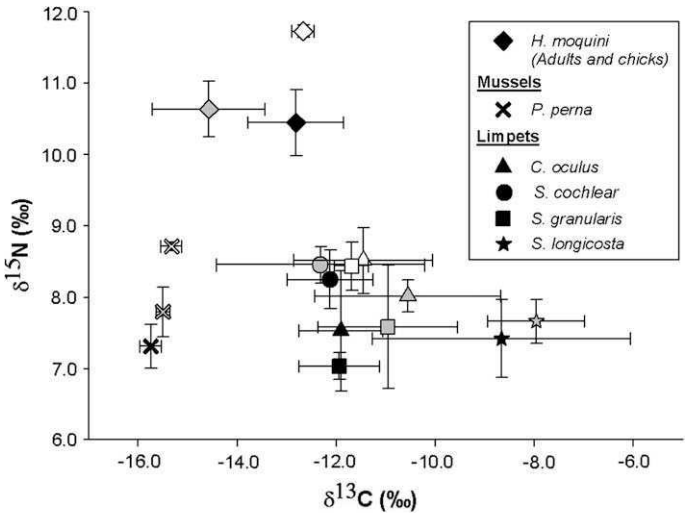

Fig. 3. Mean carbon and nitrogen isotopic signatures (±SD) in oystercatchers and prey species in East London (black), Kenton (gray) and Port Elizabeth (white).

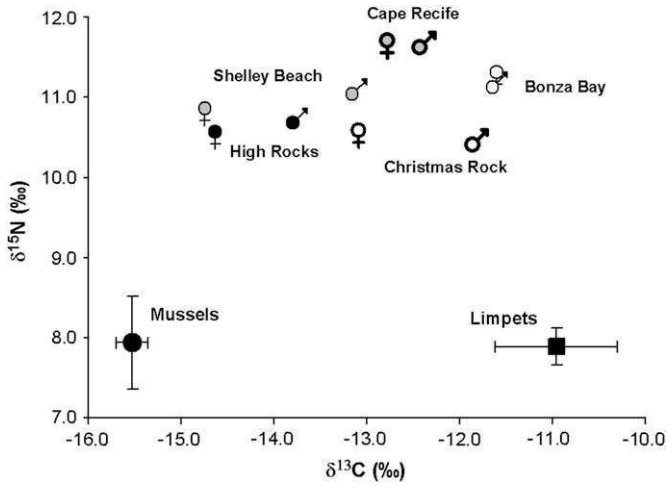

Fig. 4. Carbon and nitrogen isotope signatures in five breeding pairs (females ♀; males ♂) and average isotope signatures of mussels and limpets in the Eastern Cape.

considered, *Scutellastra longicosta*, *Cymbula oculus*, *Scutellastra barbara* and *Scutellastra granularis*, were also present in higher proportions in middens than on foraging areas, but did not seem to be particularly preferred by oystercatchers. These species are present at low densities on feeding territories but are found on the middle and upper shore (Branch and Branch, 2005), and so are accessible for longer period than either mussels or *S. cochlear*. The invasive Mediterranean mussel was found at the Swartkops River Mouth in Port Elizabeth. On the rocky shore there, where four breeding pairs feed, *P. perna* was about 10 times more abundant than the Mediterranean mussel. Interestingly, however, the invasive species formed a higher proportion of the two sets of middens examined and was the most abundant prey item in one of them (59.5%). The increasing importance of the invasive Mediterranean mussel in ABOs diet has previously been noted on the west coast of South Africa (Hockey and Van Erkom Schurink, 1992), where it is virtually the only mussel in the intertidal zone, although no active selection by the oystercatchers has previously been demonstrated. The species has enhanced mussel biomass above pre-invasion levels because it forms particularly dense, multi-layered beds (Van Erkom Schurink and Griffiths, 1990; Griffiths et al., 1992; Robinson et al., 2005). As a consequence, it seems to have had a positive influence on population densities of ABOs (Hockey and Van Erkom Schurink, 1992; Vernon, 2004; Hockey et al., 2005). Zardi et al. (2007) highlighted differences in attachment strength between the Brown Mussel and the Mediterranean mussel, the latter being easier to detach from the substratum. Therefore, the Mediterranean mussel is an abundant prey that is relatively easy for ABOs to collect when feeding their chicks, although other energetic considerations must not be excluded. These indications of prey selectivity by breeding oystercatchers are however restricted to the feeding of chicks and may not reflect the feeding behavior of adults when they are feeding themselves.

4.2. Regional variations in isotope signatures of African Black Oystercatchers and prey

^{15}N and ^{13}C isotope signatures in mussels, limpets and oystercatchers give a clear picture of the trophic structure of rocky-shore ecosystems in the study area. $\delta^{15}N$ values in consumers both integrate the signature at the base of the food web and the trophic position of the consumer. In marine food webs, 3–4‰ increases between a prey and its predator are standard values, and are characteristic for seabirds (DeNiro and Epstein, 1981; Hobson et al., 1994; Kelly, 2000; Cherel et al., 2005). Therefore in our study, the difference of an average of 3‰ between intertidal organisms and oystercatchers, confirms their relationship as prey and predator on these shores. ^{13}C isotope signatures show segregation between filter feeding (mussels) and grazing organisms (limpets). Mussels showed relatively depleted ^{13}C values, reflecting the contribution of pelagic waters as a carbon source (Hill et al., 2006), whereas limpets show relatively enriched $\delta^{13}C$ values, highlighting the importance of intertidal primary production as a carbon source for these organisms. Middens clearly show that oystercatchers prey on both, consequently showing an intermediate $\delta^{13}C$ signature.

At a regional scale, mussels showed an east–west trend of enrichment in ^{13}C and ^{15}N. The same trend was observed in Brown and Mediterranean mussels, and SPM in nearshore waters at a larger scale (1000 km), between Sodwana Bay (Kwazulu-Natal, South Africa) and Walvis Bay (Namibia) (Hill et al., 2006; Hill and McQuaid, 2008). In the present study, limpets also showed an overall east to west enrichment in ^{15}N, though this was not significant, but their ^{13}C signatures showed high variability both within and between sites. The observed ^{13}C gradient in mussels and nearshore primary producers was interpreted by Hill et al. (2006) to be a result of progressive change in coastal hydrography whereas ^{15}N gradients reflected a switch from oligotrophic conditions on the east coast to eutrophic conditions farther west. ^{15}N enrichment between East London and Port Elizabeth was also observed in oystercatchers, leading to the conclusion that small-scale changes in water productivity penetrate to the top of the food web where the top predator is highly residential.

4.3. Trophic segregation within breeding pairs

Sexual dimorphism related to culmen shape and length has been reported for the ABO (Hockey, 1981; Hockey and Underhill, 1984; Hockey et al., 2005). Sexual differences in the foraging behavior of seabirds and shorebirds are also well documented, and are related to optimization of resource exploitation (Durell et al., 1993; Durell, 2000; Lewis et al., 2002). In the present study, differences in ^{13}C signatures between the male and female of the same pair were observed for four out of five pairs and reflect the difference observed between mussels and limpets. These observations lead to the hypothesis that, while both sexes will include both organisms in their diet, females preferentially feed on mussels whereas males primarily select limpets. A similar observation was made on the west coast based on visual observations (Hockey and Underhill, 1984), where females selected the indigenous mussel *Aulacomya ater* and males fed on the limpet *Scutellastra granularis*. In Bonza Bay, the male and the female had similar ^{13}C signatures. At that particular site, mussels are limited to a very small colony of small individuals as a result of harvesting by local people (C. Vernon, pers com.). Limpets such as *S. granularis*, *Scutellastra longicosta*, and *Cymbula oculus* therefore form the primary prey for both sexes of oystercatchers. The carbon signatures of these individuals were similar to those of limpets, reinforcing the conclusion that these are the main prey at that site. Sex-related feeding specialization has also been documented for the Eurasian Oystercatcher, *Haematopus ostralegus* (Durell et al., 1993). Males and females use different techniques related to their bill shape to open their main prey *Mytilus edulis*, thus avoiding direct competition by exploiting different weaknesses in mussels (Durell et al., 1993; Durell, 2000; Nagarajan et al., 2002a,b). Sex-related feeding strategies allow the optimization of feeding territory exploitation by minimizing competition within breeding pairs (Durell et al., 1993; Durell, 2000; Lewis et al., 2002). The sex-related differences in carbon isotope signatures of oystercatchers associated with the differences in their bill shape and size seem to indicate that segregation in food resources also occurs in this species

and is most likely related to optimal exploitation of the resources in the territory. However, based on five pairs only, it is difficult to conclude whether these trophic segregations can be seen as individual cases of specialization or as a common behavior among breeding pairs in the overall ABO population. A larger sample of breeding pairs would be required to confirm this phenomenon.

5. Conclusion

African Black Oystercatchers on the south–east coast of South Africa showed strong selection of certain prey, such as the Mediterranean mussel *Mytilus galloprovincialis* and the limpet *Scutellastra cochlear*, when they were feeding their chicks. Both prey species are abundant and relatively large bodied. Selection of these prey also presumably reflects the fact that, of the two mussels on this coast, the invasive *M. galloprovincialis* shows much weaker attachment strength than the indigenous species, while *S. cochlear* is a territorial limpet, occurring at exceptionally high densities, allowing birds to minimize foraging times. Stable Isotope analysis revealed that consistent sex-related feeding specialization occurs in ABOs during breeding, probably allowing optimization of exploitation of the feeding territory and thus reducing minimum territory size and/or intra-pair competition. Isotope analysis also revealed that differences in productivity occurring on a scale of 300 km have perceptible effects on a top predator. Further studies should focus on sex-related feeding strategies at larger scales and within different kind of feeding territories. Biogeographic gradients of stable isotope signatures in ABOs should also be investigated along the whole coast of South Africa in order to highlight the influence of large scale differences in coastal hydrography and primary production on the top of the food chain.

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Annexe 5

Geographic variation in the trophic ecology of an avian rocky shore predator, the African Black Oystercatcher along the southern African coastline

Sophie A. Kohler, Maëlle Connan, Jaclyn M. Hill, Cécile Mablouké, Bo Bonnevie, Katrin Ludynia, Jessica Kemper, Johan Huisamen, Les G. Underhill, Yves Cherel, Christopher D. McQuaid & Sébastien Jaquemet (in press)

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Geographic variation in the trophic ecology of an avian rocky shore predator, the African Black Oystercatcher along the southern African coastline

Running head: Trophic ecology of African Black Oystercatchers

Sophie A. Kohler[1,2*], Maëlle Connan[2], Jaclyn M. Hill[2], Cécile Mablouké[1], Katrin Ludynia[3], Jessica Kemper[4], Johan Huisamen[5], Leslie G. Underhill[3], Yves Cherel[6], Christopher D. McQuaid[2], Sébastien Jaquemet[1].

[1]Université de La Réunion, Laboratoire ECOMAR, 97400 Saint Denis, La Réunion, France
[2]Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa
[3]Animal Demography Unit, Department of Zoology, University of Cape Town, Rondebosch 7701, South Africa
[4]African Penguin Conservation Project, Lüderitz 9000, Namibia
[5]CapeNature, Garden Route, George 6530, South Africa
[6]Centre d'Etudes Biologiques de Chizé, UPR 1934 du CNRS, 79360 Villiers-en-Bois, France

KEY WORDS: $\delta^{13}C$, $\delta^{15}N$, shorebirds, biogeography, *Haematopus moquini*, mussels, limpets, stable isotope mixing model

ABSTRACT: The reflection of baseline isotopic signals along marine food chains up to higher trophic levels has been widely used in the study of oceanic top-predators but rarely for intertidal predators. We investigated variation in the $\delta^{13}C$ and $\delta^{15}N$ ratios of a sedentary rocky shore predator, the African Black Oystercatcher (*Haematopus moquini* - ABO) over approx. 2000km of the southern African coastline, which is characterized by strong biogeographic patterns in primary productivity and intertidal communities. Blood and feathers from breeding adults and chicks and muscle tissues from primary prey items (mussels and limpets) were sampled between southern Namibia and the south-east coast of South Africa. ^{15}N enrichment was observed between the south-east and west coasts in oystercatcher tissues and their prey, mirroring an isotope shift between the oligotrophic Agulhas Current on the east coast and the eutrophic Benguela Upwelling System on the west coast. Oystercatcher blood showed $\delta^{13}C$ values varying between the carbon-depleted mussels and the carbon-enriched limpets along the coastline, which reflected changes in the proportion of grazers and filter-feeders in their diet across the sampling range. The geographic shift in diet, dominated by mussels on the west coast and composed of mixed proportions of mussels and limpets on the south-east coasts, strongly reflects regionally high abundances of the invasive Mediterranean mussel *Mytilus galloprovincialis*. Finally, isotope signatures of blood and feathers displayed strong correlation throughout the study area, indicating seasonal stability in environmental conditions and feeding habits of the adults. There were, however, local discrepancies on the south coast that indicate movement of adults outside the breeding season in possibly in response to lower food abundance in this region. Overall the results indicate that the influence of regional oceanic conditions on the

base of the food web can penetrate to a predator, but that local effects can be embedded within this.

50 INTRODUCTION

51 Spatial distributions of carbon and nitrogen stable isotopes at the base of
52 marine food webs are affected by oceanic parameters such as sea surface
53 temperature and CO_2 concentration (Rau et al. 1982, Goericke & Fry 1984),
54 biochemical processes and the composition of primary producers (Saino & Hattori
55 1980). This baseline signal is then transmitted along the food chain in a predictable
56 manner and is ultimately reflected in organisms at higher trophic levels (Cherel &
57 Hobson 2007). This effect has been widely used to investigate spatial and temporal
58 aspects of the feeding ecology of oceanic predators (Burton & Koch 1999, Quillfeldt
59 et al. 2005, Cherel & Hobson 2007), but rarely in large-scale studies involving
60 higher trophic level organisms of intertidal ecosystems (but see Atkinson et al.
61 2005). $\delta^{13}C$ has been particularly exploited at the lower trophic levels to distinguish
62 between the two main potential sources of carbon in intertidal habitats: nearshore
63 benthic and offshore pelagic primary production (Fry & Sherr 1984, France 1995,
64 Post 2002). Recently, based on the ^{13}C and ^{15}N signatures of rocky shore primary
65 producers and consumers, Hill et al. (2006) and Hill & McQuaid (2008) described
66 four isotopic regions and continuous gradients of $\delta^{13}C$ and $\delta^{15}N$ ratios between the
67 Mozambican and Namibian coasts (Fig. 1). These reflected variations in coastal
68 hydrographic features along the coastline and the shift between oligotrophic and
69 eutrophic conditions set respectively by the Agulhas Current bringing warm waters
70 from the Mozambique Channel along the east and south coasts (Lutjeharms 2004)
71 and the nutrient-rich Benguela Upwelling system that flows northwards along the
72 west coast (Shannon 1985).

73 The trophic structure of southern African rocky shores has also been
74 profoundly influenced by the accidental introduction of the Mediterranean mussel

Mytilus galloprovincialis to the west coast of South Africa in the 1970s (Grant and Cherry 1985). The arrival of this invasive species has caused major changes in the structure and functioning of intertidal communities on these rocky shores (Robinson et al. 2007). Because of its higher physiological performances, dispersal rates and ability to colonize free space (Branch & Steffani 2004, Erlandsson et al. 2006), the invasive species has replaced the indigenous mussels *Aulocomya ater* and *Choromytilus meridionalis* as the dominant mussel on the mid- and low-shore on the west coast (Robinson et al. 2007). Moreover *M. galloprovincialis* outcompetes adult limpets (*Scutellastra argenvillei* and *S. granularis*) for primary space on exposed rocky shores on the west coast (Hockey & Von Erkom Schurink 1992, Steffani & Branch 2003). The Mediterranean mussel was also introduced for aquaculture in Port Elizabeth on the south coast in 1988 (McQuaid & Phillips 2000). The distributions of the indigenous *Perna perna* and *M. galloprovincialis* now overlap in this region but where they co-occur, they exhibit partial spatial segregation, with *M. galloprovincialis* dominating the upper mussel zone, *P. perna* the lower zone and a mix of the two species in the mid-mussel zone (Bownes & McQuaid 2006). At the start of the 21st century, *M. galloprovincialis* occurred along 2000 km of shoreline from Namibia to South Africa, and dominated intertidal biomass on the west coast (Robinson et al. 2005).

Although the arrival of *M. galloprovincialis* on the Southern African coasts had mostly negative effects for the rocky shore communities, it has benefited a near-threatened endemic shorebird species, the African Black Oystercatcher (*Haematopus moquini*, ABO). Since the 1980s the reproductive output of ABOs has increased in response to a combination of conservation measures and enhanced mussel biomass due to the invasive species on the west coast (Hockey & Van

100 Erkom Schurink 1992, Hockey 1997, Williams et al. 2004, Tjørve & Underhill 2006).
101 As a consequence, in the past 30 years, the overall population has increased from
102 4,800 (Hockey 1983) to approximately 6,000 birds (Hockey et al. 2005), which might
103 be an underestimation of the present population size. The breeding range of this
104 shorebird has also expanded eastwards (Vernon 2004, Brown & Hockey 2007).
105 This seems to reflect a spill-over effect, with vagrant individuals from the burgeoning
106 west coast populations spreading farther east (Vernon 2004), rather than a direct
107 consequence of the eastward spread of *M. galloprovincialis* as this mussel is
108 present at only low abundances at most sites on the south-east coast (von der
109 Meden et al. 2008). The breeding range of ABOs now extends from the Lüderitz
110 region of southern Namibia to the south-east coast of South Africa, with a gap
111 between the Lüderitz region and Cape Columbine on the west coast (Hockey et al.
112 2005, Fig. 1). ABOs are non-migratory and are territorial during the breeding
113 season, which extends from October to March in South Africa (Hockey et al. 2005)
114 and from January to June in Namibia (JK, *pers obs*). Finally they depend exclusively
115 on intertidal invertebrates, mostly mussels and limpets for their food (Hockey &
116 Underhill 1984). This set of features makes them excellent biological model
117 organisms to study the influence of physical processes and biological perturbation
118 on intertidal communities. In particular it makes them ideal for the study of how
119 conditions at the base of the intertidal food web are transmitted to higher trophic
120 levels under different environmental conditions.

121 Here we investigate the trophic ecology of this rocky shore predator across
122 the full extent of its breeding range, relating this to spatial changes in the local
123 assemblages of prey species in its habitat and to larger oceanic processes.
124 Analysis of stable carbon and nitrogen isotope signatures allows us to examine the

125 balance between biogeographic and local effects and to test whether the ABO
126 responds more strongly to large-scale oceanic characteristics, conforming to
127 previously defined isotopic provinces (Hill et al. 2006), or whether local physical and
128 biological conditions have a more powerful influence.

MATERIALS AND METHODS

Sample collection. Breeding oystercatchers and their chicks were sampled during three consecutive breeding seasons (from December 2007 to April 2010), at 13 sites from Lüderitz (26°38.8' S, 15°9.2 'E) on the south coast of Namibia to East London (33°3.2' S, 27°52.4' E) on the south-east coast of South Africa (Fig. 1). Adults were caught at the nest during incubation using a walk-in trap and chicks (10 days to 7 weeks old) were caught by hand. Blood samples (0.5 ml) were taken from the tarsal vein of both adults and chicks and subsequently preserved in 70% ethanol. Five to eight body feathers were collected from each adult and large chicks (5 to 7 weeks old). All captured birds were tagged with a unique engraved ring (SAFRING) before their release. In addition, potential prey species were collected at each site for stable isotope analysis. Collection focused on mussel and limpet species as they are known to form the bulk of oystercatcher diet on rocky shores (Hockey Underhill 1984, Hockey & Van Erkom Schurink 1992, Kohler et al. 2009). Five similarly sized specimens of each species were collected at each breeding area and stored at –20°C until further processing. Across the whole study area, the prey species collected comprised the mussels *Perna perna, Mytilus galloprovincialis, Choromytilus meridionalis, Aulocomya ater* and the limpets *Cymbula oculus, Scutellastra argenvillei, S. cochlear, S. granatina, S. granularis and S. longicosta*. Not all of these species occur throughout the study region which comprises two major biogeographic provinces. In addition, the Benguela system and the Agulhas Current give rise to broad geographic differences in nutrient concentration, intertidal primary production and ultimately species assemblages and biomass along the coastline (Emanuel et al. 1992; Bustamante & Branch 1996): Intertidal biomass is greater on the west coast than on the south and east coasts

154 which are in turn characterized by higher species richness. Local hydrography plays
155 an important role in the ecosystem dynamics of rocky shore communities (Menge et
156 al. 2003). On the South African coastline in particular, it has been suggested that
157 temporal variability in hydrographic processes may profoundly affect the
158 composition and distribution of nearshore suspended particular matter (SPM) and
159 subsequently its ^{13}C signatures (Hill et al. 2008). Consequently, prey species and
160 oystercatchers at a given site were sampled during the same breeding season as
161 far as possible to limit temporal effects on isotope signatures. However in order to
162 cover the entire study area (~2000km) and sample sufficient numbers of birds, it
163 was logistically necessary to sample over 3 breeding seasons (see Table 1).

164 **Sample preparation and isotope analysis.** Whole blood has a rapid turnover rate
165 and for birds, gives information on the diet integrated over a few weeks prior to
166 sampling (Hobson & Clark 1992a, Bearhop et al. 2002). Isotopic signatures of blood
167 collected in summer were therefore used as a proxy for the diet of adults and chicks
168 during the breeding season. Adult feathers are produced during moult and remain
169 metabolically inert once fully grown (Mizutani et al. 1990). No published data exist
170 on the moult of ABOs, however, it is believed that this takes place from March to
171 September, i.e. during the non-breeding season (LGU, *pers obs*). Moreover, other
172 shorebirds (Klaassen et al. 2001, Atkinson et al. 2005) and oystercatcher species
173 (Dare & Mercer 1974, Hulscher 1977) are known to moult during the wintering/non-
174 breeding season. Therefore we assume that the isotopic composition of adult body
175 feathers reflects their diet during the non-breeding season (Jaeger et al. 2009).
176 Different tissues have different protein turnover rates and routings. Consequently,
177 $\delta^{13}C$ and $\delta^{15}N$ signatures vary from one tissue to the other and this must be taken
178 into consideration when comparing isotopic signatures of different tissues (Tieszen

et al. 1983, Vanderklift & Ponsard 2003, Cherel et al. 2005). In large chicks, the isotopic composition of blood and newly grown feathers is representative of the diet integrated over about the same period of time. For this reason, in addition to blood, body feathers were also collected on 20 large chicks to estimate differences in diet–tissue isotopic discrimination between blood and feathers. Prey species were analysed using muscle tissues because of their slow isotopic turnover rate and the fact that they are unlikely to be affected by short-term environmental fluctuations (Gorokhova & Hansson 1999). Consequently, the adductor muscle of mussels and the foot muscle of limpets were analysed for their isotopic composition, to provide an isotopic signal integrated over a period of months (Hill & McQuaid 2009). A limpet's foot represents the majority of their body mass, while the adductor tissue of a mussel is only a small part of the whole animal. However, adductor tissue and whole mussels only differ by a ^{13}C-enrichment of 0.5 ‰ in their stable isotope signature (Koher et al. unpub data). Therefore conclusions regarding geographic changes in the stable isotope signatures of benthic invertebrates and outputs of stable isotope mixing models (see below) are likely to be unaltered (Lefebvre et al. 2009). Blood samples were dried (60°C, 24h) and reduced to a homogenous powder. Pooled body feathers from a given individual were cleaned of surface contaminants and lipids by immersion in a chloroform/methanol solution (2:1) placed in an ultrasound bath for 2 minutes and then rinsed with distilled water and dried (60°C, 24h). Muscle tissues of mussels and limpets were cut out, rinsed thoroughly with distilled water and dried (60°C, 24h). All dried samples were then reduced to a homogenous powder. Relative isotope abundance of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) were determined from ~1 mg sub-samples of the homogenous powder in a continuous flow isotope ratio mass spectrometer (IRMS),

after sample combustion in online Carlo-Erba preparation unit. Results are expressed relative to the international standards of Pee Dee Belemnite for carbon and atmospheric N_2 (air) for nitrogen. The standard notation is $\delta \mathrm{X} = \left(\left[\frac{R_{sample}}{R_{standard}}\right] - 1\right) \times 1000$ (‰), where X is the element considered and R is the ratio of heavy to light isotope. Precision of replicate determinations was < 0.10 ‰ for carbon and < 0.13 ‰ for nitrogen. All samples were analyzed at the Stable Light Isotope Unit of the University of Cape Town, South Africa.

Trophic Enrichment factors (TEF). Isotopic enrichment between diet and consumer tissues results from isotopic fractionation during assimilation, protein synthesis and excretion (Ponsard & Averbuch 1999). The estimation of prey contribution using stable isotope mixing models requires knowledge of an estimated TEF. These can vary among species or taxa and have been widely investigated in seabirds (Hobson & Clark 1992b, Bearhop et al. 2002, Cherel et al. 2005), but to our knowledge in only one shorebird species, the dunlin (*Calidris alpina pacifica;* Evans Ogden et al. 2004). TEFs found between diet and whole blood of dunlins were +1.3 ‰ for $\delta^{13}C$ and +2.9 ‰ for $\delta^{15}N$. As $\delta^{13}C$ is the major discriminant between mussels and limpets (Kohler et al. 2009), the TEF for $\delta^{13}C$ needs to be as reliable as possible (Dalerum & Angerbjörn 2005). Therefore, we estimated the TEF for $\delta^{13}C$ and $\delta^{15}N$ by comparing the isotopic compositions of oystercatcher blood and their prey at four sites where only one type of prey (either mussels or limpets) was available and where extensive feeding observations confirmed that this unique prey was the main food ingested by oystercatchers (Kohler unpub. data). Results showed TEFs of + 0.2 ‰ (±0.4 ‰) for $\delta^{13}C$ and + 2.7 ‰ (± 0.4 ‰) for $\delta^{15}N$, which are within the range of values found for other marine birds (Hobson & Clark 1992b,

228 Bearhop et al. 2002, Cherel et al. 2005), but TEF for $\delta^{13}C$ was noticeably different
229 from dunlins (Evans Ogden et al. 2004).

230 **Prey contributions.** To investigate variations in the relative contribution of mussels
231 and limpets to the diet of oystercatchers along the coastline, we used the Bayesian
232 stable isotope mixing model SIAR. The SIAR package (Parnell et al. 2010; available
233 at http://cran.r-project.org/web/packages/siar/index.html), running on the statistical
234 software R (R Development Core Team 2009), allows the incorporation of standard
235 deviations of mean sources and consumers signatures as well as uncertainty
236 regarding diet-consumer discrimination. We used mean (± SD) signatures of
237 oystercatcher blood (Table 1) and prey (Table 2) and the TEFs given above to
238 calculate prey contributions at each location. No limpets were present on the
239 feeding grounds at De Hoop, DanaBaai and Goukamma but for reasons of
240 comparison, limpet signatures from nearby areas (less than 50km away) were
241 included to run the model for these sites (see footnotes in Table 2). With the SIAR
242 outputs, an *a-posteriori* aggregation (Phillips et al. 2005) was carried out to pool
243 results for limpet species on one side and for mussel species on the other side.

244 **Statistical analyses.** All statistical analyses were performed using R Statistical
245 software (R Development Team Core 2009). When data sets did not meet the
246 assumptions of normal distribution (Shapiro-Wilk test, $p < 0.05$) or homoscedasticity
247 (Bartlett test, $p < 0.05$), non-parametric procedures were used. Although the
248 purpose of this study was not to investigate differences between individuals at a
249 local scale, we tested local differences between age groups to see whether adults
250 and chicks from the same site could be considered as a homogenous local
251 population. A two-way ANOVA ($\alpha = 0.05$) was performed with sites ($n = 13$) and age
252 (chicks or adults) as factors and $\delta^{13}C$ or $\delta^{15}N$ as response variables for each site.

There was a significant effect of site on individuals for both $\delta^{13}C$ ($F_{12,123} = 13.66$, $p < 0.01$) and $\delta^{15}N$ ($F_{12,123} = 24.57$, $p < 0.01$) values. Chicks were slightly but significantly depleted by – 0.4 ‰ in ^{13}C ($F_{1,122} = 5.85$, $p=0.02$) and by – 0.3 ‰ in ^{15}N ($F_{1,122} = 30$, $p < 0.01$) compared to adults. There was no interaction between site and age ($\delta^{13}C$: $F_{11,\ 122} = 1.27$, $p = 0.25$; $\delta^{15}N$: $F_{11,122} = 1.46$, $p = 0.15$) and adult and chick isotope signatures showed very strong correlations ($\delta^{13}C$: $R^2_{adults\text{-}chicks} = 0.85$, $p < 0.01$; $\delta^{15}N$: $R^2_{adults\text{-}chicks} = 0.93$, $p < 0.01$), meaning that adult and chick signatures co-varied along the coastline. Geographic variations of chick and adult blood signatures are represented separately and correlation tests were performed for each age group. We pooled chicks and adults for the estimation of the contributions of limpet and mussel to the diet of ABOs along the coastline (see "prey contributions" in Material and Methods) because the SIAR model incorporates individual variability in the output. Geographic grouping of $\delta^{13}C$ and $\delta^{15}N$ values of adult tissues were analyzed using a K-means cluster analysis, subsequently tested with a discriminant function analysis (DFA). We also tested if the presence of *M. galloprovincialis* and/or limpets on the feeding grounds had an effect on the overall contribution of mussels (estimated from SIAR) to the ABO diet, using a two-way ANOVA ($\alpha = 0.05$).

272 **RESULTS**

273 **Benthic invertebrates: isotopic variation among sites, trophic groups and**
274 **species**

275 Across the study region, individual carbon isotope signatures ranged from –
276 18.9 ‰ (*Choromytilus meridonalis*, Lüderitz) to – 13.7 ‰ (*Mytilus galloprovincialis*,
277 Tsitsikamma) for mussels and from – 16.1‰ (*Scutellastra granatina*, Lüderitz) to –
278 5.3 ‰ (*S. longicosta*, East London) for limpets. Filter-feeders and grazers were
279 separated by their $\delta^{13}C$ values with mussels being depleted in carbon at all sites
280 compared to limpets (Fig 2). Differences in their carbon isotope signatures,
281 however, were not always significant (Table 2) and in Lüderitz, *M. galloprovincialis*
282 and the limpet *S. granatina* had both a mean $\delta^{13}C$ ratio of – 15.7 ‰. Overall no
283 consistent separation in the $\delta^{15}N$ values of mussels and limpets was observed
284 (Table 2, Fig 2.). However, west of Cape Agulhas (Namibia excluded), the only
285 mussel present, *M. galloprovincialis*, was significantly depleted in ^{15}N compared to
286 the dominant limpets, *S. argenvillei* or *S. granularis* (Table 2).

287 The invasive mussel *M. galloprovincialis* and the indigenous brown mussel
288 *Perna perna* co-occurred at six locations (Table 2). No significant differences in
289 carbon or nitrogen isotope ratios were recorded between the two species at a local
290 scale (Table 2, Fig. 2). In Namibia, *M. galloprovincialis* was significantly enriched in
291 ^{13}C compared to the indigenous mussels *C. meridionalis* and *Aulocomya ater* (Table
292 2). When *S. longicosta* was present, this limpet was always enriched in ^{13}C
293 compared to other limpets (Table 2, Fig. 2). Overall, the different limpet species had
294 similar $\delta^{15}N$ values throughout the sampling area (Table 2).

295 Muscle $\delta^{13}C$ values of mussels and limpets did not show any geographic
296 trends along the coastline. The lowest mean ^{13}C signatures for both mussels and

297 limpets were observed in Lüderitz, while the highest signatures were in Tsitsikamma
298 for mussels and Arniston, near Cape Agulhas for limpets. However it is worth noting
299 that the mean $\delta^{13}C$ signatures of limpets presented in Fig. 3a were affected by the
300 presence or absence of *S. longicosta,* which was particularly enriched in ^{13}C.

301 Unlike carbon signatures, nitrogen-isotope signatures showed a clear
302 geographic pattern. The $\delta^{15}N$ values of mussels varied from 9.6‰ in Lüderitz (West
303 coast, Namibia) to 7.1 ‰ in East London (south-east) and they displayed a
304 significant depletion (Pearson's correlation test, $R^2_{mussels\text{-}longitude} = 0.80$, $p < 0.01$)
305 from the west to the south-east coast (Fig 3b). Geographic patterns in limpets $\delta^{15}N$
306 signatures were not as clear and a marginally significant depletion was only
307 observed from Arniston (close to Cape Agulhas) eastwards (Pearson's correlation
308 test, $R^2_{limpets\text{-}longitude} = 0.76$, $p = 0.05$). Particularly high ^{15}N signatures were observed
309 for both mussels and limpets at Langebaan on the west coast compared to
310 neighbouring sites and to a lesser extent, this was also the case on the south coast
311 for Cape Recife compared to Kenton and Tsitsikamma (Fig. 3b). In Walker Bay,
312 limpets displayed depletion in ^{15}N compared to those sampled at the nearest sites,
313 Koeberg to the west and and Arniston to the east (Fig 3b).
314

315 **African Black Oystercatchers: geographic and tissue-specific variations in**
316 **their isotopic signatures**

317 Altogether 136 oystercatchers (53 % adults and 47 % chicks) were sampled
318 during this study. Oystercatcher blood showed $\delta^{13}C$ values (from – 16.7 ‰ in Dana
319 Baai to – 10.8 ‰ in East London) that were intermediate between those of mussels
320 and limpets (Fig. 2). $\delta^{15}N$ values ranged from 9.3 ‰ (East London) to 13.8 ‰
321 (Langebaan) and on average were enriched by + 2.7 ‰ (± 0.4) compared to benthic

322 invertebrates (Fig. 2). Blood-feather discrimination in adults was + 0.5 ‰ (± 0.5) for
323 $\delta^{13}C$ and + 1.6 ‰ (± 0.4) for $\delta^{15}N$. (n = 71). Mean blood-feather isotopic
324 discrimination of the 20 largest chicks sampled was not strongly different: + 0.9 ‰
325 (± 0.3) for $\delta^{13}C$ and + 1.2 ‰ (± 0.3) for $\delta^{15}N$.

326 No significant correlation existed between the geographic variations of $\delta^{13}C$
327 values of mussels or limpets and the blood of ABOs (Spearman's rank correlation
328 test; Adults: $R^2_{blood\text{-}mussels} = 0.41$, $p = 0.16$, $R^2_{blood\text{-}limpets} = 0.01$, $p = 0.98$; Chicks:
329 $R^2_{blood\text{-}mussels} = 0.47$, $p = 0.10$, $R^2_{blood\text{-}limpets} = 0.20$, $p = 0.55$), nor did blood display
330 clear geographic patterns in ^{13}C signatures. However, an increase in the ^{13}C
331 signatures in blood was visible between Plettenberg Bay and the more easterly
332 sites. Overall, blood $\delta^{13}C$ values varied between the mean values of mussels and
333 limpets along the coastline, suggesting that the ^{13}C signatures of ABOs were
334 dependent on the relative consumption of filter-feeders or grazers. Blood and
335 feather carbon-isotope signatures of adults displayed identical patterns across the
336 ABO breeding range (Fig. 3a.) and showed a strong correlation (Pearson's
337 correlation test, $R^2_{blood\text{-}feathers} = 0.92$; $p < 0.01$).

338 The $\delta^{15}N$ variations of ABO tissues along the coastline showed very similar
339 patterns to mussels (Pearson's correlation test, Adults: $R^2_{blood\text{-}mussels} = 0.86$, $p <$
340 0.01; Chicks: $R^2_{blood\text{-}mussels} = 0.85$, $p < 0.01$). Significant depletion was observed from
341 Lüderitz to East London in the blood of adults and chicks (Pearson's correlation
342 test, Adults: $R^2_{blood\text{-}longitude} = 0.61$, $p = 0.03$; Chicks: $R^2_{blood\text{-}longitude} = 0.69$, $p < 0.01$)
343 and in adult feathers (Pearson's correlation test, $R^2_{feathers\text{-}longitude} = 0.57$, $p = 0.04$).
344 Blood and feathers of adults displayed very significant correlations along the
345 coastline (Pearson's correlation test, $R^2_{blood\text{-}feathers} = 0.81$, $p < 0.01$) between
346 Namibia and the south-east coast of South Africa (Fig. 3b).

K-means classifications based on the $\delta^{13}C$ and $\delta^{15}N$ ratios of blood and feathers of adults showed a similar biogeographic pattern between tissues (Fig 4a & b). Classifications were subsequently confirmed by a DFA with 100% accuracy. Group A was characterized by enriched ^{13}C signatures in blood (Group A centroids: $\delta^{13}C$ = – 13.1 ‰, $\delta^{15}N$ = 11.4 ‰) and grouped 3 of the 4 most eastern sites together (Tsitsikamma being at the eastern limit of the south-west coast) (Fig. 4a). Group B had intermediate ^{13}C signatures and enriched ^{15}N signatures (Group B centroids: $\delta^{13}C$ = – 14.7‰, $\delta^{15}N$ = 11.9‰) compared to other groups and was composed of all the western sites but also Kenton (south-east coast) and De Hoop (south-west coast). Group C was exclusively composed of south-west coast sites and was defined by depleted ^{13}C signatures and ^{15}N signatures similar to those of Group B (Group C centroids: $\delta^{13}C$ = – 15.3‰, $\delta^{15}N$ = 11.3‰). Feather classification displayed a similar pattern, with the exception of Cape Recife that fell into Group B with the western sites, De Hoop and Kenton.

Trophic relationships between benthic invertebrates and African Black Oystercatchers along the coastline

The relative contributions of mussels and limpets to the diet of ABOs varied greatly across the sampling area, with a contrast between the west/south-west coasts and the south-east coast (Fig. 5). ABOs relied almost exclusively on mussels between Langebaan (95.0 %) and Goukamma (91.7 %) while the contributions of mussels and limpets were more balanced in Namibia (60.1 and 39.9 % respectively) and at the eastern sites, between Plettenberg Bay and Kenton ($Min_{mussels}$ = 38.2 ± 14.8 %; $Max_{mussels}$ = 72.1 ± 7.4 %). In East London, 74.1 % of the overall diet of ABOs was composed of limpets.

371 The presence/absence of limpets on feeding grounds (see Fig. 5) had no
372 effect on the overall dietary composition of birds (ANOVA; $F_{1,11} = 2.20$, $p = 0.17$).
373 The presence of *M. galloprovincialis* however had a significant effect expressed as
374 an increase in the relative contribution of mussels to ABOs diets (ANOVA, $F_{1,11} =$
375 5.54, $p = 0.04$). Additionally there was no significant interaction between the effects
376 of *M. galloprovincialis* and whether limpets were present (ANOVA, $F_{2,10} = 3.27$, $p =$
377 0.08).

378

DISCUSSION

The $\delta^{13}C$ and $\delta^{15}N$ signatures of ABOs in this study discriminated between birds from different biogeographic locations, grouping them together in three distinct clusters. Birds from the west coast were enriched in ^{15}N, birds from the south-east coast were enriched in ^{13}C and birds from the south-west coast had depleted $\delta^{13}C$ ratios (see Fig 4). This clear isotopic pattern in biogeography is similar to previous studies conducted from lower trophic levels to top predators in the region (Hill et al. 2006, Hill & McQuaid 2008, Jaquemet & McQuaid 2008), where organisms from the Agulhas and Benguela systems could be segregated by their carbon and nitrogen signatures. Furthermore, differences in $\delta^{13}C$ signatures of oystercatchers among sites reflected variations in the relative consumption of mussels and limpets associated with changes in prey community structure (Hockey & Von Erkom Schurink 1992, Bustamante & Branch 1996).

Oligotrophic versus productive systems

Clear ^{15}N enrichment was observed between the south-east and west coasts in oystercatchers and mussels, and to a lesser extent in limpets. This westwards enrichment was previously described for rocky shore mussels and other benthic filter-feeders on the South African coastline (Hill et al. 2006, Hill & McQuaid 2008) and for Cape Gannets (*Morus capensis*) on offshore islands (Jaquemet & McQuaid 2008). Presumably the $\delta^{15}N$ gradient between organisms from the regions dominated by the Agulhas current and the Benguela upwelling system mirrors the isotope shift described by Saino & Hattori (1980) between waters that are oligotrophic (reliance on recycled nitrogen – ^{15}N depleted) to those that are eutrophic (rich in nitrates – ^{15}N enriched). Surprisingly, however, the southeast – west coast increase in $\delta^{15}N$ was disjointed and samples collected in Cape Recife,

404 just outside Port Elizabeth, and Langebaan located within Saldanha Bay displayed
405 high nitrogen-isotope ratios compared to adjacent sampling sites. This may be the
406 result of increased nitrogen-loading through anthropogenic inputs (Heaton 1986,
407 Schaal et al. 2010) associated with urban, industrial and tourist activities in these
408 areas. Another discrepancy was observed in Walker Bay where the limpet *S.*
409 *granularis* displayed ^{15}N-depleted signatures. We do not have a clear explanation
410 for this pattern other than possible local depletion in de δ^{15}N ratios of the benthic
411 algae on which this limpet grazes. Overall local and large-scale patterns of nitrogen-
412 isotope ratios in benthic invertebrates and oystercatchers confirm that large scale
413 physical processes affecting patterns of primary productivity are transmitted up
414 through the intertidal food web to a rocky shore predator.

415 Carbon signatures of ABOs and their prey showed clear differences from
416 biogeographic patterns of ^{13}C enrichment in SPM and mussels from the east coast
417 to Cape Agulhas, which were suggested to mirror changes in the overall
418 composition of nearshore SPM (phytoplankton vs. macroalgae detritus; Hill et al.
419 2006, see also Bode et al. 2006). Our mussel data showed consistent δ^{13}C ratios
420 across the board of approximately – 15.7 ‰ (± 0.5) between Arniston and East
421 London, with one exception (Tsitsikamma = – 14.2 ± 0.2 ‰). This difference from
422 previous studies probably reflects the type of local and inter-annual changes in
423 coastal hydrography described by Hill et al. (2008). In contrast, the δ^{13}C depletion in
424 mussels, limpets and oystercatchers sampled off the Namibian coast conformed to
425 expected biogeographic patterns (Hill et al. 2006) and thus appears to be consistent
426 through time and visible at multiple levels of the intertidal food web. The
427 mechanisms behind this depletion are not well understood and further isotopic
428 investigations into nutrient dynamics and upwelling processes of the Benguela

429 ecosystem are needed. With the exception of Lüderitz, the geographic variations of
430 limpet $\delta^{13}C$ ratios (Fig. 3a) appeared to be linked to the species pool rather than
431 environmental conditions. For example, the territorial limpet *Scutellastra longicosta*
432 displayed particularly ^{13}C-enriched signatures, which confirmed its reliance on
433 gardens of *Ralfsia verrucosa* (McQuaid & Froneman 1993, Hill & McQuaid 2008)
434 and clearly departed from the $\delta^{13}C$ displayed by other species. This obviously
435 increased the mean $\delta^{13}C$ values for limpets on the south west and south east coast
436 when *S. longicosta* was present (see Table 2). Some significant localized variations
437 and large standard deviations in limpets (see Table 2) also suggested local and
438 micro-scale variability, either in the composition of the benthic algae and/or the
439 conditions (e.g. carbon source, light intensity, temperature) affecting photosynthesis
440 and therefore isotopic fractionation of the benthic primary producers on which the
441 limpets graze (Wong & Sackett 1978, Burkhardt et al. 1999).

442 Large scale $\delta^{13}C$ patterns at the base of marine food webs in relation to
443 spatial variability of CO_2 concentration, water temperature and growth rates of
444 primary producers (Rau et al. 1982, Goericke & Fry 1994) have been widely used to
445 investigate animal migration patterns (see review in Hobson 1999) and foraging
446 movements in marine predators (Burton & Koch 1999, Quillfeldt et al. 2005). $\delta^{13}C$
447 ratios can also be used to identify the ultimate sources of carbon for consumers
448 when the ^{13}C signatures of food sources differ (Post 2002), and in the case of
449 higher level predators, can help to determine the main component of the diet. This
450 latter aspect was clearly shown in this study, with the blood $\delta^{13}C$ variations in ABOs
451 not correlating with the geographic variations displayed by either mussels or
452 limpets, but instead oscillating between the contrasting ^{13}C signatures of the two
453 main prey items. This confirms the fact that although primary/secondary consumer

454 ratios may reflect geographic differences in nutrient/primary productivity regimes,
455 variations in the $\delta^{13}C$ signatures of ABOs are primarily due to the proportion of
456 grazers and filter-feeders in their diet across the sampling range.
457
458 **Impact of prey assemblages on the diet of African Black Oystercatchers**
459 The blood $\delta^{13}C$ signatures of oystercatchers varied significantly along the
460 coastline, ranging between approximately – 11.0 ‰ and – 17.0 ‰, with maximum
461 $\delta^{13}C$ values observed between Tsitsikamma and East London, and lowest value on
462 the south-west coast. Limpets were enriched in ^{13}C compared to mussels
463 throughout the study area, which is an isotopic segregation typically observed
464 between grazers and filter-feeders (Post 2002, Schaal et al. 2008). In contrast, the
465 ^{15}N signatures of mussels and limpets were very similar at a local scale, with the
466 exception of the west coast, and varied mostly in relation to changes in primary
467 production processes associated with the Benguela and Agulhas ecosystems.
468 Broadly contrasting $\delta^{13}C$ ratios and local differences in $\delta^{15}N$ ratios between
469 prey allowed the application of the stable isotope mixing model SIAR to relate
470 geographic variations in ABO isotope signatures to potential changes in the
471 assimilation of mussels or limpets in their diet along the coastline. The SIAR model
472 revealed a biogeographic pattern in the contribution of different prey to the diet of
473 ABOs with the diet largely dominated by mussels on the west and south-west
474 coasts of South Africa and a mixed diet of mussels and limpets in Namibia and on
475 the south-east coast of South Africa. Finally, on the eastern boundary of the study
476 area, limpets made up nearly 75 % of the prey items assimilated by ABOs (Fig. 5).
477 This shift in diet along the coastline indicates that ABO prey selection is influenced
478 by prey availability, which reflects biogeographic trends in species composition and

abundances along the coastline (Bustamante & Branch 1996). The extremely high abundances of the invasive Mediterranean mussel on the west coast have a particularly clear effect on bird diets (see results).

The west coast supports a higher intertidal invertebrate biomass than the south and east coasts, reflecting the higher productivity of the Benguela upwelling system as opposed to the oligotrophic Agulhas current. Following the arrival of the invasive Mediterranean mussel on the west coast in the 1980's (Grant & Cherry 1985), the benthic biomass on rocky shores in this region became largely dominated by this species (Robinson et al. 2007). In Saldanha Bay, a change in the feeding habits of ABOs following the invasion by *M. galloprovincialis* in the 1980's has been described for three offshore Islands, based on direct observations or collection of emptied molluscs shells left by adults feeding their chicks (Hockey & Van Erkom Schurink 1992, Coleman & Hockey 2008). ABOs had shifted from a mixed diet of mussels (the ribbed mussel *Aulocomya ater* and the black mussel *Choromytilus meridionalis*) and limpets (mainly S*. granularis* on these islands) prior to the invasion, to a diet dominated by *M. galloprovincialis* in the late 1980s and 1990s. Our results show an even more extreme scenario in Langebaan in 2009 (also situated in Saldanha Bay, but on the mainland), where *M. galloprovincialis* accounts for 95% of the prey versus 5% for the limpet *S. argenvillei*. In Walker Bay and Koeberg, similar preference of the invasive mussel was observed (Fig. 5), despite the presence of the limpets *S. granularis* or *S. argenvillei* previously favoured by ABOs (Hockey & Underhill 1984). During the 1979/1980 breeding season in the Lüderitz region (Namibia), the diet of ABOs was almost exclusively composed of limpets (average 96.8%; Hockey & Underhill 1984). *M. galloprovincialis* is now well established on the southern Namibian coast and

504 dominates rocky shores in the Lüderitz region (B. Currie, *pers. com.*). Results from
505 this study show that mussels have become the predominant source of food for
506 ABOs here, although limpets still contribute significantly (39.9%±0.6). Although the
507 diet of oystercatchers remains more balanced in Namibia than on the South African
508 west coast, the increasing reliance on the Mediterranean mussel reflects a clear
509 dietary shift in response to changes in prey availability. On the south-west coast,
510 mussels also dominated the diet of ABOs (between 72% and 95%), except at the
511 eastern boundary of the region (only 40%), in Tsitsikamma (see Fig. 5). This is not
512 surprising as limpets were scarce or even absent from oystercatchers feeding
513 grounds between De Hoop and Goukamma. The inverse proportions of filter-
514 feeders and grazers in the diet of ABOs between Plettenberg Bay (Mussels = 72 %;
515 Limpets = 28 %) and Tsitsikamma (Mussels = 38 %; Limpets = 62 %) is however
516 surprising considering that the two sites are separated by only ~ 50 km (see Fig. 1).
517 Bownes & McQuaid (2006) investigated the potential for *M. galloprovincialis* to
518 replace the indigenous mussel *P. perna* on the south coast, in Plettenberg Bay and
519 Tsitsikamma. They observed that mussel abundance was significantly lower in
520 Tsitsikamma than in Plettenberg Bay, which forms a focal point of high *M.*
521 *galloprovincialis* abundance along this coast (von der Meden et al 2008) and mixing
522 model outputs from our study support these finding. *P. perna* and *M.*
523 *galloprovincialis* co-occurred at six sites, but were sometimes the only prey
524 available. Based on empty shell and feeding area analysis, Kohler et al. (2009)
525 reported active selection of the invasive mussel by ABOs feeding their chicks rather
526 than the indigenous mussel at Port Elizabeth, probably because *M. galloprovincialis*
527 has weaker attachment strength than *P. perna* (Zardi et al. 2007). Unfortunately, the
528 lack of differences in $\delta^{13}C$ and $\delta^{15}N$ signatures between these two mussel species

529 prevented confirmation of this selective behaviour further west where they often co-
530 occur. This emphasizes the need to combine stable isotope analyses with more
531 conventional techniques (e.g. feeding behaviour observations, collection of food
532 remains) in the study of marine predators when possible.

533 The diet of ABOs on the south-east coast was characterized by a significant
534 contribution of limpets; however the brown mussel *P. perna* was also well
535 represented, specifically in Kenton (72 %). This is consistent with a previous study
536 (Kohler et al. 2009), where *P. perna* represented between 84 and 97 % of the
537 relative prey abundance on three of the feeding grounds sampled in this area for the
538 present study. Indeed mussel dominance on rocky shores is driven by wave
539 exposure (Bustamante & Branch 1996), which is strong in Kenton (McQuaid &
540 Lindsay 2007). *M. galloprovincialis* remains scarce and site-specific on this part of
541 the coastline (Bownes & McQuaid 2006) and no invasive mussel >16 mm (minimum
542 shell size for consumption by ABOs, see Hockey & Underhill 1984) were found on
543 feeding grounds sampled at Cape Recife, Kenton or East London. Thus, as
544 opposed to the south-west and west coasts sites, breeding sites sampled on the
545 south-east coast have so far effectively been unaffected by the *M. galloprovincialis*
546 invasion. Thus the feeding behaviour of ABOs on the south-east coast can also be
547 regarded as “unaltered”, but will be mediated by extrinsic factors such as wave
548 action and sex-specific or individual specialization, as documented for other
549 oystercatcher species (Baker 1974, Goss-Custard & Sutherland 1984, Lauro & Nol
550 1995).

551

552 **Seasonal variation in the trophic ecology of the African Black**
553 **Oystercatcher**

554 Variations in stable isotope ratios of blood and feathers, displayed very
555 strong correlations along the coastline for both $\delta^{13}C$ and $\delta^{15}N$. Since adult ABOs are
556 known to be territorial year-round (Hockey 1996), this suggests an overall seasonal
557 stability in the environmental conditions influencing rocky shore food webs along the
558 coastline and a consistency in the feeding behavior of adults throughout the year.
559 However, some local discrepancies were observed between the blood and feather
560 ratios. In East London for example, the blood-feather $\delta^{15}N$ discrimination factor was
561 + 0.6 ‰ (as opposed to + 1.6 ‰ (± 0.4) for adults throughout the study area and +
562 1.2 ‰ (± 0.3) for large chicks). This indicates either a seasonal shift in feeding
563 behaviour, or that outside the breeding season, ABOs from East London feed in
564 areas with lower $\delta^{15}N$ ratios at the base of the food web than in their breeding site.
565 Another clear blood-feather shift was in DanaBaai (+ 2.6‰) which indicated that
566 adults there seem to feed in a wintering habitat with a higher basal $\delta^{15}N$ than the
567 breeding habitat.
568 Climate variations between seasons are mild in the study region compared to the
569 north hemisphere, where oystercatchers have to endure harsh winters and often
570 migrate southwards (Goss-Custard et al. 1996). Consequently, like the other
571 southern hemisphere oystercatcher species, breeding ABOs do not migrate after
572 reproduction, but remain territorial year-round and, especially those birds that breed
573 on offshore islands on the west coast of South Africa, (Hockey 1996, Tjørve &
574 Underhill 2006, Coleman & Hockey 2008). However color-ringed birds have been
575 resighted in flocks over 10 km east from their breeding site during the non-breeding
576 season in the East London region (SAFRING), while in Kenton, color-ringed pairs
577 are rarely spotted on their breeding site outside the breeding season (SAK, *pers*
578 *obs*). Similarly in Goukamma and Plettenberg Bay, breeding pairs do no stay on

579 their breeding site, instead large flocks of birds gather around river mouths and on
580 beaches during winter (JH & CDM, *pers obs*). Therefore it seems that on the south-
581 west and south-east coasts, adults move around substantially outside the breeding
582 season. This again reflects a contrast between the west coast and the rest of the
583 ABOs breeding range. One potential explanation may be that breeders are not
584 bound to their feeding territory and their confines during winter and may choose to
585 move to more advantageous feeding areas. Conversely, on the west coast, feeding
586 territories may be profitable for year-round occupation, because of high food
587 biomass (Hockey & Van Erkom Schurink 1992, Bustamante & Branch 1996).
588 Further investigation of the wintering movement strategies of ABOs would require
589 complementary techniques such as radio-telemetry (Warnock & Takekawa 2003,
590 Wilson et al. 2009)
591
592 **Conclusion**
593 Overall we show that carbon and nitrogen stable isotope ratios in a rocky
594 shore avian predator, the African Black Oystercatcher, were able to integrate a
595 balance of large scale patterns of oceanic productivity and local-scale prey
596 assemblages. This indicates that the influence of major large-scale current systems
597 penetrates to the top of the food web, but that local-scale effects embedded within
598 this framework can be important. The $\delta^{15}N$ variations of the tissues of ABOs were
599 indicative of changes in intertidal nutrient quality in relation to major oceanic
600 influences along the southern African coastline and local anthropogenic
601 perturbations. $\delta^{13}C$ ratios and stable isotope mixing models revealed geographic
602 changes in the main diet of ABOs that were strongly influenced by the presence of
603 the invasive mussel, *M. galloprovincialis*. ABOs demonstrated plasticity in their

604 trophic ecology in connection with biogeographic provinces, changes in prey
605 communities and seasonality. In the context of global changes and overexploitation
606 of marine resources, this could help them face future changes in their trophic
607 environment.
608

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List of tables and figures

862 Table 1. *Haematopus moquini*. Carbon and nitrogen stable isotope values of blood (adults
863 and chicks) and body feathers (adults only) of African black Oystercatchers.
864 Values are mean ± SD

Sites	Blood (Adults + chicks)		Feathers (Adults only)		N			Sampling seasons*
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Adults	Chicks	Total	
Lüderitz	-15.2 ± 0.5	12.4 ± 0.7	-13.8 ± 0.2	13.6 ± 0.9	3	1	4	2010
Langebaan	-14.9 ± 0.2	13.2 ± 0.4	-14.5 ± 1.0	14.9 ± 0.3	4	2	6	2009
Koeberg	-14.6 ± 0.6	11.6 ± 0.3	-13.8 ± 0.4	13.2 ± 0.1	4	4	8	2008 and 2009
Walker Bay	-14.4 ± 0.1	11.6 ± 0.2	-13.5	12.8	1	3	4	2009 and 2010
Arniston	-15.6 ± 0.3	11.3 ± 03	-14.9 ± 0.3	12.8 ± 0.2	6	1	7	2009
De Hoop	-14.8 ± 0.6	11.8 ± 0.4	-14.9 ± 0.3	12.8 ± 0.2	5	7	12	2009
Dana Baai	-15.9 ± 0.5	10.5 ± 0.4	-15.8 ± 0.3	13.8 ± 0.1	2	8	10	2009
Goukamma	-15.5 ± 0.5	11.4 ± 0.4	-15.0 ± 0.4	13.3 ± 0.3	8	9	17	2009
Plettenberg Bay	-15.3 ± 0.8	11.0 ± 0.6	-14.9 ± 0.6	12.8 ± 0.2	5	2	7	2009
Tsitsikamma	-13.2 ± 0.0	11.3 ± 0.2	-12.3	12.8	1	1	2	2010
Cape Recife	-13.6 ± 0.8	11.9 ± 0.4	-13.1 ± 1.0	13.5 ± 0.4	12	6	18	2008 and 2009
Kenton	-14.4 ± 0.9	11.2 ± 0.4	-13.7 ± 0.9	12.7 ± 0.4	10	7	17	2008 and 2009
East London	-13.0 ± 1.4	10.5 ± 0.6	-11.6 ± 1.6	11.4 ± 0.5	11	13	24	2008

**The breeding season spans consecutive years, therefore "2008", "2009" and "2010" correspond respectively to the 2007-2008, 2008-2009 and 2009-2010 austral summers*

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Table 2. Carbon (a) and nitrogen (b) stable isotope values of mussels and limpets along the southern African coastline. Values are mean ± SD (‰). ^{a,b,c} indicate homogenous groups of species with non-significant differences in their $\delta^{13}C$ or $\delta^{15}N$ values (Kruskal-Wallis *H* test, Dunn post-hoc test and Bonferroni corrections, $p > 0.05$)

a. $\delta^{13}C$ Sites	Mussels				Limpets					
	A. ater	*C. meridionalis*	*M. galloprovincialis*	*P. perna*	*C. oculus*	*S. argenvillei*	*S. cochlear*	*S. granatina*	*S. granularis*	*S. longicosta*
Lüderitz	-17.9 ± 0.2^{a}	-17.4± 1.0^{a}	-15.7± 0.1^{a,b}	-	-	-	-	-15.7± 0.6^{a}	-11.8± 0.3^{b}	-
Langebaan	-	-	-15.0± 0.1^{a}	-	-	-11.6± 0.4^{b}	-	-	-	-
Koeberg	-	-	-15.0± 0.1^{a}	-	-	-12.7± 0.2^{b}	-	-	-	-
Walker Bay	-	-	-14.7± 0.2^{a}	-	-	-	-	-	-11.2± 0.6^{b}	-
Arniston	-	-	-15.4± 0.1^{a}	-15.6± 0.1^{a}	-8.3± 0.8^{a,b} **	-	-	-	-	-6.2± 0.2^{b} **
De Hoop	-	-	-15.9± 0.1^{a}	-16.3± 0.1^{a}	-	-	-	-	-	-
Dana Baai	-	-	-15.5± 0.6^{a}	-16.5± 0.2^{a}	-	-		-	-	-
Goukamma	-	-	-15.2± 0.5^{a,b}	-15.6± 0.5^{a}	-10.9± 0.6^{b,c} *	-	-11.6± 0.3^{b,c} *	-	-	-7.2± 1.7^{c} *
Plettenberg Bay	-	-	-15.2± 0.4^{a}	-15.9± 0.3^{a}	-13.1± 0.7^{b}	-	-	-	-13.4± 1.1^{b}	-
Tsitsikamma	-	-	-14.0± 0.3^{a,b}	-14.3± 0.1^{a}	-12.1± 1.1^{a,b,c}	-	-11.1± 0.5^{b,c}	-	-11.3± 0.3^{a,b,c}	-9.8± 1.2^{c}
Cape Recife	-	-	-	-15.9± 0.1^{a}	-10.5± 1.3^{a,b}	-	-11.6± 0.7^{a,b}	-	-11.9± 0.2^{a,b}	-8.4± 1.9^{b}
Kenton	-	-	-	-15.2± 0.1^{a}	-12.8± 0.7^{b,c}	-	-11.8± 0.6^{b}	-	-12.4± 1.6^{b,c}	-8.2± 1.0^{c}
East London	-	-	-	-15.8± 0.1^{a}	-13.2± 1.1^{a,b}	-	-13.0± 0.1^{b,c}	-	-11.9± 0.6^{b,c}	-8.2± 0.6^{c}

b. $\delta^{15}N$ Sites	Mussels				Limpets					
	A. ater	*C. meridionalis*	*M. galloprovincialis*	*P. perna*	*C. oculus*	*S. argenvillei*	*S. cochlear*	*S. granatina*	*S. granularis*	*S. longicosta*
Lüderitz	10.2± 0.2^{b}	9.2± 0.3^{a,b}	9.3± 0.3^{a,b}	-	-	-	-	7.7^{a,b}± 0.3	8.5± 0.1^{a}	-
Langebaan	-	-	10.1± 0.2^{a}	-	-	11.1± 0.4^{b}	-	-	-	-
Koeberg	-	-	8.6± 0.3^{a}	-	-	9.5± 0.2^{b}	-	-	-	-
Walker Bay	-	-	8.8± 0.1^{a}	-	-	-	-	-	7.4± 0.8^{b}	-
Arniston	-	-	8.5± 0.5^{a}	9.0± 1.2^{a}	9.0± 0.6^{a} **	-	-	-	-	8.3± 0.7^{a} **
De Hoop	-	-	8.9± 0.2^{a}	9.2± 0.2^{a}	-	-	-	-	-	-
Dana Baai	-	-	8.4± 0.2^{a}	8.7± 0.3^{a}	-	-	-	-	-	-
Goukamma	-	-	8.6± 0.5^{a,b}	8.8± 0.5^{a,b}	8.7± 0.2^{a,b} *	-	9.4± 0.2^{b} *	-	-	8.2± 0.2^{a} *
Plettenberg Bay	-	-	8.1± 0.3^{a}	8.6± 0.6^{a,b}	8.8± 0.4^{b}	-	-	-	8.2± 0.2^{a,b}	-
Tsitsikamma	-	-	7.8± 0.3^{a}	7.7± 0.1^{a}	8.4± 0.3^{a,b}	-	8.4± 0.2^{a,b}	-	8.3± 0.3^{a,b}	8.6± 0.2^{b}
Cape Recife	-	-	-	8.7± 0.1^{a}	8.7± 0.5^{a}	-	8.6± 0.4^{a}	-	8.9± 0.2^{a}	8.2± 0.4^{a}
Kenton	-	-	-	8.1± 0.2^{a}	8.0± 0.0^{a,b}	-	9.2± 0.3^{b}	-	7.3± 0.9^{a}	7.7± 0.3^{a}
East London	-	-	-	7.1± 0.1^{a}	8.1± 0.4^{b}	-	8.2^{b}± 0.0	-	7.6±0.1^{a,b}	8.0± 0.3^{b}

**Not present on the feeding grounds and collected ~10km eastwards. Limpet data used to run SIAR for Goukamma and Dana Baai*
***Limpet data used to run SIAR for De Hoop*

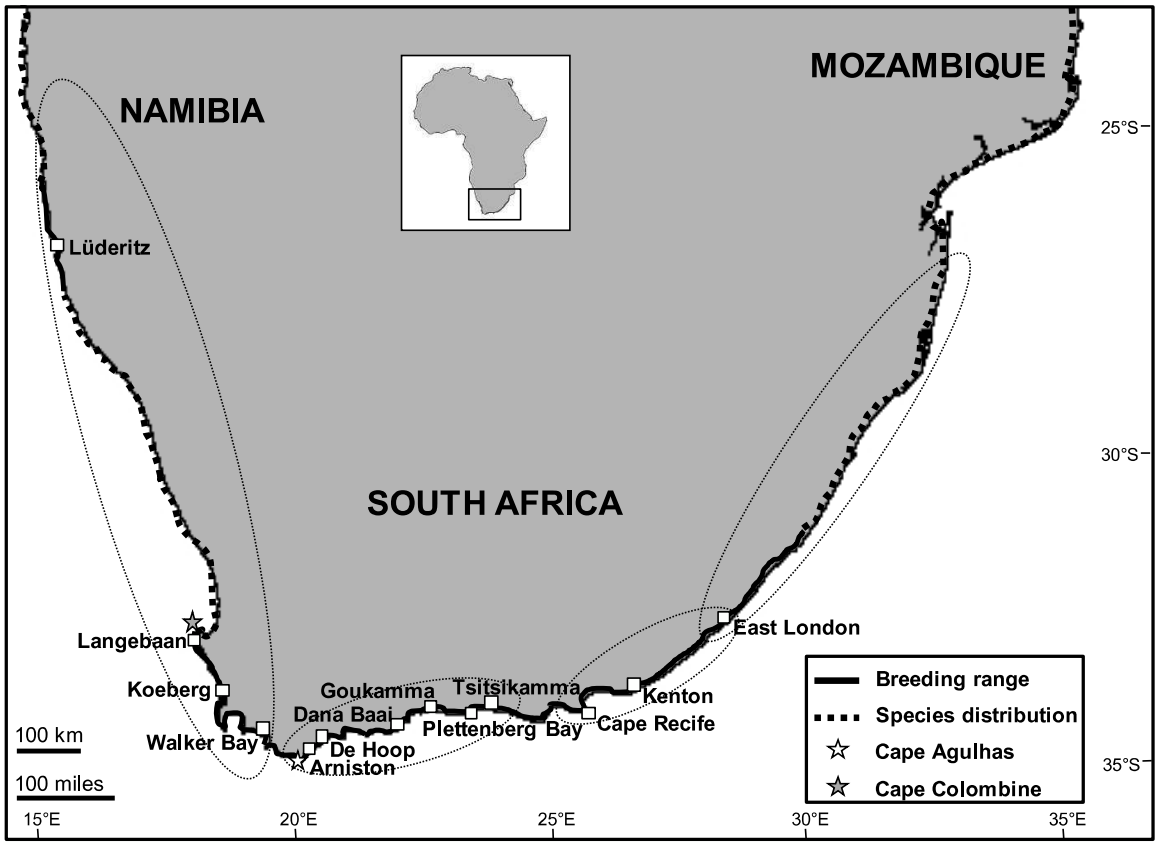
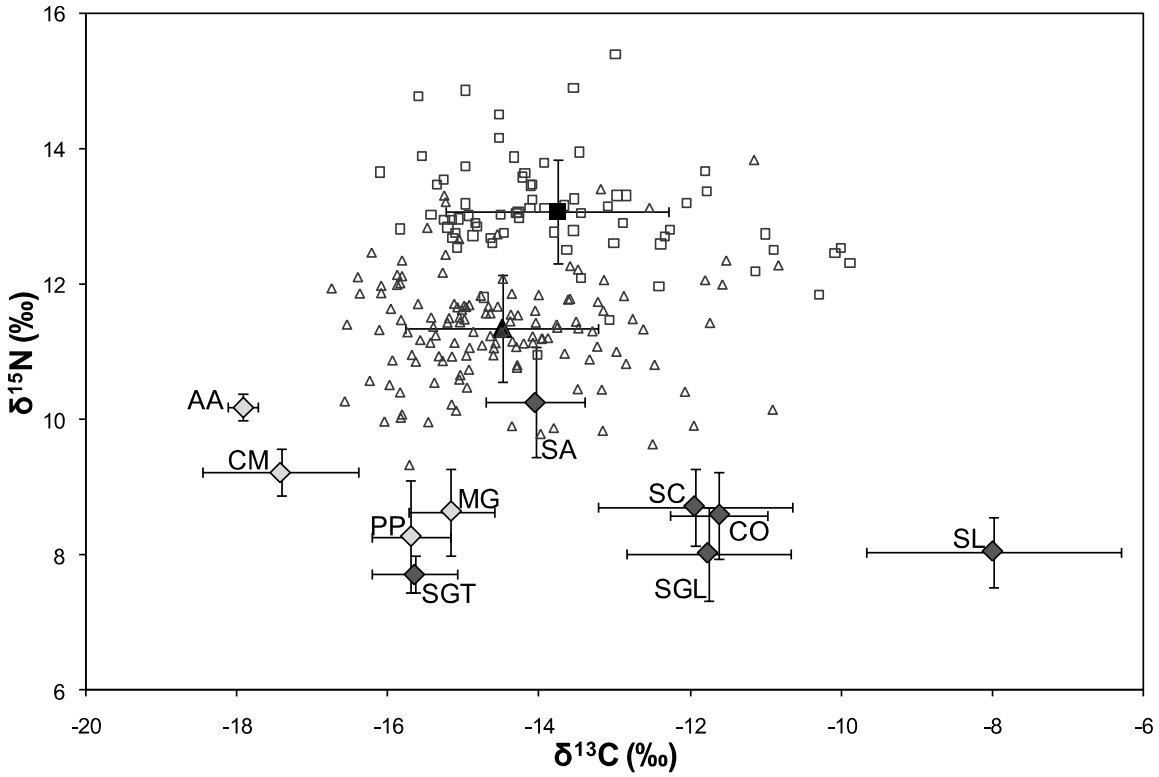


Fig. 1. Location of the breeding sites where African Black Oystercatchers and prey were sampled. Isotopic regions described in Hill et al. (2006) and Hill & McQuaid (2008) are delineated by dotted circles



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879 Fig. 2. Stable carbon and nitrogen isotope ratios (‰) of African Black Oystercatchers,
880 mussels and limpets across the sampling area. (△) and (□): Individual isotope ratios of
881 blood (adults and chicks, n = 136) and feathers (adults, n = 72) respectively. (▲) and (■
882): Mean ± SD isotopic values of blood (adults+chicks) and feathers (adults) respectively.
883 (◇) and (◆): Mean ± SD isotopic values of mussels (AA: *Aucolomya ater*; CM:
884 *Choromytilus meridionalis*; MG: *Mytilus galloprovincialis*; PP: *Perna perna)* and limpets
885 species (CO: *Cymbula oculus* ; SA: *Scutellastra argenvillei*; SC: *S. cochlear*; SGT: *S.*
886 *granatina*; SGL: *S. granularis*; SL: *S. longicosta)* respectively

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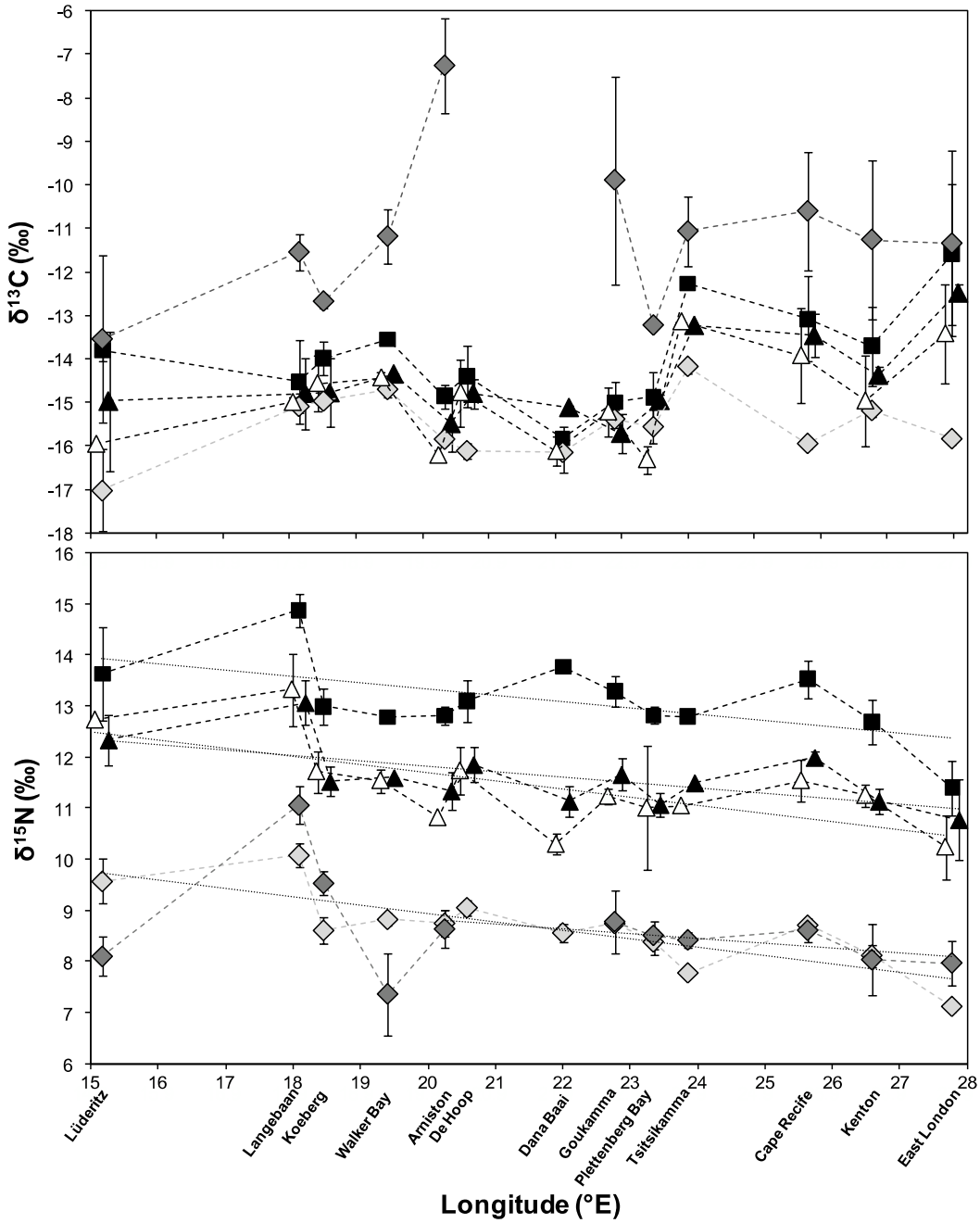

Fig. 3. Stable carbon (a) and nitrogen (b) isotope ratios (‰) of blood (▲) and feathers (■) of adult oystercatchers, blood of chicks (△), mussels (◇) and limpets (◆) along the coastline. Values are mean ± SD. Dotted lines indicated significant correlation with longitude. Adults and chicks signatures are voluntarily shifted for more clarity

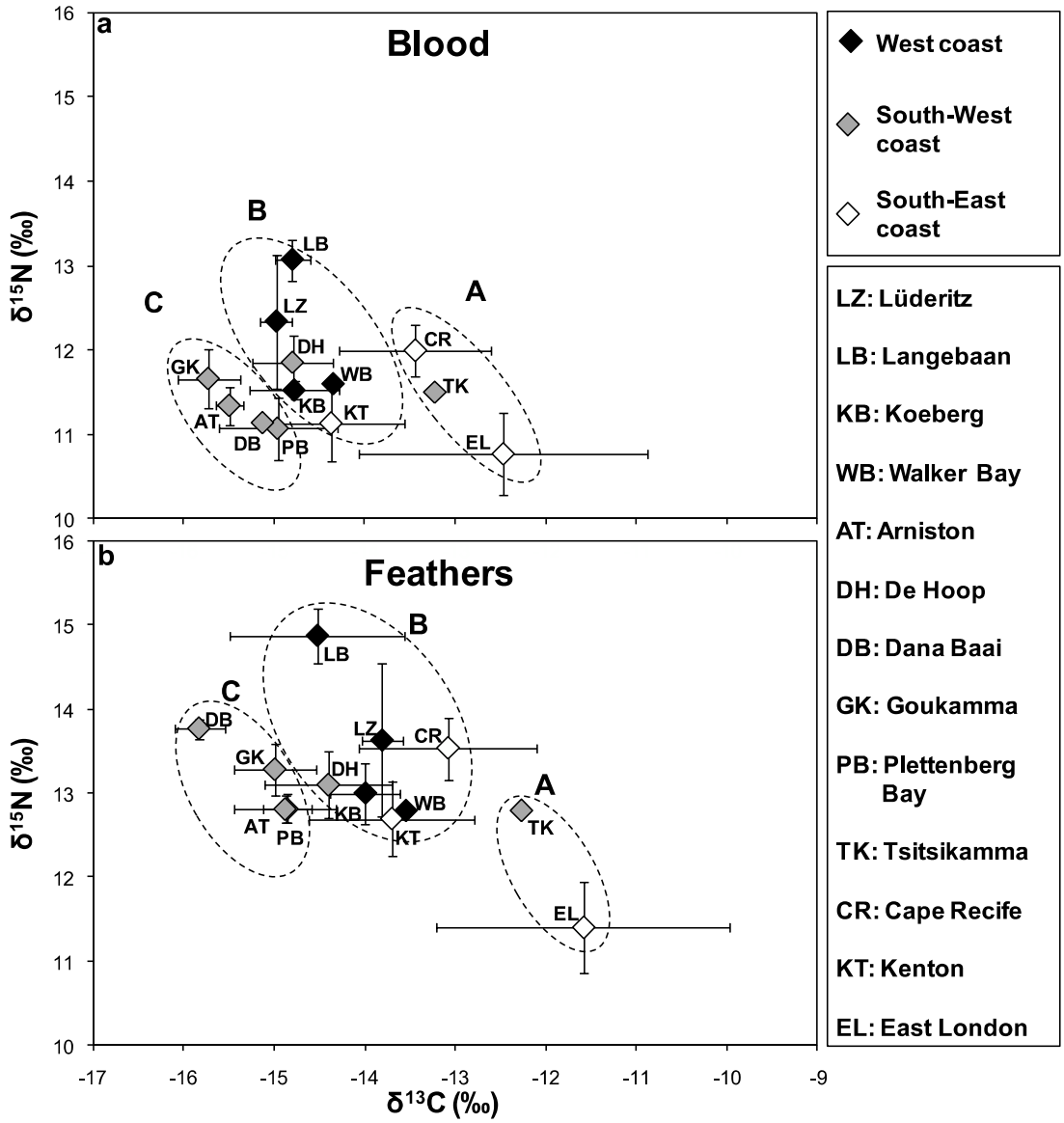

Fig. 4. *Haematopus moquini.* $\delta^{13}C$ and $\delta^{15}N$ ratios in blood (a) and feathers (b) of adult birds. Dotted circles indicate grouping of sites accroding to k-means cluster analysis and confirmed by a discriminant function analysis. Shading of diamonds shows the biogeographic regions described by Hill et al. (2006)

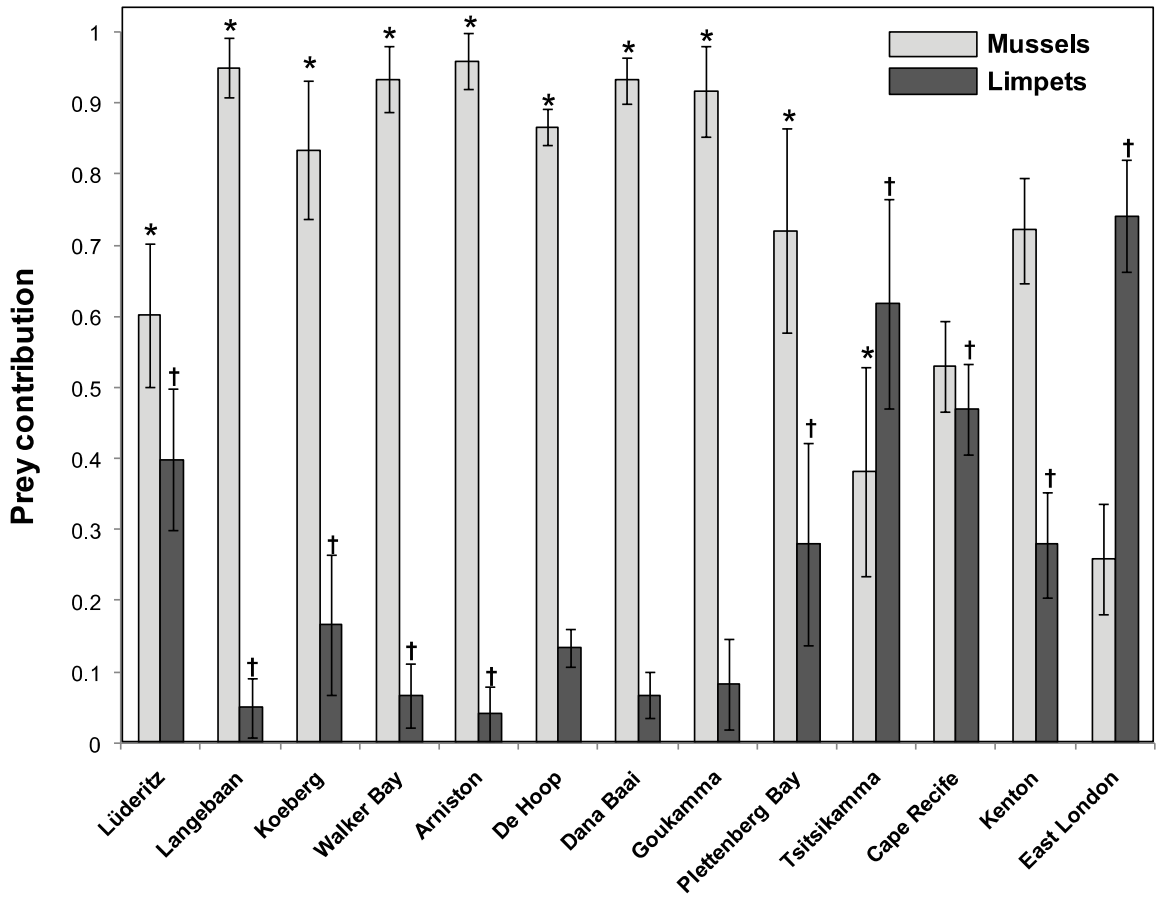

Fig. 5. *Haematopus moquini*. Contributions of mussels and limpets to the African Black Oystercatchers diet along the coastline. Values are mean ± SD estimated from Bayesian mixing models (SIAR). Blood isotope signatures of African Black Oystercatchers and potential sources used in the model are presented in Tables 1 and 2. Results for mussel species and limpet species were pooled for each site according to Phillips et al (2005) *a posteriori* aggregation. Trophic enrichment factors (see method for TEF estimations in "Materials and Methods") used were + 0.2 (± 0.4) ‰ for $\delta^{13}C$ and + 2.7 (± 0.4) ‰ for $\delta^{15}N$. * and † indicate sites where *Mytilus galloprovincialis* and limpets were present on the feeding grounds, respectively.

Annexe 6

Minimal sex-related trophic segregation in a sexually dimorphic shorebird, the African Black Oystercatcher (*Haematopus moquini*) revealed by stable isotope analyses.

Sophie A. Kohler, Maëlle Connan, Joanna Kolasinski, Yves Cherel, Christopher D. McQuaid & Sébastien Jaquemet

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Minimal sex-related trophic segregation in a sexually dimorphic shorebird, the African Black Oystercatcher (*Haematopus moquini*) revealed by stable isotope analyses

Sophie A. Kohler[1,2*], Maëlle Connan[2], Joanna Kolasinski[1,3], Yves Cherel[4], Christopher D. McQuaid[2] and Sébastien Jaquemet[5]

[1]Université de La Réunion, Laboratoire ECOMAR, 97400 Saint Denis, La Réunion, France
[2]Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa
[3]Department of Botany, Rhodes University, Grahamstown 6140, South Africa
[4]Centre d'Etudes Biologiques de Chizé, UPR 1934 du CNRS, 79360 Villiers-en-Bois, France
[5]UMR-EME 212, IRD, Department of Botany, Rhodes University, Grahamstown 6140, South Africa

*Corresponding author: kohler84@gmail.com

Abstract

Sexual dimorphism occurs in all oystercatcher species and is characterized by a longer and more pointed bill in females compared to males. This has been related to sex-specific segregation in their feeding habits in several of these shorebird species, including the African Black Oystercatcher. For the latter, however, studies concerned only a small number of breeding pairs and/or were done prior the invasion of the South African rocky shores by the Mediterranean mussel. In this study, we investigated sexual dimorphism in the African Black Oystercatcher and, using stable isotopes of carbon and nitrogen, related this to diet segregation between sexes in relation with changes in foraging habitats along the South African coastline. Males and females were sampled during incubation on the west, south-west and south-east coasts of South Africa. Potential prey (mussels, limpets, polychaetes and ascidians) were also collected and their isotopic ratios measured. Bill dimorphism was consistent with the general pattern previously described and occurred throughout the study area. Males and females displayed little differences in their $\delta^{13}C$ ratios and in the relative contribution of the different prey to the diet composition throughout the study area, except on the south-east coast where the most abundant prey elsewhere (the Mediterranean mussel) is rare and males were slightly depleted in ^{13}C relative to females. 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 suggest instead that this $\delta^{15}N$ divergence could be related to differences in physiological requirements between males and females during the pre-laying and incubation periods. The overall slight sex-specific food segregation could result from the lack of food limitation in foraging habitats brought by the invasion of the Mediterranean mussel on the west and south-west coasts. The persistence of bill dimorphism in this species could be genetically fixed or driven by sexual selection or unidentified behaviours affecting the bill abrasion differently in males and females.

Introduction

Food partitioning as a way of reducing competition in a limited resource environment, and optimizing energy intake and fitness is widespread in animals (Stephens and Charnov 1982), particularly in both terrestrial and aquatic birds (Donald et al. 2007, Masello et al. 2010). Mechanisms of food segregation among birds involve the targeting of food items of different sizes or species, the use of different foraging methods and behaviour or the use of different foraging areas or strata (Selander 1966). These mechanisms are often related to phenotypic differences in morphology, skills and social status especially in shorebirds (Durell 2000). During the breeding season, energy demand is high for parents and physiological and behavioural constraints often differ between males and females (Drent and Daan 1980, Meijer and Drent 1999). As a consequence, sex-related differences in diet and foraging strategies frequently occur (Andersson and Nordberg 1981, Forero et al. 2005). In this situation sexual dimorphism can be a way of reducing intersexual food competition. In seabirds, sexual dimorphism is mostly related to differential body size (Székely et al. 2000, Gonzales-Solis et al. 2000) and in colony-based species, males and females are known to differ in their foraging ranges (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, males and females can also differ in their body sizes, but most sex-specific diet and feeding techniques have been related to differences in the 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, in terms of both diet and handling techniques, and how these relate to bill morphology (Hulscher 1996, Sutherland et al. 1996): individuals with pointed bills typically specialize on polychaetes, while birds with chisel-shaped and blunt bills specialize on stabbing and hammering shellfish respectively. Beside *H. ostralegus,* there are 10 oystercatcher species throughout the world and one presumed to be extinct. Despite their scattered distribution (Eurasia, Australasia, North and South America, Southern Africa), oystercatcher species share many ecological

and morphological similarities (Hockey 1996). They are highly territorial during the breeding season, monogamous, form long-term pair bonds and provide full biparental care (Hockey 1996). 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 with bill morphology has been reported on the basis of direct observations for Eurasian oystercatchers (Durell et al. 1993, Van de Pol et al. 2010) and for the two species occurring in Australia (Lauro and Nol 1995). In the case of the African Black Oystercatcher (ABO), which is a non-migrating species that breeds exclusively along the coastlines of Namibia and South Africa, Hockey and Underhill (1984) also reported sex-specific dietary differences, but in two breeding pairs only.

On southern African rocky shores, ABOs can encounter a wide range of potential prey and this includes mussels, limpets, polychaetes, chitons, isopods, barnacles and ascidians (Hockey and Underhill 1984). The structure of these rocky shore communities however is 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 that flows along the east and south coasts (Shannon 1985, Lutjeharms 2004). Overall this gives rise to broad differences in nutrient concentration and intertidal biomass, which are greater on the West coast, while species richness is greater on the east coast (Bustamante and 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). On the West coast, the invasive mussel has replaced the indigenous species as the dominant mussel in the low- and mid-shore where it outcompetes adult limpets for primary rocky space (Hockey and Van Erkom Schurink 1992, Steffani and 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 (Bownes and McQuaid 2006). 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 ABO population dynamics on the west coast by increasing the overall food biomass available to this bird (Hockey and Van Erkom Schurink 1992). The natural variability of coastal habitats in southern Africa and their recent perturbation by the invasive mussel constitute a unique opportunity to investigate sex-specific foraging strategies in the ABO. More precisely, variations in abundance and diversity of food sources across the breeding range of ABOs could result in geographic variation in the prevalence of food limitation, so that optimal foraging theory would predict consequences for the degree of dietary segregation between males and females.

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 have the disadvantage of being very time-consuming and can only give a snapshot of the diet for a limited number of individuals of the population. On the other hand in the study of oceanic birds, 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 and Angerbjörn 2005, Cherel and Hobson 2007, Jaeger at al. 2009). The use of carbon and nitrogen stable isotopes relies on the fact that their ratios (denoted as $\delta^{13}C$ and $\delta^{15}N$) in consumer tissues reflect those of their prey in a relatively predictable manner (DeNiro and Epstein 1978, 1981). $\delta^{13}C$ varies little along the food chain and is therefore a good indicator of baseline sources. This is especially interesting 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 and Rasmussen 1999). On the other hand the shift in $\delta^{15}N$ between a prey

and its consumer varies between 2‰ and 5‰ (DeNiro and Epstein 1981, Bearhop et al. 2002, McCutchan et al. 2003) and is often used to infer the trophic position of organisms within a food chain (Cherel et al. 2008).

Our primarily aim in this study was to investigate the segregation of resources between sexes and within pairs of the ABO, and its possible variation in relation to changes in their foraging habitats. For this purpose we combined the analysis of biometric measurements to assess the degree of sexual dimorphism in this species and the analysis of food segregation between male and female oystercatchers breeding on the South African coastline using carbon and nitrogen stable isotope ratios in their tissues and their potential prey.

Material and Methods

Study areas. Fieldwork was carried out during 3 consecutive breeding seasons (December 2007 to February 2010) in the rocky shore habitats of ABOs in South Africa. Birds and their potential prey were sampled in 3 distinct regions in South Africa: the south-east coast (from East London to Port Elizabeth), the south-west coast (from Plettenberg Bay to Arniston) and the west coast (Koeberg and Langebaan) (Fig. 1).

Sampling of oystercatchers and potential prey. Breeding males and females were captured during incubation using walk-in traps on nests. Efforts were made to capture as many complete breeding pairs as possible. For each bird, 0.5 ml of blood was taken from the tarsal vein and preserved in 1 ml of 70% alcohol to measure the stable isotope ratios of carbon and nitrogen. Five to eight feathers were cut from the neck of each adult and stored in plastic bags until further measurement of their stable-carbon and stable-nitrogen isotopic ratios. The tarsus and bill (from the feather line) lengths were measured to the nearest 0.1 mm using callipers and the wing length was measured to the nearest 1 mm with a ruler. Birds were weighted 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 photos. After handling, birds were tagged with a unique engraved ring (SAFRING) and released. Each photo was scaled using CPCe software (Kohler and 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 photo (Fig. 2). Although most oystercatchers can be sexed in the field according to morphological features, such as bill morphology and eyeflecks (Hockey 1981; Kohler et al. 2009a), we used molecular sexing based on the CHD1W and CHD1Z introns located on the sex chromosomes (Fridolfsson and Ellegren 1999) to confirm the sex of birds.

Collection of the potential prey to sample was based on the literature (Randall and Randall 1982, Hockey and Underhill 1984) but also on prior visual observations of the feeding behaviour of ABOs at the different study sites. 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 when present on feeding grounds. Mussels and limpets compose the bulk of oystercatcher's diets (Hockey & Underhill 1984, Hockey & Van Erkom Schurink 1992, Kohler et al. 2009b); polychaetes however are also considered in the literature to be an occasional prey (Hockey & Underhill 1984). In Port Elizabeth, oystercatchers were regularly observed scavenging on beached ascidians, *Pyura stolonifera*; hence, 3 specimens were collected at this site and body was sorted from the thick tunic. In addition, stable isotope ratios of the suspension-feeding polychaete worm *Gunnarea capensis* were taken from Hill and McQuaid (2008), who collected specimens from three sites between the west and south-east coasts of South Africa (see Fig. 1). Fifteen individuals of the mussel *P. perna* (five per size class: 20, 40 and 65 mm in shell length), the limpet *C. oculus* (20, 40 and 60 mm) and the limpet *S. cochlear* (20, 40 and 55 mm) were additionally collected in Kenton to test for ontogenic changes in the stable isotope compositions of these invertebrates in relation with size (hereafter called small, medium and large).

Stable isotope analysis. Whole blood of birds has a rapid turnover (Hobson & Clark 1992, 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 remain isotopically inert once fully grown (Mizutani et al. 1990). Feathers can be therefore used as proxy for the diet during the non-breeding season (Jaeger et al. 2009). Pooled body feathers from each individual were cleaned of surface contaminants by immersion in a chloroform/methanol solution (2:1) placed in an ultrasound bath for 2 minutes and then rinsed with deionized water and dried (60°C, 24h). In marine invertebrates, muscle tissues have a slow turnover rate and are unlikely to be affected by short-term changes in environmental conditions (Gorokhova and Hansson 1999). For this reason, adductor and foot tissue were collected from mussels and limpets respectively. For ascidians, after removal of the body from the discarded tunic, a tissue sample was taken from the region of the buccal siphon and used for stable isotope

195 analysis. Lipids are depleted in ^{13}C compared to other tissue components and show variable
196 concentrations among animals and tissue types (DeNiro and Epstein 1977, Tieszen et al.
197 1983, Post et al. 2007). These properties can induce bias when comparing $\delta^{13}C$ ratios
198 between species, social groups or tissues that have different lipid contents, as indicated by
199 the C/N mass ratio (Cherel et al. 2005b). Nevertheless whole blood, feathers and muscle
200 tissues are typically poor in lipids, so that their $\delta^{13}C$ ratios should not be affected in this way
201 (McCutchan et al. 2003, Cherel et al. 2005b, Kojadinovic et al. 2008). Similarly, the lipid
202 content of ascidians represents only 4% of their dry mass (McClintock et al. 2004). For these
203 reasons and because their C/N ratios were low, no delipidation or posterior lipid-
204 normalization (Post et al. 2007) was performed for any tissue sample. All samples were
205 rinsed, dried in an oven (60°C, 24h) and individually ground into a fine homogenous powder.
206 Relative isotope abundances of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) were determined
207 from ~1 mg sub-samples of the homogenous powder with a continuous flow isotope ratio
208 mass spectrometer (IRMS). Results are expressed relative to the international standards of
209 ^{13}C in Pee Dee Belemite and ^{15}N in atmospheric air. Size-class specimens and ascidian
210 samples were analyzed at IsoEnvironmental cc at Rhodes University, Grahamstown (South
211 Africa). All other samples were analyzed at the Stable Light Isotope Unit of the University of
212 Cape Town (South Africa). Precision of replicate determinations was < 0.17 ‰ for carbon and
213 < 0.20 ‰ for nitrogen for both laboratories.
214 **Data analysis**. All statistical analyses were performed using R statistical Software (available
215 at www.r-project.org). When datasets did not meet the required assumptions of normality
216 (Shapiro-Wilk's test, $p > 0.05$) and homoscedasticity (Levene's test), we performed non-
217 parametrical tests. Two-way ANOVAs were used with $\delta^{13}C$ (‰) or $\delta^{15}N$ (‰) ratios as
218 response variables and sex and breeding site (see Fig. 1) as fixed factors to test for
219 significant differences in the blood stable isotope compositions of males and females. In
220 cases of significant differences, we used Tukey's Honest Significant Difference test (Tukey
221 HSD) for post-hoc multiple comparison. The Wilcoxon test was used to investigate $\delta^{13}C$ and
222 $\delta^{15}N$ differences between the blood and feather tissues of paired individuals. We used two-

223 way ANOVAs to investigate variations in morphometric parameters of oystercatchers, related
224 to gender and location, except for bill length, for which the non-parametric Scheirer-Ray-Hare
225 procedure, a two-way extension of the Kruskall-Wallis test, was used. Finally to test for
226 differences in the $\delta^{13}C$ and $\delta^{15}N$ ratios of size classes of prey, we used a Kruskal-Wallis test
227 (H, $\alpha = 0.05$) and a multiple-comparison post-hoc test in cases of significant differences.
228 To estimate the relative contribution of the different types of prey (mussels, limpets,
229 polychaetes and ascidians) to the diet of males and females, the IsoSources stable isotope
230 mixing model software was used (Phillips and Gregg 2003, available at
231 http://www.epa.gov/wed/pages/models.htm.). We used mean blood signatures of males and
232 females, mean signatures of potential prey species at each site and trophic enrichment
233 factors (TEFs) of + 0.2‰ for $\delta^{13}C$ and + 2.7‰ for $\delta^{15}N$ (Kohler et al., *in press*) to run the
234 model for each sex at each study site. The outputs were aggregated *a posteriori* to pool
235 mussel species together and limpet species together (Phillips et al. 2005).
236

RESULTS

A total of 63 breeding ABOs, including 30 females, 33 males and 20 breeding pairs, were sampled from 9 different breeding sites grouped into 3 coastal regions along the South African coastline (Fig. 1).

Biometrics. Males and females displayed significantly high levels of dimorphism for all biometric parameters except for the bill depth. Females were about 40 g heavier than males and had longer tarsi, wings and bills than males (Table 1). On the other hand males had significantly deeper bill-tips and higher bill-tip depth / bill length ratios than females (Table 1, Fig. 3). There was no evidence of geographic changes in the morphology of either sex (Table 1, Fig. 3).

Stable isotope composition of prey. Mean (±SD) carbon and nitrogen stable isotope values of potential prey in each coastal regions are presented in Fig. 4 a, b and c. On the three coastlines, limpet species (from – 16.8 to – 5.3‰) were enriched in ^{13}C compared to mussels (from – 16.7 to – 14.3‰) and polychaete worms (from – 15.4 to – 14.2‰). Conversely the polychaete *Gunnarea capensis* was enriched in ^{15}N (from 9.9 to 11.2‰) compared to mussels (6.4 to 10.9‰) and limpets (from 5.8 to 11.5‰). On the south-east coast, ascidians were ^{13}C-depleted (mean = - 17.1 ± 0.9‰) and ^{15}N-enriched (mean = 10.5 ± 0.7‰) compared to other benthic invertebrates.

Small, medium and large mussels had very similar $\delta^{13}C$ (- 16.0 ± 0.4‰, - 15.7 ± 0.2‰ and – 15.8 ± 0.1‰ respectively) and $\delta^{15}N$ values (7.1 ± 0.2, 7.4 ± 0.3 and 7.3 ± 0.3‰ respectively) that did not differ significantly (H = 2.27 and 2.90 for $\delta^{13}C$ and $\delta^{15}N$ respectively, $p > 0.05$ for both tests). Although small and medium-sized specimens of the limpet *S. cochlear* displayed a wide range of $\delta^{13}C$ values (- 13.5 ± 2.5‰ and – 12.7 ± 2.2‰ respectively), they were not significantly different from large specimens (- 12.2 ± 0.6‰, H = 1.52, $p > 0.05$) and all size classes had similar nitrogen stable isotope composition (8.3 ± 0.3, 8.5 ± 0.3 and 8.3 ± 0.3‰ for small, medium and large specimens respectively; H = 1.34, p

263 >0.05). Finally small individuals of the limpet *C. oculus* were significantly depleted in $\delta^{15}N$
264 (7.2 ± 0.5) compared to both medium and large specimens (8.1 ± 0.3 and 8.2 ± 0.5‰
265 respectively; H = 8.66, p = 0.01) but the $\delta^{13}C$ ratios of the 3 size classes were similar (small =
266 -11.4 ± 0.8‰, medium = - 10.3 ± 0.8‰ and large = - 10.1 ± 0.7‰; H = 5.11, p > 0.05).

267

268 **Stable isotope composition of birds.** Mean (±SD) blood $\delta^{13}C$ and $\delta^{15}N$ ratios of males and
269 females from the nine study sites are also presented by regions in Fig. 4. On the south-east
270 coast (Fig. 4a), birds from East London, Kenton and Port Elizabeth displayed different $\delta^{13}C$
271 ratios (from – 17.1 to – 10.8 ‰) with East London birds being significantly enriched in ^{13}C
272 compared to those from Kenton and Port Elizabeth (Tukey HSD, p < 0.001) (Table 2). On
273 this coastline, $\delta^{15}N$ ratios of birds ranged from 10.4 to 13.4 ‰ and individuals from Port
274 Elizabeth had significantly higher $\delta^{15}N$ values than individuals from both Kenton and East
275 London (Tukey HSD, p < 0.001). Females were depleted in ^{13}C at the 3 breeding sites and
276 enriched in ^{15}N compared to males in Port Elizabeth and East London (Fig. 4a), though not
277 significantly so (Table 2).

278 On the south-west coast, $\delta^{13}C$ values of oystercatchers ranged from -16.1 to -14.0‰
279 and individuals from Goukamma were significantly depleted in ^{13}C compared to De Hoop
280 (Tukey HSD, p = 0.01) and Plettenberg Bay (Tukey HSD, p = 0.04). The $\delta^{15}N$ values ranged
281 from 10.6 to 12.3‰ with values of $\delta^{15}N$ for birds from Plettenberg Bay being significantly
282 depleted compared to De Hoop (Tukey HSD, p < 0.01) and Goukamma (p = 0.02). At the
283 same sites no sex-related differences in $\delta^{13}C$ values were recorded (Fig. 4b, Table 2).
284 Conversely, females displayed slightly but significantly higher $\delta^{15}N$ ratios than males (Fig. 4b,
285 Table 2). Post-doc Tukey HSDs, however, revealed that this was due to significant
286 differences between males from Plettenberg Bay and females from De Hoop (p = 0.02) and
287 Goukamma (p = 0.03), rather than a clear sex-related trend in $\delta^{15}N$ values from a same site.

On the west coast, individuals from Koeberg and Langebaan had similar $\delta^{13}C$ values (from –15.6 to – 14.2 ‰, Fig. 4c, Table 2) and differed significantly in their $\delta^{15}N$ values (from 11.4 to 13.3‰, Table 2), with birds from Langebaan being relatively enriched in ^{15}N. At Langebaan males and females had similar values of both $\delta^{13}C$ and $\delta^{15}N$ (Fig. 4c, Table 2) and at Koeberg females were slightly (but not significantly) depleted in ^{13}C compared to males (Table 2).

Breeding pairs. There were significant differences in the $\delta^{13}C$ ratios of males and females from the same breeding pair 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 its mate (blood: $\delta^{13}C$ = - 12.6 ‰, feathers: $\delta^{13}C$ = -12.9‰) (Fig. 5, pair indicated by an arrow). When this pair was excluded from the analysis, significant differences between paired birds disappeared (Fig. 5a and c). Breeding partners displayed significant differences in their $\delta^{15}N$ ratios (Fig. 5b) for blood with an overall enrichment in ^{15}N (average + 0.3‰) in females, while their feather $\delta^{15}N$ were not significantly different (Fig. 5d). The trend persisted even when the pair from Port Elizabeth was excluded from the analysis (Fig. 5b and d).

Diet. The IsoSource outputs indicated that mussels and limpets contributed the bulk of the diet of ABOs, and that their relative contributions varied mostly between sites and regions rather than between sexes (Fig. 6). On the south-west and west coasts, mussels dominated the diet (range = 40 – 100%; Fig. 6a) while on the south-east the contribution of limpets was substantial though variable (range = 7 - 100%; Fig. 6b). With the exceptions of Port Elizabeth (range = 0-74%) and Langebaan (range = 43-60%), the contribution of polychaetes was low (range = 0 - 44%, Fig. 6c). There was much overlap in the range of feasible contributions (represented by whiskers in Fig. 6) and in the interquartile ranges (represented by boxes in Fig. 6) of males and females from the same sites. However in Kenton, females seem to feed more on mussels (median = 66%; range = 47 - 83%) than males (median = 43%, range = 13 – 69%), which fed more on limpets (Males: median = 36%; range = 15 – 52%; Females:

315 median = 18%, range = 7 – 28%). One female sampled in Port Elizabeth had very different
316 stable isotope signatures compared to other females from the same area, and was not
317 pooled with them in the stable isotope mixing model (Fig. 6, individual indicated with an
318 arrow). The IsoSource outputs revealed a much higher consumption of ascidians (*Pyura*
319 *stolonifera*) for this female (range = 75 – 95%) than for other birds (range = 0 – 61%) from
320 Port Elizabeth (Fig. 6d).

321

DISCUSSION

The main result emerging from this study is that despite clear sexual dimorphism, especially in bill morphology, male and female ABOs displayed very little differences in their stable isotope signatures during either the breeding and non-breeding periods. Although the pattern was not significant, at most locations, males tended to be enriched in ^{13}C compared to females, which in turn were slightly ^{15}N-enriched compared to males. Between breeding mates, $\delta^{13}C$ segregation was only observed on the south-east coast in blood and to a lesser extent in feather tissue. In addition, one breeding pair from Port Elizabeth displayed extreme sex-related $\delta^{13}C$ differences (+ 4.5‰ in the female) but this seems to have reflected individual idiosyncrasy in feeding preference of the female. Finally, mild ^{15}N enrichment in females compared to their breeding partners was visible, and only concerned blood tissues. Sexual dimorphism has already been described in several oystercatcher species including the ABO (Hockey 1996). This has mostly been attributed to the need for diet segregation to reduce competition within pairs (Hockey and Underhill 1984, Lauro and Nol 1995) and to increase winter survival and fitness (Durell et al. 1993). The fact that we found only slight sex-related differences in stable isotope signatures raises the question of whether sexual dimorphism in ABOs is really driven by food partitioning between partners.

Carbon and nitrogen stable isotopes have successfully demonstrated sex-specific food partitioning in a wide variety of seabird taxa, including alcids, penguins, procellariforms, and skimmers (Forero et al. 2005, Bearhop et al. 2006, Paredes et al. 2008, Mariano-Jelicich et al. 2008), but has rarely been used for this purpose for shorebirds. Variations in stable isotope ratios of marine predators can result from: 1) environmental changes affecting the isotopic composition of the basis of the food web (Cherel and Hobson 2007), 2) differences in the relative consumption of isotopically distinct prey (Gannes et al. 1998) or 3) physiological status and diet-tissue fractionation (McCutchan et al. 2003). At one level we can eliminate the first possibility as we compared territorial males and females feeding on

territories or on the scale of 0-1 km of coastline. Persistent environmental changes in food web baseline stable isotope ratios at such a small scale are unlikely. At larger scales on the other hand significant differences in carbon- and nitrogen-stable isotope ratios were observed between ABOs from different sites and regions. Those are related to the broad differences in primary production and structure of rocky intertidal communities between the two large marine ecosystems surrounding the South African coastline, the Benguela Upwelling System on the west coast and the Agulhas Current on the south and east coasts of southern Africa (Bustamante and Branch 1996). These large-scale patterns have already been shown to affect the stable isotope composition of nearshore primary producers and benthic invertebrates (Hill and McQuaid 2008) as well as oceanic (Jaquemet and McQuaid 2008) and coastal avian predators (Kohler et al. *in press*).

In term of dietary preferences, potential food sources 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 enriched in ^{13}C compared to mussels and polychaetes and this $\delta^{13}C$ segregation is typically observed between inshore grazing and filtering organisms (France 1995, Vander Zanden and Rasmussen 1999). Furthermore, the suspension-feeding polychaete *Gunnarea capensis* was consistently enriched by ~ 2‰ in ^{15}N compared to mussels. Finally the filter-feeding ascidian *Pyura stolonifera*, additionally sampled in Port Elizabeth, clearly differed from mussels, polychaetes and limpets in their $\delta^{13}C$ and $\delta^{15}N$ values. Conversely, the lack of clear differences in stable-carbon isotope composition of males and females or in the relative contribution of the different types of prey to their diet as shown by the mixing models (Fig 6) suggest that sex-specific diet segregation in ABOs is not as widespread as in other oystercatchers species (Durell et al. 1993; Lauro and Nol 1995). Two exceptions were observed on the south-east coast: the stable isotope mixing model outputs suggested that females in Kenton were feeding more on mussels and males on limpets. This correlates with previous findings on the feeding ecology of ABOs on the south-east coast of South Africa

(Kohler et al. 2009b). In addition, one female from Port Elizabeth fed almost exclusively on ascidians, while other males and females from this area seemed to feed on a mixed diet of polychaetes, limpets and ascidians. The solitary ascidian *P. stolonifera* forms dense beds from the low littoral to a depth of about 10 m on rocky reefs (Fielding and Weerts 1994), which can be dislodged locally by wave action and brought high on the shore by the tide where they become accessible for oystercatchers. Pacheco and Castilla (2001) described similar feeding behaviour in American Pied Oystercatchers (*Haematopus palliatus*) exploiting ascidians *Pyura praeputialis* in Chile. This requires a combination of feeding techniques to perforate the tunic and then to extract the animal: striking, hammering, prying, cavity food searching and swallowing (Pacheco and Castilla 2001). Direct observations of similar sequence of feeding techniques were made on African Black Oystercatchers foraging on ascidians in Port Elizabeth (S. Kohler, pers. obs.).

Female oystercatchers were slightly enriched in ^{15}N by an average + 0.3 ‰ compared to their breeding partners and this could indicate that females feed on prey at higher trophic levels than males, and more specifically feed differentially on larger prey size classes or on different species (Bearhop et al. 2006). Eurasian oystercatchers are known to select against small bivalves (Zwarts et al. 1996) for their own diets and the American oystercatcher (*Haematopus bachmani*) and ABOs select larger prey when feeding their chicks than the modal size available on the feeding grounds (Randall and Randall 1982, Hockey and Underhill 1984). Ontogenetic shifts in $\delta^{15}N$ related to changes in diet, feeding habitats and trophic levels have been observed in several marine consumers such as fish (Kolasinski et al. 2009), shrimps (Pakhomov et al. 2004) and squids (Cherel et al. 2009). In the present study, however, there were no obvious isotopic differences between the size classes of mussels and limpets typically targeted by ABOs, i.e. > 30 mm (Randall and Randall 1982, Hockey and Underhill 1984), which correspond to our medium and large prey-size classes. Hence if female ABOs were eating larger mussels or limpets, this would not be reflected in their $\delta^{15}N$ ratios. The different types of prey sampled in this study displayed different $\delta^{15}N$ ratios. Specifically polychaete worms were enriched by ~2 ‰ compared to mussels and

405 limpets. Outputs from the stable isotope mixing model did not however detect any consistent
406 differences in the relative consumption of *G. capensis* by males and females. This suggests
407 that $\delta^{15}N$ differences between partners are not strongly linked to dietary differences. On the
408 other hand, variations in $\delta^{15}N$ between sexes could result from differential ^{15}N diet-tissue
409 fractionation, related to their physiological status (Gannes et al. 1997). Food deprivation has
410 been shown to induce ^{15}N increases in fasting breeding King penguins (Cherel et al. 2005a)
411 and Ross' Geese (Hobson et al. 1993), which literally "feed on themselves" during this
412 period. Conversely, other studies have demonstrated that moderate nutritional stress can
413 result in decreased diet-consumer ^{15}N fractionation in seabirds (Williams et al. 2007, Sears et
414 al. 2008). More generally, the level of nitrogen-use efficiency, in other words the ratio
415 between the ^{15}N depleted nitrogenous waste excreted (uric acid in the case of birds) and the
416 dietary ^{15}N assimilated through protein catabolism, affects the nitrogen fractionation in
417 consumer's tissues (Vanderklift and Ponsard, 2003). In this study, individuals were caught
418 during incubation, which lasts for about 30 days in this species (Parsons 2006). Whole blood
419 has a turnover of 4 to 5 weeks in aquatic birds (Bearhop et al. 2002), therefore, the stable
420 isotope composition of blood tissue in oystercatchers reflects the diet integrated over the pre-
421 laying, laying and incubation periods. Male and female oystercatchers have different energy
422 allocation and requirements during the breeding season, specifically regarding the production
423 of eggs (Meijer and Drent 1999, Morissey et al. 2010) and this could result in differences in
424 nitrogen fractionation between genders. A relation between nitrogen fractionation and sex in
425 breeding oystercatchers is further suggested by the lack of consistent sex-specific
426 differences in $\delta^{15}N$ in feathers, which are grown during the non-breeding season. The
427 difference in $\delta^{15}N$ between breeding partners was small (0.3‰) and not significant at the
428 scale of the whole study, and so may not be biologically meaningful. Nevertheless, it may be
429 precisely because breeding partners displayed little diet segregation that we were able to
430 observe this $\delta^{15}N$ variation. In Kenton where females seemed to prefer mussels and males
431 limpets, there was no such observed sex-specific difference in $\delta^{15}N$. While many studies
432 have focused on the energy allocation to the egg-production in different organisms (Hendry

et al. 1999, Klaassen et al. 2004) to our knowledge, no study has demonstrated the effect of egg-production on female nitrogen stable isotope composition and fractionation in their own tissues. These findings emphasize the need for more experimental and field studies on the allocation of stable isotopes in non-fasting and resident breeding birds.

Records of sex-specific feeding behaviour in ABOs prior to the invasion of South African rocky shores by the Mediterranean mussel *Mytilus galloprovincialis* are limited to observations made on 2 breeding pairs on Marcus Island in 1979/1980 (Hockey and Underhill 1984). Hence, it is difficult to extrapolate this pattern to the rest of the ABO 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* (47.3% vs. 62.9% for males and females respectively), but males consumed more limpets and whelks (50.1 vs. 6.2% for females) and females more polychaetes (0.9 and 19.3% for males and females respectively). 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 would be better equipped for removing limpets from rocks. Since then, numerous studies have been published on the close association between individual or sex-related diet specialization and bill shape in Eurasian Oystercatchers (*Haematopus ostralegus*) (Goss-Custard and Sutherland 1984, Durell et al. 1993, Van de Pol et al. 2010). Feeding specializations in this species are not only prey-type related (polychaetes vs hard-shelled prey), but also characterized by different handling techniques (stabbing, ventral hammering or dorsal-hammering of bivalves, Sutherland et al. 1996). Conversely there is no evidence of different prey-handling techniques among ABOs. In middens (piles of empty shells left by oystercatchers while feeding their chicks) collected to quantitatively study the diet of African Black Oystercatcher (Randall and Randall 1982, Hockey and Underhill 1984, Kohler et al. 2009b), mussels and limpets shells are mostly found intact (S. Kohler pers. obs.), which suggests the use of only stabbing to open mussels and prying to dislodged limpets. Recently, in a study of the feeding ecology of ABOs breeding on sandy shores on the West coast,

Parsons (2006) observed that all birds, males and females, mostly ate polychaetes and small crustaceans and that overall bill morphology and sex did not seem to play an important role in the feeding behaviour of breeding oystercatchers, which fed opportunistically on the most abundant prey (the polychaete *Scololepsis* sp). Similarly the lack of association between sex (and bill-shape) with one type of prey in African Black Oystercatcher was recently suggested by Coleman and Hockey (2008) on Marcus Island off the west coast, where males and females seem to have converged towards a diet almost exclusively composed of the invasive mussel.

All these lines of evidence lead to the conclusion that breeding ABOs display very little sex-specific food segregation, despite the potential for feeding specialization in such a species. This could result from the lack of food limitation in their foraging habitat possibly caused by the invasion of rocky shores by the Mediterranean mussel (Hockey and Van Erkom Schurink 1992), which greatly increased the biomass of mussels, a food item historically favoured by African Black Oystercatchers (Randall and Randall 1982, Hockey and Underhill 1984). Such hypothesis is supported by the slight food segregation observed on the south-east coast where the invasive mussel is virtually absent, and where overall prey biomass is lower than further west (Bustamante and Branch 1996). Moreover, although the population has been increasing for the past 20 years and extended its breeding range further east (Vernon 2004, Tjørve and Underhill 2006, Brown and Hockey 2007, Kemper 2007), presumably as a result of this mussel invasion, the breeding population as a whole may not have reached the carrying capacity of their rocky shore habitats and therefore intra-specific competition and need for food partitioning could be relaxed. Thus sexual dimorphism in ABOs, especially bill dimorphism, could be maintained genetically or by other ultimate factors than food partitioning.

The relative influence of sexual selection and/or ecological processes in sexual dimorphism especially in Charadrii (gulls, shorebirds and alcids) remains controversial (Hedrick and Temeles 1989, Shine 1989, Székely et al. 2000, Van de Pol et al. 2010). There

was overlap in the distribution of bill length between the two sexes (Table 1), however within breeding pairs, females always had longer bills than their breeding partners, with differences ranging from + 2.6 to +18.3 mm. The same observations were made by Hockey and Underhill (1984) for ABOs and by Baker (1975) for New Zealand oystercatchers. These authors suggested that sex recognition and pair formation could be the ultimate causes. If females had longer bills than males, the bill-depth (halfway down) however was similar between sexes. Therefore, intuitively, males had deeper bill-tips than females. The shape of bill-tips in oystercatchers is the combined result of continuous growth (average of 0.44 mm per day) and abrasion rate (Hulscher 1996). Behaviours, other than strictly feeding-related, such as territory defence, differing between males and females could result in differential abrasion rate, but are yet to be identified.

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516

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767

List of Tables and Figures

- Table 1. Biometric measurements of male and female African Black Oystercatchers. A two-way ANOVA (*F*, α=0.05) was used on all biometric measurements, except bill length, with sex and sites as co-factors. For bill length, the non-parametric Sheirer-Ray-Hare procedure (*H*, α=0.05) was used.

- Table 2. Two-way ANOVAs (*F, α* = 0.05) on the $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values of blood for male and female African Black Oystercatchers on the south-east, south-west and west coasts

- Fig. 1 Location of the sampling sites for African Black Oystercatchers and their prey (1 to 9) on the South African coastline. A, B and C indicate the sampling sites for the polychaete *Gunnarea capensis* (Hill and McQuaid 2008)

- 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 and McGill 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)

- Fig. 3 Bill-tip depth/ bill length ratios of male (black diamonds) and female (grey diamonds) African Black Oystercatchers at the 9 study sites (from east to west, as coded in Fig. 1)

- Fig. 4 Carbon and Nitrogen stable isotope values (mean ± SD) for 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*)

- 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) coast. The arrows indicate a pair sampled in Port Elizabeth with contrasted stable isotope compositions. A Wilcoxon rank-sum test (*W*, α = 0.05) was used to test for differences in $\delta^{13}C$ and $\delta^{15}N$ between breeding partners. Values

804 between brackets indicate the *p-value* when the pair indicated by an arrow was removed
805 from the analysis.
806 - Fig. 6 Relative Contribution of a) mussels, b) limpets, c) polychaetes and d) ascidians to the
807 diet of male and female oystercatchers at the 9 study sites (as coded from east to west in
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809 within represent median values. Whiskers represent ranges of feasible contributions. The
810 arrows indicate contributions estimated individually for the female with contrasting stable
811 isotope signatures sampled at Port Elizabeth (see Fig. 5).
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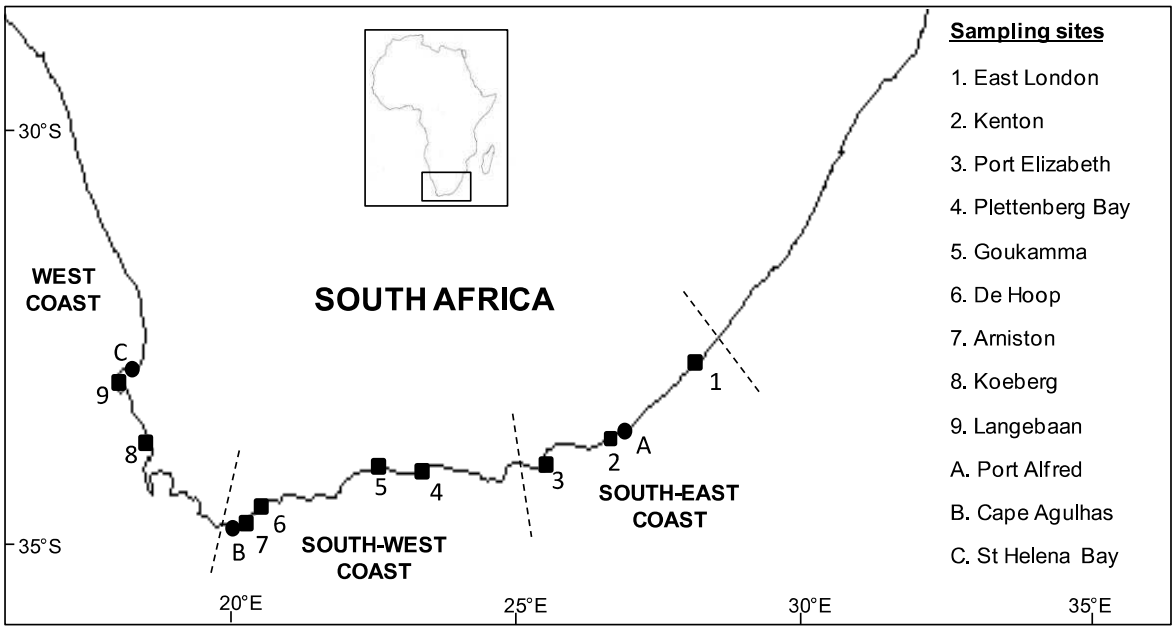

Fig. 1 Location of the sampling sites for African Black Oystercatchers and their prey (1 to 9) on the South African coastline. A, B and C indicate the sampling sites for the polychaete *Gunnarea capensis* (Hill and McQuaid 2008)

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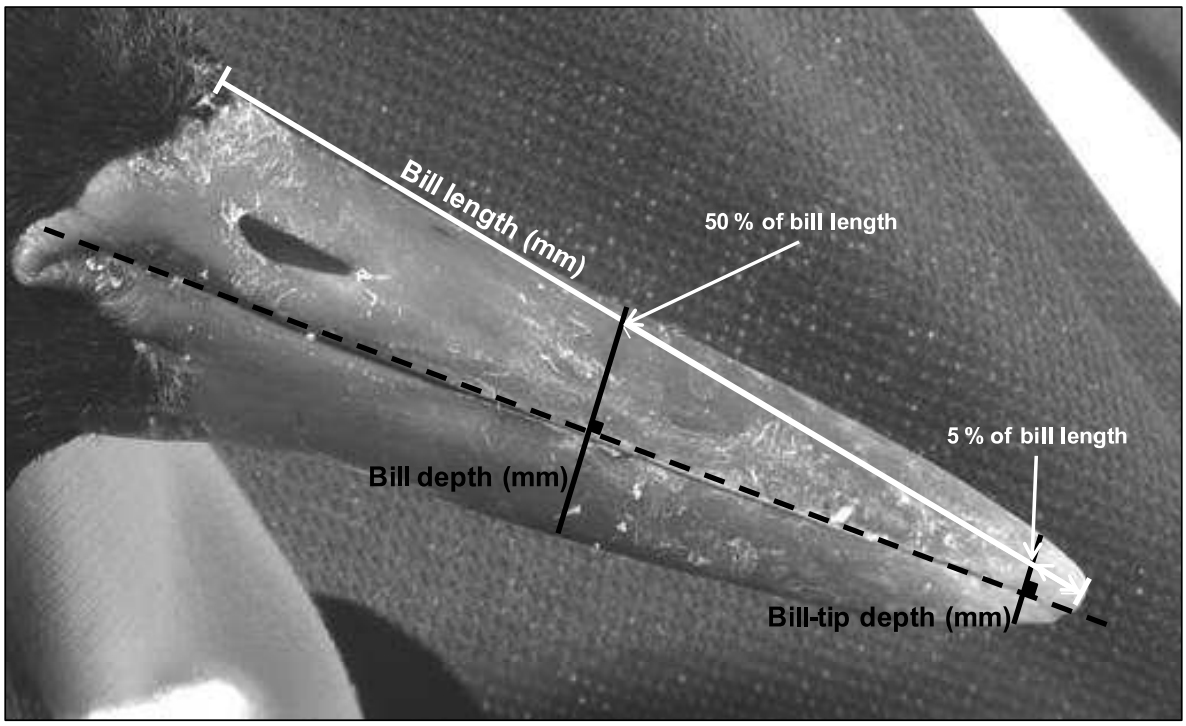

Fig. 2 Lateral photo of an African Black Oystercatcher's bill. Bill length was measured in the field and used to scale the picture with CPCe (Kohler and McGill 2006). A mark was made at 5% and 50% of the bill length, from the bill-tip, to estimate the bill depth halfway down and the bill-tip depth respectively,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

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Table 1. Biometric measurements of male and female African Black Oystercatchers. A two-way ANOVA (*F*, α=0.05) was used on all biometric measurements, except bill length, with sex and sites as co-factors. For bill length, the non-parametric Sheirer-Ray-Hare procedure (*H*, α=0.05) was used.

	Females		Males		Statistical outputs								
					Sex			Sites			Sex X Sites		
	Mean ± SD (range)	*n*	Mean ± SD (range)	*n*	*Df*	*F/H*	*p-value*	*Df*	*F/H*	*p-value*	*Df*	*F/H*	*p-value*
Mass (g)	701 ± 39 (630 – 775)	29	660 ± 36 (580 – 730)	32	1	16.70	***	8	1.07	n.s.	8	0.50	n.s.
Wing (mm)	269 ± 4 (260 – 277)	30	265 ± 6 (253 - 282)	33	1	9.81	**	8	1.16	n.s.	8	0.72	n.s.
Tarsus (mm)	58.2 ± 2.1 (54.5 - 62.2)	30	56.7 ± 2.5 (52.7 - 66.3)	33	1	6.67	*	8	1.06	n.s.	8	0.53	n.s.
Bill length (mm)	72.6 ± 3.2 (64.0 – 78.0)	30	64.1 ± 2.6 (58.7 - 69.8)	33	1	51.70	***	8	5.27	n.s.	8	– 6.49	n.s.
Bill depth (mm)	12.3 ± 0.7 (11.1 – 14.1)	25	12.3 ± 0.9 (10.0 – 14.4)	26	1	0.76	n.s.	8	1.96	n.s.	8	0.83	n.s.
Bill-tip depth (mm)	5.6 ± 0.5 (4.6 - 6.8)	25	6.0 ± 0.7 (4.5 - 7.2)	26	1	7.88	**	8	1.48	n.s.	8	0.59	n.s.
Bill-tip depth / Bill length	0.08 ± 0.01 (0.06 - 0.09)	25	0.09 ± 0.01 (0.07 - 0.11)	26	1	51.12	***	8	1.18	n.s.	8	0.51	n.s.

821 ** p < 0.05 ; ** p< 0.01 ; *** p < 0.001 ; n.s. non-significant differences*

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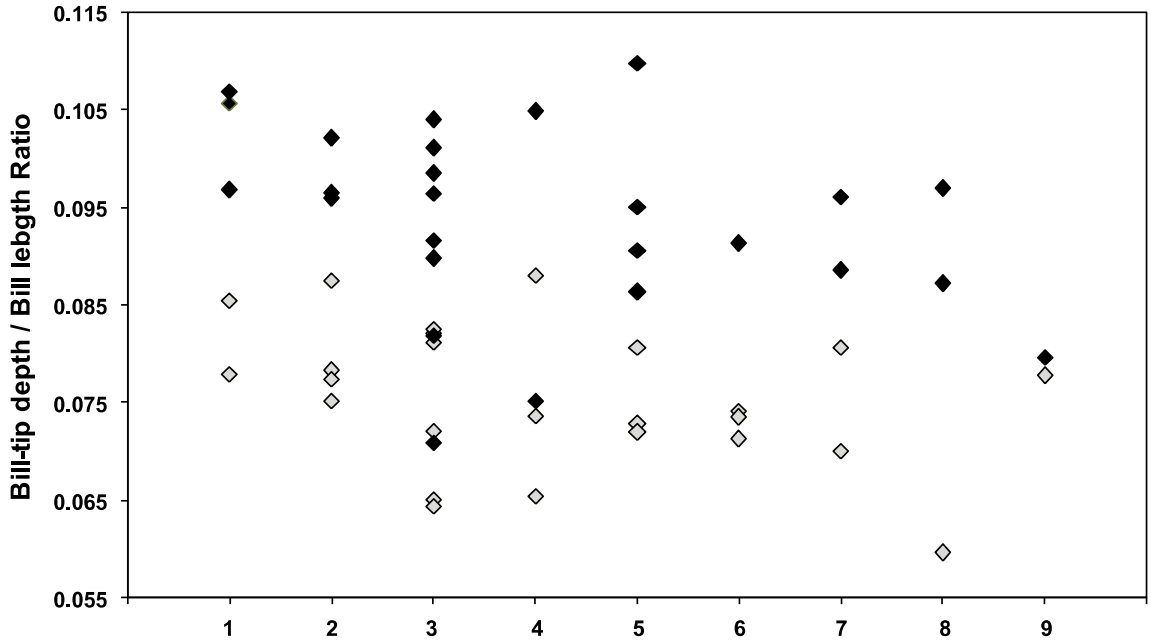

Fig. 3 Bill-tip depth/ bill length ratios of male (black diamonds) and female (grey diamonds) African Black Oystercatchers at the 9 study sites (from east to west, as coded in Fig. 1)

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Table 2. Two-way ANOVAs (*F, α* = 0.05) on the $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values of blood for male and female African Black Oystercatchers on the south-east, south-west and west coasts

			Sex			Sites			Sex x Sites		
		n	*Df*	*F*	*p-value*	*Df*	*F*	*p-value*	*Df*	*F*	*p-value*
South-east coast	$\delta^{13}C$	*31*	*1*	2.90	n.s.	2	16.41	***	2	0.26	n.s.
	$\delta^{15}N$			0.92	n.s.	2	21.62	***	2	0.48	n.s.
South-west coast	$\delta^{13}C$	23	*1*	0.96	n.s.	3	5.77	**	3	0.57	n.s.
	$\delta^{15}N$			6.45	*	3	5.91	**	3	0.12	n.s.
West coast	$\delta^{13}C$	9	*1*	0.81	n.s.	1	0.33	n.s.	1	0.91	n.s.
	$\delta^{15}N$			0.36	n.s.	1	76.23	***	1	0.55	n.s.

828 * *p < 0.05 ; ** p< 0.01 ; *** p < 0.001 ; n.s. non-significant differences*

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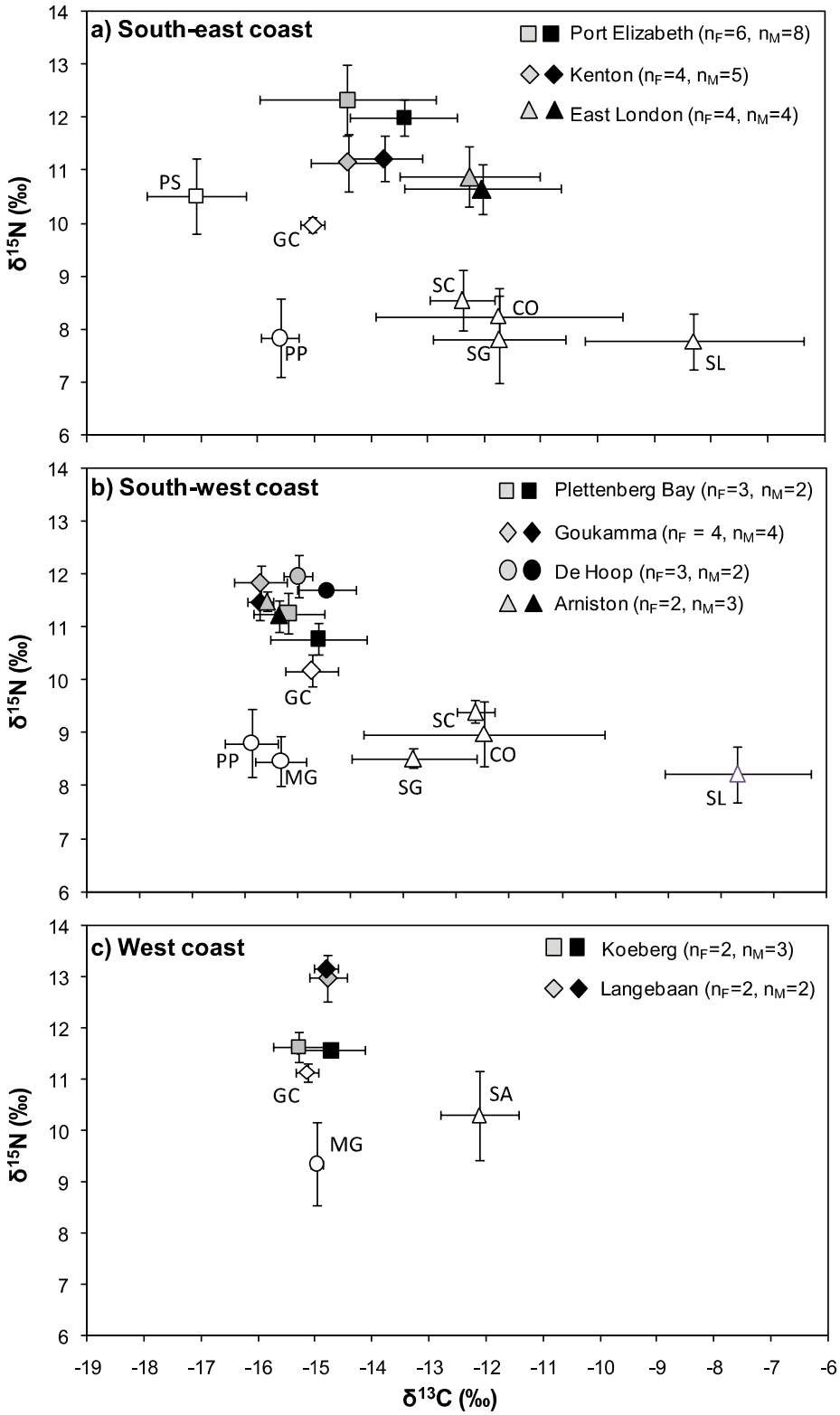

Fig. 4 Carbon and Nitrogen stable isotope values (mean ± SD) for male (black symbols) and female (grey symbols) oystercatchers, mussels (open circles – PP = *Perna perna*, MG = *Mytilus galloprovincialis*), limpets (open triangles - CO = *Cymbula oculus*, SA = *Scutellastra argenvillei*, SC = *S. cochlear*, SG = *S. granularis*, SL = *S. longicosta*), polychaetes (open diamonds – GC = *Gunnarea capensis*), and ascidians (open square – PS = *Pyura stolonifera*)

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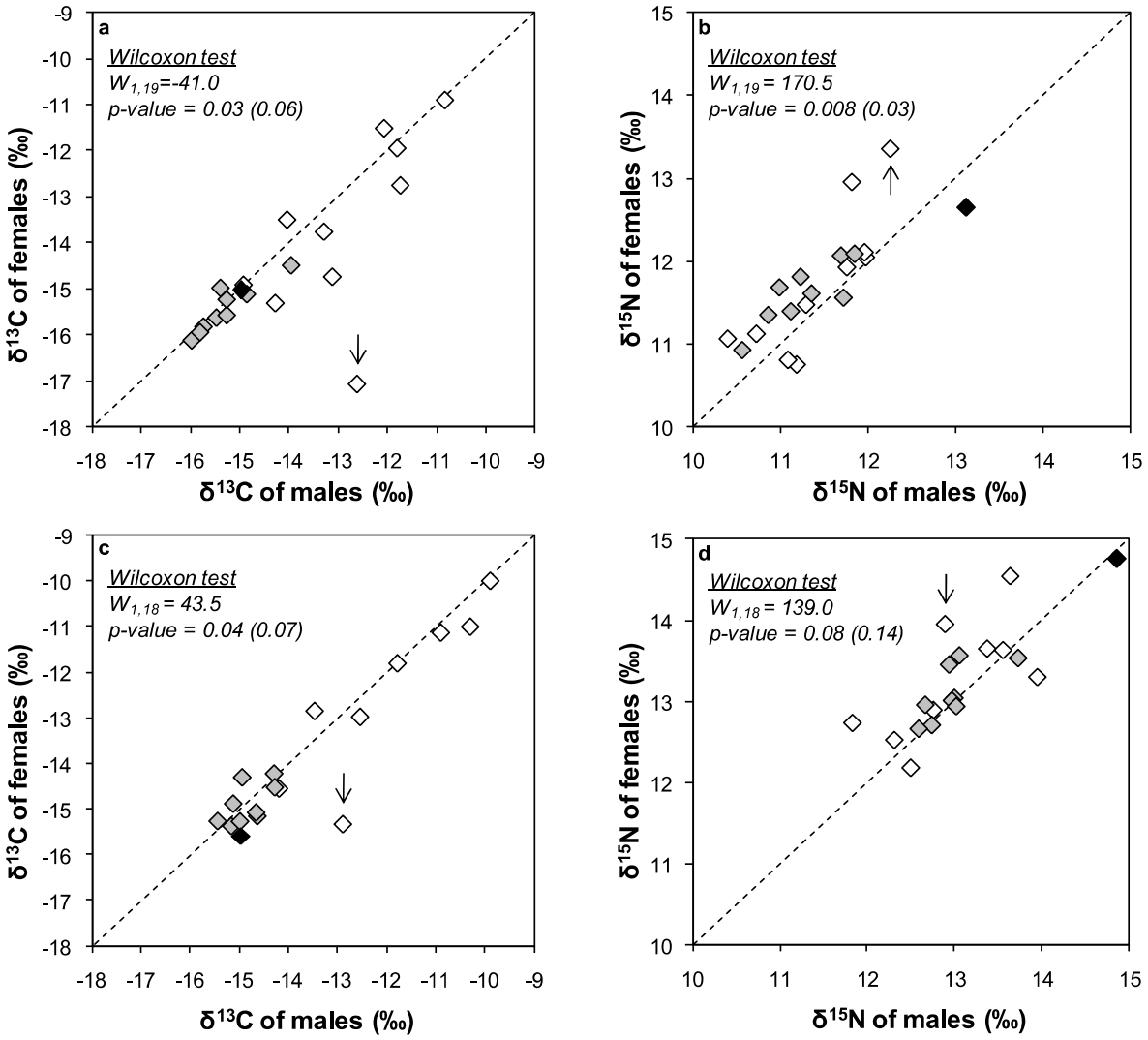

Fig. 5 Blood carbon (a) and nitrogen (b) and feather carbon (c) and nitrogen (d) stable isotope signatures of breeding pairs from the south-east (open diamonds), south-west (grey diamonds) and west (black diamond) coast. The arrows indicate a pair sampled in Port Elizabeth with contrasted stable isotope compositions. A Wilcoxon rank-sum 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.

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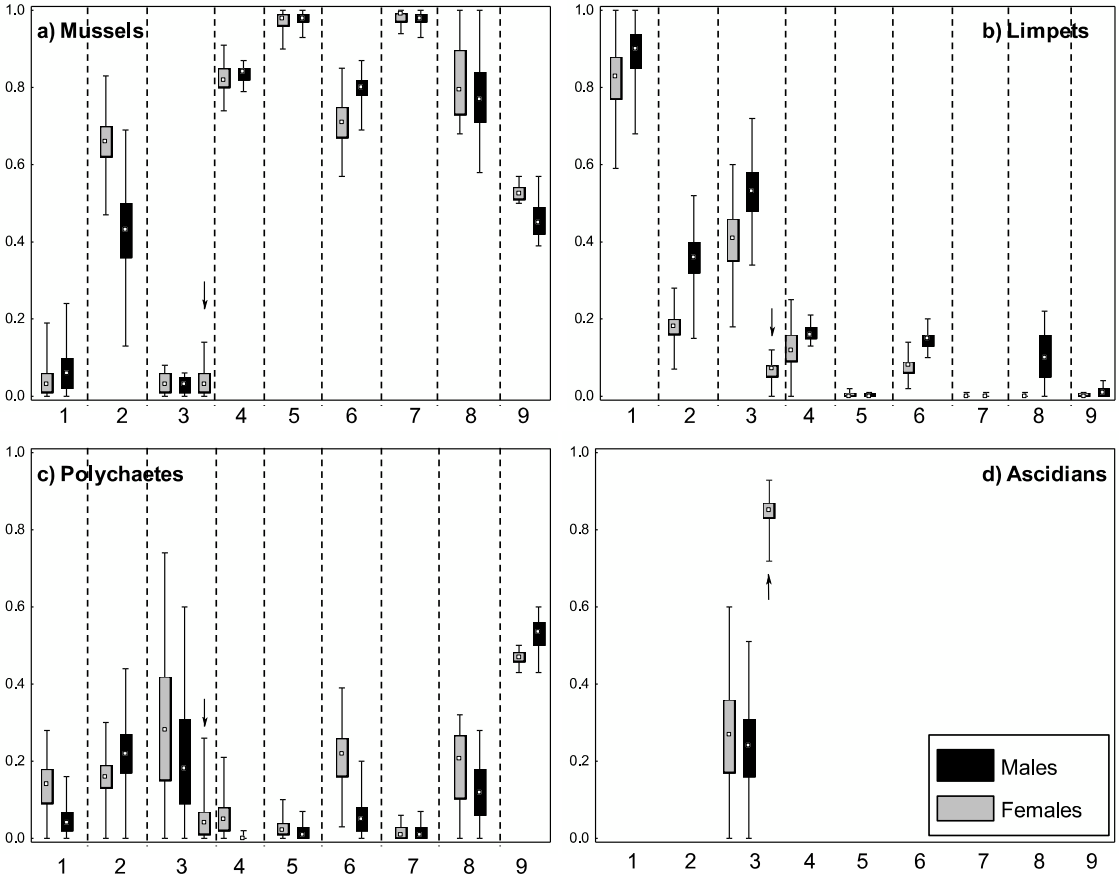

Fig. 6 Relative Contribution of a) mussels, b) limpets, c) polychaetes and d) ascidians to the diet of male and female oystercatchers at the 9 study sites (as coded from east to west in Fig. 1), estimated from IsoSources. Boxes represent interquartile ranges and white squares within represent median values. Whiskers represent ranges of feasible contributions. The arrows indicate contributions estimated individually for the female with contrasting stable isotope signatures sampled at Port Elizabeth (see Fig. 5).

Annexe 7

LETTERS

SOPHIE KOHLER

SCRAMBLING EGG

This image was taken on the morning of 26 January 2010 at Keurbooms River, in the Western Cape. A CapeNature ranger, Petrus, and I were monitoring African Black Oystercatchers at the Keurbooms River Nature Reserve, where these birds breed within a large Kelp Gull colony. As we were walking forward, looking for nests and chicks, we noticed that the gulls and oystercatchers were very agitated. A pair of oystercatchers were clearly in conflict with the gulls and I observed one of them pick up something in the grass and fly off with it.

As it did so, I managed to take an opportunistic photograph of it, but it was only once I enlarged the image that I saw that the oystercatcher had in fact flown off with an egg. The bird that removed the egg returned to its mate in less than 20 seconds. We think that one of the gulls may have stolen the egg and the oystercatcher reclaimed it and took it back its nest. Petrus, who had previously monitored this nest, believed that it lay in the direction the bird flew while carrying the egg.

As we had already caused considerable disturbance in the area, we decided to leave and did not check that particular nest. From the photograph it seems as though the bird's top mandible is inserted in the egg; maybe it had been damaged by the gulls or perhaps the chick was hatching.

SOPHIE KOHLER
RHODES UNIVERSITY
GRAHAMSTOWN, EASTERN CAPE

Professor Phil Hockey comments: The egg the bird is carrying is definitely an oystercatcher egg and not a Kelp Gull egg, and there is no doubt that this is extremely unusual behaviour. In 30 years of watching oystercatchers I have never seen one carry an egg, although they do sometimes move eggs along the ground if, for example, they become dislodged from the nest.

One or both mandibles (the bill looks closed) must have punctured the shell; in any case, if the egg had been stolen by a gull, it would probably already have been punctured/fractured. Alternatively, as the observer suggests, the egg may have been in the process of hatching and was already 'pipped'.

The most likely prompt for such behaviour is that the egg was about to hatch. Chicks call from within the egg for a few days before hatching and this strengthens the adults' 'attachment' to the egg. The desire to protect eggs increases with the age of the egg, because every additional day of incubation heightens the investment that the pair has made in that reproductive attempt.

Egg-carrying behaviour is rare among birds – it's documented in ducks and (bizarrely) Peregrines and nightjars. Some questionable evidence exists for it in quails, coucals and jacanas.

RESUME : La distribution d'espèces benthiques intertidales est contrainte par l'océanographie côtière. On connaît moins les effets sur l'écologie des prédateurs. Les côtes sud de l'Afrique sont caractérisées par des contrastes de production primaire et d'assemblages intertidaux dus aux deux courants majeurs qui les longent. Le prédateur apical de ces côtes est un oiseau limicole endémique, l'huîtrier noir africain (*Haematopus moquini*), qui présente un polymorphisme favorable à la spécialisation alimentaire. Ces travaux ont étudié l'effet des variations spatiales de structure de communautés benthiques sur l'écologie alimentaire de l'huîtrier à l'aide des isotopes stables. Les oiseaux répondent aux fluctuations qualitative et quantitative des communautés de proies à plusieurs échelles. A large échelle ils montrent de forts contrastes entre les côtes ouest et sud-ouest où le régime alimentaire est dominé par les moules, notamment l'espèce invasive *Mytilus galloprovincialis* et le sud-est où un mélange de moules et patelles est consommé. Localement les individus montrent des différences faibles d'alimentation liées à l'abondance relative des moules et patelles. Cela s'explique par le caractère généraliste de l'espèce et le relâchement de compétition intra-spécifique pour les ressources. La transition alimentaire d'*H. moquini* vers une consommation quasi-exclusive à l'ouest d'une moule introduite et la multitude de comportements alimentaires ailleurs indiquent un fort potentiel d'adaptation aux modifications de son habitat d'alimentation. En revanche la dégradation des plages par l'Homme augmente la compétition pour l'espace et affecterait aujourd'hui le succès reproducteur de l'espèce.

MOTS-CLEF : Afrique du Sud, Benguela, Courant des Aiguilles, Estrans rocheux, Huîtrier, Limicoles, Ecologie trophique, Invasion biologique, Isotopes stables

ABSTRACT: The distribution of intertidal benthic species is constrained by coastal oceanography. Less is known about the effects on the ecology of predators. Along the southern coasts of Africa the two main currents constraint both the patterns of primary production and the structure of benthic communities. The top predator on these coasts is an endemic shorebird, the African Black Oystercatcher (*Haematopus moquini*), which exhibits a polymorphism favourable for food specialization. This study investigates the effect of spatial variations in benthic community structure on the feeding ecology of oystercatchers using stable isotopes. Birds respond to changes in quality and quantity of prey at multiple scales. At large scale they show strong contrasts between west and southwest coasts where the diet is dominated by mussels, including the invasive species *Mytilus galloprovincialis*, and south-east shores where a mixture of mussels and limpets is consumed. Locally individuals show weak dietary differences related to relative abundances of mussels and limpets. This reflects the generalist foraging behaviour of the species and the release of intra-specific competition for resources. The dietary shift of *H. moquini* on the west coast toward the invasive mussel and the multiplicity of foraging behaviours elsewhere reveal strong capacities to face changes in its foraging habitat. On the other hand the degradation of beaches by humans increases the competition for space and today affects the reproductive success of the species.

KEY WORDS: Southern Africa, Benguela, Agulhas, Rocky shores, Oystercatcher, Shorebirds, Trophic ecology, Biological invasion, Stable isotopes