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UNIVERSITY OF GHANA

COLLEGE OF BASIC AND APPLIED SCIENCES

SCHOOL OF BIOLOGICAL SCIENCES

# FORAGING ECOLOGY OF SANDERLING *CALIDRIS ALBA* ON THE WESTERN COAST OF GHANA

BY

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THIS THESIS IS SUBMITTED TO THE SCHOOL OF GRADUATE STUDIES IN PARTIAL FULFILLMENT OF THE REQUIREMENT FOR THE AWARD OF DOCTOR OF PHILOSOPHY DEGREE IN BIODIVERSITY AND CONSERVATION SCIENCE

DEPARTMENT OF ANIMAL BIOLOGY AND CONSERVATION SCIENCE

DECEMBER 2018

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# DECLARATION

I hereby declare that this thesis and the work presented in it are entirely my own and have been produced by me as the result of research work undertaken under supervision.

I certify that to the best of my knowledge, this thesis has neither been presented wholly nor partially to any other University for a degree. With the exception of other peoples' work that have been duly referenced and any help received acknowledged accordingly, I confirm that this work contains no material previously published or written by another person.

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# ABSTRACT

Migration is an important process in the annual cycle of shorebirds that enables them to escape unfavourable conditions at certain times of the year and provides them opportunity to breed in one area and spend the non-breeding season in other latitudes. The selection of a suitable non-breeding habitat by migrants is dependent on a number of factors which define the quality of the habitat, namely: levels of disturbances, predatory risk, suitable environmental and climatic conditions such as depth and temperature of water, abundance and availability of food. The Esiama beach on the Ghana coast is important for sanderlings of the East Atlantic Flyway during the non-breeding season, supporting 40-70% of all sanderlings along the Ghana coast. The overall aim of this study was to investigate and document the foraging ecology of sanderlings on the western coast of Ghana; and using the species as a model, describe and assess the quality of Esiama beach as a suitable and preferred non-breeding site for sanderlings in Ghana. Specifically, this study sought to measure the variations in the distribution, availability and quality of benthic macroinvertebrates as prey for sanderlings and assess the spatio-temporal variation in the distribution of sanderlings in relation to food availability. The study also focused on describing foraging behaviour and strategies employed by sanderlings, determine prey preference and evaluate the impact of human disturbances and other pressures on the foraging behaviour of sanderlings. Data for this study were obtained through direct field observations of foraging birds, benthic macroinvertebrate sampling, mist netting, faecal collection; laboratory analysis of macroinvertebrates and estimation of biomass; as well as experiments to determine intake rates and prey preference of captive sanderlings. A total of 62,000 macroinvertebrates belonging to four Phyla: Mollusca (*Donax pulchellus*, *D. rugosus*, *Hastula aciculina* and *Agaronia acuminata*), Arthropoda/ Crustacea (*Excirolana chiltoni*, *Emerita talpoida*, Mysid shrimp), Annelida (*Glycera* spp., *Nereis* sp.) and Nemertea were recorded in benthic samples. *Donax pulchellus*, *E. chiltoni* and *Glycera*

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spp. constituted 91.66%, 6.45% and 1.40% respectively of all individuals in benthic samples. About 95.0% of all macroinvertebrates in benthic samples were present in the top 3 cm depth and therefore were considered available to sanderlings. About 99.18% of all *D. pulchellus* individuals were available to sanderlings. About 99.68% of all available macroinvertebrates were distributed within the low- and inter-tidal zones and was dominated by *D. pulchellus*. *Excirolona chiltoni* was the most abundant prey within the high tide zone. The diet of sanderlings from the analysis of faecal samples was made up of bivalves, gastropods, polychaetes, isopods and fish. *Donax pulchellus* was the most abundant prey found in droppings of sanderlings, occurring in about 78.0% of all faecal samples and constituted of 79.0% of the total number of prey items found in faecal samples. The mean length, biomass and quality of *D. pulchellus* were 6.9 ± 1.7 mm, 1.42 ± 0.04 mg $AFDM_{flesh}$ and 1.04 kJ/ g and for *E. chiltoni* 5.2 ± 1.4 mm, 1.44 ± 0.06 mg $AFDM_{flesh}$ and 7.75 kJ/g. There were two recruitment periods for *D. pulchellus*; between July – October and January – March. Peak densities of *D. pulchellus* occurred in August – October and January – March, which explained the occurrence of high numbers of sanderlings along the beach, coinciding with the autumn and spring migrations respectively. Spatially, densities of *D. pulchellus* declined towards the estuaries ($p < 0.001$) with mean densities up to 15,509 individuals/ $m^2$ whiles densities of *E. chiltoni* increased towards the Ankobra estuary ($p < 0.001$) with mean densities up to 960 individuals/ $m^2$. The spatial distribution of sanderlings was explained by the densities of *D. pulchellus* ($p < 0.001$), but not *E. chiltoni* ($p = 0.91$). Sanderlings spent 60.45%, 36.93%, 1.15% and 1.48% of the 12-hour day time foraging, resting, in locomotion and engaged in comfort activities respectively. The time-activity budgets of sanderlings could be explained by the tidal cycle, diurnal time, number of sanderlings on the beach and density of prey. For example, more sanderlings foraged between 0600 – 0900 GMT and 1500 – 1700 GMT which coincided with 2 hours before and after high tide. Such observation suggests that

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sanderlings take an optimal course of foraging action, maximizing foraging opportunities presented by tidal action. Three foraging methods were described for sanderlings in exploiting their prey: pecking, probing and sewing. Pecking was a visual foraging method whereas probing and sewing were tactile methods. Sanderlings in captivity were also observed to use sewing methods to search for the appropriate prey size. Foraging rates of sanderlings varied with prey densities and sanderling numbers. For example, sanderlings pecked more when density of prey was high (25.24 ± 19.29 pecks/min) than when prey densities was lower (15.19 ± 13.74 pecks/min; $p < 0.0001$), and also when sanderlings were abundant on the beach (25.04 ± 19.01 pecks/min) than when there were fewer sanderlings (17.66 ± 16.16 pecks/min; $p < 0.0001$). Sanderlings also spent more time probing when bird numbers were high (9.80 ± 12.74 s/min) than when they were low (6.23 ± 8.19 s/min). Foraging rates of sanderlings increased with flock size below 28 individuals ($p < 0.0001$), beyond this threshold, foraging rates declined ($p = 0.04$). Due to competition for limited resource. Foraging rates of sanderlings also increased with nearest neighbour distance for conspecifics foraging in flock size greater than 28 individuals. Highest foraging rates were observed for sanderlings immediately upon arrival on the beach and peak sanderling count periods. The variation in foraging rates could be explained by competition for food in line with actual or apparent decline of prey densities. There was no significant difference in foraging rates in the field (23.68 ± 18.54 pecks/min) and in captivity (25.13 ± 14.03 pecks/min; $W = 3810$, $p = 0.37$). The intake rate of *D. pulchellus* by sanderlings in captivity was 1.61 ± 0.73 individuals/ min but varied between small size (1.61 ± 1.03 individuals/min) and medium size (0.44 ± 0.36 individuals/min). The estimated biomass of prey consumed in a 12-hour period from faecal samples were: *D. pulchellus* (0.72 ± 0.62 g AFDM), *E. chiltoni* (0.49 ± 0.42 g AFDM) and *Glycera* spp. (0.36 ± 0.26 g AFDM) making a total of 1.57 ± 0.96 g AFDM. The biomass of *E. chiltoni* was likely to be underestimated due to the time of faecal collection. Therefore,

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using estimates of intake rates of isopods from literature, a value of 7.34 g AFDM was estimated as the total biomass consumed in a 12-hour period. Sanderlings showed preference for *E. chiltoni* to *D. pulchellus* ($p = 0.01$). Between small and medium size *D. pulchellus*, sanderlings preferred the former ($p < 0.001$). Several disturbance activities were observed along the beach: human related activities (74.0%); predators such as yellow-billed kite *Milvus migrans parasitus* (13.0%) and dogs (6.0%); scavengers (5.0%) and engine-driven machines (2.0%). Out of the proportion of human-related disturbances, fishing activities, passers-by, shellfish harvesting and recreational activities accounted for 45.0%, 37.0%, 14.0% and 4% respectively of the observed activities. The mean encounter rate of fishing activity was 0.5±0.3 activity/km with an average human density of 21±11 individuals/activity. The spatial distribution of sanderlings was related to distribution of *D. pulchellus* ($p < 0.05$), human densities ($p < 0.001$) but not *E. chiltoni* ($p = 0.6$). The impact of the disturbances along the beach by sanderlings was determined using the Minimal Approach Distance (MAD) method. Sanderlings could tolerate approaching humans up to a distance of 25.51±10.03 m and kites up to a height of 11.93 ± 6.29 m beyond which they showed signs of being disturbed. Multiple linear regression of all possible factors indicated that the MAD for sanderlings to humans depended on flock size and width of the beach for foraging sanderlings ($R^2 = 0.27$, df=5, $p = 0.0002$). The findings of this study provide additional information on the foraging ecology of sanderlings along the Esiama beach, describe the quality of the Esiama beach as a habitat for sanderlings and make a case for protection of the Esiama beach and associated Amansuri wetlands as a Ramsar site (i.e. an internationally important wetland).

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# DEDICATION

I dedicate this work to my future leaders; Dedilord, Beishia, Lorisabel, Treasure, Drusilla and the very special Jessie. Please make sure you surpass this hallmark. I believe in you.

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# ACKNOWLEDGEMENT

I am most grateful to the Almighty God for how far He has brought me.

I will like to appreciate my supervisory committee for the wonderful work done. Especially to Prof. Yaa Ntiamoa-Baidu, who aside being my Principal, was more of a mother to me. The enormous knowledge and skills obtained from my co-supervisors cannot go unmentioned.

A lot of work and training went into this study and I will like to appreciate all the folks at the Netherlands Institute for Sea Research (NIOZ) for the pep talks and advices that helped in shaping this study. Most importantly, Thomas Oudman for all the help with the R software. To Roeland, Tim, Piet and Michelle, I say a big ‘thank you’. I appreciate the support of all members of the International Wader Study Group. A special appreciation goes to Jeroen Reneerkens, Prof. Francis Gbogbo, Dr. Fred Aboagye, Dr. Maxwell Billah, Dr. Ben Ofori and Mr. Yahaya Musah for all the critiquing and wonderful suggestion offered me.

To my colleagues at the Centre for African Wetlands, I say a big thank you. A special one to Dr. Kofi Amponsah-Mensah and Emmanuel Taye for the healthy talks and ideas shared on the corridors during the hot afternoons. To Hannah, you are the best. Words cannot express how much I appreciate Mr. Alfred Ali Nuoh for the wonderful assistance in the field. Mr William Tetteh and Mr Joseph Sassah, may God bless you.

I acknowledge the financial support received from the University of Ghana-Carnegie Corporation of New York Next Generation of Academics in Africa Project.

To my parents Mr & Mrs Quartey, Joel, Judy, Bro Charles, David, Gloria and the entire family, I really appreciate your support. Finally, to my best friend, Belinda, I could not have done this without you. Hard work and patience pay, but for your intercessory prayers, I owe you big time.

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# LIST OF ABBREVIATIONS

| | | |
|---|---|---|
| a | - | Assimilation Efficiency |
| AFDM | - | Ash Free Dry Mass |
| AFDW | - | Ash Free Dry Weight |
| AIC | - | Akaike Information Criterion |
| AM | - | Ash Mass |
| BMR | - | Basal Metabolic Rate |
| CM | - | Contingency Model |
| cm | - | Centimeter |
| d | - | Energy density |
| DEE | - | Daily Energy Expenditure |
| df | - | Degree of Freedom |
| DM | - | Dry Mass |
| DRM | - | Digestive Rate Model |
| e | - | Energy content |
| EAF | - | East Atlantic Flyway |
| ECBAS | - | Ethics Committee for Basic and Applied Sciences |
| EURING | - | European Union for Bird Ringing |
| g | - | Gram |
| GRS | - | Ghana Ringing Scheme |
| h | - | Handling time |
| ind | - | Individual |
| IUCN | - | International Union of Conservation of Nature |
| IWSG | - | International Wader Study Group |

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| | | |
|---|---|---|
| k | - | Shell Mass |
| kJ | - | Kilojoule |
| km | - | Kilometer |
| m | - | Meter |
| MAD | - | Minimal Approach Distance |
| mg | - | Milligram |
| mm | - | Millimeter |
| n | - | Number of samples |
| NEI | - | Net Energy Intake |
| PHC | - | Population and Housing Census |
| Q | - | Prey Quality |
| SD | - | Standard Deviation |
| WD | - | Wildlife Division |

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# CHAPTER ONE

# INTRODUCTION

## 1.1 Background Information

Migration is an important process in the annual cycle of shorebirds that enables them to escape unfavourable conditions at certain times of the year and provides them opportunity to breed in one area and spend the non-breeding season in other latitudes (Møller *et al.*, 2010)**.** Changing climatic conditions at a given location give rise to seasonal variations, which stimulate migration in different species of animals. The timing of migration is important for species because an early or late arrival on either wintering or breeding sites may have consequential impact on species survival and fitness (Møller *et al.*, 2010).

Migrant birds embark on annual migration exploiting different conditions across relatively short or long distances. Shorebird migration is an interesting phenomenon, where different species of shorebirds move from one place (usually breeding sites) to another (non-breeding sites) on a regular annual basis with varying degrees of site fidelity. However, some individuals within the same population may decide to skip migration if they do not meet the required conditions. For example, some first year birds may either delay or skip migration back to their breeding grounds, because they have not stored enough fat to provide adequate energy needed for a successful journey (Summers *et al.*, 1995; Hockey *et al.*, 1998; Reneerkens *et al.*, 2009a). Other individuals may attempt the process but may not be successful due to a number of reasons which include inexperience on the part of some individuals mostly juveniles and stress from either reproduction or survival strategies on non-breeding grounds.

Migrant birds may select habitats for staging and non-breeding purposes based on a number

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of factors. Staging sites are essential when species are embarking on long distant migration and need to refuel, because the amount of stored fat they possess cannot support their energy requirement for a non-stop flight. Some staging sites may double as non-breeding sites for individuals of the same population. For example, during southern autumn migration, some individual sanderlings of the East Atlantic Flyway population use the sandy beaches of the Wadden Sea as a wintering site and use the nearby intertidal mudflats for migratory fuelling. Other individuals may only use the intertidal mudflats in replenishing lost energy and continue migrating further south (Loonstra *et al.*, 2016). Ghana's coast also serve as a stopover site for sanderlings possibly migrating to the Walvis Bay in Namibia (Reneerkens *et al.*, 2009a).

The selection of a suitable non-breeding site may depend on the quality of the habitat measured by levels of disturbances, predatory risk, suitable environmental and climatic conditions such as depth and temperature of water, abundance and availability of food (Yates *et al.*, 2000; Piersma, 2012). There has always been a strong correlation between densities of prey and occurrence of shorebirds both on a macro- and/or microhabitat scale (Piersma *et al.*, 1995; van Gils *et al.*, 2006). That is to say, shorebirds are attracted to areas rich in food. This is because staging areas are purposely meant for replenishing lost energy. However, non-breeding sites go beyond that by offering shorebirds the necessary support and favourable conditions during the non-breeding season.

Some habitats have been observed to support high densities of food which serve as prey for shorebirds. However, such habitats may even be regarded as 'poor' in quality because of a number of factors which do not encourage shorebirds to inhabit such areas (van Gils *et al.*, 2006). A number of studies have shown that foraging efficiency of shorebirds reduces in the presence of other competitors, high predation risk and when the energy cost involved in predator avoidance is more than the energy obtained from food (Goss-Custard, 1977; Ens & Goss-Custard, 1984; Dolman, 1995; Stillman *et al.*, 1997; Yates *et al.*, 2000). In such

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instances, shorebirds may be forced to desert such habitats.

Furthermore, most habitats exploited by shorebirds are also depended on by humans for a number of reasons. Such wetlands support the livelihoods of surrounding communities (Ntiamoa-Baidu, 1991a; van Roomen *et al.*, 2014; van Roomen *et al.*, 2015). Increasing human population and infrastructural development have impacted on the ecological processes of these habitats. Recreational facilities along coastal beaches have attracted large number of people into using the beaches at different times. Other pressures along shorebird habitats may either be mere disturbances, for example shellfish harvesting and fishing, or as threats, for example hunting, to shorebirds (van Roomen *et al.*, 2015). In addition to the threats that directly influence mortality rate of shorebirds, the other forms of pressures may indirectly produce a similar fate. The influx of people together with their various activities on shorebird habitats influence the behaviour of foraging shorebirds and ultimately affect the amount of energy obtained through foraging (Thomas *et al.*, 2003).

Shorebirds spend a greater portion of their time on non-breeding grounds foraging (Castro *et al.*, 1992; Grond *et al.*, 2015). Different species of shorebirds employ different strategies in obtaining prey in time and space. Shorebirds portray different behaviours towards disturbances and approaching threats whilst foraging. In addition to these, shorebirds may resolve to ecological adaptations to increase their chances of foraging (Burger & Gochfeld, 1991b; Thomas *et al.*, 2003). Most of these constraints, if not all, have negative impacts on energy budgets of foraging birds.

The Ghana coast has been observed as an important non-breeding and staging area for different species of migrant shorebirds of the East Atlantic Flyway (Ntiamoa-Baidu, 1991b; Gordon, 1995; Ntiamoa-Baidu *et al.*, 1998; Ntiamoa-Baidu *et al.*, 2000; Ryan & Ntiamoa-Baidu, 2000; Ntiamoa-Baidu *et al.*, 2001; Ntiamoa-Baidu *et al.*, 2014a). The entire 550

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kilometre stretch of Ghana coast is known to harbour different species of waterbirds, and certain habitats support internationally important populations of some species, for example the sanderling *Calidris alba*. Migrant birds arrive in Ghana in August, population peaks in September/October, with a decline in November/December as a result of southern migration of a proportion of observed birds which uses the Ghana coast as a stopover site. Prior to the final departure of shorebirds to their breeding grounds in April/May, there may be another peak between January and March during the northern spring migration (Ntiamoa-Baidu & Hepburn, 1988; Ntiamoa-Baidu, 1991b; Reneerkens *et al.*, 2009a; Ntiamoa-Baidu *et al.*, 2014a).

The earlier counts of shorebirds led to the designation of five of several coastal wetlands in Ghana as Ramsar sites and as such received the necessary protection. More than 70 species of waterbirds (including waders, ducks, terns and herons) were recorded along Ghana's coast (Ntiamoa-Baidu, 1991b; Gordon, 1995). Out of this number, 15 wader and tern species were recorded in internationally significant numbers; greenshank *Tringa nebularia*, black-tailed godwit *Limosa limosa*, pied avocet *Recurvirostra avosetta*, spotted redshank *Tringa erythropus*, ringed plovers *Charadrius hiaticula*, sanderling *Calidris alba*, little stint *Calidris minuta*, black-winged stilt *Himantopus himantopus*, roseate tern *Sterna dougallii*, royal tern *Thalasseus maximus*, little tern *Sternula albifrons* amongst others (Ntiamoa-Baidu, 1991b; Ntiamoa-Baidu *et al.*, 2014a). Over the years, population dynamics of the different species have shown declining, stable and increasing population trends. One of such species observed to be increasing in numbers is the sanderling (Ntiamoa-Baidu *et al.*, 2014a; Ntiamoa-Baidu *et al.*, 2015).

The sanderling is a long distant migrant which breeds in the coldest part of the world and spends the non-breeding season in the temperate and tropical regions (Reneerkens *et al.*, 2009a). Sanderlings are generalists whose diet on the non-breeding grounds include

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crustaceans, polychaetes, bivalves, insects and annelids (Myers *et al.*, 1980; Akiyama, 2000; Petracci, 2002; Nuka *et al.*, 2005; Reneerkens *et al.*, 2009a; Grond *et al.*, 2015; Loonstra *et al.*, 2016). Other records of sanderling diet include seeds, plant buds, algae and mosses (Richards, 1988). Sanderlings have been observed to even act as scavengers of remains of prey of other waterbirds (Petracci, 2002). However, in Ghana, the main prey of sanderling is the surf clam or bivalve *Donax pulchellus*, which constitutes about 90% of invertebrates, found in benthic samples (Ntiamoa-Baidu *et al.*, 2014b; Grond *et al.*, 2015).

The most important non-breeding site for sanderlings in Ghana is a 13 kilometre sandy beach between the Ankobra and Amansuri estuaries (hereafter known as Esiama beach). The temporal variation of *D. pulchellus* along the Esiama beach correlates with the seasonal pattern of occurrence of sanderlings the in Ghana (Ntiamoa-Baidu *et al.*, 2014b). However, relying on just the abundance of *D. pulchellus* as a measure of the carrying capacity of Esiama beach as a suitable habitat for sanderlings may not be enough when the availability, accessibility and quality of this prey have not been determined (van Gils *et al.*, 2003a; van Gils *et al.*, 2005a). Nonetheless, Ntiamoa-Baidu *et al.* (2014a) observed that, despite the fact that sanderling numbers along the Esiama beach increase with increasing numbers along the Ghana coast, there is a possible movement of individuals between sites. In other words, sanderlings are likely to move from higher quality sites onto poorer ones, implying that, either the Esiama beach has simply reached its carrying capacity or there are possible changes in the habitat condition of the beach.

Sanderling studies in Ghana have been intensified over the past two decades with some demography studies through a colour-ringing scheme. Regular monitoring of uniquely colour marked individuals has shown some level of site fidelity by sanderlings (Ntiamoa-Baidu, unpubl) and movement in between sites. The presence of colour-marked sanderlings provides an opportunity to carry out several ecological studies at the individual level. High densities of

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food may explain the reason behind Esiama beach being a preferred habitat for sanderlings.

## 1.2 Justification

Biodiversity is being lost at an alarming rate (Asafu-Adjaye, 2003). Anthropogenic influences have always been implicated in the destruction and reduction of habitat quality (Naughton-Treves *et al.*, 2005). Recently, climate change has added another twist to this observation, accelerating the rate at which habitats and biodiversity are being lost. Migrant birds also stand a greater risk of this annihilation process. Climate change has been observed to influence prey distribution and availability and this has altered the migration pattern and ranges of certain populations of migrant birds (Jenni & Kéry, 2003; Gordo, 2007; Miller-Rushing *et al.*, 2008; Visser *et al.*, 2009; Møller *et al.*, 2010). A migrant's decision to migrate to and from a particular site is rather more complex than it seems to be. Nevertheless, the decision to select a particular habitat as a preferred one and desert another due to its 'poor' state depends on knowledge of the migratory birds about the relative quality of all available sites, cost-benefit analysis of the resources available and how to exploit such resources. For non-breeding birds, food is the most important resource and any other factor that hinders the exploitation of this resource may be identified as disturbance.

Ecological studies are important in providing basic but relevant information on species interactions with their environment, the interdependency of humans on their environment and the consequences of human activities on the environment. Failure to understand ecological processes today, will eventually affect how ecosystems work and may affect species associations and assemblages. Therefore, in order to monitor and provide timely management practices for different ecosystems, the use of different species or groups of species as bio-indicators of their immediate environments is very necessary. The presence, absence and

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population dynamics of bio-indicator species could provide a rapid assessment of the ecological health of their habitat (Parmar *et al.*, 2016). In addition to serving as bio-indicators of the environment at the local scale, migratory birds provide connections between different latitudes and reflect the status and trends affecting a wider biodiversity. For example, the reproductive success of American redstarts *Setophaga ruticilla* on their temperate breeding grounds is limited by the quality of their tropical non-breeding habitats (Norris *et al.*, 2004).

Sanderling studies are not just limited to the Ghana coast, rather it involves a consortium of researchers studying the ecology of this bird on different latitudes. Recognized locations of sanderlings studies along the East-Atlantic Flyway include Zachenburg in Greenland, Wadden Sea in the Netherlands, Banc d'Arguin in Mauritania, Esiama in Ghana and Walvis Bay in Namibia. Other important areas are found in Iceland, France and Portugal. As part of the ecological studies carried out by this consortium of researchers include capturing, colour-marking and re-sighting of colour marked individuals to monitor the migration patterns of individual sanderlings and the population as a whole. Re-sightings also provide historical records of marked individuals for demographic and survival analysis studies (Reneerkens *et al.*, 2009a). These sort of studies enables us to get data on the importance of migration of birds as sentinels of the environment. For example, part of the history of the sanderling R3GWYR shows that, this bird was first captured and ringed in Ghana on 7th March, 2008 on the Esiama beach. It was observed in Norway on 11th August, 2009 during the autumn migration and having travelled a minimum distance of 6000 km in five days was re-sighted in Ghana again on 16th August, 2009 (Smeets, 2010; Ntiamoa-Baidu, unpubl.). Such information is key in supporting the assumption that long-distance movements of migrating animals can enhance geographic spread of pathogens amongst wild animals including that which are of zoonotic importance and of public health concern e.g. West Nile virus, avian influenza viruses and multiple endoparasitic worms in waterfowls (Altizer *et al.*, 2011).

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The long distance migration of this rather small bird is highly dependent on energy. Feeding contributes to the changes in prey distribution and as such there is a need to assess variation in prey densities so as to provide information of reliable sources of prey and biomass contribution of such prey. Non-breeding shorebirds spend most of their time foraging in order to support daily energetic budgets and have adequate storage of fat and protein for migration (Lindström & Piersma, 1993). The proportion of time migrants spend foraging on non-breeding grounds may basically be explained by the abundance, availability, searching and handling time of prey (van Gils, 2004). However, some studies have shown that other factors such as the quality of prey and anti-predatory strategies of prey, predation risk and human disturbances influence foraging time of shorebirds (Yates *et al.*, 2000; Piersma *et al.*, 2003; Thomas *et al.*, 2003; van Gils *et al.*, 2003a; van Gils *et al.*, 2005a). There are fewer studies in Ghana that have investigated the effect of such parameters on the foraging behaviour and ecology of shorebirds (Gbogbo *et al.*, 2008; Grond *et al.*, 2015).

Ghana's coast support between 3-4% the 1990s EAF sanderling population estimated at 123,000 individuals between September and October during autumn migration (Reneerkens *et al.*, 2009a; Ntiamoa-Baidu *et al.*, 2014a). More than two-thirds of 'Ghanaian sanderlings' exploit resources along the Esiama beach. Studies have shown that, the most important prey for sanderlings along the Esiama beach is *Donax pulchellus* (Ntiamoa-Baidu *et al.*, 2014a; Grond *et al.*, 2015). It is important to monitor the distribution, abundance and availability of *D. pulchellus* on a regular basis in relation to population dynamics of sanderlings, and observe how sanderlings obtain food in time and space. Such observations will help provide understanding on the energy acquisition and expenditure of non-breeding sanderlings and their success to migration. Such observations can also provide an indication of the ecological state of the Esiama beach on a yearly basis and allow for comparison and timely intervention in case of deterioration.

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The Esiama beach, despite its importance to sanderling population in Ghana, is an unprotected wetland. The continuous re-sightings of colour-marked sanderlings on the Esiama beach give an indication of side fidelity (Ntiamoa-Baidu & Hepburn, 1988; Ntiamoa-Baidu, 1991b; Reneerkens *et al.*, 2009a; Reneerkens *et al.*, 2009b; Ntiamoa-Baidu *et al.*, 2014a). In going forward, there is a need to protect the Esiama beach which will enhance the conservation of sanderlings and the ecological integrity of the beach. Meanwhile it is important to study the ecology of sanderlings along the beach to provide a better understanding of factors that influence the selection of this beach by sanderlings. Information from such studies will assist in developing management practices for the beach and sanderlings to ensure a proper habitat-species conservation.

Foraging is an important activity of birds on non-breeding grounds. It is therefore ideal to do an in-depth study on the foraging ecology of sanderlings. It is crucial to analyse food distribution and availability and how sanderlings exploit this resource in time and space. The quality of food, is an integral factor in explaining constraints to foragers, which may help us understand the choices and decisions of sanderlings. It is of the view that sanderlings, like most shorebirds, are likely to prefer foraging on high quality prey, which enhances and supports their energy needs. However, for a mollusc-eating bird like the sanderling, it can be expected that the species will face digestive constraints from shells when feeding. How sanderlings manage to overcome this constraint along the Esiama beach is unknown. Whether sanderlings chose between different prey types and sizes as an efficient and effective way of obtaining energy remains a hypothesis yet to be tested. Such information will provide a better understanding to the success story of non-breeding sanderlings in Ghana.

Global human population increase especially in coastal areas has caused widespread influxes of humans and human-related activities along coastal beaches and wetlands, which provide refuge for shorebirds at different times of the year. For an unprotected wetland like the Esiama

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beach, it is expected that disturbances caused by humans and human-related activities will be much higher than that of protected areas. With time, these disturbances may exceed a threshold which may lower the quality of the habitat and influence the distribution of shorebirds. It is therefore important to investigate how disturbances affect the foraging ecology and behaviour of sanderlings and how sanderlings accommodate these disturbances. As a model species, such information will be key in managing similar shorebird species, e.g. curlew sandpiper, ringed plover and little stint, and sites in Ghana.

## 1.3 General Objective

To investigate and document the foraging ecology of sanderlings on the western coast of Ghana; and using the species as a model, describe and assess the quality of Esiama beach as a suitable and preferred non-breeding site for sanderlings in Ghana.

### 1.3.1 Specific Objectives

i. To measure the variation in the distribution, availability and quality of benthic macroinvertebrates as prey for sanderlings.

ii. To assess the spatio-temporal variation in the distribution of sanderlings in relation to food availability.

iii. To describe and measure when, where and how non-breeding sanderlings forage; a functional and aggregate response to prey and predator densities.

iv. To determine prey type and size preference of non-breeding sanderlings.

v. To determine and evaluate the impact of human disturbances and other pressures on the foraging behaviour of sanderlings.

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## 1.4 Research Questions

i. What possible prey items are available for sanderlings?
ii. Does prey distribution influence that of sanderlings?
iii. When, where and how do sanderlings forage?
iv. How much biomass do sanderlings obtain from available prey?
v. Which prey species is preferred by sanderlings?
vi. What pressures exist on the Esiama beach?
vii. What impact do these pressures have on foraging activity of sanderlings?

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# CHAPTER TWO

# LITERATURE REVIEW

## 2.1 Wetlands as habitats for waterbirds

Wetlands are “areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters” (Ramsar Convention, 1971). Wetlands are productive ecosystems, which provide different services that include the provision of refuge for waterbirds. The varying diversities of waterbirds in this ecosystem make them good bio-indicators of the health and value of wetlands (Rose & Scott, 1997). The ecological importance of wetlands to waterbirds has generated research interests all over the world, and the findings been used in education and management of this important ecosystem.

The status of a wetland, according to the Convention on Wetlands of International Importance especially as Waterfowl Habitat (Ramsar, 1971), has over the years helped in the conservation of both the habitats and their biological diversity. Despite the fact that there are four different criteria on which the evaluation of a wetland is based on, according to the Ramsar Convention, only two of these are objective and provide quantitative support to the argument. These are criteria (3a) which states that a wetland should support at least 20,000 waterfowls at any one time and criteria (3c) which requires a wetland to supports 1% of individuals of a migratory waterfowl flyway population (Rose & Scott, 1997). Wetlands that qualify under any of these two criteria, as well as any of the other criteria, may be classified as a wetland of international importance that may be designated as a Ramsar site.

The coastlines of many countries serve as important hubs for shorebirds (van Roomen *et al.*, 2014; van Roomen *et al.*, 2015). The varying habitat types; estuaries, open and closed lagoons,

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harbours, mud and sand flats as well as sandy beaches, remain important habitats for both migrant and resident birds. Studies have shown that the phenomenon of migration ensures that the coasts, and occasionally, inland wetlands harbour small to large populations of waterbirds at different times of the year. A typical example is the western coast of Africa, which is an important non-breeding ground for migrant shorebirds of the East Atlantic Flyway (EAF) during the northern autumn migration (Wetlands International, 2012; van Roomen *et al.*, 2015).

Furthermore, there is a clear indication of temporal and spatial habitat preferences by shorebirds. For example, Sagar *et al.* (1999) observed that depending on the time of year, some estuaries in New Zealand were inhabited by up to 50% of the populations of migrant species such as the bar-tailed godwit *Limosa lapponica* and red knot *Calidris canutus,* as well as up to 85% of resident shorebirds. Elsewhere in Great Britain, a little over a third of the estimated 16,000 wintering sanderlings *Calidris alba* were distributed along non-estuarine coasts (Musgrove *et al.*, 2011). Ghana's coast supports ca. 5000 sanderlings that represents about 3.5% of the population of the EAF (Reneerkens *et al.*, 2009a; Wetlands International, 2012; Ntiamoa-Baidu *et al.*, 2014a). However, the selection of a wetland as a suitable habitat during the non-breeding season is dependent on a list of factors that defines the quality of the habitat.

Ghana's wetland ecosystems may be classified under three broad categories; coastal/marine, inland and man-made wetlands (Ministry of Lands and Forestry, 1999). Coastal/Marine wetland systems in Ghana have been given more attention than inland and man-made wetland types, evidenced by several studies and literature in that regard (Ntiamoa-Baidu, 1991a; Ntiamoa-Baidu *et al.*, 1998; Ntiamoa-Baidu *et al.*, 2000; Gbogbo, 2007; Gbogbo *et al.*, 2008; Ntiamoa-Baidu *et al.*, 2014a; Gbogbo & Otoo, 2015; Gbogbo *et al.*, 2017). There are over 100 coastal/ marine wetlands along the 550 km Ghana coast, out of which five of them have

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been designated as Ramsar sites based on supporting over 20,000 waterbirds at any one time: Keta lagoon complex, Songor lagoon, Sakumo lagoon, Densu delta and Muni-Pomadze lagoon (Ntiamoa-Baidu, 1991b). To the western coast of the country lies a 13 km sandy beach between the Amansuri and Ankobra estuaries (hereafter referred to as Esiama beach) which is internationally important based on the sanderling populations it supports (Ntiamoa-Baidu *et al.*, 2014a), but this site is not protected.

### 2.2 Waterbird as bio-indicators of wetlands

Waterbirds are species of birds that depend on wetlands (Rose & Scott, 1994, 1997; Wetlands International, 2012). Before proceeding further, it is important to define and clarify the different semantics one may come across reviewing literature on waterfowls. Such keywords include waders, shorebirds, seabirds, waterfowls and waterbirds.

Seabirds are pelagic birds that occasionally visit the coastal areas to breed, but then spend a greater percentage of their time out at sea (Hobson, 1993; Quillfeldt *et al.*, 2005). Shorebirds on the other hand, are mostly migratory birds that depend on the shore to forage, roost and sometimes breed (Piersma, 2008). There are several definitions for waders, but for the purpose of this study, waders are shorebirds that are capable of moving and feeding in water (Barlow & Dodman, 2015).

A bio-indicator is an organism or community of organisms whose presence or absence, population dynamics, function or status can be used in a qualitative assessment of the health of an environment (Sutton *et al.*, 2004). Shorebirds are important sentinels of the coastal wetland ecosystem, because of their ability to track short- or long-term changes within the environment (Rendón *et al.*, 2008). For example, in their study in the Mar Menor lagoon of south-eastern Spain, Fernández *et al.* (2005) observed an increase in the numbers of the great crested grebe *Podiceps cristatus*, in relation to an increase in nutrients in the wetland caused

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by agricultural effluents. Shorebirds are keystone predators of benthic macroinvertebrate communities, and as such, they can be used as indicator species to assess changes in the lower trophic levels. Shorebirds are also important predators of fishes which are also harvested by humans. Therefore levels of exploitation of shorebirds through hunting by humans may provide information on the nesting success of birds (Miller *et al.*, 1988), whiles the fitness of birds may give an indication of fish stocks (Einoder, 2009). The constant interaction between shorebirds and humans allows changes in shorebird behaviour and populations, which may provide an indication of the level of pressure on the ecosystem (Amat & Green, 2010). The distribution of shorebirds within wetland ecosystems and the regular monitoring of population of shorebird species is a simple, but effective way, of assessing changes within such habitats caused by anthropogenic and naturally related influences.

### 2.3 Distribution of shorebirds in Ghana

Out of the 647 different populations of the 290 species of waterbirds recorded along the East-Atlantic Flyway (van Roomen *et al.*, 2015), about 70 of these species have been recorded on the Ghana coast. These include waders, terns, ducks and herons/egrets (Ntiamoa-Baidu, 1991a; Ntiamoa-Baidu *et al.*, 2001; Dodman & Diagana, 2003). The earlier counts of shorebirds on the Ghana coast provided data on its international importance to certain species of shorebirds that use the EAF. Shorebirds occurring in internationally important numbers on the Ghana coast included the spotted redshank *Tringa erythropus*, greenshank *Tringa nebularia*, common ringed plover *Charadrius hiaticula*, curlew sandpiper *Calidris ferruginea*, sanderling *Calidris alba*, little stint *Calidris minuta*, black-tailed Godwit *Limosa limosa*, avocet *Recurvirostra avosetta* and black-winged stilt *Himantopus himantopus* (Ntiamoa-Baidu, 1991a). However, recent counts of two of these species, black-tailed Godwit and pied avocet show a collapsed population, whilst species such as the sanderling and curlew

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sandpiper have increased in numbers (Ntiamoa-Baidu *et al.*, 2015).

## 2.4 Classification and conservation status of sanderling

Sanderling is one of the wader species that occur in internationally significant numbers along the Ghana coast. Sanderlings are waders that breed in very cold areas of the high Arctic tundra (for example the Taimyr peninsula, Greenland, Canada) and spend the non-breeding season in a wide range of habitats within the temperate and tropical regions (Soloviev & Tomkovich, 1995; Reneerkens *et al.*, 2009a). Taxonomically, sanderlings belong to the order Charadriiformes, family Scolopacidae and the genus *Calidris*. There are two subspecies of sanderlings, based on morphological and plumage descriptions, and these are *Calidris alba alba* and *Calidris alba rubidus* (Engelmoer & Roselaar, 1998).

### *2.4.1* The species *Calidris alba*

The two sub-species of *Calidris alba* have distinct breeding areas (Stroud *et al.*, 2004; Reneerkens *et al.*, 2009a). *Calidris alba alba* breeds in Greenland, Siberia and North-eastern Canada and spends the non-breeding season along the Atlantic coast of Europe and West Africa (the East Atlantic Flyway population), West and Central Asia, as well as East Africa (West Asia/East African Flyway). The other sub-species, *C. a. rubidus*, is more or less associated with the neo-tropics. *Calidris a. rubidus* breeds in Alaska and in Canada and uses the American coasts as non-breeding grounds (Reneerkens *et al.*, 2009a). The subspecies occurring on the Ghana coast and the subject of this study is the nominate species *Calidris alba alba* (hereafter referred to as sanderling).

### 2.4.2 Conservation status and population trend of sanderling

The International Union of Conservation of Nature (IUCN) categorises the sanderling as a “Least Concerned” species (Birdlife International, 2016). The EAF sanderling population is

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known to be increasing (Figure 2.1) in both the long- (4% since 1979) and short- term (6% since 2003). The European non-breeding sanderling population increased at a rate of 5% per year whereas the West African non-breeding population increased at a rate of 1% per year since 1979. The EAF sanderling population currently is estimated at 200,000 individual birds (van Roomen *et al.*, 2015).

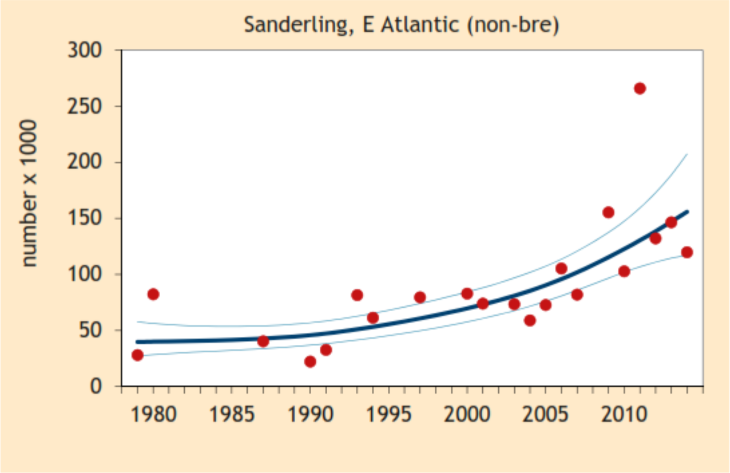

**Figure 2.1 Sanderling population trend along the East Atlantic Flyway** (van Roomen *et al.*, 2015).

## 2.5 Biometrics of sanderling

Biometric measurements of sanderlings provide a measure of the size range of individuals, which may define the demography of different populations as well as relate seasonal and annual variations in body conditions (Summers *et al.*, 1987; Gudmundsson *et al.*, 1991; Soloviev & Tomkovich, 1995). The maximum wing and bill lengths offer near accurate measurements of the size of sanderlings. Therefore, sanderlings have been observed to demonstrate varying sizes in different seasons and geographical location, indicating unique population (Engelmoer & Roselaar, 1998) or effect of biological/ ecological processes (van Gils *et al.*, 2016). For example, birds of Taimyr Peninsular share similar biometrics with that

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of Poland, however, Soloviev and Tomkovich (1995) observed the former to be characterised by longer wing length, an observation which is as a result of wear of primaries through migration (Meissner & Wlodarczak, 1999). The same explanation applies to adults possessing longer wings than juveniles on the south African coast (Summers *et al.*, 1987). The average bill length of sanderlings observed in South Africa (non-breeding area) was longer than that measured in Taimyr (breeding area), suggesting a geographical effect on bill length. Maximum bill length of non-breeding sanderlings are observed between November and January when they are repairing their heavily worn plumage (Summers *et al.*, 1987; Soloviev & Tomkovich, 1995). In addition to geographical variation in sizes of sanderlings, and the fact that sanderlings are not sexually dimorphic in terms of plumage variation in the non-breeding season, females tend to be bigger than males (Soloviev & Tomkovich, 1995). Summers *et al* (1987) observed a mean bill length of 24.9 ± 1.1 mm in males compared to 26.2 ± 1.0 mm in females.

There is a wide variation in the body mass of sanderlings, which has a lot to do with seasonal changes and to a large extent geographical location (Kersten & Piersma, 1987; Castro *et al.*, 1992). Changes in average masses of sanderlings have been observed at various stages of life of this migrant bird. For example, sanderlings were observed to be heavier during the incubation period in breeding season, than during the pre-nesting and brood-rearing periods (Soloviev & Tomkovich, 1995, 1997). Al-Mansour (2004) attributed the variation in body mass of sanderlings to environmental cues, such as photoperiod and temperature rather than availability of food. The mean body mass of sanderlings on non-breeding grounds, prior to storage of fat for migration, was between 50.3 to 54.1 g in South Africa, with no disparity between adults and juveniles (Summers *et al.*, 1987). Furthermore, sanderlings tend to be heavier than average, approximately 80 g or more, during the late non-breeding period as they embark on migration, due to storage of fat (Summers *et al.*, 1987; Zwarts *et al.*, 1990b;

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Gudmundsson *et al.*, 1991) and enlargement of flight muscles (Underhill & Summers, 1993; Al-Mansour, 2004), as there are hardly any seasonal changes in lean body mass (Summers *et al.*, 1987). Adult sanderlings increase their body mass more than juveniles during this period at a rate of approximately 1 g/day (Summers *et al.*, 1987; Al-Mansour, 2004). Variation in body mass can also be related to energy budgets (Serra *et al.*, 2006; Loonstra *et al.*, 2016). For example, in their study in the Wadden Sea, Loonstra *et al.* (2016) observed that moulting sanderlings were lighter in weight as compared to their non-moulting counterparts.

## 2.6 Migration of sanderling

Shorebirds breed in areas that vary in distance from their non-breeding areas. Variation in climatic conditions defines the pattern and timing of migration adopted by birds. Nevertheless, the factors that define the actual distances travelled by migrant birds remain a puzzle (Piersma, 2007; Reneerkens *et al.*, 2009a). Several theories have been propounded as the underlying factors that determine migration distances. These include predation risk (Lank *et al.*, 2003), inter and intra-specific competition (Moore *et al.*, 2005; Skagen, 2006), availability and accessibility of prey (Piersma, 2012; Duijns *et al.*, 2014) and latitudinal variation in foraging habitats (Díaz *et al.*, 2013; Grond *et al.*, 2015). Furthermore, the pattern of migration may be species, age and/or physiologically related (Hockey *et al.*, 1998). For example, juveniles that decide to migrate back to breeding grounds within their first year may increase their success by rather engaging in several short-distant flights, refuelling at each stop, than one long flight (Myers, 1981; Pienkowski & Evans, 1985). The disadvantages of this approach are that, several short flights may result in a late arrival on the breeding ground and may negatively affect breeding success.

Migration normally occurs along certain routes designated as flyways. A migratory flyway may be defined in the broad context as "…the biological systems of migration paths that

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directly link sites and ecosystems in different countries and continents" (Boere & Stroud, 2006). There are nine different flyways used by different migrant populations on an annual basis (Figure 2.2). The flyway of interest for this study is the East Atlantic Flyway (EAF).

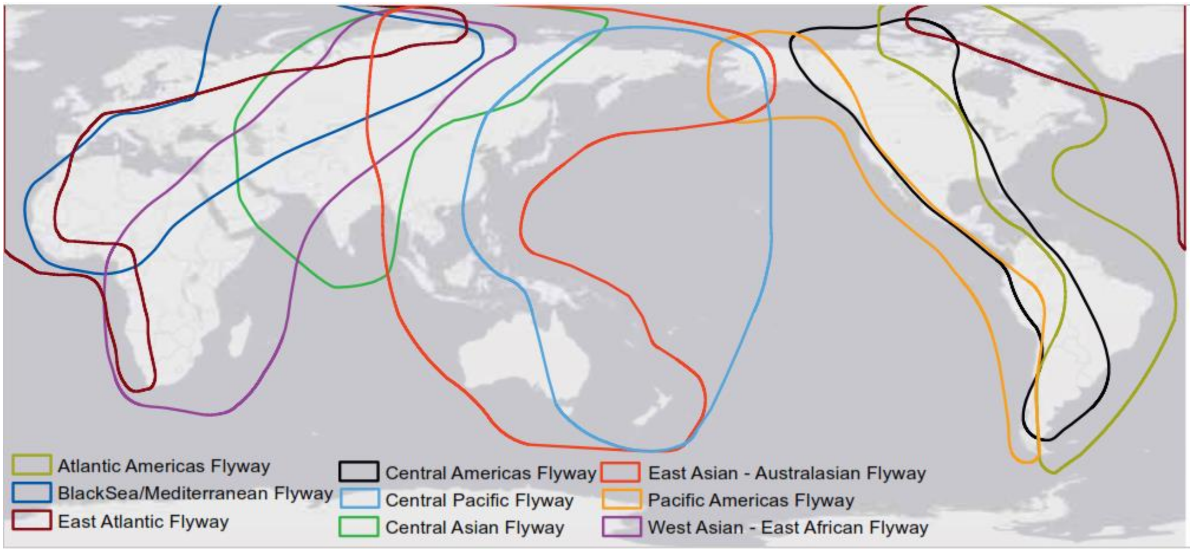

**Figure 2.2 Major flyways of waterbirds based on migratory routes of shorebirds** (Wetlands International, 2012)

Sanderlings migrate from their breeding grounds in the high arctic areas and spend the non-breeding season in the temperate and tropical regions. The sanderling's decision to spend the non-breeding season in the temperates appear to be based on energetic costs in migrating long distances. However, such stress and energy expenditure is compensated for by a more stable climatic condition in the tropical regions. The temperate non-breeding sanderling population have to deal with the harsh climatic condition, through constant thermoregulation that is accompanied by high energy expenditure (Castro *et al.*, 1992). This could be one of the reasons why van Roomen *et al.*, (2015) estimated that, more than 60% of the EAF sanderling population preferred to spend the non-breeding season in Africa.

Adult sanderlings arrive on non-breeding grounds earlier than juveniles (Meissner & Wlodarczak, 1999). This is because, adults are better migrants than juveniles due to

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experiences obtained from previous migrations. In addition to this, adults are by far better foragers (Hockey *et al.*, 1998; van den Hout *et al.*, 2014) and are able to build enough energy to support longer flights times on their journey to non-breeding grounds. Juveniles, on the other hand, are born as 7 grams heavy chicks, which have to grow up and become independent and capable of making their first migratory flight in their life within a few months after they were born. During the time the juveniles are ready to migrate, most adults have either lost their offspring already in the egg phase and can prepare for an early migration southwards without still having to grow. Even adults that guide their chicks until they fledge have had the possibility to prepare for southward migration while raising the chicks, which at that time, still need to fuel for southward migration. Therefore it is essential that juveniles have to make short bouts of flights, refuelling as and when needed, before finally arriving on non-breeding grounds (Myers, 1981).

Information from ring recoveries suggest that sanderlings show high fidelity to non-breeding sites (Spaans, 2006). Adults are more site faithful than juveniles owing to their accumulated knowledge of wintering areas and/or dominance of older animals (Lourenço *et al.*, 2016a). Juveniles often skip migration to breeding grounds in their first year. For example, most sanderlings observed along the coast of southern Africa between June and July were juveniles, suggesting an over ‘wintering’ juvenile population (Summers *et al.*, 1987; Summers *et al.*, 1995).

The timing of migration is influenced by temperature (Møller *et al.*, 2010), although the onset of migration is believed to be endogenous. Migrants advance migration dates in response to changes in temperature either on non-breeding or breeding grounds. In other words, there is an inverse correlation between temperature and median dates of arrival of migrants (Dunn & Winkler, 2010). For example, long-distant migrants arrive a day earlier for every 1°C increase in spring temperatures (Marra *et al.*, 2005). The temperate non-breeding populations of

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migrant species show quicker response to such changes in temperature than their tropical non-breeding counterparts (Dunn & Winkler, 2010).

Different scenarios are under operation during north- and southbound migrations, both of which operate under different time constraints (Dinsmore & Collazo, 2003). Whereas southbound migrants seek to travel to the farthest point which will enable them maximize overwinter survival (Gudmundsson *et al.*, 1991), northbound migrants seek to acquire all nutritional requirements needed for successful migration and reproduction, bearing in mind the have limited time at their disposal to reach the breeding grounds earlier enough to compete for resources that enhance successful reproduction (Johnson & Herter, 1990).

The duration spent at stopover sites in relation to migration, to a large extent, depends on the body condition of shorebirds. Stopover or staging sites are important in the migration process to enable individuals replenish lost energy. Two hypothesis have been proposed regarding the time shorebirds spend on migration. These are the time-selection and energy-selection hypotheses (Alerstam & Lindström, 1990; Gudmundsson *et al.*, 1991). The time-selection hypothesis simply predicts that shorebirds prefer to replenish lost energy at high quality sites where energy gains are greater, and thus reduce time spent on migration by avoiding lower quality sites. In this case, birds are more likely to arrive at stopover sites in better condition which is also accompanied by less time spent refuelling at these high quality sites. The energy-selection hypothesis, on the other hand, predicts that shorebirds make use of the next available stopover sites, irrespective of the quality of such sites, as soon as their fat deposits runs out, to replenish lost energy. In this context, the duration of migration is longer as more lower-quality sites are visited and the time spent refuelling on lower quality prey is much longer. Nevertheless, both hypotheses are based on the body condition of birds. This means that, regardless of the hypotheses shorebirds follow, individuals in better body condition are likely to spend less time on stopover sites and depart earlier than birds in poorer body condition.

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Spring migration, which aims at reproduction, is more likely to operate under the time-selected migration hypothesis, whereas the autumn migration will follow the energy-selection migration hypothesis, as suggested by Lyons and Haig (1995).

Sanderlings oftern migrate from breeding areas to non-breeding areas in June-August. Early migrants on the coast of the Wadden Sea in the Netherlands are observed in late July. There is a high turnover rate, which can span until September (Loonstra *et al.*, 2016). Individuals leaving the temperate areas to ‘winter’ further south arrive along the western coast of Africa from August. Ntiamoa-Baidu *et al.* (2014a) observed arrival of sanderlings along the Ghana coast in the first week of August. In southern Africa, the early migrants arrived along the coast of the western Cape in the second week of December (Summers *et al.*, 1987).

## 2.7 Distribution of sanderlings in Ghana

Sanderlings are distributed along the entire stretch of the Ghana coast, especially along sandy beaches, coastal lagoons and mudflats (Ntiamoa-Baidu, 1991a). The Ghana coast supports up to 3.5% of the sanderling population of the East Atlantic Flyway (Reneerkens *et al.*, 2009a; Wetlands International, 2012; Ntiamoa-Baidu *et al.*, 2014a). Out of this proportion, between 40-70% of non-breeding sanderlings in Ghana use the Esiama beach in the Western Region of Ghana (Ntiamoa-Baidu *et al.*, 2014a; Figure 2.3).

Sanderlings are observed along Ghana’s coast between August and April each year, with peak numbers between September and November during the southern autumn migration. There is a decline in numbers of sanderlings observed along the Ghana coast in November, because of further southward migration of staging individuals. However, a second sanderling peak count may be observed between January and March during the northern spring migration (Figure 2.3). The lean period of sanderling occurrence in Ghana is between May-July (Ntiamoa-

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Baidu, 1991a; Reneerkens *et al.*, 2009a; Ntiamoa-Baidu *et al.*, 2014a; Grond *et al.*, 2015). Trend analysis of long-term sanderling count data shows an increasing sanderling population on the Ghana coast (Figure 2.3).

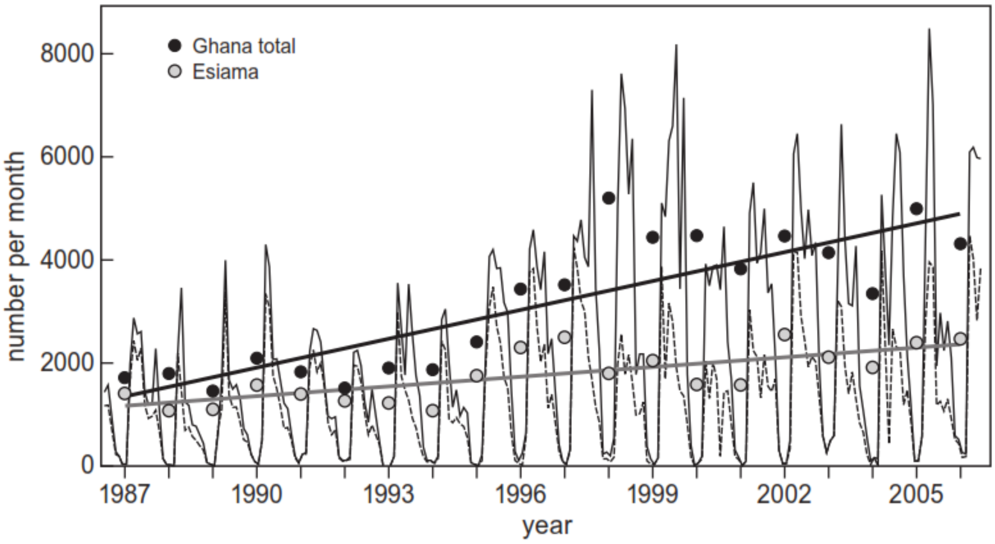

**Figure 2.3 Sanderling population trends along the Ghana coast.** (Solid and broken lines represent total monthly sanderling counts for the entire Ghana coast and on the Esiama beach respectively; Ntiamoa-Baidu *et al.*, 2014a)

### 2.8 Time-activity budgets of sanderlings

Shorebirds spend most of their time either foraging or resting on non-breeding grounds. Very little of their time is spent on other comfort or maintenance activities such as flying, bathing, fighting and preening (Nol *et al.*, 2014). Sanderlings spend more time foraging on non-breeding grounds in order to obtain enough energy to maintain a constant internal environment and build enough energy for migration and reproduction (Morrier & McNeil, 1991; Summers *et al.*, 1995; Lourenço *et al.*, 2015). Castro *et al.* (1992) observed sanderlings to spend between 40% and 90% of their time foraging in four different locations: Panama, Peru, New Jersey and Texas. Shorebirds spend more time foraging in temperate areas than in the tropics, because of higher energy demands for thermoregulation in the temperate regions.

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For example, sanderlings spent about 40% of their time foraging in Ghana (a tropical non-breeding site) and 80% of their time foraging in the Netherlands, a temperate non-breeding site (Grond *et al.*, 2015). In between these two regions is Portugal, where sanderlings spent approximately 60% of their time foraging (Lourenço *et al.*, 2015). This observation suggests that, time spent on foraging is also influenced by latitudinal gradient, accompanied by varying climatic conditions (Kersten & Piersma, 1987; Alves *et al.*, 2013). However, not all observations confirm the positive relationship between latitudinal variation and time spent foraging by shorebirds. For example, Castro *et al.* (1992) observed a negative correlation between latitudinal variation and foraging time. They observed sanderlings to spend 55% and 90% of their time foraging in New Jersey (39°55′ N) and Texas (29°30′ N) respectively. Other factors such as body size (Nol *et al.*, 2014), prey availability and quality (van Gils *et al.*, 2005a; Grond *et al.*, 2015) are equally important in explaining the time-activity budgets of shorebirds. That is to say smaller shorebirds tend to spend more time foraging; also foraging time increases in habitats associated with low prey quality and less prey availability.

## 2.9 Habitat quality

The selection and preference of a suitable habitat by an organism purposed for ecological or biological processes, plays a fundamental role in explaining the success of species in an ecosystem. The extensive global distribution of shorebirds along and across migratory routes highlights the use of different types of habitats from the arctic to the tropics at different times of the year (Rose & Scott, 1997; Stroud *et al.*, 2004; Piersma *et al.*, 2005; Reneerkens *et al.*, 2009a). There is a high complexity in the choices of migrant birds in habitat selection in relation to the intra- and inter-specific interactions (Piersma, 2012).

Piersma (2012) outlined the factors that shorebirds consider in selecting suitable non-breeding

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sites. He modelled these factors schematically with four different axes, each axis describing a collection of measureable factors under a thematic area (Figure 2.4). The four areas considered by Piersma (2012) as important in defining the quality of a habitat which may influence the selection process of a suitable habitat by shorebirds include energy management, water management, danger management and social management.

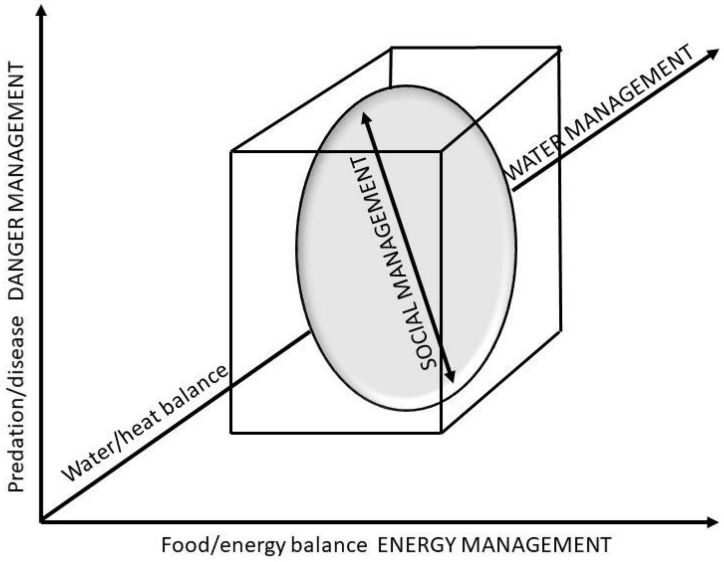

**Figure 2.4 Factors defining the quality of a habitat for migratory birds (Piersma, 2012).**

### 2.9.1 Energy demands and management by non-breeding sanderlings

All processes in the life cycle of birds require use of energy. The most energy-dependent phases are that of migration and reproduction. The decision of a sanderling to spend the non-breeding season in the tropics or temperate regions is arguably related to energy expenditure. Energy acquisition is dependent on the abundance, availability, accessibility and quality (ratio of digestible to indigestible matter) of prey. The abundance and/or quality of prey is just enough to explain the success and fitness of individuals as well as the demography of an entire shorebird population (Ruthrauff *et al.*, 2013).

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Shorebirds are faced with a rather extreme energy-demanding lifestyle when perceived from the kinds of habitats they inhabit. Unlike terrestrial birds, who can regulate their body temperatures through behavioural changes such as resting in shady environments, shorebirds are not privileged to do so and mostly regulate their body temperature physiologically, which is costly (Klaassen, 1995; Gutiérrez *et al.*, 2015). Castro *et al* (1992) observed that energy expenditure negatively correlated with ambient temperature and postulated that it was costlier for sanderlings to spend the non-breeding season in temperate areas than the tropics.

Quite a number of studies have been conducted to understand the energy demands of shorebirds, how they acquire energy and how the energy translates into successful migration and reproduction (Castro, 1987; Kersten & Piersma, 1987; Castro *et al.*, 1992). Critical components of the energy demands of shorebirds, such as the minimum energy requirement to ensure proper day-to-day functioning of the body is basic and very important. Castro (1987) estimated the Basal Metabolic Rate (BMR; defined as the rate at which a resting animal in a thermo-neutral environment consumes oxygen as a measure of energy expenditure) of sanderlings to be 48.1 kJ/day.

The harsh conditions of the temperate regions during the autumn and winter require that sanderlings need to increase their metabolic cost in order to maintain a high body temperature of approximately 40°C even when ambient temperature is extremely low. Therefore to be able to meet this energy demand, sanderlings have to change their foraging behaviour to increase their intake rates, as well as feed on high quality prey (Grond *et al.*, 2015). As stated by Piersma (2012), food intake must reflect energy requirement and the net energy gain must be profitable in relation to the cost involved in obtaining food. In this regard, some species of shorebirds avoid rich prey habitats, especially when they have to fly over longer distances between their roost and foraging sites. For example, red knots were practically absent on some tidal flats in the Wadden sea enriched with high densities of prey, but distant from roost sites

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and rather foraged on tidal flats which were less richer in prey availability, but closer to roost sites which they deemed cost effective (van Gils *et al.*, 2006).

A simple rule that non-breeding shorebirds have to follow is that energy income must be able to meet energy expenditure. The need for more energy to sustain the Daily Energy Expenditure (DEE) should reflect in the time budget of foragers. The DEE is defined as the amount of energy expended by a shorebird in a day, excluding that invested into tissue repair (Tjørve *et al.*, 2008). Non-breeding sanderlings in the tropics have lower DEE than those in temperate areas. Castro *et al.* (1992) recorded a 100 kJ/d as DEE for sanderlings in Panama, which was about half the DEE of sanderlings wintering in New Jersey (200kJ/d, value about four times the Basal Metabolic Rate, BMR). Kersten & Piersma (1987) observed similar relationship between DEE and BMR for some shorebirds in the temperate areas. The extensive variation in DEE between the tropic and temperate zones was strongly related to ambient temperature (Kersten & Piersma, 1987; Castro *et al.*, 1992) and fat reserves of sanderlings (Castro *et al.*, 1992). That is to say, a homoeothermic organism such as a sanderling thermoregulates in low thermal conditions by increasing energy expenditure, relying on fat reserves.

Meanwhile, sanderlings that winter in the temperate regions are heavier in mass than tropical non-breeding sanderlings (Castro *et al.*, 1992). This increase in body mass of shorebirds is due to increase in nutritional reserves, such as fats and proteins (Summers *et al.*, 1987; Zwarts & Wanink, 1993). Furthermore, increase in body size reduces heat loss to the environment, because of the smaller surface area to volume ratio of larger animals (James, 1970; van Gils *et al.*, 2016). The increase in body size also comes with an increase in food consumption and Net Energy Intake (NEI). According to Kersten & Piersma (1987), each gram of increase in body weight demands between 1.3-2.6 g of additional food in daily consumption, which is accompanied by a 45.66 kJ of additional energy. They explained that, additional weight

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gained by shorebirds is composed of 85% fat, 5% non-fat nutrient such as protein and 10% water, which gives the proportion of energy intake that is deposited in body tissue and assimilated to be 75% and 85% respectively, resulting in an assimilation efficiency of 88% (75/85*100).

In order to increase the nutritional reserves, sanderlings tend to spend more time foraging in the temperate areas (55%/9h in New Jersey, 90%/9h in Texas, 79%/12h in the Netherlands, 51.7%/12 h in Portugal) than the tropical non-breeding sites (35%/9.0h in Ghana, 40%/9.0h in Panama, 45%/9h in Peru, 51%/12.4h in Kenya) (Castro *et al.*, 1992; Fasola & Biddau, 1997; Grond *et al.*, 2015; Lourenço *et al.*, 2015), and preferably, on better quality prey (Grond *et al.*, 2015). Sanderlings foraged mainly on polychaetes in the Netherlands, which were of higher quality (110.6 ± 1.9 kJ $g^{-1}$ $DM_{shell}$), but less available (biomass of 7.4 ± 1.6 g AFDM $m^{-2}$) than the bivalve, *Donax pulchellus* (prey quality of 4.59 ± 0.12 kJ $g^{-1}$ $DM_{shell}$, biomass of 77 g AFDM $m^{-2}$) that is the primary prey sanderlings forage on in Ghana (Grond *et al.*, 2015). The high cost in processing *D. pulchellus* and the low caloric gain renders the bivalve a low quality prey.

In Ghana, the number of foraging sanderlings is not influenced by prey availability, because prey is readily available (Chapter 4), and the energy intake of sanderlings is estimated as 1.64 mg AFDM $s^{-1}$ (36.27 J $s^{-1}$) (Grond *et al.*, 2015). Elsewhere in Portugal, sanderlings on non-estuarine habitats were observed to forage on a number of prey items in order to achieve their required daily energy (6.1 g AFDM in 12 h). About 90% of the required daily energy was obtained by sanderlings foraging on a combination of different prey (such as bivalves, gastropods, crustaceans, polychaetes and insects) on different substrates in an estuarine environment, as compared to only 57% of the required daily energy obtained by foraging in a non-estuarine environment (Lourenço *et al.*, 2015). Most high quality prey are difficult to obtain because of their unavailability through prey depression strategies and naturally

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occurring in lower densities (Zwarts & Wanink, 1993; van Gils, 2004). Other factors such as predator avoidance, social interactions and interference influence the amount of energy obtained from foraging (Goss-Custard, 1980; Ens & Goss-Custard, 1984; Skalski & Gillman, 2001; Lank *et al.*, 2003; van den Hout *et al.*, 2014).

The amount of energy needed to be obtained by shorebirds from their daily food consumption can be determined from BMR, assimilation efficiency and caloric content of prey. For example, Vanermen *et al*. (2009) estimated the number of polychaete worms needed to be consumed by a sanderling wintering along a coastal beach in Belgium in order to fulfil its daily energy demands. With a BMR of 48.1kJ/day (Castro, 1987), a NEI of 136-277kJ/day (2.4-4.9 times the BMR) and a 85% assimilation efficiency (Kersten & Piersma, 1987), a sanderling foraging exclusively on polychaetes (dry weight between 1.6 and 3 mg AFDW, caloric content between 22 and 26 kJ/g; Zwarts & Wanink, 1993), requires 1735-7650 individual polychaete to meet its daily energy needs. In addition to this, red knot feeding on horseshoe crab eggs need about 24,000 eggs per day to be able to replace fat used during previous migration (Haramis & Link, 2007). In so doing, knots have to spend a greater portion of their time foraging, preferably, in areas with high densities of horseshoe crab eggs. According to Gillings *et al.* (2007), an ideal foraging area may be one that supports more than 360 eggs per square meter on the surfaces of the substrate or about 19,000 buried eggs per square meter.

### 2.9.2 Diversity and distribution of macroinvertebrates as prey for sanderlings

Most shorebirds are generalists in their diet, meaning that they feed on any prey they encounter, provided the prey is available and easy to access. However, when offered a choice, shorebirds prefer higher quality prey, which provide more energy per unit mass and does not entail any digestive constraints.

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The most common prey for shorebirds include molluscs, polychaetes, amphipods, insects and sea grass. Sanderlings have been observed feeding on horseshoe crab eggs (Karpanty *et al.*, 2011), polychaetes and bivalves which they swallow whole (Dekinga & Piersma, 1993; van Gils *et al.*, 2003a; van Gils *et al.*, 2005a; Reneerkens *et al.*, 2009a; Onrust *et al.*, 2013; Ntiamoa-Baidu *et al.*, 2014b; Oudman *et al.*, 2014; Grond *et al.*, 2015).

Sandy beaches are associated with high densities of invertebrates and are important for non-breeding shorebirds populations (Myers *et al.*, 1985). Invertebrate distribution may be influenced by several terrestrial and marine factors such as ambient temperature and ocean currents resulting in upwelling systems that provides nutrients for invertebrate development and growth (Summers *et al.*, 1987). Density dependent factors affect size distribution of invertebrates as prey for shorebirds. Selection of particular invertebrate size classes, e.g. smaller sizes, may leave out larger size classes of prey which may be more profitable in energy content (Zwarts & Wanink, 1993; Yasué, 2005).

Benthic macroinvertebrates form the bulk of prey for non-breeding shorebirds. The accessibility and availability of prey are equally as important as their abundance and densities. That is to say, it is more profitable for shorebirds to forage in areas supporting prey which are available and accessible, but of low densities, than areas with high prey densities but inaccessible and unavailable to birds. Zwarts and Wanink (1993) observed that bivalves are readily available to shorebirds than polychaetes, because the former hardly burrow deeper into the substrate, hence available to a wide group of waders, and are less mobile to be evading predators. Burying depth of macroinvertebrates is also size related, and larger sized prey tend to burrow deeper into the substrate than smaller ones (Reading & McGrorty, 1978).

Variation in distribution of invertebrates as prey for shorebirds may be temporal/ seasonal or spatial. Zwarts & Wanink (1993) observed seasonal variation in the total biomass and body

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condition (weight at same length) of some prey items of shorebirds. They observed poor body conditions, which resulted in lower total biomass of invertebrates in winter than in summer. Zwarts and Wanink (1993) attributed this observation to the burying depth of prey species at different temporal scales.

Predation on macroinvertebrates by shorebirds and other forms of predators influences densities and distribution of prey. In Portugal, decline in densities of the polychaete *Hediste diversicolor* was a function of predation by birds and nektons (Rosa *et al.*, 2008). Elsewhere in Southern Africa, variation in densities of invertebrates was not only caused by predation from sanderlings, but from the ghost crabs *Ocypode africana* and *O. cursor* (Penrith & Kensley, 1970; Kensley & Penrith, 1980), which implies a competitive relationship between sanderlings and ghost crabs.

As shorebirds continually exploit prey at particular sites over certain periods, declines in densities of the prey reach a threshold below which it is not profitable for birds to stay and feed at the same site and therefore have to relocate. This threshold is known as the ‘giving-up density’ (Gawlik, 2002; van Gils *et al.*, 2005a; Karpanty *et al.*, 2011).

### 2.9.3 Sanderling’s diet composition

Several methods have been employed in studying the diets of shorebirds. These include methods that inflict pain and discomfort to the birds such as flushing the gut content (Tsipoura & Burger, 1999), or involving the death of individual birds through dissection and examination of the alimentary canal (Dierschke *et al.*, 1999). Modern methods of studying the diet of birds, though expensive and time consuming, but very effective, involves the use of radioactive isotopes on feather or blood samples of birds (Espoz *et al.*, 2008). However, a simpler and effective method of assessing the diet of birds involves the analysis of regurgitates and faecal matter of birds (Dekinga & Piersma, 1993; Verkuil & Burg, 1996; Lourenço, 2007;

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Onrust *et al.*, 2013). This approach is based on the knowledge that most bird species have a short digestive tract, which ensures a faster digestion process, and as such, digestive remains can provide a fair idea of ingested food (Dekinga & Piersma, 1993). Direct field observation, recording prey consumed is also a cheaper and quicker method of diet assessment. However, this approach is effective for birds that feed slowly and on large prey items (Lourenço *et al.*, 2017).

Bivalves and gastropods can be easily identified in droppings using indigestible shells and hinges or parts of shell whorls (Dekinga & Piersma, 1993; Onrust *et al.*, 2013); arthropods by using appendages and exoskeleton (Nuka *et al.*, 2005); polychaetes by using chaetae and mandibles (Zwarts & Wanink, 1993) and vertebrates by using bones (Kloskowski *et al.*, 2000). Diet assessment through analysis of faecal droppings has been observed to be very effective and easy to use in molluscivores as the shells are easily seen in the faeces of shorebirds. Dekinga & Piersma (1993) observed that the hinges of bivalves are intact in the droppings of red knots and the consumed size of bivalve can be reconstructed using calibrated equations. Similar approach was used to reconstruct the diet of sanderlings in Portugal (Lourenço *et al.*, 2015) and Guinea-Bissau (Lourenço *et al.*, 2017). Based on the frequency of occurrence and numerical frequency (explained as the mean percentage of each prey type per dropping), the biomass of prey consumed could be estimated and the energy budget of sanderlings constructed (Lourenço *et al.*, 2015; Lourenço *et al.*, 2017). Although diet analysis of faecal droppings is not easy to use on soft bodied prey such as amphipods and polychaetes (Onrust *et al.*, 2013), such prey may still be identified and reconstructed by pairing mandibles of similar sizes of polychaetes and thoraxes of insects (Lourenço, 2007).

Sanderlings are generalists in their diet (Petracci, 2002; Reneerkens *et al.*, 2009a) and opportunistic in feeding on prey that are readily available and easily accessible (Lourenço *et al.*, 2015). Sanderlings feed mostly on local prey that occur in high densities (Reneerkens *et*

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*al.*, 2009a; Grond *et al.*, 2015) and are capable of sharing such prey items with other foragers (Zwarts, 1985). The type of diet exploited by sanderlings does not necessarily depend on the geographical location, but the time or season (Summers *et al.*, 1987; Nuka *et al.*, 2005). With a wide span of non-breeding locations, and breeding areas, it is not surprising to see sanderlings feeding on probably any edible and accessible food they come across. From the breeding sites in the northern hemisphere to the southernmost non-breeding areas, the diet of sanderlings consists of a wide list of prey items: insects, crustaceans (amphipods and isopods), horseshoe crab eggs, bivalves, anemones, surf clams or bivalves and polychaetes (Table 2.1).

With bivalves as diet, sanderlings swallow their prey whole and rely on their muscular gizzards to crush and breakdown the shell of the ingested prey. In Ghana, sanderlings have been observed to feed exclusively on the surf clam *Donax pulchellus* that are abundant and readily available (Reneerkens *et al.*, 2009a; Ntiamoa-Baidu *et al.*, 2014a; Grond *et al.*, 2015). In Guinea-Bissau, another tropical country close to Ghana, sanderlings were observed foraging on *Dosinia isocardia* (Table 2.1). Elsewhere in Belgium, sanderlings were observed feeding on *D. vittatus* (Vanermen *et al.*, 2009). In their study on the Belgian coast, Vanermen *et al.* (2009) also observed sanderlings scavenging leftover mussels from Oystercatchers.

### 2.9.4 Variations in shorebird densities and prey densities

The abundance and distribution of prey have been shown to correlate with the distribution and abundance of shorebirds. High numbers of shorebirds, for example on the Taimyr Peninsula in Siberia, have been observed to be associated with higher abundance of lemmings in different years (Summers, 1986). Thus, in years with high abundance of lemmings, predators such as the arctic foxes have enough lemmings to feed on allowing shorebirds to breed successfully, however in years with low lemming abundance, predatory foxes tend to complement their diets with eggs and young of breeding shorebirds. Karpanty *et al.* (2011) observed decline in red knot population in years associated with decline in densities of

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horseshoe crab (*Limulus polyphemus*) eggs in the Delaware Bay. Also in the Delaware Bay, Niles *et al*. (2009) and

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**Table 2.1: Diets of sanderlings recorded at some selected sites along the migration flyway.**

| **Location** | **Country** | **Site** | **Prey** |
|---|---|---|---|
| Banc d'Arguin | Mauritania | Non-breeding | *Hydrobia* sp, Polychaete, Bivalve (Lourenço *et al.*, 2016) |
| Belgian coast | Belgium | Non-breeding | Polychaete *Scolelepis squamata, D. vittatus* (Speybroeck *et al.*, 2007; Vanermen *et al.*, 2009) |
| Bijagós archipelago | Guinea Bissau | Non-breeding | Polychaete *Nereis* sp., *Glycera* spp., Amphipoda, *Hydrobia* sp, *Dosinia isocardia* (Lourenço *et al.*, 2017) |
| Bodega Bay | California | Non-breeding | Sandcrab *Emerita analoga* and Isopod *Excirolana linguifrons* (Maron & Myers, 1985; Thomas *et al.*, 2003) |
| Cádiz Bay National Park | Spain | Non-breeding | Brine shrimp *Artemia* spp (Estrella *et al.*, 2007) |
| Coast of Southern Africa | Namibia & South Africa | Non-breeding | Polychaete *Nereidae* sp; Amphipods *Ampelisca palmata*, *Urothoe grimaldii*; Insects; Bivalve *Donax serra* and Mysid shrimp *Gastrosaccus psyammodytes* (McLachlan *et al.*, 1980; Summers *et al.*, 1987) |
| Delaware Bay | United States of America | Non-breeding | Horseshoe crab eggs *Limulus Polyphemus* (Castro *et al.*, 1989; Castro & Myers, 1993; Tsipoura & Burger, 1999; Gillings *et al.*, 2007) |
| Griend | The Netherlands | Non-breeding | Brown shrimp *Crangon crangon* (Loonstra *et al.*, 2016) |
| Kujukuri beach | Japan | Non-breeding | Surf clam *Donax semigranosus*, Isopod *Excirolana chiltoni* and Mysid shrimp *Archaeomysis vulgaris* (Nuka *et al.*, 2005) |
| Monte Hermoso | Argentina | Non-breeding | Coleoptera, Mussels *Brachydontes rodriguez*, Clams *Corbula* sp and Diptera (Petracci, 2002) |
| Taimyr | Siberia | Breeding | Diptera (Myers & Pitelka, 1979) |
| Tejo estuary | Portugal | Non-breeding | Bivalves *Scrobicularia plana*, *Donax trunculus, Mytilus galloprovincialis;* Polychaete; Staphylinids; Chironomid larvae and Gastropod *Hydobia ulvae* (Lourenço *et al.*, 2015) |
| Vlieland | The Netherlands | Non-breeding | Polychaete *Scolelepis squamata* (Reneerkens *et al.*, 2009b; Grond *et al.*, 2015) |
| Zackenberg | Greenland | Breeding | Diptera (Reneerkens *et al.*, 2011) |

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Baker *et al.* (2004) observed declines in population of red knots in relation to decline in densities of horseshoe crab eggs as a result of overharvesting of horseshoe crabs. In Southern Africa, densities of sanderlings correlated with biomass of invertebrates. Summers *et al.* (1987) observed beaches with low invertebrate biomass supported sanderling densities of 4 individuals/ km, whereas beaches with very high invertebrate densities, comprising mostly *Donax* spp (McLachlan, 1977), supported densities of more than 10 sanderlings/ km.

### 2.9.5 Prey choice and size selection

Shorebird habitats, such as intertidal systems, support high densities of different species of macroinvertebrates which serve as prey for birds. This provides shorebirds with the opportunity to choose between different prey types at different times of the year. In cases where the habitat is dominated by a single macroinvertebrate species, denying shorebirds the luxury of choosing between prey, size selection of prey becomes critical. When species of birds are able to define particular resources they exploit, it helps in coexistence and utilization of similar resources by different species, but on the temporal and spatial scale (Sih & Christensen, 2001).

The selection and choice of prey may go beyond the abundance and availability of macroinvertebrates. The searching and handling time of prey are key explanatory components of classical models used in explaining predator-prey interactions (Smallegange & van der Meer, 2010). One of such models is the contingency model (CM). The CM has helps to explain and predict foraging and intake rates in many ecological contexts. The CM describes optimal diets that maximize intake rates of foragers, depending on the searching and handling times of prey (MacArthur & Pianka, 1966). This model explains energy intake and maximization for foragers whose constraints depend solely on the profitability of prey. Profitability of prey (e/h) in this context may be expressed as a gain in the long-term average intake rate of prey whose energy content (e) exceeds unit searching and/or handling time (h).

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The CM best predicts energy intake amongst foragers that spend all or more of their time searching and handling prey. Such foragers have been described as "handling-limited" (Farnsworth & Illius, 1998). According to Jeschke *et al.* (2002), the main constraint for foragers that follow the CM is the rate at which prey is handled externally.

However in some other studies, e.g. van Gils *et al.* (2005b), foragers were observed to take digestive pauses when foraging, due to digestive bottleneck that arise when energy intake rates are constrained by digestive rates rather than handling times. The CM could not predict such observation, but then an alternative model, the digestive rate model (DRM) could (Jeschke *et al.*, 2002). The DRM best predicts high quality prey (e/k) that maximizes long-term energy intake rate (e) in circumstances where foragers are faced with a digestive constraint (shell or ballast mass, k). This means that the long term energy intake rate of a predator foraging on a 'poor-quality' prey will be less than one foraging on a 'high-quality' prey. According to Verlinden and Wiley (1989), foragers that follow the CM could only maximize energy intake in the short- but not the long-term, especially when prey differ in their assimilation rate. Therefore, foragers following the DRM, select prey of higher quality, which allows them to forage for longer periods, maximizing use of time which should have been used in taking digestive breaks.

The choice of prey can therefore be said to depend on prey characteristics such as, energy content, ballast mass and handling time. The long term energy and ballast intake rates are also dependent on the processing rate of prey, which is a function of the gizzard mass or size (van Gils *et al.*, 2005a). Shorebirds have a glandular stomach (proventriculus) which is filled as the bird forages. The rate at which this organ fills up is steeper for prey with more shell or ballast material than soft-bodied prey (De Leeuw, 1999). van Gils *et al.* (2005b) observed energy intake rates of red knots to be supported by the DRM when foraging on smaller bivalves which are of higher quality than larger ones. However in another study by Gommer

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*et al.* (2018), when presented with different prey types, crab plovers foraged on food with a higher profitability and as their digestive organs filled up, they switched to prey of higher quality so as to continue foraging when they would be expected to take a digestive break. Most molluscivores which swallow their prey whole follow the DRM. However, the oystercatcher *Haematopus ostralegus*, another molluscivore satisfies the CM, because of its foraging style, which involves opening up bivalves and feeding on the flesh increasing handling time (Wanink & Zwarts, 2001).

### 2.9.6 Availability, accessibility and quality of sanderling prey

The quality of food eaten by shorebirds is dependent on a number of factors. According to Yang *et al.* (2013), prey quality is expressed as $Q = (a \times d \times AFDM_{flesh})/DM_{shell}$, where ‘a’ is the assimilation efficiency and ‘d’ is the prey energy density. Prey quality is not only dependent of the ratio of the ash-free dry mass (AFDM) of the flesh to the dry mass (DM) of the shell, but also on the product of the assimilation efficiency and energy density of the prey.

The energy density of prey is the amount of energy stored in a well-dried flesh of a macroinvertebrate that has been combusted in a calorimeter. The energy density of macroinvertebrates is dependent of the species, season and regional variation in macroinvertebrate distribution (Zwarts & Wanink, 1993). Fat content of macroinvertebrates varies with latitude. Therefore, invertebrates of the same species found at higher latitudes are more likely to possess more fat, and as such have higher energy densities than those of lower latitudes (Rumohr *et al.*, 1987; Wacasey & Atkinson, 1987). For example, Pekkarinen (1983) observed twice the fat content in *Macoma balthica* in the Baltic sea as in those in the Wadden sea. The difference in the nutritional composition of macroinvertebrates also relates to their energetic density. Macroinvertebrates richer in fat content have higher energy density than those richer in either carbohydrates or proteins. For example, the energy content of the amphipod *Corophium volutator* with a fat content of approximately 2%, is less than that of

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bivalves which have on average 10% fat content. Zwarts and Wanink (1993) observed lower energy densities in macroinvertebrates during the winter than in the summer. They attributed this observation to starvation in winter and spawning in summer. During spawning, gametes are likely to add more weight to the flesh of the macroinvertebrate which increases its energy density (Zwarts & Wanink, 1991). The average energy densities of all invertebrates, according to Zwarts and Wanink (1993), is 22 $kJg^{-1}$ AFDM (21 - 23 $kJg^{-1}$ AFDM).

## 2.10 The prey, *Donax pulchellus*

*Donax pulchellus,* a surf clam or bivalve, is the most important prey for non-breeding sanderlings along the Ghana coast (Ntiamoa-Baidu *et al.*, 2014a; Grond *et al.*, 2015).

### 2.10.1 Taxonomy and description of *Donax pulchellus*

The surf clam *Donax pulchellus* is a bivalve (Phylum Mollusca, Class Bivalvia) of the family Donacidae (Ansell, 1983). There are several genera of the family Donacidae, however of the three most prominent genera, *Donax*, *Egeria* and *Iphogenia* (Laudien *et al.*, 2001; Laudien, 2002), *Donax* is the most common (Brown & McLachlan, 2006).

Species of the genus *Donax* are somehow similar in appearance. They are characterised by a triangular shell with heights almost equal to half their full length and a nearly straight ventral edge. The length of *D. pulchellus* at maturity ranges from 10 – 15 mm (Edmunds, 1978). In Ghana, Akita *et al.* (2014) observed a maximum shell length of 11 mm for matured *D. pulchellus*. The shell of *Donax* spp is generally smooth with varying colouration, although some species or individuals are generally white. The shell colour of *D. pulchellus* include white, purple and sometimes with radiating bands. The posterior end of the shell is usually characterised by a radiating ridge. *Donax* spp possess a cardinal tooth each in each valve and another small lateral tooth (Ansell, 1983). *Donax* spp possess elongated shells which

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accommodates their large foot that aid in rapid burrowing into sand (Stanley, 1970).

### *2.10.2* Distribution of *Donax pulchellus*

According to McLachlan (1996) and Laudien (2002), *Donax* spp are mostly present within the intertidal zones of most sandy beaches. *Donax* spp are important consumers of phytoplankton and may serve as good bio-indicators of primary production on sandy beaches (McLachlan, 1996). Ocean upwelling, characterised by systems rich in nutrients, support high phytoplankton production which stimulate high densities of *Donax* spp along sandy beaches. Most of the suitable upwelling beaches are geographically positioned along the western coasts of continents associated with high currents (Laudien, 2002). According to Ansell (1983), more than 70% of *Donax* spp are distributed along sandy beaches within the tropics, with about 20% in the temperate regions.

Only two of the 64 species of *Donax* spp in the world occur in Ghana. These are *Donax pulchellus* and *D. rugosus* (Ansell, 1983). *Donax rugosus* is bigger in size with a length at maturity ranging from 15 – 60 mm. Apart from the distinct variation in size, both species are similar in many physical characteristics such as colouration and shape of shell. However, *D pulchellus* is mostly associated with sand with finer grains, whereas *D. rugosus* burrows in coarser grain sand (Edmunds, 1978). For example, Akita *et al.* (2014) observed *D. pulchellus* to inhabit the intertidal zone of the La beach with a characteristic fine grain size. However, *D rugosus* was observed along the Chorkor beach associated with coarse grain sizes. Other records of *D. pulchellus* in Ghana have been reported along the Esiama beach in the Western Region of Ghana (Ntiamoa-Baidu *et al.*, 2014a; Grond *et al.*, 2015), where they occur in high densities. For example Grond *et al.* (2015) observed *D. pulchellus* to thrive in shell banks of 1-3 m wide, with densities of about 170,000 ind/ $m^2$.

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### 2.10.3 Factors influencing the distribution of *Donax pulchellus*

Several environmental factors influence the distribution, growth and survival of *Donax* spp. Temperature, availability and abundance of food are very important factors that influence the growth of *Donax* spp. Other equally important environmental factors include salinity and predation. *Donax* spp that inhabit the intertidal zone of beaches have been observed to show high degree of tolerance to temperature variation than their subtidal counterparts (Ansell *et al.*, 1980). Furthermore, a decline or increase in salinity may be detrimental to the survival of some *Donax* spp. For example *D. vittatus* could hardly tolerate low levels of salinity accompanied by high temperature, but the intertidal *D. trunculus* shows a greater tolerance to these conditions (Ansell, 1983). Low phytoplankton availability has been observed to influence reduction in growth rate of some species of surf clams. Several environmental factors may operate together to influence significantly the ecology of *Donax* spp. For example the growth of *D. trunculus* was observed by Gaspar *et al.* (1999) to be influenced by the interactions of temperature, salinity and food availability.

In Ghana, the distribution and growth of *D. pulchellus* is influenced by salinity, nitrate content and grain size (Akita *et al.*, 2014). In their study along the La and Chorkor beach, Akita *et al.* (2014) observed that *D. pulchellus* shells increased in length in relation to increasing salinity of surface sea water and decreasing sediment temperature. Furthermore, the mass of *D. pulchellus* declined with increasing temperature of surface sea water. *Donax pulchellus* also prefer to burrow in sandy beaches with finer grain sizes (Edmunds, 1978). The growth of *D. pulchellus* also increase with higher concentration of nitrate, a measure of food availability (Akita *et al.*, 2014).

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## 2.11 Feeding styles, strategies and habitats of sanderlings

Sanderlings are circadian foragers (Ntiamoa-Baidu *et al.*, 1998), spending most of their time feeding. Sanderlings exhibit different foraging styles and techniques in obtaining prey depending on the behaviour and ecology of the prey, time of the day and the environmental condition of the habitat (Burger *et al.*, 1977; Burger & Gochfeld, 1991a). Three different foraging styles and techniques have been identified for sanderlings; namely pecking, probing and sewing/threading. These foraging styles are based on visual, tactile and/or mechanoreceptor sensors. Sanderlings' visual foraging styles are exclusively pecking and sometimes probing. Tactile and mechanoreceptor styles of foraging include probing and sewing/threading (Ntiamoa-Baidu *et al.*, 1998; Nuka *et al.*, 2005; Grond *et al.*, 2015; Lourenço *et al.*, 2015). Sanderlings may employ probing and sewing as a technique in search of prey on dry sand and substrate covered with thin film of water.

Pecking yields higher success rates than probing and sewing (Lourenço *et al.*, 2015; Lourenço *et al.*, 2017). However, probing and sewing enhances the capturing rate of sedentary polychaetes by shorebirds (Kelsey & Hassall, 1989). The type of substrate and densities of prey may cause a predator to switch foraging technique from visual to tactile to increase prey capture success (Piersma, 2011; Lourenço *et al.*, 2016b; Lourenço *et al.*, 2017). For example, sanderlings showed higher pecking rate of 50.6 ± 10.9 pecks/min along a sandy beach to 37.7 ± 9.2 pecks/min in muddy-sand habitat (Lourenço *et al.*, 2015).

Sanderlings show characteristic fast runs or chase after wave breaks when foraging along sandy beaches. These runs are in pursuit of prey that are exposed to the surface after each wave break (Grond *et al.*, 2015). Using their eyes, sanderlings are able to identify prey trying to burrow into the sand or readily lying on the surface of the sand, and attack them with either a single or multiple pecks prior to consumption. Sanderlings employ short flights to increase

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their chances of obtaining and capturing prey identified short distances away.

Foraging efficiency of sanderlings may be related to the tidal cycle. Sanderlings spend less time foraging close to high tide when most of the foraging area are submerged under water and *vice-versa* (Vanermen *et al.*, 2009). Grond *et al*. (2015) observed sanderlings to forage more during low tide when most part of the beach can be accessed. Sanderlings may combine several actions in order to obtain prey. To maximise intake rate along sandy beaches, sanderlings chase after outgoing waves and quickly peck on exposed invertebrates before they burrow into the sand. Sanderlings, like most waders, practice kleptoparasitsm, stealing prey from other conspecifics or heterospecifics, especially when foraging on larger prey items (Zwarts *et al.*, 1990a).

Sanderlings prefer to spend the non-breeding season along beaches with sandy substrate (Ntiamoa-Baidu & Hepburn, 1988; Ntiamoa-Baidu, 1991b; Petracci, 2002; Nuka *et al.*, 2005; Ntiamoa-Baidu *et al.*, 2014a). On the contrary, most sandpipers, such as curlew sandpipers *Calidris ferruginea*, prefer beaches with muddy substrates (Ntiamoa-Baidu, 1991b). A critical environmental parameter of shorebird habitats that influences foraging is the depth of water (Ntiamoa-Baidu *et al.*, 1998). Other important parameters could be the ambient temperature (Castro *et al.*, 1992), tidal effect (Grond *et al.*, 2015) and morphology of beach (Castro *et al.*, 1992). Morphologically, the tarsus length explains which species can successfully forage in a particular depth of water. In other words, the depth of water may limit foraging prowess of some species whilst enhancing that of other species. Sanderlings forage in water up to a depth of 3 cm (Ntiamoa-Baidu *et al.*, 1998). The depth of water is also important in determining the densities of invertebrates. As water depth decreases especially in coastal habitats such as lagoons, estuaries and tidal flats, the salinity increases. High salinity could be detrimental to benthic invertebrates (Ntiamoa-Baidu *et al.*, 1998; Battley *et al.*, 2003), which form bulk of the diet of waders and other waterbirds. Such high saline environments may be rendered as

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poor foraging environments for waterbirds, because of the limited food supply and also because getting rid of the excess salt is energetically expensive.

## 2.12 Interference and prey depletion

Interference refers to decline in intake rates of prey by a predator (Goss-Custard, 1980). There may be several factors that may lead to interference amongst foraging shorebirds. These include the presence of con- and hetero-specifics (Ens & Goss-Custard, 1984; Goss-Custard *et al.*, 2006; van den Hout *et al.*, 2014), presence of humans (Thomas *et al.*, 2003), predation, anti-predatory strategies of the prey (Goss-Custard, 1970b), use of poorer foraging microhabitats (Goss-Custard, 1970a; van den Hout *et al.*, 2014) and kleptoparasitism (Goss-Custard, 1980). As predation intensifies, which may or may not be related to increase in bird densities, the effect of intense predation may lead to prey depletion. Prey depletion also then leads to declines in intake rates (Goss-Custard, 1980). The variation in prey and predator densities provide a good foundation for discussion under the ‘optimal foraging theory’. Two of the key discussions under this theory are the ‘functional’ and ‘aggregate/ numerical response’ of predators to prey densities (van Gils, 2004; Gilg *et al.*, 2006; McKinnon *et al.*, 2014).

### 2.12.1 Functional and aggregate response of shorebirds to prey distribution

The distribution of shorebirds has been shown to be highly correlated with prey distribution (Piersma, 1987; Thomas *et al.*, 2003; Piersma & Lindström, 2004; Piersma *et al.*, 2005; van Gils *et al.*, 2006; Piersma, 2012). Habitats associated with high densities of prey are preferred by birds to those with lower densities. For example, spatial distribution of red knots has been shown to be positively correlated with spatial distribution of its main prey in different years; they tend to aggregate and explore areas rich in high quality prey (Piersma, 2012).

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The detection and aggregation of shorebirds in areas of higher prey densities have been studied extensively and explained in different ways in relation to different species. In red knots and other sandpipers, detection of buried invertebrates is achieved by the ability to sense buried prey from a distance (Piersma *et al.*, 1995). Other species such as the Eurasian Oystercatcher *Haematopus ostralegus* perceives buried prey with the help of probing bills. The different approaches used by different species have to do with the specialised features associated with the bills of shorebirds (Piersma *et al.*, 1998).

The Ideal Free Distribution (IFD) theory suggests that as food is uniformly distributed in the environment, predators also aggregate themselves in response to pry such that the number of predators on each patch is directly proportional to the available food resource (Sutherland, 1983; Tregenza, 1995). Therefore under such a condition, there is no need for foragers to switch foraging patch (van Gils & Piersma, 2004). However, hardly is there such an ideal situation observed in nature. Predators are limited in foraging as prey distribution is patchy and there is a very high variation in densities of prey. Predators, through the dynamics of prey availability, spend time searching and handling prey, which definitely influences intake rates.

Functional response deals with a predator’s intake rate in response to variation in prey distribution and densities, whereas aggregate/numerical response explains how predators are distributed in response to prey availability (Stephens & Krebs, 1986). These two responses shape communities of social foragers and drive fitness and survival amongst individuals. Through the functional response of conspecifics, other individuals foraging in a flock (for example, community of waterbirds) may learn of profitable areas to visit and forage (Ruthrauff *et al.*, 2013).

Several models have been postulated and tested on the functional response of shorebirds (Sutherland, 1983; Piersma *et al.*, 1995; Tregenza, 1995; Cummings *et al.*, 1997; van Der

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Meer & Ens, 1997; Skalski & Gillman, 2001; Jeschke *et al.*, 2002; Vucetich *et al.*, 2002); however, the simplest of them, the Holling's disc equation, entails the searching and handling time of prey. In this model, the intake rate of a predator is dependent on the extent to which prey is handled externally (Holling, 1959). Modification of this model has given rise to more complex models that take different variables into consideration. Predators do not just have to deal with the external handling of prey, but whilst searching for prey, predators receive competition from other predators in the process. This competition or interference is explained by the increase in predator numbers and/or decline in prey densities, because of impact of predation intensity or adaptive strategies of prey to predation. Another twist to the modified models is the incorporation of digestive constraints that predators encounter when foraging (Jeschke *et al.*, 2002; Piersma *et al.*, 2003; van Gils *et al.*, 2003a; van Gils *et al.*, 2003b; van Gils *et al.*, 2005a). Predators have to pay the price by spending time processing ingested poor quality prey which results in a reduction of intake rates of predators.

For example, van Gils & Piersma (2004), using the red knot *Calidris canutus*, a species closely related to the sanderling in foraging behaviour, as a study subject proposed and tested experimentally, modified models of the Holling's disc equation. Their modified models were based on the presence and absence of interference in a 'digestion-limited' and 'handling-limited' paradigms of foraging knots. Out of the four models van Gils and Piersma (2004) tested, the best model in explaining the functional response of a predator under experimental condition was the one which described foraging birds having to compete with other conspecifics for space and prey and are digestively constrained. In testing this model in the field, the aggregate response of knots showed that selection of foraging patches with high prey densities was not really an issue. This was because the long-term foraging rates of knots were rather controlled by digestive constraints and as such, the presence of high numbers of prey did not matter, but how many can be ingested and processed at a time was the issue.

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Therefore, little interference was observed amongst huge flocks of foraging knots, recognising also that knots receive protection when foraging in large flocks (van Gils & Piersma, 2004).

Other studies have also shown that predators switch to alternative prey when they realise that the total response (thus functional response x aggregate response) to prey distribution has significantly declined (Wilson & Bromley, 2001). Nevertheless, the switching of prey or foraging patches may not necessarily be related to significant decline in prey numbers. Age-related interference observations have been reported in a number of wader studies and clearly, juveniles are always presented with less profitable sites or patches to forage in, which is another factor that explains the lower survival rates in juveniles compared to adults (Boyd & Piersma, 2001; Baker *et al.*, 2004). The quality of juvenile foraging patches may be related either to high predation risk or lower prey availability. For example, van den Hout *et al* (2014) observed juvenile red knots to forage nearshore, areas marked by high predation risk, because adults had selected areas between offshore and nearshore which were of lower predation risk. However, the juvenile knots failed to increase intake rates in line with the idea of food-safety trade-off (i.e. individuals pay off the cost of foraging in dangerous areas by maximising their energy intake), similar to that observed in juvenile redshanks (Cresswell, 1994a). Piersma *et al.* (1998) associated this observation with the inexperience and lack of skills of juveniles in competing with adults for prey.

## 2.13 Danger management by foraging shorebirds

The habitats of shorebirds are compromised from time to time by several factors which influence the behaviour and populations of shorebirds either positively or negatively. These factors may either be natural or anthropogenic. Amongst such factors include tidal action, coastal erosion through sea level rise, natural predation risk, threat posed by human densities

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and related activities, prey densities and availability, invertebrate predator-evasion strategies, presence and interactions amongst conspecifics and/or heterospecifics, and noise levels (Thomas *et al.*, 2003; Yasué, 2005). The response by shorebirds to potentially disturbing factors may be species specific, age- and sex related (Cresswell, 1994a; Leyrer *et al.*, 2012; van den Hout *et al.*, 2014) and dependent on the frequency, type and agent of disturbance (Fitzpatrick & Bouchez, 1998; Lafferty, 2001a). Therefore, shorebirds may learn from repeated pattern of occurrence of disturbances and habituate to them accordingly.

### 2.13.1 Foraging shorebirds and human disturbances

Human densities within shorebird habitats have increased significantly over the years and there has always been a continuous interaction between populations of shorebirds and that of humans. These interactions become problematic when they pose threat to shorebird populations, for example, competition for space. The increase in human densities has been attributed to urbanization and coastal development, which have decreased the quality of shorebird habitats. The impact of human disturbances on shorebird populations depend on the type of human activity (Burger & Gochfeld, 1991a; Burger, 1994; Lafferty, 2001a, 2001b; Thomas *et al.*, 2003; Yasué, 2005) and position of the activity on the beach (Lafferty, 2001a).

Shorebirds that forage mostly by the watermark at low tide are likely to be disturbed more by humans than those foraging and roosting at the upper beach, because of spatial distribution in occurrence and activities of humans. Studies have also shown that shorebird populations have suffered significant decreases in numbers that is strongly correlated to the intensity of development projects within their habitats (Howe *et al.*, 1989; Thomas *et al.*, 2003; van Roomen *et al.*, 2015).

Several studies have been carried out on the impact of human activities on the behaviour of certain species of shorebirds and how these activities influence the survival of birds. These

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include studies on sanderlings (Burger & Gochfeld, 1991a; Thomas *et al.*, 2003), western snowy plovers *Charadrius alexandrinus nivosus* (Lafferty, 2001b), piping plovers *Charadrius melodus* (Burger, 1987), semipalmated plovers *Charadrius semipalmatus* (Burger, 1997; Yasué, 2005), least sandpipers *Calidris minutilla* (Yasué, 2005) and oystercatcher *Haematopus palliatus* (Vines, 1992). Populations of shorebirds may resort to different behavioural strategies in order to accommodate disturbances from humans to certain degrees, beyond which they would be forced to desert the said area, in which case the habitat may no longer be described as a good quality habitat.

Coastal communities depend very much on coastal wetlands for their livelihoods. The availability of such resources within coastal wetlands ensures the continuous presence of humans within such areas. Among the commonest human-related beach activities include fishing, shellfish harvesting, walking leisurely either with or without pets such as dogs, use of manual or engine-driven automobiles, recreational activities such as swimming, surfing, amongst others. These activities have been shown to influence the behaviour of shorebirds, and to some extent pose as threats to foraging and resting birds (Burger & Gochfeld, 1991a; Thomas *et al.*, 2003; Yasué, 2005; Yasué *et al.*, 2008). The threats become worse if the said habitat doubles as a tourist attraction site.

Shorebirds may spend twice as much time foraging in the absence of humans as in the presence of humans (Burger, 1994). The frequency with which disturbances are perceived by foraging birds may explain their increased alertness and reaction to disturbances. Thomas *et al* (2003) observed that human densities, human activities and proximity, reduced the foraging time and rates of sanderlings significantly. Burger and Gochfeld (1991) also observed foraging rates of sanderlings to be reduced by human activities. In their explanation, they claimed that the sanderlings had to apportion more time to being vigilant, thereby reducing time spent on foraging. The time spent on vigilance by shorebirds is dependent on the

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occurrence of disturbance factors (Burger & Gochfeld, 1991a; Lafferty, 2001a, 2001b; Frid & Dill, 2002). Thomas *et al* (2003) observed about 96% of sanderlings within up to 30 meters of human disturbance responding to such disturbance either by running or flying every 15 minutes. This means that there is less time for foraging, but more energy expended through escape activities.

The inefficiency of shorebirds in foraging because of disturbances may affect survival and reproduction due to inadequate rate of storage of fat for other life processes (Burger, 1994). Burger & Gochfeld (1991) observed that lost foraging time used in managing or accommodating disturbances may be accounted for by nocturnal foraging by some species of shorebirds when human disturbances are relatively low. The decision to forage at night depends on a trade-off between starvation and threat to survival (Burger & Gochfeld, 1991a; Lima, 1998; Yasué, 2005). Therefore, the decision to forage at night must reflect the fact that energy cost to avoidance of humans or other forms of disturbances within the limits of foraging areas during the night is lower than during day time. Night foragers need to meet certain criteria to increase their efficiency in feeding at night. Such a bird must have a better nocturnal vision and foraging ability at night (Yasué, 2005; see also Burger & Gochfeld, 1991a; Dodd & Colwell, 1998; Rojas *et al.*, 1999). For example, the semipalmated plover was observed to respond to human densities with a decline in diurnal foraging rates, which was accounted for by foraging at night (Yasué, 2005).

Shorebirds have been observed generally to tolerate high human densities (Burger & Gochfeld, 1991a; Burger, 1994). However, if the impact of the densities of humans on shorebirds become extreme, shorebirds flee from such environments (Vines, 1992) if there are no alternative feeding sites (Gill *et al.*, 2001). Vines (1992) observed oystercatchers to flee onto islands near to their main habitat to forage and nest when they could no longer tolerate the increase in human densities in Florida. Thomas *et al.* (2003) observed a significant

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difference in the Minimal Approach Distance (MAD) sanderlings could tolerate to the number of people around and this was indicative of the difference in foraging times spent by sanderlings. The extent of tolerating human activities by foraging birds may be dependent not only on the number of people present, but also on the type of activity. Fast motion human activities such as jogging are likely to initiate a quicker response by foraging or roosting birds than slow motion activities (Lafferty, 2001a; Thomas *et al.*, 2003).

Furthermore, shorebirds find solace in foraging in large flocks, which increases their foraging rates even in the presence of humans and other disturbing factors. This is because, each individual within a large flock is a potential threat perceiver and contributes to minimizing the net threat by providing additional support to the detection of an attack (Elgar, 1988; Cresswell, 1994b). These scenarios support the optimal foraging theory and associated predator dilution effect (Goss-Custard, 1980; Stephens & Krebs, 1986).

Foraging rate is inversely related to density of humans present at the foraging site. Yasué (2005) showed that foraging rates of the semipalmated sandpiper decreased with increasing human densities. However, shorebirds may only conform to this observation when some other conditions such as flock size, abundance and availability of food are controlled for. For example, Yasué (2005) observed that the feeding rates of the least sandpiper decreased under conditions of high human densities and large flock size, but increased under conditions of high human and prey densities. Foraging birds are slow to respond to intruders when feeding in areas with high prey density; are reluctant to leave such profitable spots, because trading off high foraging rates to survival by foraging in areas with lower prey density may be costly in terms of their energy demands (Yasué, 2005).

### 2.13.2 Foraging shorebirds and dogs

There have been studies also on the extent of impact of other pressures or activities on

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shorebird population within their habitats. The presence of dogs within shorebird habitats have been reported to be more problematic than that of humans. The densities of dogs within shorebird habitats may not necessarily provide a clear indication on the level of disturbance they cause to foraging birds. This is because, unlike the case of humans, where disturbance is high as human density increases, a single dog can actively chase shorebirds around and eventually cause significant impacts on the energy acquisition and expenditure of shorebirds (McCrary & Pierson, 2000; Lafferty, 2001a, 2001b). Because of this, shorebirds are more sensitive to and react quicker to presence of dogs than to humans. For example, Lafferty (2001b) observed snowy plovers to be more alert to dogs and responded to the presence of dogs at distances twice what they reacted to in the case of humans.

### 2.13.3 Foraging shorebirds and predatory and scavenging birds

Evidence of disturbances from predatory and scavenging birds on foraging and roosting shorebirds also have been reported. Increase in human population in developing countries have been implicated in the over production and improper disposal of garbage in and around public recreational and business centres. The presence of garbage has also been strongly connected to the presence of scavenging birds, such as crows and vultures (Lafferty, 2001a). However, the presence and abundance of scavengers along coastal beaches, may influence the foraging behaviour of waders, reducing their foraging time and affecting the energy build-up and reserves. Shorebirds may also experience danger and predation risk, especially within non-breeding areas, because individuals are always on the move foraging, thereby exposing them to predators.

A non-breeding site may be termed ‘dangerous’ due to high numbers of predators as well as the habitat structure, but ‘risk’ involves the possibility of an individual bird being captured by a predator, which is also a measure of the danger and anti-predatory strategies employed by the prey (Lank & Ydenberg, 2003; van den Hout *et al.*, 2014; van Roomen *et al.*, 2014).

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Danger and risk of predation at non-breeding sites have been observed to be age-related (van den Hout *et al.*, 2014), where juveniles are forced to forage and inhabit areas associated with higher danger. Such areas may include nearshore and sand dunes close to the peripheral vegetation (Dekker & Ydenberg, 2004; Rogers *et al.*, 2006; van den Hout *et al.*, 2008; van den Hout *et al.*, 2010). Predatory birds are known to roost in the peripheral vegetation. Hence, surprise attacks within nearshore areas are higher than areas closer to the shoreline, and this puts juveniles at a higher risk (Cresswell, 1994a; van den Hout *et al.*, 2014).

### 2.13.4 Shorebirds tolerance to disturbances

Some studies have shown that, months that support peak counts of shorebirds double as the busiest months for human use of the same wetland (as reviewed by Yasué, 2005). In tolerating human densities, their activities and other sources of disturbances, shorebirds concentrate foraging and roosting activities in areas within the larger habitat that supports fewer people and lower frequencies of other sources of disturbances. Shorebirds also decide to keep a minimal approach/flight distance (MAD/MFD) from humans and their activities, but this distance is species and site specific (Lafferty, 2001a, 2001b; Thomas *et al.*, 2003; Yasué, 2005).

## 2.14 Conclusion

There is clearly a large volume of literature on shorebird ecology resulting from the great number of studies carried out on shorebirds and their wetland habitats. This review has focused on studies relevant to the general foraging ecology of shorebirds as well as the focal species for this thesis, the sanderling. The literature review has covered wetlands as habitats for waterbirds; waterbirds as bio-indicators of wetlands; distribution of shorebirds in Ghana; classification and conservation status of sanderling; biometrics of sanderlings; migration of

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sanderlings and distribution of sanderlings in Ghana. It also covered review on time-activity budgets of sanderlings; habitat quality; energy demands and management by non-breeding sanderlings; diversity and distribution of macroinvertebrates as prey for sanderlings; sanderling's diet composition; variations in shorebird densities and prey densities; prey choice and size selection; availability, accessibility and quality of sanderling prey; the prey, *Donax pulchellus*; feeding styles, strategies and habitats of sanderlings; interference and prey depletion, and danger management by foraging shorebirds.

Based on the available knowledge presented in the literature review, the key gaps, with particular reference to sanderling foraging ecology in coastal Ghana have been identified, and this informed the focus of this thesis.

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# CHAPTER THREE

# GENERAL METHODOLOGY

## 3.0.1 Study Area

### 3.1.1 Location and demography of the study area

The study was conducted along a 13 km sandy beach between the Ankobra (4°53'57.49"N, 2°16'11.13"W) and Amansuri (4°56'31.49"N, 2°22'58.58"W) estuaries in the Ellembelle district (Longitude 2° 05″W and 2° 35″W, Latitude 4° 40″N and 5° 20″N) in the Western Region of Ghana (hereafter referred to as Esiama beach; Figure 3.1). The Esiama beach constitutes part of the bigger Amansuri wetland which comprises an open water lagoon, raffia palm *Raphia vinifera* swamp forest, mangrove swamps and beaches (Ntiamoa-Baidu *et al.*, 2001). The Ellembelle district is about 360 km west of Accra. The Ellembelle district is bounded to the south by a 70 km stretch of sandy beach along the Gulf of Guinea, Wassa Amenfi West district in the north, Jomoro district in the west, and Tarkwa-Nsuaem district to the east. The population of the Ellembelle district is 87,501 constituting about 4% of the entire Western Region's population according to the 2010 Population and Housing Census (PHC). This district is more rural than urban as 80% of the entire populace reside in rural areas (Ghana Statistical Service, 2014). There is a high degree of movement of people in this district mainly due to search for jobs, especially during the fishing and farming seasons, as well as for mining prospects.

The Esiama beach experiences a semi-diurnal tide; meaning there are two equal high and low tides in a day. During spring low tide, the portion of the beach, between the watermark and the base of the sand dune or peripheral vegetation could measure up to 150 m. Most part of the Esiama beach may be classified as a dissipative beach characterised by the gentle beach slope, fine sand grains and a wide surf zone. However, other parts of the beach, especially

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towards the Amansuri estuary or Azuleloanu is characterised by steep gradient, narrow beach width and coarse sand to the west, which satisfies the description of a reflective beach. These different beach types create conditions that support different invertebrate species in varying densities (Akita *et al.*, 2014).

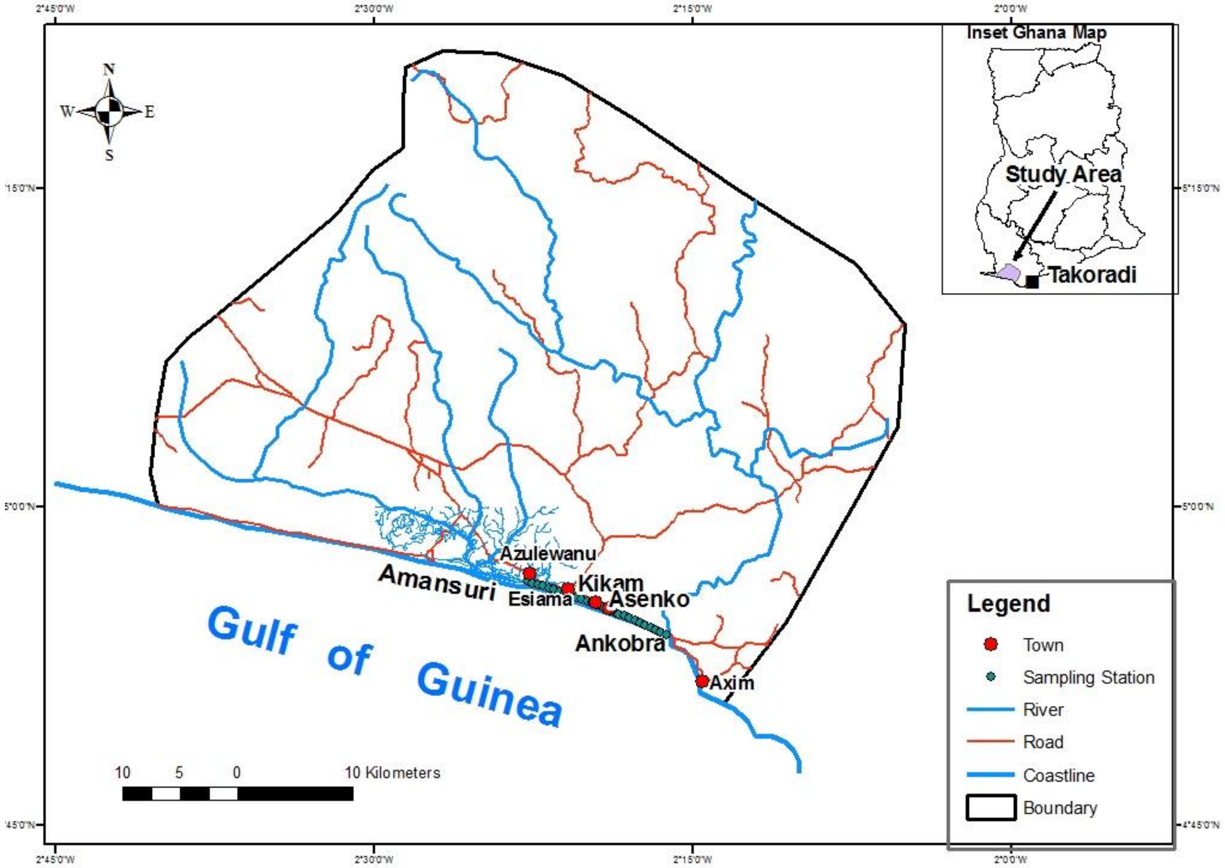

**Figure 3.1 Map of the Ellembelle district and the study area.** (Note that the study area is the sandy beach between Amansuri and Ankobra estuaries).

There are seven different villages along the 13 km-Esiama beach. From east to west, the villages are Ankobra, Asanta, Bobrama, Asemko, Kikam, Esiama and Azuleloanu. The total human population living in these villages is estimated at 18,375 according to the 2010 PHC (Ghana Statistical Service, 2012). Human population dynamics over the past five decades shows an increase of over 300% (Figure 3.2).

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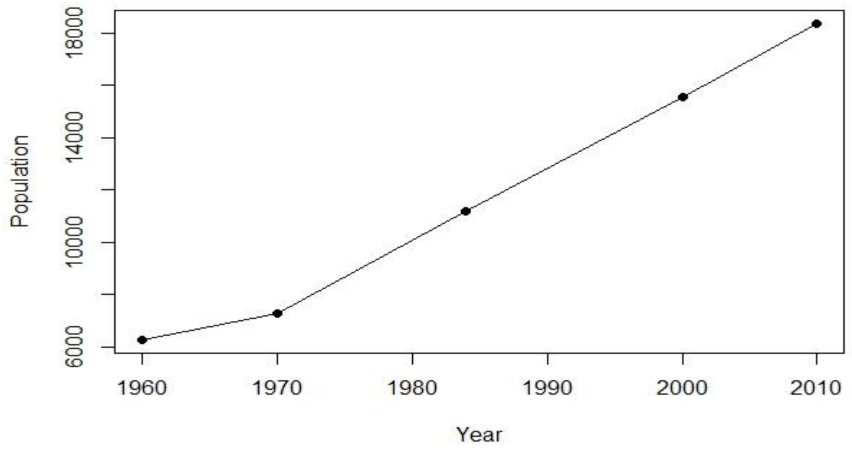

**Figure 3.2 Population trends of the seven communities along the Esiama beach.** (Data obtained from the Ellembelle District Assembly and the Ghana Statistical Services)

### 3.1.2 Topography, geology and pedology of the Ellembelle district

The topography of the Ellembelle district is such that the highest point is about 140 meters above sea level. The geology of the Ellembelle district shows that the rocks contain economic minerals such as gold, sandstones, kaolin and silica (Ghana Statistical Service, 2014). The underlying rocks are also important in the provision of freshwater, which supports both economic and domestic livelihoods of surrounding communities (Hughes, 1992). The soil type supports cultivation of several cash crops including oil palm, coconut, cocoa and coffee as well as food crops such as plantain and cassava (Ghana Statistical Service, 2014).

### 3.1.3 Drainage system of the Ellembelle district

The Ellembelle district is characterised by a well-established drainage system, which have given rise to vast areas of swamps and marshlands. The study area supports some of the important rivers in Ghana. One of the major rivers that flows through the area is the Ankobra River with Ahama and Nwini as its major tributaries. To the south-western part of the study area is the Amansuri River with its characteristic blackish colour. The northern part of the

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area supports the Ankasa and Draw Rivers with their tributaries clearly defining the territory and boundaries of the Ellembelle district (Turner, 1980).

The two estuarine areas (Amansuri and Ankobra estuaries) receive sediments from upstream of their respective rivers, as well as the ocean, creating vast sand deposits that serve as foraging and roosting sites for waders and tern species. Nevertheless, these areas of sand deposits are lost at certain times of the year because of the dynamic nature of beaches. Several smaller seasonal streams flow into the sea thereby truncating the continuity of the beach (Plate 3.1).

**Plate 3.1 A stream that drains one of the communities along the Esiama beach into the sea.** (Kindly note the blockage of the stream by sand deposited by tidal action).

### 3.1.4 Climate of the Ellembelle district

The Ellembelle district lies in the wet-equatorial climatic zone of the West African region characterised by two distinct rainfall seasons, between May and July and between September and November. The total annual rainfall ranges from 1,900 mm to 2,100 mm (Hackman,

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2014). The average temperature of the Ellembelle district is 29.40°C and the relative humidity ranges from 26.6% to 27.9% (Ghana Statistical Service, 2014).

### 3.1.5 Ecological habitats, vegetation types and floral composition

There are three distinct vegetation types in the Ellembelle district. The northern part of the district includes a semi-deciduous rain forest which transforms to secondary forest going south mainly due to anthropogenic activities such as tree logging and farming (Ghana Statistical Service, 2014). The coastal area is mainly savanna vegetation characterised by extensive coconut *Cocos nucifera* plantations initially cultivated purposely for commercial production of coconut oil (Plate 3.2A). The coconut trees are predominantly the emergents reaching heights of about 22 m. The tall coconut trees are ecologically important for predatory birds such as the yellow-billed kite *Milvus migrans parasitus* (Plate 3.2 D), Lanner falcon *Falco biarmicus*; and scavenging birds such as the hooded vulture *Necrosyrtes monachus* (Plate 3.2 E), palm-nut vulture *Gypohierax angolensis* and pied crows *Corvus albus*. Other important tree species include timber species such as *Elaies guineensis* and non-timber species such as bamboo, raffia palm, large spiny aroid *Cyrtosperma senegalense*, *Baphia nitida*, *Uvaria ovata,* and *Borassus palm.* There is well as extensively established mangrove vegetation along the coastal areas, the various rivers and swamps (Ntiamoa-Baidu *et al.*, 2001; Amlalo, 2006; Ghana Statistical Service, 2014). There are interspersed grasslands, which are liable to flood during the rainy season. The dominant grass species include *Hyparrhenia subplumosa* with associated sedges such as *Rhyncospora waliichiana* (Owusu, 2014).

### 3.1.6 Faunal composition

The different vegetation zones within the district support different faunal species. The varying habitat types provides several micro- and macro-habitat conditions for different faunal species to inhabit leading to an assemblage of a large and quite diverse faunal community. For example, the forests, freshwater, swamps, ocean, lagoon and even farmlands, provide animals

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with various ecological niches to occupy. The coastal beaches are important nesting grounds for marine turtles (Mensah, 2008). About 128 species of birds belonging to 33 families have been reported from the Amansuri wetland, excluding the Esiama beach (Owusu, 2007). About 50 species of waterbirds make use of the sandy Esiama beach and the Amansuri estuary at certain times of the year (Ntiamoa-Baidu *et al.*, 2001). Some commonly occurring waterbird species within the study area include waders such as Sanderling *Calidris alba*, Grey plover *Pluvialis squatarola*, Ruddy turnstone *Arenaria interpres* and Common ringed plover *Charadrius hiaticula*. The Esiama beach regularly supports ca. 20 individuals of the Near Threatened Eurasian oystercatcher *Haematopus ostralegus*, the largest count on all monitored local waterbird non-breeding sites. Some regularly observed tern species also include Sandwich tern *Thalasseus sandvicensis*, Royal tern *Thalasseus maxima*, Common tern *Sterna hirundo* and Black tern *Chlidonias niger* (Gordon, 1995; Ntiamoa-Baidu *et al.*, 2001). Mammals species reported to occur in the area include Mona monkey *Cercopithecus mona*, Red river hog *Potamochoerus porcus*, Bushbuck *Tragelaphus scriptus*, Maxwell duiker *Philantomba maxwellii* and Western black and white colobus monkey *Colobus vellerosus*. Reptile species that occur in the area include the Nile monitor lizard *Varanus niloticus*, Dwarf crocodile *Osteolamus tetraspis* and the Slender-snouted crocodile *Mecistops cataphractus*. About twenty-eight species of fish also occur in the study area (Ghana Wildlife Society, 1998; Owusu, 2014). The Amansuri wetland supports a large community of benthic invertebrates that include different species of insects (Dipterans and Trichopterans), Annelids (Oligochaetes, Polychaetes, Hirudines), crustaceans such as shrimps, hermit crabs and amphipods (Aggrey-Fynn *et al.*, 2011).

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**A. Peripheral coconut vegetation**

**B. Fishing activity**

**C. Shellfish collection**

**D. Yellow-billed kites**

**E. Hooded vulture**

**F. Recreational facilities**

**Plate 3.2 The Esiama beach**

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### 3.1.7 Economic livelihoods of communities within the Ellembelle District

The main economic activity of communities within the district is agriculture (including fishing and forestry) engaging about 35% of the population (Ghana Statistical Service, 2014). Fishery is concentrated on both freshwater and marine areas. On the Esiama beach, fishing involves the use of canoes and seine fishing in the surf zone (Plate 3.2 B). There are several taboos that regulate fishing activities in the study area to ensure sustainable extraction of fish stock (Ntiamoa-Baidu *et al.*, 2001). There are two major marine upwelling along Ghana's coast and these occur between June/July-September/October and January-March. These conditions influence fish catch in coastal fishing communities (Armah & Amlalo, 1998). The periods of marine upwelling explain the peak fishing seasons within the study area; the major fishing season being between July and September and the minor season between November and January. Other important economic activities on the Esiama beach include shellfish harvesting (Plate 3.2 C), sand winning, recreational (Plate 3.2 F) and industrial developments, commercial trading and coconut oil production. Mining activities and cultivation of cash crops occur in the northern part of the district (Amlalo, 2006).

## 3.2 Study design and data collection

The study was carried out from September 2015 to February 2018. The methods used included direct field observations, experiments with captive sanderlings and laboratory analyses. All field sampling were carried out along the 13 km transect between the Amansuri and Ankobra estuaries.

### 3.2.1 Macroinvertebrate sampling

To map out and document macroinvertebrates and their respective abundances available for sanderlings as prey, benthic sampling techniques as described by Akita *et al.* (2014) and

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Ntiamoa-Baidu *et al*. (2014) were employed with some modification to suit the purpose of this study.

Benthic macroinvertebrates were sampled with a hand corer, with a base diameter of 14.9 cm, at every 500 m from the Amansuri estuary to the Ankobra estuary every month at spring low tide from September 2015 to December 2017. Samples were taken from 27 different locations identified by their GPS coordinates (Plate 3.3). Each sampling location was visited every month during the sampling period.

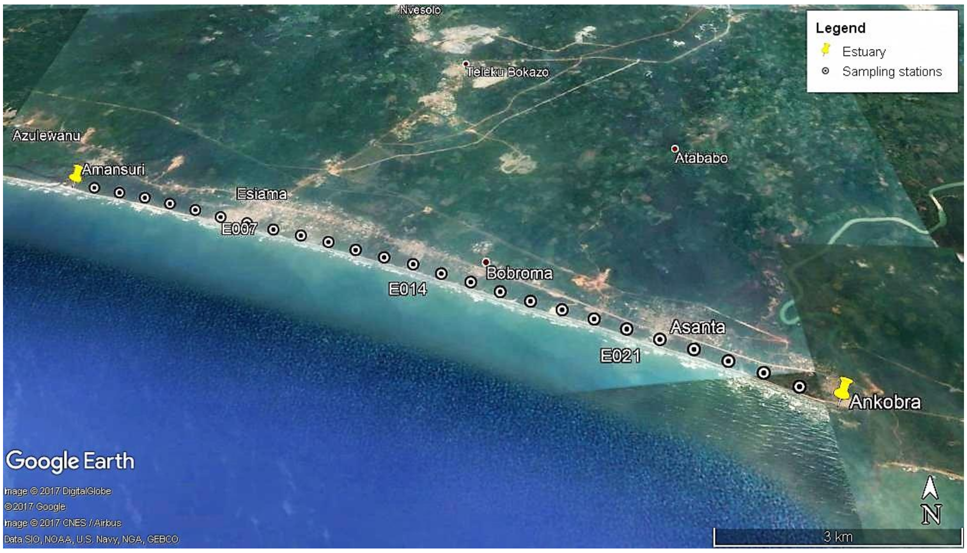

**Plate 3.3 Sampling locations along the Esiama beach in the Western Region of Ghana** (Google earth, 2017).

Three different replicates were taken at each sampling location, at the high tide (nearshore), low tide (shoreline) and within the intertidal zone of each sampling location (Figure 3.3). Samples were taken up to a depth of 10 cm (Plate 3.4 A); and the first 3 cm layer was treated separately from the remaining 7 cm (Plate 3.4 B). This was done to determine densities of macroinvertebrates accessible to sanderlings, because with an average bill length of 2.5 cm, foraging sanderlings could be expected to reach a depth not exceeding 3cm below the ground level.

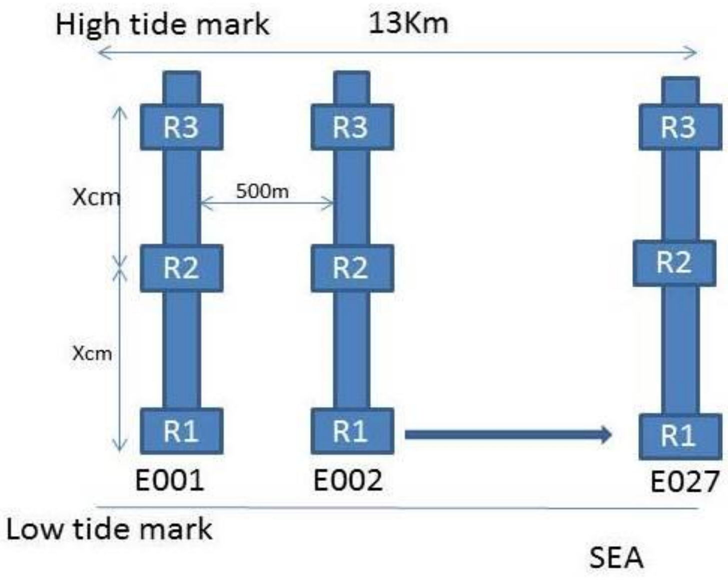

**Figure 3.3 Schematic representation of benthic sampling design employed along the 13 km-Esiama beach.** (Each 'R' represents a replicate and each 'E' represents a sampling station. E001 and E027 represent sampling locations closest to the Amansuri and Ankobra estuaries respectively).

In total, 81 different samples each for the top 3 cm and bottom 7 cm were collected along the beach on monthly visits. Samples were washed in-situ through a 1 mm-mesh size sieve (Plate 3.4 C). All macroinvertebrates found in the sieve were fixed in 10% formaldehyde solution, labelled appropriately and transported to the laboratory for sorting and identification.

In the laboratory, invertebrates were taken out of the fixative and air dried for 30 minutes to reduce the chances of individual invertebrates clinging onto each other as well as reduce the pungent smell of formaldehyde on samples. The samples were sorted into broader taxonomic classes (based on morphological features). Species were identified and classified with the help of keys and guides (Akita *et al*., 2014; "WoRMS taxon details", 2015) and confirmed by laboratory technicians from the African Regional Postgraduate Programme in Insect Science (ARPPIS) of the University of Ghana. The different species per each sampling station were recorded together with their abundances. A sub-sample of each species was taken from each

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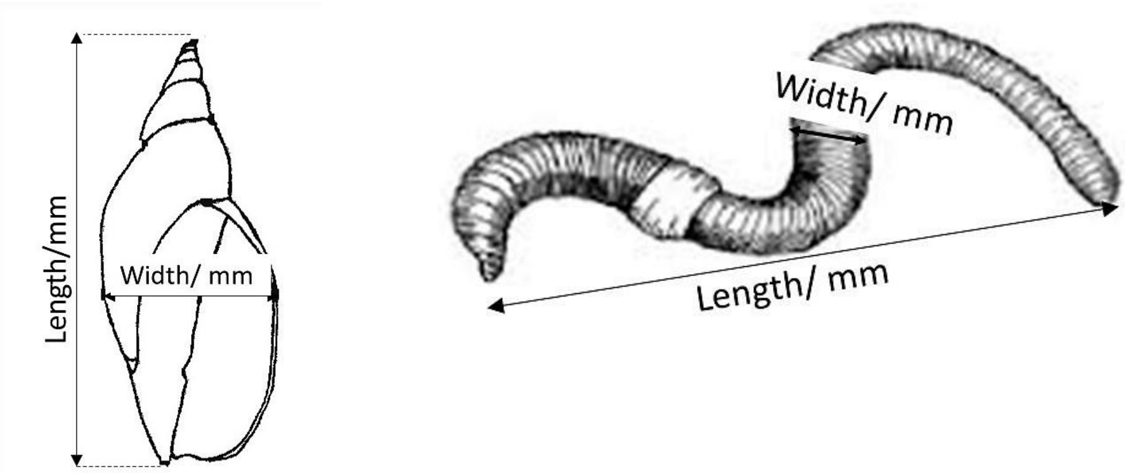
sample and morphometric parameters such as the height, length and width of macroinvertebrates were measured using a Wiha tools 150 mm Dial caliper 0.1 mm. The mass of macroinvertebrates was measured using a VWR LA 164i analytical balance to a 0.0001 g (Plate 3.4 D). The length of macroinvertebrates was measured as the longest distance along the surface of the invertebrate, whilst the width referred to the distance across the surface of the invertebrate. For example, the length of bivalves was measured as the longest distance along the anterior-posterior axis, with the width being the maximum lateral distance across the hinge of a closed shell and the height as the maximum distance across the dorsal-ventral axis (Gaspar *et al.*, 2001; Gaspar *et al.*, 2002). The length or height of gastropods was measured as the maximum distance from the apex to the siphonal canal along its central axis, whereas the width was measured as the maximum measurement of the shell perpendicular to the central axis (Allen, 2014). The length of polychaetes was measured as the maximum distance between the prostomial part of the head and the anal region of the tail of its body at full stretch (Rouse & Pleijel, 2001).



**A. Gastropod** **B. Polychaete**

**Figure 3.4 Schematic diagram of a gastropod (A) and polychaete (B) showing biometric measurements taken**

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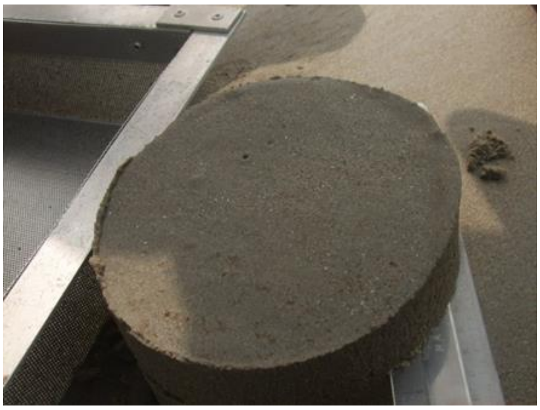
A. Hand corer used in collecting sand to a depth of 10 cm

B. Top 3 cm of corer sample to be processed separately



C. In-situ washing of sample in a 1 mm mesh size sieve

D. Weighing of mass of invertebrates

**Plate 3.4 Benthic macroinvertebrate sampling and processing**

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### 3.2.2 Biomass and quality of macroinvertebrates

Sanderlings swallow bivalves whole (Reneerkens *et al.*, 2009a; Grond *et al.*, 2015). The prey is crushed and processed in the muscular gizzard, after which the indigestible shells are excreted in the droppings. This process of food consumption also applies to other ingestible prey (small enough to be swallowed completely). Biomass was expressed as Ash Free Dry Mass of flesh ($AFDM_{flesh}$) for each macroinvertebrate and used in estimating prey quality (Dekinga & Piersma, 1993; van Gils *et al.*, 2003a; van Gils *et al.*, 2005a; Onrust *et al.*, 2013; van den Hout *et al.*, 2014; Grond *et al.*, 2015). For bivalves, ten individuals *Donax pulchellus* per each length class of 1.0 mm (range from 2.0-12.0 mm) were selected and the actual length measured to the nearest 0.1 mm, shell opened and flesh separated from the shell. Both shell and flesh were dried in separate crucibles to constant mass in a drying oven at 55-60 °C for 3 days and masses measured to obtain $DM_{shell}$ (Dry Mass of Shell) and $DM_{flesh}$ (Dry Mass of Flesh) respectively. The dried flesh was incinerated in a furnace at 550°C for 2 hours (Plate 3.5 A), and the ash content (Plate 3.5 B) measured as $AM_{flesh}$ (Ash Mass of flesh). The ash-free dry mass of flesh ($AFDM_{flesh}$) was determined as the difference between the dry mass of flesh and the ash mass ($AFDM_{flesh} = DM_{flesh} - AM_{flesh}$). The prey quality (Q) was estimated as the ratio of the average $AFDM_{flesh}$ to average $DM_{shell}$. That is;

$Q = (a \times d \times AFDM_{flesh}) / DM_{shell}$, (van Gils *et al.*, 2005a; Yang *et al.*, 2013)

where 'a' represents assimilation efficiency of 0.8 (Kersten & Piersma, 1987; Castro *et al.*, 2008) and 'd' is the energetic density of the flesh, equivalent to 22 kJ/ g $AFDM_{flesh}$ (Zwarts & Wanink, 1993; Yang *et al.*, 2013).

The procedure was repeated for the other macroinvertebrates. There was no measurement for $DM_{shell}$ for soft-bodied invertebrates such as amphipods and polychaetes, hence prey quality was determined as;

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$Q = (a \times d \times AFDM_{flesh}) / DM_{flesh}$.

For gastropods, the flesh could not be separated from the shell. Therefore, the $AFDM_{flesh}$ and $DM_{shell}$ were determined after the whole shell and the flesh were oven dried and incinerated together.

**A. Incineration of invertebrates in a furnace at 550°C**

**B. Ashes of isopods after incineration**

**Plate 3.5 Determination of biomass of macroinvertebrates**

### 3.2.3 Sanderling capture and colour marking

The Esiama sanderling population contains colour-marked individuals either marked in Ghana under the Ghana Ringing Scheme (GRS) or from other ringing schemes from countries along the East Atlantic Flyway, denoted by the colour of the plastic flag carried by a sanderling. All these colour marking schemes follow protocols accepted by the International Wader Study Group (IWSG) Sanderling Colour Ringing Scheme and European Union for Bird Ringing (EURING).

Sanderlings were captured using four two-shelved 12-meter and one 18-meter two-shelved mist nets. There was no reason for using mistnets of different lengths as these were the only

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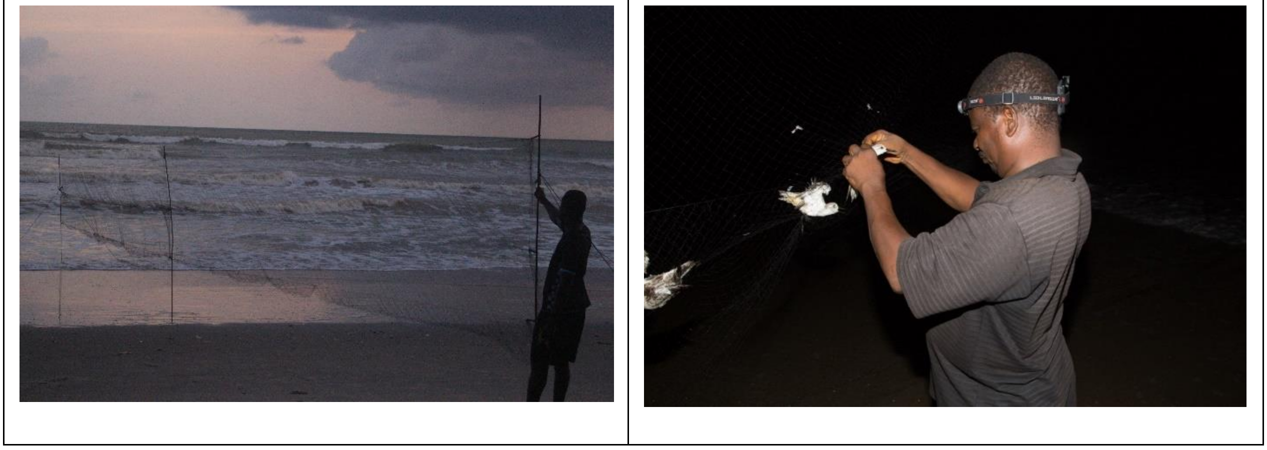
nets available at the time of trapping. The mist nets were set perpendicular to the shoreline at neap low tide (during which period the tidal range between high and low tide is at its minimal and tidal height is very low). This prevented mist nets from being submerged in the water at high tide and ensured captured birds could be removed safely at any time. To increase the capture rate of sanderlings, trapping was done during the first three nights of the crescent phase of the moon, when moonlit was lower allowing for a better concealment of mist nets. Two sets of mist nets were set perpendicular to the shoreline. The two sets of nets were set at a distance of 150 m apart. The first set of nets comprised of one 18-meter and one 12-meter mist nets. The second set of nets included three 12-meter nets. Mist nets were erected on 2.2-m iron poles anchored to the ground by two 1 m iron pegs (Plate 3.6 A). Mist nets were set late afternoon, opened at dusk, and closed at dawn for three consecutive nights every trapping month. Mist nets were inspected every two hours due to the distance of the location of the nets and the field processing site. Captured birds were carefully removed from the nets by trained technicians (Plate 3.6 B). Captured birds were placed individually in bird bags and transported to a research camp established 1 km away from the nets.



**A. Mist nets**

**B. Technician removing trapped sanderling**

**Plate 3.6 Mist netting of sanderlings along the Esiama beach**

At the research camp, the captured birds were quickly processed to avoid imposing any

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additional stress on them. Captured birds were carefully removed from the bird bags, held in the palm and the species identified using field guides (Borrow & Demey, 2013; Barlow & Dodman, 2015) where necessary. External body condition of sanderlings was carefully examined and morphometric measurements taken (Plate 3.7 A). Measurements recorded included wing length (the maximum chord length measured as the distance between the scapula and tip of the longest primary feather of a well-straightened wing), tarsus length (from the back edge of the tibio-tarsal joint and the intertarsal joint), tarsus and toe length (from the bottom edge of the longest toe to the back edge of the tibio-tarsal joint), bill length (from the back edge of frontal shield to the tip of the bill), total head length (from the back of the skull to the tip of the bill) and mass of each bird (Wood, 1987). The wing and tarsus plus toe lengths were measured with a stopped ruler to the nearest 1 mm whereas tarsus, bill and total head lengths were measured with a veneer caliper to the nearest 0.1 mm.  Body mass of sanderlings and other captured birds was measured with a digital balance to the nearest 1 g. The age of captured sanderlings was determined through plumage characteristics (Prater *et al.*, 1977; Reneerkens *et al.*, 2009a; Lemke *et al.*, 2012). State of moulted primary and breast feathers were assessed and scored on a scale of 0 to 5; 0 representing old feathers that needed to be replaced and 5 for fully-grown new feathers (Waltner, 1976).

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A. Total head measurement

B. Colour-ringed sanderling

**Plate 3.7 Biometric measurement (A) and colour ringing (B) of sanderling**

Each captured bird received the appropriate GRS metal ring size on the right tarsus except sanderlings, which received the metal rings on the tibia to make room for the plastic coloured rings on the tarsus. Individual sanderlings were uniquely colour marked before release. Each sanderling tarsus received two plastic colour rings and an additional red plastic flag placed on one of the tarsus according to the EURING and IWSG Colour Ringing Scheme (Plate 3.7 B). The red flag represents a sanderling first captured and coloured marked in Ghana. The position of the flag and the order of the colour rings are important in giving each sanderling a unique identity.

The release of birds into the wild was done before sunrise in order to avoid or reduce the chances of being captured by predators. Birds were either released close to a large flock of conspecifics so that, through a dilution effect (Cresswell, 1994b), the chances of being predated on will be reduced or at areas characterised by large beach width at the time of release.

## 3.3 Sanderling feeding studies

Feeding studies on sanderlings formed the core subject of this thesis. Combinations of

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different methods and protocols were employed to address specific aims and objectives of the study (for example, Dekinga & Piersma, 1993; Ntiamoa-Baidu *et al.*, 1998; Thomas *et al.*, 2003; van Gils *et al.*, 2003a; van Gils *et al.*, 2005a; van Gils *et al.*, 2006; Onrust *et al.*, 2013; Grond *et al.*, 2015; Lourenço *et al.*, 2015; Lourenço *et al.*, 2017). The methods and protocols under description were selected because, they have been used on the same species (sanderling) or closely related species (other sandpipers), under similar settings (tropical sandy beaches) and similar prey type (bivalves and crustaceans).

### 3.3.1 Sanderling feeding behaviour and strategies

Studies on the feeding behaviour of sanderlings involved a combination of direct field observation and experiments with captive sanderlings. Sanderling feeding styles and techniques were closely observed in the field through a 15-60x Swarovski spotting telescope from a 50-meter distance in the peripheral vegetation to avoid the observer being seen by the foraging birds. The foraging techniques exhibited by sanderlings were identified and described following Grond *et al.* (2015) and Ntiamoa-Baidu *et al.* (1998).

Upon sighting a flock of sanderlings, a 5-minute period was allowed for the birds to process and react to any form of disturbance. Sanderling feeding methods were classified as pecking (single movement of the bill), probing (continuous movement of the bill with a clear penetration in the sand) or sewing/threading (probing accompanied by a drag in the sand) in their approach to obtain prey. The latter has also been described as stitching (Lourenço *et al.*, 2008). Pecking was solely a visual strategy, probing comprised visually identifying a prey, but obtaining it through tactile means, whereas sewing/threading was totally a tactile foraging strategy (Ntiamoa-Baidu *et al.*, 1998; Lourenço *et al.*, 2015).

Important information such as the date and time of observation, the flock size of sanderlings, other shorebird species present and their abundance, and the part of the beach where

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sanderlings were foraging were recorded. Groups of foraging sanderlings were considered as different flocks if they were more than 50 m apart. The date and time of observation helped to document the preferred foraging style adopted by sanderlings during a particular time of the day, in relation to the tidal cycle and seasonal variation in prey and predator (sanderlings) densities. The part of beach utilized by sanderlings provided an idea of the type of prey exploited.

### 3.3.2 Foraging rates

It was not possible to actively measure successful intake rates of prey in the field because of the small sizes of macroinvertebrates exploited by sanderlings, which made observation of successful ingestion of prey practically impossible, even in captivity. However, intake rates were measured whenever sanderlings were foraging on larger preys. As a proxy, in this study, foraging rates was through observation and estimation of number of pecks made per minute and the time spent on probing and sewing. Foraging rates were measured using a focal individual approach following Thomas *et al.* (2003).

Amongst other parameters recorded prior to focal observation included: the date and time of observation, the feeding location (in relation to invertebrate sampling stations), the part of the beach where sanderling was foraging (in relation to the cross-tidal invertebrate sampling replicates), the flock size, other shorebird species present and their abundances, nearest neighbour distance (for both conspecifics and heterospecifics) and width of the beach (from the peripheral vegetation to the watermark). The approach used in estimating the nearest neighbour distance followed method used by Thomas *et al* (2003). Field observers were trained in estimating previously measured distances repeatedly to guarantee estimates were similar to actual measurements. In the field, the distance between a focal bird and the closest conspecific or heterospecific neighbour was estimated by averaging three replicated measurements either with a Nikon Forestry Pro Range Finder or directly with the unaided

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eye.

Within each encountered flock, an individual sanderling was selected and observed. Preference was given to colour marked sanderlings if present, in order to avoid repeated observations on the same individual. Focal observations were carried out with an 8 x 42 Texel optical binocular, a 15-60x Swarovski spotting telescope, a Zoom H1 handy voice recorder or a x60 optical zoom HD Lumix video camera. The binocular and telescope were used together with the voice recorder. Once an individual sanderling was identified, it was followed and observed for 1 minute, recording all feeding activities, which included the following; pecking, probing, sewing, running, staying vigilant/alert, aggressive interference behaviour and successful prey intake. Any observation that could not last for the entire 1 minute because of losing the focal bird through any form of disturbance or missed in a flock was discarded or treated as unsuccessful.

### 3.3.3 Experiment on feeding behaviour with captive sanderlings

In order to measure intake rates of prey by sanderlings, an experiment with captive sanderlings was designed in a safe and humane atmosphere. The welfare of the captive birds was taken into account and observed closely.

Six of the sanderlings mist-netted along the Esiama beach were colour banded for unique identification. These colour marked sanderlings were aged and weighed each day from day of capture, 23rd January 2017, to the day of release, 31st January 2018. Assessment of primary and breast feather moult was also done in order to exclude moulting birds who are likey to feed more due to the energy demands associated with moulting from the experiment. Sanderlings were kept in an experimental unit, which measured 120 x 80 x 40 cm and was made out of a wooden frame and plastic mesh. The experimental unit was kept indoors at the research centre located about 10 km away from the beach. The experimental unit was sub-

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divided into six compartments with each compartment measuring 40 x 40 x 40 cm. Adjacent compartments were separated by a wooden frame whereas opposite compartments were separated by a transparent plastic mesh. The bottom of each compartment was covered with sand sieved through a 1 mm mesh sieve to eliminate all buried invertebrates or plant materials that may serve as food for the birds. The top of the experimental unit was covered with a small mesh size fish net hooked to pegs at the edges of the wooden frame.

The initial stages of the experiment involved keeping a number of sanderlings together in a single compartment of the experimental unit. This was done to de-stress and condition them for the experiment, knowing that sanderlings are social birds and keeping them together in a flock is likely to hasten the conditioning process. Individual sanderlings were assigned separate compartments in the experimental unit after 24 hours, however they were rotated from time to time in these compartments to help familiarise them to the cage (National Research Council, 1996).

The most important prey for sanderlings along the Esiama beach is the surf clam *Donax pulchellus* (Ntiamoa-Baidu *et al.*, 2014a). Therefore, the main prey offered to captive sanderlings in the experiment to determine intake rate was *D. pulchellus*. Subsequent studies to determine prey preference involved an additional prey, the isopod *Excirolana chiltoni*, the second most abundant prey in benthic samples. The experimental methodology on prey preference is explained in detail in Chapter 7. A supplementary diet consisting of freshly cut gastropod *Agaronia acuminata* was offered sanderlings to help keep their body masses near average (Plate 3.8). Fresh water was offered *ad libithum*.

Four out of the six captive sanderlings were used in feeding trials following methods by Dekinga and Piersma (1993) and Onrust *et al.* (2013). These four sanderlings were observed to be fit for the trials, because they actively fed when offered food and showed little signs of

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stress and discomfort. The other two sanderlings which were not included in the feeding trials were monitored closely and released in the field at the point of capture. They were observed after a week of release actively foraging and flocking with other conspecifics on the beach.

For the maximum intake experiment, each of the four sanderlings was offered two different size classes of the surf clam *Donax pulchellus*; small-sized (3.5-5.5 mm) and medium-sized (6.5-8.5 mm). These size classes were selected based on two reasons:

i. The range of sizes of *D. pulchellus* in the field was between 2.0-12.3 mm, but it was difficult to obtain representative samples for the extreme size classes.

ii. The mean size class of *D. pulchellus* is between 6 and 8 mm and it is ideal to use this range as one of the size.

A third size class, large (9.5-11.5 mm) was exempted from the feeding trials, because it was impossible to obtain enough individuals of this size class. Sanderlings were also offered a mixture of sizes of *D. pulchellus* in another set of trials. The sizes of about 100 individuals of prey offered each captive bird was measured before and after each trial. Each feeding trial lasted for an hour. Only flesh of shellfish was offered to the captive birds to avoid having any shells in their gut on experimental days. Therefore, any shells observed in droppings were sure to be coming from prey offered the birds during the trial period. After the one-hour period for each trial, any left-over prey was taken away from the sanderling and counted. Sanderlings were allowed 3 hours to empty their gut after which droppings of sanderlings were collected.

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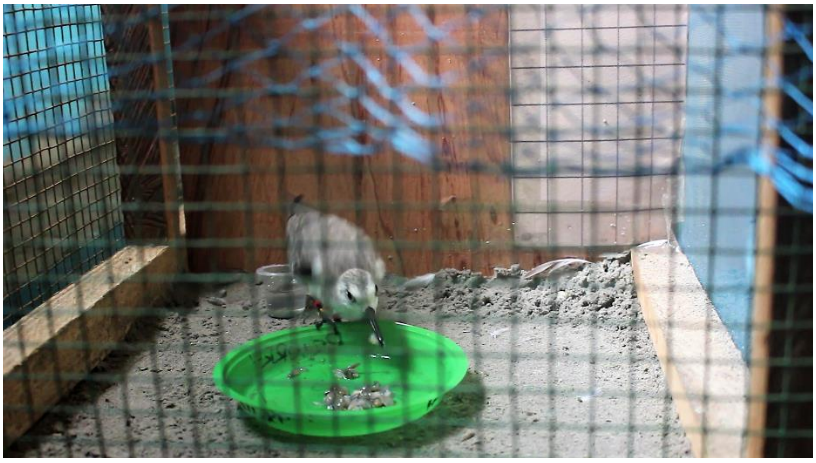

**Plate 3.8 Captive sanderling feeding on freshly cut *Agaronia acuminata***

To avoid birds from trampling on droppings, a plastic mesh platform (30 cm x 30 cm) was placed 1 cm above the base of the experimental unit. This platform allowed droppings to pass through a 10 mm plastic mesh sieve and faeces were collected on a nylon material placed beneath the plastic platform. The droppings were stored in a freezer prior to analysis in the laboratory. A x60 optical zoom HD Lumix video camera was used in recording each trial and later analysed with Solomon Coder beta 17.03.22.

### 3.3.4 Assessment of diet of sanderling

The diet of sanderling was assessed by direct field observation and by analysis of faecal droppings. Direct field observation, relied on information from spatial distribution of macroinvertebrate species, with the assumption that sanderlings were foraging on a particular macroinvertebrate species based on the part of the beach where prey was captured and consumed. Large prey items that could easily be identified using spotting telescopes also were recorded.

Faecal droppings were collected along the Esiama beach in November 2016 and November 2017 when sanderlings on the beach were considered to be part of the “true” non-breeding population. Faecal samples were collected at roost sites, an hour after foraging sanderlings

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had been observed to commence roosting (Lourenço *et al.*, 2015). The roosting birds were displaced for some time and droppings collected with forceps and each dropping placed in a zip lock bag. The time, day and position along the beach was recorded. Faecal samples were frozen to avoid unpleasant smell and subsequently were sieved through a 300µm sieve to separate sand particles from indigestible matter (Dekinga & Piersma, 1993; Onrust *et al.*, 2013). Remains of faecal matter on the sieve were observed under a compound microscope and parts of ingested invertebrates identified, recorded and compared to reference materials obtained from benthic collection of macroinvertebrates.

Bivalves and gastropods were identified from indigestible shells and hinges or last whorl of shells (Dekinga & Piersma, 1993; Onrust *et al.*, 2013), polychaetes from chaetae and mandibles (Zwarts & Wanink, 1993; Weber & Haig, 1997; Scheiffarth, 2001) and isopods from setae and posterior appendages known as uropods (Ramer, 1985). Other less frequently observed prey in the diet of sanderlings were identified as fish from scales and arthropods from exoskeleton (Weber & Haig, 1997; Nuka *et al.*, 2005). The abundance of each identified prey in sieved faecal samples were estimated as well (Lourenço, 2007). Hinges of bivalves were sorted as pairs of similar sizes (right and left halves) and the minimum number of each prey estimated as the maximum number of hinges observed for either pair. The number of polychaetes was estimated based on the number of mandibles (Scheiffarth, 2001). Polychaetes sampled in this study were observed to possess 4 mandibles, hence the number of polychaetes consumed by sanderlings was based on the number of mandibles divided by 4. The total number of the last whorl of gastropod shells were used in estimating the number of gastropods ingested. The number of uropods were also used in determining the number of amphipods consumed.

### 3.3.5 Reconstruction of sanderling diet

The recognizable parts of *Donax pulchellus* in faecal samples or regurgitates of sanderlings

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included the hinges and broken shells. The hinge of this invertebrate is tough enough to be recovered whole and used in estimating the number of bivalves consumed as well as reconstruct the ingested prey size. The latter is possible through the use of allometric equations derived from hinge and prey size estimates (Dekinga & Piersma, 1993; Onrust *et al.*, 2013; Lourenço *et al.*, 2017).

The first step to reconstructing sanderling diet was to develop calibrated curves or regression equations from representative samples of each size class of *D. pulchellus*. About 10 individuals of each 1 mm size class (range: 2.0 to 12.0 mm) *D. pulchellus* were sorted, length measured and biomass as $AFDM_{flesh}$ determined using method described under section 3.2.2. A calibration curve and regression equation was determined for the biomass $AFDM_{flesh}$ against length of shell.

Secondly, the height of both hinges plus top (right and left halves of shell) was measured using a Leica EZ4 HD camera microscope and the average used in plotting a calibration curve to avoid pseudo-replication. The hinge plus top (a swelling above the hinge called umbo) was used for the estimated height because hinges were observed in faecal samples together with the umbo. A calibration curve and a regression equation from the length of shell and the height of hinge plus top was plotted and determined respectively.

Heights of hinges plus top of *D. pulchellus* observed in faecal samples collected in the field or from captive experiments were measured, shell length and biomass determined using developed allometric equations.

## 3.4 Ethical considerations and consent processes

Aspects of this study involved the capture, ringing and experiments on captive sanderlings. Ethical clearance was obtained from the Ethics Committee for Basic and Applied Sciences

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(ECBAS) of the University of Ghana, under the permit number ECBAS 040/17-18. Permission was also obtained from the Wildlife Division of the Forestry Commission of Ghana (WD/A.30/VOL.10/57). The study was executed following approved protocols and techniques and efforts were put into ensuring that sanderlings were treated safely and with minimal physical pain and stress.

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# CHAPTER FOUR

# DISTRIBUTION, AVAILABILITY AND QUALITY OF BENTHIC MACROINVERTEBRATES AS PREY FOR NON-BREEDING SANDERLINGS.

## 4.1 Introduction

Migration and reproduction, two of the most energy-driven activities, are important processes in the annual cycle of shorebirds (García-Peña *et al.*, 2009). During the non-breeding season, migrant shorebirds select and rely upon certain habitats for their ecological needs (Delany *et al.*, 2009). Such habitats may be revisited over and over again. Leyrer *et al.* (2006) indicated that some shorebirds show high fidelity to foraging and roosting spots due to a number of factors such as food predictability and absence of diurnal/ nocturnal predation pressure. One of the most important factors that influences the selection of a suitable non-breeding site is the abundance and availability of food (Piersma, 2012).

Coastal wetlands are mostly preferred by shorebirds because they support huge stocks of macroinvertebrates which serve as sustainable prey during the non-breeding period (Piersma & Lindström, 2004; van de Kam *et al.*, 2004). Shorebirds are therefore keystone predators of intertidal macroinvertebrate communities, and regular predation influences densities of macroinvertebrates in time and space (Wootton, 1997). In the process, shorebirds are affected through competition, should densities of macroinvertebrates decline (e.g. Piersma *et al.*, 1993; van Gils, 2004; Lourenço *et al.*, 2017).

Some sites selected by migrating shorebirds, outside the breeding season, may double as staging areas for refuelling and as actual non-breeding sites, where birds spend the entire non-breeding season (e.g. Ntiamoa-Baidu *et al.*, 2014a). The presence and abundance of communities of shorebirds on such sites may depict the health of the environment (Amat & Green, 2010). In other words, shorebirds are bio-indicators of such ecological systems and

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may provide an indirect measure of densities of macroinvertebrates within the system. Inferring from the behaviours of shorebirds, aggression and resource partitioning could provide information on habitats which support less prey (Karpanty *et al.*, 2011). The ability for shorebirds to switch between preferred prey types, sizes of prey, temporal and spatial foraging strategies also may ensure co-existence of a rather diverse bird community (Lourenço *et al.*, 2017).

Good quality habitats are characterised by higher densities of available prey, higher prey quality, lower disturbances, lower predation risks and lower risk of diseases and infections (Buehler *et al.*, 2010; Piersma, 2012; Ntiamoa-Baidu *et al.*, 2014a). All the attributes of an ideal non-breeding site have linkages with food. Shorebirds therefore prefer quality habitats because of the significant increase in foraging rates and energy acquisition associated with such environments which prepares them for subsequent migration and/or reproduction. The intake rates of prey may therefore be expressed as a function of prey densities, availability, quality and sizes of prey (Dekinga & Piersma, 1993; Onrust *et al.*, 2013; Oudman *et al.*, 2014).

The amount of energy obtained from prey is dependent on the quality of the prey and rate of intake by a shorebird. Prey quality is a measure of the ratio of the digestible to indigestible parts of prey. In molluscs, it is referred to as the flesh-to-shell ratio. The higher the flesh-to-shell ratio, the higher the prey quality (Dekinga & Piersma, 1993; Piersma *et al.*, 2003; van Gils *et al.*, 2003a; van Gils *et al.*, 2005a; Onrust *et al.*, 2013).

Sanderling, a long-distant migrant, can be described as a generalist in its diet, hence makes use of prey that is available and abundant within the habitats it finds itself (e.g. Tsipoura & Burger, 1999; Nuka *et al.*, 2005). The sanderling is able to switch easily between prey types, hence the enormous list of invertebrates observed as important food sources for the species on non-breeding grounds. Amongst the array of prey items are bivalves, gastropods,

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crustaceans, insects, polychaetes, spiders, and in some cases, plant materials (Tsipoura & Burger, 1999; Nuka *et al.*, 2005; Reneerkens *et al.*, 2009a; Vanermen *et al.*, 2009; Loonstra *et al.*, 2016; Lourenço *et al.*, 2016b). There are variations in biomass and energy content of this wide variety of prey items that sanderlings feed on (Grond *et al.*, 2015; Lourenço *et al.*, 2017). Several foraging strategies of sanderlings ensure the ingestion of different prey (Myers *et al.*, 1979; Lourenço *et al.*, 2015) and the processing of prey is likely to be a function of their (sanderlings') physiological plasticity (van Gils *et al.*, 2005a).

Sanderlings arrive in Ghana in August, populations peak in September/October followed by a decline in November. Part of the observed sanderling population only use Ghana's coast as stopover site to refuel on their way further south, accounting for declines in numbers in November. However, the other remaining part of the population spend the entire non-breeding season along Ghana's coast, with high concentrations recorded along the Esiama beach. In some years sanderling numbers increase in March to levels observed in September/ October (Ntiamoa-Baidu, 1991b; Ntiamoa-Baidu *et al.*, 2014a).

The most important prey for sanderling in Ghana is the surf clam *Donax pulchellus*. This prey occurs in high densities, about 14,000 individuals/m$^2$ (Grond *et al.*, 2015). Such densities of macroinvertebrates are important in providing adequate energy to support shorebird migration. However, the quality and sustainability of this prey is equally important in qualifying the site as a high quality site. Besides, high predation leads to declines in densities of prey and alternative sources of prey becomes imperative.

This chapter seeks to measure the temporal and spatial dynamics in the distribution, availability and quality of benthic macroinvertebrates as prey for sanderlings.

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## 4.2 Methodology

### 4.2.1 Study area

The study was conducted along a 13 km sandy beach between the Amansuri and Ankobra estuaries, known as the Esiama beach in the Western Region of Ghana. Detailed description of the study area has been provided in Chapter Three of this thesis. All field and laboratory investigations were carried out between September 2015 and December 2017.

### 4.2.2 Study design and data collection

The study entailed field surveys along the Esiama beach and laboratory investigations. Twenty-seven different sampling locations were established at 500 m intervals along the beach. Field surveys included benthic macroinvertebrate sampling. Laboratory analysis comprised sorting, identification, measuring of biometrics, biomass and quality assessment of macroinvertebrates.

### 4.2.3 Macroinvertebrate sampling

Benthic macroinvertebrates were sampled at 500 m intervals along the 13 km Esiama sandy beach following methodology in Akita *et al.* (2014) and Ntiamoa-Baidu *et al.* (2014b). Detailed description of benthic sampling, identification and measurement of biometric parameters of the macroinvertebrates collected from the benthic samples are provided in Chapter Three of this thesis.

Benthic macroinvertebrates were sampled the first week of every month during the study period at each of the 27 sampling locations. Three replicates were taken at each location cross-tidally, each time separating and treating the top 3 cm sand differently from the bottom sample. Therefore, a total of 162 benthic samples were taken from the study site every month, macroinvertebrates collected were identified and measured.

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### 4.2.4 Biomass of macroinvertebrates

Biomass was estimated as either fresh biomass (both shell and flesh) or Ash Free Dry Mass of the flesh ($AFDM_{flesh}$) of the various size classes of all macroinvertebrates found in the benthic samples as described in Chapter Three of this thesis.

## 4.3 Data Analysis

Data was tested for normality using Shapiro-Wilk test. The distribution of densities of macroinvertebrates ($W = 0.18$, $p < 0.001$) and abundance of sanderlings ($W = 0.76$, $p < 0.001$) were not normally distributed, hence such data were subjected to non-parametric statistical tests, unless successfully transformed. All data on biometric measurements and biomass followed a normal distribution. Such parametric data were represented as mean ± SD. Data was analysed using a number of computer softwares: RStudio version 1.1.447 operating under R version 3.5.0, PRIMER 6 & PERMANOVA+ version 1.0.3, QGIS version 2.18.9 and Microsoft Office, Excel® 2016.

### 4.3.1 Abundance and density of macroinvertebrates

The relative abundance of the different species of macroinvertebrates were expressed as percentages of the total number of macroinvertebrates in benthic samples. The density of macroinvertebrates was estimated as the number of individuals per each species in the benthic sample per unit area:

Density = Number of individuals per species/ Base area of hand corer (A),

where $A = \pi d^2/4$ and d = base diameter of hand corer (14.9 cm).

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### 4.3.2 Frequency of size distribution and densities of macroinvertebrates

The length of all macroinvertebrates was used as a measure of size. A 1 mm size class was used in plotting and showing the temporal variation in size distribution of the most abundant species. Monthly and spatial densities of most abundant prey were graphically displayed.

### 4.3.3 Statistical analysis

Kruskal-wallis H-test and Analysis of Variance (ANOVA) test were used to check for spatio-temporal variations in the densities and sizes of the most abundant invertebrates respectively. All decisions and inferences on statistical analyses were based on a 5% significance level and computed in R statistical software (R Core Team, 2018).

As a follow up to the differences in the spatial distribution of macroinvertebrate species, a cluster analysis, with log(x+1) transformation, was performed on all sampling stations along the beach following Delgado *et al.* (2008) in PRIMER 6 & PERMANOVA software. A dendogram to display level of similarity amongst sampling locations was plotted based on Bray-Curtis similarity index estimated for the distribution of macroinvertebrates along the Esiama beach.

Regression equations for biomass-size and prey quality-size relationships were determined through linear models using the '*lm ()*' function in R statistical software (R Core Team, 2018). Estimates of non-linear relationships were obtained following a $\log_{10}$ transformation of the predictors and response variables.

Pearson's correlation coefficient was used to show the relationship between any two of the biometric measurements of *D. pulchellus*: length, width and height. Spearman's rank correlation was used to assess the relationship between distribution of densities of *D. pulchellus* and *E. chiltoni* against distance to estuaries.

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## 4.4 Results

### 4.4.1 Composition of macroinvertebrates in benthic samples

A total of 62,000 macroinvertebrate individuals belonging to four Phyla (Mollusca, Arthropoda/ Crustacea, Annelida and Nemertea) were collected from the benthic samples during the 24-month survey. Six of these macroinvertebrates were identified to the species level: the gastropods *Agaronia acuminata* (Lamarck, 1811 as cited on WORMS, 2018a) and *Hastula aciculina* (Lamarck, 1822 as cited on WORMS, 2018g), the surf clams *Donax pulchellus* (Hanley, 1843 as cited on WORMS, 2018b) and *Donax rugosus* (Linnaeus, 1758 as cited on WORMS, 2018c), the sand or mole crab *Emerita talpoida* (Say, 1817 as cited on WORMS, 2018d) and the isopod *Excirolana chiltoni* (Richardson, 1905 as cited on WORMS, 2018e). Polychaetes belonging to the genus *Glycera* (Lamarck, 1818 as cited on WORMS, 2018f) and ribbon worms belonging to the phylum Nemertea could be identified to the genera and phyla (Plate 4.1). Other species observed occasionally included polychaetes *Nereis* sp. (Linnaeus, 1758 as cited on WORMS, 2018h) and Mysid shrimp.

### 4.4.2 Relative abundance of benthic macroinvertebrates available for sanderlings

*Donax puchellus* was the most abundant species accounting for 91.66% of all invertebrates in benthic samples, followed by *E. chiltoni* (6.45%) and *Glycera* spp. (1.40%) (Table 4.1). Together these three macroinvertebrate species made up 99.51% of all benthic macroinvertebrates sampled during the study period. The gastropods *Hastula aciculina* and *Agaronia acuminata* and the bivalve *D. rugosus* occurred in smaller proportions of 0.24%, 0.01% and 0.12% of the total benthic macroinvertebrates respectively. The ribbon worms Nemertea were also present in low numbers accounting for about 0.02% of all benthic samples. The other macroinvertebrates recorded, the Mysid shrimp (Order Mysidacea) and the annelid *Nereis* sp., together accounted for less than 0.01% of all benthic macroinvertebrates (Table 4.1).

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All benthic macroinvertebrates except *A. acuminata* were recorded in the top 3 cm depth of sand, *Nereis* sp. and the Mysid shrimp were absent in the bottom 7cm depth of sand. Macroinvertebrates within the top 3 cm of sand were understood to be available for sanderlings, based on the average bill length of sanderlings which averages 2.5 cm. More than 95.0% of the macroinvertebrates in the benthic samples were present in the top 3 cm depth, indicating a high proportion of prey items available for sanderlings. *Donax pulchellus* was observed to be the most important prey item for sanderlings based on both its abundance and availability in benthic samples. About 99.18% of all *D. pulchellus* individuals in benthic samples were present in the top 3 cm depth of sand. Furthermore, 94.77% of all benthic samples available for sanderlings was made up of *D. pulchellus*. The top three macroinvertebrates in benthic samples from this study; *D. pulchellus*, *E. chiltoni* and *Glycera* spp., were equally observed to be important prey and available for sanderlings. These species also formed the bulk of macroinvertebrates in the bottom segment (Table 4.1).

**Table 4.1: Relative abundance and availability of benthic macroinvertebrates along the Esiama beach**

| **Species** | **Numbers recorded in** | | **Total** |
|---|---|---|---|
| | **(≤ 3 cm)** | **(> 3 cm)** | |
| *Donax pulchellus* | 56363 | 467 | 56830 |
| *Excirolana chiltoni* | 2744 | 1254 | 3998 |
| *Glycera* spp. | 136 | 729 | 865 |
| *Hastula aciculina* | 130 | 19 | 149 |
| *Donax rugosus* | 47 | 26 | 73 |
| *Emerita talpoida* | 47 | 18 | 65 |
| Nemertea | 7 | 6 | 13 |
| *Agaronia acuminata* | | 5 | 5 |
| Others | 2 | | 2 |
| **Total** | **59476** | **2524** | **62000** |

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### 4.4.3 Biometric measurement of benthic macroinvertebrates

There was high correlation amongst the various biometric parameters of *D. pulchellus*. Pearson's correlation coefficients of 0.96, 0.96 and 0.95 were estimated between length and height, length and width as well as height and width of *D. pulchellus* shells respectively. The high correlation coefficient values show that each of the biometric measurements could be used as a measure of size of the species. For this study, the length of *D. pulchellus* shell, as well as that of other benthic macroinvertebrates, was used as a measure of size.

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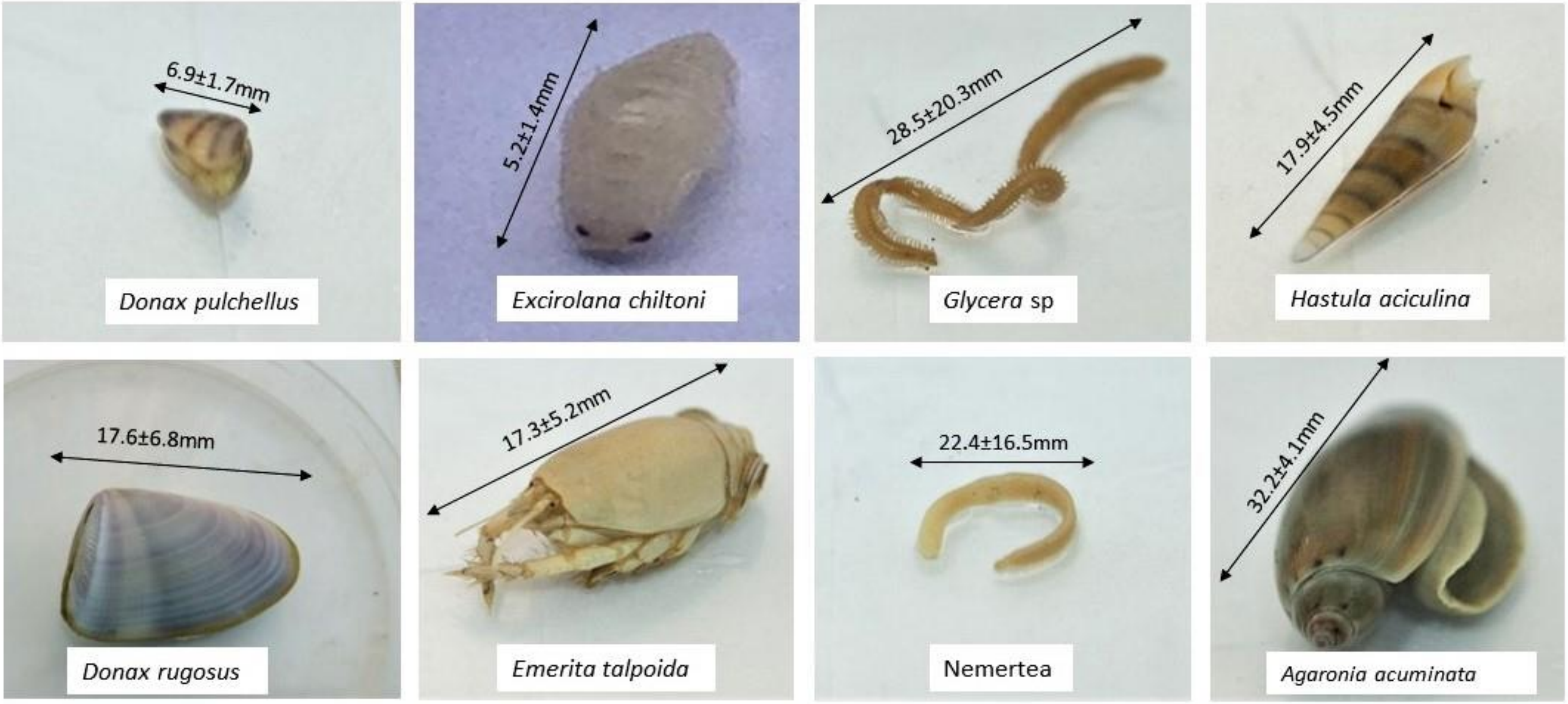

**Plate 4.1: Macroinvertebrates in benthic samples along the Esiama beach**

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The mean size of *D. pulchellus* observed during the study period was 6.9 ± 1.7 mm, *E. chiltoni* was 5.2 ± 1.4 mm and *Glycera* spp. was 28.5 ± 20.3 mm. The mean length of the other macroinvertebrates was 17.9 ± 4.5 mm for *H. aciculina*, 17.6 ± 6.8 mm for *D. rugosus*, 17.3 ± 5.2 mm for *E. talpoida*, 22.4 ± 16.5 mm for Nemertea and 32.2 ± 4.1 mm for *A. acuminata* (Table 4.2).

**Table 4.2 Mean length of benthic macroinvertebrates along the Esiama beach**. (SD is the standard deviation and 'n' is the sample size of macroinvertebrates measured)

| Species | Mean length/ mm | SD/ mm | n | Range/ mm |
|---|---|---|---|---|
| *E. chiltoni* | 5.2 | 1.4 | 1173 | 1.5 – 8.8 |
| *D. pulchellus* | 6.9 | 1.7 | 11937 | 2.0 - 12.3 |
| *E. talpoida* | 17.3 | 5.2 | 36 | 7.8 - 26.3 |
| *D. rugosus* | 17.6 | 6.8 | 40 | 9.9 - 31.8 |
| *H. aciculina* | 17.9 | 4.5 | 83 | 4.6 - 29.4 |
| Nemertea | 22.4 | 16.5 | 19 | 5.3 - 59.1 |
| *Glycera* spp. | 28.5 | 20.3 | 125 | 4.8 - 79.4 |
| *A. acuminata* | 32.2 | 4.1 | 4 | 26.7 - 36.5 |

### 4.4.4 Accessibility of benthic macroinvertebrates to sanderlings

Accessibility of macroinvertebrates to sanderlings was based on the depth to which prey items were buried, the mean size of prey and the body structure of the prey. All macroinvertebrates which were available to sanderlings were presumed to be accessed by sanderlings. This means that *A. acuminata* was the only one of the invertebrate species recorded which could not be accessed by sanderlings, because it was buried at depths beyond the top 3 cm of sand. Sanderlings may prefer to swallow their prey whole, hence the mean size of prey was important. All prey with a mean length below 12.0 mm was presumed to be easily ingested

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whole by sanderlings, making them accessible. Therefore, *D. pulchellus* and *E. chiltoni* could easily be accessed by sanderlings. This may not necessarily apply to soft-bodied prey which have a different body structure. For such species the process of ingestion may vary. Macroinvertebrates longer than 12.0 mm may still be accessed by sanderlings, but the prey may have to be externally handled and processed before ingestion. Such prey included *Glycera* spp., Nemertea and occasionally *E. talpoida*. Smaller individuals of *Hastula aciculina* were also possible prey to be utilized by sanderlings. This means that, at least, about 95.6% of all macroinvertebrates present in benthic samples were accessible to sanderlings.

### 4.4.5 Biomass and quality of macroinvertebrates

The relationship between biomass and size distribution of macroinvertebrates is mostly allometric (e.g. Dekinga & Piersma, 1993), and expressed as a power function in the form $Y = aX^b$, where 'Y' is the biomass, 'X' is the prey size, 'a' is the intercept and 'b' is the growth rate (e.g. Gaspar *et al.*, 2001). The results from this study also showed a similar pattern for seven of the sampled macroinvertebrates.

A curvilinear relationship existed between the Ash Free Dry Mass of flesh ($AFDM_{flesh}$) and length of *D. pulchellus* (Figure 4.1 A) and *E. chiltoni* (Figure 4.2 B). For *D. pulchellus*, there was a gradual increase in biomass for smaller size individuals below 6 mm, however the change in biomass per unit increase in length was accompanied by a steep increase for individuals greater than 6 mm. A similar pattern was observed for *E. chiltoni*. However, the regressional plots showed that biomass of the isopod *E. chiltoni* was higher than that of the bivalve *D. pulchellus*, for similar prey sizes.

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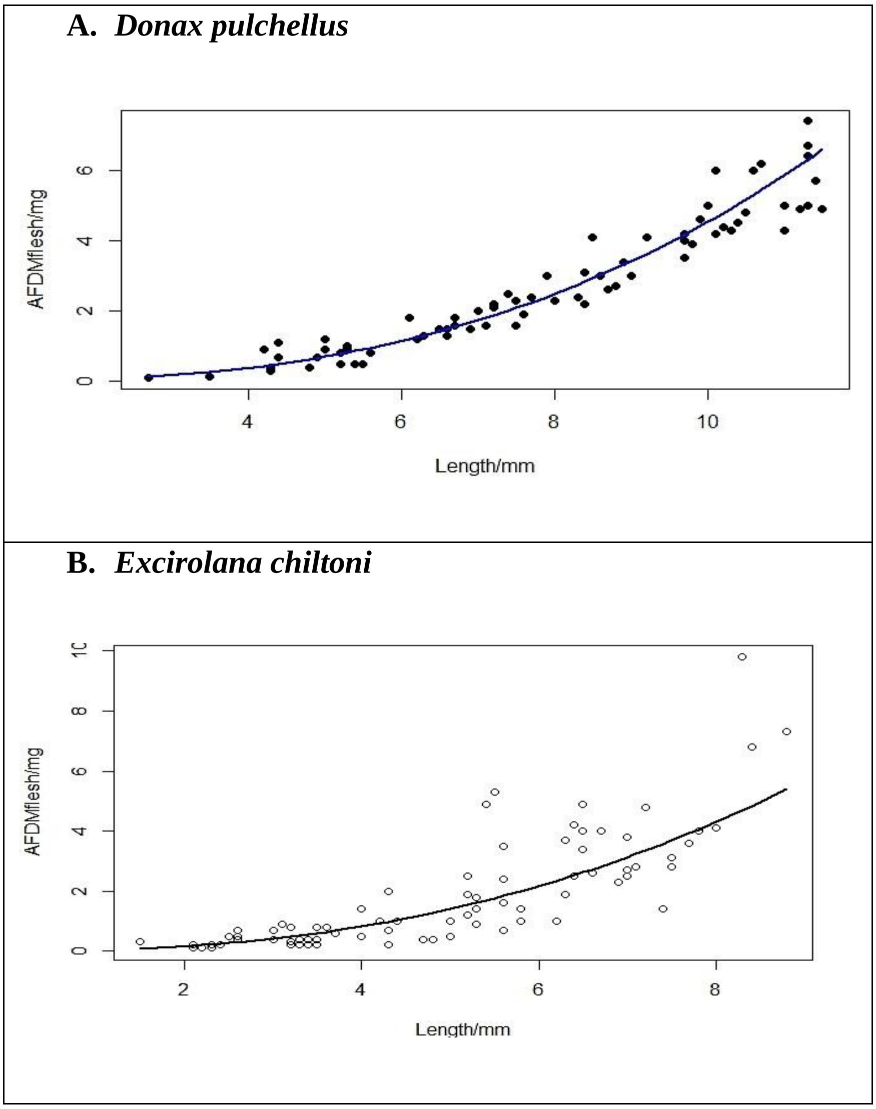

**Figure 4.1 Curvilinear relationship between AFDM$_{\text{flesh}}$ in mg and length in mm of the two most abundant benthic macroinvertebrates along the Esiama beach: *D. pulchellus* in top panel (A) and *E. chiltoni* in bottom panel (B).** (Regression equations are provided in Table 4.3).

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**Table 4.3 Regression equations between Ash-Free Dry Mass of flesh (AFDMflesh in mg) and length (L in mm) of benthic macroinvertebrates observed along the Esiama beach.** (The degrees of freedom (df), proportion of variance explained by the equation ($R^2$), the F-statistic (F), level of significance (p-value) and size range (in mm) are presented for each equation.)

| Invertebrate | Equations | df | $R^2$ | F | p-value | size range/ mm |
|---|---|---|---|---|---|---|
| *D. pulchellus* | $AFDM = 0.009L^{2.69}$ | 69 | 0.92 | 784.7 | < 0.001 | 2.7-11.5 |
| *E. chiltoni* | $AFDM = 0.028L^{2.39}$ | 75 | 0.72 | 199.6 | < 0.001 | 1.5-8.8 |
| *Glycera* spp. | $AFDM = 0.078L^{1.22}$ | 71 | 0.54 | 84.76 | < 0.001 | 7.8-75.9 |
| *H. aciculina* | $AFDM = 0.004L^{2.83}$ | 34 | 0.57 | 47.92 | < 0.001 | 4.5-29.0 |
| *D. rugosus* | $AFDM = 0.002L^{3.35}$ | 23 | 0.98 | 1049 | < 0.001 | 13.0-39.4 |
| *E. talpoida* | $AFDM = 0.075L^{2.44}$ | 19 | 0.85 | 118.5 | < 0.001 | 6.1-28.2 |
| *A. acuminata* | $AFDM = 0.018L^{2.85}$ | 12 | 0.70 | 31.79 | < 0.001 | 22.3-36.4 |

Following the equations in Table 4.3, the $AFDM_{flesh}$ of the mean sizes of benthic macroinvertebrates along Esiama beach are as follows:

i. *D. pulchellus* – 1.62 ± 0.04 mg $AFDM_{flesh}$
ii. *E. chiltoni* – 1.44 ± 0.06 mg $AFDM_{flesh}$
iii. *Glycera* spp. – 4.65 ± 3.07 mg $AFDM_{flesh}$
iv. *H. aciculina* – 14.05 ± 0.28 mg $AFDM_{flesh}$
v. *D. rugosus* – 29.75 ± 1.23 mg $AFDM_{flesh}$
vi. *E. talpoida* – 78.69 ± 4.19 mg $AFDM_{flesh}$
vii. *A. acuminata* – 356.99 ± 1.00 mg $AFDM_{flesh}$.

It important to note the high biomass of the molluscs *D. rugosus* and *A. acuminata*, which are the main harvested shellfishes by humans along the Esiama beach.

There was also a curvilinear relationship between the mass of dry shell ($DM_{shell}$) and size of

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bivalves and gastropods. Following the regression equations in Table 4.4, the $DM_{shell}$ of the mean sizes of benthic bivalves and gastropods along Esiama beach are as follows:

i. *D. pulchellus* – 30.04 ± 0.04 mg $DM_{shell}$

ii. *H. aciculina* – 168.83 ± 5.28 mg $DM_{shell}$

iii. *D. rugosus* – 571.98 ± 25.28 mg $DM_{shell}$

iv. *A. acuminata* – 2321.47 ± 9.08 mg $DM_{shell}$.

Table 4.4 Regression equations between Dry Mass of shell ($DM_{shell}$ in mg) and length (L in mm) of molluscs observed along the Esiama beach.

| **Invertebrate** | **Equations** | **df** | **$R^2$** | **F** | **p-value** | **size range/ mm** |
|---|---|---|---|---|---|---|
| *D. pulchellus* | $DM_{shell} = 0.127L^{2.83}$ | 69 | 0.94 | 1074 | < 0.001 | 2.7-11.5 |
| *H. aciculina* | $DM_{shell} = 0.121L^{2.51}$ | 75 | 0.97 | 1320 | < 0.001 | 4.5-29.0 |
| *D. rugosus* | $DM_{shell} = 0.047L^{3.28}$ | 71 | 0.99 | 12650 | < 0.001 | 13.0-39.4 |
| *A. acuminata* | $DM_{shell} = 0.204L^{2.69}$ | 34 | 0.95 | 258.8 | < 0.001 | 22.3-36.4 |

The quality of benthic macroinvertebrates, a function of the ratio of digestible to indigestible material of an invertebrate, also followed curvilinear relationships for all the benthic macroinvertebrates sampled (e.g. *E. chiltoni*; Figure 4.2 A) with the exception of *D. pulchellus*, which followed a linear regression (Figure 4.2 B). An inverse relationship was observed between the size of *D. pulchellus* and quality. The quality of *D. pulchellus* individuals below 4 mm was however observed to be relatively lower. This observation should be noted that, these values are averages of a number of individuals within a 1 mm size class since it was quite difficult to work on individual shells of such sizes in isolation. On the other hand, a positive relationship was observed between the sizes of *E. chiltoni* and its quality. The quality of *E. chiltoni* was several folds (between 5 and 9 times) higher than that of *D. pulchellus*.

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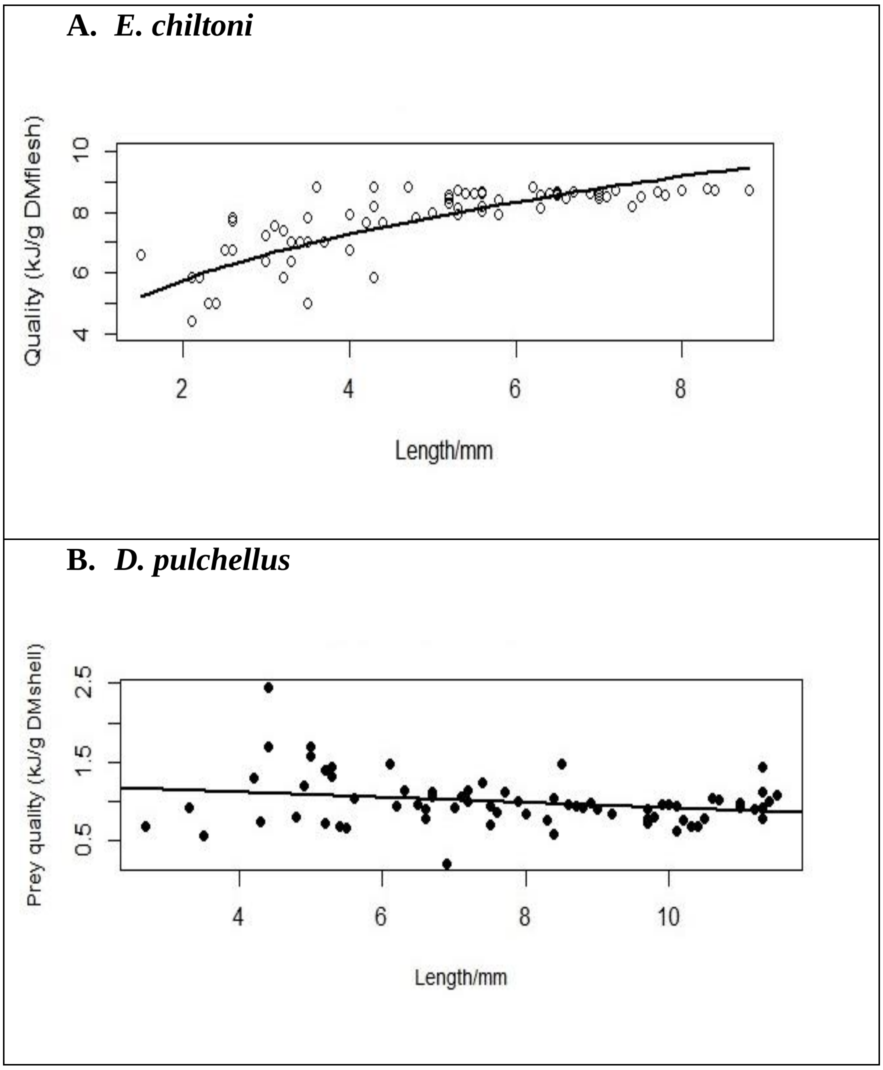

**Figure 4.2 Relationship between prey quality, Q in kJ/ g and length, L in mm of the two most abundant benthic macroinvertebrates along the Esiama beach: *E. chiltoni* in top panel (A) and *D. pulchellus* in bottom panel (B).** (Note the difference in prey quality, Q scales for the two species. Regression equations are provided in Table 4.5).

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**Table 4.5: Regression equations and averages between the Quality in kJ/ g and length** (L in mm) of benthic macroinvertebrates observed along the Esiama beach.

| Invertebrate | Equations | df | $R^2$ | F | p-value | Size range/ mm |
|---|---|---|---|---|---|---|
| *D. pulchellus* | $Q = 1.25 – 0.03L$ | 69 | 0.05 | 4.32 | 0.04 | 2.7-11.5 |
| *E. chiltoni* | $Q = 4.57L^{0.33}$ | 75 | 0.57 | 102.3 | < 0.001 | 1.5-8.8 |
| *Glycera* spp. | $Q = 11.22L^{0.11}$ | 71 | 0.14 | 12.85 | < 0.001 | 7.8-75.9 |
| *H. aciculina* | $Q = 0.56L^{0.32}$ | 34 | -0.01 | 0.66 | 0.42 | 4.5-29.0 |
| *D. rugosus* | $Q = 0.69L^{0.07}$ | 23 | -0.02 | 0.48 | 0.50 | 13.0-39.4 |
| *E. talpoida* | $Q = 9.95L^{-0.04}$ | 19 | 0.48 | 19.77 | < 0.001 | 6.1-28.2 |
| *A. acuminata* | $Q = 1.53L^{0.16}$ | 12 | -0.07 | 0.16 | 0.70 | 22.3-36.4 |

### 4.4.6 Spatial distribution of benthic macroinvertebrates

#### i. Cross-tidal distribution of macroinvertebrates

About 46,516 individuals representing 78.21% of all macroinvertebrates in benthic samples available to sanderlings were distributed along the low tide water mark. About 10,694 individual macrobenthic organisms representing 17.98% of all benthic macroinvertebrates were within the intertidal areas and 2,266 individual macrobenthic organisms representing 3.81% the total macro-benthos in samples distributed around the high tide water mark. About 99.68% of all *D. pulchellus* available to sanderlings were sampled within the low tide and intertidal zone of the beach. The high tide area of the beach was dominated by the isopod *E. chiltoni*, supporting about 89.23% of the macrobenthic community along beach (Table 4.6).

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**Table 4.6: Cross-tidal distribution of abundance of benthic macrobenthic community along the Esiama beach**

| Species | Low tide zone | Intertidal zone | High tide zone | Total |
|---|---|---|---|---|
| *D. pulchellus* | 46287 | 9896 | 180 | 56363 |
| *E. chiltoni* | 96 | 626 | 2022 | 2744 |
| Glycera spp. | 49 | 31 | 56 | 136 |
| *H. aciculina* | 22 | 106 | 2 | 130 |
| *D. rugosus* | 26 | 21 | | 47 |
| *E. talpoida* | 29 | 14 | 4 | 47 |
| Nemertea | 5 | | 2 | 7 |
| Others | 2 | | | 2 |
| **Total** | **46516** | **10694** | **2266** | **59476** |

### ii. Longitudinal distribution of densities of macrobenthic community along the Esiama beach.

Some macroinvertebrates were observed in the benthic samples across all the sampling stations but others were confined to a selected few. *Donax pulchellus* was the only macroinvertebrate observed in the benthic samples from all the 27 sampling stations. *Excirolana chiltoni* and *Glycrea* spp were encountered in 26 of the sampling stations, whereas *E. talpoida* and *H. aciculina* were present in 25 and 22 of the sampling stations respectively. The other macroinvertebrates were sparsely distributed along the beach (Figure 4.3). However, it is important to mention that most of the *D. pulchellus* observed in the benthic samples were most abundant at the western end of the beach towards the Amansuri estuary.

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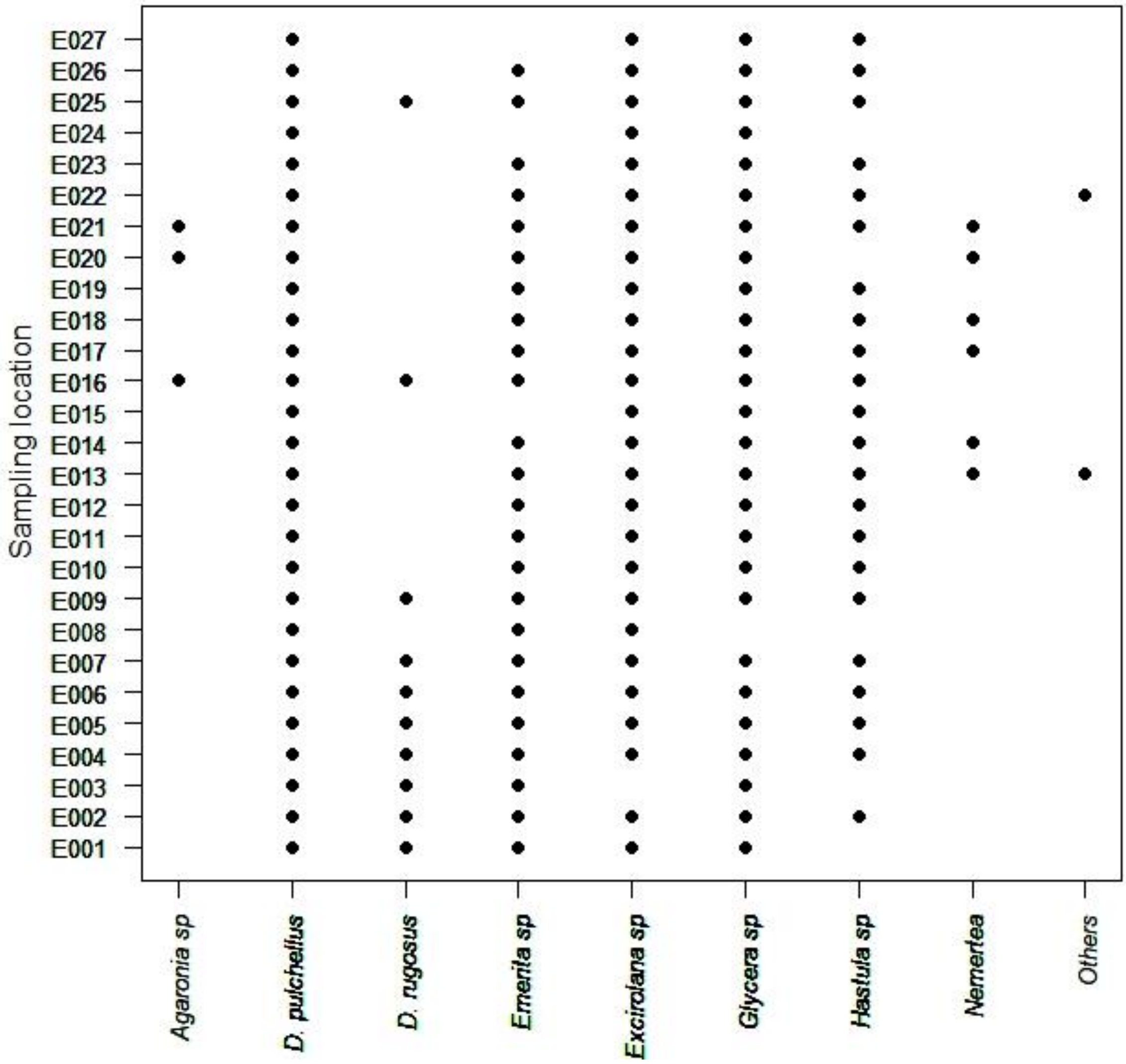

**Figure 4.3 Distribution of benthic macroinvertebrates along the Esiama beach**

The communities of benthic macroinvertebrates distributed along the 27 sampling stations along the Esiama beach demonstrates how similar certain parts of the beach are and how important they may be for foraging sanderlings. A Bray-Curtis similarity index of all sampling locations, based on different species of macroinvertebrates present and their relative abundances, shows that the Esiama beach may be divided into four main similar sections; sampling stations within a kilometre to the Amansuri estuary (E001, E002 and E003), showed a 60.0% similarity in terms of macroinvertebrate distribution. The other group of sampling locations were areas within a 1.5 – 5.0 km from the Amansuri estuary, which showed 80.0%

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similarity in macroinvertebrates distribution. Sampling stations within the middle section of the beach (5.5 – 10.0 km) from the Amansuri estuary are also similar, 87.48% similarity index. The final group was composed of a number of selected location in no particular order which were 87.43% similar in benthic macroinvertebrate distribution (Figure 4.4). A rather distinct pattern was observed between the sampling station at Ankobra estuary and those located within a kilometre from the estuaries. The spatial distribution of the two most abundant species were used to further explain these observations.

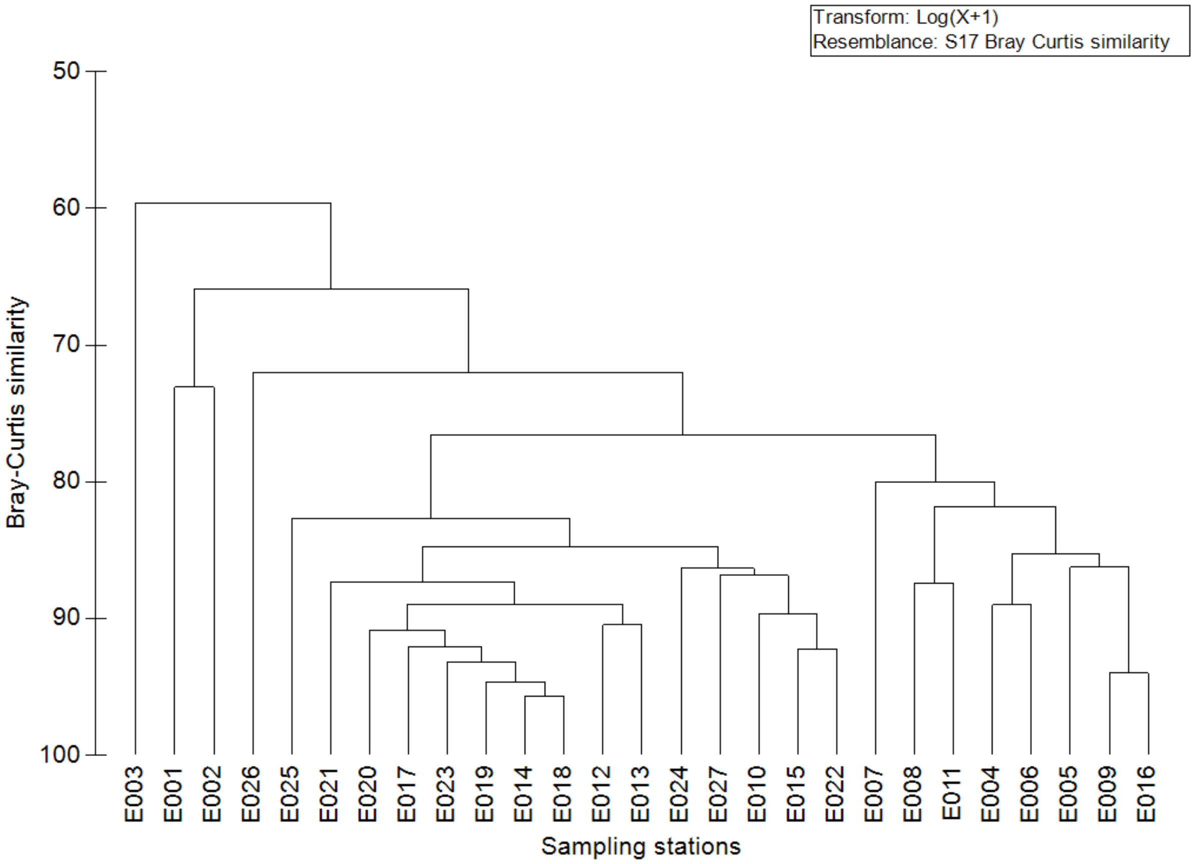

**Figure 4.4 Bray-Curtis similarity of sampling locations along the Esiama beach based on macroinvertebrate distribution**

- ***Donax pulchellus***

*Donax pulchellus* was distributed in varying densities along the entire beach. The mean densities of *D. pulchellus* along the beach ranged between 5 and 15,509 individuals/ m$^2$.

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Spatial variation in densities of *D. pulchellus* showed that areas within the middle part of the beach supported higher densities of this species as compared to sampling stations a kilometre to the estuaries (Figure 4.5). For example, the very middle sampling station, about 6.5 km from either estuaries, supported on average 15,509 *D. pulchellus* individuals/ $m^2$ whereas the lowest densities of *D. pulchellus* were observed at or close to the estuaries. The difference in spatial variation of densities of *D. pulchellus* was significantly different (Kruskal-wallis chi-squared = 122.47, df = 26, p-value < 0.001).

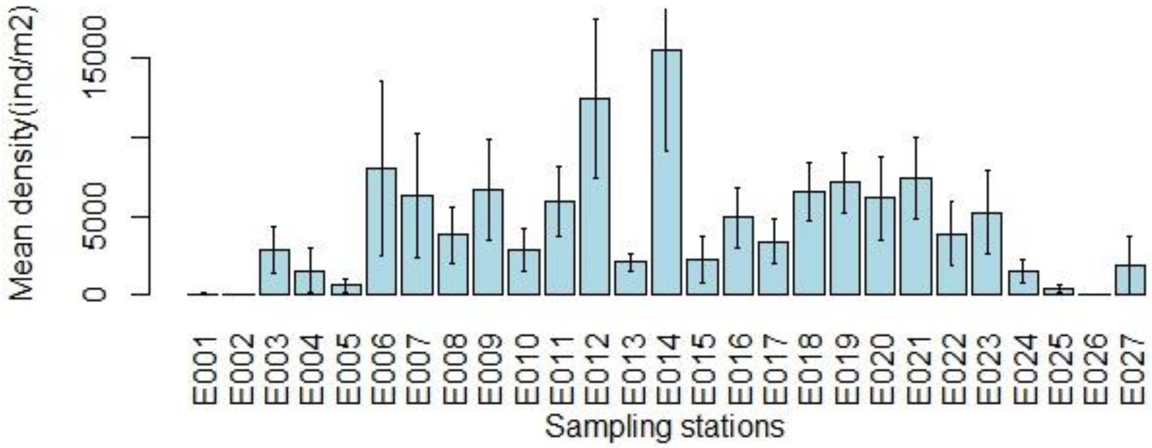

**Figure 4.5 Spatial distribution of densities of *Donax pulchellus* along Esiama beach** (Error bars represent as standard errors of mean).

- ***Excirolana chiltoni***

*Excirolana chiltoni* was also distributed in varying densities along the entire beach. The mean densities of *E. chiltoni* along the beach ranged between 0 and 960 individuals/ $m^2$. Higher densities of *E. chiltoni* recorded from the middle part (maximum of 960 individuals/ $m^2$) to the eastern end of the beach. For the estuarine areas, higher densities of *E. chiltoni* were observed along the Ankobra end of the beach (305 – 378 individuals/ $m^2$) than the Amansuri end (0 – 77 individuals/ $m^2$; Figure 4.6). There was a significant difference in the spatial

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distribution of densities of *E. chiltoni* observed along the beach (Kruskal-wallis chi-squared = 258.54, df = 26, p-value < 0.001).

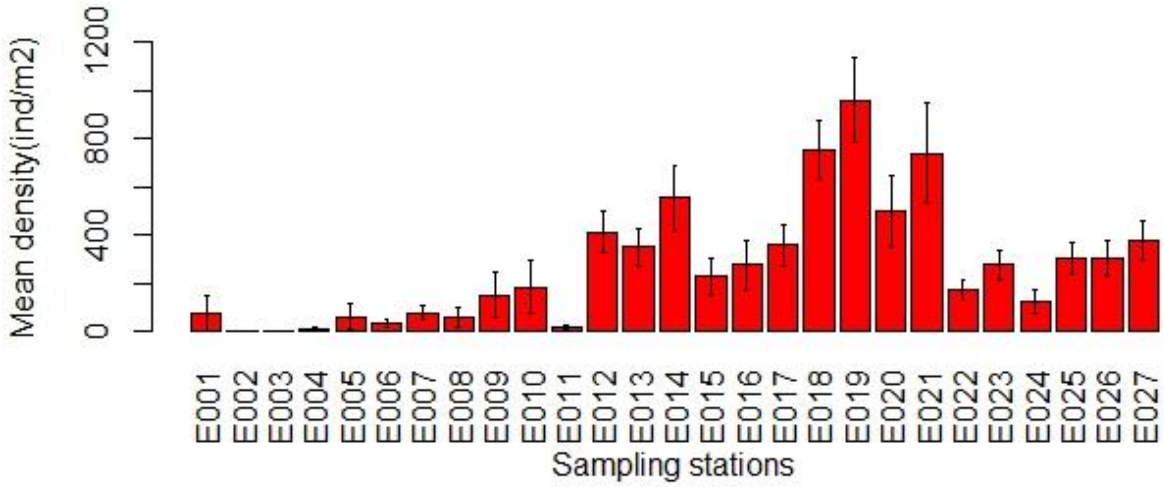

**Figure 4.6 Spatial distribution of densities of *Excirolana chiltoni* along Esiama beach** (Error bars represent as standard errors of mean).

### 4.4.7 Densities of macroinvertebrates in relation to the estuaries

A high correlation was observed between the densities of *D. pulchellus* and distance to the estuaries ($r_s = 0.61$, $p = 0.02$). The densities of *D. pulchellus* were lowest a kilometre to the estuaries, increasing by three folds as you move away from the estuaries to about 4.5 km and again increased by two folds towards the middle part of the beach (Figure 4.7 A). On the other hand, a weaker relationship was observed between densities of *E. chiltoni* and distance to the estuaries ($r_s = 0.35$, p-value = 0.2). Lower densities of *E. chiltoni* were observed close to the estuaries and the middle part of the beach whiles highest densities were observed between 3 km and 5 km away from the estuaries (Figure 4.7 B).

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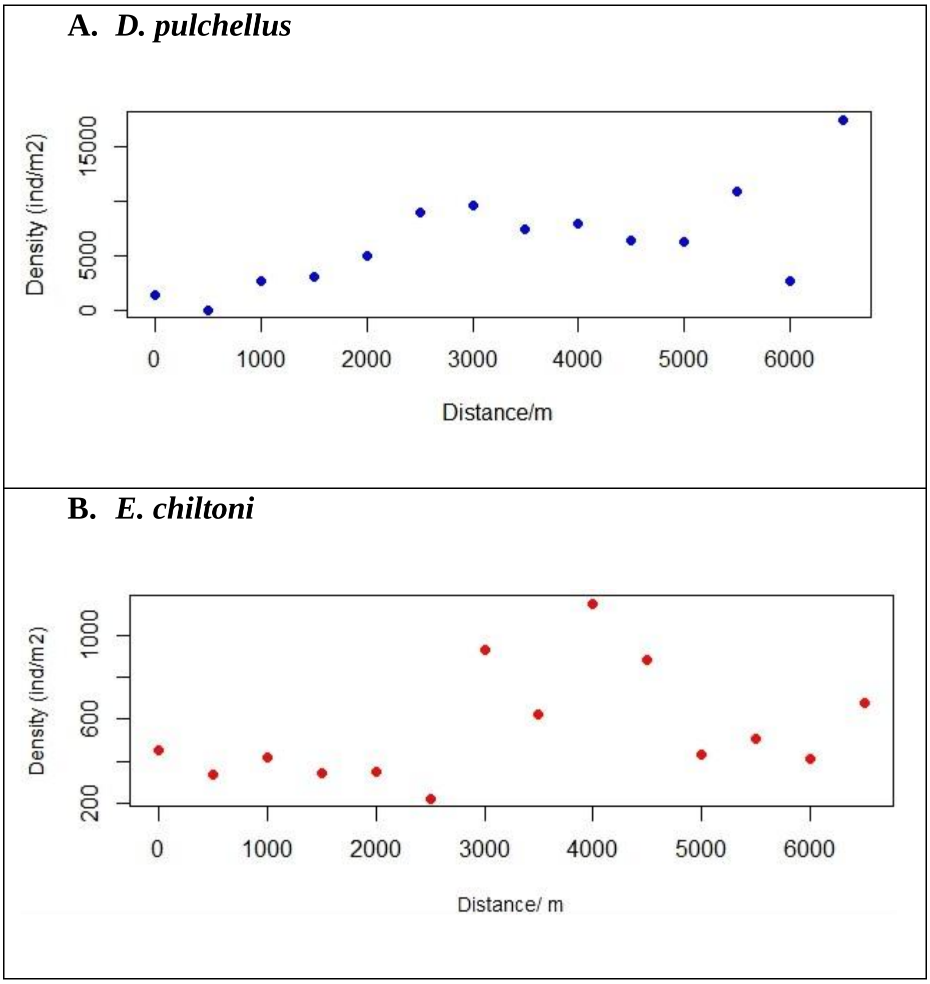
**A. *D. pulchellus***

**B. *E. chiltoni***

**Figure 4.7 Densities of *D. pulchellus* (A) and *E. chiltoni* (B) in relation to distance from estuary.**

### 4.4.8 Temporal variation in densities of *D. pulchellus* and *E. chiltoni*

The densities of *D. pulchellus* ranged between 16 and 15,837 individuals/ m$^2$ in the different months surveyed. There was a significant difference in the monthly variation of densities of *D. pulchellus* (Kruskal-wallis chi-squared = 132.29, df = 23, p < 0.001). There were two seasonal peak periods for the abundance of *D. pulchellus*; August-October and January-March. The densities between these two peaks were observed to alternate between years. For example, the two peaks of densities of *D. pulchellus* in 2015/2016 season were observed in October 2015 (5,888 individuals/ m$^2$) and March 2016 (12,742 individuals/ m$^2$). However, in

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2016/2017, the two peaks of densities of *D. pulchellus* were observed in September 2016 (15,837 individuals/ m$^2$) and March 2017 (5,040 individuals/ m$^2$). There was always a sudden decline in densities of *D. pulchellus* the month succeeding peak months. The lowest densities were observed in either November or July with magnitudes ranging between 16 – 1,797 individuals/ m$^2$ (Figure 4.8).

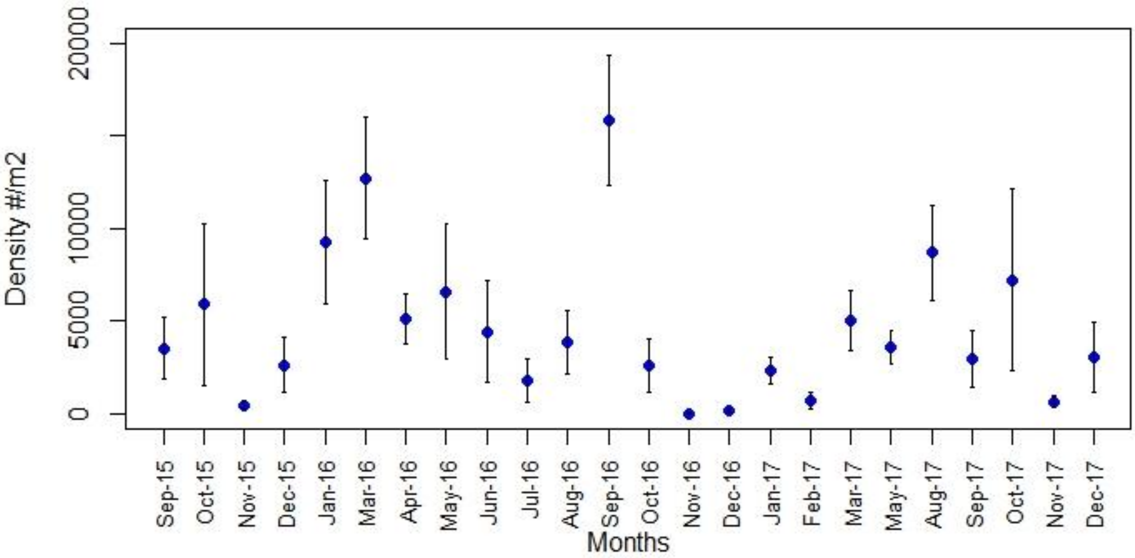

**Figure 4.8 Temporal variation in densities of *Donax pulchellus* along the Esiama beach.**

(Error bars represent standard errors of mean values)

There was also significant variation in the temporal distribution of densities of *E. chiltoni* (Kruskal-wallis chi-squared = 59.13, df = 23, $p < 0.001$). The results showed a decline in densities of *E. chiltoni* between August and September, accompanied by an increase in densities in October. The highest peaks were observed in November and July. These months, however were the lean periods for the most abundant benthic macroinvertebrate, *D. pulchellus*. There were other peaks in March/April accompanied by gentle declines in May/June (Figure 4.9).

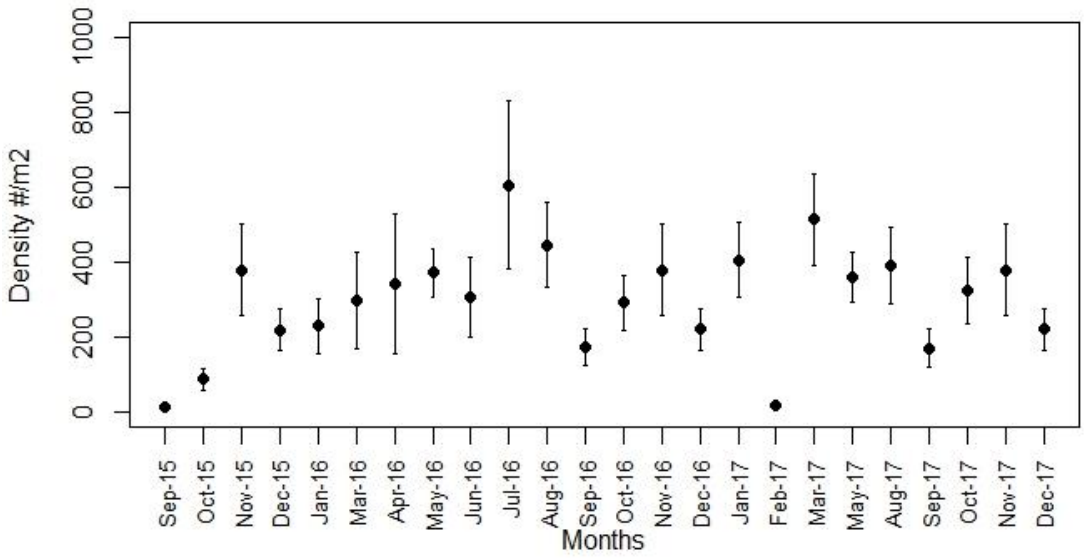

**Figure 4.9 Temporal variation in densities of *Excirolana chiltoni* along the Esiama beach.** (Error bars represent standard errors of mean values)

### 4.4.9 Temporal variation in sizes of *D. pulchellus*

The sizes of *D. pulchellus* ranged from 2.0 – 12.3 mm in length. New recruits were considered as individual *D. pulchellus* shells with measurements between 2.0 – 4.0 mm. Figure 4.8 shows the presence of different sizes of *D. pulchellus* in benthic samples at different times of the year. The results from this study showed two main recruitment periods for *D. pulchellus*. The first recruitment occurred in July and new recruits were observed in benthic samples until October. The second recruitment occurred in January and extended until March. June and November were characterised by the least number of *D. pulchellus* in benthic samples. However whereas the former was devoid of new recruits, the latter was very important for new and smaller *D. pulchellus* individuals.

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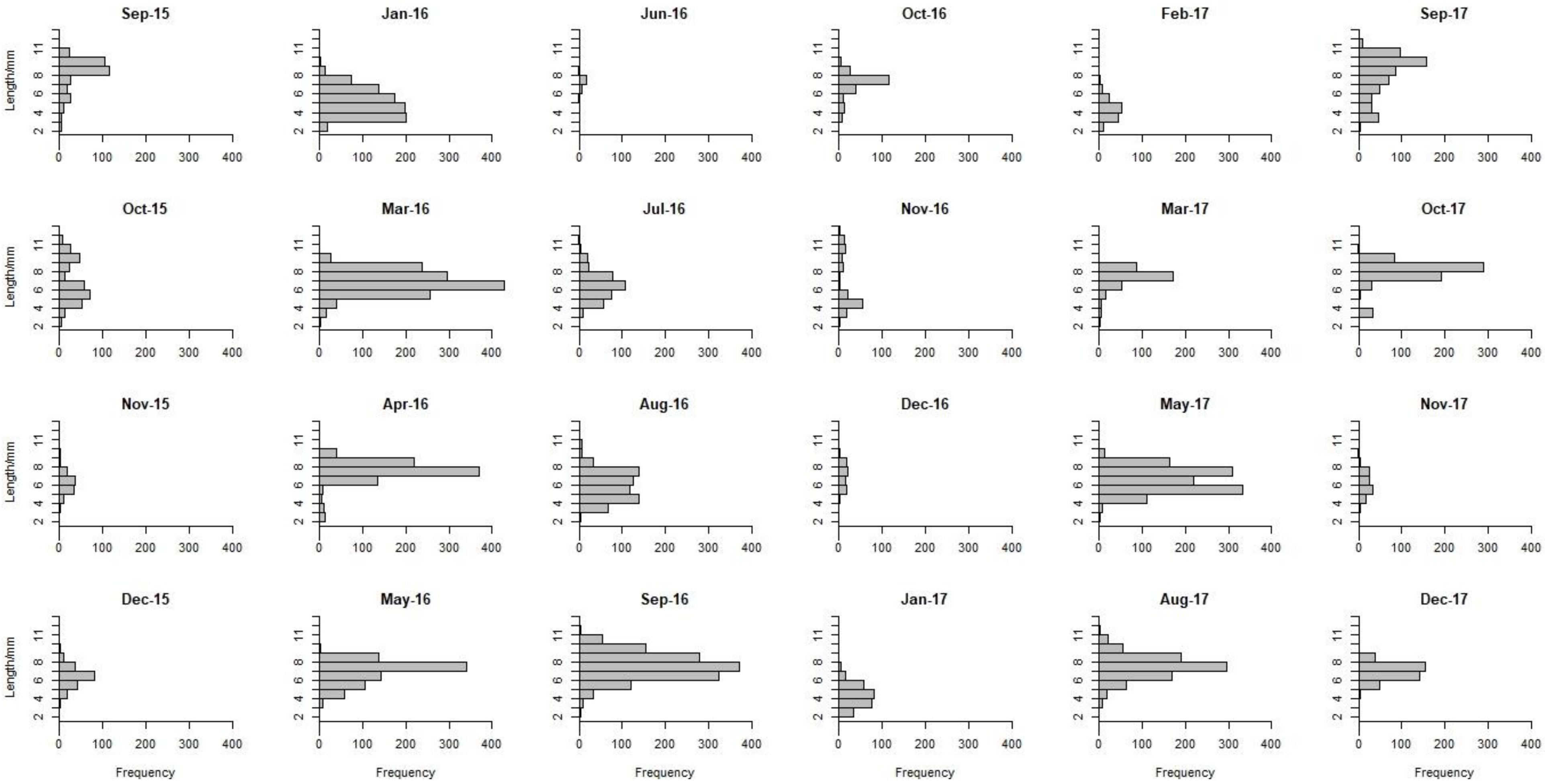

Figure 4.8 Temporal variation in sizes of *Donax pulchellus* along the Esiama beach

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**Table 4.7 Relative monthly and overall growth rates of *D. pulchellus*.** (Included in the table are the mean length ± SD, mean mass ± SD, the mass-length equation, the coefficient of determination $R^2$, the confidence interval CI of the growth rate b, degrees of freedom df, level of significance p-value and the mass-length relationship. '+ve' and '-ve' represents positive and negative.)

| Month | Mean Length ± sd | Mean mass ± sd/ g | Mass-Length equation | $R^2$ | b (95% CI) | df | p-value | Relationship |
|---|---|---|---|---|---|---|---|---|
| September | 9.3 ± 1.4 | 0.0965 ± 0.0417 | $M = 0.00011L^{3.0}$ | 0.95 | 0.05 | 205 | < 0.001 | Isometric |
| October | 8.4 ± 2.7 | 0.0908 ± 0.0573 | $M = 0.00017L^{2.8}$ | 0.98 | 0.03 | 267 | < 0.001 | -ve allometric |
| November | 6.4 ± 2.8 | 0.0527 ± 0.0576 | $M = 0.00016L^{2.9}$ | 0.99 | 0.03 | 135 | < 0.001 | -ve Allometric |
| December | 5.0 ± 1.3 | 0.0237 ± 0.0256 | $M = 0.00016L^{3.0}$ | 0.98 | 0.05 | 90 | < 0.001 | Isometric |
| January | 4.4 ± 1.1 | 0.0150 ± 0.0115 | $M = 0.00014L^{3.0}$ | 0.94 | 0.05 | 268 | < 0.001 | Isometric |
| February | 4.4 ±1.1 | 0.0148 ± 0.0116 | $M = 0.00013L^{3.1}$ | 0.97 | 0.04 | 144 | <0.001 | +ve allometric |
| March | 5.6 ± 1.4 | 0.0246 ± 0.0215 | $M = 0.00013L^{2.9}$ | 0.93 | 0.04 | 467 | < 0.001 | -ve allometric |
| April | 6.9 ± 2.0 | 0.0550 ± 0.0428 | $M = 0.00009L^{3.2}$ | 0.97 | 0.09 | 37 | < 0.001 | +ve allometric |
| June | 7.3 ± 0.8 | 0.0411 ± 0.0124 | $M = 0.00012L^{2.9}$ | 0.88 | 0.21 | 25 | < 0.001 | -ve allometric |
| July | 6.8 ± 1.4 | 0.0394 ± 0.0208 | $M = 0.00028L^{2.5}$ | 0.9 | 0.21 | 14 | < 0.001 | -ve allometric |
| Overall | 6.9 ± 1.7 | 0.0451 ± 0.0479 | $M = 0.00017L^{2.8}$ | 0.97 | 0.01 | 1670 | < 0.001 | Allometric |

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### 4.4.10 Growth rate of *D. pulchellus*

The overall growth rate (Mass-Length relationship in the form $M = aL^b$, where 'M', 'L', 'a' and 'b' are mass, length, intercept and slope of the graph respectively) of *D. pulchellus* was allometric. Allometric growth is a type of growth whereby different parts of the bivalve grow at different rates whereas isometric growth is one in which all the parts of the bivalve grow at approximately the same rate (Gaspar *et al.*, 2001). The curvilinear relationship showed that there was a gradual increase in the fresh or wet mass of *D. pulchellus* for every unit increase in length below 6.0 mm, above which there was a sudden increase in mass of *D. pulchellus* for every unit increase in length (Figure 4.9). *Donax pulchellus* showed isometric growth rates in September, December, January to March and June. *Donax pulchellus* showed negative allometric growth rates in October, November and July whereas a positive allometric growth was observed in April (Table 4.7). Values of 'b' = 3 represents isometric growth whereas values on either side of the relationship 3 > b > 3 represents negative and positive allometric relationship respectively.

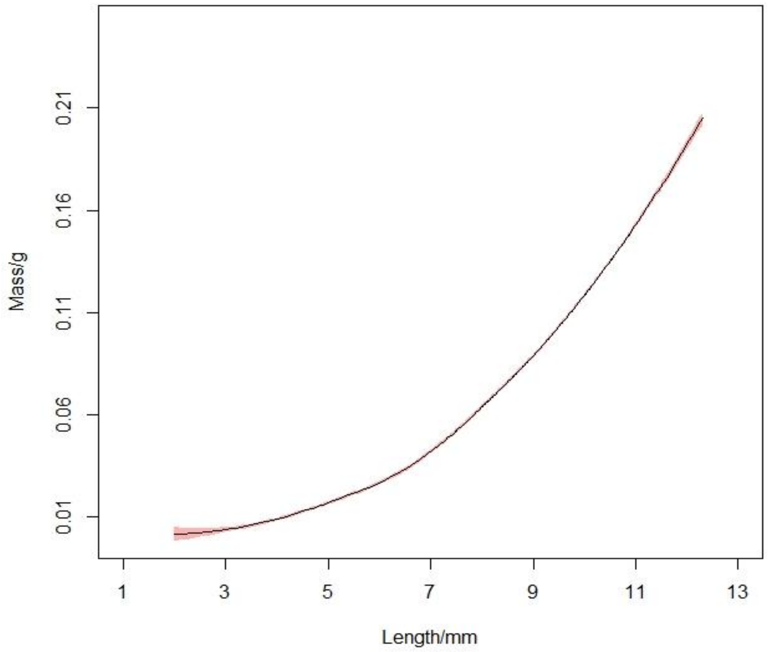

**Figure 4.9 Relative growth rate of *D. pulchellus* along the Esiama beach**

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## 4.5 Discussion

### 4.5.1 Composition of benthic macroinvertebrates as prey items for sanderlings

*Donax* spp are important bivalves on most coastal beaches in tropical Africa (e.g. McLachlan *et al.*, 1980; Summers *et al.*, 1987; Lourenço *et al.*, 2017). From this study, *D. pulchellus* constituted more than 90.0% of the total numbers of macroinvertebrates in benthic samples. The high densities of *D. pulchellus* observed during this study confirms the findings from other studies along Ghana's coast and other geographical locations. For example Grond *et al.* (2015) reported maximum *D. pulchellus* densities of 14,300 individuals/ $m^2$ along the Esiama beach. Akita *et al.* (2014) also observed a maximum density of 111 *D. pulchellus* individuals/ $m^2$ along a sandy beach located about 300 km east of Esiama beach. Elsewhere in southern Africa, Summers *et al.* (1987) observed high densities of *Donax serra* as important prey for sanderlings. In Portugal, Lourenço *et al.* (2015) also observed high densities of *Donax trunculus* as important prey for sanderlings in a non-estuarine habitat.

The mud snail *Hydrobia ulvae* was reported by Grond *et al.* (2015) as the second most abundant benthic macroinvertebrate along the Esiama beach, but this species was absent in the composition of benthic macroinvertebrates recorded during the study period. However, other gastropods such as *Hastula aciculina* and *Agaronia acuminata* were recorded in the benthic samples.

This study provides additional information on documented benthic macroinvertebrates which are possible prey items for sanderlings. In addition to *Donax pulchellus* which had been reported in previous studies (Reneerkens *et al.*, 2009a; Ntiamoa-Baidu *et al.*, 2014a; Grond *et al.*, 2015), the Esiama beach supported more than seven species of macroinvertebrates. Most of the macroinvertebrate species recorded in this study have been recorded as important prey for

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sanderlings at different geographical locations. For example, Lourenço *et al.* (2017) observed the polychaetes *Nereis* sp. and *Glycera* spp., and the gastropod *Hydrobia* sp, as well as some crustaceans and isopods as important prey for sanderlings in Guinea-Bissau. In another locality, the Banc d' Arguin in Mauritania, Lourenço *et al.* (2016b) observed sanderlings to feed on *Hydrobia* sp, some polychaetes and bivalves. In southern Africa, Summers *et al.* (1987) observed the polychaete *Nereis* sp, isopods *Ampelisca palmate* and *Urothoe grimaldii*, insects, bivalve *Donax serra* and the Mysid shrimp *Gastrosaccus psyammodytes* as important prey of sanderlings. Elsewhere in Japan, important sanderling prey included *Donax semigranosus*, the isopod *Excirolana chiltoni* and the mysid shrimp *Archaeomysis vulgaris* (Nuka *et al.*, 2005). Sanderlings have also been observed to forage on amphipods, polychaetes, insects, fish larvae and seeds of *Ruppia maritima* on other mudflats in Ghana (Piersma & Ntiamoa-Baidu, 1995; Reneerkens *et al.*, 2009a).

Most of the benthic macroinvertebrates (about 95.0%) were found in the top 3 cm depth of sand. This indicates abundance of available food for sanderlings. A little over a quarter of this proportion of prey was found at the low tide water mark and a high percentage of these was *D. pulchellus*. This would explain the foraging behaviour of sanderling in relation to tidal cycle. As the tide comes in, most parts of the intertidal zone are submerged in water and unavailable to foraging sanderlings. However, the muscular foot of *D. pulchellus* which aids in movement, anchorage and floating in water may allow the species to position itself against wave action (Ansell & Trueman, 1973). Such position may allow the bivalve to be easily transported with the tide and through that means, some *D. pulchellus* individuals become available to sanderlings during high tide. Otherwise, sanderlings that forage during high tide may have to feed on prey located by the high tide water mark.

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The distinct distribution of benthic macroinvertebrates may provide a quick assessment of the kind of prey sanderlings may be feeding on depending on their location. It is highly possible that sanderlings foraging along the high tide water mark or the sand dunes may be taking in the isopod *E. chiltoni*. This is because this species formed the bulk of macroinvertebrates sampled from that part of the beach. Sanderlings are known to be important predators of *E. chiltoni* along the Washington coast (EOL, 2018 August). On the other hand, sanderlings foraging within the intertidal zone and by the low tide water mark are likely to be feeding on *D. pulchellus*.

### 4.5.2 Sizes of benthic macroinvertebrates

The size range of *D. pulchellus* was between 2.0 and 12.0 mm, which is similar to that observed by Akita *et al.* (2014) along the La sandy beach in Ghana. The mean size of *D. pulchellus* sampled in the current study was 6.9 ± 1.7 mm. Grond *et al.* (2015) estimated mean size of *D. pulchellus* to be approximately 7.0 mm, which is similar to that estimated from the current study. Sanderlings are likely to consume such prey sizes whole, in which case they will have to deal with digestive constraints. Therefore, they may have to forage for shorter periods and spend more time going through a digestive break in order to process prey ingested. Furthermore, sanderlings may have to develop larger gizzards to enable them to crush such prey sizes easily. Nevertheless, the mean size of *E. chiltoni* is appropriate for easy consumption and their soft-bodied structure even enhances the process of ingestion. The sizes of all other benthic macroinvertebrates were out of the ingestion range of sanderlings, to allow swallowing whole prey. But then, the soft-bodied prey such as Nemertea and *Glycera* spp. could still be an important prey item for sanderlings, only that, their ingestion would entail a longer external handling time; during which time, other sanderlings may initiate aggressive interference, especially when prey densities are lower.

Temporal variation in size distribution of *D. pulchellus* showed that there are two major

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recruitment periods; September-October and January-March. Akita *et al.* (2014) also observed two recruitment periods for *D. pulchellus* along the La beach, which were October-November and March. These periods are very similar and coincides with important migration periods for non-breeding sanderlings. The southern autumn migration of sanderlings and arrival on the Ghana coast coincides with the September-October recruitment period whiles the northern spring migration and passage through the Ghana coast coincides with the January-April recruitment period.

### 4.5.3 Spatio-temporal variation of densities of benthic macroinvertebrates

The study provided information on the annual and seasonal variation of densities of macroinvertebrates along the Esiama beach. Higher densities of *D. pulchellus* were observed during the 2015/2016 and 2017/2018 seasons but the highest *D. pulchellus* density of 15,837 individuals/ $m^2$ was observed in September 2016. Zwarts and Wanink (1993) also observed significant annual variation in densities of macroinvertebrates in the Wadden Sea. They attributed such variation to the varying degrees of successful prey recruitments. The two recruitment periods observed from the results of this study coincided with important migration periods for the sanderling. The data suggests that the first recruitment which occur in July ensure enough food (*D. pulchellus*) supply for the southern autumn migration that occur between August and November. The second recruitment which occur in January to March coincide with the northern spring migration which commences just about that period.

Predation is an important factor for explaining seasonal variations in densities of prey. High predation could also influence the ecological behaviour of prey in an attempt to escape predators. High predation of *D. pulchellus* between September and October, when sanderling numbers were highest, could have accounted for the lower densities of this prey between November and January.

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During these months, larger individuals were observed than smaller ones because the larger prey are difficult to be ingested by sanderlings (Zwarts & Wanink, 1993). The seasonal variation in densities of *D. pulchellus* may best be explained by intensity in predation. Because *D. pulchellus* is relatively less mobile compared to the isopod *E. chiltoni*, the former is more vulnerable to predation. *E. chiltoni* individuals may tend to bury further deep into the substrate, thus eluding predators. This may have accounted for the unclear pattern in the variation of densities of this prey, which would imply that the lack of detection of such prey in certain months may be apparent, rather than real due to anti-predatory strategies.

### 4.5.4 Growth rate of Donax pulchellus

Some studies have shown that a number of factors such as availability of nutrients and temperature influence the growth rate of *D. pulchellus* (Ansell *et al.*, 1980; Gaspar *et al.*, 1999). Akita *et al.* (2014) also suggested that variation in densities and growth rate of *D. pulchellus* in Ghana could be due to predation. This study showed that, there were variations in the relative growth rate of *D. pulchellus* from, e.g. isometric growth in September just when sanderling numbers began to peak to negative allometric relationship in October, when prey densities declined. The change in relative growth rate could be related to a possible intense predation during periods characterised by higher sanderling numbers along the study beach. The effect of a possible intense predation by a large number of sanderlings might have influenced a prey size selection process, whereby smaller individuals within the local *D. pulchellus* cohort were predated upon leaving behind larger individuals with a disproportionate weight-length ratio (Zwarts & Wanink, 1993). The effect of predation was a potential cause of the variation in sizes of the local *D. pulchellus* population from which monthly sampling was made. Nonetheless, as population densities of *D. pulchellus* increases, and carrying capacity within areas along the

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Esiama beach is reached, growth rate of *D. pulchellus* is influenced when mortality of individuals (either through predation or natural causes) within the population causes growth increment of individuals (Ansell *et al.*, 1985).

In other studies, that focused on reproduction of benthic macroinvertebrates, spawning was accompanied by a decline in body mass due to the release of oocytes (Bartels-Hardege & Zeeck, 1990). The lowest growth rates for *D. pulchellus* were observed in June/July. Similar observations were made by Zwarts and Wanink (1993) for other macroinvertebrates. The decline in body mass (or body condition) of some *D. pulchellus* individuals was probably due to weight changes in reproductive and other body tissues. Therefore, the low growth rates observed in June/ July for this study could probably be due to spawning. Further investigations would be needed to substantiate this observation.

### 4.5.5 Biomass of macroinvertebrates

There were differences in the biomass of the different macroinvertebrates sampled from the Esiama beach. The AFDM estimates showed that *A. acuminata* was the heaviest macroinvertebrate followed by *E. talpoida* and *D. rugosus* in that order. The readily accessible macroinvertebrates; *Glycera* spp., *D. pulchellus* and *E. chiltoni* rather had lower biomass. The data also showed a direct relationship between biomass and size of macroinvertebrates. The high biomass of *A. acuminata* and *D. rugosus* explains the importance of these macroinvertebrates in the shellfish harvesting business along the Esiama beach. These two macroinvertebrates serve as important protein source in the diet of surrounding communities.

According to Zwarts and Wanink (1993), the total biomass of benthic macroinvertebrates in the substrate is dependent on their body condition and densities of the different size classes. The

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maximum biomass of *D. pulchellus* was estimated at 26.29 g AFDM $m^{-2}$; that of *E. chiltoni* was 1.40 g AFDM $m^{-2}$. These estimates suggest that *D. pulchellus* could be a staple food for sanderlings due to its high biomass. *Excirolana* sp could, however, be a supplement diet at certain periods of the season as well as certain times of the day, especially during incoming tides, when the low tide areas have been submerged. The biomass of 26.29 g AFDM $m^{-2}$ was a third of that (77 g AFDM $m^{-2}$) reported by Grond *et al.* (2015) despite the similar densities reported. This difference could be due to the body condition and average sizes of the macroinvertebrate at the time of sampling. It is therefore important to determine the biomass of *D. pulchellus* at various times of the year as it has been documented that macroinvertebrates show temporal variation in growth rate and body condition (e.g. Beukema, 1985; Zwarts & Wanink, 1993). Nevertheless, the reported biomass of 26.29 g AFDM $m^{-2}$, contributed by only *D. pulchellus*, falls within the range of total biomass (5 and 80 gAFDM$m^{-2}$) reported for temperate and tropical intertidal foraging sites by Piersma *et al.* (1993). It is also five times higher than the total estimated biomass of 5.2 g AFDM $m^{-2}$ at the Bijagós archipelago in Guinea-Bissau that hosts about 35,000 sanderlings every year, together with other shorebird species (Lourenço *et al*. unpubl; as cited in Lourenço *et al*., 2017).

### 4.5.6 Prey quality and profitability

Prey quality assessment showed that the soft-bodied macroinvertebrates (e.g. *E. chiltoni* and *Glycera* spp.) were of higher quality than the hard-shelled prey such as bivalves and gastropods. This means that, it will be energetically beneficial for sanderlings to feed on soft-bodied prey than the hard-shelled ones. The quality of hard-shelled macroinvertebrates is compromised by the hard shell structure and this pose digestive constraints in the diet of shorebirds as they mostly swallow prey whole (van Gils *et al.*, 2003a; Yang *et al.*, 2013). The quality of *E. chiltoni* was

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observed to be 5-9 times higher than that of *D. pulchellus*. For the bivalves and gastropods, the quality of these macroinvertebrates was inversely related to their sizes. Therefore, there is a higher profitability in feeding on smaller bivalves than larger ones. On the contrary, a positive relationship was observed between the quality of soft-bodied macroinvertebrates such as *E. chiltoni* and *Glycera* spp. and size. This suggests a higher profitability for sanderlings to forage on larger soft-bodied prey than smaller ones (Zwarts & Wanink, 1991).

Soft-bodied prey is energetically worth consuming than shelled prey. In addition to this, larger soft-bodied prey is more profitable than smaller soft-bodied prey. However, due to anti-predatory strategies, it is more difficult for shorebirds to access larger soft bodied prey. For example, Zwarts and Wanink (1993) observed larger *Mya arenaria* (approximately 80.0 mm long) to burrow 20.0 cm deep into the substrate, whereas *Scrobicularia plana* (about 40.0 mm long) could only burrow to a maximum depth of 12.0 cm. Furthermore, they observed the bivalves in their study (maximum length of 30.0 mm) to burrow to a maximum depth of 2.0 cm. Their result showed a direct relationship between prey quality and the burying depth of prey; thus the higher the prey quality the deeper the burying depth. *Excirolana* sp which are energetically worth consuming, according to this study, could burrow up to more than 10 cm in depth (EOL, 2018 August), which is beyond the reach of sanderlings. The results from the current study also showed an appreciable amount of this prey beyond the first 3 cm depth of the substrate. Furthermore, *D. pulchellus* which is less energetically profitable is readily available and occurred in higher densities.

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# CHAPTER FIVE

# SPATIO-TEMPORAL VARIATION IN THE DISTRIBUTION OF SANDERLINGS AND THEIR INVERTEBRATE PREY

## 5.1 Introduction

Shorebirds are involved in several life processes, however the most energy-demanding ones include migration and reproduction (e.g. Bromley & Jarvis, 1993). The periods before and after successive migrations are so important that shorebirds need to be adequately prepared for and make decisions that will enhance successful future migration and survival. It is generally assumed that birds in better physical and physiological conditions stand a better chance of accomplishing other energy-demanding life processes than those in poorer conditions (e.g. Lindstrom *et al.*, 2000; Dinsmore & Collazo, 2003). From this perspective, it is expected that non-breeding shorebirds, in their quest to obtain sufficient energy, would choose habitats which are ecologically favourable to provide them with enough available and profitable food resources that would support their energy demands (Piersma & Lindström, 2004; Piersma, 2012).

A number of factors define the quality of habitats selected by shorebirds for non-breeding or breeding purposes. Food abundance and availability are arguably the most important resources that influence selection of a habitat by non-breeding shorebirds (Burger & Olla, 1984). The abundance and/or quality of prey within selected habitats help to explain the success and fitness of individuals as well as the demography of an entire shorebird population (Ruthrauff *et al.*, 2013).

According to the Optimal Foraging Theory (MacArthur & Pianka, 1966; Stephens & Krebs,

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1986), predator-prey interactions may be centred around functional and numerical/aggregate responses of predators (Gilg *et al.*, 2006). The former explains intake rates in response to prey densities whereas the latter considers predator abundance and distribution in relation to prey densities (Goss-Custard, 1977).

The distribution of prey is aggregated and territorial (Dolah, 1978). Spatial distribution of non-breeding shorebirds reflect distribution and densities of prey, especially on large spatial scales (Goss-Custard, 1970b; Colwell & Landrum, 1993). This is because prey abundance and condition decreases during the non-breeding season in the temperate areas (Zwarts & Wanink, 1993) but the cost of maintenance through thermoregulation is rather high (Kersten & Piersma, 1987). The abundance and availability of prey to support the energy needs of non-breeding shorebirds is therefore crucial to their survival. High quality microhabitats created as a result of high prey densities, may therefore be selected by shorebirds to enhance feeding success (Myers *et al.*, 1979; van Gils, 2004). However, across sampling sites on smaller spatial scales, weak (Wilson, 1990) or inverse (Kelsey & Hassall, 1989) relationships have been observed between shorebird numbers and prey densities.

The spatial distribution of densities of prey also explains the behaviour of shorebirds (Goss-Custard, 1980; Goss-Custard *et al.*, 1984; Yates *et al.*, 2000). Intense predation on prey over time leads to decline in prey densities. As prey densities fall below certain thresholds, known as giving-up-densities (GUD), shorebirds abandon such foraging spots (Gawlik, 2002; van Gils *et al.*, 2005a; Karpanty *et al.*, 2011).

This chapter investigates how spatio-temporal variation in the distribution of prey explains the occurrence of sanderlings along the Esiama beach.

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## 5.2 Methodology

### 5.2.1 Study area

The study was conducted along a 13 km sandy beach between the Ankobra and Amansuri estuaries, hereafter known as Esiama beach. The Esiama beach is known to support between 40 - 70% of the total number of sanderlings observed along the Ghana coast (Ntiamoa-Baidu *et al.*, 2014a). Detailed description of the study area has been provided in Chapter three of this thesis. Data collection was by field survey that included counting of sanderlings and sampling of benthic macroinvertebrates along the study beach, and laboratory identification of macroinvertebrates collected in benthic samples. Data were collected between September 2015 and December 2017.

### 5.2.2 Macroinvertebrate distribution

Benthic macroinvertebrates were sampled with a hand corer with a base diameter of 14.9 cm, every month, at 500 m intervals along the 13 km sandy beach. There were 27 different sampling locations from where benthic samples were taken. Samples were washed in situ, fixed in 10% formaldehyde solution and transported to the laboratory for identification and estimation of relative abundance of each species. The detailed description of benthic macroinvertebrate sampling is provided in Chapter three.

### 5.2.3 Sanderling count and distribution

The number of sanderlings along the 13 km Esiama beach were counted the first week of each month during the study period using both line and point transect counting methods as reported by Sutherland *et al.* (2004) and Ntiamoa-Baidu *et al.* (2014a). Line transect counts were used to estimate the total number of sanderlings along the 13 km Esiama beach on a monthly basis, whereas point counts were used to estimate the spatial distribution of sanderlings in relation to

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distribution of benthic macroinvertebrates. For line transects, two field personnel walked almost at constant pace in an estimated 4-hour duration along the 13 km Esiama beach, once in the first week of every month, between September 2015 and December 2017. Counts were done in the mornings of spring low tides, at the time sanderlings were actively foraging. Each sanderling encountered during the transect walk within a perpendicular distance of 200 m from the watermark offshore and up to the peripheral vegetation onshore, was counted with a 15-60x Swarovski spotting telescope. For point counts, sanderlings were observed and counted in relation to the 27 benthic invertebrate sampling locations (see chapter three for more details) for 5 minutes after a 1-minute allowable time for birds to settle upon reaching each counting point.

### 5.2.4 Data presentation and statistical analysis

Data were tested for normality using Shapiro-Wilk test at a significance level of $p = 0.05$. The distribution and abundance of sanderlings ($W = 0.68$, $p < 0.05$) and densities of *D. pulchellus* ($W = 0.88$, $p = 0.01$) were not normally distributed, hence all analysis on abundance of sanderlings and densities of *D. pulchellus* were subjected to non-parametric tests, unless transformed accordingly. However, data on densities of *E. chiltoni* were normally distributed around the mean ($W = 0.96$, $p = 0.5$), hence such data were represented by mean ± SD and analysed using parametric statistics.

Density of prey (*D. pulchellus* and *E. chiltoni*) was estimated as number of individuals per base area of hand corer and expressed as number/ $m^2$. The base area of the hand corer was calculated from Area = $(\pi d^2)/4$, where d is the base diameter of the corer = 14.9 cm; hence the base area of the corer was estimated as 0.0174 $m^2$.

The monthly survey data were grouped into four different seasons that explained the migratory

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pattern of sanderlings. These were ‘northern autumn’ which included data collected during the arrival and peak counts periods of sanderlings and spanned between August and October; ‘northern winter’ for data collected between November and February and also represented that fraction of sanderling population that were considered to actually spend the non-breeding season in Ghana along the Esiama beach; ‘northern spring’ which covered sanderlings that were preparing for migration to the breeding grounds and entailed data collected between March and May; and finally, ‘northern summer’ which included data collected in June and July and represented the lean period of sanderling counts along the Esiama beach.

Linear regression was used to derive models that explained the spatio-temporal variation in numbers of sanderlings along the Esiama beach, with appropriate data transformations to satisfy the assumptions of a linear regression model. Variations in the spatial distributions of sanderlings and *D. pulchellus* were also assessed with a Kruskal-wallis non-parametric test, but that of *E. chiltoni* was done with an Analysis of Variance (ANOVA) test. All statistical analyses were carried out and graphs plotted in RStudio version 1.1.447 operating under R version 3.5.0 (R Core Team, 2018). All statistical tests were done at a significance level of p = 0.05.

## 5.3 Results

### 5.3.1 Temporal distribution of sanderlings along Esiama beach

A total of 13,727 sanderlings were observed across the 22 sampling months between September 2015 and December 2017. These sanderlings occurred in a total of 265 flocks, with flock sizes ranging between 1 to 650 individuals. The largest flock sizes of 650 and 600 individuals were observed in September 2015 and October 2015 respectively. Another flock size of 400 individuals was observed in January 2016 (Figure 5.1).

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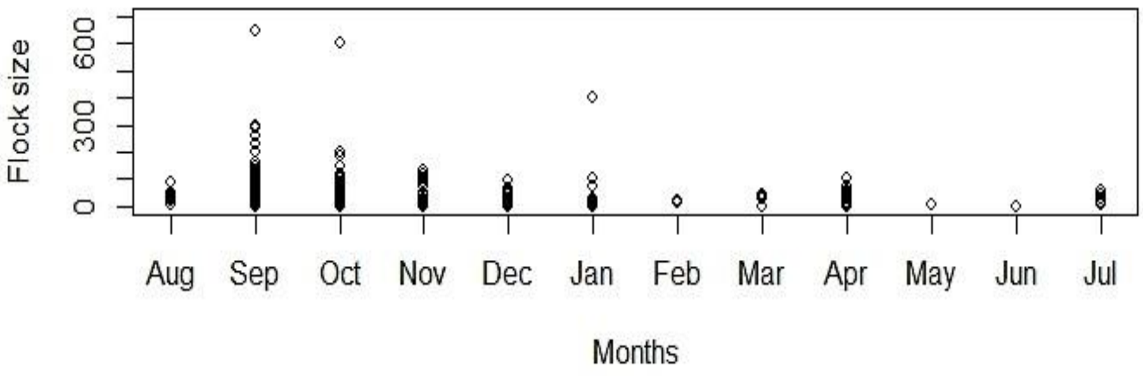

**Figure 5.1 Monthly variation in flock sizes of sanderlings along the Esiama beach**

Sanderlings occurred along the Esiama beach throughout the study period in varying numbers except in the month of June. When present, the total numbers of sanderlings recorded in any monthly count at the Esiama beach during the study period ranged between 14 and 1,794 individuals (Figure 5.2). Sanderlings were observed to arrive along the Esiama beach in August, however some individuals were also observed earlier in July following zero counts in June the same year. The numbers of sanderlings mostly peaked in September and/or October. The peak counts of sanderlings declined sharply in November, and a further gentler decline was observed in December. The numbers of sanderlings then increased marginally in January, followed by a rather inconsistent pattern until May when most sanderlings were observed to have departed from the Esiama beach, possibly to their breeding grounds (Figures 5.1, 5.2 and 5.3).

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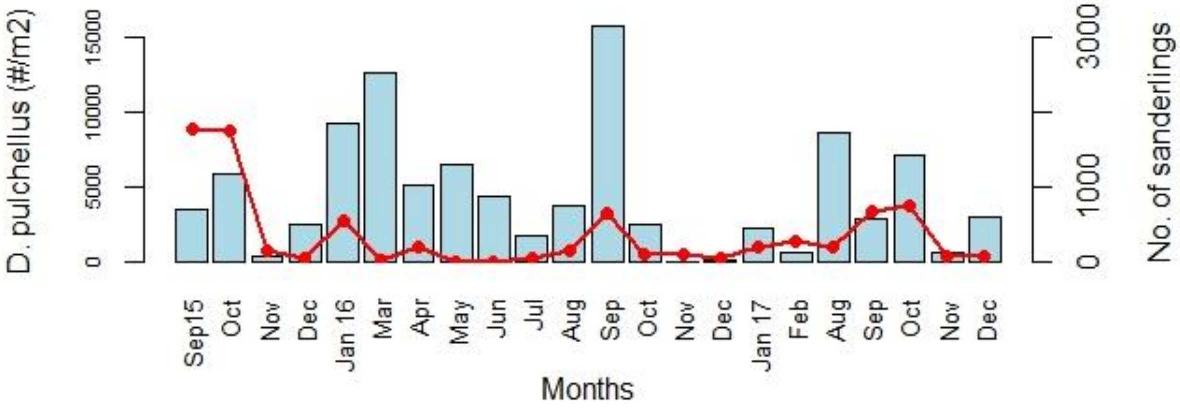

**Figure 5.2 Temporal variation in distribution of densities of *Donax pulchellus* and sanderling count.** (Bar graphs represents densities of *D. pulchellus* and line graph represents counts of sanderlings).

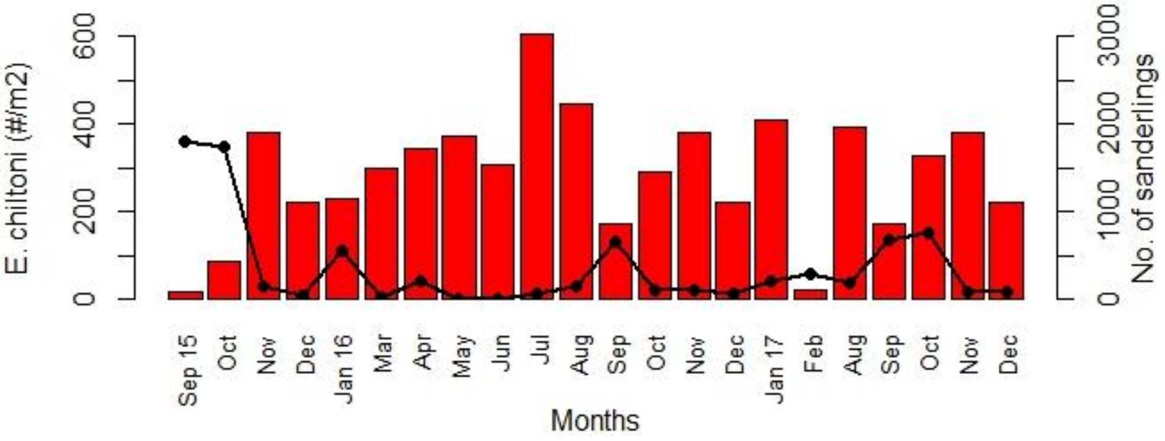

**Figure 5.3 Temporal variation in distribution of densities of *Excirolana chiltoni* and sanderling count.** (Bar graphs represents densities of *E. chiltoni* and line graph represents counts of sanderlings).

There was a seasonal effect in the occurrence of sanderlings along the Esiama beach (Table 5.1). Season, as an explanatory variable, explained 47.0% of the variation in sanderling numbers observed along the beach during the study period. Sanderlings were more abundant along the

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Esiama beach in northern autumn with an average count of 767.38 ± 672.97 individuals (slope = 2.69, t = 9.96, $p < 0.001$). This number declined to 183.00 ± 162.29 (slope = -0.55, t = -1.49, p = 0.15) and 85.00 ± 109.41 (slope = -1.05, t = -2.02, p = 0.06) individuals in the northern winter and northern spring respectively. The lowest counts of sanderlings were recorded during the northern summer, with an average of 36.00 ± 50.91 individuals (slope = -2.77, t = -4.57, p = 0.0002; Table 5.1). Occurrence of sanderlings along the Esiama beach did not vary across years.

**Table 5.1 Possible explanatory variables of the temporal variation in occurrence of sanderlings along the Esiama beach.** (‘Prey’ refers to both *Donax pulchellus* and *Excirolana chiltoni*)

| **Variable** | **df** | **$R^2$** | **F-statistic** | **p-value** |
|---|---|---|---|---|
| Season | 3 | 0.47 | 7.32 | 0.002 |
| Year | 2 | -0.04 | 0.64 | 0.54 |
| *Donax pulchellus* (#/ $m^2$) | 1 | -0.05 | 0.03 | 0.87 |
| *Excirolana chiltoni* (#/ $m^2$) | 1 | 0.04 | 1.97 | 0.18 |
| Prey + Season + Year | 7 | 0.37 | 2.78 | 0.049 |

### 5.3.2 Temporal variation in the distribution of benthic macroinvertebrates

The most important macroinvertebrates in benthic samples were the surf clam *Donax pulchellus* and the isopod *Excirolana chiltoni*. Together, these two macroinvertebrates accounted for 98.11% of all macroinvertebrates in benthic samples (see chapter four for more details). *Donax pulchellus* was distributed along the beach in varying densities during the entire study period. Temporal variation in densities of *D. pulchellus* showed that monthly densities of this prey over

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the 27 sampling locations, ranged between 15.61 ± 81.11 and 15,836.53 ± 21,57.30 individuals/ $m^2$ (Figure 5.2). Peak densities of *D. pulchellus* were observed between August and October as well as between January and March. Sharp declines in densities of *D. pulchellus* were observed mostly in the month succeeding peak months. Even though peak *D. pulchellus* densities tend to support peak sanderling numbers, the overall relationship between occurrence of sanderlings and monthly variation in densities of *D. pulchellus* was not significant (Table 5.1). Similarly, the temporal variation in densities of *E. chiltoni* showed that monthly densities of this prey over the 27 sampling locations ranged between 7.03 ± 31.13 and 607.30 ± 1,232.96 individuals/ $m^2$ (Figure 5.3). There was also no significant relationship between occurrence of sanderlings and densities of *E. chiltoni* along the Esiama beach (Table 5.1).

### 5.3.3 Spatial variation in the distribution of sanderlings and densities of benthic macroinvertebrates

Sanderlings along the Esiama beach were observed to be selective of the part of the beach used most. The data showed that distribution of sanderlings along the Esiama beach was non-random. Flocks of sanderlings were observed to aggregate around the middle part of the beach. The numbers of sanderlings declined in the direction of the estuaries (Figure 5.4; Kruskal-wallis $\chi^2$ = 39.13, df = 26, p = 0.047). Densities of *D. pulchellus* were also higher within the middle part of the beach and declined towards the estuaries (Figure 5.4; Kruskal-wallis $\chi^2$ = 95.74, df = 26, $p < 0.001$). There was a significant positive relationship in the spatial distribution of sanderling numbers and densities of *D. pulchellus* ($\log_{10}\text{Sanderling} = 0.11\log_{10} Donax - 1.30$; $R^2 = 0.04$, df = 562, F = 27.1, $p < 0.001$; Figure 5.4) along Esiama beach. There was also a significant pattern in the spatial distribution of *E. chiltoni* (F = 4.37, df = 26, $p < 0.001$), where higher densities of this benthic macroinvertebrate were distributed towards the eastern end of the beach. However,

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there was no significant relationship between the spatial distribution of sanderling numbers and densities of *E. chiltoni* (F = 0.01, df = 562, p = 0.91).

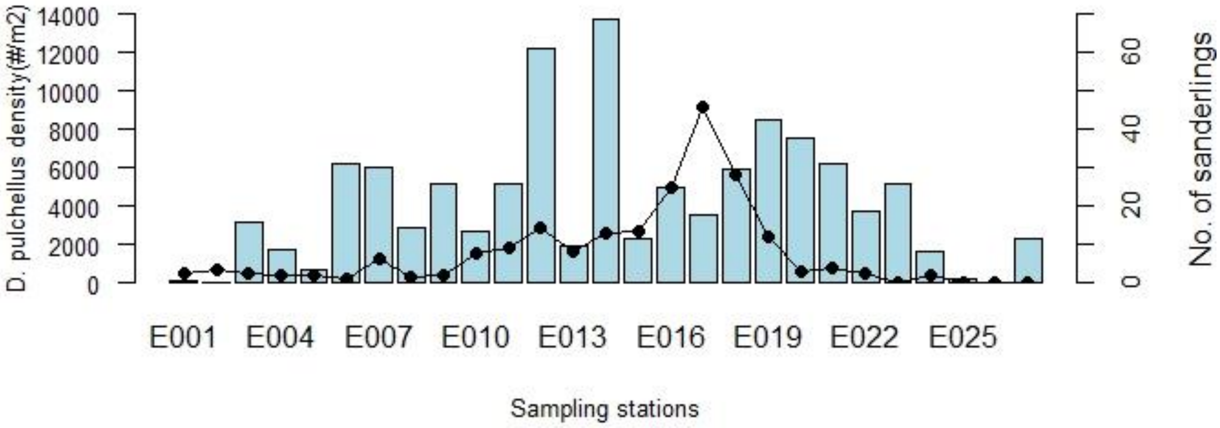

**Figure 5.4 Spatial distribution of densities of *D. pulchellus* and sanderling count**

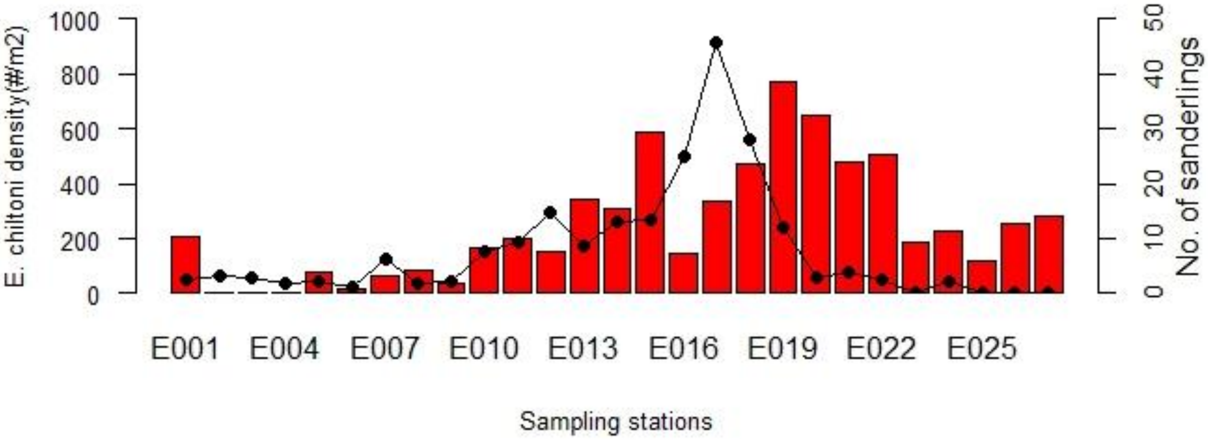

**Figure 5.5 Spatial distribution of densities of *E. chiltoni* and sanderling count**

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## 5.4 Discussion

### 5.4.1 Spatio-temporal variation in the distribution of sanderlings and available prey

Pattern in local abundance of sanderlings along the Ghana coast has been documented over the years and clearly reported to follow a regular pattern. Sanderlings start arriving on Ghana's coast from August, their population peak in September/ October with another peak occasionally observed between January and March during the northern spring migration, with final departure to breeding grounds between April and May (Ntiamoa-Baidu, 1991b; Ntiamoa-Baidu *et al.*, 2014a). The results from this study confirm the reported patterns. Sanderlings were observed along the Esiama beach between July and May. Peak densities of sanderlings were observed in September/ October each sanderling year, however, the peak observed in January/February was not as conspicuous as that in September/ October.

The high numbers of sanderlings observed in September/October may be attributed to the Esiama beach serving the dual purpose as staging (areas where migrants stop to replenish lost energy; also known as stopover sites) and non-breeding shorebird habitat during the southern autumn migration. Therefore, it is possible that assemblages of sanderling populations intending to spend the entire non-breeding season along the Esiama beach (non-breeding "wintering" populations) and those that are only passing through to southern Africa (staging populations) could have been present. Furthermore, the varying numbers of sanderlings observed between January and March, with peak numbers in January/February could be attributed to different migration strategies employed by different sanderling populations en route to their breeding grounds. Thus, the highly unlikely passage through the Ghana coast of sanderling populations that spend the non-breeding season in southern Africa (J. Reneerkens, personal communication, October, 2018; see also Reneerkens *et al.*, 2019) or the more likely passage of sanderlings that spent the non-breeding

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season in other habitats on the Ghana coast or possibly from elsewhere in West Africa, including neighboring countries, such as Ivory coast, may have caused the slight peak counts observed between January-February. The lower peaks observed at this time could be explained by the ability of some "southern" individuals which are able to prepare adequately for the northern-spring migration embark on direct flights to their arctic breeding grounds without stopping over to use resources along the Esiama beach, but of course, stage on temperate stopover sites (Summers *et al.*, 1987; Reneerkens *et al.*, 2019).

Sanderling numbers along the Esiama beach varied independently of prey densities. Variation in prey densities does not always translates into prey availability (Boutin, 1990). Therefore, the bulk of prey observed at the Esiama beach could have been unavailable and inaccessible, probably due to larger prey size, especially in the case of *D. pulchellus*, or faster mobility leading to prey depressions as in the case of *E. chiltoni*.

However, checking the data carefully, some months supported peak counts of both sanderlings and *D. pulchellus*. Possible intense predation by sanderlings on *D. pulchellus* in such months may have resulted in the observed sharp decline in densities of *D. pulchellus* in the immediate succeeding months. The carried over effects of prey depletion in the succeeding months may explain the decline in sanderling numbers along the beach during such periods. Prey densities then recovered in subsequent months, probably due to low predation. Such depletion in densities of the most abundant prey as a result of predation, is a classic example of predator-prey interaction. Such observations have been reported in a wide range of studies; e.g. bird community and nektons feeding on the polychaete *Hediste diversicolor* (Rosa *et al.*, 2008). In the case of shorebirds, declines in densities of prey may lead to a decline in numbers of birds (Goss-Custard, 1980). For example, Karpanty *et al.* (2011) observed that densities of sanderlings declined in

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relation to lower densities of horseshoe crab (*Limulus polyphemus*) eggs, caused by an earlier intense predation. Baker *et al.* (2004) and Niles *et al.* (2009) also observed declines in red knot *Calidris canutus* populations in relation to lower densities of horseshoe crab eggs due to overharvesting of horseshoe crabs.

Spatially, sanderlings were very selective of parts of the beach they utilised. The results suggest that distribution of prey, especially *D. pulchellus*, explained the decision behind sanderlings selecting certain parts of the beach. This observation suggests that even though, temporal variation in distribution of *D. pulchellus* could not explain the numbers of sanderlings on the beach, sanderlings were able to identify areas along the beach which supported high densities of prey to enhance intake rates. *Donax pulchellus* were distributed within the first 3 cm depth of the substrate and as such, were readily available for sanderlings. Identifying good spots to forage will more than likely increase the chances of a forager to increase its intake rates, since a chunk of the food is readily available. In their study of the Mad river estuary in California, Colwell and Landrum (1993) observed different species of shorebirds to aggregate at areas within the habitat that supported high densities of prey.

Furthermore, the topography of the Esiama beach is such that, the mid areas of the beach were wider at low tide, but became narrower towards the estuaries. However, the estuarine areas themselves were wide and extensive at most times but not stable for longer periods due to the frequent deposit and transport of sediment load. These areas were mostly avoided by foraging sanderlings possibly because of the low densities of *D. pulchellus*, but not *E. chiltoni*. Occasionally, a few sanderlings were observed roosting within the estuarine areas, mostly during high tide and probably when preferred roost sites are under severe disturbances, explaining the very few numbers of sanderlings observed along the Amansuri estuary (E001; see chapter 3, Plate

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3.3). Nevertheless, the most preferred roosting site for sanderlings is by the sand dunes within the middle part of the beach, which is closer to areas supporting high densities of prey. Similar observation was made by Rogers *et al.* (2006) at Roebuck Bay on the coast of north-western Australia, where they observed shorebirds to roost close to sources of food.

In contrast, the spatial distribution of sanderlings was independent of the densities of *E. chiltoni*. The unclear pattern between the spatial distribution of sanderlings and densities of *E. chiltoni* may suggest that, *E. chiltoni* could not be the most important prey for sanderlings, but may serve as an alternative source of food during the lean season of *D. pulchellus*. However, a more prudent explanation for the independent association between sanderling numbers and densities of *E. chiltoni* may be the anti-predatory strategies of this prey. *Excirolana chiltoni* is a very mobile species of macroinvertebrates which could easily elude sanderlings by burrowing deeper into the substrate, unlike *D. pulchellus*, which is available and easily accessible in the substrate within an average depth of 1.09 ± 0.72 cm (Grond *et al.*, 2015). This means that, at some point in time, *E. chiltoni* becomes unavailable to sanderlings. Goss-Custard (1970b) and Yates *et al.* (2000) observed that increasing flock size of foraging sanderlings resulted in an increase in predation intensity. Through prey depression as an anti-predatory strategy in response to increasing predation intensities, mobile preys became unavailable to sanderlings which resulted in a decline in foraging rates of sanderlings. Such interference may influence the decision of shorebirds to either abandon such foraging spots or switch to other available preys within the area. Therefore, prey depression as an anti-predatory strategy could influence the decision of sanderlings, by avoiding eluding prey and concentrating on that which is readily available.

Another plausible reason, why sanderlings avoided the eastern estuarine part of the beach which supported higher densities of *E. chiltoni*, could be due to disturbance, especially from humans,

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which would interfere in their foraging activities. Thomas *et al.* (2003) observed foraging rates of sanderlings to decline as human densities increased and Yasué *et al.* (2008) observed foraging birds to abandon areas with higher human disturbances to forage within areas with lower levels of human disturbances.

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# CHAPTER SIX

# DESCRIPTION AND MEASUREMENT OF WHEN, WHERE AND HOW NON-BREEDING SANDERLINGS FORAGE; A FUNCTIONAL AND AGGREGATE RESPONSE TO PREY AND PREDATOR DENSITIES.

## 6.1 Introduction

The East Atlantic Flyway (EAF) sanderling population breed in the arctic regions of Siberia, Greenland and Canada and the non-breeding population covers a wide geographical spread between the temperate and tropic regions (Delany *et al.*, 2009; Reneerkens *et al.*, 2009a). The tropical non-breeding population may have to migrate longer distances, but then are presented with a much favourable climatic condition and as such have little to do with thermoregulation (Castro, 1987; Castro *et al.*, 1992). On the other hand, the temperate non-breeding population is presented with a shorter migratory distance from the breeding ground, however there is a trade-off with maintenance as more energy is spent on thermoregulation (Kersten & Piersma, 1987). In both cases, energy is a key driving force. Therefore, the identification, acquisition and assimilation of food form an integral aspect of the annual life cycle of migrant shorebirds (Breed, 2001).

Migrant shorebirds spend a large part of the non-breeding season either foraging or resting (e.g. Morrier & McNeil, 1991; Nol *et al.*, 2014). The amount of time spent foraging and resting is dependent on a number of factors including: abundance and quality of food, flock size, tidal cycle and predation (e.g. Reneerkens *et al.*, 2009a; Piersma, 2012; van den Hout *et al.*, 2014; Grond *et al.*, 2015; Lourenço *et al.*, 2016b). A number of studies have shown that the seasonal occurrence of some wader species strongly correlates with the distribution of their main prey, especially

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during the lean season of other alternative prey items (Goss-Custard, 1970b; Goss-Custard & Le V. dit Durell, 1983; Maron & Myers, 1985).

Due to the patchiness in food resource allocation, densities of shorebirds are also aggregated, rather than randomly or uniformly distributed. Variation in the prey intake rates of shorebirds is therefore, a function of predator (shorebird) densities, prey densities and size distribution, inter- and intra-specific competition and disturbances (van Gils, 2004; Lourenço *et al.*, 2015; Lourenço *et al.*, 2016b; Lourenço *et al.*, 2017). The searching time, handling time, prey quality and digestive constraints may influence the short- and long-term intake rates of shorebirds (van Gils *et al.*, 2005b; Gommer *et al.*, 2018).

To maximize prey intake in view of all the above listed constraints, shorebirds have devised foraging techniques and styles used in exploiting prey. For sanderlings, three different foraging techniques have been described: pecking, probing and sewing/threading/stitching (e.g. Petracci, 2002; Nuka *et al.*, 2005; Grond *et al.*, 2015; Lourenço *et al.*, 2015). Pecking is solely a visual foraging technique, whereas probing and sewing/threading/stitching are tactile foraging methods. Visual foraging methods are used when prey are easily visible to the bird, whilst tactile methods are used when searching for buried prey (Lourenço *et al.*, 2015). In addition to the foraging techniques and styles, phenotypic plasticity of some internal organs (e.g. gizzard) allows certain shorebird species the comfort to exploit a wide variety of food resources (van Gils *et al.*, 2003a; van Gils *et al.*, 2005a; van Gils *et al.*, 2005b; Yang *et al.*, 2013; Oudman *et al.*, 2014).

The diet of shorebirds is important in understanding the various relationships within the food chain and as such, provide a better understanding of the community structure of habitats on a micro- or macro-scale. Assessment of shorebird diet can be done in several ways. However, an

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easier, cost-effective and a faster way of assessing diet of shorebirds, aside direct observation of prey consumed, is by analysing undigested materials in their faecal matter, especially when prey fragments can be recognized in droppings (Barrett *et al.*, 2007). In such circumstances, the frequency of occurrence of prey fragments in droppings may allow for an estimation of the amount of prey consumed (Dekinga & Piersma, 1993; Lourenço *et al.*, 2015). However, in situations where recognizable prey fragments are affected by digestive processes, then analysis of droppings should be done with some reservations. To address this problem, calibration studies may be employed to provide more accurate estimations (Onrust *et al.*, 2013). Otherwise, more expensive and time consuming techniques such as stable isotope (Bearhop *et al.*, 2004) and genetic markers (Bradley *et al.*, 2007) may be used.

Mollusc-eating shorebirds have been used as models in calibration studies from shell fragments in their droppings. The red knot is one that has been widely studied (e.g. Dekinga & Piersma, 1993; van Gils *et al.*, 2003a; van Gils *et al.*, 2005a; Onrust *et al.*, 2013; Oudman *et al.*, 2014). The sanderling, a closely related species to the knot (Zwarts & Wanink, 1993), may be considered a molluscivore at certain non-breeding sites (Nuka *et al.*, 2005; Ntiamoa-Baidu *et al.*, 2014a; Grond *et al.*, 2015). In recent times, sanderlings have also been used as models in calibration studies in both the tropics and temperate areas (Lourenço *et al.*, 2015; Lourenço *et al.*, 2017). In Ghana, sanderling forages exclusively on the surf clam *Donax pulchellus* (Ntiamoa-Baidu *et al.*, 2014a; Grond *et al.*, 2015), and the macroinvertebrate assessment (refer to chapter four) confirmed the importance of this prey, as it constituted more than 90% of the total composition of macroinvertebrates in benthic samples.

This chapter presents descriptions and measurements of when, where and how non-breeding sanderlings forage, a functional and aggregate response to prey and predator densities.

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## 6.2 Methodology

### 6.2.1 Study site

The study was conducted along the 13 km sandy beach between the Amansuri and Ankobra estuaries in the Western Region of Ghana, hereafter referred to as the Esiama beach. Detailed description of the study area has been provided in Chapter 3 of this thesis. All field and laboratory investigations were carried out between September 2015 and February 2018.

### 6.2.2 Time-activity budgets

Time-activity budgets were constructed for sanderlings along the Esiama beach from August 2015 to July 2016 following methods described by Ntiamoa-Baidu *et al*. (1998) and Grond *et al*. (2015). A 12-hour daily survey was conducted once each month at specific locations along the 13 km beach; recording the time, location (in relation to the 27 sampling locations used for invertebrate sampling) and activities or behaviours of each sanderling encountered. The selected areas were known from the transect surveys to support continuously high densities of sanderlings (see Chapter 5). Flocks of sanderlings were scanned with a 15-60x Swarovski spotting telescope for a period of 10 minutes every hour during the day, from 0600 to 1800 GMT and all activities portrayed by sanderlings and the proportion of birds involved in a particular activity were recorded. Sanderlings were observed either by driving along the beach in a vehicle or by using multiple observers at different locations recording at the same time. It was assumed that the proportion of individual sanderlings engaged in a particular activity was equal to the proportion of time sanderlings spent on that activity. The various activities recorded included:

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I. Foraging: birds actively searching for (also included short runs chasing after prey) and ingesting prey through exhibition of different foraging strategies such as probing, pecking and sewing

II. Resting: birds not involved in active foraging, but lying, sitting, squatting, standing or sleeping, with little or no movement.

III. Locomotion (active runs, walking, hoping and flying)

IV. Comfort activities such as preening and bathing.

An individual sanderling was assigned a particular behaviour if it spent the majority of the time under observation on such activity.

### 6.2.3 Foraging behaviour

Detailed behavioural parameters of foraging sanderlings in the field were studied through direct observation with a 15-60x Swarovski spotting telescope and 1-minute video recordings with a x60 optical zoom HD Lumix video camera. Sampling was based on a focal individual approach and followed Thomas *et al.* (2003). Video recordings were analysed with Solomon Coder beta 17.03.22. Detailed description of methods used are described in Chapter 3.

### 6.2.4 Calibration studies

Following the protocol and samples used in the biomass-size calibration study (see chapters 3 and 4), the heights of hinges plus 'top' of individual *D. pulchellus* were regressed against the length. The 'top' refers to the extended part of both halves of the bivalve above the hinge line known as umbo. The hinge + top was used in this study because more than 70% of the identifiable hinges in sanderling droppings had the umbo in place. Furthermore, the hinge + top was a good explanatory variable of the length of *D. pulchellus* explaining more than 90% of the variation in

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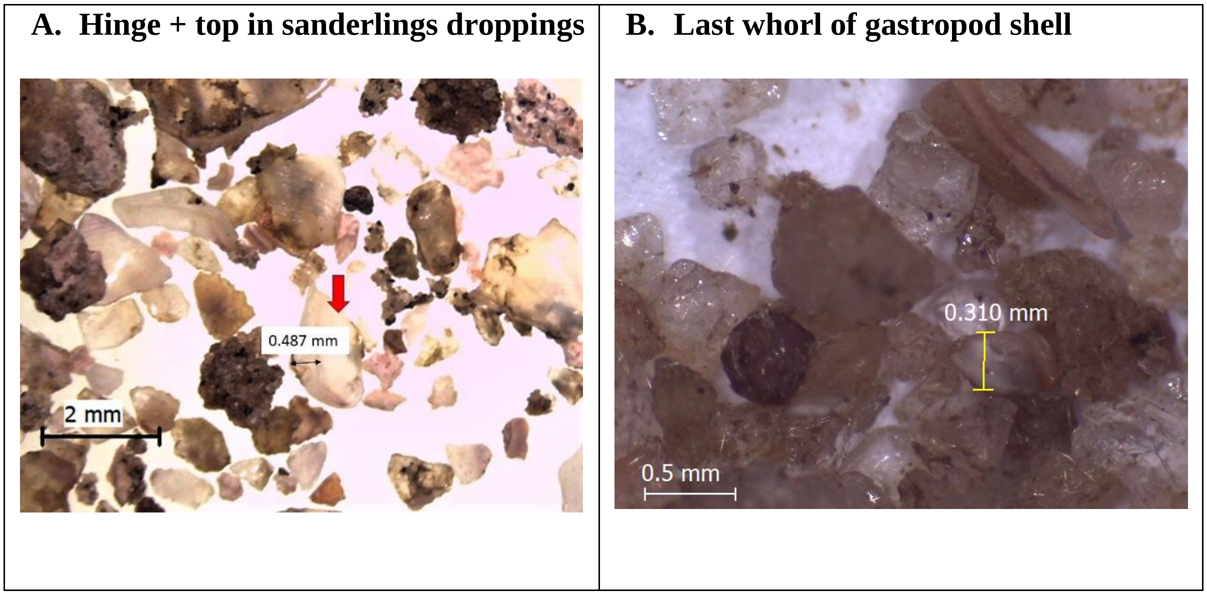
the size of the bivalve. To avoid pseudo-replication, the heights of both left and right hinges + top were measured with a Leica EZ4 HD camera microscope and the mean value used in the regression plot against corresponding sizes of *D. pulchellus*. The regression equation was later used in the reconstruction of length of ingested *D. pulchellus* from hinges + top found in faecal droppings of sanderlings.

### 6.2.5 Assessment of diet of sanderlings

The diet of sanderlings was assessed through direct observation and identification of prey consumed by sanderlings in the field whenever possible. However, in most cases, the prey was too small to be identified with a telescope, therefore an indirect approach of analysing faecal droppings was employed. A total of 177 sanderling droppings were collected along the beach on two occasions; in November 2016 and November 2017, mostly at roost sites immediately after sanderlings were observed foraging, in order to be certain that faecal matter was actually from sanderlings. Droppings were analysed for undigested and identifiable parts of prey (see Chapter 3 for detailed description of diet assessment including methodologies followed).

From the droppings, the different types of prey consumed were identified. Bivalves were identified in droppings from broken shells and hinges (Plate 6.1 A), and the number of bivalves consumed was estimated from the number of paired hinges + top of similar sizes following Lourenço (2007). It was not easy identifying and estimating the number of isopods and polychaetes in faecal samples, because of their soft bodies which enhanced their easy digestion. However, polychaetes were identified from chaetae and mandibles (Zwarts & Wanink, 1993; Weber & Haig, 1997; Scheiffarth, 2001) and isopods from setae and posterior appendages known as uropods (Ramer, 1985). Other less frequently observed prey in the diet of sanderlings such as fish were also identified in the faecal samples from scales and gastropods from the last whorl of shell (Figure 6.1 B) (Weber & Haig, 1997; Nuka *et al.*, 2005; Onrust *et al.*, 2013).


**A. Hinge + top in sanderlings droppings**

**B. Last whorl of gastropod shell**

**Plate 6.1 Indigestible materials in faecal droppings of sanderlings.** (A - Hinge + top confirm *Donax pulchellus* as part of sanderlings diet, and B - presence of other less occurring prey such as the gastropod *Hastula aciculina* in sanderling's faecal droppings).

The abundance of each identified prey in faecal samples was estimated as well (Lourenço, 2007). Hinges of bivalves were sorted as pairs of similar sizes (right and left halves) and the minimum number of bivalves per faecal sample was estimated as the maximum number of hinges recorded for either pair. The height of the hinge + top was measured to the nearest 0.001 mm with a Leica EZ4 HD camera microscope with a magnification of x32. The number of polychaetes was estimated based on the number of mandibles recorded (Scheiffarth, 2001). Polychaetes sampled in this study were observed to possess four mandibles, hence the number of polychaetes consumed by sanderlings was based on the number of mandibles divided by four. The total number of the last whorl of gastropod shells was used in estimating the number of gastropods ingested. The number of uropods was also used in determining the number of isopods consumed.

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The occurrence and proportions of the various macroinvertebrates constituting the diet of sanderlings were estimated as frequency of occurrence (FO) and numerical frequency of each prey consumed (NF) following Lourenço *et al.* (2015). Because sanderling droppings were collected at low tide and most isopods were expected to be consumed during high tide, there is a possibility of underestimating the number of isopods consumed by sanderlings. Furthermore, there could also be underestimation of soft-bodied prey such as isopods and polychaetes as most parts of the prey were likely to have been digested before passing out of the bird's gut.

### 6.2.6 Intake rates and energy budget

Prey intake rate of foraging sanderlings was difficult to estimate in the field due to the small sizes of ingested prey. In order not to over- or under- estimate prey intake rates from only direct observations, information from diet analysis of faecal droppings was also used. Regurgitates were very rarely observed in this study. The proportion of each prey in the droppings of sanderlings was determined, focusing mainly on the most abundant prey parts in sanderlings' faecal droppings namely; *D. pulchellus*, *Excirolana chiltoni* and *Glycera* spp.. These prey were used in estimating the total biomass of prey consumed, based on size class and intake rates. The sizes of *D. pulchellus* consumed by sanderlings were reconstructed from hinges + top using regression equation developed through calibration studies. It was not possible to construct such calibrations for isopods and polychaetes, therefore size estimation was based on average length estimated for these species during macroinvertebrate sampling (Chapter 4).

As a result of the difficulty in determining intake rates through direct observations, the intake rates of *D. pulchellus* was determined experimentally with captive sanderlings. The intake rates of *E. chiltoni* and *Glycera* spp. could not be estimated experimentally, because there were not enough individuals of this prey in samples to be used under experimental conditions. Therefore,

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in determining the intake rates of *E. chiltoni* and *Glycera* spp., it was assumed that the proportion of these prey in the faecal matter was a representative of the number of prey consumed over a period of time. Knowing the intake rate of *D. pulchellus* experimentally, and the proportion of this prey in sanderlings droppings in relation with other prey items, the intake rates of polychaetes and isopods could be estimated.

The intake rates of sanderling feeding on the main prey *D. pulchellus*, was determined with captive sanderlings. Four sanderlings were captured with mist nets on 23rd January 2017, colour marked and used in captive experiments that lasted for a period of nine days, after which the birds were released at the point of capture on 31st January, 2017 (see chapter 3 for more details). The mean of the biometrics of these sanderlings were:

i. Wing length - 125.25 ± 3.69 (range 121 - 130 mm)
ii. Bill length - 23.13 ± 2.61 (range 19.8 - 25.7 mm)
iii. Total head length - 50.85 ± 2.53 (range 47.7 - 53.4 mm)
iv. Tarsus length - 25.83 ± 1.37 (range 24.2 - 27.1 mm)
v. Tarsus and toe length - 45.00 ± 1.41 (range 44 - 47 mm).

The average body mass of the four sanderlings at capture prior to the experiment was 53.50 ± 5.00 g, which declined to and was kept constant at around 45.25 ± 4.57 g over the one week of experimentation. The average body mass of the captive birds, however increased to 46.50 ± 3.11 prior to their release in the field after the experiment (Figure 6.1). No leg cramps were observed for any of the captive birds and these birds easily conditioned to the set up and commenced feeding after 12 hours in captivity.

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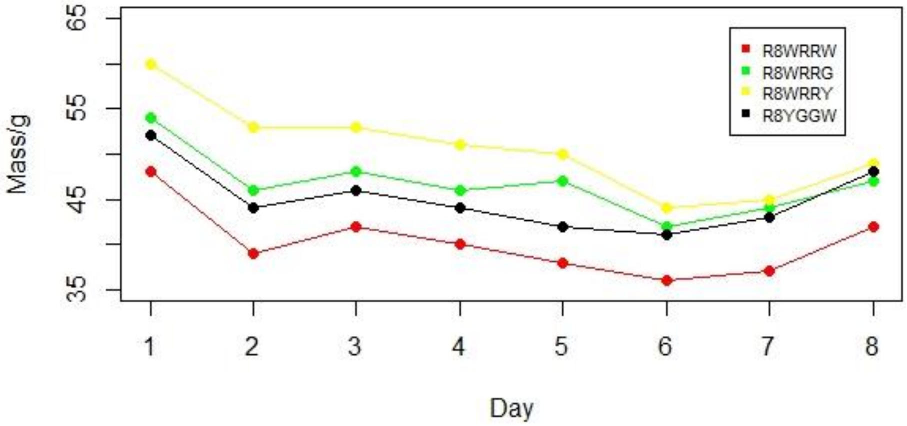

**Figure 6.1 Variation in body mass of captive sanderling over the experimental period**

The prey that was offered to the captive birds was mainly made up of a mixture of *D. pulchellus* and some *E. chiltoni*, enough to condition them into getting used to both prey items. *Donax pulchellus* formed the bulk of the diet as this prey was the most abundant in the field. Freshly cut flesh of *Agaronia acuminata* was offered to the sanderlings as supplementary diet to help maintain their body mass just around the mean value. A total of 52 trials were carried out on the four captive sanderlings, offering them different sizes of *D. pulchellus*: 28 trials with mixed size *D. pulchellus* (1.0 mm size class), 12 trials with small-size *D. pulchellus* and 12 trials with medium-size *D. pulchellus*. The average sizes of *D. pulchellus* consumed was determined from the difference in proportion of the different size classes of *D. pulchellus* offered before and after the experiment. The *D. pulchellus* ingested in the experiment was then compared to that obtained from reconstruction of *D. pulchellus* sizes from the faecal analysis.

The ingested biomass per size class was estimated as a product of the intake rate per minute and size-specific biomass in relation to the time spent foraging estimated from the time-activity budget. The sizes of *D. pulchellus* were estimated from regression equation using hinge + top in

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faecal samples. For isopods and polychaetes, the mean length of these species was used to estimate the biomass. The estimates obtained per minute were subsequently extrapolated into biomass intake per 12-hour period in relation to the proportion of time spent foraging as estimated from the time-activity budgets of sanderlings in the field.

In estimating the biomass, some assumptions were made, which means it is only under such conditions would the estimated biomass of prey consumed by sanderlings along the Esiama beach hold. It was assumed that the intake rate of *D. pulchellus* under experimental condition was similar to that in the field. Nevertheless, such intake rates only hold at low tides and four hours before and after low tide. This is because the bulk of *D. Pulchellus* are available to sanderlings only during this period. During high tide, the bulk of *D. pulchellus* is no longer available to sanderlings and it was assumed that the most important prey during this period was *E. chiltoni*. There were no estimates of intake rates for *E. chiltoni* and *Glycera* spp., so it was assumed that the intake rates of *Glycera* spp. and *E. chiltoni* would reflect the proportion of these prey items in the faecal droppings.

## 6.3 Data analysis

The data were tested for normality using Shapiro-Wilk test and the appropriate statistical tests were applied. The RStudio version 1.1.447 operating under R version 3.5.0 (R Core Team, 2018) was used to analyse the data; all bar charts with error bars and scatter plots were created graphically with this software. Stacked bar charts for time-activity budgets were plotted with Microsoft Excel® 2016.

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### 6.3.1 Time-activity budgets

The proportions of sanderlings engaged in a particular activity were expressed as percentages of the total flock size under observation. Time-activity budgets were constructed for sanderlings with the following as explanatory variables: hours to low tide, diurnal time (time of the day), monthly variation, densities of prey and numbers of sanderling.

### 6.3.2 Foraging and Intake rates

The Solomon Coder beta 17.03.22 was used in transcribing video recordings on foraging sanderlings both in the field and under experimental conditions. The output frequencies and durations obtained from the transcription were expressed as ratios of the total time under observation. Foraging and intake rates, as well as foraging durations were expressed as mean ± SD.

### 6.3.3 Statistical analysis

All linear regression models were computed with the '*lm()*' function in R software and the '*summary(model)*' provided the necessary inferential statistical information such as F-values, degree of freedom (df), coefficient of determination ($R^2$) and p-values. Linear regression was used to determine the relationships between foraging rates and densities of prey, densities of sanderlings, age of sanderlings, cross-tidal distribution of sanderlings, flock size and nearest neighbour distance (both conspecifics and heterospecifics). Kruskal-wallis was also used to test for the relationship between intake rates and prey size. Dunn's test of multiple comparisons was carried out as a post-hoc test on significant relationship between any two explanatory variables. Wilcoxon rank sum test was also used to test for relationship between foraging rates of sanderlings under experimental and field conditions. The proportion of each prey item in faecal dropping was presented as a percentage of the total number of prey items in the faecal sample.

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All decisions and inferences on statistical analyses were based on a 5% significance level and computed in R statistical software (R Core Team, 2018).

## 6.4 Results

### 6.4.1 Time-activity budgets

A total of 378 scans were made in 12 days over a 12-month period in the field, identifying 34,298 individual sanderlings in different flocks with sizes ranging between 1 to 1,200 individuals. Out of the total number of sanderlings observed, 20,732 were engaged in foraging activity, 12,666 were resting, 394 were in locomotion and 506 were exhibiting comfort activities. Thus sanderlings spent 60.45%, 36.93%, 1.15% and 1.48% of the 12-hour day time foraging, resting, in locomotion and engaged in comfort activities respectively (Figure 6.2). This implies that, sanderlings foraged for about 7.01 hours, rested for 4.59 hours, moved around for 0.08 hours and spent 0.31 hours out of the 12-hour day time on comfort activities. Furthermore, the activity pattern of sanderlings varied with the tidal cycle. The results showed that foraging activities of sanderlings increased during the first 3 hours of ebb tide, reduced thereafter until low tide and started to increase again with the incoming tide.

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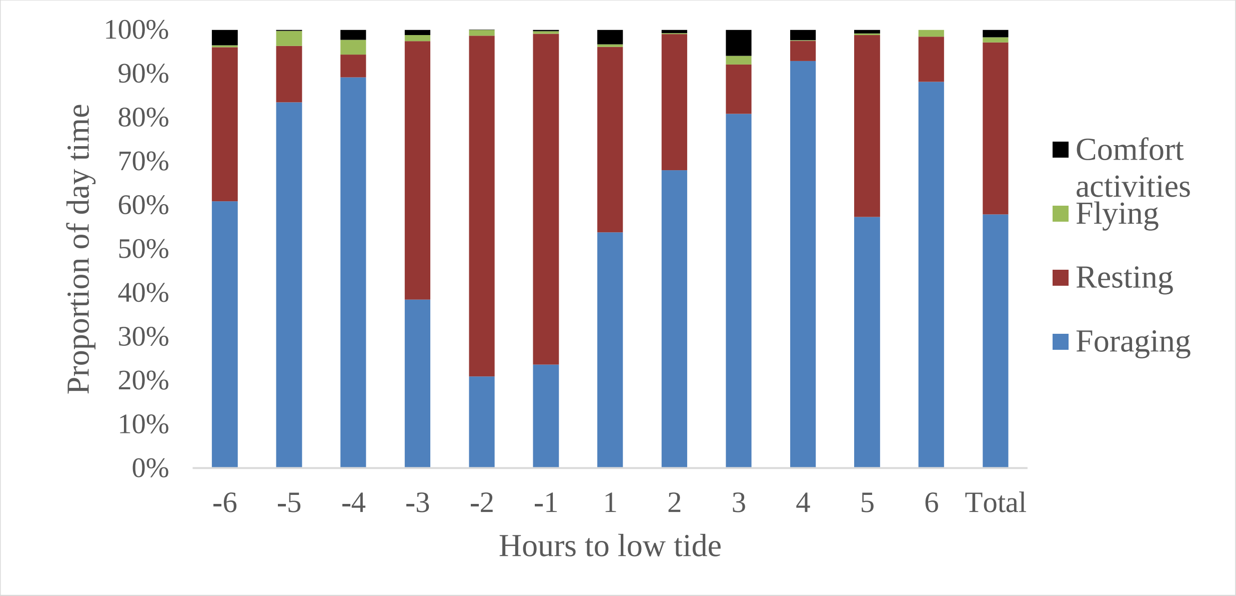

**Figure 6.2 Time-activity budget of sanderlings along the Esiama beach in relation to tidal cycle.**

The time-activity budget of sanderlings was subjected to a different perception, analysing the data with respect to diurnal time. A time-activity budget was constructed for sanderlings along the beach from morning 0600 GMT to evening 1800 GMT (Figure 6.3). The result showed that sanderlings spent more time (between 70.0% and 100.0%) foraging in the early hours of the day. The amount of time spent foraging gradually decreased with time until midday (1200 GMT), when sanderlings spent the least time foraging. Although sanderlings foraging activity increased after midday until dusk, the proportion of time spent foraging at this time was relatively lower than in the mornings.

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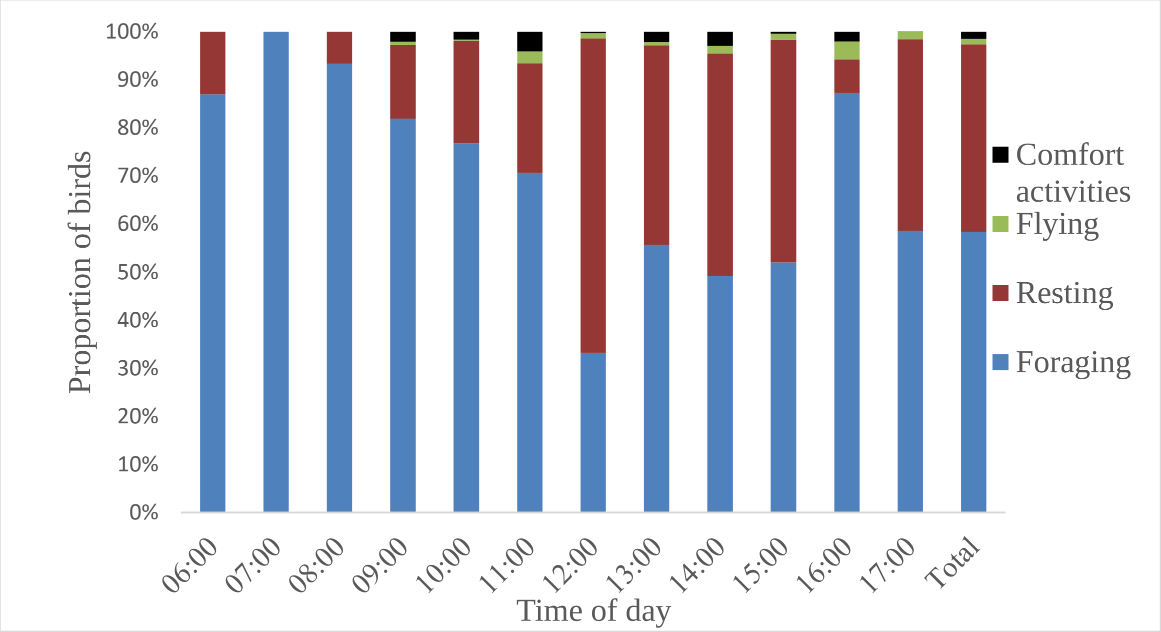

**Figure 6.3 Time-activity budget of sanderlings along the Esiama beach in relation to diurnal time.**

The proportion of foraging sanderlings was analysed in a contour plot as a third variable against the time of day (diurnal time) and time to low tide (Figure 6.4). The results confirmed that, sanderlings preferred to forage during the early and late hours of day light, i.e. between 0600 and 0900 as well as 1500 and 1700 GMT. These periods also coincided with the tidal cycle, showing an interesting pattern, such that, the foraging activities of birds were concentrated between two and six hours before and after low tide. The pattern clearly showed increase in foraging activities as the tide comes in (Figure 6.4).

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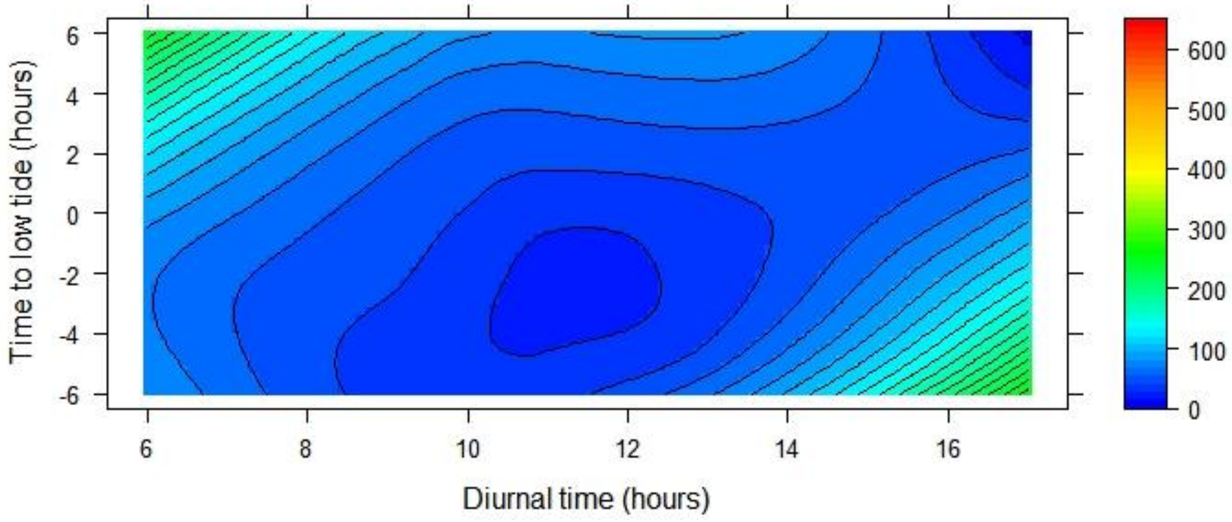

**Figure 6.4 Proportion of sanderlings in relation to diurnal time and tidal cycle.** (Colour gradient scale shows number of foraging sanderlings where blue represents 0 sanderlings and red 600 foraging sanderlings).

Upon arrival on the Esiama beach in August, sanderlings spent more time foraging, this declined in September to about half the hours of day light. The time spent foraging increased in October and November and sanderlings were observed to spend about 80% of day time foraging. Between December and January, sanderlings spent about half of the entire day light hours foraging, increasing gradually in subsequent months. No sanderlings were observed along the Esiama beach in June 2016. Nevertheless, sanderlings that were present in July spent two-thirds of diurnal time foraging (Figure 6.5).

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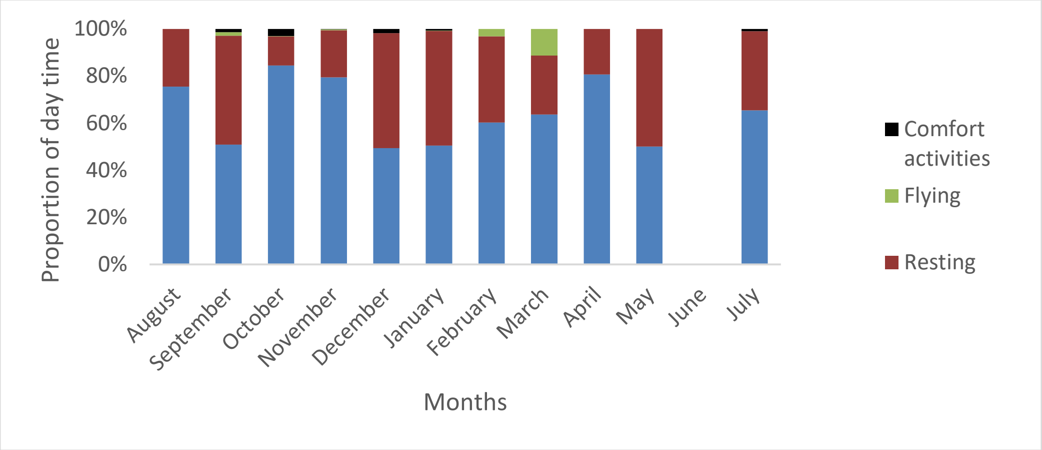

**Figure 6.5 Temporal monthly variation in the time-activity budget of sanderlings along Esiama beach**

The time–activity budget of sanderlings was also influenced by density dependent factors. Sanderlings were observed to forage more during the lean season of prey abundance (76.87%) than during the peak season of prey abundance (51.01%). Sanderlings also spent more time foraging during the low season of sanderling occurrence (69.26%) than during the peak season (56.42%, Figure 6.6).

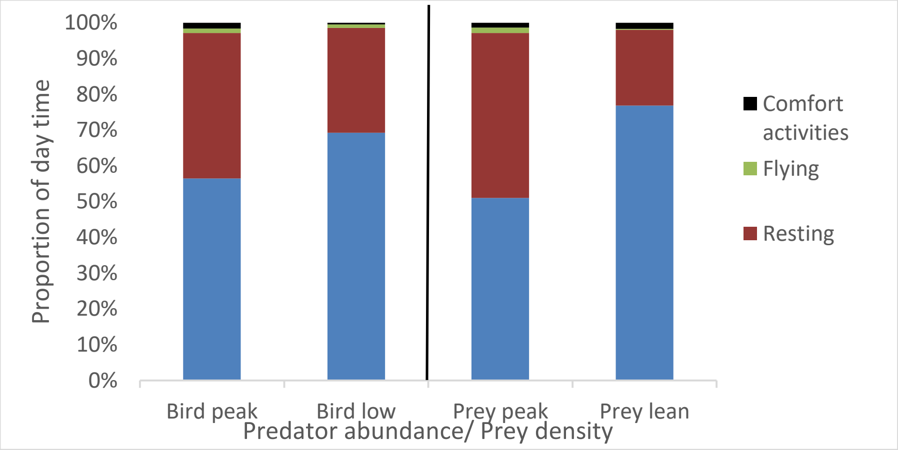

**Figure 6.6 Time-activity budgets of sanderlings in relation to prey density and sanderling abundance**

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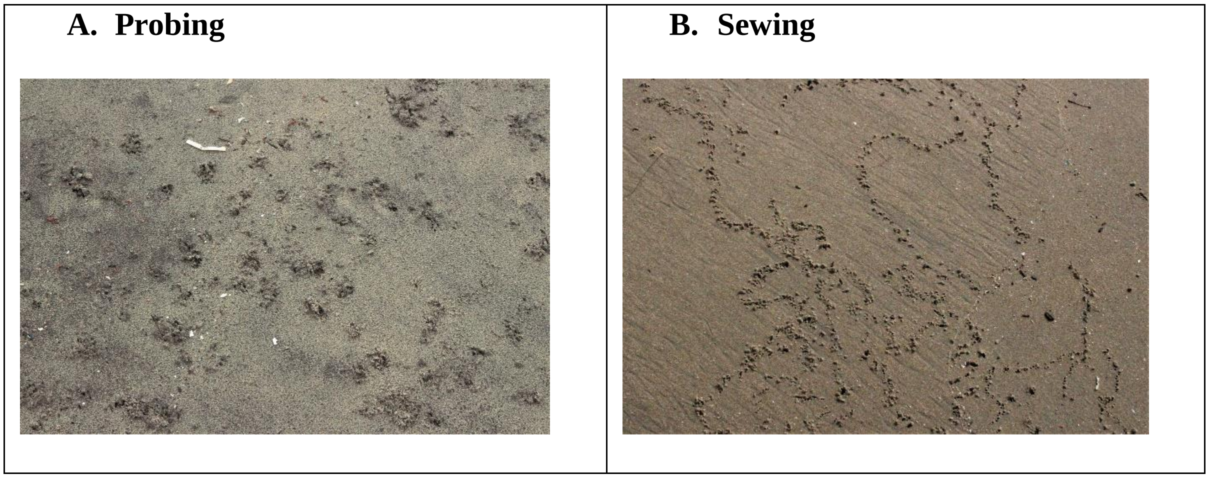
### 6.4.2 Foraging methods and strategies

Sanderlings were observed to employ both visual and tactile foraging methods in exploiting their prey. Three foraging methods were identified during the study period and these included pecking, probing (Plate 6.2 A) and sewing (Plate 6.2 B). ‘Sewing’ has also been referred to as threading or stitching in other studies (e.g. Grond *et al.*, 2015).

Sanderlings used the entire beach, from the peripheral vegetation to the watermark for foraging purposes. Sanderlings were observed foraging mostly along the edge of the water and they would run or chase after receding tides to forage on exposed macroinvertebrates. Sanderlings foraging in between the watermark and the peripheral vegetation during low tides were observed to use more tactile methods. Depending on the condition at the high tide watermark areas, sanderlings were observed to employ both tactile and visual foraging methods. For example, sanderlings foraging within the high tide zone during low tides were observed to probe or sew more in search of prey. However, sanderlings foraging within the high tide zone during high tide, were observed to peck more as the water kept gashing in on the sand dune. Sanderlings in captivity were observed to spend more time probing and sewing when foraging on larger prey items.


**A. Probing**

**B. Sewing**

**Plate 6.2 Signs of probing (A) and sewing activities (B) of sanderlings**

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### 6.4.3 Foraging rates and duration

In this study, foraging rate was measured as number of pecks made by sanderlings per minute. Foraging rates of sanderlings varied with densities of prey (*D. pulchellus*) and number of sanderlings present along the beach. Sanderlings pecked more (25.24 ± 19.29 pecks/min) when densities of prey were higher than when densities of prey were lower (15.19 ± 13.74 pecks/min; F = 32.92, df=1, p < 0.0001; Figure 6.7). Similarly, sanderlings pecked more (25.04 ± 19.01 pecks/min) when they were abundant on the beach than when they were fewer (17.66 ± 16.16 pecks/min; F = 17.73, df = 1, p < 0.0001; Figure 6.7).

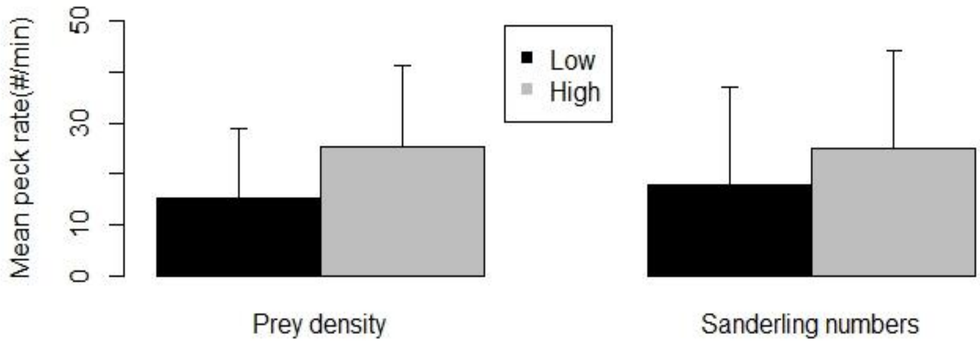

**Figure 6.7 Foraging rates of sanderlings in relation to densities of prey and numbers of sanderlings.** (Black bars represent low prey density and bird numbers whereas grey bars represent high prey density and bird numbers. Standard deviations are shown with error bars).

The results also showed a significant difference (F = 11.42, df =1, p = 0.0008; Figure 6.8) in the time spent probing for prey by sanderlings between the low season of bird numbers (6.23 ± 8.19 s/min) and the peak season of bird numbers (9.80 ± 12.74 s/min). However, there was no difference (F = 0.05, df = 1, p = 0.82; Figure 6.8) in the time spent probing for food during the

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lean season of prey density (7.79 ± 10.52 s/min) and the peak season of prey density (8.03 ± 10.92 s/min; Figure 6.8).

In the case of time spent by sanderlings sewing, the data showed a significant difference (F = 20.2, df =1, p < 0.0001; Figure 6.9) in the time spent sewing between the low season of bird numbers (8.09 ± 12.12 s/min) and the peak season of bird numbers (3.33 ± 8.73 s/min). However, there was no significant difference (F = 0.08, df = 1, p = 0.78; Figure 6.9) in the time spent sewing for prey during the lean season of prey density (6.00 ± 11.32 s/min) and the peak season of prey density (5.69 ± 10.61 s/min).

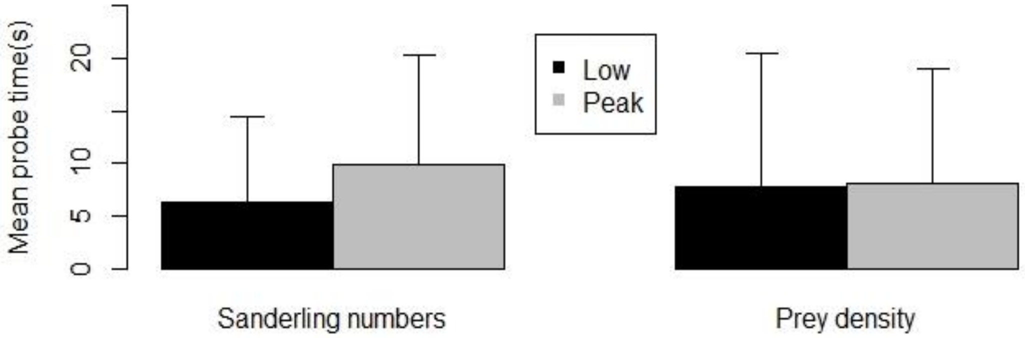

**Figure 6.8 Time spent probing by sanderlings in relation to densities of prey and numbers of sanderlings.**

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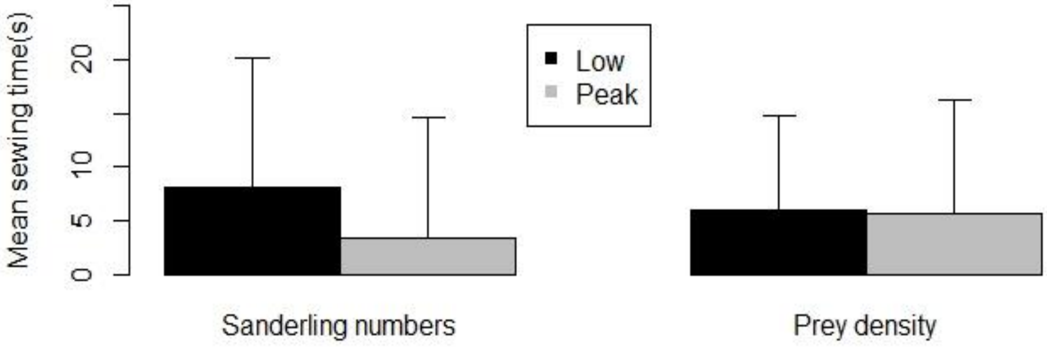

**Figure 6.9 Time spent sewing by sanderlings in relation to densities of prey and numbers of sanderlings.**

Whiles foraging along the edge of the water, sanderlings were observed to employ the pecking foraging method. There was no significant difference (Table 6.1) in mean pecking rate across the beach; 17.30 ± 16.91, 19.03 ± 16.80 and 22.79 ± 20.57 pecks/min estimated at the low, intertidal and high tide zones of the beach respectively. Though juveniles pecked more (28.13 ± 22.19 pecks/min) than adults (22.73 ±17.52 pecks/min), there was no significant difference in their foraging rates (Table 6.1).

**Table 6.1 Relationship between foraging rates of sanderlings and other explanatory variables**

| Parameter | df | F-statistic | p-value* |
|---|---|---|---|
| Cross tidal | 2 | 1.57 | 0.21* |
| Age | 1 | 3.35 | 0.07* |
| Flock size | 339 | 1.27 | 0.26* |
| Conspecific distance | 327 | 3.19 | 0.08* |
| Heterospecific distance | 47 | 0.90 | 0.35* |

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* *None of the p-values was significant.*

Furthermore, there was no significant relationship between flock size of sanderlings and pecking rate (Table 6.1). The mean flock size of foraging sanderlings varied significantly across the beach (F = 3.04, df = 2, p = 0.049); low tide zone – 28.4 ± 33.3 individuals, intertidal zone – 21.36 ± 20.4 individuals and high tide zone – 16.4 ± 19.9 individuals. Therefore, using the highest mean flock size of 28 individuals as a threshold, a positive significant relationship was observed between pecking rate and flock size below this threshold (F = 17.89, df = 243, p < 0.0001), but a negative significant relationship was observed between pecking rate and flock size greater than 28 individuals (F = 4.37, df = 94, p = 0.04; Figure 6.10).

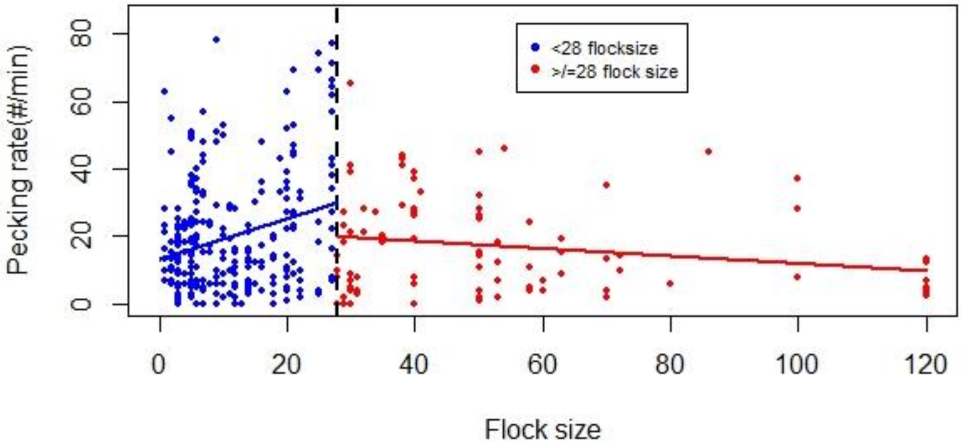

**Figure 6.10 Foraging rate of sanderlings in relation to flock size.** (Blue dots and line are peck rates and model line for flock size less than 28 individuals respectively; red dots and line represents peck rates and model line for flock size greater than or equal to 28 individuals respectively. Broken black line represents the threshold flock size of 28 individuals).

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There was no significant relationship between pecking rate and distance between a foraging sanderling and the nearest conspecific neighbour (Table 6.1). However, sanderlings foraging in flock size greater than or equal to 28 individuals, pecked more as the distance between foraging conspecifics increased (F = 19.02, df = 84, $p < 0.0001$). There was no significant relationship between pecking rate and distance between a foraging sanderling and other conspecifics in flock sizes less than 28 individuals (F = 1.55, df = 219, p = 0.21). Furthermore, there was no significant relationship between pecking rate and distance between foraging sanderlings and heterospecifics (Table 6.1).

The highest foraging rates of sanderlings were observed in August (29.45 ± 21.00 pecks/min) and September (28.90 ± 18.38 pecks/min), periods marking arrival and peak counts of sanderlings respectively. The foraging rates declined suddenly and significantly in successive months until November (H = 68.18, df = 10, $p < 0.001$) when the least foraging rate of 11.75 ± 12.07 pecks/min was estimated. Sanderlings then maintained a rather steady foraging rate between 13.22 ± 5.87 and 19.67 ± 14.93 pecks/min between December and July (Figure 6.11).

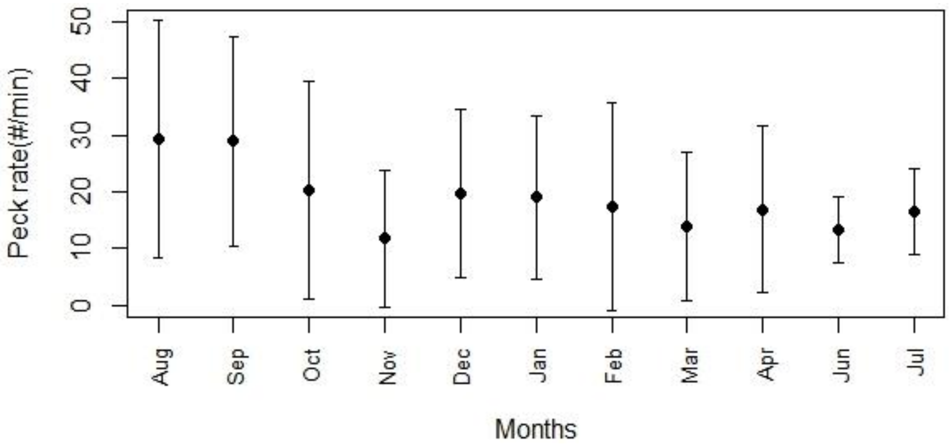

**Figure 6.11 Temporal variation in foraging rates of sanderlings along Esiama beach** (Error

bars represents standard deviation).

### 6.4.4 Diet analysis and reconstruction of prey

The diet of sanderlings was analysed through direct observation in the field and indirectly through faecal droppings of sanderlings. For direct field observations, only conspicuous prey items were identified to be consumed by sanderlings. Amongst such prey were polychaetes (Plate 6.3), *Emerita talpoida*, small fishes and occasionally, strands of the sea weed *Sargassum* spp. The frequencies of prey consumption estimated through direct observation was very low because sanderlings foraged mostly on small prey items making it difficult to observe ingestion.

**Plate 6.3 Sanderling feeding on a polychaete.** (In the picture are other sanderlings aggressively trying to interfere with the ingestion of the polychaete).

Out of the 177 sanderling droppings collected from the field and analysed, 162 of them representing 92.05% contained an indigestible material of at least one prey species. The frequency of occurrence of each prey item varied from one faecal sample to the other. *Donax*

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*pulchellus* was the most frequently occurring prey item in the faecal samples and was found in 78% of the total number of faecal samples analysed. This was followed by *E. chiltoni* (15%), *Glycera* spp. (10%), *H. aciculina* (2%) and fish (1%). *Donax pulchellus* also accounted for 79% of the total number of prey items found in faecal samples. *Excirolana chiltoni* and *Glycera* spp. also accounted for 12% and 8% respectively of the total number of prey items in faecal samples. *Hastula aciculina* and fish were amongst the least observed in terms of numbers of prey items in faecal samples, and together, they accounted for less than 2% of the total number of prey items in faecal samples (Table 6.2).

**Table 6.2 Sanderling diet composition based on analysis of faecal samples.** (FO = Frequency of occurrence and NF = Numerical frequency are expressed as a proportion of 1. For *E. chiltoni*, *Hastula aciculina* and *Glycera* spp., mean lengths of each from benthic macroinvertebrate sampling was used).

| **Prey** | **FO** | **NF** | **Size range/ mm** | **AFDM/ mg** |
|---|---|---|---|---|
| *D. pulchellus* | 0.78 | 0.79 | 2.76-10.21 | 1.28 ± 1.39 |
| *E. chiltoni* | 0.15 | 0.12 | 5.2 | 1.44 ± 0.06 |
| *Glycera* spp. | 0.10 | 0.08 | 28.5 | 4.65 ± 3.07 |
| *Hastula aciculina* | 0.02 | 0.01 | 17.6 | 14.05 ± 0.28 |
| Fish | 0.01 | 0.00 | | |
| **Total faecal samples** | **177** | **718** | | |

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From the calibration study, a curvilinear relationship existed between the length of *D. pulchellus* and the height of the hinge + top (Figure 6.12).

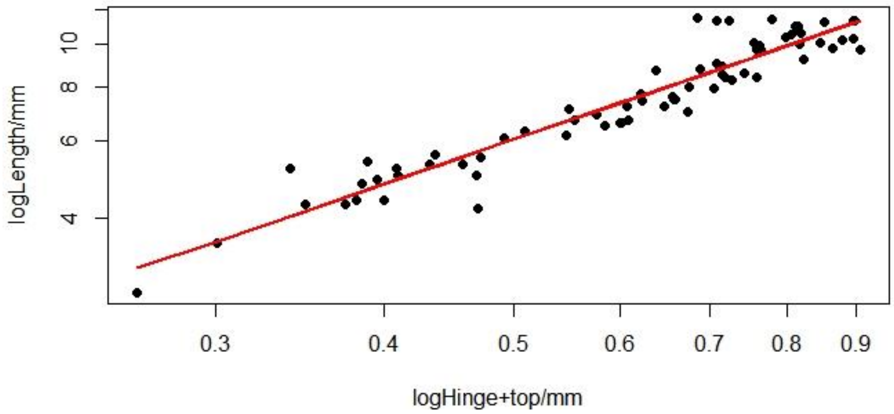

**Figure 6.12 Calibrated relationship between length in mm, and height of hinge + top in mm of *D. pulchellus*.** (Note the logarithm scales of both axes. The regression line is represented by $\log_{10}$ Length = 12.51 + 1.054 $\log_{10}$ Hinge + top; $R^2 = 0.91$, F = 668.3, df = 69, $p < 0.0001$).

### 6.4.5 Intake rates

As a result of the small sizes of prey, intake rates could hardly be observed and estimated under field conditions. Nonetheless, it was possible to estimate intake rate of *D. pulchellus* under experimental conditions with captive sanderlings. Such estimates may then be useful in determining intake rates in the field, based on the assumption that similar foraging rates occurred under both field and experimental conditions. The data depicted no significant difference in foraging rate of sanderlings under field (23.68 ± 18.54 pecks/min) and experimental (25.13 ± 14.03 pecks/min; W = 3810, p = 0.37) conditions (Figure 6.13), which justified the assumption made.

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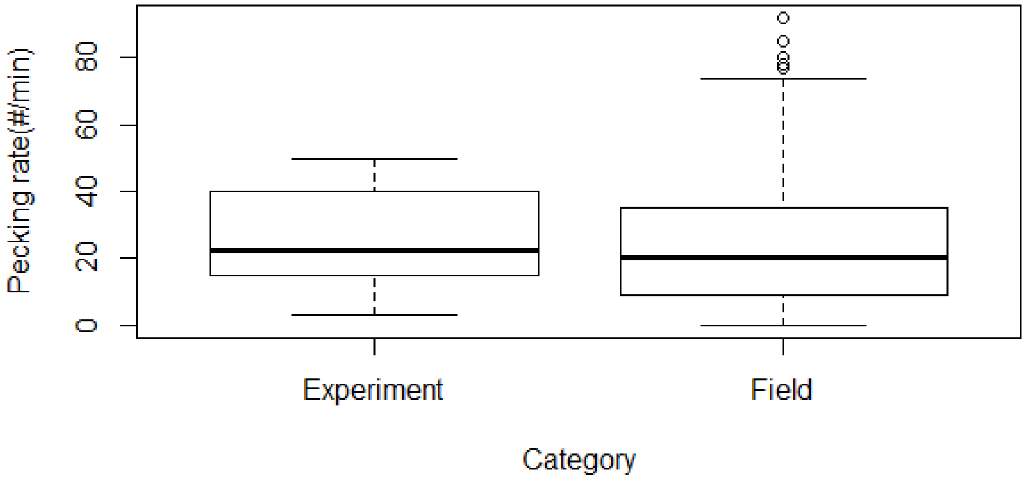

**Figure 6.13 Foraging rates of sanderlings under experimental and field conditions**

The rate of intake of *D. pulchellus* by sanderlings varied with size of prey. There was a significant difference in intake rates of the different sizes of *D. pulchellus* ($H = 18.28$, df = 2, $p = 0.0001$). Sanderlings consumed 1.61 ± 0.73, 1.61 ± 1.03 and 0.44 ± 0.36 *D. pulchellus* individuals/min of mixed-size, small-size (3.5-5.5 mm) and medium-size (6.5-8.5 mm) *D. pulchellus* respectively (Figure 6.14). A post-hoc test showed that sanderlings consumed more of the mixed-size ($p < 0.0001$) and small-size ($p = 0.0005$) *D. pulchellus* than the medium-size prey. This implies that there is a possible prey size selection for smaller-size than medium-size and probably larger-size *D. pulchellus*.

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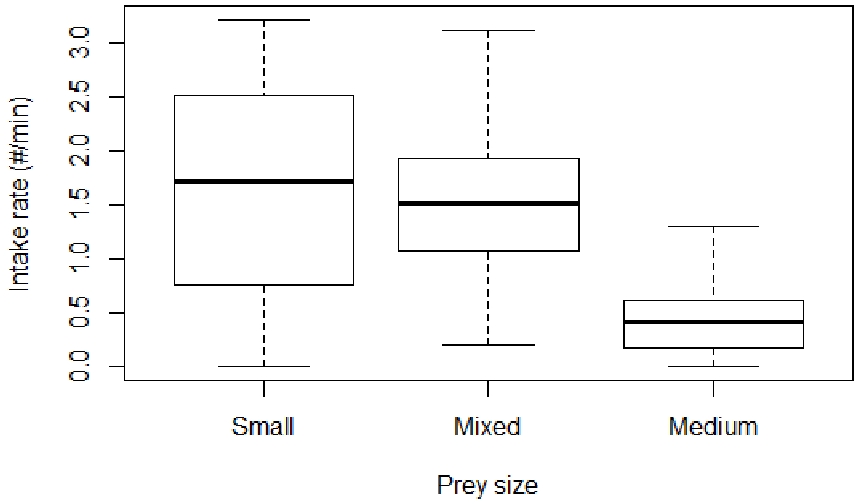

**Figure 6.14: Intake rates of *Donax pulchellus* by captive sanderlings.**

Sanderlings were observed to select more small-size (< 5.5 mm) *D. pulchellus* than medium-size (6.5-8.5 mm) and large-sized (9.5-11.5 mm) individuals. The most consumed size classes of *D. pulchellus* under experimental condition were 4.0-4.9, 5.0-5.9 and 6.0-6.9 mm, whereas that under field condition were 3.0-3.9, 4.0-4.9 and 5.0-5.9 (Figure 6.14).

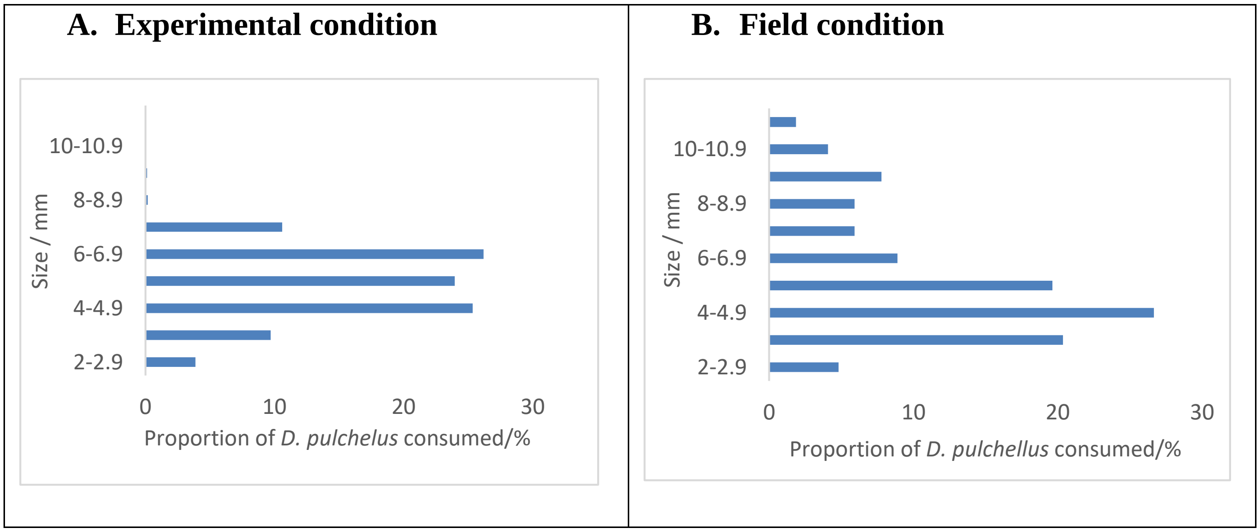

**Figure 6.14: Proportion of different size classes of *Donax pulchellus* consumed by sanderlings under experimental (A) and field (B) conditions**

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### 6.4.6 Biomass and energy consumption of sanderlings along Esiama beach

Biomass of prey consumed was estimated for the three most abundant prey in the diet of sanderlings. Sanderlings consumed on average an estimated 1.57 ± 0.96 gAFDM$_{\text{flesh}}$ of prey in a 12-hour diurnal period, of which *Donax pulchellus*, *E. chiltoni* and *Glycera* spp. constituted 46.01%, 31.18% and 22.81% of the total biomass consumed, respectively (Figure 6.15).

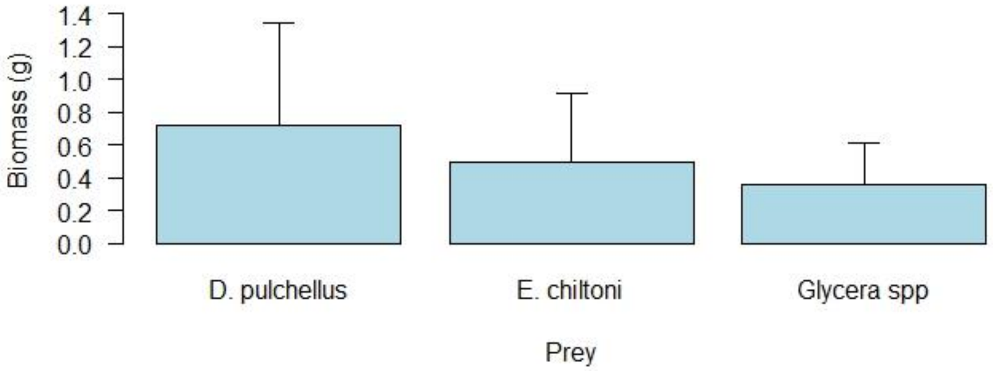

**Figure 6.15: Estimated biomass of prey items consumed by sanderlings in a 12-hour diurnal period**

## 6.5 Discussion

### 6.5.1 Time-activity budgets

The results from this study showed that non-breeding sanderlings along the Esiama beach spent 60% of the day time foraging. The amount of time recorded in this study to be spent by sanderlings foraging was higher than the approximated 40% of day time recorded by Grond *et al.* (2015) at the same study site, but similar to the 63% of day time reported by Ntiamoa-Baidu *et al.* (1998) at other wetlands along Ghana's coast. The time budget of sanderlings from this study was estimated once a month for 12 months and showed temporal variations in the proportion of

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time spent foraging. Grond *et al.* (2015) studied sanderlings along the Esiama beach from January to March in 2008 and in January and February in 2009. In the same month period, this study reported 50-60% of day time spent foraging. The difference in the proportion of time spent foraging could be due to the different times the studies were conducted, the tidal phase, the densities of prey, the condition of the prey and the ambient temperature (Castro *et al.*, 1992; Zwarts & Wanink, 1993).

Another important factor which could influence the amount of time spent by sanderlings foraging is disturbance from humans and human activities along the beach. Several studies have shown that foraging rates decline with disturbances, resulting in shorebirds foraging for longer hours if they cannot find better foraging areas to relocate to (Lafferty, 2001a, 2001b; Thomas *et al.*, 2003; Yasué, 2005; Yasué *et al.*, 2008). Shorebirds may even resort to nocturnal foraging in order to meet their energetic needs (Burger & Gochfeld, 1991a).

Sanderlings were observed to spend more time foraging in certain months which coincided with timing of migration; thus arrival (in August) and northern spring migration (between February and May). Similar observations were reported by Zwarts *et al.* (1990a) in Mauritania for several species of shorebirds, who increased foraging time in response to timing of migration.

More sanderlings were observed foraging during the early hours of the day. This observation could mean that sanderlings were either not foraging at night or even if they did, nocturnal foraging was less efficient. Sanderlings are primarily visual foragers and foraging efficiency of such foragers are low at night (Grond *et al.*, 2015). Elsewhere in California, Lafferty (2001b) observed a high proportion of western snowy plovers *Charadrius alexandrinus nivosus* to forage more in the morning before 10:30am than later in the afternoon. He attributed this to the relatively

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little human disturbances in the mornings than later in the day.

The time-activity budget of sanderlings could be explained also by the tidal cycle. More sanderlings were observed to forage during high tide (2 hours before and after high tide). Sanderlings were likely to be foraging on the isopod *E. chiltoni* during this period. This fast moving macroinvertebrate could easily evade sanderlings by burrowing deeper into the substrate, beyond the reach of sanderlings. However, during high tide, water gushed onto the sand dunes, forcing buried isopods to come out of their burrows and become visible to sanderlings for easy capture and ingestion. The results also showed that more sanderlings foraged after low tide. This observation could be explained by the action of the incoming tide causing partial erosion of the substrate and thereby, exposing buried *D. pulchellus*. As the bivalves try to burrow back into the substrate, their movements are noticed by sanderlings and they are captured. The study showed that sanderlings take an optimal course of foraging action, maximizing foraging opportunities presented by the tidal action.

### 6.5.2 Foraging methods, rates and strategies

Foraging sanderlings were observed to employ three main methods in obtaining prey: pecking, probing and sewing/threading. These three foraging methods have been described in a number of studies that involved sanderlings (Ntiamoa-Baidu *et al.*, 1998; Goss-Custard *et al.*, 2006; Grond *et al.*, 2015; Lourenço *et al.*, 2015). Pecking is a visual foraging method used on surface dwelling prey, whereas probing and sewing are predominantly tactile foraging methods used for searching and consuming buried prey. However, probing could involve some visual cues where sanderlings may observe prey prior to the insertion of their bills in the substrate to search for the prey. Lourenço *et al.* (2015) differentiated between probing and sewing as non-random probe (NRP) and random probe (RP) respectively.

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The results of this study suggest that sanderlings pecked more when prey densities were higher and when sanderling numbers were also higher. Assuming there is a positive correlation between foraging rates and intake rates, then such an observation will be a classic example of a functional response of sanderlings to prey densities. Nevertheless, sanderlings were also observed to use more tactile approach as bird densities increased, even when prey density was known to be high and such an observation suggests that: (i) individual sanderlings within a foraging flock may experience competition or interference from other members of the flock, which result in an increase in time spent searching for prey using tactile foraging methods, (ii) the high numbers of sanderlings might influence anti-predatory strategies such as prey depression, causing limited prey availability, resulting in the use of tactile foraging methods. The latter may also be the reason behind the observation of no significant difference in time spent probing or sewing by sanderlings during peak and lean seasons of prey densities.

These observations confirm that of Goss-Custard (1980) and Goss-Custard *et al.* (2006). In his review of studies carried out in the Ythan estuary in north-east Scotland, Goss-Custard (1977) observed higher foraging rates for redshanks *Tringa totanus* feeding on the amphipod *Corophium volutator* when prey densities were higher. The intense predation on the amphipod by redshanks led to depletion of the prey, leading to enhanced competition and increased interference amongst foraging birds. Duijns and Piersma (2014) also observed anti-predatory response in the form of prey depression by lugworms *Arenicola marina* which were fed on by bar-tailed godwits *Limosa lapponica* in the Wadden Sea as foraging rates increased, leading to prey depletion.

Sanderlings foraging in flock sizes less than 28 individuals did so with little interference. Some studies have shown higher foraging rates of shorebirds in larger flocks (e.g. Elgar, 1988). In this study, foraging rates increased with increasing flock size up to a threshold of 28 birds in a flock.

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It appears that beyond this threshold, foraging rates of sanderlings were no longer just dependent on the combined efforts of individual birds towards protection against predation, which allowed them to spend less time watching out for potential predators and more time foraging. Foraging rates at that level may depend on competition for food resources. According to Silliman *et al.* (1977), optimum flock size is determined by competition for food when resources are limited. The results from this study showed that beyond a flock size of 28 individuals, there was a negative influence of increasing numbers in a flock on foraging rates. Aggression amongst foraging individuals was not observed frequently, probably because of the small sizes of *D. pulchellus* and *E. chiltoni* sanderlings fed on. The external handling time of such small prey items was so little that prey was almost swallowed instantly after capture. However, few aggressive behaviours were however observed, when sanderlings were foraging on polychaetes, which were larger and demanded longer external handling time. So as competition and interference intensifies in larger flock sizes, sanderlings increased their nearest neighbour distances in order to maximize intake rates. Such distances were significantly greater, when the nearest neighbour was a conspecific, probably to avoid aggressive interaction over shared resources.

### 6.5.3 Reconstruction of prey item in sanderling diet

The relationship between size of a bivalve and indigestible parts such as hinge + top in droppings is mostly allometric and expressed as a power function in the form $Y = aX^b$, where ‘Y’ is the size of the bivalve which is a measure of the length, ‘X’ is the indigestible hinge + top in faecal droppings, ‘a’ is the intercept and ‘b’ is the slope (e.g. Dekinga & Piersma, 1993; Onrust *et al.*, 2013; Lourenço *et al.*, 2015; Lourenço *et al.*, 2017). The results of this study also followed a similar pattern.

Allometric equation for reconstructing prey size from indigestible material in droppings was done

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for only *D. pulchellus*. The data from prey consumed under experimental and field conditions showed that sanderlings consumed *D. pulchellus* of all sizes (size range = 2.0-12.0 mm). However, there was variation in the proportion of the different size classes of *D. pulchellus* that were consumed. Sanderlings consumed more small size *D. pulchellus* than medium and large size individuals. This observation suggests that, it was easier for smaller prey size to be ingested than medium and large *D. pulchellus*. Smaller size *D. pulchellus* could also be more profitable than medium and larger ones, and would be more profitable to select such prey size, especially when sanderlings are foraging in a foraging patch with a higher interference and competition for food.

### 6.5.4 Biomass of prey consumed by sanderlings

Diet of sanderlings consisted of bivalves, gastropods, crustaceans, polychaetes and fish. These prey items have been reported in the diet of sanderlings by other studies (e.g. Nuka *et al.*, 2005; Vanermen *et al.*, 2009; Lourenço *et al.*, 2015). The observation from this study supports the idea that sanderlings are generalists in their dietary needs and they make use of the most abundant prey within their habitats (Nuka *et al.*, 2005). The most frequently observed and most abundant prey item in the faecal samples was *D. pulchellus*. However, it is not conclusive that *D. pulchellus* was the most consumed prey item, because there is a possibility that, most of the soft-bodied prey that were consumed by sanderlings had already been digested in the gut of the bird and as such, could not have been observed in the droppings of these birds.

The data from this study showed that the total estimated biomass consumed by sanderlings in a 12-hour diurnal period was 1.57 ± 0.96 g AFDM, out of which *D. pulchellus* constituted 46.01% equivalent to 0.72 ± 0.62 g AFDM. The biomass consumed by sanderlings contributed by *D. pulchellus* according to this study was much lower than the 26.57 g AFDM estimated by Grond *et al.* (2015). The difference in the estimated biomass of *D. pulchellus* from this study and that of

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Grond *et al.* (2015) could be due to the very low intake rates of *D. pulchellus* in this study. In this study, the intake rate of *D. pulchellus* was estimated from the experimental trials with captive sanderlings as 0.03 mg AFDMs$^{-1}$, whereas that estimated by Grond *et al.* (2015) in the field was 1.64 mg AFDMs$^{-1}$. The latter is equivalent in biomass to a 6.9 mm *D. pulchellus* estimated from the calibrated allometric equation derived in this study. Meaning that sanderlings consumed one medium-size *D. pulchellus* every second according to the estimates of Grond *et al.* (2015). This study estimated such biomass (1.61 mg AFDM) to be consumed in one minute. Grond *et al.* (2015) estimated the intake rate of *D. pulchellus* through observation of the fast movement of the head of foraging sanderlings which they assumed that each upright movement of the head resulted in a successful intake. Such an assumption could have accounted for the extremely high biomass estimates, because it was observed in the captive experiment that several foraging attempts made by sanderlings did not result in successful prey intakes. The experimental results also showed that sanderlings took between 1 and 3 digestive breaks every 30 minutes when foraging on *D. pulchellus*. Each digestive break lasted for about 490.17 ± 124.50 s. In the field, the estimated mean time taken by sanderlings for a digestive break was 513.16 ± 361.32 s. Although Grond *et al.* (2015) were quick to mention the importance of digestive breaks by waders foraging on bivalves, this was not factored in their estimation of ingested biomass which was calculated to be 5.9 g AFDM h$^{-1}$ compared with the 0.14 g AFDM h$^{-1}$ obtained in this study. Clearly, these estimates show that the time taken to process ingested shell mass by digestively constrained sanderlings is very important in determining the total biomass of prey consumed.

In another non-breeding site, Lourenço *et al.* (2015) estimated a total biomass of 6.1g AFDM consumed by sanderlings on a sandy beach in Portugal. Out of this proportion, 85% of the prey items that contributed to the 6.1 g AFDM biomass was from the consumption of polychaetes. In

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this study, the ingested biomass of *E. chiltoni* and *Glycera* spp. were 0.49 ± 0.42 g AFDM and 0.36 ± 0.26 g AFDM respectively. In their study, Lourenço *et al.* (2015) observed that polychaetes were the most abundant prey in benthic samples on the beach, but the bivalve *Donax trunculus* was the most abundant prey item in faecal samples. However, the average biomass of a polychaete was about 45 times that of an individual *D. trunculus* leading to the higher contribution of polychaetes to the total ingested biomass estimated by Lourenço *et al.* (2015).

The lower total ingested biomass estimated by this study could also be explained by underestimation of the importance of other prey items in the diet of sanderlings. The assumptions in estimating the intake rates of *E. chiltoni* and *Glycera* spp. may have resulted in underestimation of the actual biomass of these prey consumed. In other studies where waders were observed foraging on crustaceans, Goss-Custard (1977) estimated the intake rates of redshanks feeding on the amphipod *Corophium volutator* at the Ythan estuary in north-east Scotland to be 22 individuals/ min when they were foraging in areas with amphipod densities of 1000 individuals/ $m^2$, but only 2.4 individuals/ min when feeding in areas with less than 200 individuals/ $m^2$ respectively. Dierschke *et al.* (1999) also reported about 21 individuals of the amphipod *Hyperia galba* in the gut of dunlins *Calidris alpina* in a dietary study using stomach flushing method on the island of Langenwerder in Germany. Certain areas along the Esiama beach supported densities of 1000 individual isopods/ $m^2$ and the size range of *E. chiltoni* (1.5 – 9.0 mm; Chapter 4) is similar to that of *C. volutator* (1.0 – 10.0 mm) and *H. galba* (2.0 – 12.0 mm). If we assume that sanderlings in our study also consumed 22 and 2.4 individuals of *E. chiltoni* during high tide (±2 hours) and low tide (±4 hours) respectively, then the total biomass of isopods consumed in a 12-hour tidal cycle will be 6.25 g AFDM. If the overall total biomass consumed by sanderlings is estimated based on intake of both isopods and bivalves, a figure of 7.34 g AFDM is obtained,

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which is similar to what was observed by Lourenço *et al.* (2015).

The lower estimated biomass of prey consumed by sanderlings in this study as compared with the estimates reported by Grond *et al.* (2015) may also be due to the condition of the macroinvertebrates. Zwarts and Wanink (1993) observed temporal variation in the condition of macroinvertebrates in the Wadden Sea. It is possible that the macroinvertebrates used in estimating the biomass of prey in this study and those used in the Grond *et al.* (2015) study were sampled within different seasons or months and therefore the estimates may not be comparable. It would be informative to estimate the biomass of benthic macroinvertebrates along the Esiama beach on a monthly basis to determine seasonal variations in their condition with time.

There were probably some other macroinvertebrates which were not identified in faecal samples. The period for the collection of the faecal droppings coincided with the lean season of prey densities along the Esiama beach (Chapters 4 & 5) and lowest foraging rates of sanderlings. These estimates could also have been influenced by the total ingested biomass. Sanderlings could have been feeding on some other important prey items which were not observed in both benthic macroinvertebrate sampling and faecal droppings. For instance, sanderlings were observed to feed on the seasonal sea weed *Sargassum* spp which was not taken into consideration in estimating the total biomass. Some studies have shown that smaller waders consume significant amount of biofilm on the surface of the sediment (Kuwae *et al.*, 2008; Jardine *et al.*, 2015; Jiménez *et al.*, 2015; Lourenço *et al.*, 2017) and benthic meiofauna (Sutherland *et al.*, 2000), which may supplement their dietary and energetic intakes. Mathot *et al.* (2010) examined the stomach contents of western sandpipers *Calidris mauri* and dunlins at the Fraser River delta in British Columbia, Canada, and observed that less than 25% of ingested prey by these species comprised of macroinvertebrates. They also observed that between 40 and 75% of the stomach

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contents were made up of sediments, diatoms and organic detritus, which implies that a significant proportion of the ingested biomass by those waders were made up of biofilm.

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# CHAPTER SEVEN

# PREY TYPE AND SIZE PREFERENCE OF SANDERLINGS

## 7.1 Introduction

Prey selection is an important component of predator-prey relationship which in effect influences community ecology. With the process of natural selection shaping interactions within a community, a predator's choice of prey is important in maximizing its survival and fitness (Gill, 2003). Easy as it may sound, the process of energy transfer within a community is quite complex and dependent on several components or actors which play key roles in an all-inclusive interaction. Nevertheless, the basic components of predator-prey relationship include predator/ prey densities, searching and handling of prey (Vucetich *et al.*, 2002) as well as a prey- selection or preference component (Stephens & Krebs, 1986).

The foraging behaviour of many organisms are dependent on the abundance and availability of prey, as well as the number of predators that depend on the prey resource (Wilson & Bromley, 2001). Competition amongst foragers, due to limited food supply, is one of the major underlying factors explaining resource partitioning and prey switching in an ecosystem (van den Hout *et al.*, 2014). The main goal of most foragers is to maximize long term intake rates, which translates into enough energy to satisfy their daily energy demands, as well as provide reserves for other life processes (van Gils, 2004). Therefore, for shorebirds staging in certain habitats, whose energy budget are time-bound and who need to maximize intake rates within the shortest possible time, the preference and selectivity of prey are of paramount importance. In systems that support high densities of food, the type and quality of prey may also define the intake rates of shorebirds. These explanations may satisfy the predictions of several foraging models that define the foraging

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and intake rates of foragers in a spatio-temporal dynamic system (Gill, 2003).

Several models have been designed to help with the understanding of predator-prey interactions and prediction of prey choice/ selection amongst foragers (e.g. Holling, 1959; Ayala *et al.*, 1973; Belovsky, 1986). However, the two most important models for this study are the contingency model (CM) and the digestive rate model (DRM). These models operate on the following characteristics of prey; prey type or size ($i$), metabolizable energy or digestible part ($e$), shell/ ballast mass or indigestible part ($k$) and searching and/or handling time ($h$). The CM, also known as the Basic Prey Model (BPM) (Hughes, 1997), describes optimal diets that maximize intake rates of foragers, depending on the handling times of prey (MacArthur & Pianka, 1966). Profitability of prey ($e_i/h_i$) in this context may be expressed as a gain in the long-term average intake rate of prey whose energy content exceeds unit searching and/or handling time (Stephens & Krebs, 1986; Hughes, 1997). The main constraint for foragers that follow the CM, according to Jeschke *et al.* (2002), is the rate at which prey is handled externally .

The digestive rate model (DRM), on the other hand, describes prey that maximizes long term energy intake for foragers constrained by digestion rate (Jeschke *et al.*, 2002). The DRM therefore best predicts prey of high quality ($e_i/k_i$) to be selected for by foragers that aim at maximizing long-term energy intake rate ($e$) in circumstances where foragers are faced with a digestive constraint (ballast mass, $k$).

For shorebirds that feed on shelled- or hard exoskeleton- prey by swallowing their prey whole, the energy intake rate is dependent on the rate of processing the swallowed prey, a condition termed ‘digestive bottleneck’ (Piersma *et al.*, 2003; van Gils *et al.*, 2003a) rather than external handling time. Studies have shown that, digestive constraint forces such predators to pause

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feeding in order to provide time for processing swallowed prey, thereby reducing the total energy intake in the long-term (van Gils *et al.*, 2005b). However, the DRM predicts foragers to forage on high-quality prey in order to maximize their long term energy intake.

The main diet of sanderlings along the Esiama beach is the surf clam *Donax pulchellus,* which is swallowed whole. An alternative diet is the isopod *Excirolana chiltoni*, which occurs in lower densities. The swallowing of *D. pulchellus* whole means that the stomach of sanderling is likely to fill up early, demanding time taken off to process ingested prey, and as such, affecting long-term intake rate. This chapter seeks to investigate prey choice by sanderlings as predicted by the contingency and digestive rate models.

## 7.2 Methodology

### 7.2.1 Study Site

The study was conducted along the 13 km sandy beach between the Amansuri and Ankobra estuaries in the Western Region of Ghana, hereafter known as Esiama beach. Detailed description of the study site has been provided in Chapter 3 of this thesis. The research design was an experimental one with a set-up located about 10 km away from the beach.

### 7.2.2 Captive birds

The birds held in captivity were captured in mist nets on 23rd January 2017 and released on 31st January 2017 as described in Chapter three. Four adult sanderlings were involved in the captive experiments. The average body mass of the four sanderlings at capture prior to the experiment was 53.50 ± 5.00 g, which declined to and was kept constant at around 45.25 ± 4.57 g over the experimental week. The average body mass however increased to 46.50 ± 3.11 prior to release in

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the field after the experiment (see Chapter 6). No leg cramps were observed for any of the captive birds and these birds easily conditioned to the set up and commenced feeding after half a day in captivity. The diet provided to the captive birds was made up mainly of a mixture of *D. pulchellus* with some *E. chiltoni*, enough to condition them into getting used to both prey items. *Donax pulchellus* formed the bulk of the diet as this prey was more abundant in the field. Freshly cut flesh of *Agaronia acuminata* was offered to sanderlings as supplementary diet to help maintain their body mass just around the mean value. In parameterizing the CM, the handling time of each prey species by the captive birds was estimated. A maximum intake experiment was also conducted to parameterize the DRM. Preference of prey type (between *D. pulchellus* and *E. chiltoni*) and size (only *D. pulchellus*) was determined in an experiment using a dichotomous set up (van Gils *et al.*, 2005b; Gommer *et al.*, 2018).

### 7.2.3 Prey species

*Donax pulchellus* and *Excirolana chiltoni* were the two preys used in the experiments. *Donax pulchellus* was used in the maximum intake experiment because of the high densities of this prey along the beach. Length was used as a measure of size (see chapter 4) and two size classes were used: small-sized (3.5-5.5 mm) and medium-sized (6.5-8.5 mm). The large size class (9.5-11.5 mm) was excluded as it was difficult to get enough samples there. These two size classes provided the necessary basis to determine profitability and digestive quality of prey in relation to size. Following van Gils *et al.* (2005b) and Gommer *et al.* (2018), estimations of the metabolizable energy content or digestible part of prey was based on ash free dry mass of flesh $AFDM_{flesh}$, assuming that the assimilation efficiency and energetic density of macroinvertebrates was constant across prey species and sizes. Also the indigestible part of prey was assumed to be the dry mass of shell $DM_{shell}$ of *D. pulchellus*. For soft-bodied prey such as *E. chiltoni*, it was not

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possible to separate the flesh from other body parts. Hence the quality of this prey was expressed as a ratio of the AFDM and dry mass of the whole prey, $Q = \frac{\mathrm{AFDM}}{\mathrm{DMtotal}}$. The procedure for estimating these parameters are clearly outlined in Chapter 3 and regression models for predicting estimates are presented in Chapter 4. In the dichotomous test, six individuals of each size class of *D. pulchellus* and six individuals each of *D. pulchellus* and *E. chiltoni* were offered to captive sanderlings for the size preference test and the prey preference test respectively.

### 7.2.4 Contingency model

The Contingency model predicts optimal prey that maximizes long term energy intake rates in predators that are 'handling limited'. In order to make predictions based on the CM, the handling time ($h_i$) of each unburied prey individual offered to sanderlings was estimated from the time a prey is being attacked until the time it is swallowed. Time spent on pauses in prey attack was exempted from the estimation. Videos were recorded for each trial with a x60 optical zoom HD Lumix video camera and analysed with Solomon Coder beta 17.03.22. The energy content ($e_i$) of each prey was estimated as $\mathrm{AFDM}_{\mathrm{flesh}}$ from the allometric regression equations calibrated for prey size (Chapter 4). Profitability of prey was therefore estimated as the ratio of energy content to handing time, ($e_i / h_i$).

### 7.2.5 Digestive rate model

The digestive rate model predicts optimal prey that maximizes long term intake rates for foragers that face digestive constraints. Therefore, in making such predictions, experimental trials were carried out to determine which parameter ($\mathrm{AFDM}_{\mathrm{flesh}}$ and $\mathrm{DM}_{\mathrm{shell}}$) served as ballast mass that digestively constrained intake rates in sanderlings, assuming that rate of processing ballast mass is constant across all prey (van Gils *et al.*, 2005b; Gommer *et al.*, 2018).

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According to Gommer *et al.* (2018) and van Gils *et al.* (2005b), the ash content of crustaceans and the dry mass of the shell bivalves were responsible for digestive constraints in birds. Therefore, to parameterize the DRM, profitability ($e_i$ /$h_i$) was regressed against ballast intake ($k_i$/$h_i$), where k is the ballast mass of prey using dry mass of shell $DM_{shell}$ (according to the results of this study). According to van Gils *et al.* (2003a), the intake rate of prey can be expressed as y = $\frac{1}{x}$ c, where y is the number of prey consumed per unit time (IR), x is the ballast mass represented by either AFDM or DM of prey and c is the digestive constraint.

### 7.2.6 Maximum intake experiment

*Donax pulchellus* was the only prey used in the maximum intake rate experiment. Captive sanderlings were offered 200 unburied individuals of small size and 150 unburied individuals of medium size *D. pulchellus* for a period of one hour. The difference in the number of the different sizes *D. pulchellus* individuals offered sanderlings was due to the fact that sanderlings were observed from pre-trials to forage more on smaller size prey than medium sized ones. A total of 24 trials were carried out (4 birds x 2 diets x 3 replicates). However, another set of trials (28 in total; 7 trials x 4 birds) using a mixture of prey sizes (prey of all sizes randomly selected) were performed on the expectation that sanderlings intake rates will be based on size distribution of the whole lot; i.e. they will show preference for some prey sizes and reject others. It was difficult to measure the cumulative intake rates due to the very small sizes of the prey. Therefore, attempts to estimate this from the video recordings could result in either overestimates or underestimates of prey intake rate. As such, the overall IR was determined as the difference between prey offered and prey left after the experiment. The overall IR for each trial (log transformed) was plotted against $AFDM_{flesh}$ and $DM_{shell}$ (all parameters log transformed) of prey eaten to determine the slope and intercept following the equation y = $\frac{1}{x}$ c. A log-log regression of this equation produces

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an intercept which is equal to the digestive constraint of the forager and a slope of -1. Therefore, if the slope of this study is significantly different from -1, then the explanatory variable of the model (AFDM or DM) can simply not be the parameter that is responsible for digestive constraint, c, in this forager on the said prey type.

### 7.2.7 Dichotomous prey choice experiment

Captive sanderlings were offered six pairs of two different prey types (*D. pulchellus* and *E. chiltoni*) in 20 trials to determine the type of prey preferred by sanderlings. In another set of experiments, captive sanderlings were offered six pairs of two different prey sizes; small and medium sizes of *D. pulchellus* in 20 trials (Plate 7.1); each trial lasted over a period of 5 minutes. The twelve individual prey items were randomly assigned to each of the cavities in each trial. The sizes of each prey used in the different trials in both experiments were measured. Sanderlings were allowed to walk in from adjacent compartments of the experimental unit to select from the offered prey. Video recordings were taken for each trial and later analysed with Solomon Coder beta 17.03.22 for the order of preference. Statistical prey preference test followed Van der Meer (1992) and cardinal preference rank was determined for the first choice of prey.

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**Plate 7.1 Sanderling selecting a prey in a dichotomous experimental set up**

## 7.3 Statistical analysis

Data were checked for normality using Shapiro test and normally distributed data were subjected to parametric test, otherwise data were transformed appropriately or analysed using non-parametric tests. Normally distributed data, such as size of prey, handling time, profitability, AFDM, DM and quality were presented as mean ± SD.

The difference between mean values of the parameters being compared was either tested with students' t-test or Analysis of Variance (ANOVA). To compare the relationship between profitability and prey size, a linear mixed effect model with prey size as a fixed effect and bird ID as a random effect was carried out. Similarly, to compare relationship between profitability and prey type, a linear mixed effect model was carried out with prey type as a fixed effect and bird ID as a random effect. To determine the parameter that digestively constrained sanderlings,

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a linear mixed effect model was fitted for the relationship, IR against AFDM or DM, with bird ID as a random effect.

The results from statistical tests such as the t- or F-values, degrees of freedom (df) and p-values were presented as such. Graphical plots either showed individual scatter plots or mean values with error bars indicating SD or SE. All statistical tests and graphs were computed and plotted in R statistical package (R Core Team, 2018).

## 7.4 Results

### 7.4.1 Contingency model

The average size of *E. chiltoni* (5.03 ± 1.24 mm) used in the experiment was significantly larger ($t = 3.13$, $df = 157$, $p = 0.002$) than that of the small-sized *D. pulchellus* (4.61 ± 0.64 mm) but significantly smaller ($t = -10.56$, $df = 25$, $p < 0.001$) than medium size *D. pulchellus* (6.97 ± 0.33 mm). Sanderlings spent more time ($W = 7694$, $df = 1$, $p = 0.002$) handling *D. pulchellus* (0.52 ± 0.72 s) than *E. chiltoni* (0.35 ± 0.34 s). Specifically, sanderlings spent significantly more time ($W = 6906$, $df = 1$, $p = 0.003$) handling small sized *D. pulchellus* (0.48 ± 0.66 s) to *E. chiltoni* (0.35 ± 0.34 s) as well as significantly more time ($W = 208$, $df = 1$, $p = 0.002$) handling medium sized *D. pulchellus* (1.54 ± 1.23 s) to *E. chiltoni*. Furthermore, sanderlings spent significantly more time ($W = 966$, $df = 1$, $p = 0.03$) handling medium-sized *D. pulchellus* to small sized D. pulchellus (Table 7.1) and in the process rejected 93.43% of the medium sized *D. pulchellus* offered them in the dichotomous prey preference experiment. The results also showed that the prey *E. chiltoni* was more profitable than *D. pulchellus* ($t = 7.90$, $df = 143$, $p < 0.001$; grouped mean profitability of *D. pulchellus* = 2.48 ± 2.31 mgAFDM/s and *E. chiltoni* = 6.78 ± 5.53 mgAFDM/s). There was a significant positive effect of size on profitability of *E. chiltoni* ($R^2 =$

0.4, F = 68.97, df = 114, $p < 0.001$) as well as small sized *D. pulchellus* ($R^2 = 0.1$, F = 20.31, df = 149, $p < 0.001$), but a negative significant effect for that of medium-sized *D. pulchellus* ($R^2 = 0.9$, F = 35.34, df = 5, p = 0.002; Figure 7.1).

### 7.4.2 Digestive Rate Model

The different ballast masses were regressed against the intake rate of *D. pulchellus*. The slope of the linear regression between the log-transformed intake rate and $AFDM_{flesh}$ was marginally significantly different from -1 (slope = -0.08, p = 0.06) and not significantly different from -1 for $DM_{shell}$ (slope = -1.47, p = 0.15; Figure 7.2). Therefore, the variation in long term intake rates of *D. pulchellus* by sanderlings is dependent on the shell mass of the prey. From the linear mixed effect model estimates ($\log_{10} IR = -4.34 - 1.47\log_{10} DMshell$), sanderlings are expected to be digestively constrained at 0.05 mg of shell mass per second.

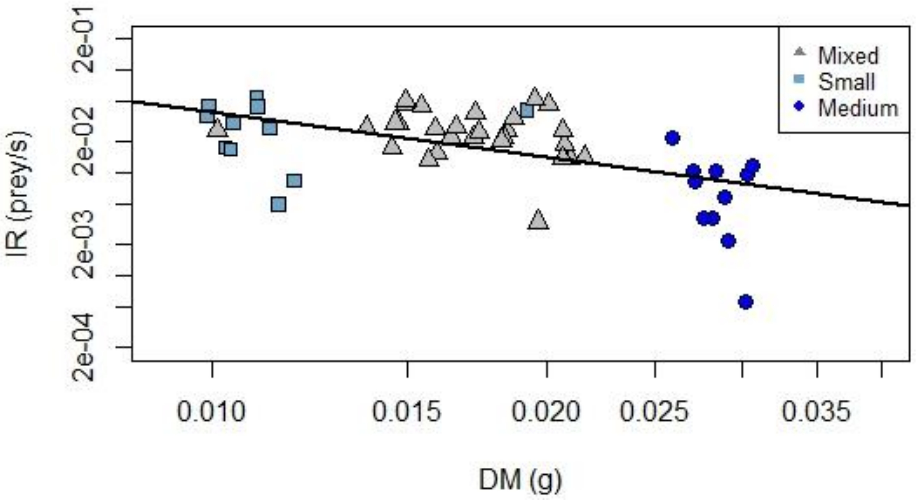

**Figure 7.2 Numerical intake rate of *Donax pulchellus* against ballast mass.** (Ballast mass is measured as dry mass of shell $DM_{shell}$; the regression equation for the model is $\log_{10} IR = -4.34 - \log_{10} DMshell$).

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**Table 7.1 Characteristics of prey offered sanderlings in a dichotomous prey choice experiment.** (In the table are the number of prey type offered (n), the mean size of prey (mean ± SD/ mm), energy content reported as ash free dry mass AFDM (mean ± SD/ mg), mean dry mass DM (mean ± SD) of either whole prey (for *E. chiltoni*) or shell (for *D. pulchellus*) in mg, handling time (mean ± SD/ s), mean profitability ($e_i/h_i$; mean ± SD) in mg/ s and mean digestive quality ($e_i/k_i$; mean ± SD) where $k$ is DM of either whole prey (*E. chiltoni*) or shell (*D. pulchellus*)

| **Prey** | **n** | **Size (mm)** | **AFDM (mg)** | **DM (mg)** | **Handling time (s)** | **Profitability (ei/hi)** | **Digestive quality (ei/ki)** |
|---|---|---|---|---|---|---|---|
| *E. chiltoni* | 116 | 5.03 ± 1.24 | 1.47 ± 0.85 | 3.16 ± 1.58 | 0.35 ± 0.34 | 6.78 ± 5.53 | 0.45 ± 0.04 |
| Small *D. pulchellus* | 151 | 4.61 ± 0.64 | 0.57 ± 0.19 | 10.05 ± 3.54 | 0.48 ± 0.66 | 2.28 ± 2.01 | 0.06 ± 0.00 |
| Medium *D. pulchellus* | 7 | 6.97 ± 0.33 | 1.68 ± 0.21 | 31.09 ± 4.10 | 1.54 ± 1.23 | 1.82 ± 1.13 | 0.05 ± 0.00 |

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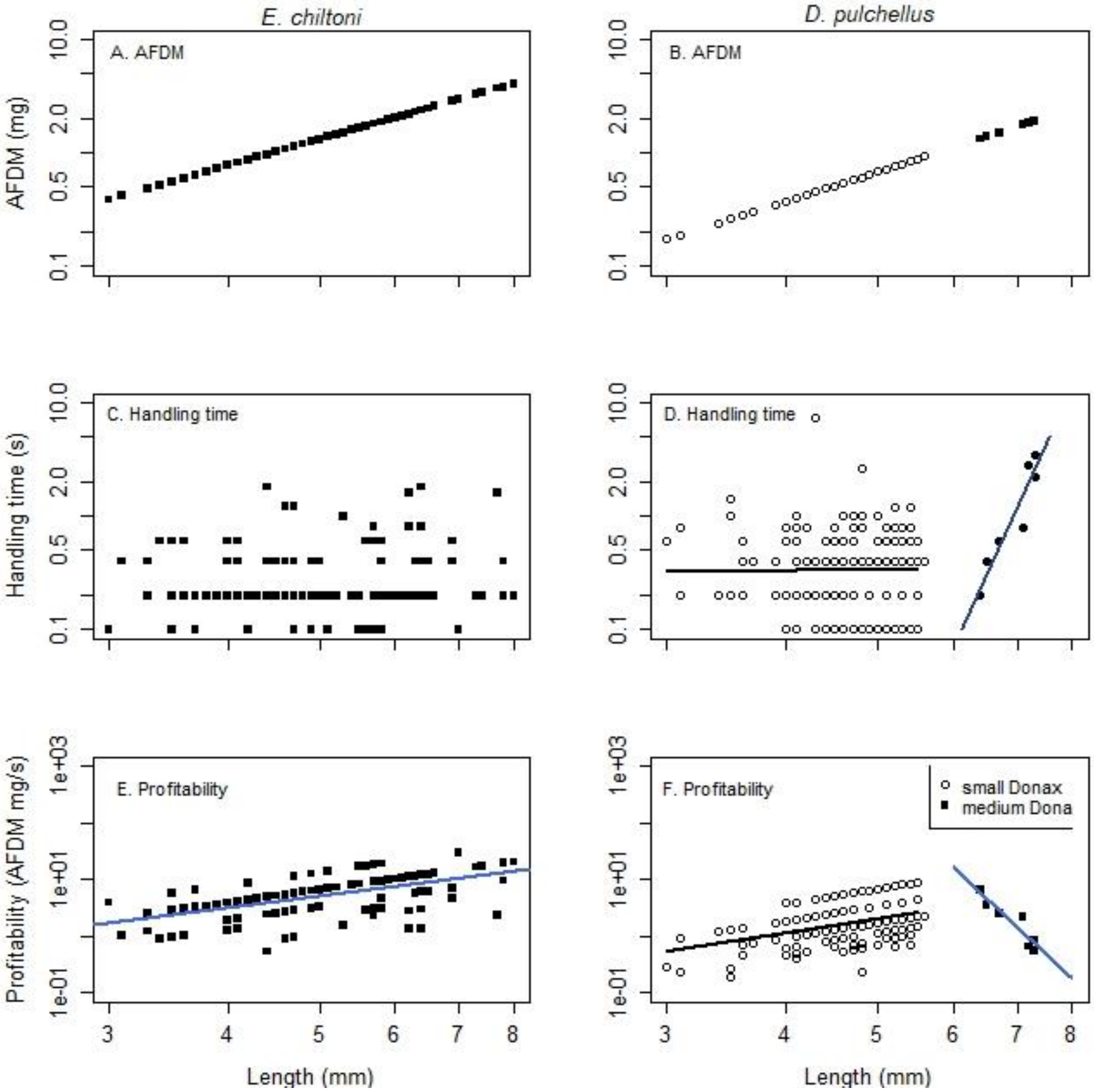

**Figure 7.1 Characteristics of sanderling prey and size variation.** (Note the logarithmic scales. Energy content represented as AFDM plotted against size of (A) *E. chiltoni* and (B) *D. pulchellus*. Handling time regressed against size of prey (C) *E. chiltoni* ($y = 5.98x^{0.27}$), (D) small-sized *D. pulchellus* ($y = 0.26x^{-0.16}$) and medium-sized *D. pulchellus* ($y = 2.17e\text{-}16x^{18.63}$). Profitability regressed against prey size of (E) *E. chiltoni* ($y = 0.17x^{2.12}$), (F) small-sized *D. pulchellus* ($y = 0.03x^{2.53}$) and medium-sized *D. pulchellus* ($y = 4.14e14x^{-15.94}$)).

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The digestive rate model predicted *E. chiltoni* as the most preferred prey, which was also the most profitable prey according to the CM. However, between the small and medium size *D. pulchellus* (the most abundant prey along the Esiama beach), the DRM predicted the medium-sized *Donax* to be a better choice over small-sized *Donax*, if sanderlings want to maximize long term energy intake rate while handling the prey in relation to digestive constraint. This was contrary to the prediction of the CM, which predicted small *Donax* to be preferred over medium sized *Donax* due to the former having a higher profitability than the latter. The ballast intake of each of the three prey types was greater than the digestive constraint ($k_i/h_i$) > c, where c is the digestive constraint (0.05 mg/s), represented by the vertical grey line (Figure 7.3).

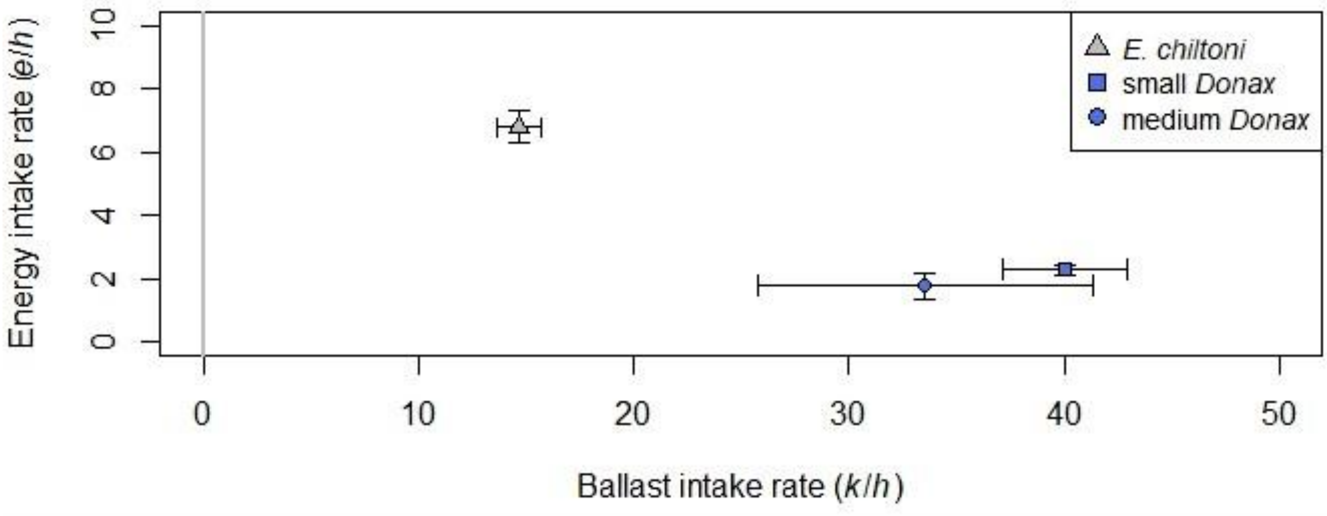

**Figure 7.3 The digestive rate model: energy intake rate against ballast intake rate.** (Grey line represents digestive constraint on foraging on *Donax pulchellus*. Ballast intake rate for *Excirolana chiltoni*, the isopod, was estimated from dry mass of flesh rather than shell mass that was used in the case of the bivalve).

### 7.4.3 Dichotomous prey choice experiment

When offered *D. pulchellus* and *E. chiltoni*, sanderlings preferred the latter to the former (t =

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2.87, $p = 0.01$; Figure 7.4A) depicted by a higher cardinal preference rank. *Donax pulchellus* was set to 0 in the Generalized linear model, glm (family = quasibinomial; link = logit) as *E. chiltoni* was compared to *D. pulchellus*. Sanderlings also preferred small sized *Donax* to medium sized ones ($t = 111.4$, $p < 0.001$; Figure 7.4B), shown by the higher cardinal preference rank. Sanderlings actually selected small-sized *Donax* as their first preference throughout the 20 trials. Medium-sized *Donax* was also set to 0 in the glm for comparison with small-sized *Donax*.

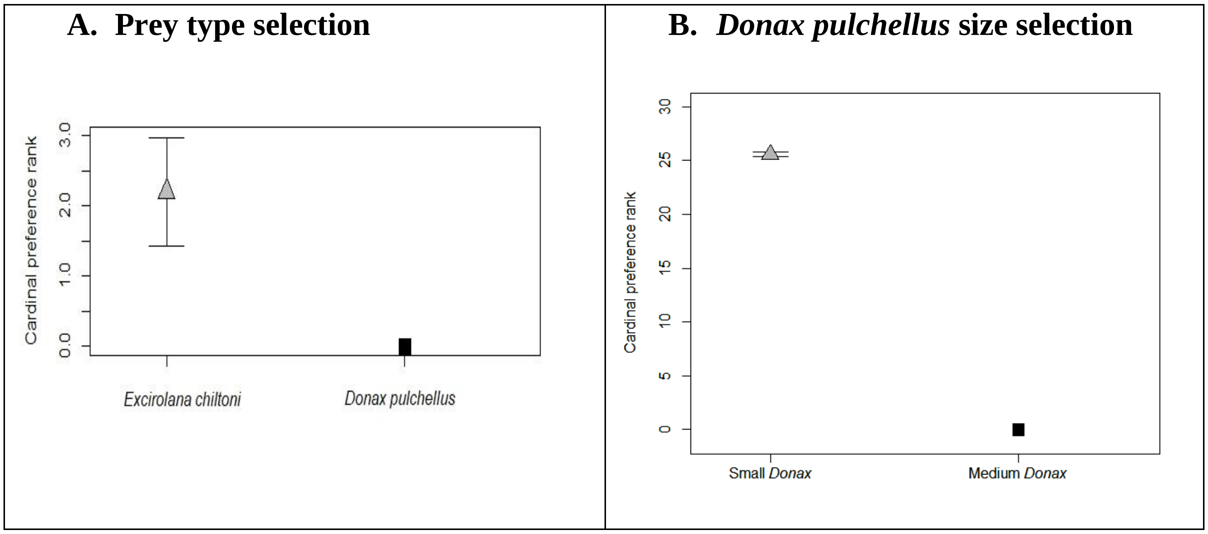

**Figure 7.4 Dichotomous prey choice selection of two different prey type *Excirolana chiltoni* and *Donax pulchellus* (A); and prey size selection Small *Donax* and medium *Donax* (B).**

## 7.5 Discussion

The contingency model predicts prey with a higher profitability to be selected by foragers who are handling limited. The results from this study suggests that sanderlings should select the isopod *E. chiltoni* followed by small-sized *Donax* and then medium-sized *Donax* because of the differences in profitability. Sanderlings were observed to spend very little time in handling

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isopods as compared to small- and medium-sized *Donax* externally. The time spent on handling isopod and small-sized *Donax* did not also relate to their sizes, but was significantly related to size of medium-sized *Donax*. This observation confirms that of Gill (2003), who observed fishes that also swallow their prey whole to spend more time in handling larger prey. However, the profitability of sanderlings foraging on *E. chiltoni* is about thrice that of small-sized *D. pulchellus*. This means that, in maximizing long term intake rate, in the presence of high prey densities, sanderlings will be able to obtain thrice the amount of energy they would obtain in selecting isopods over small-sized *Donax*. The CM do not support sanderlings selecting medium sized *Donax* due to the extensive time spent on handling this prey externally.

The digestive rate model, on the other hand, predicts foragers who are digestively constrained to select prey of higher quality in their quest to maximize long-term energy intake, otherwise they are expected to take breaks whilst foraging in order to process ingested prey. In terms of prey quality ($e_i/k_i$), the isopod *E. chiltoni* was the higher quality prey, followed by small-sized *Donax*. The DRM, as expected, predicted sanderlings to select isopods over small and medium sized *Donax*. Similar observation was made by Gommer *et al.* (2018) on crab plovers that preferred high-quality *Portunus segnis* to low-quality *Macrophthalmus sulcatus*. There was however no clear distinction for preference for small sized *Donax* over medium sized *Donax*. In a similar study by van Gils *et al.* (2005b), red knots were observed to select small sized bivalves to larger individuals. Crab plovers were also observed to select small-sized prey over larger ones simply because larger prey (crabs) has more ballast mass and as such, the long term numerical intake of such prey is expected to be lower than the small-sized prey with less ballast mass (Gommer *et al.*, 2018). The indistinct observation between small and medium sized *Donax* could be explained be explained by the handling time of the different size classes of *Donax*. It should be recalled that

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whereas there was a negative relationship between size and handling time of medium-sized *Donax*, there was no relationship between size and handling time of small-sized *Donax*.

The long-term ingested ballast mass could increase at a faster rate when consuming small prey size than medium-sized prey, which already has external handling time as a constraint. The external handling time of the medium-sized prey could compensate for the ballast intake, and sanderlings could go on foraging for longer periods without necessarily having to take longer digestive breaks. On the other hand, sanderlings may be forced to take longer digestive breaks when ingesting smaller-sized prey, as ballast mass accumulates in the stomach, filling up the stomach faster because there is less time spent on external handling of prey which could have been used for processing already ingested prey (Gill, 2003). In addition to this, the lower ballast intake rate whilst handling the medium-sized *Donax* will provide sanderlings enough time to stay vigilant for predators whilst they spend more time handling prey externally (Heller & Millinski, 1979).

Prey choice may be influenced by motivational state or satiation level (Gill, 2003). In maximizing long term intake rate, sanderlings may have to switch between preys. Due to the high abundance of *Donax* along the Esiama beach, sanderlings could forage on such prey on an empty stomach. However, the best approach could be to select the smaller-sized *Donax,* which is more profitable due to less time required for handling, and switch to the medium-sized ones as their stomachs fill up. Such was the observation from the dichotomous study. The isopod, the most preferred prey according to the DRM, could be selected for when the stomach of sanderling is almost full and there is a need to take digestive breaks. In simple terms, the motivational state of the predator may influence choice of prey (Hart & Gill, 1992; Gill & Hart, 1994; Gill, 2003). Such an ideal scenario was observed in crab plovers who switched prey from highly profitable ones to high

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quality prey upon realizing stomach fullness on foraging on the former prey (Gommer *et al.*, 2018).

It is important to note that the searching time of prey was not factored into this experiment as prey was provided *ad libitum*. However Donax in the field is probably available to sanderlings *ad libithum*, especially when tide recedes. Besides, one of the limitations of the CM is that, it assumes all prey are vulnerable to capture during the searching phase (Gill, 2003). Therefore, expecting such preferences of prey in the field may simply not hold, especially for the fast moving isopod *E. chiltoni* which may elude predators (Sih & Christensen, 2001). Some factors may affect the searching efficiencies of prey and ultimately influence prey choice (Gommer *et al.*, 2018). Among such factors include variation in densities of prey; in this case *Donax* happened to more abundant than the isopods (Chapter four; Ball, 1994), presence of other competitors for similar prey (Svanbäck & Bolnick, 2005) and effect of tidal cycle that influences the distribution and availability of prey at certain times (van Gils, 2004).

Prey choice may also be influenced by migration cycle. There are two “different” sanderling populations that visit the Esiama beach: “true” non-breeders and staging population. Individuals that need to replenish lost fuel and continue migration further south (staging population) are time-limited in their energy acquisition. For such foragers, prey which demand longer searching and/or handling time would not be an ideal choice. The other sanderling population, the “true” non-breeders, who can afford all the time needed to search for more quality prey, could follow the DRM in maximizing energy intake (Bergman *et al.*, 2001).

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# CHAPTER EIGHT

# HUMAN DISTURBANCES AND OTHER PRESSURES ON FORAGING BEHAVIOUR OF SANDERLINGS

## 8.1 Introduction

Coastal wetlands are amongst the most globally diverse ecosystems (Haines-Young & Potschin, 2010). These systems serve as suitable habitats for migrants and residents shorebirds, nesting sites for marine turtles, nesting and spawning environments for some fish species, and a large host of benthic organisms. However, these environments have been under serious threats from anthropogenic influences. The status of these threats have exacerbated in the wake of climate change through sea level rise (Galbraith *et al.*, 2002; Austin & Rehfisch, 2003). The impacts of these threats on biodiversity have been extensively studied in the temperate areas, however, a lot more studies are needed within the tropics to provide a holistic understanding of this global issue on the conservation of biodiversity.

Urbanization and infrastructure development due to human population increase have had their own share of impacts on landscapes. Coastal habitats have not been exempted as they have also suffered changes either through direct infrastructural development or through tourism and other related activities (Sorice *et al.*, 2006; Delgado *et al.*, 2010). The natural ecological character of most coastal habitats has been questioned seriously over the years, and although not conclusive, some of these habitats may have lost their ecological integrity (UNEP/GPA, July 2006).

Coastal habitats are important staging and non-breeding sites in the annual migration cycle of shorebirds. These habitats may serve as critical foraging areas for birds, but also are of critical

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importance in supporting the livelihoods of surrounding communities. This means that, it is eminent for foraging shorebirds to come into contact with humans and human activities constantly. It is of no problem if this interaction is within levels compactible to the ecological accommodation and resilience of biodiversity (Yasué *et al.*, 2008). However, various studies have shown that, the densities of humans along coastal habitats have significantly increased over the past few decades and activities to support livelihoods go beyond the wise-use concept. Such disturbances, together with other natural activities, have changed what used to be "shorebird utopias" into unpleasant and harsh environments (Sorice *et al.*, 2006; Borgmann, 2010).

The impacts of disturbances on the ecological behaviour of shorebirds have been studied extensively in the temperates, moderately in the neo-tropics and a few in the afro-tropics (Burger & Gochfeld, 1991a; Burger, 1994; Thomas *et al.*, 2003; Yasué, 2005; Burger *et al.*, 2007; Yasué *et al.*, 2008; van den Hout *et al.*, 2014). Amongst the ecological impacts of disturbances include reduction in foraging time, with an increase in energy expenditure through escape strategies portrayed towards such disturbances. Clearly, an energy imbalance is created and shorebirds need to find ways and means of compensating for energy lost through insufficient foraging time or disturbance accommodation to be able to meet their daily energy requirements, as well as prepare for other important life processes (Vines, 1992; Burger, 1993). In as much as possible, shorebirds try to avoid such disturbances by avoiding areas with high human concentrations (Burger & Gochfeld, 1991a; Burger, 1994).

This chapter seeks to determine and evaluate human disturbances and other pressures on foraging behaviour of sanderlings and describes associated responses.

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## 8.2 Methodology

### 8.2.1 Study area

The study area is a 13 km sandy beach between the Amansuri and Ankobra estuaries, hereafter known as the Esiama beach. This beach supports livelihoods of at least seven communities; Ankobra, Asanta, Bobrama, Asemko, Kikam, Esiama and Azuleloanu (Amansuri). Human population in these areas have significantly increased over 300% in the past three decades (Ghana Statistical Service, 2014). Detailed description of the study area has been provided in Chapter three of this thesis. Data collection was by field survey between September 2015 and December 2017.

### 8.2.2 Transect survey

Monthly transect surveys of all activities along the 13 km beach and within a 200 m stretch offshore were carried out for at least a single day within the first week of every month by an individual on foot with an 8 x 42 optical power binocular. The frequency of each activity and the total number of agents involved in each activity were recorded. Furthermore, flocks of sanderlings were also scanned and flock size estimated. All records were made in reference to the 27 sampling location used for the benthic macroinvertebrate sampling (Chapter 3).

### 8.2.3 Sanderling distribution

Spatial distribution of sanderlings was estimated by counting the total number of sanderlings within a 200 m radius in relation to the 27 macroinvertebrate sampling location during the first week of every month throughout the entire study period, from September 2015 to December 2017. The detailed description of methodology is provided in Chapter three of this thesis.

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### 8.2.4 Macroinvertebrate distribution

Benthic macroinvertebrates were sampled with a hand corer with a base diameter of 14.9 cm every month during the survey period. Samples were washed in situ, fixed in 10% formaldehyde solution and transported to the laboratory for identification and morphometric measurements. The detailed description of benthic macroinvertebrate sampling is provided in Chapter three.

### 8.2.5 Foraging rates of sanderlings

Observations of foraging sanderlings were made along the 13 km stretch of beach each month during the study period. Sampling was based on a focal individual approach and followed Thomas *et al.* (2003) and Burger and Gochfeld (1991a). At the beginning of each observation, the following parameters were taken: date, time of day, the observation location in relation to the 27 sampling stations used for benthic macroinvertebrate sampling, flock size of sanderlings, other species of shorebirds present and their numbers, width of the exposed beach (distance from the peripheral vegetation to the water mark) and density of humans within a 50 m radius. An individual sanderling was selected at random (preference given to colour marked sanderlings so as to avoid repetitive sampling), followed for one minute and a video of foraging activity recorded with a x60 optical zoom HD Lumix video camera and analysed with Solomon Coder beta 17.03.22.

### 8.2.6 Minimal Approach Distance (MAD)

The impact of all encountered disturbances on foraging sanderlings was assessed using the minimal approach distance (MAD) approach (Roberts & Evans, 1993). The MAD provides an estimation of how close foraging sanderlings could allow agents of a particular disturbance or pressure get to them before changing their behaviour. Change in behaviour was assumed to be any of the following: walking, running, jumping or flying away. The assumption for using the

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MAD is that, the closer an agent of a particular activity gets to a sanderling, the less susceptible sanderlings are to that activity. In estimating the MAD, an individual sanderling was selected and focused on. In most cases it was the closest sanderling to an approaching agent of disturbance. The point at which the focal sanderling changes its behaviour was identified and the distance between this point and that of the approaching intruder was estimated. The distance moved by the displaced sanderling was also estimated. Other important records taken included the number of agents involved in the disturbance and the displacement activity. Prior to this exercise, trial sessions were carried out where the observer estimated distances and these values were compared with actual measurements. This preparation was carried out on several occasions in order to increase the precision of estimates before the field work. Measurements were also taken with a Nikon Forest Pro Range Finder where possible. It is important to note that this study was not based on experiments, but actual field observations with minimal influence from the researcher. Therefore, the researcher hid in the peripheral vegetation, unknowing to any agent of disturbance, whilst recording.

### 8.2.7 Data presentation and statistical analysis

Data were tested for normality using Shapiro-Wilk test and all normally distributed data were presented as mean ± SD and subjected to parametric tests. Data which were not normally distributed were either transformed where possible or analysed with non-parametric statistics. Count data were presented as proportions, percentages or densities (number/ area). All activities along the beach were identified and spatial distributions of mean densities of agents of each activity were plotted in QGIS version 2.18.9. Spatial distribution of benthic macroinvertebrates was also plotted in QGIS version 2.18.9.

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To test for relationship between human densities, prey densities and sanderling densities, a generalised linear model was run on log-transformed variables. A small value of "0.01" was added to all the individual values so as to correct for the error generated from transforming zeros. Generalised linear regression was also used to test for relationship between the MAD and several explanatory variables such as flock size, beach width and prey densities. The relationship between displacement of sanderlings in response to activities of kites or passers-by was also tested in a generalised linear regression. Similarly, the relationship between foraging rate and human density was also determined in a linear regression.

Generalised linear regression was used to derive models that best explained the minimal approach distance, MAD, a sanderling could allow a passer-by using the 'glm' function from the package "MASS" of the R software. Appropriate models were selected based on a stepwise deletion of irrelevant terms from selected variables that were observed to be significant in explaining the MAD from simple linear regressions. The selected parameters were again confirmed in a multiple regression of the full model which contained all the explanatory variables. Model selection was based on Akaike Information Criterion (AIC). Coefficient of determination $R^2$ was employed to estimate the proportion of data explained by the selected linear models. All statistical tests were done at a significance level of $p = 0.05$.

## 8.3 Results

### 8.3.1 Frequency of occurrence of human activities and other pressures

A total of 447 activities or pressures were observed along the study beach during the study period. Human-related activities were the most frequently observed activity along the beach and constituted 74.0% of all activities observed (Figure 8.1). This was followed by the sighting of the

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Yellow-billed kite *Milvus migrans parasitus* (13.0%; hereafter referred to as kite), dogs (6.0%), scavengers (5.0%) and engine-driven machines (2.0%). The palm-nut vulture *Gypohierax angolensis*, hooded vulture *Necrosyrtes monachus* and pied crow *Corvus albus* were grouped together as scavengers. The palm-nut vulture was regarded as a scavenger for this study because it was mostly seen feeding on carrion along the beach. The most frequently observed human activity was fishing (45.0%; both canoe and dragging of seine nets along the shore), followed by passers-by (37.0%; people moving from one end of the beach to the other without engaging in any of the other stated activities), shellfish harvesting (14.0%) and recreational activities (4.0%; mainly swimming activities). The mean encounter rate of fishing activities observed along the Esiama beach was 0.5 ± 0.3 fishing activity/km with an average human count of 21 ± 11 individuals per each fishing activity. Therefore, it is estimated that an average of 147 individuals were engaged in fishing activities every day along this stretch of beach.

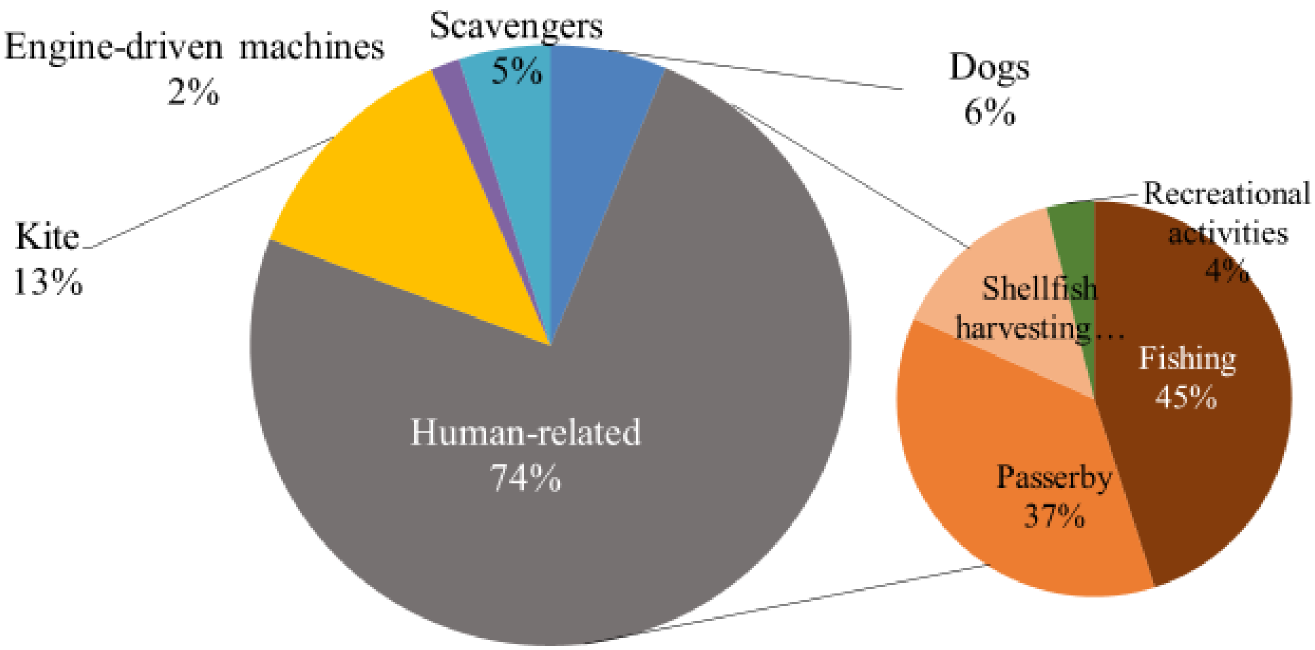

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**Figure 8.1 Frequency of occurrence of different activities along the Esiama beach.** (Smaller circle shows frequency of occurrence of different human related activities).

### 8.3.2 Spatial distribution of human, sanderling and prey densities

Human related activities were the most frequently observed along the beach. A spatial plot of mean human densities across the beach showed that human densities were highest (Kruskal-wallis chi-squared = 75.83, df = 26, $p < 0.001$) towards the eastern end of the beach (Ankobra estuary; Plate 8.1 A). Sanderlings were mostly observed within a 2.5 km radius from the middle part of the beach, thus the Kikam village (Kruskal-wallis chi-squared = 160.05, df = 26, $p < 0.001$; Plate 8.1 B). Some sanderlings were also observed along the stretch of beach by the Esiama village. There was spatial variation in the distribution of the two most abundant prey species along the beach. For *Donax pulchellus* (hereafter referred to as *Donax*), the highest densities were distributed between Kikam and Asanta villages with very little found towards both estuaries (Kruskal-wallis chi-squared = 122.47, df = 26, $p < 0.001$, Plate 8.1 C). However, for *Excirolana chiltoni* (hereafter referred to as *Excirolana*), densities were more aggregated towards the eastern end of the beach as well as the Amansuri estuary end of the beach (Kruskal-wallis chi-squared = 258.54, df = 26, $p < 0.001$, Plate 8.1 D).

Furthermore, there was a significant inverse relationship between the spatial distribution of densities of humans and that of sanderlings ($\log_{10}\text{Sanderling density} = -0.13 - 0.80\ \log_{10}\text{Human density}$, $R^2 = 0.06$, F = 17.32, df = 275, $p < 0.001$). There was a positive significant relationship between the spatial distribution of densities of *Donax* and that of sanderlings ($\log_{10}\text{Sanderling density} = 0.16\log_{10} Donax\ \text{density} - 1.44$, $R^2 = 0.11$, F = 76.48, df = 622, $p < 0.001$). However, there was no significant relationship between the spatial

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distribution of sanderling density and that of *Excirolana* ($\log_{10} \text{Sanderling density} = -1.47 - 0.01\log_{10} Excirolana \text{ density}$, $R^2 = -0.001$, F = 0.24, df = 622, p = 0.6).

### 8.3.3 Minimal approach distance, MAD

In order to measure the tolerance of certain activities along the beach by sanderlings, the minimal approach distance MAD was used. Sanderlings responded to activities on the beach by walking (12.5%), running (51.3%) or flying (36.2%) away from their original positions. From the study, the average MAD varied between 8.15 ± 1.41 m and 59.42 ± 35.86 m depending on the type of activity. Sanderlings were more tolerant to stationary people. Sanderlings could accommodate such people up to a distance of 8.15 ± 1.41 m.

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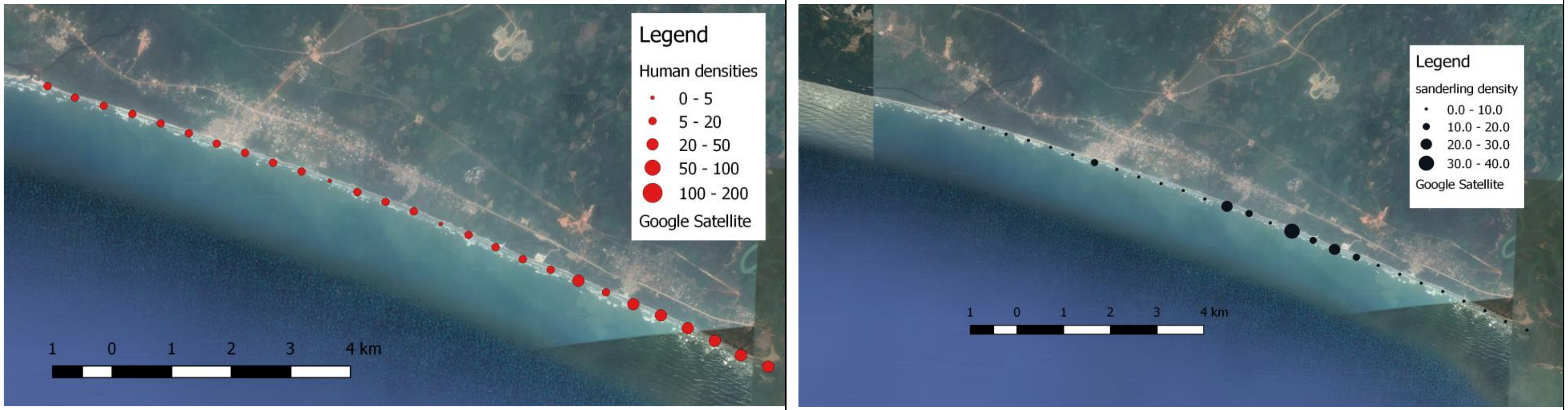
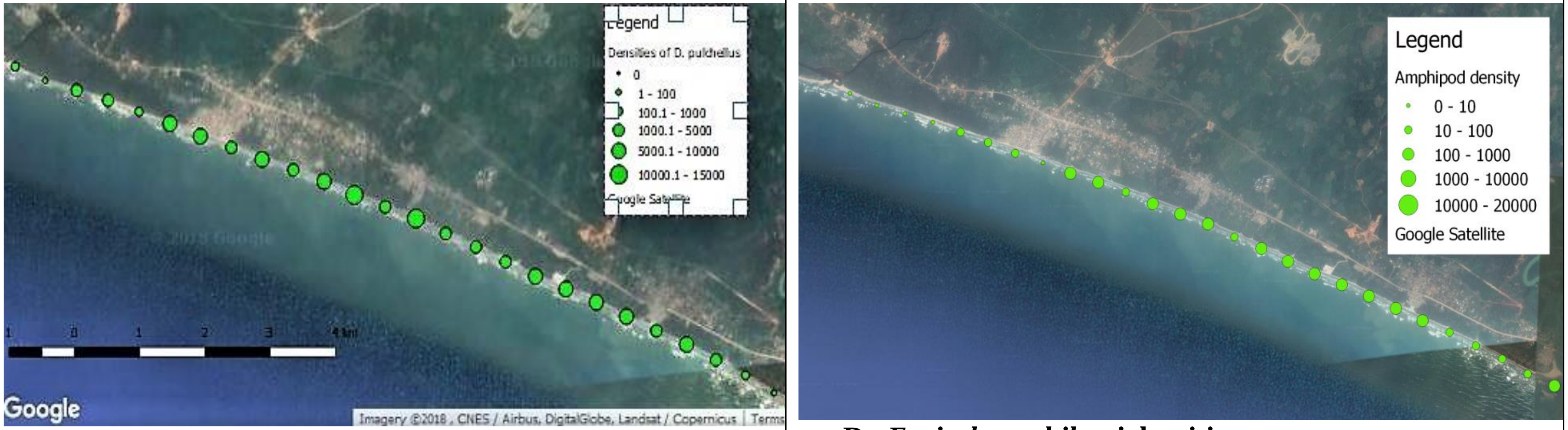


**A. Human densities**

**B. Sanderling densities**



**C. *Donax pulchellus* densities**

**D. *Excirolana chiltoni* densities**

**Plate 8.1 Spatial distribution of human, sanderling and prey densities along the Esiama beach**

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For aerial agents of disturbances, sanderlings were more sensitive to the kites (Plate 8.2 A). Sanderlings could tolerate kites up to a vertical height of 11.93 ± 6.29 m before responding to their presence. For other human-induced activities, sanderlings were more sensitive to shellfish harvesting (33.50 ± 9.19 m; Plate 8.2 B), followed by passers-by (25.51 ± 10.03 m) and fishing activities (dragging of seine nets, 20.19 ± 8.03 m). Sanderlings were also sensitive to unleashed dogs along the beach (Plate 8.2 D), responding to their presence at a distance of 31.20 ± 17.22 m. Sanderlings showed the highest sensitivity to engine-driven machines such as tricycles and vehicles moving along the beach. Sanderlings reacted to such activities at a distance of 59.42 ± 35.86 m (Table 8.1). The relatively large sample size of activities involving passers-by and kites provided the opportunity to carry out further analyses on the MAD that sanderlings reacted to these.

**Table 8.1: Minimal approach distance MAD to sanderlings to activities along the Esiama beach**

| **Activity** | **n** | **Mean MAD ± SD/ m** |
|---|---|---|
| Stationary person | 6 | 8.15 ± 1.41 |
| Scavenger | 2 | 10.00 ± 5.94 |
| Yellow-billed kite | 19 | 11.93 ± 6.29 |
| Fishing | 8 | 20.19 ± 8.03 |
| Passer-by | 121 | 25.51 ± 10.03 |
| Dogs | 5 | 31.20 ± 17.22 |
| Shellfish harvesting | 2 | 33.50 ± 9.19 |
| Engine-driven machines | 9 | 59.42 ± 35.86 |

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A. A kite hovering above foraging sanderlings

B. Shellfish harvesting

C. Fishing activity

D. Unleashed dog chasing after a flock of sanderlings and plovers

**Plate 8.2 Activities of disturbance to sanderlings along the Esiama beach**

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### 8.3.4 Yellow-billed kite

The yellow-billed kite was the most common aerial predator of sanderlings along the Esiama beach. There were no sightings of kites during the arrival and early peak months of sanderling counts in August and September respectively. Kites were sighted along the Esiama beach from October through June. Kites were therefore absent from the study beach between July and September (Figure 8.2).

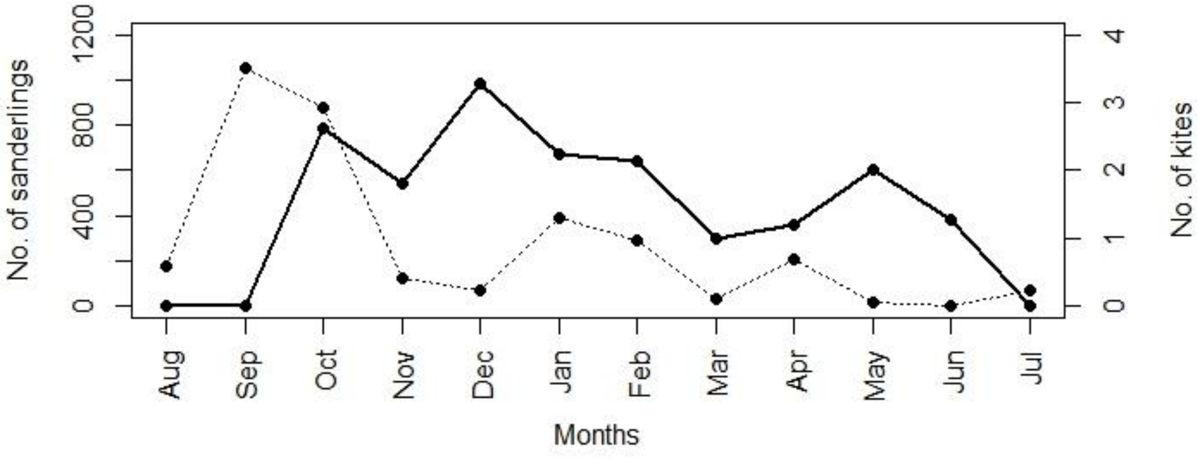

**Figure 8.2 Sanderling and yellow-billed kite occurrence along the Esiama beach.** (Black solid line graph represents mean counts of yellow-billed kites and black broken line represents mean counts of sanderlings).

The MAD to sanderlings was regressed against flock size (F = 0.57, df = 17, p = 0.46), width of the beach (F = 0.03, df = 13, p = 0.87), densities of *Donax* (F = 0.07, df = 17, p = 0.79) and *Excirolana* (F = 4.13, df = 17, p = 0.06), and none of the relationships was significant. However, there was a significant negative relationship between MAD to sanderlings and distance moved or displacement from original position (Figure 8.3).

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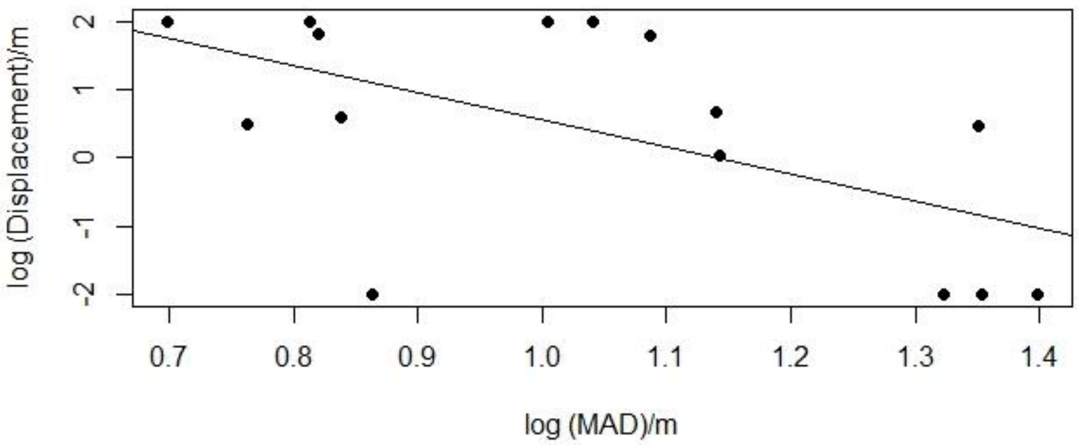

**Figure 8.3 Minimum approach distance and displacement of sanderlings approached by yellow-billed kites.** (Note the logarithm transformation of both axes with a correction of +0.01 for zero values. The regression line is represented by $\log_{10}\text{Displacement} = 4.51 - 3.95\log_{10}\text{MAD}$, $R^2 = 0.28$, $F = 6.41$, $df = 13$, $p = 0.03$).

### 8.3.5 Passers-by

There was a significant difference between the MAD to foraging and resting sanderlings by passers-by ($t = -3.58$, $df = 46.37$, $p = 0.0008$). This means, foraging sanderlings were more tolerant to passers-by (23.03 ± 7.27 m, n = 84) than resting sanderlings (31.13 ± 12.91 m, n = 37). Therefore, the data were analysed separately for foraging and resting sanderlings. There was a significant positive relationship between MAD to sanderlings and flock size ($F = 6.30$, $df = 82$, $p = 0.01$; Table 8.2). There seems to be a threshold flock size of 35 individuals which separated the same data into two sets (Figure 8.4). Although there was a negative relationship between MAD and flock size less than 35 individuals, this observation was not significant ($\text{MAD} = 20.28 – 0.02\text{Flock size}$, $R^2 = -0.02$, $F = 0.05$, $df = 58$, $p = 0.83$). Nevertheless, there

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was a significant inverse relationship between MAD and flock size larger than 35 individual birds (F = 4.76, df = 22, p = 0.04; Figure 8.4).

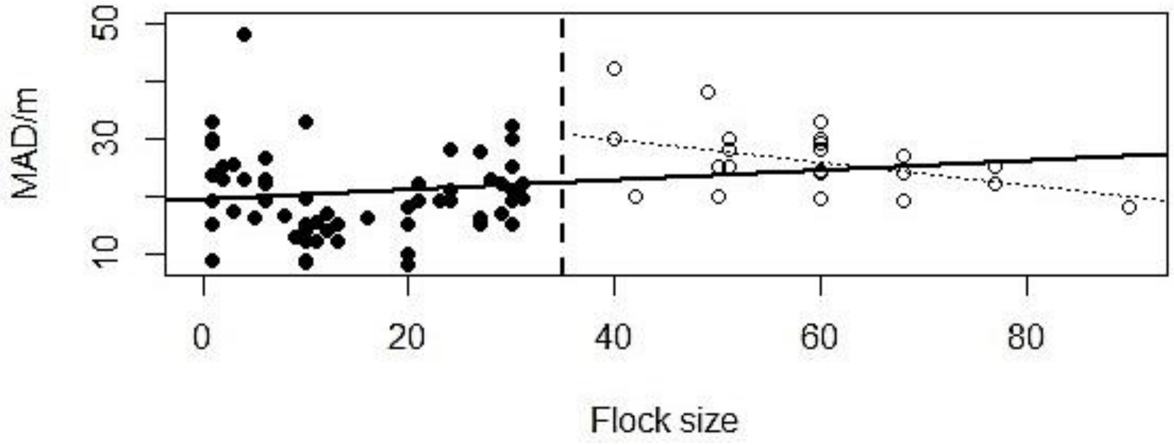

**Figure 8.4 Minimal approach distance and flock size of sanderlings.** (The vertical broken line represents a threshold flock size of 35 individual sanderlings before and beyond which the data showed different patterns. The filled black circle represents data below a flock size of 35 whereas the open circles represents data for flock size 35 and above. The bold regression line is represented by MAD = 19.38 + 0.09 Flock size, $R^2$ = 0.07. The dotted regression line is represented by MAD = 37.71 – 0.20 Flock size, $R^2$ = 0.14).

The number of passers-by observed to approach foraging sanderlings varied between 1 and 6 people. However, the number of passers-by did not influence the MAD to sanderlings (Table 8.2). The displacement of sanderlings from their original foraging spots by passers-by did not also explain the MAD to sanderlings (Table 8.2). There was however a significant positive relationship between MAD and width of the beach used by sanderlings (F = 14.06, df = 53, p = 0.0004; Figure 8.5). There was a significant inverse relationship between MAD to sanderlings and densities of *Donax* ($\log_{10}$ MAD = 21.20 – $\log_{10}$ Donax, $R^2$ = 0.04, Table

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8.2), however the relationship between MAD to sanderlings and densities of *Excirolana* was not significant (F = 3.76, df = 81, p = 0.06).

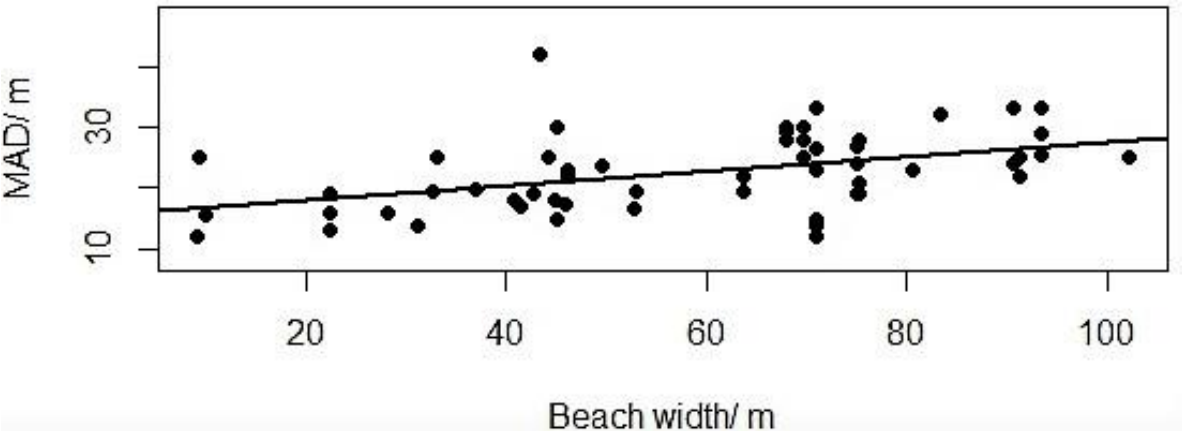

**Figure 8.5 Minimal approach distance and width of beach used by foraging sanderlings.**

(Regression line represented by MAD = 15.60 + 0.12 Beach width, $R^2$ = 0.19).

For resting sanderlings, there was no significant relationship between MAD and flock size (Table 8.2). Between 1 and 8 passers-by were observed to approach resting sanderlings and there was a positive significant relation between MAD to resting sanderlings and the number of passers-by (MAD = 21.10 + 4.37Number of passers-by, $R^2$ = 0.3; Table 8.2). There was no relationship between the MAD to resting sanderlings and how far sanderlings moved from their original position after being displaced by passers-by (F = 1.77, df = 24, p = 0.20). The width of the beach used by resting sanderlings did not explain the MAD to sanderlings by passers-by (F = 1.73, df = 12, p = 0.21).

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**Table 8.2: Linear regression between MAD and a list of explanatory variables for foraging and resting sanderlings.**

| Variable | Foraging sanderlings | | | Resting sanderlings | | |
|---|---|---|---|---|---|---|
| | **df** | **F-statistic** | **p-value** | **df** | **F-statistic** | **p-value** |
| Flock size | 82 | 6.30 | 0.01 | 35 | 2.03 | 0.16 |
| Number of people involved | 82 | 0.22 | 0.64 | 35 | 16.25 | 0.0003 |
| Displacement/ m | 70 | 1.19 | 0.28 | 24 | 1.77 | 0.2 |
| Beach width/ m | 53 | 14.06 | 0.0004 | 12 | 1.73 | 0.21 |
| *Donax* (ind/ $m^2$) | 81 | 4.40 | 0.04 | | | |
| *Excirolana* (ind/ $m^2$) | 81 | 3.76 | 0.06 | | | |

The three most important explanatory variables of the MAD to foraging sanderlings based on significant p-values were used in a multiple regression against the MAD to establish which variables or combination of factors influenced the MAD to sanderlings. The outcome showed that flock size and width of the beach were the most important variables that explained the MAD to sanderlings (Table 8.3).

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**Table 8.3: Candidate models that explained the MAD to foraging sanderlings.** (Included in the table are the degrees of freedom (df), coefficient of determination ($R^2$), Akaike Information Criterion (AIC) and level of significance (p-value).

| **Models** | **df** | **$R^2$** | **AIC** | **ΔAIC** | **p-value** |
|---|---|---|---|---|---|
| Flock size + Beach width | 4 | 0.24 | 348.8 | 0 | 0.0003 |
| Flock size + Beach width + *Donax* | 5 | 0.23 | 350.6 | 1.8 | 0.001 |
| Beach width | 3 | 0.19 | 350.9 | 2.1 | 0.0004 |
| Flock size | 3 | 0.06 | 573.3 | 224.5 | 0.01 |
| Null/ Intercept | 2 | | 577.5 | 208.7 | < 0.0001 |

### 8.3.6 Foraging rates and human density

The impact of human disturbance, measured in this context as human density within a 50 m radius to the focal foraging bird on the foraging rates (measured as pecking rate) of sanderlings was assessed. Pecking rate declined as number of humans per unit area increased ($F = 5.39$, $df = 138$, $p = 0.02$; Figure, 8.6).

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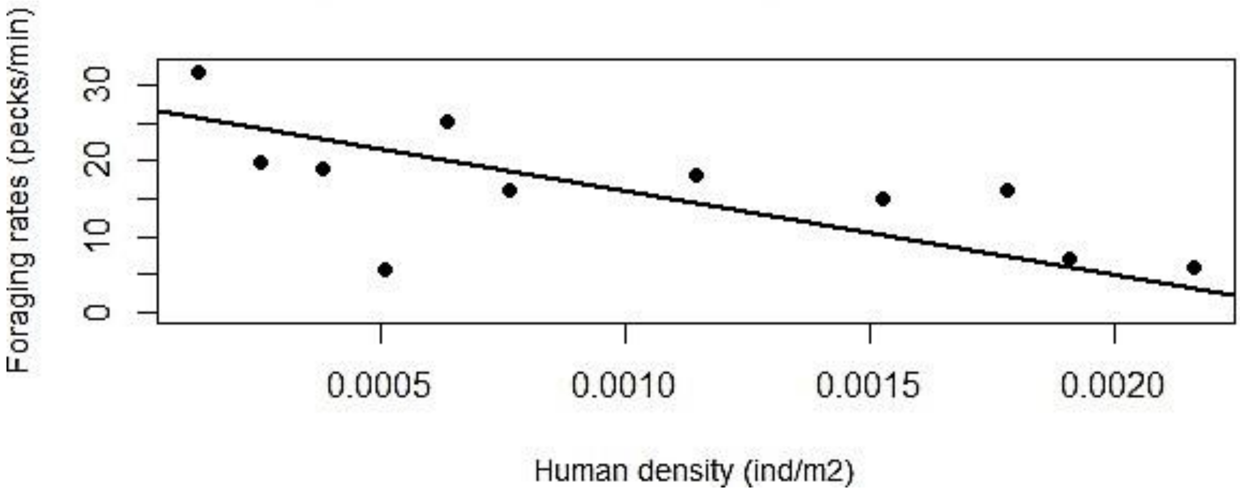

**Figure 8.6 Foraging rates of sanderlings and human density.** (The regression line is represented by Foraging rate = 27.12 – 11091.52 Human density, $R^2 = 0.03$. Each point represents mean foraging rate per human density).

## 8.4 Discussion

This study assessed the various activities along the Esiama beach, identified those that disturbed either foraging or resting sanderlings, how sanderlings responded to and accommodated these activities, as well as the influence of such activities on the foraging rates of sanderlings. It was not surprising that human-related activities dominated the beach and especially, that at least 60% of human-related activities were of fishing and related activities (including shellfish harvesting). The most recent census in Ghana reported that, most communities along the coast in the study area depended on the beach for their livelihoods (Ghana Statistical Service, 2014). In recent times, infrastructural developments along the beach has also created an aesthetic environment for recreational activities. Various studies have shown that beaches and other wetlands around the globe have been inhabited and/or used rather more often by humans and this has influenced the behaviour of shorebirds, which

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further translates into individual fitness and population dynamics of birds (e.g. Lord *et al.*, 1997; Frid & Dill, 2002; Thomas *et al.*, 2003; Yasué, 2005; Yasué *et al.*, 2008).

The results of this study suggests that sanderlings were selective in the part of the beach they frequently used. Their selection, according to the results, was based on prey distribution and disturbances (human densities). Sanderlings were ready to trade off high quality prey (*E. chiltoni*) which was abundant towards the eastern end of the beach to their survival by feeding on *D. pulchellus* within the middle part of the beach. This observation is similar to that by Yasué *et al.* (2008) who observed low wader densities within habitats that supported higher densities of worms and some bivalves. In the Yasué *et al.* (2008) study, they observed that the displaced birds inhabited adjacent habitats which supported appreciable prey densities, but lower rates of human disturbances. Sanderlings along the Esiama beach have been observed to use the entire beach for different activities depending on the levels of disturbances. They were observed to roost along the Amansuri estuary when levels of disturbances were high within their preferred foraging and roosting points.

The most important aerial predator of sanderlings along the Esiama beach is the yellow-billed kite. The results of this study showed that sanderlings migrated ahead of kites. Sanderlings arrived on the Esiama beach two months before kites did. This offered sanderlings, especially individuals staging at the site, some time to forage undisturbed by kites. Lank *et al.* (2003) also observed migration of sandpipers to precede that of peregrine falcon *Falco peregrinus* by a month. However, during such early periods of arrival, sanderlings were also anxious of other agents of disturbances, especially the pied crows. Lafferty (2001b) also observed crows as an important agent of disturbance for snowy plovers *Charadrius nivosus.* Sanderlings were able to accommodate crows over time, which showed some level of habituation. Fitzpatrick and Bouchez (1998) also observed some waders to become habituated to disturbances that occurred frequently along the Jordanstown beach in Northern Ireland.

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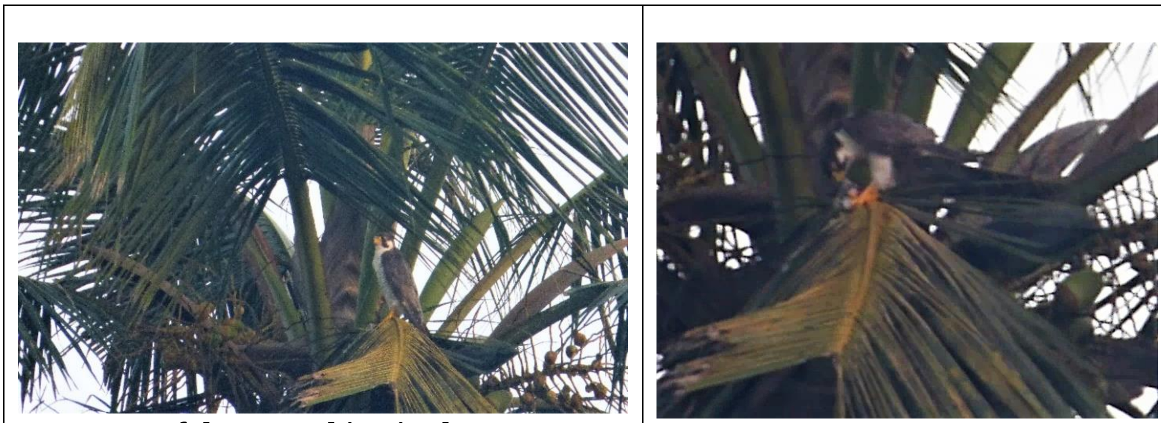
Predation risk was expected to decrease with increasing beach width (van den Hout *et al.*, 2014), however this was not in the case from this study. This could probably be due to either the small sample size of data on the MAD to kites or the fact that kites made themselves visible to sanderlings all the time as they hover in the air. Assuming the latter happens to be the case, then it means that the presence of kites was easily noticed by sanderlings and as such they (sanderlings) avoided possible attacks by moving further away from kites as the kites drew closer. Elsewhere in Mauritania, van den Hout *et al.* (2014) observed red knots foraging close to the edge (away from the shoreline) to be at higher risk of predation to falcons than those foraging away from the edge. There was no single observation of a lanner falcon *Falco biarmicus* in the transect survey, however it was once captured on camera to have captured a sanderling (Plate 8.3). The success of the falcon could be due to their mode of attack, which involves hiding in the trees and surprising their prey in an attack.



**A. Lanner falcon perching in the coconut tree**

**B. Lanner falcon devouring a captured sanderling**

**Plate 8.3 Lanner falcon along the Esiama beach**

There were lots of fishing activities observed along the beach, but only few of such activities impacted on the behaviour of sanderlings. The nature of fishing along the Esiama beach, which involved dragging of seine nets along the shore, hardly influenced the behaviour of

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sanderlings, because the nets are dragged perpendicular to the shoreline. In this case, only a small area is covered in relation to the shoreline, hence sanderlings can easily forage close to fishing activities and would not show any signs of displacement.

Foraging sanderlings were observed to be more tolerant than resting sanderlings. This is probably because foraging sanderlings were always on the move and could easily escape predators and other sources of disturbances, unlike resting individuals who seemed more vulnerable. The most important factors that influenced the MAD to foraging sanderlings were flock size and width of the beach. The results showed that sanderlings preferred foraging in larger flock size (35 individuals and above) to smaller ones (less than 35 individuals). Individuals in larger flocks feels safer because the risk of predation is shared amongst each member within the flock (Cresswell, 1994b). Therefore, approaching disturbances are easily picked up early enough and information transferred amongst members within the flock early enough to elicit response.

Sanderlings foraging on wider beaches were more sensitive to approaching passers-by. This supported observation by Lafferty (2001b), who reported snowy plovers on wider beaches to be more sensitive to agents of disturbances. According to him, plovers could not accommodate other beach users on a wider beach, however on narrower beaches, plovers were more tolerant because they cannot afford to be displaced. The variation in beach width was primarily a function of tidal movement and seasonal distribution of sand. To add to this explanation, based on results from this study, sanderlings' increasing sensitivity with increasing beach width could be a function of resource (food) distribution. Cross-tidally, sanderlings have the option of feeding on different preys. Therefore, in other to coexist with other beach users, sanderlings could afford a temporal displacement on wider beaches, by moving across the beach in order to avoid approaching agent of disturbance. Sanderlings can continue foraging on other prey types and possibly return to their original position once the

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agent of disturbance has departed often at a cost to such movements. The larger the number of humans along the beach, the less foraging rates observed for sanderlings. This observation supports that of Yasué (2005) and Yasué *et al.* (2008). The former observed swallowing rates of semipalmated plovers *Charadrius semipalmatus* to decline with human counts whereas the latter observed the intake rates of Eurasian curlew *Numenius arquata* to decline as the number of dogs and humans increased along the beach. The simple reason behind such observations was that foragers spent more time on the lookout, acknowledging the presence of intruders, thereby having less time to forage. As a follow-up, even though fishing activities were tolerated by sanderlings, due to relatively lower MAD, the presence of large numbers of people could interfere with the intake rates of sanderlings. This may have severe consequences on the long-term intake rate and energy acquisition of sanderlings. Sanderlings may probably have to forage at night to compensate for the lost time foraging in the day. However, it was not possible to undertake night observations because of limited resources to obtain the appropriate equipment.

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# CHAPTER NINE

# GENERAL DISCUSSION

## 9.1 Introduction

The sanderling *Calidris alba* breeds in the artics, Greenland, Siberia and spends the non-breeding periods in the temperate and tropical coasts. The annual long-distance movement of this little bird, which weighs on average 50 g, demonstrates the global linkages between the artic, temperate and tropical regions.

Migratory birds act as sentinels of the environment picking and disseminating biological and environmental cues from the wide range of habitats and ecosystems they exploit in their annual cycle. The population of sanderling and other waterbirds have been monitored on the Ghana coast for well over 30 years beginning from the 1980s (Ntiamoa-Baidu & Hepburn, 1988; Ntiamoa-Baidu, 1991b; Ntiamoa-Baidu *et al.*, 1998; Ntiamoa-Baidu & Gordon, 2000; Ntiamoa-Baidu *et al.*, 2000; Ntiamoa-Baidu *et al.*, 2014a).

The Ghana coast has been shown to support internationally important numbers of several species of waterbirds, including the sanderling (Reneerkens *et al.*, 2009a; Reneerkens *et al.*, 2009b; Ntiamoa-Baidu *et al.*, 2014a). The stretch of beach between the Ankobra and Amansuri rivers in the Western Region of Ghana, known as the Esiama beach, is the most important site along the Ghana coast for sanderlings supporting 40-70% of the non-breeding population, estimated to constitute 3.5 % of the East Atlantic Flyway population. Despite the qualification of the Esiama beach and associated Amansuri wetland for designation as a Ramsar site (wetland of international importance) under the Ramsar Convention’s criterion of 1% waterbirds population threshold, the site remains unprotected. With the discovery of oil in the Western Region of Ghana and the rapidly growing petroleum industry in the region,

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the Esiama beach has become highly vulnerable to the potential adverse impacts of the extraction industries. Thus the status of sanderling and other waterbirds using the Esiama beach offer good biological indication of the health of the wetland. There is already an indication of Esiama beach reaching its carrying capacity and as such surplus sanderlings are then forced to use other sites along the Ghana coast (Ntiamoa-Baidu *et al.*, 2014a). This thesis provides comprehensive study on the foraging ecology of the sanderling along the Esiama beach and aims to contribute to the ecological requirements of the species, thereby, providing a solid biological information base on monitoring the health of not only the sanderling population but also the wetlands on which the sanderling and other shorebirds depend.

The purpose of this thesis therefore was to study the foraging ecology of non-breeding sanderlings in Ghana. The specific objectives of the study were designed to augment the information available on the distribution, abundance, availability and quality of prey along the Esiama beach. Furthermore, the objectives were to provide information on exploratory behaviours of sanderlings, the prey selection process and disturbances that influence the foraging efficiency of sanderlings. The findings of the study have been presented under the objectives in five chapters of the thesis namely;

I. Distribution, availability and quality of benthic macroinvertebrates as prey for non-breeding sanderlings
II. Spatio-temporal variation in the distribution of sanderlings and their invertebrate prey
III. Description and measurement of when, where and how non-breeding sanderlings forage; a functional and aggregate response to prey and predator densities
IV. Sanderlings' prey type and size preference
V. Human disturbances and other pressures on foraging behaviour of sanderlings

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This final discussion chapter provides a commentary on key findings of the study and integrates these with existing knowledge on the foraging ecology of sanderlings and habitat quality. First, the chapter discusses the ecological processes and ecosystem functions of the Esiama beach, and the role of sanderlings in this context. Secondly, the chapter synthesizes the complexity of species interaction, explaining the social roles and strategies that enhance the foraging efficiency of the species in the ecosystem. Thirdly, the chapter discusses energy management of sanderlings, highlighting how prey availability and choice influence the energy budgets of sanderlings along the Esiama beach, relating the outcome to annual migration. Finally, the implication of the findings to the protection of the Esiama beach and conservation of sanderlings locally, and along the East Atlantic flyway (EAF) are discussed.

## 9.2 Ecological processes and ecosystem functions of the Esiama beach

Ecosystems are important in the provision of ecological and socio-economic support to human communities. Changes in the ecosystem may impose stress on the system, but if the stress is beyond the capacity of the ecosystem, then the ecosystem may lose its integrity (Davis & Brock, 2008). The ecological integrity/ character of an ecosystem refers to the long-term capacity of the system to support and maintain the ecological processes or interactions among the physical, biological and chemical elements of the system. When ecological processes operate optimally, then the ecosystem is in a better condition to provide better goods and services (Balvanera *et al.*, 2006).

The ecosystem functions of the Esiama beach and associated wetlands fall under the four categories described by the Millennium Ecosystem Assessment: production, regulation, habitat and informational functions (Leemans & De Groot, 2003; Sarukhan *et al.*, 2005). This study shows that the Esiama beach is an important habitat for the long-distant migrant

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shorebird, the sanderling, during the non-breeding season that lasts for about nine months (from August to April) each year. In their study on the Esiama beach, Ntiamoa-Baidu *et al.* (2014a) described the importance of Ghana's coast to sanderlings and in particular the Esiama beach. They showed that, the beach supports more than 1% the sanderlings population of the East Atlantic Flyway, which qualifies the Esiama beach as a Ramsar site and therefore needs to be protected. The findings of this study also shows that the Esiama beach is important for at least 10 benthic macroinvertebrates: *Donax pulchellus* and *D. rugosus* (bivalves), *Hastula aciculina* and *Agaronia acuminata* (gastropods), *Emerita talpoida* and *Excirolana chiltoni* (crustaceans), *Glycera* spp. and *Nereis* sp. (polychaetes), Nemertea and Mysid shrimp, which are important food sources for animal life and humans.

The Esiama beach also supports regulatory functions which ensure equilibrium among the various actors and processes along the beach. Large numbers of shorebirds including the sanderling use the beach and are important predators of the macroinvertebrates stock on the beach. In terms of biological control, the sanderling prey on the surf clam *D. pulchellus* which occurs in high densities, with records of about 15,000 individuals/ $m^2$ (Chapter 4). The study showed that, there was a significant relationship between the spatial distribution of sanderlings and *D. pulchellus* ($F = 27.1$, $df = 562$, $p < 0.001$; Chapter 5). The control of densities of *D. pulchellus* by sanderlings could help to keep the densities of the bivalve below the carrying capacity of the beach which, when reached, will cause high mortality of the prey and may also have severe impact on the nutrient cycle in the water (Ansell *et al.*, 1980). As reported by Akita *et al.* (2014), the relative growth rate of *D. pulchellus* is influenced by food availability which they measured indirectly as nutrient load in the system. They explained that increase in primary productivity influences the growth of *D. pulchellus*. This implies that in the absence of a key predator of the bivalve, such as the sanderling, a trophic cascading effect may arise in the food chain, which may affect densities of *D. pulchellus*, algae and

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phytoplankton that are sources of food for the bivalve, and nutrient load in the system. High nutrient load may lead to eutrophication of the system, affecting animal life. Up the food chain, predatory birds such as the yellow-billed kite may have to find other sources of prey (Chapter 8). The diet analysis of sanderlings from this study showed that sanderlings consumed also Mysid shrimps and fish. The consumption of these prey may be through scavenging on leftovers after fishing activities. Such foraging behaviour of sanderlings are likely to help in cleaning.

## 9.3 The complexity of species interaction; are sanderlings on top?

Since no single organism can live on its own without interacting with other organism, it is imperative for species to tolerate and coexist with others within a defined space over a period of time. However, to be able to coexist, organisms must adapt to certain features and processes that will enhance their chances of survival. Most shorebird species are communal and often forage and roost in small to large flock sizes (Silliman *et al.*, 1977). Whilst foraging in varying flock sizes on the Esiama beach individual birds may learn of good foraging areas based on the intake rates of their neighbours (van Der Meer & Ens, 1997). The intake rates of shorebirds increase with flock size (Powell, 1974; Yasué, 2005). The findings of this study show that sanderlings are social birds and occurred in varying flock sizes from 1 to 650 individual birds (Chapter 5). They formed smaller flock sizes of up to 120 individuals when foraging. The results showed that, foraging rates increased with flock size, but only when the flock size was below 28 individuals (Chapter 6). Beyond this threshold, sanderlings had to adopt other forms of strategies to increase their intake rates. Amongst such strategies included; increasing the nearest neighbour distances, changing foraging strategies from visual to tactile methods or relocating from the selected patch. The decision to relocate would be the foragers' last resort because, it is costlier to let go of good foraging grounds. Besides, there is no guarantee of

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finding another better foraging patch. Moreover, foraging in larger flocks also has its advantages. Each individual within the larger flock is a potential threat perceiver and as such sanderlings foraging in larger flocks are able to respond quicker to agents of disturbances than those foraging in smaller flocks. In this study, sanderlings foraging in flock size greater than 35 individuals responded quicker to humans than those foraging in smaller flock sizes.

### 9.4 Energy management of foraging sanderlings along the Esiama beach

Sanderlings, like other shorebirds, make several decisions of which the selection of a suitable non-breeding habitat is key. For a long distant migrant like the sanderling that travels thousands of kilometers on an annual basis, the quality of selected habitats provides a good basis for explaining the success of such species in the environment. One of such factors that defines the quality of the habitat is the energy management (Piersma, 2012). Energy acquisition and expenditure is a crucial component of the migration process of sanderlings. Energy acquisition depends primarily on the abundance, availability of prey and quality of prey, and how sanderlings exploit such prey in time and space. Most coastal beaches support high densities of macroinvertebrates which serve as prey for shorebirds (e.g. Nuka *et al.*, 2005). However, availability and accessibility of prey on a temporal scale influences the community dynamics within the coastal beach environment. Furthermore, the spatial distribution of prey also explains the aggregate responses of predators. Between the two most abundant macroinvertebrates in benthic samples in this study, *Excirolana chiltoni* was heavier in biomass (measured as Ash Free Dry Mass, AFDM) and of more quality than *D. pulchellus* of similar sizes. The mean biomass of *E. chiltoni* was 1.44 ± 0.06 mg $\text{AFDM}_{\text{flesh}}$ for a mean size of 5.2 mm, whereas for a similar size of *D. pulchellus*, the mean biomass was 0.68 ± 0.04 mg $\text{AFDM}_{\text{flesh}}$. The total biomass of *D. pulchellus* along the beach was estimated at up to

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26.29 gAFDMm$^{-2}$ and up to 1.40 gAFDMm$^{-2}$ for *E. chiltoni*. However, spatial distribution of sanderlings along the beach was rather explained by the distribution of *D. pulchellus* ($F = 27.1$, $p < 0.001$). This means that, the distribution of sanderlings was primarily influenced by abundance, availability and total biomass of prey rather than quality of prey. The low biomass or densities of *E. chiltoni* on the beach could be either actual densities which means lower densities of *E. chiltoni* on the Esiama beach, or due to anti-predatory strategies such as prey depression, which ensured fewer individuals present in benthic samples.

The diet of shorebirds provides information of energy flow and the position of a species in the food chain. Such information helps in understanding the community ecology of the studied ecosystem. The abundance of prey species has been used to explain the carrying capacities of specific habitats of shorebirds (Summers & Underhill, 1987). Ntiamoa-Baidu *et al.* (2014a) and Grond *et al.* (2015) observed sanderlings along the Esiama beach to exclusively feed on the prey *D. pulchellus*. Their observations were supported by the high biomass and abundance of *D. pulchellus* along the beach. This study, however, presents a different dietary profile for sanderlings along the Esiama beach. Diet analysis through faecal samples showed that sanderlings were generalists in their diet selection and consumed practically anything they came across. However, the bivalve *D. pulchellus,* was the most observed and abundant prey in their diet, accounting for 79.0% of all prey items in faecal samples. The isopod *E. chiltoni* accounted for 12.0% of all prey in faecal samples. The proportion of *E. chiltoni* was very likely to be underestimated, primarily because, they are soft-bodied prey which were likely to be digested before egestion. The information from the diet analysis, however, confirmed that sanderlings are keystone predators of *D. pulchellus* and *E. chiltoni* along the Esiama beach.

The size of prey consumed by shorebirds helps in accurately predicting the energy obtained from consumed prey. This is because an allometric relationship exists between prey size and biomass. Such prey size-biomass allometric equations are species- and site- specific.

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Information on the sizes of prey consumed helps in addressing questions on prey size selection and profitability of prey, and provide a more accurate estimation of the energy budgets of predators. Furthermore, the niche of a study species can be defined and where there are overlaps with other species, identified accordingly and studied to understand how species are successful in their ecological roles within selected ecosystems. There are several indigestible parts of prey items in faecal droppings. Some can be used in estimating the original sizes of prey consumed (Onrust *et al.*, 2013), whereas others cannot (Lourenço *et al.*, 2017). This depends on the variation amongst indigestible parts in the droppings and the fact that there exist an allometric relationship between the indigestible parts and the original sizes of prey. This study provides the first reported allometric equations between sizes of macroinvertebrates in benthic samples along the Esiama beach and the dry biomass of their flesh. This thesis also provides the first reported allometric equations that estimate the quality of macroinvertebrates in benthic samples along the Esiama beach from the sizes of macroinvertebrates. But more importantly, this thesis provides the first calibration study which can be used in estimating the size and biomass of ingested *D. pulchellus* from indigestible 'hinge plus top' in faecal sample. The estimated biomass of *D. pulchellus* consumed by sanderlings can be estimated from the number and heights of hinges + top in the faecal droppings of sanderlings.

Most studies on the foraging behaviour of sanderlings have described three different foraging strategies for the species. On the Esiama beach, Grond *et al.* (2015) described pecking, probing and sewing as the main foraging strategies used by sanderlings in exploiting prey. Elsewhere in Portugal, Lourenço *et al.* (2015) also identified pecking, probing and sewing as foraging strategies used by sanderlings. However in their study, Lourenço *et al.* (2015) classified probing as non-random probes (NRPs) and sewing as random probes (RPs). Probing and sewing or NRP and RP have been generally defined as tactile foraging methods mostly

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used in searching for hidden and buried prey. This study also supports such information on foraging strategies employed by sanderlings. This thesis also provides additional information from the experiments with captive sanderlings which showed that sanderlings do not only employ probing and sewing foraging methods in searching for buried prey, but the latter is used especially in searching for appropriate sizes of prey (*D. pulchellus*) even when prey has been offered unburied. How sanderlings are able to identify appropriate prey sizes has not been described as yet. Some studies have already shown sensory structures around the bill of red knots (Piersma *et al.*, 1998) and ibises (Cunningham *et al.*, 2010) that help the birds in their search for prey.

Time-activity budgets provide information on the proportion of time organisms spend on specific activities, thereby providing a basis for estimating energetic budgets of shorebirds. Time-activity budgets could also provide information on the temporal partitioning and utilization of resources by a community of shorebird species and could further explain coexistence and survival of sympatric species. This study estimated that sanderlings along the Esiama beach spend about 60% of the diurnal period foraging. The time-activity budgets showed high foraging activity during high tide. The distribution of macroinvertebrates also suggests that the most available prey during this period was *E. chiltoni* (Chapter 6). Experimental investigation also showed that sanderlings preferred the isopod *E. chiltoni* to the bivalve *D. pulchellus*, because of the profitability and digestive quality of the former to the latter (Chapter 7). However, estimation of biomass from prey consumed in faecal droppings suggested that intake rates of *E. chiltoni* were underestimated, because of the time of collection of the faecal droppings. It was therefore evident from the estimation of ingested biomass that the intake rates of sanderlings could be more than that estimated from faecal droppings. Simply because, the intake rate of *D. pulchellus* could not provide enough biomass for sanderlings to meet the estimated minimum daily energy requirement of 10.2 g AFDM

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reported for similar wader species by Kersten and Piersma (1987). However, with assumptions of intake rates of *E. chiltoni* from other studies (Goss-Custard, 1977; Dierschke *et al.*, 1999), the estimated biomass ingested of 7.34 g AFDM per 12-hour period was similar to the 6.1 g AFDM that was reported by Lourenço *et al.* (2015).

The energy budget of shorebirds is very important as it provides a quick evaluation of the welfare of birds and helps to predict their success on other biological processes such as reproduction. The energy budgets of shorebirds may also provide an indication of upcoming events such as migration and tell whether a bird is ready for a direct flight or not (Zwarts *et al.*, 1990a; Piersma *et al.*, 2005). Nevertheless, it is always paramount that the minimum energy requirement for the proper functioning of the body is obtained. Castro *et al.* (1992) estimated the daily energy expenditure (DEE) of sanderlings as 100 kJ/day and the basal metabolic rate (BMR) as 48.1 kJ/day in a tropical non-breeding habitat in Panama. Assuming the conditions in Panama is similar to that of Ghana, it implies that the minimum amount of energy needed by sanderlings in a day on the Esiama beach is 100 kJ/ day. Therefore, the net energy intake (NEI) of prey items should at least approximate to the DEE. In this study, estimated biomass of 7.3 g AFDM per 12 h (estimate includes intake rates of *E. chiltoni* from Goss-Custard, 1977; Dierschke *et al.*, 1999) and 1.57 g AFDM per 12 h (estimate include intake rates of *E. chiltoni* from faecal samples) was consumed by sanderlings. If it is assumed that the energetic density of prey is 22 kJ/g for all macroinvertebrate species (Zwarts & Wanink, 1993), and an assimilation efficiency of 85% (Kersten & Piersma, 1987), then the net energy intake (NEI = biomass per 12 h x energetic density x assimilation efficiency) of sanderlings is estimated at 136.51 kJ/12h or 29.34 kJ/ 12h for biomass of 7.3 g AFDM per 12h or 1.57 g AFDM per 12h respectively (Figure 9.1). The estimated NEI is either approximately 2.83 times the BMR and 1.37 times that of the DEE (estimate includes intake rates of *E. chiltoni* from Goss-Custard, 1977; Dierschke *et al.*, 1999) or 0.61 times the BMR

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and 0.29 times that of the DEE (includes intake rates of *E. chiltoni* from faecal samples). From the two estimations, a biomass of 1.57 g AFDM per 12h would not be enough to meet the daily energy needs of sanderlings, but a biomass of 7.3 g AFDM per 12 h is enough for sanderlings to meet its daily energy without engaging in nocturnal foraging.

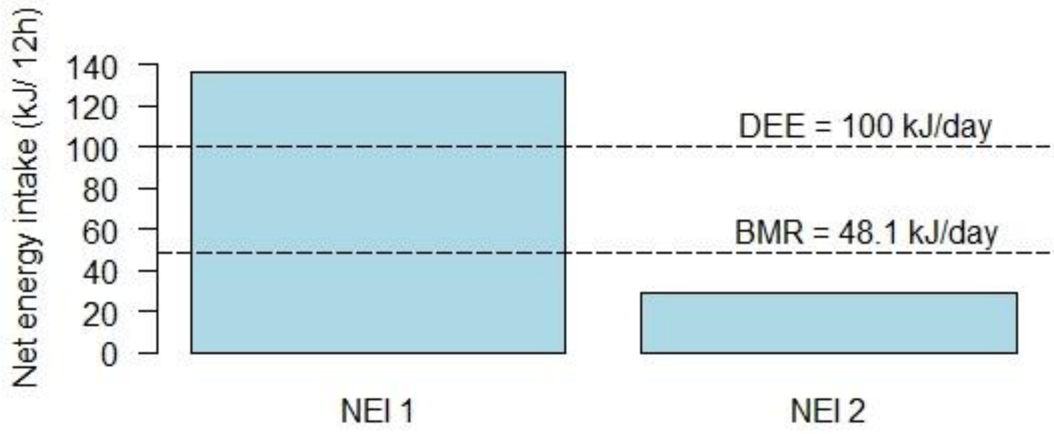

**Figure 9.1 Estimated Net Energy Intake (NEI) of sanderlings.** [NEI 1 is the estimated NEI of sanderlings with estimates of intake rate of *E. chiltoni* obtained from (Goss-Custard, 1977; Dierschke *et al*., 1999) and NEI 2 is NEI with estimates of intake rate of *E. chiltoni* from faecal samples. Note the horizontal axis is NEI in 12 hours whereas the BMR and DEE thresholds are estimated in KJ/ day from (Castro *et al*., 1992)].

The low intake rates of *D. pulchellus* may be as a result of ballast mass filling the stomach (proventriculus) of the birds faster. The efficiency of gizzard depends on its mass, and the absence of data on gizzard mass made it difficult to say if the intake rates of sanderlings on bivalves reflect intake rates when the bird is about to embark on migration. van Gils *et al.* (2005a) observed phenotypic plasticity of the gizzard mass in the red knots which allowed the birds to forage on different prey types of different qualities.

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## 9.5 Implications of findings for sanderlings conservation in Ghana and along the East Atlantic Flyway

It is quite difficult for the ordinary person to understand ecological concepts, especially when such studies are not directly linked to human benefits such as provision of food, water, monetary income and other raw materials. To the political governing bodies of developing countries, which most at times operate on tight budgets in funding developmental projects, ecological research on biodiversity must meet certain criteria, e.g. conservation of threatened species and protection of national monuments, in order to receive some considerations. Otherwise, such research becomes irrelevant, to the government especially when its findings do not address any of the Sustainable Development Goals of the United Nations (UN). The SDGs addresses three key areas: social, ecological and economic aspects, and deliveries on these three key areas has faced lots of challenges, which has led to some trade-offs being made in order to achieve desired goals (Gupta & Vegelin, 2016). Several concepts have been developed in attempt to optimize all three areas under a single operational system. One of such concept is the 'inclusive development' which brings together the social inclusiveness, ecological inclusiveness and economic inclusiveness dimensions to achieve a developmental goal (Gupta & Vegelin, 2016).

The findings of this study may not provide a direct developmental achievement, but rather provides basic information that are relevant to the protection and conservation of the Esiama beach and sanderlings (SDGs 13, 14 and 15, which represents Climate change, Life below water and Life on land respectively) in relation to the well-being of communities along the beach. The findings of this study outlines the ecological importance of the Esiama beach to sanderlings during the non-breeding season and macroinvertebrates such as shellfishes, as well as the economic and social importance of the Esiama beach to surrounding communities.

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Going forward, changes in the population dynamics of sanderlings could be used as a measure of the ecological health of the Esiama beach vis-à-vis the impact of developmental pressures on the beach on the foraging behaviour of sanderlings. The long-term effect of pressures which are not sustainable to the ecological processes of the beach is that the economic livelihoods of surrounding communities such as shellfish harvesting, may be lost should the Esiama beach ecosystem lose its ecological integrity.

The ecological health of several habitats are important to the conservation of sanderlings along the East Atlantic Flyway (EAF). Because resources are limited in their distribution, shorebirds are distributed in aggregation rather than uniformly or randomly. For non-breeding shorebirds, the selection of suitable non-breeding sites depends on the food availability as well as other ecological processes such as danger from natural predators; anthropogenic pressures such as human interactions and infrastructural developments (Piersma, 2012). The understanding of the interaction of these pressures on the behaviour of migrants is essential in defining the local survival of birds as well as in totality the fitness (survival and reproduction) of these birds on their breeding ground (Baker *et al.*, 2004; van Roomen *et al.*, 2015). Once the quality of a non-breeding habitat is lost, shorebirds may either decide to abandon that habitat or endure the changing conditions, especially where there is competition on other non-breeding sites. Such decisions by migrants may either influence the population of the flyway positively or negatively (van Roomen *et al.*, 2015).

The findings of this study show how important the Esiama beach is to the foraging ecology of sanderlings. This study also documents the impact of human pressures on the Esiama beach on the foraging behaviour of sanderlings and how sanderlings manage these pressures. The Esiama beach may continue to be important for sanderlings and the EAF, if the energetic demands of sanderlings are met even in the presence of all the identified pressures, and the site continues to maintain its ecological integrity. The findings of this study may also be used

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to push for the designation of the Esiama beach and associated wetlands as a Ramsar site in order for the site to receive formal protection status. In the meantime, the findings of this study can be used in managing the site either by the local communities, the local fishers' associations and traditional rulers of surrounding communities.

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# CHAPTER TEN

# CONCLUSIONS, RECOMMENDATIONS AND CONTRIBUTION TO KNOWLEDGE

## 10.1 Conclusions

The general objective of this study was to investigate and document the foraging ecology of sanderlings on the western coast of Ghana; and using the species as a model, describe and assess the quality of Esiama beach as a suitable and preferred non-breeding site for sanderlings in Ghana. The specific objectives of this study were to;

I. To measure the variations in the distribution, availability and quality of benthic macroinvertebrates as prey for sanderlings.

II. To assess the spatio-temporal variation in the distribution of sanderlings in relation to food availability.

III. To describe and measure when, where and how non-breeding sanderlings forage; a functional and aggregate response to prey and predator densities.

IV. To determine prey type and size preference of non-breeding sanderlings.

V. To determine and evaluate the impact of human disturbances and other pressures on the foraging behaviour of sanderlings.

At least ten macroinvertebrate species were recorded in this study; these were the bivalves *Donax pulchellus* and *D. rugosus*, the gastropods *Hastula aciculina* and *Agaronia acuminata*, the crustaceans *Excirolana chiltoni* and *Emerita talpoida*, the polychaetes *Glycera* spp. and *Nereis* sp., the ribbon worms Nemertea and Mysid shrimp. *Donax pulchellus*, *E. chiltoni* and *Glycera* spp. were the three most abundant macroinvertebrates in benthic samples, constituting 91.66%, 6.45% and 1.40% respectively of all macroinvertebrate individuals recorded. Cross-tidally; about 78.21%, 17.98% and 3.81% of all macroinvertebrates in

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benthic samples were recorded within the low tide, intertidal and high tide zones; *D. pulchellus* being the most abundant macroinvertebrate within the low tide and intertidal zones and *E. chiltoni* the most abundant in the high tide zone. More than 95.0% of the recorded macroinvertebrates in benthic samples were present in the top 3 cm depth, out of which 94.77% were made up of *D. pulchellus*. The mean size of *D. pulchellus* was 6.9 ± 1.7 mm (range 2.0 – 12.3), a mean biomass of 1.62 ± 0.04 mg $AFDM_{flesh}$ and a quality of 1.20 kJ/g; the mean size of *E. chiltoni* was 5.2 ± 1.4 mm (range 1.5 – 9.0), a biomass of 1.44 ± 0.06 mg $AFDM_{flesh}$ and a quality of 5.15 kJ/g. This is the first study that calibrated and developed regression equations in estimating the biomass of macroinvertebrate from the size of the prey as well as the quality of the prey from its biomass on the Esiama beach.

This study documented mean densities of *D. pulchellus* up to 15,509 ind/$m^2$ and that of *E. chiltoni* up to 960 ind/$m^2$. The densities of *D. pulchellus* were highest in August-October and January-March and lowest in November and July. On the other hand, the densities of *E. chiltoni* were highest in November and July. *Donax pulchellus* were distributed away from the estuaries whereas *E. chiltoni* were distributed towards the Ankobra estuary. The transect counts showed that sanderlings occurred in flocks with sizes ranging between 1 and 600 individuals. Occurrence of sanderlings along the beach was seasonal; sanderlings were mostly abundant in September/ October and occasionally in January-March. The spatial distribution of *D. pulchellus* explained the spatial distribution of sanderlings along the beach.

The time-activity budget studies showed that sanderlings spent 60.54%, 36.93%, 1.15% and 1.48% of the 12-hour day time foraging, resting, in locomotion and exhibiting comfort activities. The tidal cycle, time of day, number of birds on the beach and prey densities explained the amount of time sanderlings spent foraging. The feeding studies showed that sanderlings exhibited three foraging methods; probing, pecking and sewing. Sanderlings pecked more were prey densities were high (25.24 ± 19.29 pecks/ min) but less when prey

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densities were low (15.19 ± 13.74 pecks/ min). Sanderlings pecked more when they were abundant on the beach (25.04 ± 19.01 pecks/min) than when they were fewer (17.66 ± 16.16 pecks/ min). Foraging rates of sanderlings increased with flock size up to a threshold of 28 birds in a flock, above which foraging rates declined. Nearest neighbour distances increased when sanderlings were foraging in flock sizes above 28 individuals. The dietary studies showed that the diet of sanderlings was made up of *D. pulchellus*, *E. chiltoni*, *Glycera* spp., *H. aciculina* and fish. The experiments with captive sanderlings showed that the intake rates of sanderlings in captivity was 1.61 ± 0.73 ind/ min and varied between small size (1.61 ± 1.03 ind/ min) and medium size (0.44 ± 0.36) *D. pulchellus*. The estimated biomass consumed by sanderlings was 1.57 ± 0.96 g AFDM per 12-hour from faecal samples and 7.34 g AFDM per 12-hour from substituted intake rates of *E. chiltoni* from literature.

The prey choice and preference study showed that *E. chiltoni* was a more profitable prey (6.78 ± 5.53 mgAFDM/s) than *D. pulchellus* (2.48 ± 2.31 mgAFDM/s). Small size *D. pulchellus* was also more profitable (2.28 ± 2.01 mgAFDM/s) than medium size *D. pulchellus* (1.82 ± 1.13 mgAFDM/s). Therefore, the contingency model predicted *E. chiltoni* as a preferred prey to *D. pulchellus*. The digestive rate model predicted *E. chiltoni* as a preferred prey over *D. pulchellus*. The maximum intake experiment showed that shell mass of prey constrained foraging sanderlings. In the dichotomous study, sanderlings preferred *E. chiltoni* over *D. pulchellus* and small size *D. pulchellus* over medium size *D. pulchellus*.

Human-related activities were the most frequently observed activity along the Esiama beach accounting for 74.0% of all activities observed followed by the sighting of yellow-billed kites (13.0%). The transect survey on disturbances along the Esiama beach showed that sanderlings avoided areas along the beach with high human densities ($p < 0.001$). The minimal approach distance study showed that sanderlings were more sensitive to engine-driven machines (59.42 ± 35.86 m) but tolerated fishing activities (20.19 ± 8.03 m). The MAD between sanderlings

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and passers-by was 25.51 ± 10.03 m as well as 11.93 ± 6.29 m with kites. The flock size of sanderlings and width of the beach explained the level of tolerance of sanderlings to passers-by ($R^2 = 0.27$, df = 5, AIC = 347.1, $p = 0.0002$). Foraging rates of sanderlings decreased in the presence of high human densities ($F = 5.39$, df = 138, $p = 0.02$).

## 10.2 Recommendations

The findings of this study have provided important information for the understanding of the foraging ecology of sanderlings along the Esiama beach. Out of these information come four different recommendations for policy consideration and sensitization. These include:

I. The entire 13 km stretch of Esiama beach is important for sanderlings and needs to be protected.

II. Local authorities should help protect sensitive foraging areas along the beach (at least 3 km stretch between Kikam and Asanta villages) for sanderlings.

III. Beach users should be sensitized on the need to avoid disturbing flocks of foraging sanderlings otherwise keep to a distance of 30 m away from foraging sanderlings.

IV. Residents should be sensitized enough on the need to leach their dogs that visit the beach.

V. Beach users should avoid direct contact with sanderlings so as to prevent potential transmission of any pathogens they may be carrying.

The findings of this study also have raised further research questions in the process which could add to the knowledge on the foraging ecology of sanderlings and its importance to sanderling migration. Key questions include:

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I. Does the condition of benthic macroinvertebrates on the Esiama beach vary with time and if so, how does the variation in body condition of macroinvertebrates influence the energy intake and foraging time of sanderlings?

II. To what extent does the seasonal sea weed (*Sargassum* spp) influence the ecology of sanderlings on the beach?

III. What is the turnover rate of sanderling population on the Esiama beach and how does the local food stock influence the body conditions of the birds?

IV. How does phenotypic plasticity of body organs of sanderlings explain their foraging behaviour and migration process?

V. What are the estimated intake rates of *E. chiltoni* and *Glycera* spp. by sanderlings?

VI. Do sanderlings on the Esiama beach graze on biofilm and what contribution does the biofilm make to the energy intake of sanderlings.

VII. Do sanderlings forage at night?

VIII. Does the bill of sanderling possess any special features that aid the bird select the appropriate or preferred prey size?

Answers to some of these questions will give a better understanding of the foraging behaviour, migration process and survival of sanderlings that use the Esiama beach as a stopover site or an actual non-breeding site. In investigating these questions, future studies should use holistic methods through interdisciplinary approaches. Such holistic approach could include investigating beach profile dynamics, pollution (both solid and liquid waste), pathogenic occurrence and transmission, and livelihood and social demography of communities within the catchment of the wetland.

As a result of time and financial constraints, this study could not look at the factors that influenced the distribution of macroinvertebrates along the beach, which could have provided explanations to some of the observations and results. It was also not possible to do a molecular

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genetic or isotopic analyses of the diet of sanderlings, to confirm or augment the information obtained from the faecal analysis.

The Esiama beach and associated Amansuri wetland has continually supported internationally important numbers of sanderlings. This study identified important areas along the beach that support high densities of prey and lower densities of humans. Such areas may be regarded as hot spots for foraging birds and may be vital in the preparation towards migration. The findings of the study provide additional information that defines the quality of the Esiama beach for foraging sanderlings. However, in order for humans and sanderlings to coexist harmoniously on the beach, management practices need to be put in place to ensure the right balance. The Esiama beach and associated Amansuri estuary, therefore need to be designated as a Ramsar site (i.e. wetland of international importance) and protected, so that such important foraging areas along the coast of Ghana and the East Atlantic Flyway as a whole, will continue to provide ecological support for migrant birds at different time periods. The protection of the Esiama beach and associated Amansuri wetland will allow site managers to tap into the technical information provided from this thesis and help conserve this wetland and ensure the sustainable utilization of resources by communities within the wetland through the ‘wise-use’ concept.

## 10.3 Contribution to knowledge

In the nutshell, this study has contributed to scientific knowledge through:

I. Provision of additional information on foraging ecology of sanderlings on Esiama beach.

II. Establishing a basis for monitoring sanderling prey distribution.

III. Demonstrating high prey biomass available for sanderlings on Esiama beach, however exploitation of this biomass is constrained by prey processing or digestion.

IV. Identification of important areas along the Esiama beach that support high densities

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of prey and lower densities of humans, thereby providing additional description on quality of the site.

V. Establishing the international importance of Esiama beach and associated Amansuri wetland, which provides further justification for the protection of the site.

VI. Determining the distribution of these migrants and the potential spread of any pathogens they may be carrying.

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# REFERENCES

Aggrey-Fynn, J., Galyuon, I., Aheto, D., & Okyere, I. (2011). Assessment of the environmental conditions and benthic macroinvertebrate communities in two coastal lagoons in Ghana. *Annals of Biological Research, 2*(5), 413-424.

Akita, L. G., Laudien, J., & Armah, A. K. (2014). *Donax pulchellus and Donax rugosus on sandy beaches, Ghana*: LAP Lambert Academic Publishing.

Akiyama, A. (2000). Foraging behaviours of coastal shorebirds in the Ichinomiya tidal estuary. *Aquabiology, 22*(4; ISSU 129), 332-339.

Al-Mansour, M. I. (2004). Seasonal variation in Basal Metabolic Rate and Body Composition Within Individual Sanderling Bird *Calidris alba*. *Journal of Biological Sciences, 4*(4), 564-567.

Alerstam, T., & Lindström, Å. (1990). Optimal bird migration: the relative importance of time, energy, and safety *Bird migration*. Springer, 331-351

Allen, H. (2014). *Correlation Between Shell Size and Presence and Size of Apertural Teeth in the Low-Intertidal Zone Snail, Nucella lamellosa*. Friday Harbor Laboratories. University of Washington. Retrieved from http://hdl.handle.net/1773/27270

Altizer, S., Bartel, R., & Han, B. A. (2011). Animal migration and infectious disease risk. *Science, 331*(6015), 296-302.

Alves, J. A., Gunnarsson, T. G., Hayhow, D. B., Appleton, G. F., Potts, P. M., Sutherland, W. J., & Gill, J. A. (2013). Costs, benefits, and fitness consequences of different migratory strategies. *Ecology, 94*, 11-17.

Amat, J. A., & Green, A. J. (2010). Waterbirds as bioindicators of environmental conditions *Conservation Monitoring in Freshwater Habitats*. Springer, 45-52

University of Ghana http://ugspace.ug.edu.gh

Amlalo, D. S. (2006). The protection, management and development of the marine and coastal environment of Ghana. *Administering Marine Spaces: International Issues, 148*.

Ansell, A., Angus, I., & Robb, L. (1985). Variations in shell morphology and growth of the banded wedge shell *Donax vittatus* in populations in Lewis and Harris. *A report to Comhairlenan Eilean. SMBA Internal Reports*(131).

Ansell, A., Barnett, P., Bodoy, A., & Massé, H. (1980). Upper temperature tolerances of some European molluscs II. *Donax vittatus*, *D. semistriatus* and *D. trunculus*. *Marine biology, 58*(1), 41-46.

Ansell, A., & Trueman, E. R. (1973). The energy cost of migration of the bivalve *Donax* on tropical sandy beaches. *Marine Behavioural Physiology, 2*, 21-32.

Ansell, A. D. (1983). The biology of the genus *Donax*. In: McLachlan, A. & Erasmus, T. (Eds.), *Sandy beaches as ecosystems*. The Hague, The Netherlands: Springer, 607-635

Armah, A., & Amlalo, D. (1998). *Coastal zone profile of Ghana*: Ministry of Environment, Science and Technology.

Asafu-Adjaye, J. (2003). Biodiversity loss and economic growth: a cross-country analysis. *Contemporary Economic Policy, 21*(2), 173-185.

Austin, G. E., & Rehfisch, M. M. (2003). The likely impact of sea level rise on waders (Charadrii) wintering on estuaries. *Journal for Nature Conservation, 11*(1), 43-58.

Ayala, F. J., Gilpin, M. E., & Ehrenfeld, J. G. (1973). Competition between species: theoretical models and experimental tests. *Theoretical Population Biology, 4*(3), 331-356.

Baker, A. J., González, P. M., Piersma, T., Niles, L., do Nascimiento, I., Atkinson, P. W., Clark, N., Minton, C., Peck, M. K., & Aarts, G. (2004). Rapid population decline in

University of Ghana http://ugspace.ug.edu.gh

red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society B, 271*, 875-882.

Ball, J. P. (1994). Prey choice of omnivorous canvasbacks: imperfectly optimal ducks? *Oikos*, 233-244.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology letters, 9*(10), 1146-1156.

Barlow, C. R., & Dodman, T. (2015). *African East Atlantic Flyway Guide - Photographic Field Guide to Waterbirds and Seabirds of Africa's Western Coastline*. Common Wadden Sea Secretariat, Wilhelmshaven, Germany; BirdLife International, Cambridge, United Kingdom; Programme Rich Wadden Sea; Leeuwarden, The Netherlands.

Barrett, R. T., Camphuysen, C. J., Anker-Nilssen, T., Chardine, J. W., Furness, R. W., Garthe, S., Hueppop, O., Leopold, M. F., Montevecchi, W. A., & Veit, R. R. (2007). Diet studies of seabirds: A review and recommendations. *ICES J. Mar. Sci, 64*, 1675-1691.

Bartels-Hardege, H. D., & Zeeck, E. (1990). Reproductive behaviour of *Nereis diversicolor* (Annelida: Polychaeta). *Marine biology, 106*, 409-412.

Battley, P., Poot, M., Wiersma, P., Gordon, C., Ntiamoa-Baidu, Y., & Piersma, T. (2003). Social foraging by waterbirds in shallow coastal lagoons in Ghana. *Waterbirds, 26*(1), 26-34.

Bearhop, S., Adams, C. E., Waldrons, S., Fuller, R. A., & Macleod, H. (2004). Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology, 73*, 1007-1012.

Belovsky, G. E. (1986). Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. *Oecologia, 70*(1), 35-52.

University of Ghana http://ugspace.ug.edu.gh

Bergman, C. M., Fryxell, J. M., Gates, C. C., & Fortin, D. (2001). Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology, 70*, 289-300.

Beukema, J. J. (1985). Zoobenthos survival during severe winters on high and low tidal flats in the Dutch Wadden Sea. In: Gray, J. S. & Christiansen, M. E. (Eds.), *Marine biology of polar regions and effects of stress on marine organisms*. Chichester: John Wiley, 351-361

Birdlife International. (2016). *Calidris alba*. doi: http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22693369A86614145.en Retrieved 01 December 2018

Boere, G. C., & Stroud, D. A. (2006). The flyway concept: what it is and what it isn't. *Waterbirds around the world*, 40-47.

Borgmann, K. L. (2010). A review of human disturbance impacts on waterbirds. *Audubon California, 376*.

Borrow, N., & Demey, R. (2013). *Field guide to the birds of Ghana*: Bloomsbury Publishing.

Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology*, *68*(2), 203-220.

Boyd, H., & Piersma, T. (2001). Changing balance between survuval and recruitment explains population trends in red knots *Calidris canutus islandica* wintering in Britain, 1969-1995. *Ardea*, *89*, 301-317.

Bradley, B. J., Stiller, M., Doran-Sheehy, D. M., Harris, T., Chapman, C. A., Vigilant, L., & Poinar, H. (2007). Plant DNA sequences from feces: Potential means for assessing diets of wild primates. *Am. J. Primatol*, *69*, 699-705.

Breed, M. D. (2001). *Animal Behaviour, An Online Text Book*. http://www.animalbehaviouronline.

University of Ghana http://ugspace.ug.edu.gh

Bromley, R. G., & Jarvis, R. L. (1993). The energetics of migration and reproduction of Dusky Canada Geese. *The Condor*, 193-210.

Brown, A. C., & McLachlan, A. (2006). *Ecology of Sandy Shores*. Elsevier, Amsterdam.

Buehler, D. M., Tieleman, B. I., & Piersma, T. (2010). How do migratory species stay healthy over the annual cycle? A conceptual model for immune function and for resistance to disease. *Integrative and Comparative Biology, 50*(3), 346-357.

Burger, J. (1987). Physical and social determinates of nest-site selection in piping plover in New Jersey. *The Condor, 89*, 811-818.

Burger, J. (1993). Shorebird squeeze. *Natural History, 102*, 8-12.

Burger, J. (1994). The effect of human disturbance on foraging behaviour and habitat use in piping plover (*Charadrius melodus*). *Estuaries, 17*(3), 695-701.

Burger, J. (1997). Effect of oiilg on feeding behaviour of sanderlings and semipalmated plovers in New Jersey. *The Condor, 99*, 290-298.

Burger, J., Carlucci, S. A., Jeitner, C. W., & Niles, L. (2007). Habitat choice, disturbance, and management of foraging shorebirds and gulls at a migratory stopover. *Journal of Coastal Research*, 1159-1166.

Burger, J., & Gochfeld, M. (1991a). Human activity influence and diurnal and nocturnal foraging of sanderlings (*Calidris alba*). *The Condor, 93*, 259-265.

Burger, J., & Gochfeld, M. (1991b). Human activity influence and diurnal and nocturnal foraging of sanderlings (*Calidris alba*). *The Condor, 93*, 259-265.

Burger, J., Howe, M. A., Hahn, D. C., & Chase, J. (1977). Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. *The Auk*, 743-758.

Burger, J., & Olla, B. L. (1984). *Shorebirds: migration and foraging behaviour* (Vol. 6):

University of Ghana http://ugspace.ug.edu.gh

Plenum Publishing Corporation.

Castro, G. (1987). High basal metabolic rate in Sanderlings (*Calidris alba*). *Wilson Bull, 99*, 267-268.

Castro, G., Myers, J. P., & Ricklefs, R. E. (1992). Ecology and energetics of sanderlings migrating to four latitudes *Ecology, 73,* 833-844.

Castro, M., Masero, J. A., Megina, C., Amat, J. A., & Pérez-Hurtado, A. (2008). Energy and macronutrient assimilation efficiencies of Snowy Plover (*Charadrius alexandrinus*) feeding on the polychaete ragworm *Nereis diversicolor*. *The Auk, 125*(2), 368-373.

Colwell, M. A., & Landrum, S. L. (1993). Nonrandom shorebird distribution and fine-scale variation in prey abundance. *The Condor*, 94-103.

Cresswell, W. (1994a). Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology, 63,* 589-600.

Cresswell, W. (1994b). Flocking as an effective anti-predation strategy in redshanks, *Tringa totanus. Animal Behaviour, 47,* 433-442.

Cummings, V., Schneider, D., & Wilkinson, M. (1997). Multiscale experimental analysis of aggregative responses of mobile predators to infaunal prey. *Journal of Experimental Marine Biology and Ecology, 216*(1), 211-227.

Cunningham, S. J., Alley, M. R., Castro, I., Potter, M. A., Cunningham, M., & Pyne, M. J. (2010). Bill morphology of ibises suggests a remote-tactile sensory system for prey detection. *The Auk, 127*(2), 308-316.

Davis, J., & Brock, M. (2008). Detecting unacceptable change in the ecological character of Ramsar wetlands. *Ecological Management & Restoration, 9*(1), 26-32.

De Leeuw, J. J. (1999). Food intake rates and habitat segregation of tufted duck Aythya fuligula and scaup Aythya marila exploiting zebra mussels *Dreissena polymorpha*.

University of Ghana http://ugspace.ug.edu.gh

*Ardea, 87*(1), 15-31.

Dekinga, A., & Piersma, T. (1993). Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the knot *Calidris canutus*. *Bird Study, 40*(2), 144-156.

Dekker, D., & Ydenberg, R. C. (2004). Raptor predation on wintering dunlins in relation to the tidal cycle. *Condor, 106*, 415-419.

Delany, S., Scott, D., Dodman, T., & Stroud, D. (2009). An atlas of wader populations in Africa and Western Eurasia. *Brit Birds, 102*, 639-642.

Delgado, F., Escobar, C., Verschuuren, B., & Hiemstra, W. (2010). Sacred natural sites, biodiversity and well-being: the role of sacred sites in endogenous development in the COMPAS network. *Sacred natural sites: conserving nature and culture. Earthscan, London*, 188-197.

Delgado, J. D., Riera, R., Monterroso, O., & Nunez, J. (2008). Distribution and abundance of meiofauna in intertidal sand substrata around Iceland. *Aquatic Ecology*, 13. doi: 10.1007/s10452-008-9200-0

Díaz, M., Møller, A. P., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., Markó, G., & Tryjanowski, P. (2013). The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS ONE, 8*(5), e64634.

Dierschke, V., Kube, J., Probst, S., & Brenning, U. (1999). Feeding ecology of dunlins *Calidris alpina* staging in the southern Baltic Sea, 1. Habitat use and food selection. *Journal of Sea Research, 42*(1), 49-64.

Dinsmore, S. J., & Collazo, J. A. (2003). The influence of body condition on local apparent survival of spring migrant sanderlings in coastal North Carolina. *The Condor, 105*(3), 465-473.

Dodd, S. L., & Colwell, M. A. (1998). Environmental correlates of diurnal and nocturnal

University of Ghana http://ugspace.ug.edu.gh

foraging patterns of non-breeding shorebirds. *The Wilson Bulletin*, 182-189.

Dodman, T., & Diagana, C. H. (2003). *African Waterbird Census 1999, 2000 & 2001* (Vol. 16). Wageningen, The Netherlands: Wetland International Global Series.

Dolah, R. F. V. (1978). Factors regulating the distribution and population dynamics of the amphipod *Gammarus palustris* in an intertidal salt marsh community. *Ecological monographs, 48*, 191-217.

Dolman, P. M. (1995). The intensity of interference varies with resource density: evidence from a field study with snow buntings, *Plectrophenax nivalis*. *Oecologia, 102*(4), 511-514.

Duijns, S., Gils, J. A., Spaans, B., Horn, J., Brugge, M., & Piersma, T. (2014). Sex-specific winter distribution in a sexually dimorphic shorebird is explained by resource partitioning. *Ecology and evolution, 4*(20), 4009-4018.

Duijns, S., & Piersma, T. (2014). Interference competition in a sexually dimorphic shorebird: prey behaviour explains intraspecific competition. *Animal Behaviour, 92*, 195-201.

Dunn, O. P., & Winkler, D. (2010). Effects of climate change on timing of breeding and reproductive success in birds. In: Møller, A. P., Fiedler, W. & Berthold, P. (Eds.), *Effects of climate change on birds*. USA: Oxford University Press, 113-128

Edmunds, J. (1978). *Sea shells and other molluscs found on West African shores and estuaries*: Ghana Universities Press.

Einoder, L. D. (2009). A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research, 95*(1), 6-13.

Elgar, M. A. (1988). Predator vigilance and group size in mammals and birds: a critical review of the empirical eveidence. *Biol Rev, 64*, 13-33.

Engelmoer, M., & Roselaar, C. S. (1998). *Geographical variation in waders*. Dordrecht, the

University of Ghana http://ugspace.ug.edu.gh

Netherlands: Kluver Academic Publishers.

Ens, B., & Goss-Custard, J. (1984). Interference among oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. *The Journal of Animal Ecology*, 217-231.

EOL. (2018 August). *Excirolana chiltoni*. from http://eol.org/pages/347597/details#distribution. Retrieved 31/08/2018

Espoz, C., Ponce, A., Matus, R., Blank, O., Rozbaczylo, N., Sitters, H., Rodríguez, S., Dey, A., & Niles, L. (2008). Trophic ecology of the red knot *Calidris canutus* rufa at Bahía Lomas, Tierra del Fuego, Chile. *Wader Study Group Bulletin, 115*(2), 69-76.

Estrella, S. M., Masero, J. A., & Pérez-Hurtado, A. (2007). Small-prey profitability: field analysis of shorebirds' use of surface tension of water to transport prey. *The Auk*, *124*(4), 1244-1253.

Farnsworth, K. D., & Illius, A. W. (1998). Optimal diet choice for large herbivores: an extended contingency model. *Functional Ecology*, *12*, 74-81.

Fasola, M., & Biddau, L. (1997). An assemblage of wintering waders in coastal Kenya: activity budget and habitat use. *African Journal of Ecology, 35*(339-350). doi: 10.1111/j.1365-2028.1997.087-89087.x

Fernández, J. M., Selma, M. A. E., Aymerich, F. R., Sáez, M. T. P., & Fructuoso, M. F. C. (2005). Aquatic birds as bioindicators of trophic changes and ecosystem deterioration in the Mar Menor lagoon (SE Spain). *Hydrobiologia*, *550*(1), 221-235.

Fitzpatrick, S., & Bouchez, B. (1998). Effects of recreational disturbance on the foraging behaviour of waders on a rocky beach. *Bird Study, 45*(2), 157-171.

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology, 6,* 11-26.

University of Ghana http://ugspace.ug.edu.gh

Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B., & Page, G. (2002). Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. *Waterbirds, 25*(2), 173-183.

García-Peña, G. E., Thomas, G. H., Reynolds, J. D., & Székely, T. (2009). Breeding systems, climate, and the evolution of migration in shorebirds. *Behavioural Ecology, 20*(5), 1026-1033.

Gaspar, M., Ferreira, R., & Monteiro, C. (1999). Growth and reproductive cycle of *Donax trunculus L.*,(Mollusca: Bivalvia) off Faro, southern Portugal. *Fisheries Research, 41*(3), 309-316.

Gaspar, M. B., Santos, M., & Vasconcelos, P. (2001). Weight–length relationships of 25 bivalve species (Mollusca: Bivalvia) from the Algarve coast (southern Portugal). *Journal of the Marine Biological Association of the United Kingdom, 81*(5), 805-807.

Gaspar, M. B., Santos, M. N., Vasconcelos, P., & Monteiro, C. C. (2002). Shell morphometric relationships of the most common bivalve species (Mollusca: Bivalvia) of the Algarve coast (southern Portugal). *Hydrobiologia, 477*(1), 73-80.

Gawlik, D. E. (2002). The effects of prey availability on the numerical response of wading birds. *Ecological monographs, 72*(3), 329-346.

Gbogbo, F. (2007). The importance of unmanaged coastal wetlands to waterbirds at coastal Ghana. *African Journal of Ecology, 45*(4), 599-606.

Gbogbo, F., Oduro, W., & Oppong, S. K. (2008). Nature and pattern of lagoon fisheries resource utilisation and their implications for waterbird management in coastal Ghana. *African Journal of Aquatic Science, 33*(3), 211-222. doi: 10.2989/AJAS.2008.33.3.3.615

Gbogbo, F., & Otoo, S. D. (2015). The concentrations of five heavy metals in components of an economically important urban coastal wetland in Ghana: public health and

University of Ghana http://ugspace.ug.edu.gh

phytoremediation implications. *Environmental monitoring and assessment, 187*(10), 655.

Gbogbo, F., Otoo, S. D., Huago, R. Q., & Asomaning, O. (2017). High levels of mercury in wetland resources from three river basins in Ghana: a concern for public health. *Environmental Science and Pollution Research, 24*(6), 5619-5627.

Ghana Statistical Service. (2012). *2010 Population and Housing Census Final Results*. Ghana Statistical Service Accra.

Ghana Statistical Service. (2014). *2010 Population and housing census*. Ghana Statistical Service Accra, Ghana.

Ghana Wildlife Society. (1998). *Ghana Wildlife Society Annual Report 1998-1999*. Ghana Wildlife Society Accra.

Gilg, O., Sittler, B., Sabard, B., Hurstel, A., Sané, R., Delattre, P., & Hanski, I. (2006). Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos, 113*, 193-216.

Gill, A. B. (2003). The dynamics of prey choice in fish: the importance of prey size and satiation. *Journal of fish biology, 63*(Supplement A), 105-116. doi: doi:10.1046/j.1095-8649.2003.00214.x, availableonline at http://www.blackwell-synergy.com

Gill, A. B., & Hart, P. J. B. (1994). Feeding behaviour and prey choice of the three-spine stickleback: the interacting effects of prey size, fish size and stomach fullness. *Animal Behaviour, 4*(921-932).

Gill, J. A., Norris, K., & Sutherland, W. J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation, 97*(2), 265-268.

University of Ghana http://ugspace.ug.edu.gh

Gillings, S., Atkinson, P. W., Bardsley, S. L., Clark, N., Love, S. E., Robinson, R. A., Stillman, R., & Weber, R. G. (2007). Shorebird predation of horseshoe crab eggs in Delaware Bay: species contrasts and availability constraints. *Journal of Animal Ecology, 76*, 503-514.

Gommer, R., Bom, R. A., Fijen, T. P., & Van Gils, J. A. (2018). Stomach fullness shapes prey choice decisions in crab plovers (*Dromas ardeola*). *PLoS ONE, 13*(4), e0194824.

Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate research (Open Access for articles 4 years old and older), 35*(1), 37.

Gordon, C. (1995). Sakumo Ramsar Site Aquatic Ecology: Ghana Coastal Wetlands Management Project, Environmental Baseline Studies. *Report prepared for the Wildlife Department, Government of Ghana*, 36.

Goss-Custard, J. (1970a). The responses of redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. *The Journal of Animal Ecology*, 91-113.

Goss-Custard, J. (1977). Predator responses and prey mortality in redshank, *Tringa totanus* (L.), and a preferred prey, *Corophium volutator* (Pallas). *The Journal of Animal Ecology*, 21-35.

Goss-Custard, J. (1980). Competition for food and interference among waders. *Ardea, 68*, 31-52.

Goss-Custard, J., Clarke, R., & Dit Durell, S. l. V. (1984). Rates of food intake and aggression of oystercatchers *Haematopus ostralegu*s on the most and least preferred mussel *Mytilus edulis* beds of the Exe estuary. *The Journal of Animal Ecology*, 233-245.

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

University of Ghana http://ugspace.ug.edu.gh

Goss-Custard, J. D. (1970b). Feeding dispersion in some overwintering wading birds. *Social behaviour in birds and mammals*, 3-35.

Goss-Custard, J. D., West, A. D., Yates, M. G., Caldow, R. W., Stillman, R. A., Bardsley, L., Castilla, J., Castro, M., Dierschke, V., dit Durell, S. E. L. V., Eichhorn, G., Ens, B., Exo, K.-M., Udayangani-Fernando, P. U., Ferns, P. N., Hockey, P. A., Gill, A. B., Johnstone, I., Kalejta-Summers, B., Masero, J. A., Moreira, F., Nagarajan, R. V., Owens, I. P. F., Pacheco, C., Perez-Hurtado, A., Rogers, D. I., Scheiffarth, G., Sitters, H., Sutherland, W. J., Triplet, P., Worrall, D. H., Zharikov, Y., Zwarts, L., & Pettifor, R. A. (2006). Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biological Reviews, 81*(4), 501-529.

Grond, K., Ntiamoa-Baidu, Y., Piersma, T., & Reneerkens, J. (2015). Prey type and foraging ecology of Sanderlings *Calidris alba* in different climate zones: are tropical areas more favourable than temperate sites? *PeerJ, 3*, e1125.

Gudmundsson, G. A., Lindström, Å., & Alerstam, T. (1991). Optimal fat loads and long-distance flights by migrating Knots *Calidris canutus*, Sanderlings *C. alba* and Turnstones *Arenaria interpres*. *Ibis, 133*(2), 140-152.

Gupta, J., & Vegelin, C. (2016). Sustainable development goals and inclusive development. *International environmental agreements: Politics, law and economics*, *16*(3), 433-448.

Gutiérrez, J. S., Soriano-Redondo, A., Dekinga, A., Villegas, A., Masero, J. A., & Piersma, T. (2015). How salinity and temperature combine to affect physiological state and performance in red knots with contrasting non-breeding environments. *Oecologia, 178*(4), 1077-1091.

Hackman, K. O. (2014). The state of biodiversity in Ghana: Knowledge gaps and prioritization. *International Journal of Biodiversity and Conservation, 6*(9), 681-701.

University of Ghana http://ugspace.ug.edu.gh

Haines-Young, R., & Potschin, M. (2010). The links between biodiversity, ecosystem services and human well-being. *Ecosystem Ecology: a new synthesis, 1*, 110-139.

Haramis, G., & Link, W. (2007). Stable isotope and pen feeding trial studies confirm the value of horseshoe crab *Limulus polyphemus* eggs to spring migrant shorebirds in Delaware Bay. *Journal of Avian Biology*.

Hart, P. J. B., & Gill, A. B. (1992). Constraints on prey size selection by the three-spined stickleback: energy requirements and the capacity and fullness of the gut. *Journal of fish biology, 40*, 205-218.

Heller, R., & Millinski, M. (1979). Optimal foraging of sticklebacks on swarming orey. *Animal Behaviour, 27*, 1127-1141.

Hobson, K. A. (1993). Trophic relationships ampng high Arctic seabirds: insights from tissue-dependent stable-isotope models. *Marine Ecology Progress Series, 95*, 7-18.

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

Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *Canadian Entomologist, 91*, 385-398.

Howe, M. A., Geissler, P. H., & Harrington, B. (1989). Population trends of North American shorebirds based on the International Shorebird Survey. *Biological Conservation, 49,* 185-199.

Hughes, R. H. (1992). *A directory of African wetlands*: IUCN.

Hughes, R. N. (1997). Diet selection. In: Godin, J.-G. (Ed.), *Behavioural Ecology of Teleost Fishes*. Oxford: Oxford University Press, 134-162

James, F. C. (1970). Geographic size variationin birds and its relationship to climate. *Ecology,*

University of Ghana http://ugspace.ug.edu.gh

*51*, 365-390.

Jardine, C. B., Bond, A. L., Davidson, P. J., Butler, R. W., & Kuwae, T. (2015). Biofilm consumption and variable diet composition of Western Sandpipers (*Calidris mauri*) during migratory stopover. *PLoS ONE, 10*(4), e0124164.

Jenni, L., & Kéry, M. (2003). Timing of autumn bird migration under climate change: advances in long–distance migrants, delays in short–distance migrants. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 270*(1523), 1467-1471.

Jeschke, J. M., Kopp, M., & Tollrian, R. (2002). Predator functional responses: discriminating between handling and digesting prey. *Ecological monographs, 72*, 95-112.

Jiménez, A., Elner, R. W., Favaro, C., Rickards, K., & Ydenberg, R. C. (2015). Intertidal biofilm distribution underpins differential tide-following behaviour of two sandpiper species (*Calidris mauri* and *Calidris alpina*) during northward migration. *Estuarine, Coastal and Shelf Science, 155*, 8-16.

Johnson, S. R., & Herter, D. R. (1990). Bird migration in the Arctic: a review. In: Gwinner, E. (Ed.), *Bird migration: physiology and ecophysiology*. Berlin: Springer-Verlag, 22-43

Karpanty, S. M., Cohen, J., Fraser, J. D., & Berkson, J. (2011). Sufficiency of horseshoe crab eggs for red knots during spring migration stopover in Delaware Bay USA. *The Journal of wildlife management, 75*(5), 984-994.

Kelsey, M., & Hassall, M. (1989). Patch selection by Dunlin on a heterogeneous mudflat. *Ornis Scandinavica*, 250-254.

Kensley, B. F., & Penrith, M. (1980). The Constitution of the Fauna of Rocky Intertidal Shores of South West Africa. Part 3. the North Coast from False Cape Frio to the Kunene River.

University of Ghana http://ugspace.ug.edu.gh

Kersten, M., & Piersma, T. (1987). High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea, 75*, 175-187.

Klaassen, M. (1995). Moult and basal metabolic costs in males of two subspecies of stonechats: the European *Saxicola torquata rubicula* and the East African *S. t. axillaris*. *Oecologia, 104*(4), 424-432.

Kloskowski, J., Grendel, A., & Wronka, M. (2000). The use of fish bones of three farm fish species in diet analysis of the Eurasian otter, *Lutra lutra*. *FOLIA ZOOLOGICA-PRAHA-, 49*(3), 183-190.

Kuwae, T., Beninger, P. G., Decottignies, P., Mathot, K. J., Lund, D. R., & Elner, R. W. (2008). Biofilm grazing in a higher vertebrate: the western sandpiper, *Calidris mauri*. *Ecology, 89*(3), 599-606.

Lafferty, K. D. (2001a). Birds at a Southern California beach: seasonality, habitat use and disturbance by human activity. *Biodiversity and Conservation, 10*(11), 1949-1962.

Lafferty, K. D. (2001b). Disturbance to wintering western snowy plovers. *Biological Conservation, 101*(3), 315-325.

Lank, D. B., Butler, R. W., Ireland, J., & Ydenberg, R. C. (2003). Effects of predation danger on migration strategies of sandpipers. *Oikos, 103*(2), 303-319.

Lank, D. B., & Ydenberg, R. C. (2003). Death and danger at migratory stopovers: problems with "predation risk". *Journal of Avian Biology, 34*, 225-228.

Laudien, J. (2002). Population dynamics and ecology of the surf clam *Donax serra* (Bivalvia, Donacidae) inhabiting beaches of the Benguela upwelling system. *Berichte zur Polar- und Meeresforschung (Reports on Polar and Marine Research), 432*.

Laudien, J., Brey, T., & Arntz, W. (2001). Reproduction and recruitment patterns of the surf clam *Donax serra* (Bivalvia, Donacidae) on two Namibian sandy beaches. *African*

University of Ghana http://ugspace.ug.edu.gh

*Journal of Marine Science, 23*, 53-60.

Leemans, R., & De Groot, R. (2003). *Millennium Ecosystem Assessment: Ecosystems and human well-being: a framework for assessment*: Island press.

Lemke, H. W., Bowler, J., & Reneerkens, J. (2012). Establishing the right period to estimate juvenile proportions of wintering Sanderlings via telescope scans in western Scotland. *Wader Study Group Bulletin, 119*, 2.

Leyrer, J., Lok, T., Brugge, M., Dekinga, A., Spaans, B., van Gils, J. A., & *et al*. (2012). Small-scale demographic structure suggests preemptive behaviour in a flocking shorebird. *Behavioural Ecology, 23*, 1226-1233.

Leyrer, J., Spaans, B., Camara, M., & Piersma, T. (2006). Small home ranges and high site fidelity in red knots (*Calidris c. canutus*) wintering on the Banc d'Arguin, Mauritania. *Journal of Ornithology, 147*(2), 376-384.

Lima, S. L. (1998). Stress and decision making under the risk of predation: recent developments from behavioural, reproductive, and ecological perspectives. *Adv Study Behav, 27*, 215-290.

Lindstrom, A., Kvist, A., Piersma, T., Dekinga, A., & Dietz, M. W. (2000). Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting and fuelling. *Journal of experimental biology, 203*(5), 913-919.

Lindström, Å., & Piersma, T. (1993). Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis, 135*(1), 70-78.

Loonstra, A. J., Piersma, T., & Reneerkens, J. (2016). Staging duration and passage population size of Sanderlings in the western Dutch Wadden Sea. *Ardea, 104*(1), 49-61.

Lord, A., Waas, J. R., & Innes, J. (1997). Effects of human activity on the behaviour of

University of Ghana http://ugspace.ug.edu.gh

northern New Zealand dotterel *Charadrius obscurus aquilonius* chicks. *Biological Conservation, 82*(1), 15-20.

Lourenço, P. M. (2007). Analysing faecal samples of Ragworm predators: not just a matter of counting mandibles. *Ardea, 95*(1), 151-155.

Lourenço, P. M., Alves, J. A., Catry, T., & Granadeiro, J. P. (2015). Foraging ecology of sanderlings *Calidris alba* wintering in estuarine and non-estuarine intertidal areas. *Journal of Sea Research, 104*, 33-40.

Lourenço, P. M., Alves, J. A., Reneerkens, J., Loonstra, A. J., Potts, P. M., Granadeiro, J. P., & Catry, T. (2016a). Influence of age and sex on winter site fidelity of sanderlings *Calidris alba*. *PeerJ, 4*, e2517.

Lourenço, P. M., Catry, T., & Granadeiro, J. P. (2017). Diet and feeding ecology of the wintering shorebird assemblage in the Bijagós archipelago, Guinea-Bissau. *Journal of Sea Research, 128*, 52-60.

Lourenço, P. M., Catry, T., Piersma, T., & Granadeiro, J. P. (2016b). Comparative feeding ecology of shorebirds wintering at Banc d'Arguin, Mauritania. *Estuaries and Coasts, 39*(3), 855-865.

Lourenço, P. M., Silva, A., Santos, C. D., Miranda, A. C., Granadeiro, J. P., & Palmeirim, J. M. (2008). The energetic importance of night foraging for waders wintering in a temperate estuary. *Acta Oecol, 34*, 122-129.

Lyons, J. E., & Haig, S. M. (1995). Fat content and stopover ecology in spring migrant Semipalmated Sandpipers in South Carolina. *Condor, 97*, 427-437.

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist, 100*(916), 603-609.

Maron, J. L., & Myers, J. (1985). Seasonal changes in feeding success, activity patterns, and

University of Ghana http://ugspace.ug.edu.gh

weights of non-breeding Sanderlings (*Calidris alba*). *The Auk*, 580-586.

Marra, P. P., Francis, C. M., Mulvihill, R. S., & Moore, F. R. (2005). The influence of climate on the timing and rate of spring bird migration. *Oecologia*, *142*(2), 307-315.

Mathot, K. J., Lund, D. R., & Elner, R. W. (2010). Sediment in stomach contents of Western Sandpipers and Dunlin provide evidence of biofilm feeding. *Waterbirds*, *33*(3), 300-306.

McCrary, M. D., & Pierson, M. O. (2000). *Influence of human activity on shorebird beach use in Ventura County, California.* Paper presented at the Proceedings of the Fifth California Islands Symposium.

McKinnon, L., Berteaux, D., & Bêty, J. (2014). Predator-mediated interactions between lemmings and shorebirds: A test of the alternative prey hypothesis. *The Auk, 131*(4), 619-628.

McLachlan, A. (1977). Composition, distribution, abundance and biomass of the macrofauna, and meiofauna of four sandy beaches. *African Zoology, 12*(2), 279-306.

McLachlan, A. (1996). Physical factors in benthic ecology: effects of changing sand particle size on beach fauna. *Marine Ecology Progress Series*, 205-217.

McLachlan, A., Wooldridge, T., Schramm, M., & Kühn, M. (1980). Seasonal abundance, biomass and feeding of shore birds on sandy beaches in the Eastern Cape, South Africa. *Ostrich, 51*(1), 44-52.

Meissner, W., & Wlodarczak, A. (1999). Autumn migration of Sanderling (*Calidris alba*) in the Puck Bay region (southern Baltic coast). *Ring, 21*(2), 57-67.

Mensah, C. (2008). *Community-based natural resources management and livelihood improvement: the case of Amansuri Conservation and Integrated Development Project (ACID) in Jomoro district in Ghana.* University of Cape Coast.

University of Ghana http://ugspace.ug.edu.gh

Miller-Rushing, A. J., Lloyd-Evans, T. L., Primack, R. B., & Satzinger, P. (2008). Bird migration times, climate change, and changing population sizes. *Global Change Biology, 14*(9), 1959-1972.

Miller, M., Beam, J., & Connelly, D. (1988). Dabbling duck harvest dynamics in the Central Valley of California - Implications for recruitment. In: Weller, M. W. (Ed.), *Waterfowl in winter*. Minneapolis, MN: University of Minnesota Press, 553-569

Ministry of Lands and Forestry. (1999). *Managing Ghana's Wetlands: A national wetland conservation strategy* Accra, Ghana.

Møller, A. P., Fiedler, W., & Berthold, P. (2010). *Effects of climate change on birds*: Oxford University Press.

Moore, F. R., Smith, R. J., & Sandberg, R. (2005). Stopover ecology of intercontinental migrants. *Birds of Two Worlds: the ecology and evolution of migration*, 251-261.

Morrier, A., & McNeil, R. (1991). Time-activity budget of Wilson's and Semipalmated Plovers in a tropical environment. *The Wilson Bulletin*, 598-620.

Musgrove, A. J., Austin, G. E., Hearn, R. D., Holt, C. A., Stroud, D. A., & Wotton, S. R. (2011). Overwinter population estimates of British waterbirds. *British Birds, 104*(7), 364.

Myers, J. (1981). A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Canadian Journal of Zoology, 59*(8), 1527-1534.

Myers, J., Connors, P., & Pitelka, F. (1979). Territory size in wintering sanderlings: the effects of prey abundance and intruder density. *The Auk*, 551-561.

Myers, J., Maron, J. L., & Sallaberry, M. (1985). Going to extremes: Why do Sanderlings migrate to the Neotropics? *Ornithological Monographs*, 520-535.

Myers, J. P., Williams, S., & Pitelka, F. (1980). An experimental analysis of prey availability

University of Ghana http://ugspace.ug.edu.gh

for sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. *Canadian Journal of Zoology, 58*(9), 1564-1574.

National Research Council. (1996). *Guide for the Care and Use of Laboratory Animals*. Washington DC: The National Academies Press.

Naughton-Treves, L., Holland, M. B., & Brandon, K. (2005). The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annu. Rev. Environ. Resour.*, *30*, 219-252.

Niles, L. J., Bart, J., Sitters, H. P., Dey, A. D., Clark, K. E., Atkinson, P. W., Baker, A. J., Bennett, K. A., Kalasz, K. S., & Clark, N. A. (2009). Effects of horseshoe crab harvest in Delaware Bay on Red Knots: are harvest restrictions working? *BioScience, 59*(2), 153-164.

Nol, E., MacCulloch, K., Pollock, L., & McKinnon, L. (2014). Foraging ecology and time budgets of non-breeding shorebirds in coastal Cuba. *Journal of Tropical Ecology, 30*(4), 347-357.

Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W., & Ratcliffe, L. M. (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*(1534), 59-64.

Ntiamoa-Baidu, Y. (1991a). Conservation of coastal lagoons in Ghana: the traditional approach. *Landscape and Urban Planning, 20*(1), 41-46.

Ntiamoa-Baidu, Y. (1991b). Seasonal changes in the importance of coastal wetlands in Ghana for wading birds. *Biological Conservation, 57*(2), 139-158.

Ntiamoa-Baidu, Y., & Gordon, C. (2000). Waterbird and wetland research and conservation in Ghana: a ten year perspective. *Ostrich, 71*(1-2), 95-95.

University of Ghana http://ugspace.ug.edu.gh

Ntiamoa-Baidu, Y., & Hepburn, I. R. (1988). Wintering waders in coastal Ghana. *RSPB Conserv. Rev, 2*, 85-88.

Ntiamoa-Baidu, Y., Nuoh, A. A., Reneerkens, J., & Piersma, T. (2014a). Population increases in non-breeding Sanderlings in Ghana indicate site preference. *Ardea, 102*(2), 131-138.

Ntiamoa-Baidu, Y., Nyame, S. K., & Nuoh, A. A. (2000). Trends in the use of a small coastal lagoon by waterbirds: Muni Lagoon (Ghana). *Biodiversity & Conservation, 9*(4), 527-539.

Ntiamoa-Baidu, Y., Owusu, E. H., Daramani, D. T., & Nuoh, A. A. (2001). Ghana. In: Fishpool, L. D. C. & Evans, M. I. (Eds.), *Important Bird Areas in Africa and associated islands: Priority sites for conservation*. Newbury and Cambridge, UK: Pisces Publications and BirdLife International, 376-389

Ntiamoa-Baidu, Y., Piersma, T., Wiersma, P., Poot, M., Battley, P., & Gordon, C. (1998). Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana. *Ibis, 140*(1), 89-103.

Ntiamoa-Baidu, Y., Quartey, J. K., & Nuoh, A. A. (2014b). Prey density explains seasonal patterns of occurrence of Sanderling *Calidris alba* on a sandy beach in Ghana [Abstract]. *Wader Study Group Bulletin, 121*(3), 213.

Ntiamoa-Baidu, Y., Quartey, J. K., Taye, E. N. A., & Nuoh, A. A. (2015). *Thriving in a diminishing world: waders of the Songhor Wetland in Ghana*. Paper presented at the Wader Study Group, Asbru, Iceland.

Nuka, T., Norman, C. P., Kuwabara, K., & Miyazaki, T. (2005). Feeding behaviour and effect of prey availability on Sanderling *Calidris alba* distribution on Kujukuri Beach. *Ornithological Science, 4*(2), 139-146.

Onrust, J., De Fouw, J., Oudman, T., Van Der Geest, M., Piersma, T., & van Gils, J. A. (2013).

University of Ghana http://ugspace.ug.edu.gh

Red knot diet reconstruction revisited: context dependence revealed by experiments at Banc d'Arguin, Mauritania. *Bird Study*, *60*(3), 298-307.

Oudman, T., Onrust, J., de Fouw, J., Spaans, B., Piersma, T., & van Gils, J. A. (2014). Digestive capacity and toxicity cause mixed diets in red knots that maximize energy intake rate. *The American Naturalist, 183*(5), 650-659.

Owusu, E. (2007). The ornithological importance of the Amansuri Community Nature Reserve in the Western Region of Ghana. *Journal of Science and Technology (Ghana), 27*(3), 72-85.

Owusu, E. H. (2014). *Ecological sensitivity of the Amanzule area.* Paper presented at the Community consultative workshop, Nkroful, Western Region, Ghana.

Parmar, T. K., Rawtani, D., & Agrawal, Y. (2016). Bioindicators: the natural indicator of environmental pollution. *Frontiers in life science, 9*(2), 110-118.

Pekkarinen, M. (1983). *Seasonal changes in condition and biochemical constituents in the soft part of Macoma balthica (Lamellibranchiata) in the Tvärminne brackish water area (Baltic Sea).* Paper presented at the Annales Zoologici Fennici.

Penrith, M., & Kensley, B. F. (1970). The Constitution of the Fauna of Rocky Intertidal Shores of South West Africa. Part 2 Rocky Point.

Petracci, P. F. (2002). Diet of sanderling in Buenos Aires province, Argentina. *Waterbirds, 25*(3), 366-370.

Pienkowski, M., & Evans, P. (1985). The role of migration in the population dynamics of birds. In: Sibly, R. M. & Smith, R. H. (Eds.), *Behavioural Ecology*. Blackwell, Oxford, 331-352

Piersma, T. (1987). Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. *Mar. Ecol. Prog. Ser.*, *38*, 187-196.

University of Ghana http://ugspace.ug.edu.gh

Piersma, T. (2007). Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology, 148*(1), 45.

Piersma, T. (2008). *Global Flyway Network: progress report for 2007* The Netherlands.

Piersma, T. (2011). From spoonbill to Spoon-billed Sandpiper: the perceptual dimensions to the niche. *Ibis, 153*(4), 659-661.

Piersma, T. (2012). What is habitat quality? Dissecting a research portfolio on shorebirds *Birds and habitat: relationships in changing landscapes*. Cambridge Cambridge University Press 383-407

Piersma, T., de Goeij, P., & Tulp, I. (1993). An evaluation of intertidal feeding habitats from a shorebird perspective: towards relevant comparisons between temperate and tropical mudflats. *Netherlands journal of sea research, 31*(4), 503-512.

Piersma, T., Dekinga, A., van Gils, J. A., Achterkamp, B., & Visser, G. H. (2003). Cost-benefit analysis of mollusc eating in a shorebird I. Foraging and processing costs estimated by the doubly labelled water method. *Journal of experimental biology, 206*(19), 3361-3368.

Piersma, T., & Lindström, Å. (2004). Migrating shorebirds as integrative sentinels of global environmental change. *Ibis, 146*(s1), 61-69.

Piersma, T., & Ntiamoa-Baidu, Y. (1995). *Waterbird ecology and the management of coastal wetlands in Ghana*. NIOZ-report 1995-6 Den Burg, The Netherlands.

Piersma, T., Rogers, D. I., González, P. M., Zwarts, L., Niles, L. J., de Lima Serrano do Nascimento, I., Minton, C., & Baker, A. J. (2005). Fuel storage rates before northward flights in Red Knots worldwide. *Birds of Two Worlds: the ecology and evolution of migration*, 262-273.

Piersma, T., van Aelst, R., Kurk, K., Berkhoudt, H., & Mass, L. R. M. (1998). A new pressure

University of Ghana http://ugspace.ug.edu.gh

sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? *Proc. R. Soc. B, 265*, 1377-1383.

Piersma, T., van Gils, J. A., De Goeij, P., & van Der Meer, J. (1995). Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. *J. Anim. Ecol., 64*, 493-504.

Powell, G. (1974). Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour, 22*(2), 501-505.

Prater, A. J., Marchant, J. H., & Vuorinen, J. (1977). Guide to the identification and ageing of Holarctic waders.

Quillfeldt, P., McGill, R. A. R., & Furness, R. W. (2005). Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Marine Ecology Progress Series, 295*, 295-304.

R Core Team. (2018). R: A language and environmental for statistical computing: R Foundation for Statistical Computing, Vienna, Australia. Retrieved from https://www.R-project.org/

Ramer, B. A. (1985). *Seasonal abundance, habitat use, and diet of selected shorebirds in Elkhorn Slough.* Calif. State University, Hayward.

Ramsar Convention. (1971). *Convention on Wetlands of International Importance especially as Waterfowl Habitat.* Retrieved from https://www.ramsar.org/search?search_api_views_fulltext=1971

Reading, C., & McGrorty, S. (1978). Seasonal variations in the burying depth of *Macoma balthica* (L.) and its accessibility to wading birds. *Estuarine and Coastal Marine Science, 6*(2), 135-144.

Rendón, M. A., Green, A. J., Aguilera, E., & Almaraz, P. (2008). Status, distribution and long-

University of Ghana http://ugspace.ug.edu.gh

term changes in the waterbird community wintering in Doñana, south–west Spain. *Biological Conservation, 141*(5), 1371-1388.

Reneerkens, J., Benhoussa, A., Boland, H., Collier, M., Grond, K., Günther, K., Hallgrimsson, G. T., Hansen, J., Meissner, W., de Meulenaer, B., Ntiamoa-Baidu, Y., Piersma, T., Poot, M., van Roomen, M., Summers, R. W., Tomkovich, P. S., & Underhill, L. (2009a). Sanderlings using African–Eurasian flyways: a review of current knowledge. *Wader Study Group Bulletin, 116*(1), 2-20.

Reneerkens, J., Grond, K., Koomson, E., Ntiamoa-Baidu, Y., & Piersma, T. (2009b). Why do some Sanderlings *Calidris alba* winter in the Wadden Sea while others prefer tropical beaches? *Limosa, 82*(3-4), 141-148.

Reneerkens, J., Versluijs, T. S., Piersma, T., Alves, J. A., Boorman, M., Corse, C., Gilg, O., Hallgrimsson, G. T., Lang, J., & Loos11, B. (2019). Low fitness at low latitudes: Wintering in the tropics increases migratory delays and mortality rates in an Arctic breeding shorebird. *J. Anim. Ecol., 00*, 1-13. doi: https://doi.org/10.1111/1365-2656.13118

Richards, A. J. (1988). *Shorebirds: a complete guide to their behaviour and migration*: Popular Culture Ink.

Roberts, G., & Evans, P. R. (1993). Responses of foraging sanderlings to human approaches. *Behaviour, 126*(1), 29-43.

Rogers, D. I., Battley, P., Piersma, T., van Gils, J. A., & Rogers, K. G. (2006). High-tide habitat choice: insights from modelling roost selection by shorebirds around a tropical bay. *Animal Behaviour, 72*, 563-575.

Rojas, L., McNeil, R., Cabana, T., & Lachapelle, P. (1999). Diurnal and nocturnal visual capabilities in shorebirds as a function of their feeding strategies. *Brain, behaviour and evolution, 53*(1), 29-43.

University of Ghana http://ugspace.ug.edu.gh

Rosa, S., Granadeiro, J. P., Vinagre, C., França, S., Cabral, H. N., & Palmeirim, J. M. (2008). Impact of predation on the polychaete *Hediste diversicolor* in estuarine intertidal flats. *Estuarine, Coastal and Shelf Science, 78*(4), 655-664.

Rose, P. M., & Scott, D. A. (1994). *Waterfowl population estimates*. Slimbridge, UK: IWRB Publication 29.

Rose, P. M., & Scott, D. A. (1997). *Waterfowl Population Estimates* (Second ed.). Wageningen, The Netherlands: Wetlands International Publ. 44.

Rouse, G., & Pleijel, F. (2001). *Polychaetes*: Oxford university press.

Rumohr, H., Brey, T., & Ankar, S. (1987). *A compilation of biometric conversion factors for benthis invertebrates of the Baltic Sea*: Institut für Meereskunde.

Ruthrauff, D. R., Gill, R. E., & Tibbitts, T. L. (2013). Coping with the cold: an ecological context for the abundance and distribution of Rock Sandpipers during winter in the upper Cook Inlet, Alska. *Arctic, 66*, 269-278. doi: 10.14430/arctic4306

Ryan, J. M., & Ntiamoa-Baidu, Y. (2000). Biodiversity and ecology of coastal wetlands in Ghana. *Biodiversity and Conservation, 9*(4), 445-446.

Sagar, P., Shankar, U., & Brown, S. (1999). Distribution and numbers of waders in New Zealand, 1983-1994. *Notornis, 46*, 1-44.

Sarukhan, J., Whyte, A., Hassan, R., Scholes, R., Ash, N., Carpenter, S., Pingali, P., Bennett, E., Zurek, M., & Chopra, K. (2005). Millenium ecosystem assessment: Ecosystems and human well-being.

Scheiffarth, G. (2001). The diet of Bar-tailed Godwits *Limosa lapponica* in the Wadden Sea: combining visual observations and faeces analyses. *Ardea, 89*(3), 481-494.

Serra, L., Clark, N. A., & Clark, J. A. (2006). Primary moult, body mass and migration of Grey Plovers *Pluvialis squatarola* in Britain. *Ibis, 148*(2), 292-301.

University of Ghana http://ugspace.ug.edu.gh

Sih, A., & Christensen, B. (2001). Optimal diet theory: when does it work, and when and why does it fail? *Animal Behaviour, 61*(2), 379-390.

Silliman, J., Mills, G. S., & Alden, S. (1977). Effect of flock size on foraging activity in wintering sanderlings. *The Wilson Bulletin*, 434-438.

Skagen, S. K. (2006). Migration stopovers and the conservation of arctic-breeding calidridine sandpipers. *The Auk, 123*(2), 313-322.

Skalski, G. T., & Gillman, J. F. (2001). Functional responses with predator inferences: viable alternatives to the Holling type II model. *Ecology, 82*, 3083-3092.

Smallegange, I. M., & van der Meer, J. (2010). Testing a stochastic version of the Beddington–DeAngelis functional response in foraging shore crabs. *Marine biology, 157*(5), 1027-1040.

Smeets, W. (2010). Vogelkoppenknipsels Nummer 57. *Het vogeljaar, 58*(1), 28-31.

Soloviev, M. Y., & Tomkovich, P. S. (1995). Biometrics of Sanderlings *Calidris alba* from the Taimyr. *Ringing & Migration, 16*(2), 91-99.

Soloviev, M. Y., & Tomkovich, P. S. (1997). Body mass changes in waders (Charadrii) in a high arctic area at northern Taimyr, Siberia. *Journal of Ornithology, 138*(3), 271-281.

Sorice, M. G., Shafer, C. S., & Ditton, R. B. (2006). Managing endangered species within the use–preservation paradox: The Florida manatee (*Trichechus manatus latirostris*) as a tourism attraction. *Environmental Management, 37*(1), 69-83.

Spaans, B. (2006). Survival and behaviour in shorebirds wintering on the Banc d’Arguin, Mauritania: Progress-report 2002–2005.

Stanley, S. M. (1970). *Relation of shell form to life habits of the Bivalvia (Mollusca)* (Vol. 125): Geological Society of America.

University of Ghana http://ugspace.ug.edu.gh

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton: Princeton University Press.

Stillman, R., Goss-Custard, J., & Caldow, R. (1997). Modelling interference from basic foraging behaviour. *Journal of Animal Ecology*, 692-703.

Stroud, D. A., Davidson, N., West, R., Scott, D., Haanstra, L., Thorup, O., Ganter, B., & Delany, S. (2004). *Status of migratory wader populations in Africa and Western Eurasia in the 1990s*: International Wader Study Group.

Summers, R. (1986). Breeding production of dark-bellied brent geese *Branta bernicla bernicla* in relation to lemming cycles. *Bird Study, 33*(2), 105-108.

Summers, R., & Underhill, L. (1987). Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. *Bird Study, 34*(2), 161-171.

Summers, R., Underhill, L., & PrysJones, R. (1995). Why do young waders in southern Africa delay their first return migration to the breeding grounds? *Ardea, 83*(2), 351-357.

Summers, R., Underhill, L., Waltner, M., & Whitelaw, D. (1987). Population, biometrics and movements of the Sanderling *Calidris alba* in southern Africa. *Ostrich, 58*(1), 24-39.

Sutherland, T., Shepherd, P., & Elner, R. (2000). Predation on meiofaunal and macrofaunal invertebrates by western sandpipers (*Calidris mauri*): evidence for dual foraging modes. *Marine biology, 137*(5-6), 983-993.

Sutherland, W. J. (1983). Aggregation and theideal free'distribution. *The Journal of Animal Ecology*, 821-828.

Sutherland, W. J., Newton, I., & Green, R. (2004). *Bird ecology and conservation: a handbook of techniques*. US: Oxford University Press.

Sutton, M., Pitcairn, C., Whitfield, C., Leith, I., Sheppard, L., van Dijk, N., Tang, S., Skiba,

University of Ghana http://ugspace.ug.edu.gh

U., Smart, S., & Mitchell, R. (2004). *Bioindicator and biomonitoring methods for assessing the effects of atmospheric nitrogen on statutory nature conservation sites*. JNCC, 232.

Svanbäck, R., & Bolnick, D. I. (2005). Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evolutionary Ecology Research, 7*(7), 993-1012.

Thomas, K., Kvitek, R. G., & Bretz, C. (2003). Effects of human activity on the foraging behaviour of sanderlings *Calidris alba*. *Biological Conservation, 109*(1), 67-71.

Tjørve, K. M., Underhill, L. G., & Visser, G. H. (2008). The energetic implications of precocial development for three shorebird species breeding in a warm environment. *Ibis, 150*(1), 125-138.

Tregenza, T. (1995). Building on the ideal free distribution. *Advances in Ecological Research, 26*, 253-307.

Tsipoura, N., & Burger, J. (1999). Shorebird diet during spring migration stopover on Delaware Bay. *Condor*, 635-644.

Turner, S. J. (1980). Draft Environmental Report on Ghana: US Man and the Biosphere Secretariat, Department of State (Washington, DC).

Underhill, L., & Summers, R. (1993). Relative masses of primary feathers in waders. *Wader Study Group Bull, 71*, 29-31.

UNEP/GPA. (July 2006). *The State of the Marine Environment: Regional Assessment*. United Nations Environment Programme, Global Programme of Action The Hague, 60.

van de Kam, J., Ens, B., Piersma, T., & Zwarts, L. (2004). *Shorebirds: an illustrated behavioural ecology*: Brill.

van den Hout, P. J., Mathot, K. J., Maas, L. R. M., & Piersma, T. (2010). Predator escape

University of Ghana http://ugspace.ug.edu.gh

tactics in birds: linking ecology and aerodynamics. *Behavioural Ecology, 21*, 16-25.

van den Hout, P. J., Spaans, B., & Piersma, T. (2008). Differential mortality of wintering shorebirds on the Banc d'Arguin, Mauritania, due to predation by large falcons. *Ibis, 150* 219-230.

van den Hout, P. J., van Gils, J. A., Robin, F., van Der Geest, M., Dekinga, A., & Piersma, T. (2014). Interference from adults forces young red knots to forage for longer and in dangerous places. *Animal Behaviour, 88*, 137-146.

Van der Meer, J. (1992). Statistical analysis of the dichotomous preference test. *Animal Behaviour, 44*(6), 1101-1106.

van Der Meer, J., & Ens, B. J. (1997). Models of interference and their consequences for the spatial distribution of ideal and free predators. *Journal of Animal Ecology*, 846-858.

van Gils, J. A. (2004). *Foraging decisions in a digestively constrained long-distance migrant, the red knot (Calidris canutus)*: Rijksuniversiteit Groningen.

van Gils, J. A., Battley, P. F., Piersma, T., & Drent, R. (2005a). Reinterpretation of gizzard sizes of red knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. *Proceedings of the Royal Society B: Biological Sciences, 272*(1581), 2609-2618.

van Gils, J. A., Lisovski, S., Lok, T., Meissner, W., Ożarowska, A., de Fouw, J., Rakhimberdiev, E., Soloviev, M. Y., Piersma, T., & Klaassen, M. (2016). Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science, 352*(6287), 819-821.

van Gils, J. A., & Piersma, T. (2004). Digestively constrained predators evade the cost of interference competition. *Journal of Animal Ecology, 273,* 386-398.

van Gils, J. A., Piersma, T., Dekinga, A., & Dietz, M. W. (2003a). Cost-benefit analysis of

University of Ghana http://ugspace.ug.edu.gh

mollusc-eating in a shorebird II. Optimizing gizzard size in the face of seasonal demands. *Journal of experimental biology, 206*(19), 3369-3380.

van Gils, J. A., Rooij, S. R. D., Van Belle, J., Van Der Meer, J., Dekinga, A., Piersma, T., & Drent, R. (2005b). Digestive bottleneck affects foraging decisions in red knots *Calidris canutus.* I. Prey choice. *Journal of Animal Ecology, 74*(1), 105-119.

van Gils, J. A., Schenk, I. W., Bos, O., & Piersma, T. (2003b). Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. *American naturalist*, *161*, 777-793.

van Gils, J. A., Spaans, B., Dekinga, A., & Piersma, T. (2006). Foraging in a tidally structured environment by red knots (*Calidris canutus*): ideal, but not free. *Ecology, 87*(5), 1189-1202.

van Roomen, M., Delany, S., Dodman, T., Fishpool, L., Nagy, S., Ajagbe, A., Citegetse, G., & Ndiaye, A. (2014). *Waterbird and site monitoring along the Atlantic coast of Africa: strategy and manual*. BirdLife International, Cambridge, United Kingdom, Common Wadeen Sea Seretariat, Wilhelmshaven, Germany, and Wetlands International, Wageningen, The Netherlands.

van Roomen, M., Nagy, S., Foppen, R., Dodman, T., Citegetse, G., & Ndiaye, A. (2015). *Status of coastal waterbird populations in the East Atlantic Flyway* Programme Rich Wadden Sea, Leeuwarden, The Netherlands, Sovon, Nijmegen, The Netherlands, Wetlands International, Wageningen, The Netherlands, BirdLife International, Cambridge, United Kingdom &, Wadden Sea Secretariat, Wilhelmshaven, Germany.

Vanermen, N., Stienen, E. W. M., De Meulenaer, B., Van Ginderdeuren, K., & Degraer, S. (2009). Low dietary importance of polychaetes in opportunistic feeding Sanderlings *Calidris alba* on Belgian beaches. *Ardea, 97*(1), 81-87.

Verkuil, Y., & Burg, D. (1996). Stomach-pumping of waders does not necessarily provide

University of Ghana http://ugspace.ug.edu.gh

more information on diet than faecal analysis. *BULLETIN-WADER STUDY GROUP*, *79*, 60-63.

Verlinden, C., & Wiley, R. H. (1989). The constraints of digestive rate: an alternative model of diet selection. *Evolutionary Ecology*, *3*(3), 264-272.

Vines, G. (1992). Florida shorebird forced to flee. *New Scientist*, *134*, 14.

Visser, M. E., Perdeck, A. C., van Balen, J. H., & Both, C. (2009). Climate change leads to decreasing bird migration distances. *Global Change Biology*, *15*(8), 1859-1865.

Vucetich, J. A., Peterson, R. O., & Schaefer, C. L. (2002). The effect of prey and predator densities on wolf predation. *Ecology*, *83*, 3003-3013.

Wacasey, J., & Atkinson, E. (1987). Energy values of marine benthic invertebrates from the Canadian Arctic. *Marine Ecology Progress Series*, 243-250.

Waltner, M. (1976). Moult in Palaearctic waders. *Safring News*, *5*, 14-16.

Wanink, J. H., & Zwarts, L. (2001). Rate-maximizing optimality models predict when oystercatchers exploit a cohort of the bivalve *Scrobicularia plana* over a 7-year time span. *Journal of Animal Ecology*, *70*(1), 150-158.

Weber, L. M., & Haig, S. M. (1997). Shorebird Diet and Size Selection of Nereid Polychaetes in South Carolina Coastal Diked Wetlands (Dieta de Playeros y Seleccion del Tamaño de Poliquetos en Areas Anegadas Formadas por Diques en Carolina del sur). *Journal of Field Ornithology*, 358-366.

Wetlands International. (2012). *Waterbird Population Estimates, Fifth Edition. Summary Report* Wetland International, Wageningen, The Netherlands.

Wilson, D. J., & Bromley, R. G. (2001). Functional and numerical responses of predators to cyclic lemming abundance: effects on loss of goose nests. *Canadian Journal of Zoology*, *79*(3), 525-532.

University of Ghana http://ugspace.ug.edu.gh

Wilson, W. H. J. (1990). Relationship between Prey Abundance and Foraging Site Selection by Semipalmated Sandpipers on a Bay of Fundy Mudflat (Relación entre la Abundancia de Presas y la Selección del Lugar de Forrajeo por parte de Calidris pusilla en un Lodazal de la Bahía de Fundy). *Journal of Field Ornithology*, 9-19.

Wood, A. (1987). Discriminating the sex of Sanderling *Calidris alba:* some results and their implications. *Bird Study, 34*(3), 200-204.

Wootton, J. T. (1997). Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecological monographs, 67*(1), 45-64.

WORMS. (2018a). *Agaronia acuminata* (Lamarck, 1811). from http://www.marinespecies.org/aphia.php?p=taxdetails&id=225436. Retrieved 23 May, 2018

WORMS. (2018b). *Donax* (*Donax*) *pulchellus* Hanley, 1843. from http://www.marinespecies.org/aphia.php?p=taxdetails&id=724666.

WORMS. (2018c). *Donax rugosus* Linnaeus, 1758. from http://www.marinespecies.org/aphia.php?p=taxdetails&id=224557.

WORMS. (2018d). *Emerita talpoida* Say, 1817. from http://www.marinespecies.org/aphia.php?p=taxdetails&id=158393.

WORMS. (2018e). *Excirolana chiltoni,* Richardson, 1905. from http://www.marinespecies.org/aphia.php?p=taxdetails&id=258416.

WORMS. (2018f). *Glycera* Lamarck, 1818. from http://www.marinespecies.org/aphia.php?p=taxdetails&id=129296.

WORMS. (2018g). *Hastula aciculina* (Lamarck, 1822). from http://www.marinespecies.org/aphia.php?p=taxdetails&id=224499.

WORMS. (2018h). *Nereis* Linnaeus, 1758. from

University of Ghana http://ugspace.ug.edu.gh

http://www.marinespecies.org/aphia.php?p=taxdetails&id=129379.

Yang, H.-Y., Chen, B., Ma, Z.-j., Hua, N., van Gils, J. A., Zhang, Z.-W., & Piersma, T. (2013). Economic design in a long-distance migrating molluscivore: how fast-fuelling red knots in Bohai Bay, China, get away with small gizzards. *Journal of experimental biology, 216*(19), 3627-3636.

Yasué, M. (2005). The effects of human presence, flock size and prey density on shorebird foraging rates. *Journal of Ethology, 23*(2), 199-204.

Yasué, M., Dearden, P., & Moore, A. (2008). An approach to assess the potential impacts of human disturbance on wintering tropical shorebirds. *Oryx, 42*(3), 415-423.

Yates, M. G., Stillman, R. A., & Goss-Custard, J. D. (2000). Contrasting interference functions and foraging dispersion in two species of shorebird (Charadrii). *Journal of Animal Ecology, 69*(2), 314-322.

Zwarts, L. (1985). The winter exploitation of fiddler crabs *Uca tangeri* by waders in Guinea-Bissau. *Ardea, 73*(1), 3-12.

Zwarts, L., Blomert, A., -M, & Hupkes, R. (1990a). Increase in feeding time in waders preparing for spring migration from the Banc d'Arguin, Mauritania. *Ardea, 78*, 237-256.

Zwarts, L., Ens, B. J., Kersten, M., & Piersma, T. (1990b). Moult, mass and flight range of waders ready to take off for long-distance migrations. *Ardea, 78*(2), 339-364.

Zwarts, L., & Wanink, J. H. (1991). The macrobenthos fraction accessible to waders may represent marginal prey. *Oecologia, 87*(4), 581-587.

Zwarts, L., & Wanink, J. H. (1993). How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands journal of sea*

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*research, 31*(4), 441-476.

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# APPENDIX: LOCATIONS OF THE 27 SAMPLING POINTS ALONG THE ESIAMA BEACH

| Location | Latitude | Longitude | Village |
|---|---|---|---|
| E001 | 4.9415 | -2.38055 | Azuleloanu/ Amansuri |
| E002 | 4.939767 | -2.37638 | |
| E003 | 4.938533 | -2.37203 | |
| E004 | 4.9373 | -2.3677 | |
| E005 | 4.935883 | -2.36342 | |
| E006 | 4.9344 | -2.35915 | |
| E007 | 4.932833 | -2.35493 | Esiama |
| E008 | 4.93145 | -2.35065 | Esiama |
| E009 | 4.92995 | -2.3464 | Esiama |
| E010 | 4.928633 | -2.34208 | |
| E011 | 4.927217 | -2.33782 | |
| E012 | 4.925533 | -2.33363 | |
| E013 | 4.92405 | -2.32937 | |
| E014 | 4.922617 | -2.3251 | Kikam |
| E015 | 4.920733 | -2.321 | |
| E016 | 4.919067 | -2.31682 | Asemko |
| E017 | 4.917217 | -2.31272 | Asemko |
| E018 | 4.915417 | -2.30858 | Asemko |
| E019 | 4.913833 | -2.30437 | |
| E020 | 4.912183 | -2.30017 | Bobrama |
| E021 | 4.910417 | -2.296 | |
| E022 | 4.908633 | -2.29187 | Asanta |
| E023 | 4.90695 | -2.28768 | |
| E024 | 4.905017 | -2.28362 | |
| E025 | 4.903117 | -2.27953 | |
| E026 | 4.900933 | -2.27558 | |
| E027 | 4.899217 | -2.27143 | Ankobra |