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Small pelagics, predatory fish and seabirds: trophic and behavioural interactions in a marine protected area in Guinea-Bissau

Doutoramento em Biologia e Ecologia das Alterações Globais
Especialidade em Biologia e Ecologia Tropical

Edna Rita de Freitas da Costa Correia

Tese orientada por:
José Pedro Granadeiro
Paulo Catry

Documento especialmente elaborado para a obtenção do grau de doutor

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Nota prévia

A presente tese apresenta artigos científicos já publicados, submetidos ou ou em preparação para publicação (capítulos 2 a 6), de acordo com o previsto no nº 2 do artigo 25º do Regulamento de Estudos de Pós-Graduação da Universidade de Lisboa, publicado no Diário da República, 2.ª série — N.º 57 — 23 de Março de 2015. Uma vez que estes trabalhos foram realizados em colaboração o candidato esclarece que participou integralmente na conceção dos trabalhos, obtenção dos dados, análise e discussão dos resultados, bem como na redação dos manuscritos.

Lisboa, Junho de 2018

Edna Rita de Freitas da Costa Correia

> “*Crer é errar. Não crer de nada serve*.”
>
> Ricardo Reis

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RESUMO

A biodiversidade marinha tem sofrido rápidos e significativos declínios, sobretudo devido à sobrepesca e às alterações globais, o que tem afectado o funcionamento dos ecossistemas marinhos por todo o mundo. Conhecer as dinâmicas das redes tróficas é assim essencial para o desenvolvimento de acções eficientes para a gestão dos ecossistemas. Na África Ocidental, este conhecimento é ainda mais urgente, uma vez que muitas populações de stocks pesqueiros estão em colapso e as populações locais dependem grandemente da pesca e do peixe para sobreviver.

A presente tese estuda as interacções tróficas da comunidade marinha do Arquipélago dos Bijagós, Guiné-Bissau. Os extensos mangais e zonas de vasa intertidal que este arquipélago continental contém, fazem dele uma área de extrema importância para uma variedade de espécies migradoras (e.g. tartarugas marinhas, aves limícolas), de espécies residentes (e.g. aves marinhas), e também como berçário de várias espécies de peixes. O seu grande valor em termos de biodiversidade levou os Bijagós a serem declarados Reserva Biosfera pela UNESCO em 1996 e sítio Ramsar em 2014. Ainda assim, poucos estudos foram realizados no seu ecossistema marinho.

Neste trabalho foram estudadas as variações entre estações, ciclos lunares e ciclos diários na comunidade dos pequenos peixes pelágicos costeiros do Arquipélago dos Bijagós. Para isso foram efectuadas pescas com rede de xávega de modo a cobrir ambas as épocas e em diferentes ilhas. Foi estudada a dieta e comportamento alimentar de predadores marinhos (peixes predadores e aves marinhas), com especial interesse nas associações facilitativas alimentares. Para o estudo da dieta foram usados métodos tradicionais, como a identificação macroscópica de restos de presas presentes nos conteúdos estomacais de peixes predadores ou nas egragópilas de aves marinhas nidificantes. Foram também usados métodos de *next-generation sequencing* aplicando DNA metabarcoding na identificação de presas nos dejectos de aves marinhas invernantes. Esta foi a primeira vez que este método foi usado para o estudo da dieta de aves marinhas migradoras nos seus locais de invernada. Foram também realizadas observações comportamentais de aves marinhas para o estudo dos seus hábitos alimentares. Devido à falta de estudos da relação comprimento-peso para determinados peixes, esta relação foi calculada para seis espécies.

O presente estudo mostrou que o ecossistema marinho dos Bijagós é fortemente dominado por uma espécie de pequeno pelágico, a *Sardinella maderensis.* Esta espécie foi a mais abundante ao longo do ano e em todas as ilhas. Foi também a espécie mais frequente na dieta de todos os predadores marinhos estudados. Em relação ao comportamento alimentar facilitativo, as diferentes espécies de aves marinhas mostraram distintos graus de dependência destas associações, variando entre completamente independente a quase obrigatória. Os resultados sugerem que o uso de associações influencia a distribuição das aves marinhas e pode aumentar o seu sucesso alimentar. Os resultados globais deste trabalho indicam que o ecossistema marinho do Arquipélago dos Bijagós é do tipo *wasp-waist*, com a *Sardinella maderensis* como espécie de pequeno pelágico chave. Assim, para uma conservação eficiente do arquipélago, deve ser considerada uma abordagem de gestão ao nível do ecossistema. Diminuições das populações tanto de peixes predadores como de pequenos pelágicos são igualmente susceptíveis a influenciar a distribuição e sucesso alimentar das aves marinhas, com impacto na sua sobrevivência e sucesso reprodutor.

Palavras-chave: Clupeidae, predadores marinhos, interacções tróficas, África Ocidental, Arquipélago dos Bijagós

ABSTRACT

Rapid and significant declines in marine biodiversity, caused by overfishing and global changes, are affecting the functioning of marine ecosystems worldwide. Understanding food-web dynamics is essential for the development of efficient ecosystem management actions. In West Africa, knowledge of food-web dynamics is particularly urgent given that fish stocks are collapsing and fisheries sustain the livelihoods of a significant part of the human population.

This thesis addresses the trophic interactions of the marine community of the Bijagós Archipelago, Guinea-Bissau. The extensive mangroves and mudflats of this continental archipelago make it an important area for several migratory species (e.g. marine turtles, waders) and resident species (e.g. seabirds), as well as a nursery area for several fish species. The great biodiversity value of the Bijagós led it to be declared as UNESCO Biosphere Reserve in 1996 and a Ramsar site in 2014. Nevertheless, few studies have been conducted in its marine ecosystem.

Seasonal, lunar tidal and diel variations of the coastal small fish community of the Bijagós Archipelago were studied through beach seining along spatial and temporal scales. The diet and foraging behaviour of marine predators (predatory fishes and seabirds) was also studied, with particular interest in their facilitative feeding associations. Traditional methods were used for diet description, such as, the macroscopic identification of prey remains from stomach contents of predatory fish and pellets of breeding seabirds. We also used next-generation sequencing, employing DNA metabarcoding on the identification of prey in the droppings of wintering seabirds. This was the first time this method was used for studying the feeding ecology on migratory birds in their wintering quarters. Additionally, behavioural focal observations of seabirds were performed to investigate their feeding habits. Given the lack of previous descriptive studies, this work also focuses the particularities of length-weight relationships of six fish species.

The present study showed that the marine ecosystem of the Bijagós is strongly dominated by a small pelagic fish species, *Sardinella maderensis*. This species was the most abundant throughout the year as well as in all the islands, and the most frequent item in the diet of all marine predators. In regards to facilitative foraging, different species of seabirds showed distinctive degrees of reliance on associations, ranging from completely independent to near-obligatory. The results also suggest that the use of associations influences the distribution of seabird species and may enhance their foraging success. The overall findings presented here indicate that the marine ecosystem of the Bijagós Archipelago is a *wasp-waist* type, with *Sardinella maderensis* as the key small pelagic species, and that an ecosystem-based approach must be considered for the adequate management of the archipelago. Declines in populations of predatory fish and small pelagic fish are both likely to influence the distribution and foraging success of seabirds, with impacts on their survival and breeding success.

Keywords: Clupeidae, marine predators, trophic interactions, facilitative behaviour, West Africa, Bijagós Archipelago

CHAPTER 1

General introduction

CHAPTER 1

General introduction

Drastic declines in biodiversity have been observed worldwide in recent years (e.g. Pereira et al. 2010, Butchart et al. 2014). In marine environments, biodiversity loss is rapidly affecting all taxa as well as the functioning of ecosystems (Cury et al. 2000, Tasker et al. 2000, Barbraud and Weimerskirch 2003, Myers and Worm 2003, Hutchings and Baum 2005). More than 80% of global fisheries are considered fully exploited, over-fished or depleted (FAO 2016). The depletion of resources caused by fisheries as well as by the effects of global changes is altering the dynamics of marine communities (Crespo and Dunn 2017).

Geographic framework

Tropical regions are prominently represented among the many important marine ecosystems experiencing disturbances even before their main components and interactions have been studied (Halpern et al. 2008, Stramma et al. 2008, Ferretti et al. 2010). The coast of Guinea-Bissau is an example of one of such regions, where the functioning of marine ecosystems is very poorly understood even though their relevance is internationally recognised (Dodman and Sá 2005, Campredon and Catry 2016).

Guinea-Bissau is located in the tropical Eastern Central Atlantic at the southern edge of one of the world's major upwelling systems, the Canary Current. This system presents high plankton production, which supports high biodiversity and biomass of marine species, particularly pelagic fish (Longhurst and Pauly 1987, Bakun 1996). Guinea-Bissau is a small country highly dependent on its natural resources. Fisheries are one of its main economic activities (Lafrance 1994, Campredon and Cuq 2001) and fish is the main source of protein for the population (Dia and Bedingar 2001, Njock and Westlund 2010). Despite increasing fishing pressure caused by the depletion of resources in neighbouring countries, Guinea-Bissau still holds important and abundant fish populations, in part due to governmental efforts for the conservation of marine biodiversity (Cuq 2001). The high relevance of Guinea-Bissau to marine resources is also strongly connected to its shallow coastal platform and the presence of a group of about 88 islands and islets, known as the Bijagós Archipelago.

The Bijagós islands form a continental archipelago that constitutes the only active deltaic archipelago on the Atlantic coast of Africa (Pennober 1999). It holds highly diverse habitats, such as extensive mangroves and mud flats that harbour substantial biodiversity, with global importance for the conservation of several species. The Bijagós support several migratory species that come from all over the world to breed here (e.g. marine turtles, Catry et al. 2009, Patrício et al. 2017) or to winter (e.g. waders and seabirds, Salvig et al. 1993, van Roomen et al. 2015), as well as for several resident species (e.g. seabirds, van Roomen et al. 2015). It is as well an important nursery area for several fish species (Arkhipov et al. 2015). The great biodiversity value of the archipelago led it to be declared as UNESCO Biosphere Reserve in 1996 and a Ramsar site in 2014. Due to its shallow waters and protected marine areas, the Bijagós are free from industrial fishing and represent one of the last refuges in West Africa for large predatory fishes. Still, artisanal fleets from neighbouring countries have been increasing in the archipelago with negative impacts for the local fish communities (Kaczynski and Fluharty 2002, Kyle 2009, Njock and Westlund 2010, Campredon and Catry 2016). A specific example of this pressure is the enduring illegal capture of sharks for their fins for the Asian market (Tous et al. 1998, Campredon and Cuq 2001, Binet et al. 2012). Therefore, the Bijagós Archipelago, due to its location and diversity of habitats, is unique in the world and represents an extremely important area for biodiversity conservation in a region that is being strongly damaged by global change and anthropogenic pressure (Alder and Sumaila 2004).

Trophic interactions

Knowledge of trophic interactions is required to understand food-web dynamics and develop ecosystem-based management approaches (Myers and Worm 2003, Frank et al. 2005, Behrenfeld et al. 2006, Ferretti et al. 2010, Katsanevakis et al. 2011). Moreover, understanding the trophic interactions of dominant species give a broad view of the functioning of communities (Frank et al. 2005). Furthermore, information about the diet and foraging behaviour of the upper-trophic-level species on a food web may reflect the abundance and distribution of their prey, therefore indicating the state of the ecosystem (Sih et al. 1998, Petchey 2000, Duffy et al. 2007, Schmitz 2007). In marine ecosystems the predator-prey interactions of the upper-trophic-level predators, such as predatory fishes and seabirds, may be used as indicators to perceive such changes in the ecosystem (Furness and Camphuysen 1997). For several of these predators, their main food sources are small pelagic fishes. The latter play thus a crucial role in their distribution and abundance. Consequently, fluctuations in small pelagic populations may affect the structure and functioning of whole ecosystems (e.g. Cury et al. 2000, Shannon et al. 2000).

Alongside with predator-prey trophic interactions, predator-predator interactions also influence the functioning of ecosystems. One type of such trophic interactions is the association between aerial and subsurface marine predators. In these associations, subsurface predators push small pelagic fish toward the surface, making it available as prey for many seabird species (Clua and Grosvalet 2001). Such facilitative associations may influence the diet and foraging range of all predator species involved (Ballance and Pitman 1999, Veit and Harrison 2017). In tropical regions, where resources are more unevenly distributed and large predatory fishes are more abundant than in temperate and polar regions, facilitative associations are more frequent (Longhurst and Pauly 1987, Ballance and Pitman 1999, Veit and Harrison 2017) and seabirds seem to be more dependent on them (Ballance and Pitman 1999). To a large extent, the complex structure of many marine tropical ecosystems arises from a healthy community of subsurface predators associating with seabirds in a rather predictable way. Such networks of dependencies imply that declines in large subsurface predators (e.g. due to fisheries) have the potential to affect other members of the community.

Therefore, understanding the feeding habits and interactions of such important elements of marine ecosystems is crucial to determine the main conditions needed for their conservation.

Previous research on our study area

Little research has been conducted in the study area addressing the themes focused here. Concerning the fish community, the most abundant species belong to the Perciformes and Clupeiformes orders, from which Clupeidae, Gerreidae, Haemulidae and Mugilidae families stand out in abundance (Lafrance 1994, van der Veer et al. 1995). The species of fish that dominate the ecosystem seem to remain largely unchanged throughout the year and along the seasons (Lafrance 1994). The Bijagós Archipelago is known to support important numbers of terns, although recent detailed counts are lacking. Among the nesting seabirds in the archipelago, Royal (*Thalasseus maximus*) and Caspian (*Hydroprogne caspia*) terns are the most numerous, counting up to around 20 000 couples (Veen et al. 2008), which represents a significant part of the breeding populations of these species in West Africa (Wetlands International 2015; van Roomen et al. 2015). The Bijagós Archipelago is also recognized as an important wintering area for birds, holding, together with other coastal islands from Guinea-Bissau, one million Afro-Palearctic migratory shorebirds during this season (Veen et al. 2008). For seabird species (Laridae) in particular, wintering numbers were estimated in 1992/1993 to be c.a. 34 000 individuals in the archipelago (Dodman and Sá 2005). The most numerous species were the ones studied in this thesis: Little, Lesser Crested, Sandwich, Common and Black terns. Apart from one study on the foraging behaviour of three tern species (Sterninae), focusing mostly on food intake rates (Brenninkmeijer et al. 2002), no studies had been done in our study area concerning the diet or foraging behaviour of predatory fishes and seabirds. However, a recent study on the diet of nesting Royal and Caspian terns in Mauritania (West Africa), based on fish otoliths identification, showed Sparidae as the most frequent prey for Royal tern and Mugilidae and Gobiidae for Caspian tern (Veen et al. 2018).

Concerning the predatory fishes, few studies have addressed the foraging ecology of Crevalle jack (*Caranx hippos*), the West African Spanish mackerel (*Scomberomorus tritor*) and the Guinean barracuda (*Sphyraena afra*) in West Africa. However, it is known that Clupeiformes are important prey in the diet of jacks, mackerels and barracudas (Fagade and Olaniyan 1973, Kwei 1978, Akadje et al. 2013).

This thesis provides detailed and robust study on the diet of ten abundant marine predators in the Bijagós Archipelago. Furthermore, it is the first study using DNA metabarcoding techniques to describe the diet of migratory birds in their wintering quarters in a completely non-invasive way to the birds.

This thesis gives new insight into the dynamics of a marine community that, albeit protected, is understudied and located in a larger region facing unprecedented depletion of resources (Belhabib et al. 2016, Polidoro et al. 2017).

Work goals

The general objective of this work was to assess the ecological significance of the relationships between schooling pelagic fish and their fish and avian predators, with relevance for the management of a West African Marine Protected Area and the conservation of migratory seabirds. Fieldwork was performed mostly in the Bijagós Archipelago, Guinea-Bissau, from 2014 to 2016, covering two dry seasons (2014/2015 and 2015/2016) and two rainy seasons (2015 and 2016).

To achieve the overall goal, I developed a study approach to tackle three main objectives, which are the basis for the five chapters in this thesis:

1. Characterise the communities of small pelagic fishes, and their spatial and temporal variation.

2. Describe the diet of the most abundant predatory fishes and seabirds.

3. Assess the factors responsible for variations in diet and foraging techniques of seabirds, with particular interest on feeding associations with predatory fish.

Papers presented

This thesis compiles a series of five papers (two published, one submitted and two manuscripts), each corresponding to a chapter (Chapters 2–6). These chapters are preceded by a general introduction to the topics focused in the papers (Chapter 1) and followed by a general discussion, where the most important findings are integrated and debated (Chapter 7).

Chapter 2

Edna Correia, José Pedro Granadeiro, Aissa Regalla, Paulo Catry. ***Seasonal, lunar and diel variations in a coastal fish community dominated by*** **Sardinella maderensis** ***in the Bijagós Archipelago, West Africa***

In this chapter I described the dynamics of a coastal small pelagic fish community. In the Eastern Central Atlantic region, where my study took place, small pelagic fishes are the most important group for fisheries, constituting almost 50% of the landings (Failler 2014, FAO 2016). Nonetheless, despite its high importance in the region, and particularly in the Bijagós Archipelago, recent studies on marine communities of small pelagics are inexistent. This knowledge gap needed to be urgently addressed in the João Vieira and Poilão Marine National Park, as understanding the functioning of coastal marine ecosystems is fundamental for their management. In order to understand the dynamics of the coastal small pelagic community, I performed beach seine fishing in different islands and periods of the year.

Chapter 3

Edna Correia, José Pedro Granadeiro, Aissa Regalla, Paulo Catry (2018) ***Length-weight relationship of fish species from the Bijagos Archipelago, Guinea-Bissau***. Journal of Applied Ichthyology. 34 (1): 177-179

In this chapter, I calculated the length–weight relationships for six fish species. For three of these fish species, this relationship was never reported before (*Citharichthys stampflii, Gerres nigri* and *Psettodes belcheri*) and for the other three species, I presented data from a wider range of sizes compared to previous reports (*Eucinostomus melanopterus, Scomberomorus tritor* and *Sphyraena afra*). Length–weight relationship data are relevant for the management of fish species as well as for fisheries. Such models enable the comparison of fish populations across space (i.e. different areas) or time (e.g. different seasons or years), and also provide information concerning variation in the overall structure of populations (Le Cren 1951, Ricker 1973, Froese 2006). In order to obtain this data, fishes were captured using three methods: angled from the beach or a boat; captured using beach seine with a mesh size ranging 0.5–1 cm; sampled with drift netting from a boat (mesh size 2 cm). Measurements and weight of different species are provided, and expand existing information available in Fishbase (Froese and Pauly 2018).

Chapter 4

Edna Correia, José Pedro Granadeiro, Aissa Regalla, Emanuel Dias, Amadeu Almeida, Paulo Catry (2017) ***Predatory pelagic fishes of the Bijagos Archipelago (Guinea-Bissau) show high overlap in diets dominated by sardinella***. African Journal of Marine Science. 39 (4): 389-396

I studied the diet of the three most abundant pelagic predatory fishes of the Bijagós Archipelago: the Crevalle jack (*Caranx hippos*), the West African Spanish mackerel (*Scomberomorus tritor*) and the Guinean barracuda (*Sphyraena afra*). These species are important along the coast of West Africa, namely for recreational fisheries, attracting sports fishermen from abroad to Guinea-Bissau

(Campredon and Catry 2016), and thus contributing to the economy of the country (Dia and Bedingar 2001, Belhabib et al. 2016). Nonetheless studies on their diet are scarce (Fagade and Olaniyan 1973, Kwei 1978, Lafrance 1994). For this study fishes were angled from the beach or a boat, their stomach contents were collected and their prey remains macroscopically identified. The prey items were identified through comparison with a large reference collection of hard structures (i.e. otoliths, vertebrae and other diagnostic bones) representing a large variety of local species.

Chapter 5

Edna Correia, José Pedro Granadeiro, Aissa Regalla, Hamilton Monteiro, Paulo Catry (Submitted)

The diet of two opportunistic seabirds (Caspian and Royal terns) confirms the importance of sardinella in West African coastal food webs

I studied the diet of the two most numerous breeding tern species: Caspian Tern (*Hydroprogne caspia*) and Royal Tern (*Thalasseus maximus*) in Guinea-Bissau. The two species are widespread breeders in the West African region with important numbers nesting in Guinea-Bissau. Nonetheless the diet of these two tern species is still poorly studied (Brenninkmeijer et al. 2002, van Roomen et al. 2015, Veen et al. 2018). I collected pellets - undigested and regurgitated prey components – from the breeding colonies and roosting sites of the two tern species. The prey items were identified using otoliths, vertebrae and other diagnostic bones, which also involved the collection of a large reference collection of fish hard structures representing most local species. I further compared two methods for quantifying the diet of both tern species, one based on the examination of all hard structures (e.g. otoliths, vertebrae, scales) and another one based only on otoliths, as their performances can vary substantially.

Chapter 6

Edna Correia, José Pedro Granadeiro, Vanessa A. Mata, Aissa Regalla, Paulo Catry. ***Trophic interactions between migratory seabirds, predatory fishes and small pelagics in West Africa***

Studies on the diet of the Afro-Palearctic populations of these species during their wintering season in West Africa are virtually inexistent, although understanding the wintering conditions experienced by migratory birds is essential for their conservation (Marra et al. 1998, Norris et al. 2004, Szostek and Becker 2015). I studied the diet and foraging behaviour of five of the most common wintering tern species in West Africa, Little (*Sternula albifrons*), Black (*Chlidonias niger*), Common (*Sterna hirundo*), Sandwich (*Thalasseus sandvicensis*) and Lesser Crested (*Thalasseus bengalensis*) Terns. Moreover, we studied the associations between these tern species and predatory fishes. This type of facilitative associations is expected to be more important in tropical regions than in temperate and polar ones, due to the former having its resources more unevenly distributed and a higher abundance of large predatory fishes (Longhurst and Pauly 1987, Ballance and Pitman 1999, Veit and Harrison 2017). Despite the importance of these feeding associations in shaping the distribution and abundance of both marine predators and prey, they have never been addressed in the tropical Atlantic. In order to study the diet and foraging behaviour of the wintering tern community in the Bijagós Archipelago, direct observation of foraging birds from the coast were performed. Furthermore, droppings of the birds from the beach roosts were collected to describe their diet using DNA metabarcoding techniques allowing the identification of prey in faeces. The fact that wintering seabirds roost together in multispecific groups makes it difficult to collect samples and know which species they belong to. With the genetic techniques used in the present work, it was possible to successfully overcome that hurdle in a completely non-invasive way to the birds, and obtain results with unprecedented detail about their diet.

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CHAPTER 2

Seasonal, lunar and diel variations in a coastal fish community assessed by beach seine in the Bijagós Archipelago, West Africa

Edna Correia, José Pedro Granadeiro, Aissa Regalla, Paulo Catry

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Abstract

In many marine ecosystems small pelagic fish exert a crucial role in controlling the dynamics of the community, mainly due to their high biomass at intermediate levels of the food web. We studied spatial, seasonal, lunar and diel variations in a coastal fish community from a marine protected area of the Bijagós Archipelago, Guinea-Bissau. Fish were sampled with 46 beach seine net sessions in 2015 and 2016. A total of 35 fish species of 25 families were captured. Fish abundance varied between years and seasons, with a higher abundance in the dry season, but not by lunar tide. Nonetheless, the community composition was broadly similar over the seasons, among islands and between lunar tides, with Clupeidae, Haemulidae and Gerreidae as the most abundant families. *Sardinella maderensis* highly dominated the captures throughout the year, with catches much higher than any other species. The differences in abundance between seasons and years may be related with movements to or from the shore due to feeding activity or to avoid predation, or else to differences in recruitment between years. There were no significant diel differences in species richness and diversity, although higher numbers of fish were captured during daytime. Mugilidae and Haemulidae were the most numerous families in nocturnal period captures which might be related to differences between species in inshore behaviour. For most species the majority of individuals captured were immature, which highlight the importance of the archipelago as nursery area for several fish species, important to support the offshore stocks of those fish species. These small pelagics, and particularly *Sardinella maderensis*, maintain several marine predators. Thus, the conservation of the small coastal pelagics of the Bijagós Archipelago may be key for the management of the Bijagós.

Keywords: beach seine, small pelagics, nursery, nearshore, Guinea-Bissau

Introduction

Small pelagic fish are essential to the functioning of marine ecosystems, connecting the lower and upper trophic levels in food webs worldwide (Rice 1995, Bakun 1996). Therefore, fluctuations in small pelagic populations may modify ecosystem structure and functioning (e.g. Cury et al. 2000, Shannon et al. 2000). Several small pelagics use coastal marine ecosystems in the near-shore as nursery grounds. Yet these ecosystems are among the most damaged by anthropogenic changes and one of the most vulnerable to future impacts of climate change (Harley et al. 2006, Martínez et al. 2007, Barbier et al. 2011, Sheaves et al. 2014).

Costal marine ecosystems, due to their dynamic structure, exhibit fluctuations in abundance and diversity of communities (Gibson 1993, Krumme 2009). This variability in number of individual may be the result of short-term migrations between different habitats for feeding, reproducing or to avoid predation and competition and are often influenced by lunar, diel and tidal cycles (e.g. Ferreira et al. 2001, Hitt et al. 2011, Krumme 2009). At a larger temporal scale, annual or seasonal migrations for feeding and spawning, may also contribute to fluctuations in coastal marine communities (Gibson et al. 1993).

In the Eastern Central Atlantic region small pelagics are the most important group for fisheries, constituting almost 50% of the landings (Failler 2014, FAO 2016). Most pelagic fish stocks are considered either fully exploited or overfished (FAO 2016). Moreover, this region is one of the most affected by illegal, unreported and unregulated fishing (Belhabib et al. 2015, Doumbouya et al. 2017, Intchama et al. 2018). Guinea-Bissau, located in the region, is strongly dependent on fisheries as one of its main economic activities (Lafrance 1994, Campredon and Cuq 2001, Belhabib et al. 2015). Fish is also the main protein source for the human population (Dia and Bedingar 2001). The Bijagós Archipelago, in particular, is recognized for its abundant fish resources and considered a nursery area for several fish species (Lafrance 1994, Arkhipov et al. 2015, Campredon and Catry 2016). The archipelago is free from industrial fishing, representing a refuge for several fish species that are harvested in neighbouring countries (Polidoro et al. 2016). Fish communities at the Bijagós Archipelago are dominated by Clupeiformes and Perciformes (Lafrance 1994, van der Veer et al. 1995). The archipelago possibly holds some resident populations since most common species are present throughout the year, although few studies have addressed its coastal fish community and related seasonal variations (Lafrance 1994, van der Veer et al. 1995).

The marine ecosystem of Guinea-Bissau is influenced by the tropical climate with two distinct seasons. The dry season (November to May) is influenced by the Canary Current and the rainy season (June to October) by the Guinean Current (Pennober 1999). The effect of the currents along with the input of organic matter from rivers, results in a relatively high productivity in the marine coastal areas of Guinea-Bissau (Berrit and Rebert 1977, Longhurst 1983, Bakun 1996, Tandstad et al. 2014). The sea-surface temperature ranges from 26 to 30 °C and salinity from 36 to 30 ppt, in dry and rainy seasons respectively (Lafrance 1994).

The first objective of this study was to characterise the inshore pelagic fish community in a relatively undisturbed area of the Bijagós, part of a Marine Protected Area. Furthermore, we explored variations in species abundance between seasons (dry and rainy), lunar cycle (spring and neap tide), and diel periods (night and day) in the coastal fish community.

Material and methods

Study area and sampling

Fieldwork was carried out in the João Vieira and Poilão Marine National Park (JVPMNP) in the southeast of the Bijagós Archipelago (Figure 1). The park covers 49,500 ha (of which only 5% are terrestrial) and comprises four main islands. The entire marine area of the JVPMNP is managed in regards to fishing activities, with two distinct zones. In Zone 1, located in the central part of the

JVPMNP and representing 19% of its total area, fishing is totally banned. In Zone 2, representing the remaining area of the park, some types of fishing nets, such as shark nets or all monofilament nets, are forbidden. Moreover, in Zone 2, access rights are reserved for members of the local community and fishing is only allowed in boats with motors up to 40c (IBAP 2007). Beach seine is not usually used for commercial or subsistence fishing in the park.

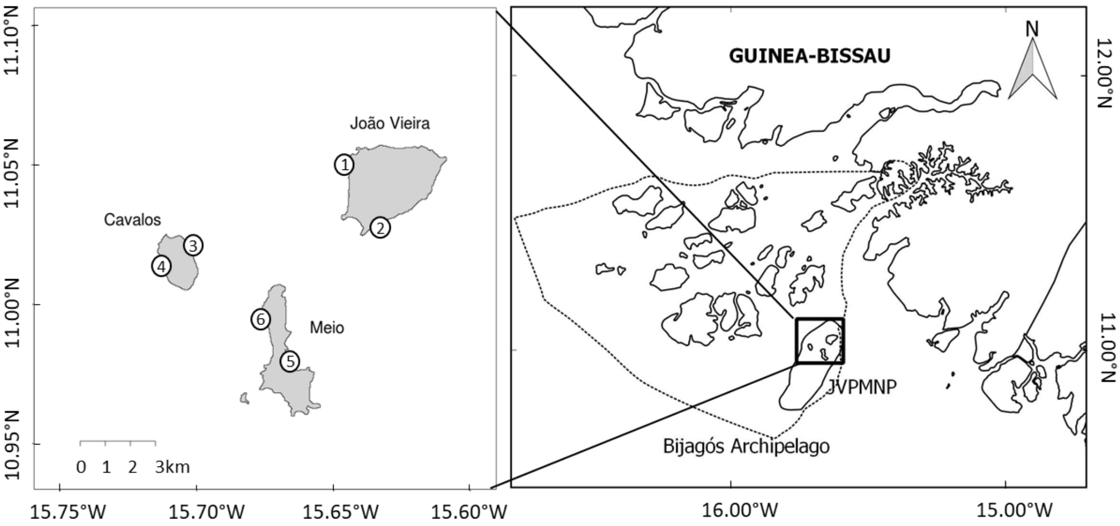

Figure 1 – Location of the six points where beach seine was performed between 2015 and 2016, dash line delimitates Bijagós Archipelago, solid line delimitates João Vieira and Poilão Marine National Park (JVPMNP)

All fishing operations were carried out using a beach seine. The net was 29.55 m in length and 1.70 m to 8.5 m in height (reaching the highest height in the central zone) with 1 cm mesh size. In the central area, it had an additional pyramid with a 1.5 m^2 base and 1 m in height with 0.5 cm mesh size (Figure 2).

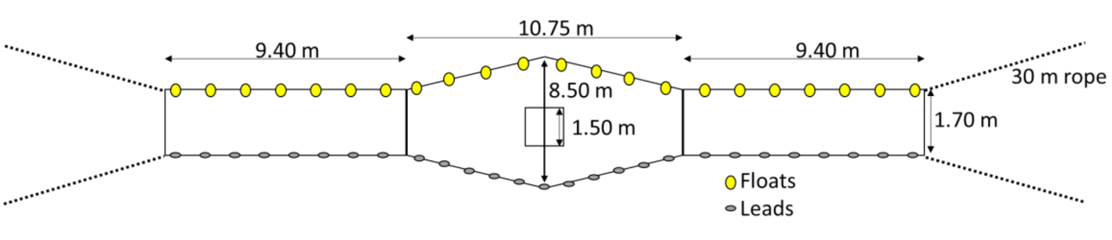

Figure 2 – Scheme of the net used to perform beach seine in the João Vieira and Poilão Marine National Park from 2015 to 2016

Net setting started from the beach using a small boat to stretch the net perpendicular to shore, always keeping the two ropes from one end ashore secured by two people, reaching approximately 35 m from the shoreline. In the farthest point from the shore the depth was on average 2.45 m. The net was then drawn towards the shore so as to form a semi-circumference. When the semi-circumference was formed two to three people on each end pulled the ropes in order to completely pull the net out from the water. This process represents one haul. We always performed four consecutive hauls approximately ten meters apart from each other. We considered each group of four hauls as one session. All samples were collected at high tide, and those obtained in the same session were pooled.

In every haul, we counted and weighted (to the nearest 0.1g) the total number of fishes by species. Furthermore, 50 random individuals from each species were measured (to the nearest 0.5 mm) and weighted (to the nearest 0.1 g). Rays (Chondrichthyes) were quickly measured on the beach and released alive and they were not weighted. Fishes were identified to the lowest possible taxonomic level following guides (Fischer et al. 1981, Schneider 1990, Paugy et al. 2003). We were not able to identify all *Pomadasys* specimens to the species level, and so we refer to them as *Pomadasys* sp. Nevertheless, we believe that most of the individuals should belong to *Pomadasys jubelini* as they were generally similar to the ones we could morphologically identify as *Pomadasys jubelini.* In the case of Mugilidae family, there were also some individuals that were only identified to the genus level.

Lunar and seasonal variation

Catches were carried out between February 2015 and September 2016. In order to explore the seasonal variation in the pelagic fish community we performed 27 sessions of beach seine in João Vieira Island between 2015 and 2016 (site 1, see Figure 1). We always fished on three consecutive days (except for one occasion when only one day was sampled, and another one when only two days were sampled due to unsuitable weather and sea conditions), (Table 1).

Table 1 - Number of sessions (N) by season and lunar tide of the beach seine performed in the João Vieira island from 2015 to 2016

N	Season	Lunar tide
9	Dry	Neap
9		Spring
5	Rainy	Neap
4		Spring

Spatial variation

In order to assess whether our main study site was representative of the whole marine park, or whether there was important spatial variation in the fish community, we sampled two different points of each of the three islands (João Vieira, Cavalos and Meio, Figure 2) in six consecutive days in January 2016.

Diel variation - day/night

We explored diel variation in the pelagic fish community by performing eight catches during both day and night periods, in João Vieira (site 1, see Figure 1), between January and March 2016.

Data analysis

The abundance of fishes corresponded to the total number of individuals captured in a session (four consecutive hauls), and the richness as the total number of species. For each species, we calculated the mean number of individuals caught per session. Their relative abundance was then calculated as a percentage of the mean of the total number of individuals captured per session. We further calculated, for each species, the mean total length and mean total mass of the individuals measured in João Vieira island between February 2015 and September 2016 at site 1 (Figure 1). To evaluate the diversity of the community, we calculated the Shannon–Wiener (H') diversity index and the Pielou's evenness index (J), (Brower and Zar 1998) following the equations:

$$H' =-\sum pi\ ei \log e\ pi;$$

$$J = H'/ \log(S);$$

where *pi* is the proportion of species *i* in relation to the total number of species; J is the Pielou's evenness index. We tested the differences between lunar tides, islands and diel period on the diversity (Shannon-Wiener and Pielou's evenness) and richness using ANOVAs. The abundance of individuals was tested accounting for species on one hand, and for lunar tides / islands or diel period on the other, using two-way ANOVAs. Concerning seasonal variations, we tested the effect of season and year on diversity and richness using two-way ANOVAs, and tested the effect of species, season and year on the abundance of individuals using three-way ANOVAs. Statistical analyses were carried out using the software R (R Core Team 2018).

Results

In total we captured 35 fish species from 25 families. The list of species with the respective threat status (IUCN 2017) is in Supplementary material (Table S1).

Lunar and seasonal variation

Sardinella maderensis accounted for more than 70% of the total of individuals captured in the dry season and c. 80% in the rainy season (Table 2), followed by *Pomadasys* sp.(19% in dry season and 3% in rainy season) and *Eucinostomus melanopterus* (8% in dry season and 10% in rainy season). Total mean mass of individuals by species and by season is presented in the Supplementary material, Table S2.

Concerning the variation between spring and neap tides, there were no differences in diversity (ANOVA: Shannon-Wiener diversity diversity - $F_{1, 25} = 0.28$, $P = 0.60$), in evenness (Pielou's evenness $F_{1,25} = 2.00 \times 10^{-3}$, $P = 0.97$), or in species richness (ANOVA: $F_{1, 25} = 2.02$, $P = 0.17$). We tested for differences in the number of individuals captured among species and between spring and neap tides. There were significant differences in the abundance of individuals by species (two-way ANOVA $F_{30,239} = 5.62$, $P < 0.001$) but not by tide ($F_{1, 239} = 1.33$, $P = 0.25$). Also, there was no significant interaction between species and tide ($F_{19, 239} = 0.39$, $P = 0.99$). Therefore, data from neap and spring tides were pooled for subsequent analyses.

There were no effect of season or year in Shannon-Wiener diversity (two-way ANOVA: season: $F_{1, 24} = 0.02$, $P = 0.90$; year: $F_{1, 24} = 0.41$, $P = 0.53$), that presented a mean of 0.92 ± 0.01 (SE). There were also no significant effect of season or year differences in Pielou’s evenness (two-way ANOVA: season: $F_{1, 24} = 0.21$, $P = 0.65$; year: $F_{1, 24} = 3.60$, $P = 0.07$), that presented a total mean of 0.40 ± 0.01 (SE). There was a significant effect of year and season on species richness (two-way ANOVA: season: $F_{1, 24} = 5.06$, $P = 0.03$; year: $F_{1, 24} = 14.66$, $P < 0.001$). The average species richness per session was 10.74 ± 0.11 (SE). We tested the effect of species, season and year on the abundance of individuals captured (three-way ANOVA). All variables had a significant effect on the abundance of individuals, however the species was the most significant (species: $F_{30, 257} = 6.23$, $P < 2.0 \times 10^{-6}$; season: $F_{1, 257} = 8.44$, $P < 0.01$; year: $F_{1, 257} = 9.31$, $P < 0.01$).

Table 2 - Mean of the total number (N) individuals captured (± standard error) and relative abundance (RA%) by species of the fishes captured during 19 sessions in the dry season and 9 sessions in the rainy season in João Vieira island from 2015 and 2016

			Dry		Rainy	
Class	**Family**	**Species**	**N ± SE**	**RA (%)**	**N ± SE**	**RA (%)**
Osteichthyes						
	Albulidae	*Albula vulpes*	5.3 ± 3.3	0.2	-	0.0
	Belonidae	*Belonidae*	-	0.0	0.3 ± 0.2	0.0
	Carangidae	*Trachinotus ovatus*	1.0 ± 0.46	0.0	5.6 ± 1.6	0.9
		Alectis alexandrinus	0.1 ± 0.1	0.0	0.1 ± 0.1	0.0
		Carangidae	-	0.0	0.1 ± 0.1	0.0
		Hemicaranx bicolor	-	0.0	0.1 ± 0.1	0.0
	Cichlidae	*Cichlidae*	0.2 ± 0.2	0.0	-	0.0
	Clupeidae	*Sardinella maderensis*	1579.6 ± 359.1	70.6	515.2 ± 130.8	79.2
		Ethmalosa fimbriata	32.1 ± 10.5	1.4	12.6 ± 6.6	1.9
		Sardinella aurita	1.8 ± 1.2	0.1	2.1 ± 2.1	0.3
	Drepanidae	*Drepane africana*	-	0.0	4.3 ± 0.7	0.7
	Elopidae	*Elops lacerta*	0.1 ± 0.1	0.0	2.4 ± 1.2	0.4
	Engraulidae	*Engraulis encrasicolus*	0.1 ± 0.1	0.0	0.1 ± 0.1	0.0
	Ephippidae	*Chaetodipterus lippei*	0.2 ± 0.2	0.0	0.9 ± 0.6	0.1
	Gerreidae	*Eucinostomus melanopterus*	162.7 ± 48.4	7.3	51.7 ± 7.8	7.9
		Gerres nigri	7.3 ± 4.2	0.3	10.4 ± 3.2	1.6
	Haemulidae	*Pomadasys* sp.	423.4 ± 105.8	18.9	19.8 ± 4.4	3.0
	Mugilidae	*Mugilidae*	6.5 ± 3.7	0.3	0.3 ± 0.2	0.0
		Mugil bananensis	0.2 ± 0.1	0.0	0.2 ± 0.2	0.0
		Mugil curema	0.2 ± 0.1	0.0	1.1 ± 0.5	0.2
		Mugil sp.	0.1 ± 0.1	0.0	-	0.0
		Liza dumerili	0.1 ± 0.1	0.0	-	0.0
		Liza falcipinis	0.1 ± 0.1	0.0	-	0.0
		Liza sp.	-	0.0	0.1 ± 0.1	0.0
	Paralichthyidae	*Citharichthys stampflii*	2.9 ± 0.5	0.1	0.1 ± 0.1	0.0
	Polynemidae	*Galeoides decadactylus*	1.1 ± 0.5	0.0	14.2 ± 4.0	2.2
	Psettodidae	*Psettodes belcheri*	1.1 ± 0.3	0.0	0.4 ± 0.2	0.1
	Scianidae	Scianidae	-	0.0	0.1 ± 0.1	0.0
	Scombridae	*Scomberomorus tritor*	8.1 ± 3.4	0.4	6.4 ± 2.7	1.0
	Sphyraenidae	*Sphyraena afra*	-	0.0	0.1 ± 0.1	0.0
Chondrichthyes						
	Dasyatidae	*Fontitrygon margarita/margaritella*	2.2 ± 0.9	0.1	1.6 ± 1.1	0.2
		Bathytoshia centroura	0.1 ± 0.1	0.0	-	0.0
	Gymnuridae	*Gymnura sp.*	0.1 ± 0.1	0.0	-	0.0
		Gymnura micrura	0.1 ± 0.1	0.0	-	0.0
	Rhinobatidae	Rhinobatidae sp.	0.2 ± 0.2	0.0	-	0.0
		Glaucostegus cemiculus	0.1 ± 0.1	0.0	0.2 ± 0.2	0.0
	TOTAL		**2236.7 ± 429.8**		**650.8 ± 142.8**	

We compared the total length between seasons and year for the three most captured families (Table 3; information on the total length and total mass of individuals of the remaining species are presented in Supplementary material, Table S3). We tested the effect of season (dry and rainy) and year (2015 and 2016) on total length with two-way ANOVAs for *Sardinella maderensis*, *Pomadasys* sp, *Eucinostomus melanopterus* and *Gerres nigri*. The total length of *Sardinella maderensis* was significantly higher in rainy season ($F_{1, 4687} = 23.45$, $P < 0.001$) and in 2016 ($F_{1, 4687} = 21.04$, $P < 0.001$). *Pomadasys* sp. and *Eucinostomus melanopterus* were both significantly larger during dry season ($F_{1, 2691} = 34.04$, $P < 0.001$; $F_{1, 1916} = 109.13$, $P < 0.001$, respectively) and in 2015 ($F_{1, 2691} = 4.51$, $P = 0.03$; $F_{1, 1916} = 63.57$, $P < 0.001$, respectively). *Gerres nigri* individuals were significantly larger during the rainy season ($F_{1, 225} = 7.20$, $P < 0.01$), but no differences were found between years ($F_{1, 225} = 0.01$, $P = 0.91$).There was a significant interaction between year and season on the total length of *Sardinella maderensis*, *Pomadasys* sp. and *Eucinostomus melanopterus* ($F_{1, 4687} = 492.11$, $P < 0.001$; $F_{1, 2691} = 258.60$, $P < 0.001$; $F_{1, 1916} = 8.95$, $P < 0.01$ respectively), but no for *Gerres nigri* ($F_{1, 225} = 0.28$, $P = 0.60$).

Table 3 – Mean total length (TL) (mm) ± standard error by year and season for the most abundant species captured by beach seine in João Vieira, N – number of individuals measured

		2015				2016			
		Dry		Rainy		Dry		Rainy	
Family	**Species**	**N**	**TL (mm) ± SE**	**N**	**TL (mm) ± SE**	**N**	**TL (mm) ± SE**	**N**	**TL (mm) ± SE**
Clupeidae	*Sardinella maderensis*	1920	59.08 ± 0.26	590	69.82 ± 0.62	872	68.13 ± 0.47	1309	60.96 ± 0.34
Gerreidae	*Eucinostomus melanopterus*	1072	78.01 ± 0.46	204	87.60 ± 1.50	380	68.82 ± 1.00	264	84.53 ± 1.58
Gerreidae	*Gerres nigri*	4	105.75 ± 8.73	30	109.17 ± 4.36	131	94.83 ± 4.23	64	110.13 ± 3.54
Haemulidae	*Pomadasys* sp.	1872	51.72 ± 0.36	30	84.93 ± 5.35	663	52.70 ± 0.51	130	35.54 ± 1.03

Spatial variation

Sardinella maderensis and *Pomadasys* sp. accounted for more than 75% of the relative abundance in all three islands (Table 4). The diversity indexes and richness by island are presented in Table

5. We tested the effect of species and island on the abundance of individuals. There were significant differences in abundance of individuals by species (two-way ANOVA $F_{19, 99} = 9.15$, $P < 0.001$) but not by island ($F_{2, 99} = 2.00$, $P = 0.14$). There was no significant interaction between species and islands, so the factor island was removed from these analyses (results not shown). Total mean mass of individuals by species and by island is presented in the Supplementary material, Table S4.

Table 4 - Mean number (N) of the individuals captured (± standard error) and relative abundance (RA%) by species of the fishes captured by islands (Cavalos, João Vieira and Meio) during 6 consecutive days in January 2016, 2 sessions by island

Family	Species	Cavalos		João Vieira		Meio	
		N ± SE	RA (%)	N ± SE	RA (%)	N ± SE	RA (%)
Albulidae	*Albula vulpes*	0.5 ± 0.5	0.0	-	0.0	-	0.0
Atherinidae	*Atherina lopeziana*	0.5 ± 0.5	0.0	0.5 ± 0.5	0.1	-	0.0
Belonidae	*Tylosurus acus*	5.0 ± 5.0	0.5	-	0.0	-	0.0
	Tylosurus crocodilus	0.5 ± 0.5	0.0	-	0.0	-	0.0
Paralichthyidae	*Citharichthys stampflii*	2.0 ± 2.0	0.2	0.5 ± 0.5	0.1	2.5 ± 2.5	0.3
Carangidae	*Trachinotus goreensis*	1.5 ± 1.5	0.1	1.0 ± 1.0	0.3	-	0.0
	Trachinotus ovatus	6.0 ± 5.0	0.6	0.5 ± 0.5	0.1	1.0 ± 1.0	0.1
Clupeidae	*Ethmalosa fimbriata*	14.5 ± 12.5	1.3	27.5 ± 20.5	7.7	62.5 ± 41.5	8.2
	Sardinella maderensis	631.0 ± 259.0	58.7	238.5 ± 76.5	66.4	291.0 ± 176.0	38.3
Gerreidae	*Eucinostomus melanopterus*	26.5 ± 16.5	2.5	9.5 ± 9.5	2.6	105.0 ± 80.0	13.8
	Gerres nigri	10.5 ± 9.5	1.0	-	0.0	3.0 ± 3.0	0.4
Haemulidae	*Pomadasys sp.*	367.5 ± 249.5	34.2	78.0 ± 7.0	21.7	282.0 ± 112.0	37.1
Monacanthidae	*Stephanolepis hispidus*	-	0.0	-	0.0	0.5 ± 0.5	0.1
Mugilidae	*Liza sp.*	2.5 ± 2.5	0.2	-	0.0	9.0 ± 9.0	1.2
	Mugil bananensis	1.0 ± 1.0	0.1	-	0.0	2.5 ± 2.5	0.3
	Mugil curema	0.5 ± 0.5	0.0	-	0.0	-	0.0
Polynemidae	*Galeoides decadactylus*	4.0 ± 4.0	0.4	1.5 ± 1.5	0.4	-	0.0
Psettodidae	*Psettodes belcheri*	-	0.0	1.0 ± 1.0	0.3	-	0.0
Scombridae	*Scomberomorus tritor*	1.0 ± 1.0	0.1	-	0.0	1.5 ± 0.5	0.2
Soleidae	*Soleidae n.i.*	-	0.0	0.5 ± 0.5	0.1	-	0.0
TOTAL		**1075.0 ± 547.0**		**359.0 ± 98.0**		**760.5 ± 12.0**	

Table 5 – Mean Shannon-Wiener diversity (H'), mean Pielou's evenness (J) diversity indexes and mean richness ± standard errors by island of the captures with beach seine in January 2016, N - number of sessions

Island	N	H'	J	Richness
Cavalos	2	0.95 ± 0.05	0.39 ± 0.00	11.50 ± 1.50
Joao Vieira	2	0.93 ± 0.04	0.48 ± 0.02	7.00 ± 0.00
Meio	2	1.17 ± 0.12	0.57 ± 0.01	8.00 ± 2.00

Diel variation - day/night

Sardinella maderensis and *Pomadasys* sp. were the most abundant during the daytime, while at night the most abundant groups were *Pomadasys* sp. and Mugilidae (Table 7).

The mean Shannon-Wiener diversity index was 1.21 ± 0.09 (SE) during daytime and 1.45 ± 0.14 (SE) during night-time, there were no differences between the two periods (ANOVA: Shannon-Wiener $F_{1, 14} = 2.17$, $P = 0.16$). The mean species richness was 10.00 ± 1.13 (SE) during daytime and 8.75 ± 0.92 (SE) during night-time and its variation was not significant (ANOVA: $F_{1,14} = 0.73$, $P = 0.41$). The Pielou's evenness index, however, varied significantly ($F_{1, 14} = 6.15$, $P = 0.03$), with a mean value of 0.54 ± 0.04 (SE) during the day and 0.68 ± 0.04 during the night period. We tested the effect of species and period in the abundance of individuals. There was a significant interaction between species and period (Two-way ANOVA: $F_{23, 336} = 6.43$, $P < 0.001$), meaning that the relationship between periods and abundance is dependent on the species. There were significant differences in the total number of individuals captured by species ($F_{23, 336} = 6.83$, $P < 0.001$), as well as by period ($F_{1, 336} = 18.34$, $P < 0.001$), with more individuals captured during the daytime except for few species (Table 6). Total mean mass of individuals by species and by island is presented in the Supplementary material, Table S5.

Table 6 - Mean number (N) of the individuals captured (± standard error) and relative abundance (RA%) by species of the fishes captured during 8 sessions in daytime and 8 sessions in night-time of beach seine in João Vieira Island in 2016

Family	Species	Daytime		Night-time	
		N ± SE	RA (%)	N ± SE	RA (%)
Albulidae	*Albula vulpes*	3.6 ± 2.4	0.5	-	0.0
Atherinidae	*Atherina lopeziana*	0.1 ± 0.1	0.0	0.8 ± 0.4	1.2
Belonidae	*Tylosurus crocodilus*	-	0.0	0.1 ± 0.1	0.1
Carangidae	*Alectis alexandrinus*	0.3 ± 0.2	0.0	0.3 ± 0.3	0.4
	Trachinotus ovatus	0.1 ± 0.1	0.0	0.6 ± 0.4	0.9
Cichlidae	*Cichlidae*	0.3 ± 0.2	0.0	1.3 ± 1.0	1.9
Clupeidae	*Ethmalosa fimbriata*	24.9 ± 8.2	3.6	5.9 ± 3.3	8.6
	Sardinella maderensis	342.1 ± 126.3	49.5	0.1 ± 0.1	0.1
Drepanidae	*Drepane africana*	0.5 ± 0.4	0.1	0.5 ± 0.2	0.7
Elopidae	*Elops lacerta*	0.1 ± 0.1	0.0	-	0.0
Gerreidae	*Eucinostomus melanopterus*	112.9 ± 51.5	16.3	1.1 ± 0.4	1.6
	Gerres nigri	3.3 ± 1.7	0.5	3.3 ± 1.2	4.8
Haemulidae	*Pomadasys* sp.	140.4 ± 31.3	20.3	26.1 ± 3.4	38.1
Mugilidae	*Liza* sp.	0.4 ± 0.3	0.1	20.4 ± 5.0	29.8
	Mugil sp.	0.5 ± 0.4	0.1	3.5 ± 1.4	5.1
Paralichthyidae	*Citharichthys stampflii*	3 ± 0.7	0.4	0.1 ± 0.1	0.1
Polynemidae	*Galeoides decadactylus*	1.3 ± 0.5	0.2	0.6 ± 0.2	0.9
Pristigasteridae	*Ilisha africana*	-	0.0	2.9 ± 1.1	4.2
Psettodidae	*Psettodes belcheri*	1.1 ± 0.5	0.2	-	0.0
Scombridae	*Scomberomorus tritor*	54.3 ± 37.5	7.9	-	0.0
Serranidae	*Epinephelus guttatus*	-	0.0	0.1 ± 0.1	0.1
Dasyatidae	*Bathytoshia centroura*	0.1 ± 0.1	0.0	-	0.0
	Fontitrygon margarita / F. margaritella	1.4 ± 0.6	0.2	0.8 ± 0.4	1.2
Rhinobatidae	*Glaucostegus cemiculus*	0.3 ± 0.3	0.0	-	0.0
TOTAL		**690.8 ± 207.6**		**68.4 ± 6.6**	

Discussion

This study showed that the coastal fish community of the Bijagós Archipelago is dominated by species belonging to the Clupeidae, Haemulidae and Gerreidae families. In particular, *Sardinella maderensis* was by far the most numerous species with a relative abundance of over 70% throughout the seasons. Furthermore, the overall fish abundance was on average c.a. three times superior during the dry season (Table 2). There were also differences between day and night periods. During the night, most species were much less abundant inshore, except for Mugilidae, which was much more numerous. The fish species captured in this study are some of the most common coastal species in the Eastern Central Atlantic West Africa (Carpenter and De Angelis 2016, Polidoro et al. 2016).

Lunar and seasonal variation

The overall diversity was low when compared to other beach seine studies in West Africa (e.g. Aggrey-Fynn and Sackey-Mensah 2012), mainly due to the much higher dominance of three species in our samples – *Sardinella maderensis*, *Pomadasys* sp. and *Eucinostomus melanopterus* (see Table 2). This is very clearly expressed in the very low values of equitability (<0.5). Most of the fish captured were immature individuals based on their total length (Table 3 and Supplementary material, Table S3; Panfili et al. 2006, Froese and Pauly 2018). This may be expected in shallow coastal areas, which can give refuge to fish from predation (Krumme 2009).

We found no differences in fish community composition between neap and spring tides. Such differences in tropical coastal ecosystems seem to be expected in heterogeneous shores, where spring tides give access to types of habitats that are not available during neap tides (Lubchenco et al. 1984, Krumme 2009). The area sampled in our study was mostly composed of sandy bottoms and the habitat made available during spring tides may not have been different from the one already available in neap tides, explaining the resemblance in fish community between the two (Castellanos-Galindo et al. 2010).

Seasonal variation in fish abundance was influenced by year and season. The interannual differences found in this study may be related to migrations to and from the coastal areas (Boely et al. 1978). Moreover, since fish recruitment is limited by food availability and spawning density, it is expected to fluctuate between years and influence inshore abundance (Cury and Roy 1989, Neill et al. 1994). The higher fish abundance found during the dry season can be related to a higher recruitment of juveniles during this season, which happens for several species in West Africa (e.g. *Sardinella maderensis*, Whitehead 1985, Cury and Roy 1989), or else, be related to migrations between adjacent inshore and offshore environments (Boely et al. 1978). The greater marine agitation felt during the rainy season may have further lowered the number of captures by destabilizing the beach seine. Some species, including *Sardinella* spp, show seasonal migrations within their main areas of abundance in West Africa. They move from Guinea-Bissau to Mauritania in May/June and the other way around in October/November; and also, from Angola to Congo during July/August and back in February/April (Boely et al. 1978, Fischer et al. 1981, Fréon 1988, Fontana 1988, Cury and Fontana 1988). Nonetheless, as only adults are expected to migrate and most of the individuals captured in this study were immatures, these movements should not have influenced our results.

The frequent capture of Chondrichthyes, particularly *Fontitrygon margarita/margaritella,* suggests that the Archipelago may be relevant for the conservation of this group, particularly since these species are considered, respectively, Endangered / Data Deficient by the IUCN. Chondrichthyes are declining rapidly worldwide and West Africa is among the priority geographic hotspots for their conservation (Dulvy et al. 2017). The Bijagós Archipelago may represent one of the most significant areas in West Africa for this fish group, holding large numbers of individuals (Tous et al. 1998, Campredon and Cuq 2001).

Spatial variation

The fish community was overall similar among the three islands and was dominated by species belonging to the Clupeidae, Haemulidae and Gerreidae families. *Sardinella maderensis* was the most abundant species in all islands (Table 4). Therefore, the results obtained from the beach seine performed in João Vieira from 2015 to 2016 may be representative of the composition and variations of the overall coastal fish community of the JVPMNP.

Diel variation - day/night

Species abundance and richness were generally higher during the daytime. However, Mugilidae was much more abundant at night, meaning that these individuals move nearer to shore during this period. Alongside Mugilidae, Haemulidae was also relatively abundant in night captures (Table 6). Due to the decrease in the dominant species, the values of equitability were significantly higher during the night, despite the maintenance of average diversity. The variation of fish behaviour along diel cycle differs between species and leads to differences in inshore catchability (Parsley et al. 1989). Therefore, some species are more prone to be captured during daytime and others during night-time (Parsley et al. 1989, Nash and Santos 1998). The behavioural differences may be related to feeding activity (Torricelli et al. 1981), or to predation / competition (e.g. Hitt et al. 2011). The use of inshore shallow waters by small fish may reduce the risk of predation by subsurface predators but may increase the predation risk by aerial marine predators (e.g. Erwin 1996, Krumme 2009). Still, shallow waters may offer less foraging opportunities for some species. Thus, different strategies may be used by different species concerning the temporal use of these areas in order to achieve an equilibrium between low predation risk and foraging success (e.g. Erwin 1996, Krumme 2009). The fact that in our study area several of the most abundant predatory fish are diurnal feeders (e.g. jacks; Kwei 1978), may explain the fact that small fish stay mostly inshore during the daytime, and move further from the shore during the night period. Nonetheless, the relatively high abundance of Mugilidae and Haemulidae in night-time captures might be related with inshore movements for feeding, as for both species, night feeding activity has already been reported (Blaber 1976, Torricelli et al. 1981, Nagelkerken et al. 2000, Dankwa et al. 2005, Krumme 2009).

Final considerations

The most abundant families, Clupeidae, Haemulidae and Gerreidae, are within the most captured in coastal areas of nearby countries (Aggrey-Fynn and Sackey-Mensah 2012). The same fish families had already been reported as the most abundant in Guinea-Bissau in previous unpublished technical reports (Lafrance 1994, Albaret et al. 2005), yet ours is the first scientific detailed analysis of a coastal community in this country.

In our study area, *Sardinella maderensis* was the most abundant species in both seasons and around all the islands. This high abundance in the Bijagós Archipelago was not limited to the shore, as some experimental fisheries with a gillnet in deeper waters (up to 30 m) also showed *Sardinella maderensis* as the most abundant species (Supplementary material, Table S6).

Sardinella maderensis is mostly present in the continental shelf, wherein immature individuals are more dependent on coastal zones and adults usually distribute farther from the shore (Boely et al. 1978). Along its distribution range, restricted to the Atlantic Ocean, from southeastern Spain to Angola (Carpenter and De Angelis 2016, Froese and Pauly 2018), *Sardinella maderensis* presents two areas of major abundance: one from Mauritania to Guinea-Bissau, and another from Gabon to the north of Angola (Brainerd 1991). Somewhat high levels of abundance of the species in the Bijagós Archipelago were therefore expected. Still, the dominance of this species in the fish communities studied here is striking and unreported for other West Africa coastal small pelagic communities (e.g. Aggrey-Fynn and Sackey-Mensah 2012). Since the dominance of one or a few species of small pelagics in a marine ecosystem is an indicator of a wasp-waist structure (Bakun 1996, Cury et al. 2000), our results suggest this type of ecosystem structure for the Bijagós Archipelago.

Sardinella maderensis first matures when its total length reaches about 170 mm (Boely 1979, Youmbi et al. 1991). From the randomly measured individuals from the beach seine in João Vieira, only one presented more than 170 mm in total length, thereby possibly being a mature individual. All others were smaller in length and therefore immature, highlighting the importance of the Bijagós Archipelago as a nursery area for this species. The archipelago is located in one of the two main nursery areas identified for *Sardinella maderensis*: one in the north of Mauritania and the other ranging from the south of Senegal to the Bijagós Archipelago (Fréon 1988, Brainerd 1991).

Despite the Bijagós Archipelago showing high levels of abundance for *Sardinella maderensis* and great potential for recruitment, fishing pressure in West Africa, coupled with the high commercial value of the species (Valdés and Déniz-González 2015, FAO 2018), have led to declines in its populations. The species is considered overfished in the region and is now classified as Vulnerable by the IUCN (FAO 2016; Polidoro et al. 2016, Corten et al. 2017).

Beyond its importance for fisheries, *Sardinella maderensis* has been shown to be the most frequent prey for several marine predators in the archipelago, such as seabirds and predatory fish (Correia et al. 2017, Correia et al. submitted, Correia et al. in prep). The fact that, in the Bijagós Archipelago, *Sardinella maderensis* is highly abundant and serves as the main link between plankton and marine predators, makes it a key species for the ecosystem. Even low levels of depletion of this species are expected to impact the functioning of the marine ecosystem (Smith et al. 2011). The conservation of this species to ensure a healthy ecosystem should therefore be a priority. The Bijagós Archipelago, by being a nursery area for *Sardinella maderensis,* contributes for the maintenance of its offshore stocks (Sheaves et al. 2014). Moreover, as the archipelago still suffers less fishing pressure than its neighbouring waters (Campredon and Cuq 2001), it represents a pivotal area for the conservation of *Sardinella maderensis*.

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Supplementary material

Table S1 – Fish species captured in João Vieira and Poilão Marine National Park with beach seine from 2015 to 2016, by Class, Family and threatened status (IUCN 2017); CR – Critically Endangered, EN - Endangered, VU - Vulnerable, NT – Near Threatened, LC – Least Convern, DD – Data Deficient, NE -Not Evaluated

Class	Family	Species	Threatened Status (IUCN)
Osteichthyes	**Albulidae**	*Albula vulpes*	NT
	Atherinidae	*Atherina lopeziana*	DD
	Belonidae	*Tylosurus acus*	
		Tylosurus crocodilus	LC
	Carangidae	*Alectis alexandrinus*	LC
		Hemicaranx bicolor	LC
		Trachinotus ovatus	LC
	Cichlidae	Cichlidae	LC/NE
	Clupeidae	*Ethmalosa fimbriata*	LC
		Sardinella aurita	LC
		Sardinella maderensis	VU
	Drepanidae	*Drepane africana*	LC
	Elopidae	*Elops lacerta*	LC
	Engraulidae	*Engraulis encrasicolus*	LC
	Ephippidae	*Chaetodipterus lippei*	LC
	Gerreidae	*Eucinostomus melanopterus*	LC
		Gerres nigri	LC
	Haemulidae	*Pomadasys jubelini*	LC
	Monacanthidae	*Stephanolepis hispidus*	DD
	Mugilidae	*Liza dumerili*	DD
		Liza falcipinnis	LC
		Mugil bananensis	LC
		Mugil curema	DD
	Paralichthyidae	*Citharichthys stampflii*	LC
	Pristigasteridae	*Ilisha africana*	LC
	Psettodidae	*Psettodes belcheri*	LC
	Polynemidae	*Galeoides decadactylus*	NT
	Sciaenidae	Scianidae	NT
	Scombridae	*Scomberomorus tritor*	LC
	Serranidae	*Epinephelus guttatus*	LC
	Sphyraenidae	*Sphyraena afra*	LC
Chondrichthyes	**Dasyatidae**	*Bathytoshia centroura*	DD
		Fontitrygon margarita / F. margaritella	EN / DD
	Gymnuridae	*Gymnura micrura*	DD
	Rhinobatidae	*Glaucostegus cemiculus*	EN

Table S2 – Mean of the total mass (TM) of the individuals captured +- standard error, during 19 sessions in the dry season and 9 sessions in the rainy season in João Vieira island from 2015 and 2016

Class	Family	Species	Dry TM (g) ± SE	Rainy TM (g) ± SE
Osteichthyes				
	Albulidae	*Albula vulpes*	61.0 ± 43.0	-
	Belonidae	*Belonidae*		0.7 ± 0.5
	Carangidae	*Trachinotus ovatus*	13.2 ± 8.8	24.9 ± 6.7
		Alectis alexandrinus	102.8 ± 102.8	58.9 ± 58.9
		Carangidae	-	0.1 ± 0.1
		Hemicaranx bicolor	-	0.8 ± 0.8
	Cichlidae	Cichlidae	0.3 ± 0.3	-
	Clupeidae	*Sardinella maderensis*	2499.8 ± 449.5	1112.4 ± 254.7
		Ethmalosa fimbriata	136.6 ± 108.3	27.4 ± 14.2
		Sardinella aurita	4.7 ± 3.1	20.5 ± 20.5
	Drepanidae	*Drepane africana*		2819.5 ± 591.6
	Elopidae	*Elops lacerta*	47.3 ± 34.9	868.7 ± 395.8
	Engraulidae	*Engraulis encrasicolus*		0.1 ± 0.1
	Ephippidae	*Chaetodipterus lippei*	129.0 ± 95.4	449.4 ± 297.3
	Gerreidae	*Eucinostomus melanopterus*	978.9 ± 308	468.0 ± 86.2
		Gerres nigri	137.5 ± 109.6	196.0 ± 61.8
	Haemulidae	*Pomadasys* sp.	728.5 ± 166.3	53.9 ± 19.3
	Mugilidae	Mugilidae	4.6 ± 2.6	1.8 ± 1.2
		Mugil bananensis	60.7 ± 36.1	28.9 ± 19.1
		Mugil curema	42.6 ± 27.5	226.4 ± 98.2
		Mugil sp.	0.1 ± 0.1	-
		Liza dumerili	14.6 ± 14.6	-
		Liza falcipinis	6.2 ± 6.2	-
		Liza sp.	-	0.2 ± 0.2
	Paralichthyidae	*Citharichthys stampflii*	16.5 ± 3.6	0.8 ± 0.8
	Polynemidae	*Galeoides decadactylus*	2.9 ± 1.5	35.3 ± 16.8
	Psettodidae	*Psettodes belcheri*	1030.0 ± 299.1	356.7 ± 141.3
	Scianidae	Scianidae	-	0.1 ± 0.1
	Scombridae	*Scomberomorus tritor*	1168.3 ± 300.1	215.0 ± 137.1
	Sphyraenidae	*Sphyraena afra*	-	46.1 ± 46.1
TOTAL			**7186.1 ± 1156.8**	**7012.5 ± 1006.2**

Table S3 - Mean total length (TL), (mm) ± standard error, minimum and maximum total length (mm) and mean total mass (TM) ± standard error, minimum and maximum total mass (g) of individually measured and weighted by fish species and season from fish captured in beach seine in Joao Vieira from 2015 to 2016, N – total number of individuals, data on Chondrichthyes correspond to the length of the disc

Class	Family	Species	N	TL (mm) ±SE	TM min	TM max	TM (g) ±SE	TM min	TM max
Osteichthyes									
	Albulidae	*Albula vulpes*	95	107.6 ± 3.6	46.0	164.0	11.6 ± 0.9	32.5	0.6
	Belonidae	*Belonidae*	3	107.0 ± 5.0	101.0	117.0	2.0 ± 0.2	2.3	1.7
	Carangidae	*Alectis alexandrinus*	2	478.5 ± 111.5	367.0	590.0	1190.0 ± 660.0	1850.0	530.0
		Hemicaranx bicolor	1	83.0	-	-	7.3	-	-
		Trachinotus ovatus	73	83.4 ± 3.1	55.0	231.0	6.7 ± 1.4	87.2	1.8
	Cichlidae	Cichlidae	4	41.3 ± 3.3	36.0	51.0	1.3 ± 0.4	2.3	0.9
	Clupeidae	*Ethmalosa fimbriata*	677	53.7 ± 0.3	36.0	123.0	1.3 ± 0.0	10.4	0.2
		Sardinella aurita	52	88.7 ± 3.1	64.0	134.0	5.2 ± 0.5	13.2	1.7
		Sardinella maderensis	4691	62.6 ± 0.2	30.0	246.0	2.3 ± 0.0	129.9	0.2
	Drepanidae	*Drepane africana*	39	276.2 ± 4.2	228.0	355.0	650.6 ± 29.8	1250.0	361.0
	Elopidae	*Elops lacerta*	26	390.4 ± 7.8	318.0	458.0	333.5 ± 19.3	585.0	175.3
	Engraulidae	*Engraulis encrasicolus*	2	53.5 ± 4.5	49.0	58.0	0.8 ± 0.2	1.0	0.6
	Ephippidae	*Chaetodipterus lippei*	12	259.8 ± 7.2	229.0	305.0	530.6 ± 31.6	720.0	390.0
	Gerreidae	*Eucinostomus melanopterus*	1920	78.1 ± 0.4	31.0	171.0	6.1 ± 0.1	57.3	0.2
		Gerres nigri	229	101.2 ± 2.7	35.0	214.0	18.5 ± 1.5	126.6	0.4
	Haemulidae	*Pomadasys* sp.	2713	51.6 ± 0.3	25.0	207.0	2.1 ± 0.1	70.3	0.1
	Mugilidae	*Liza dumerili*	1	311.0	-	-	262.8	-	-
		Liza falcipinis	1	243.0	-	-	111.5	-	-
		Mugil bananensis	6	288.2 ± 14.0	239.0	319.0	225.6 ± 31.7	298.8	128.5
		Mugil curema	14	264.3 ± 14.6	126.0	324.0	200.3 ± 19.4	292.0	55.5
		Mugilidae	118	40.7 ± 0.8	25.0	104.0	0.8 ± 0.1	10.8	0.1
	Paralichthyidae	*Citharichthys stampflii*	54	81.3 ± 3.2	42.0	136.0	5.6 ± 0.7	22.2	0.6
	Polynemidae	*Galeoides decadactylus*	147	56.7 ± 1.6	25.0	130.0	2.3 ± 0.3	21.3	0.1
	Psettodidae	*Psettodes belcheri*	23	434.6 ± 6.4	395.0	500.0	945.7 ± 45.8	1450.0	720.0
	Scianidae	Scianidae	1	49.0	-	-	1.2	-	-
	Scombridae	*Scomberomorus tritor*	191	128.4 ± 11.8	28.0	580.0	117.1 ± 20.4	1150.0	0.1
	Sphyraenidae	*Sphyraena afra*	1	453.0	-	-	415.0	-	-

Chondrichthyes								
Dasyatidae	*Bathytoshia cf centroura*	1	310.0	-	-	-	-	-
	Fontitrygon margarita / margaritella	53	199.9 ± 6.2	95.0	310.0	-	-	-
Gymnuridae	*Gymnura micrura*	1	485.0			-	-	-
Rhinobatidae	*Glaucostegus cemiculus*	6	486.7 ± 43.5	330.0	590.0	-	-	-

Table S4 – Mean of the total mass (TM) of the individuals captured ± standard error in three islands (Cavalos, João Vieira and Meio) for 6 consecutive days in January 2016, 2 sessions per island

Family	Species	Cavalos TM (g) ± SE	João Vieira TM (g) ± SE	Meio TM (g) ± SE
Albulidae	*Albula vulpes*	0.4 ± 0.4	-	-
Atherinidae	*Atherina lopeziana*	0.2 ± 0.2	0.4 ± 0.4	-
Belonidae	*Tylosurus acus*	1130.0 ± 1130.0	-	-
	Tylosurus crocodilus	40.0 ± 40.0	-	-
Paralichthyidae	*Citharichthys stampflii*	3.5 ± 3.5	6.6 ± 6.6	3.7 ± 3.7
Carangidae	*Trachinotus goreensis*	52.4 ± 52.4	74.7 ± 74.7	-
	Trachinotus ovatus	41.6 ± 34.5	0.5 ± 0.5	7.6 ± 7.6
Clupeidae	*Ethmalosa fimbriata*	21.2 ± 17.9	30.9 ± 25.1	83.0 ± 65.6
	Sardinella maderensis	1696.6 ± 938.8	593.3 ± 239.8	553.6 ± 383
Gerreidae	*Eucinostomus melanopterus*	60.8 ± 52.9	38.9 ± 38.9	153.6 ± 105.3
	Gerres nigri	16.0 ± 14.6	-	1.9 ± 1.9
Haemulidae	*Pomadasys* sp.	1101.8 ± 871.6	146.5 ± 5.9	410.4 ± 129.4
Monacanthidae	*Stephanolepis hispidus*	-	-	0.3 ± 0.3
Mugilidae	*Liza* sp.	184.2 ± 184.2	-	619.7 ± 619.7
	Mugil bananensis	67.9 ± 67.9	-	119.8 ± 119.8
	Mugil curema	134.9 ± 134.9	-	-
Polynemidae	*Galeoides decadactylus*	17.9 ± 17.9	0.7 ± 0.7	-
Psettodidae	*Psettodes belcheri*	-	88.5 ± 88.5	-
Scombridae	*Scomberomorus tritor*	515.0 ± 515.0	-	596.6 ± 113.5
Soleidae	Soleidae	-	0.2 ± 0.2	-
TOTAL		**5084.2 ± 2836.1**	**448.6 ± 317.2**	**921.9 ± 651.9**

Table S5 - Mean total mass (TM) of individuals captured ± standard error during 8 sessions during daytime and 8 sessions during nights-time of beach seine in João Vieira island in 2016

Class	Family	Species	Daytime TM (g) ± SE	Night-time TM (g) ± SE
Osteichthyes	Albulidae	*Albula vulpes*	82.3 ± 50.6	-
	Atherinidae	*Atherina lopeziana*	0.1 ± 0.1	1.7 ± 1.0
	Belonidae	*Tylosurus crocodilus*	-	11.3 ± 11.3
	Carangidae	*Alectis alexandrinus*	260 ± 183.3	189.4 ± 189.4
		Trachinotus ovatus	0.3 ± 0.3	31.4 ± 28.1
	Cichlidae	Cichlidae	3.0 ± 2.1	11.7 ± 8.0
	Clupeidae	*Ethmalosa fimbriata*	43.5 ± 12.7	31.9 ± 23.1
		Sardinella maderensis	1127.9 ± 482.5	0.2 ± 0.2
	Drepanidae	*Drepane africana*	497.5 ± 366.6	230.0 ± 93.5
	Elopidae	*Elops lacerta*	51.3 ± 51.3	-
	Gerreidae	*Eucinostomus melanopterus*	806.3 ± 379.9	3.3 ± 1.5
		Gerres nigri	140.0 ± 70.7	50.7 ± 35.0
	Haemulidae	*Pomadasys* sp.	277.7 ± 53.0	104.9 ± 21.8
	Mugilidae	*Liza* sp.	25.0 ± 24.7	1589.8 ± 437.9
		Mugil sp.	89.3 ± 81.3	119.4 ± 59.4
	Paralichthyidae	*Citharichthys stampflii*	19.7 ± 3.4	0.2 ± 0.2
	Polynemidae	*Galeoides decadactylus*	1.8 ± 0.8	162.1 ± 77.9
	Pristigasteridae	*Ilisha africana*	-	90 ± 39.8
	Psettodidae	*Psettodes belcheri*	693.4 ± 368.5	-
	Scombridae	*Scomberomorus tritor*	283.2 ± 185.6	-
	Serranidae	*Epinephelus guttatus*	-	0.4 ± 0.4
TOTAL			**4402.1 ± 1670.0**	**2628.2 ± 593.5**

Table S6 – Mean number (N) and mean total mass (TM) of individuals captured ± standard error, during 13 sessions of drifting net (9 sessions in the dry season and 4 sessions in the rainy season) around João Vieira, Cavalos and Meio islands in 2016. We used a floating gillnet that left a drift in the water with one end attached to the drifting boat for 1h30 min each session. The gillnet was 128 m on length and 2.95 to 4.9 m on height (reaching the highest height in the central zone) with 2 cm mesh size. It had floats in the upper part and leads in the lower part in order to maintain a vertical position on water.

			Dry		Rainy	
Class	**Family**	**Species**	**N ± SE**	**TM (g) ± SE**	**N ± SE**	**TM (g) ± SE**
Osteichthyes						
	Albulidae	*Albula vulpes*	-	-	1.0 ± 1.0	156.2 ± 156.2
	Ariidae	*Carlarius latiscutatus*	0.2 ± 0.2	148.9 ± 148.9	0.5 ± 0.3	725.0 ± 426.5
	Belonidae	*Ablennes hians*	2.1 ± 0.7	676.7 ± 205.5	-	-
		Tylosurus acus	0.4 ± 0.3	210.0 ± 145.3	-	-
		Tylosurus sp.	1.4 ± 1.0	483.3 ± 326.4	0.5 ± 0.3	172.5 ± 99.6
	Carangidae	*Alectis alexandrinus*	0.1 ± 0.1	76.7 ± 76.7	-	-
		Chloroscombrus chrysurus	-	-	0.8 ± 0.8	42.2 ± 42.2
	Clupeidae	*Ethmalosa fimbriata*	0.1 ± 0.1	7.3 ± 7.3	-	-
		Sardinella maderensis	7.0 ± 5.5	774.4 ± 598.0	868.8 ± 842.8	75188.6 ± 72525.8
	Echeneidae	*Echeneis naucrates*	0.1 ± 0.1	13.33 ± 13.33	-	-
	Gerreidae	*Gerres nigri*	-	-	0.8 ± 0.8	42.9 ± 42.9
	Pristigasteridae	*Ilisha africana*	-	-	1.5 ± 1.5	68.3 ± 68.3
	Scombridae	*Scomberomorus tritor*	0.8 ± 0.4	563.3 ± 298.5	-	-
	Sphyraenidae	*Sphyraena afra*	0.3 ± 0.3	86.7 ± 86.7	-	-
Chondrichthyes						
	Carcharhinidae	*Carcharhinus* sp.	-	-	0.3 ± 0.3	230.0 ± 230.0
		Rhizoprionodon acutus	0.2 ± 0.2	-	-	-

CHAPTER 3

Length-weight relationship of fish species from the Bijagós Archipelago, Guinea-Bissau

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CHAPTER 3

Length-weight relationship of fish species from the Bijagós Archipelago, Guinea-Bissau

Abstract

Length–weight relationships were estimated for six teleost fish species occurring in Bijagós Archipelago, Guinea-Bissau. Samples were collected seasonally during three dry seasons (2013/2014, 2014/2015, 2015/2016) and two rainy seasons (2015 and 2016). Fishes were captured by three methods: angled from the beach or a boat; using beach seine with a mesh size ranging 0.5 to 1 cm; drift netting from a boat (mesh size 2 cm). This work provides the length-weight relationship for three fish species that are not reported in FishBase (*Citharichthys stampflii, Gerres nigri and Psettodes belcheri*) as well as for three species from which we present a wider size range (*Eucinostomus melanopterus*, *Scomberomorus tritor* and *Sphyraena afra*).

Keywords: LWR, fisheries, West Africa

Introduction

Length–weight relationships (LWR) are useful to estimate fish biomass based on length. When the sampling procedures are standardized, the parameters of these relationships can be compared across space (i.e. among different areas) or time (e.g. among seasons or years) to provide information concerning variation in the overall structure of populations. In this contribution, we estimate the LWR for six teleost fish species from the Bijagós Archipelago, Guinea-Bissau, West Africa. Very few data are available from this region (Froese and Pauly 2017).

Material and methods

Study area and sampling

Guinea-Bissau is a small country very dependent on its natural resources, with fisheries being one of the main economic activities (Lafrance 1994, Campredon and Cuq, 2001, Campredon and Catry, 2016). Most fishing activities take place in the Bijagós Archipelago, a large group of islands off the continental coast. The archipelago is free of industrial fishing, serving as potential refuge area for several fish species, most of which are being harvested in neighbouring countries. This work was carried out in the João Vieira and Poilão Marine National Park, situated in the south-east of Bijagós Archipelago (10°57'N, 15°42' W). The local climate is tropical, with two distinct seasons: a dry season (November to May) and a rainy season (June to October).

Fishes where captured by three methods: angled from the beach or a boat; using beach seine (João Vieira island) with a mesh size ranging 0.5 to 1 cm; drift netting from a boat (mesh size 2 cm). Fieldwork was carried out between 2014 and 2016, during three dry seasons (2013/2014, 2014/2015, 2015/2016) and two rainy seasons (2015 and 2016). Fishes were individually weighed to the nearest 0.1 g (if mass < 500 g) or 10 g (if mass > 500 g) and measured with a ruler (< 500 g: nearest 0.1 cm; otherwise to 0.5 cm).

Data analysis

The parameters of LWR were estimated using a linear model on log-log transformed data, represented by $\log W = \log a + b \log TL$, where W is the total mass in g, TL the total length in cm, a the intercept and b the slope of the line (Le Cren 1951, Ricker 1973, Froese 2006). Outliers were removed by plotting log data, following Froese (2006). Statistical analyses were carried out using the software R (R Core Team 2017).

Results

The descriptive statistics and estimated parameters of length–weight relationships for the fish species are given in Table 1. The LWRs of this six fish species were highly significant ($P < 0.001$) with the coefficient of determination (r^2) greater than 0.95 for all species. All species showed a *b* value $2.5 < b < 3.5$ as expected (Froese 2006).

Table 1 - Descriptive statistics and estimated parameters of length–weight relationships ($W = aL^b$) for six species from the Bijagós Archipelago, Guinea-Bissau, captured from 2014 to 2016; N, total number of samples; Min, minimum; Max, maximum; *a*, intercept; *b*, slope; CL, confidence limits; r^2 - coefficient of determination; ^{a} Anti-log *a*.; ¶ No LWR reference in FishBase

			Total length (cm)		Total mass (g)		Regression parameters				
Family	**Species**	**N**	**Min**	**Max**	**Min**	**Max**	a^a	**CL *a* (95%)**	***b***	**CL *b* (95%)**	r^2
Gerreidae	***Eucinostomus melanopterus*** (Bleeker, 1863)	2105	3.1	17.1	0.1	57.3	0.0076	0.0074-0.0078	3.16	3.14-3.17	0.991
	Gerres nigri (Günther, 1859)¶	257	3.5	21.4	0.4	126.6	0.0074	0.0072-0.0077	3.17	3.15-3.19	0.998
Paralichthyidae	***Citharichthys stampflii*** (Steindachner, 1894)¶	55	4.2	13.6	0.6	22.2	0.0046	0.0038-0.0055	3.26	3.18-3.35	0.991
Psettodidae	***Psettodes belcheri*** (Bennett, 1831)¶	28	37.5	50.0	550.0	1450.0	0.0043	0.0015-0.0122	3.26	2.98-3.53	0.958
Scombridae	***Scomberomorus tritor*** (Cuvier, 1832)	377	6.1	96.0	1.3	5100.0	0.0068	0.0066-0.0071	2.95	2.94-2.96	0.999
Sphyraenidae	***Sphyraena afra*** (Peters, 1844)	151	45.3	127.5	415.0	8200.0	0.0061	0.0046-0.0081	2.89	2.83-2.95	0.982

Discussion

This work provides LWR parameters for six species from the Bijagós Archipelago, Guinea-Bissau. All fitted regressions were highly significant. The coefficients of determination (r^2) were very high, indicating a small dispersion of the data and so a very good predictive power. We provide the first LWR records for *Citharichthys stampflii*, *Gerres nigri* and *Psettodes belcheri*. For *Eucinostomus melanopterus*, *Scomberomorus tritor* and *Sphyraena afra* the length ranges presented in this work are wider than the previously published (Froese and Pauly 2017). Also, for *Scomberomorus tritor* and *Sphyraena afra* we present higher coefficient of determination values, indicating a smaller dispersion of the data and a better predictive power comparing with previous works (Kumolu-Johnson and Ndimele 2010, Froese and Pauly 2017).

The information provided here may be useful for future research, as well as for the management of these species.

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CHAPTER 4

Predatory pelagic fishes of the Bijagós Archipelago (Guinea-Bissau) show high overlap in diets dominated by sardinella

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CHAPTER 4

Predatory pelagic fishes of the Bijagós Archipelago (Guinea-Bissau) show high overlap in diets dominated by sardinella

Abstract

Knowledge of trophic interactions between the key components of marine communities is required to understand food-web dynamics and develop ecosystem-based management approaches. In West Africa, where fisheries sustain the livelihoods of a significant part of the human population, this understanding is even more urgent, especially in the face of rapidly expanding fisheries and some stock collapses in the region. We studied the feeding ecology of the Crevalle jack *Caranx hippos*, West African Spanish mackerel *Scomberomorus tritor* and Guinean barracuda *Sphyraena afra* in the Bijagós Archipelago, Guinea-Bissau. These are the most abundant pelagic predatory teleost fishes in the area, but little is known about their ecology despite being species with commercial and recreational value, and they likely also play an important role in various African coastal ecosystems. Our findings show a high degree of dietary overlap among these three predator species, despite some degree of segregation by prey size and type. All three predators depend on Sardinella maderensis as the most important prey, which together with other members of the Clupeidae represented 47–96% of the ingested prey items. There was little difference in the diets of the predators between the dry and rainy seasons. These novel findings suggest a 'wasp-waist'-structured ecosystem in the Bijagós Archipelago in which S. maderensis is the central small-sized pelagic fish species, and stress the need for an ecosystem-based approach to fisheries management in the region, with precautionary measures taken to avoid the overexploitation of clupeids.

Keywords: *Caranx hippos*, clupeids, predator–prey, *Sardinella maderensis*, *Scomberomorus tritor*, *Sphyraena afra*, trophic interactions, wasp-waist ecosystem, West Africa

Introduction

Marine ecosystems are being strongly affected by human activities, with major influences on their productivity, the loss of top predators, and changes in predator–prey interactions affecting several trophic levels (Myers and Worm 2003, Frank et al. 2005, Behrenfeld et al. 2006, Ferretti et al. 2010). Marine ecosystems can be described as being influenced by top-down processes when disturbances at the top of the food web, often driven by overfishing of top predators, influence the entire ecosystem by means of a trophic cascade (Frank et al. 2005). Conversely, marine ecosystems may also be regulated by bottom-up processes when disturbances to lower trophic levels spread upward in the food web (Beaugrand 2004, Frederiksen et al. 2006). However, in upwelling and coastal areas, which are often characterised by highly diverse upper and lower trophic levels and a less diverse intermediate level (Bakun 1996, Cury et al. 2000), marine ecosystems may assume a wasp-waist structure when the trophic dynamics are controlled by the dominant planktivorous small-sized pelagic fishes from the intermediate trophic level (Rice 1995).

Tropical regions are prominently represented among the many important marine ecosystems experiencing disturbances even before their main components and interactions have been studied (Halpern et al. 2008, Stramma et al. 2008, Ferretti et al. 2010). One such ecosystem is the shallow continental-shelf area off Guinea-Bissau (West Africa), on the southern edge of one of the world's major upwelling systems, the Canary Current (Bakun 1996). Guinea-Bissau is a small country relatively dependent on its natural resources; fisheries form one of its main economic activities (Lafrance 1994, Campredon and Cuq 2001) and fish is the main source of protein for the population (Dia and Bedingar 2001). The Bijagós Islands off the coast of Guinea-Bissau form a continental archipelago, comprising about 88 islands, declared a UNESCO biosphere reserve (1996) and Ramsar site (2014). The archipelago is a key area of reproduction and the nursery grounds for several species of fish, marine turtles and marine mammals (Lafrance 1994, Catry et al. 2009, Arkhipov et al. 2015), and it is also internationally recognised for its global importance for the conservation of migratory birds (Salvig et al. 1994, Dodman and Sá 2005). The tropical climate has two distinct seasons: dry (November to May) and rainy (June to October). The local climate is influenced by the Canary Current during the dry season and by the Guinean Current during the rainy season (Pennober 1999). Across the seasons, the sea-surface temperature ranges from 26 to 30 °C and salinity from 36 to 30. Despite these seasonal differences, the species of fish that dominate remain largely unchanged through the year (Lafrance 1994). Considerable efforts have been made in Guinea-Bissau regarding the conservation of marine ecosystems. With a strategy founded on the creation of marine protected areas, approximately 20% of the archipelago's territory is now classified as a nature reserve. Free from industrial fishing, the archipelago serves as a potential refuge area for numerous fish populations. Nevertheless, the increase of industrial and large-scale artisanal fishing in the wider region (Kaczynski and Fluharty 2002) and the consequent harvesting of several fish species in neighbouring areas has led to an increase in seasonal immigrant fishers to the archipelago, mostly for the capture of large predatory fishes (Campredon and Catry 2016). However, virtually nothing is known about the ecology of the fish communities in this important shallow coastal area.

This study investigated the diet of the three most abundant coastal pelagic predators in the Bijagós Archipelago: the Crevalle jack *Caranx hippos*, the West African Spanish mackerel *Scomberomorus tritor* and the Guinean barracuda *Sphyraena afra*. These fishes are important components of several ecosystems along the coast of West Africa, though few studies have addressed their foraging ecology (e.g. Fagade and Olaniyan 1973, Kwei 1978, Lafrance 1994). All three species are of commercial interest and are consumed by humans (Fischer et al. 1981), including in the Bijagós Archipelago. The species are also extremely important in terms of recreational fisheries, attracting sports fishers from abroad (Campredon and Catry 2016), thus contributing to the national economy (Dia and Bedingar 2001, Belhabib et al. 2016). Hence, understanding the foraging habits and prey types of the main predatory fishes in the Bijagós Archipelago has potential value for the management of this important marine ecosystem. Our objectives were to: (a) describe the diets of *C. hippos*, *S. tritor* and *S. afra*; (b) evaluate the trophic segregation and overlap of these three predators in the dry and rainy seasons; and (c) identify important common prey, which may have a major role in the dynamics of the regional ecosystem.

Methods

Study area

Fieldwork was carried out in João Vieira and Poilão Marine National Park (hereafter, JVPMNP), situated in the southeast section of the Bijagós Archipelago (10°57' N, 15°42' W; Figure 1). The JVPMNP consists of four islands and two islets and an extensive area of sea, and has a total surface area of 495 km^2 of which only 17 km^2 are terrestrial. The area is characterised by shallow waters, usually not exceeding 20 m depth, with several sandbanks, some of which are permanently exposed.

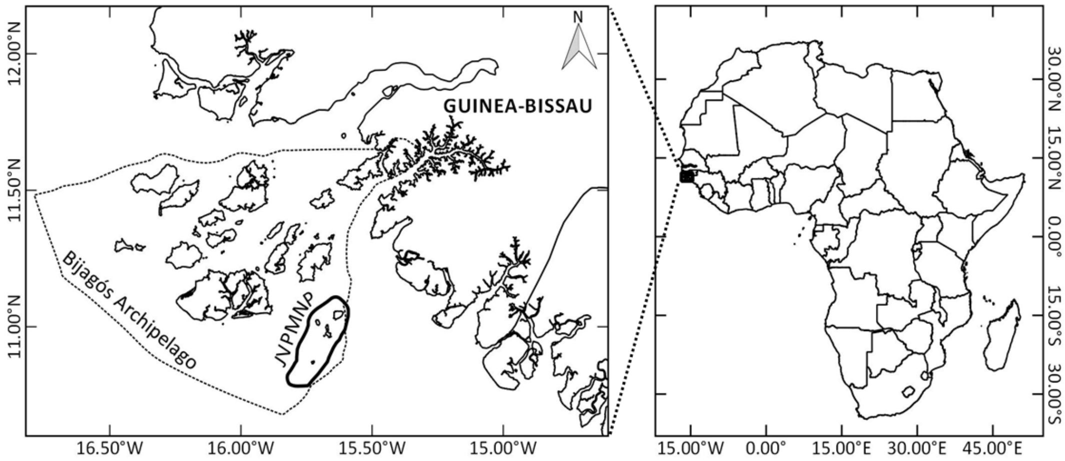

Figure 1 - Location of the João Vieira and Poilão Marine National Park (JVPMNP), indicated by a solid line; the dashed line delimits the Bijagós Archipelago Biosphere Reserve, Guinea-Bissau

Sample collection of fish and stomach contents

Fish were caught using artificial bait (lures), from the beach (João Vieira island) or from a small boat (approximately 8 m long), over a total of 140 fishing days between March 2014 and September 2016 (99 days during the dry season, and 41 during the rainy season). Live bait was never used.

All fish were weighed with a spring balance (total mass to the nearest 10 g) and measured with a ruler (total length [TL] to the nearest 5 mm). The stomach contents of each fish were collected and stored in ethanol until further processing.

Laboratory processing

Food items in the fish stomachs were sorted using a stereomicroscope, and prey were identified to the lowest possible taxonomic level. The prey items were identified through comparison with a large reference collection of hard structures (i.e. otoliths, vertebrae and other diagnostic bones) representing a large variety of local species (captured within the scope of complementary studies). Prey taxa were counted and weighed (to the nearest 0.01 g). The prey items discovered were classified according to the degree of their digestion: state I – prey item intact or nearly intact, with most skin remaining; state II – most of the skin and some of the soft parts digested; state III – most of the soft parts digested. Only prey taxa in states I and II were weighed.

Data analysis

Overlap between the diets of the predatory fishes was measured by calculating the Morisita–Horn similarity index on numerical frequency data (Morisita 1959, Horn 1966), between seasons, for each of the predator species and between the predators, following the equation:

$$C_{jk} = \frac{2 \sum_i x_{ij} x_{ik}}{\sum_i x_{ij} \sum_i x_{ik} \left(X_j + X_k\right)}$$

where x_{ij} is the number of individuals of prey i in the feeding regime of predator j, and x_{ik} is the number of individuals of prey i in the feeding regime of predator k:

$$X_j = \frac{\sum_i x_{ij}^2}{\left(\sum_i x_{ij}\right)^2} \text{ and } X_k = \frac{\sum_i x_{ik}^2}{(\sum_i x_{ik})^2}$$

This index varies from 0, indicating that feeding regimes are completely distinct, to 1, when they are identical; diet overlap can be considered to be significant when the index is greater than 0.6

(Langton 1982). The index was calculated based on prey taxa identified to the lowest possible taxonomic level.

To evaluate the diet diversity within each predator, we further calculated the Shannon-Wiener diversity index (Brower et al. 1998) based on the numerical frequency at the lowest taxonomic level identified, following the equation:

$$H' = -\sum p_i \log_e p_i \ ,$$

where p_i is the proportion of individuals from the species i in relation to all individuals found. To avoid any bias in comparing diversity indices of predators based on different sample sizes (i.e. different numbers of stomachs), we calculated rarefied diversity indices by repeatedly resampling a similar number of stomachs from each predator (N = 64, corresponding to the smallest sample in our dataset, obtained from *S. afra*). Resampling was carried out 1 000 times for each predator, and the diversity indices presented were the median of these values, and confidence intervals (CI) were calculated by the percentile method (as the 0.025 and 0.975 quantiles; Efron 1981). Taxa that occurred only once for all three predator species together were excluded from the above analysis.

In order to describe the presence and importance of each prey taxon in the diets of the three predatory fishes, we calculated the frequency of occurrence (FO%) as the number of samples with a given prey taxon, in relation to the total number of sampled fish, and the numerical frequency (N%) as the number of individuals of a given taxon in relation to the total number of prey individuals. Prey mass was not used in the calculation of an index because of the small number of prey items of digestion states I and II. An index of vacuity was used to express the number of empty stomachs encountered as a percentage of the total stomachs collected.

Feeding strategy was examined using the modified Costello diagram (Costello 1990, Amundsen et al. 1996). This diagram represents the frequency of occurrence (FO%) and prey-specific abundance of each prey taxon (P_i%), the latter reflecting the number of individuals of a prey i (S_i)

in relation to the total number of prey individuals (S_{ti}) found in stomachs containing the prey *i* (Amundsen et al. 1996), following the equation:

$$P_i = \left(\frac{\sum S_i}{\sum S_{\mathrm{ti}}} \right) \times 100$$

Information about prey importance and feeding strategy of the predator is given by the distribution of the points along the diagonals and the axes of the diagram (Figure 2). As several items could only be identified to family level, Costello diagrams were made at fish family level and at Malacostraca and Cephalopoda class level. Taxa that occurred only once were excluded.

In order to test for differences in prey species size between predatory fish, we performed an ANCOVA using the predator species as factor, predator mass as covariate and prey mass as dependent variable. Statistical analyses were carried out using the software R (R Core Team 2017).

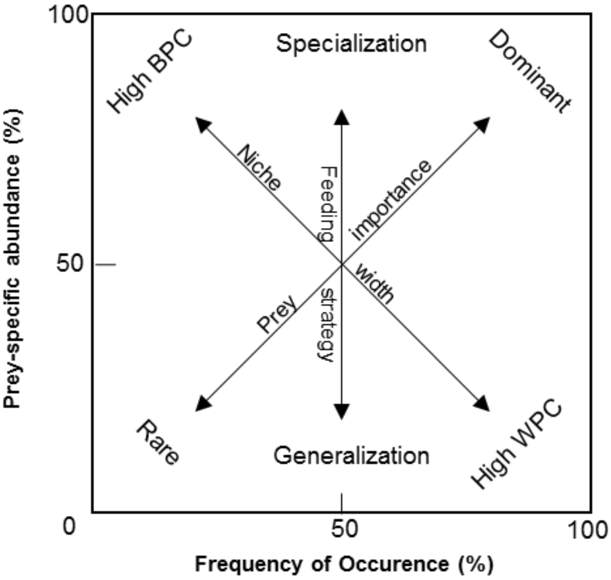

Figure 2 - The Costello diagram (modified from Figure 3 in Amundsen et al. [1996]) for interpretation of feeding strategy, niche width contribution, and prey importance. BPC = between- phenotype component; WPC = within-phenotype component

Results

A total of 130 *C. hippos*, 238 *S. tritor* and 160 *S. afra* were captured, and had vacuity indices of 9%, 50% and 53%, respectively. *Caranx hippos* had a median total length (TL) of 53.5 cm (ranging from: 42.0 to 82.5 cm) and a median total mass (TM) of 1 775 g (900 to 5 400 g); *S. tritor* had a median TL of 52.5 cm (40.0 to 76.5 cm) and a median TM of 815 g (360 to 2 650 g) and *S. afra* had a median TL of 84.8 cm (36.5 to 135.0 cm) and a median TM of 2 350 g (200 to 9 500 g).

Fishes from 14 different families were identified in sampled stomachs (Table 1). Prey that were too small and/or too digested or lacked a corresponding known item from the reference collection could not be identified. These represented approximately 15% of all prey items (Table 1).

Diet overlap between seasons for each predator was very high, indicating no differences in diet between the seasons (Horn-Morisita index between 0.89–0.98, Figure 3). The diet of *S. tritor* and *C. hippos* was rather similar, and while *S. afra* formed a separate group, the linkage value still suggested a high dietary overlap (index = 0.75, Figure 3). We therefore grouped data from the two seasons in all subsequent analysis (see Supplementary material, Table S1 and S2, for detailed data of predators in both seasons). Despite this pattern of similarity, the (rarefied) dietary diversity of *S. tritor* (median = 0.80, 95% CI = [0.65, 0.92]) was significantly lower (i.e. with no overlap in 95% CI) than that of both *C. hippos* (median = 1.81, CI = [1.57, 2.04]) and *S. afra* (median = 2.17, CI = [1.79, 2.45]).

Clupeidae was the dominant prey family for both *C. hippos* and *S. tritor*, as shown by its upper-right location on the Costello diagram (Figure 4). In terms of specialisation, all three predators showed a strong reliance on Clupeidae (upper part of the diagram). All other prey for *C. hippos* and *S. tritor* are located in the lower part of the diagram indicating that they are taken opportunistically (Figure 2). *Sphyraena afra* did not present any dominant prey (Figure 4).

Mean number of prey per stomach was 1.44 (SD 1.41) for *S. afra*, 5.74 (SD 6.15) for *C. hippos* and 5.47 (SD 5.68) for *S. tritor*. After accounting for the effect of predator mass, we found significant differences in the (log) mass of prey consumed by the three species, with *S. tritor* feeding on the lightest prey and *S. afra* consuming the heaviest items (ANCOVA: effect of prey mass, $F_{1, 108} = 79.3$, $P < 0.001$; effect of predator, $F_{2, 108} = 36.1$, $P < 0.001$).

Table 1 - Frequency of occurrence (FO%) and numerical frequency (N%) of prey in stomachs of *Caranx hippos*, *Scomberomorus tritor* and *Sphyraena afra*. Sample sizes in parenthesis represent number of stomachs analysed (for FO%) and total number of prey items (for N%). n.i. - not identified prey

		Caranx hippos		*Scomberomorus tritor*		*Sphyraena afra*	
		FO% (N=118)	N% (N=677)	FO% (N=119)	N% (N=651)	FO% (N=75)	N% (N=109)
OSTEICHTHYES							
Albulidae	*Albula vulpes*	8.5	3.3	0.8	0.2	1.3	0.9
Belonidae	Belonidae n.i.	0.9	0.1	0.8	0.2	5.3	3.7
Carangidae		1.7	0.3	0.0	0.0	1.3	0.9
	Hemicaranx bicolor	0.9	0.1	0.0	0.0	0.0	0.0
	Carangidae n.i.	0.9	0.1	0.0	0.0	1.3	0.9
Clupeidae		89.0	76.1	95.8	97.5	41.3	47.2
	Sardinella aurita	2.6	0.4	0.0	0.0	1.3	0.9
	Sardinella maderensis	61.9	47.9	83.2	73.6	34.7	40.7
	Clupeidae n.i.	49.6	27.8	41.2	24.0	6.7	5.6
Elopidae	Elops n.i.	0.0	0.0	0.0	0.0	1.3	0.9
Gerreidae		18.8	5.6	0.8	0.2	4.0	2.8
	Eucinostomus melanopterus	14.5	4.1	0.8	0.2	1.3	0.9
	Gerres nigri	6.8	1.2	0.0	0.0	2.7	1.9
	Gerreidae n.i.	0.9	0.3	0.0	0.0	0.0	0.0
Haemulidae	Pomadasys n.i.	14.5	3.8	0.8	0.3	12.0	9.3
Mugilidae		5.1	1.3	0.0	0.0	12.0	8.3
	Mugil bananensis	0.9	0.1	0.0	0.0	2.7	1.9
	Mugil curema	0.9	0.1	0.0	0.0	0.0	0.0
	Liza n.i.	0.9	0.1	0.0	0.0	0.0	0.0
	Mugil n.i.	2.6	0.7	0.0	0.0	5.3	3.7
	Mugilidae n.i.	0.9	0.1	0.0	0.0	4.0	2.8
Paralichthyidae	*Citharichthys stampflii*	0.0	0.0	0.0	0.0	1.3	0.9
Polynemidae	*Galeoides decadactylus*	12.0	2.1	0.0	0.0	13.3	10.2
Pristigasteridae	*Ilisha africana*	6.8	2.8	0.8	0.2	0.0	0.0
Sciaenidae		0.9	0.1	0.0	0.0	1.3	0.9
	Pseudotolithus elongatus	0.0	0.0	0.0	0.0	1.3	0.9
	Sciaenidae n.i.	0.9	0.1	0.0	0.0	0.0	0.0
Scombridae	*Scomberomorus tritor*	0.0	0.0	0.8	0.2	4.0	2.8
Serranidae	Serranidae n.i.	0.9	0.1	0.0	0.0	0.0	0.0
Sparidae	Sparidae n.i.	0.9	0.1	0.0	0.0	0.0	0.0
Unidentified fish		17.1	2.7	4.2	0.9	21.3	11.0
MALACOSTRACA		6.8	1.2	4.2	0.5	1.3	0.9
Decapoda	Callinectes n.i.	0.9	0.1	0.0	0.0	0.0	0.0
	Crab n.i.	3.4	0.6	0.0	0.0	0.0	0.0
	Shrimp n.i.	2.6	0.4	4.2	0.5	1.3	0.9
CEPHALOPODA							
	Cephalopoda n.i.	1.7	0.3	0.0	0.0	0.0	0.0

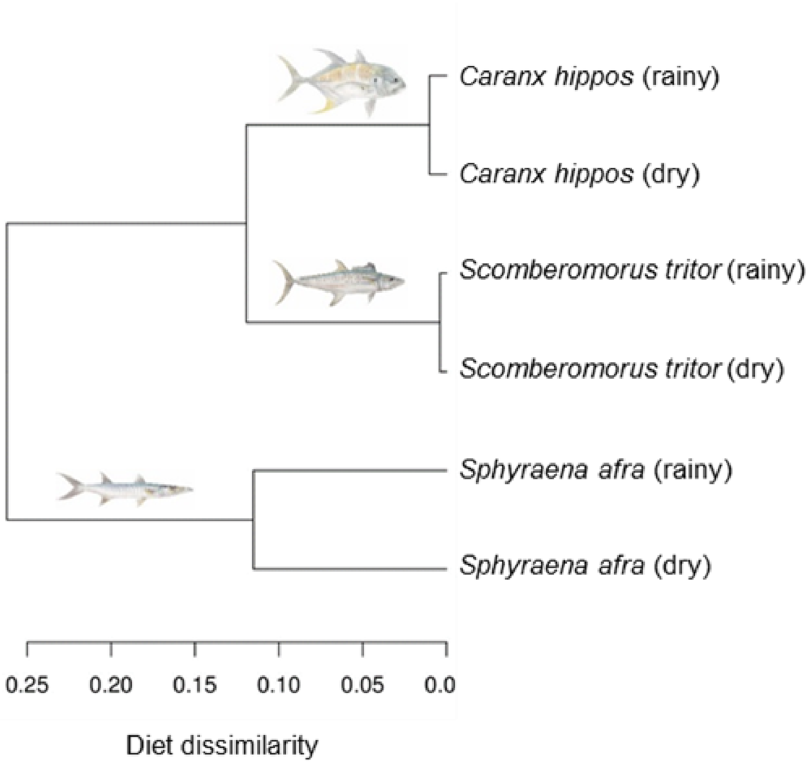

Figure 3 - Cluster analysis of diet dissimilarity, obtained by subtracting Morisita-Horn indices from '1,' as distance metrics among *Caranx hippos*, *Scomberomorus tritor* and *Sphyraena afra*, sampled at JVPMNP in each season (dry and rainy) (fish drawings by Pedro Fernandes).

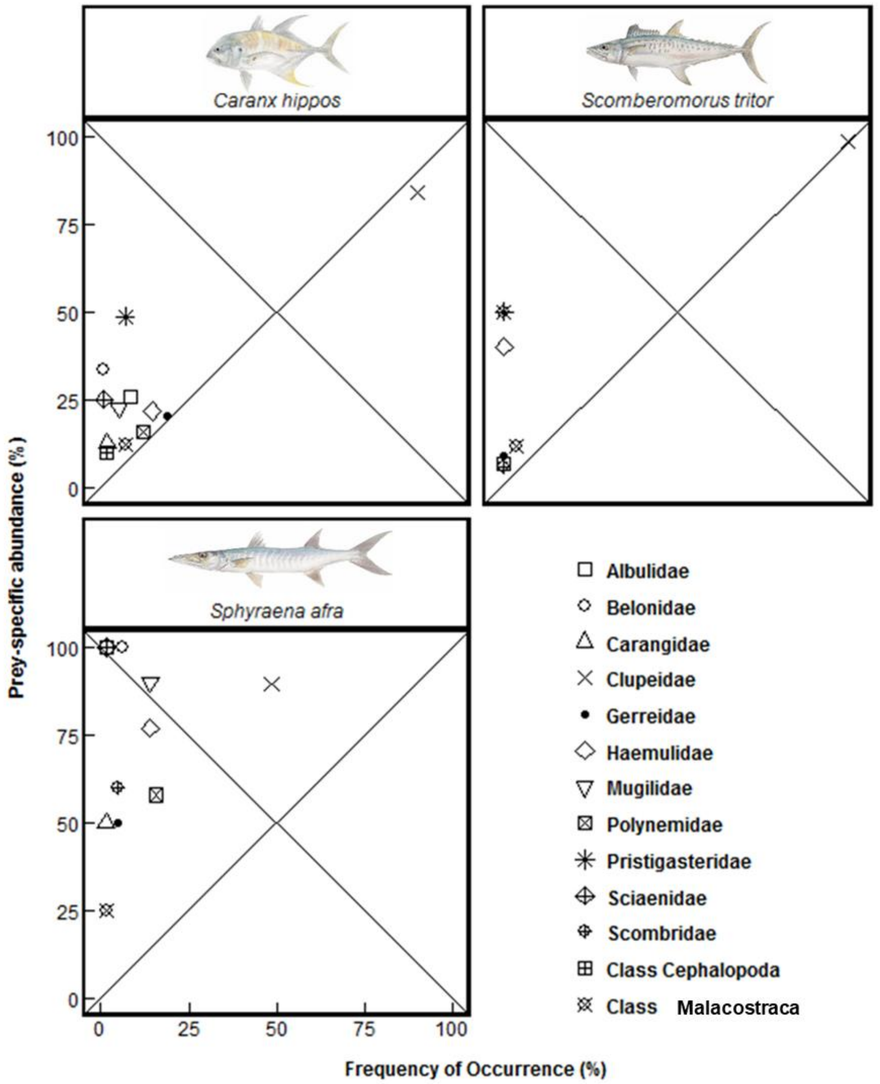

Figure 4 - Costello diagrams representing prey-specific abundance in relation to frequency of occurrence of prey taxa (fishes grouped by families, and Malacostraca and Cephalopoda grouped by classes) for *Caranx hippos*, *Scomberomorus tritor* and *Sphyraena afra* sampled at the Bijagós Archipelago. Diagonal lines represent the importance of the prey taxa (positive slope diagonal) and their contribution to niche width (negative slope diagonal) (see Amundsen et al. [1996] for details of this method), (fish drawings by Pedro Fernandes)

Discussion

This study highlights the key role of *Sardinella maderensis* in the diet of the most abundant predatory teleosts of the Bijagós Archipelago. The common reliance on sardinella indicates a high trophic overlap between predators, which may increase their dietary competition. Still, the level of competition is probably reduced since *S. afra* preys on larger individuals in relation to the other two, and *C. hippos* may segregate from *S. tritor* by exploring habitats not much used by the latter species. Our study further showed no major differences in the diet of the three predatory fishes between seasons.

Scomberomorus tritor and *C. hippos* have diets dominated only by clupeids (mainly *S. maderensis*). Moreover, these predators show a feeding strategy specialised in consuming Clupeidae, taking other types of prey more opportunistically, with the exception of Belonidae and Pristigasteridae (*Ilisha africana*) by *S. tritor* (the data- points overlap in Figure 4), and Pristigasteridae (*I. africana*) by *C. hippos* (Figure 4). This pattern is less distinct in *S. afra*, which consumes sardinella less frequently though still in high numbers. The high occurrence of Clupeidae in the diets of the three predators might be related to the high abundance of clupeids in the area. Nonetheless, a diet dominated by clupeiforms among species of *Caranx*, *Scomberomorus* and *Sphyraena* has been reported in other areas off West Africa, including Nigeria, Ghana and Ivory Coast (Fagade and Olaniyan 1973, Kwei 1978, Akadje et al. 2013).

As with most *Sphyraena* species (de Sylva 1963, Paterson 1998), *S. afra* apparently aggregates in shoals, as several individuals were often captured in quick succession in the same general area. *Caranx hippos* and *S. tritor* were often observed foraging together, hunting in large multispecific schools. On several occasions we observed schools of numerous *C. hippos and S. tritor* feeding at the sea surface, creating surface-water turbulence. Sometimes it was possible to see small pelagic fish jumping above the surface or onto the beaches (when observed in very shallow areas close to the beach) and at times we also saw the predators jumping into the air (mainly *S. tritor*). This joint feeding activity might explain the greater similarity in their diets compared with *S. afra*. The association of *Caranx* with other species for feeding is well known in other systems (e.g. Potts 1980). Clupeidae are highly abundant in the Bijagós Archipelago (Lafrance 1994), but probably have a patchy distribution, and hence, by schooling, predators are likely to increase their ability to locate, encircle and capture clupeid prey. *Scomberomorus tritor* seems to prey almost exclusively on Clupeidae, whereas *C. hippos* (and *S. afra*) have a more diverse diet. This might relate to *S. tritor* being more restricted to the epipelagic zone (Collette and Nauen 1983) whereas *C. hippos* and *S. afra* are more likely to capture prey occupying other habitats, including species that live closer to the bottom (Silvano 2001, Paugy et al. 2003). The presence of demersal prey in their diet (e.g. Mugilidae, Polynemidae; Table 1) supports this hypothesis to some extent. Differences in diet can also be related to the fact that *S. afra*, through being larger and having a wider mouth with stronger teeth, is able to capture larger prey, when compared with *C. hippos* and *S. tritor* (Paugy et al. 2003).

Caranx hippos and *S. tritor* are active feeders (Fagade and Olaniyan 1973, Kwei 1978) and they tend to prey on large numbers of smaller prey than what is consumed by *S. afra*. However, *S. tritor* presented a high vacuity index (50%). This species was observed to regularly regurgitate its prey during the capture process (although we did not quantify these events). Also, while removing the digestive tract of this species we noticed that in some individuals the stomach was completely everted towards the mouth, as has been observed in certain elasmobranch species (e.g. Sims et al. 2000, Brunnschweiler et al. 2005). These observations suggest that the high vacuity index observed for *S. tritor* may to some extent be due to this particular response. Conversely, *S. afra* and *C. hippos* were never observed regurgitating. The high vacuity index (53%) likewise found in *S. afra* may be related to the fact that barracudas are considered lie-in-wait predators, ingesting their prey in a rapid lunge (Porter and Motta 2004) and often only a single prey item at a time (de Sylva 1963, Randall 1967). All three fish predators are known to exhibit diurnal feeding patterns, and our sampling protocol of fishing during daylight hours and at times until dusk should not have affected the results (de Sylva 1963, Randall 1967, Kwei 1978).

Sardinella maderensis is considered to be one of the most important small-sized pelagic species in coastal waters of West Africa and the eastern central Atlantic region (Valdés and Déniz-González 2015). It is also one of the three most important commercial clupeids in this region, where the stock is considered to be overfished (FAO 2011, Polidoro et al. 2016). The declines observed in this species led to it being assessed as Vulnerable by the IUCN (Polidoro et al. 2016). Our study highlights the importance of *S. maderensis* as a key prey of the most abundant predator fish species in the Bijagós Archipelago, and it probably plays a key role as a forage species for these and other marine predators in this unique marine ecosystem. Wasp-waist marine ecosystems are dominated by one or a few species of pelagic fishes of intermediate trophic level, which consequently exercise a top-down control of plankton and a bottom-up control of top predators (Rice 1995). Such systems have been described in other upwelling and coastal areas (Bakun 1996, Gibbons et al. 1999, Fauchald et al. 2011), and in some cases with clupeids as the dominant pelagic fishes (Fauchald et al. 2011, Atkinson et al. 2014). Here, we suggest that the Bijagós Archipelago represents a wasp-waist ecosystem, with the population of Sardinella maderensis likely exerting a main influence on the distribution and abundance of the predator fishes as well as that of the plankton on which the clupeid feeds.

The decline of clupeid populations due to intense industrial fishing in the region (FAO 2016, Polidoro et al. 2016) may therefore have a direct impact on the distribution and abundance of several important predatory fishes, such as the three species studied here, which to date have apparently been abundant in the Bijagós Archipelago and are an important resource to the human communities there. Ultimately, shifts in the marine communities of coastal West Africa will potentially impact the small-scale artisanal, subsistence and recreational fishing sectors, affecting livelihoods in the region and local economies. Our findings highlight the need for ecosystem-based management of the fisheries in Guinea-Bissau and the West Africa region - with important consideration of the interactions and trophic links between different species, to ensure sustainable use of the natural marine resources by the generally impoverished local communities (NMFS 1996, Garcia et al. 2003). Here, we provide evidence that a collapse of the Sardinella maderensis stock (and other clupeid species) would likely impact the Bijagós Archipelago marine ecosystem as a whole and consequently the human communities on these islands.

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Supplementary material

Table S1 - Frequency of occurrence (FO%) of prey in stomachs of *Caranx hippos*, *Scomberomorus tritor* and *Sphyraena afra*, separated by dry and rainy season; Sample sizes (N) represent number of stomachs analysed. n.i. - not identified.

		Caranx hippos		***Scomberomorus tritor***		***Sphyraena afra***	
		FO% dry (93)	FO% rainy (25)	FO% dry (100)	FO% rainy (19)	FO% dry (29)	FO% rainy (46)
OSTEICHTHYES							
Albulidae	*Albula vulpes*	6.5	16.0	1.0	0.0	0.0	2.2
Belonidae	Belonidae n.i.	1.1	0.0	1.0	0.0	10.3	2.2
Carangidae		2.2	0.0	0.0	0.0	0.0	0.0
	Hemicaranx bicolor	1.1	0.0	0.0	0.0	0.0	0.0
	Carangidae n.i.	1.1	0.0	0.0	0.0	0.0	2.2
Clupeidae		89.2	88.0	95.0	100.0	41.4	41.3
	Sardinella aurita	0.0	12.0	0.0	0.0	0.0	2.2
	Sardinella maderensis	59.1	72.0	83.0	84.2	31.0	37.0
	Clupeidae n.i.	53.8	32.0	41.0	42.1	10.3	4.3
Elopidae	Elops sp.	0.0	0.0	0.0	0.0	0.0	2.2
Gerreidae		16.1	28.0	1.0	0.0	0.0	0.0
	Eucinostomus melanopterus	14.0	16.0	1.0	0.0	0.0	2.2
	Gerres nigri	5.4	12.0	0.0	0.0	0.0	4.3
	Gerreidae n.i.	1.1	0.0	0.0	0.0	0.0	2.2
Haemulidae	Pomadasys sp.	17.2	4.0	1.0	0.0	17.2	8.7
Mugilidae		3.2	12.0	0.0	0.0	13.8	10.9
	Mugil bananensis	1.1	0.0	0.0	0.0	3.4	2.2
	Mugil curema	1.1	0.0	0.0	0.0	0.0	0.0
	Liza sp.	0.0	4.0	0.0	0.0	0.0	0.0
	Mugil sp.	0.0	12.0	0.0	0.0	6.9	4.3
	Mugilidae n.i.	1.1	0.0	0.0	0.0	3.4	4.3
Paralichthyidae	*Citharichthys stampflii*	0.0	0.0	0.0	0.0	0.0	2.2
Polynemidae	*Galeoides decadactylus*	9.7	20.0	0.0	0.0	6.9	17.4
Pristigasteridae	*Ilisha africana*	5.4	12.0	1.0	0.0	0.0	0.0
Sciaenidae		1.1	0.0	0.0	0.0	0.0	0.0
	Pseudotolithus elongatus	0.0	0.0	0.0	0.0	0.0	2.2
	Sciaenidae n.i.	1.1	0.0	0.0	0.0	0.0	0.0
Scombridae	*Scomberomorus tritor*	0.0	0.0	1.0	0.0	10.3	0.0
Serranidae	Serranidae n.i.	0.0	4.0	0.0	0.0	0.0	0.0
Sparidae	Sparidae n.i.	1.1	0.0	0.0	0.0	0.0	0.0
Unidentified fish		18.3	12.0	5.0	0.0	24.1	19.6
MALACOSTRACA		6.5	8.0	0.0	0.0	0.0	0.0
Decapoda	Callinectes sp.	1.1	0.0	0.0	0.0	0.0	0.0
	Crab n.i.	4.3	0.0	0.0	0.0	0.0	0.0
	Shrimp n.i.	1.1	8.0	5.0	0.0	3.4	0.0
CEPHALOPODA							
	Cephalopoda n.i.	0.0	8.0	0.0	0.0	0.0	0.0

Table S2 - Numerical frequency (N%) of prey items found in stomachs of *Caranx hippos*, *Scomberomorus tritor* and *Sphyraena afra*, separated by dry and rainy season; Sample sizes (N) represent total number of prey (N%). n.i. - not identified.

		Caranx hippos		***Scomberomorus tritor***		***Sphyraena afra***	
		N% dry (532)	N% rainy (145)	N% dry (569)	N% rainy (82)	N% dry (41)	N% rainy (68)
OSTEICHTHYES							
Albulidae	*Albula vulpes*	3.2	3.4	0.2	0.0	0.0	1.5
Belonidae	Belonidae n.i.	0.2	0.0	0.2	0.0	7.3	1.5
Carangidae		0.4	1.4	0.0	0.0	0.0	0.0
	Hemicaranx bicolor	0.2	0.0	0.0	0.0	0.0	0.0
	Carangidae n.i.	0.2	0.0	0.0	0.0	0.0	1.5
Clupeidae		77.3	71.7	97.2	100.0	43.9	48.5
	Sardinella aurita	0.6	0.0	0.0	0.0	0.0	1.5
	Sardinella maderensis	48.5	45.5	72.8	79.3	34.1	44.1
	Clupeidae n.i.	28.2	26.2	24.4	20.7	9.8	2.9
Elopidae	Elops sp.	0.0	0.0	0.0	0.0	0.0	1.5
Gerreidae		5.6	5.5	0.2	0.0	0.0	4.4
	Eucinostomus melanopterus	4.3	3.4	0.2	0.0	0.0	1.5
	Gerres nigri	0.9	2.1	0.0	0.0	0.0	2.9
	Gerreidae n.i.	0.4	0.0	0.0	0.0	0.0	0.0
Haemulidae	Pomadasys sp.	4.7	0.7	0.4	0.0	14.6	5.9
Mugilidae		0.6	4.1	0.0	0.0	9.8	7.4
	Mugil bananensis	0.2	0.0	0.0	0.0	2.4	1.5
	Mugil curema	0.2	0.0	0.0	0.0	0.0	0.0
	Liza sp.	0.0	0.7	0.0	0.0	0.0	0.0
	Mugil sp.	0.0	3.4	0.0	0.0	4.9	2.9
	Mugilidae n.i.	0.2	0.0	0.0	0.0	2.4	2.9
Paralichthyidae	*Citharichthys stampflii*	0.0	0.0	0.0	0.0	0.0	1.5
Polynemidae	*Galeoides decadactylus*	1.7	3.4	0.0	0.0	4.9	13.2
Pristigasteridae	*Ilisha africana*	2.1	5.5	0.2	0.0	0.0	0.0
Sciaenidae		0.2	0.0	0.0	0.0	0.0	0.0
	Pseudotolithus elongatus	0.0	0.0	0.0	0.0	0.0	1.5
	Sciaenidae n.i.	0.2	0.0	0.0	0.0	0.0	0.0
Scombridae	*Scomberomorus tritor*	0.0	0.0	0.2	0.0	7.3	0.0
Serranidae	Serranidae n.i.	0.0	0.7	0.0	0.0	0.0	0.0
Sparidae	Sparidae n.i.	0.2	0.0	0.0	0.0	0.0	0.0
Unidentified fish		2.8	2.1	1.1	0.0	9.8	11.8
MALACOSTRACA		1.1	1.4	0.0	0.0	0.0	0.0
Decapoda	Callinectes sp.	0.2	0.0	0.0	0.0	0.0	0.0
	Crab n.i.	0.8	0.0	0.0	0.0	0.0	0.0
	Shrimp n.i.	0.2	1.4	0.5	0.0	2.4	0.0
CEPHALOPODA							
	Cephalopoda n.i.	0.0	1.4	0.0	0.0	0.0	0.0

CHAPTER 5

The diet of two opportunistic seabirds (Caspian and Royal Terns) confirms the importance of sardinella in West African coastal food webs

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CHAPTER 5

The diet of two opportunistic seabirds (Caspian and Royal Terns) confirms the importance of sardinella in West African coastal food webs

Abstract

Despite their importance for fisheries, livelihoods and biodiversity conservation, shelf ecosystems in West Africa are poorly known. Caspian Tern (*Hydroprogne caspia*) and Royal Tern (*Thalasseus maximus*) are two of the most numerous and widespread nesting seabirds in the region, and an understanding of the diet of these opportunistic predators may throw light on important elements of the local food webs. This study describes and compares the prey consumed by these two species in Guinea and Guinea-Bissau, and presents for the first time a comprehensive diet dataset for West African Royal Tern (*T. m. albididorsalis*), which may be split from the nominal American race in the near future. Results show that both species feed largely on clupeids (mostly *Sardinella maderensis*), which dominate the diet at all locations and seasons. This finding strengthens the recent suggestion of a wasp-waist ecosystem for our study area, with sardinella as the key prey for several predators, including seabirds and pelagic fishes, and potentially influencing their distribution and abundance.

Keywords: *Hydroprogne caspia*, *Thalasseus maximus albididorsalis*, Bijagós Archipelago, *Sardinella maderensis,* wasp-waist ecosystem

Introduction

Shelf ecosystems in West Africa south of Mauritania are poorly known, despite their importance for fisheries, livelihoods and biodiversity conservation (Campredon & Cuq 2001, Tandstad et al. 2014). In this region, Terns (Laridae) form a major component of seabird communities, which are represented by relatively few species. From Senegal to Guinea, the two most abundant and widespread nesting seabirds are Caspian (*Hydroprogne caspia*) and Royal Terns (*Thalasseus maximus*), but little has been published on their ecology, in line with the scarcity of information on most components of the ecosystems where they live (van Roomen et al. 2015). Knowledge of the diet of these representative seabird species is badly needed to enhance the current understanding of community composition and trophic interactions on the shelf marine areas of West Africa, as well as to inform seabird conservation in the region.

The Caspian Tern has a widespread distribution, with breeding populations on five continents. In West Africa the breeding population is currently estimated at 45,000 - 60,000 individuals (Wetlands International 2015; van Roomen et al. 2015). The Royal Tern is divided into two subspecies, *T. m. maximus*, present in America and *T. m. albididorsalis* in West Africa. Recent genetic evidence suggested that the West African Royal Tern subspecies should be split and considered a species on its own right (Collinson et al. 2017). The breeding range of this potential new species is restricted, extending from Mauritania to Guinea (del Hoyo et al. 1996) with a breeding population of ca. 255,000 – 315,000 birds (Wetlands International 2015, van Roomen et al. 2015). As with other seabirds nesting on low-lying islands, the West African Royal Tern suffers from important threats, from sea-level rise (leading to inundation of nesting sites; McLean and Tsyban 2001, Baker et al. 2006) to disturbance at breeding colonies, but its biology and conservation needs are still poorly documented in the literature.

Our aim here was to describe and compare the diet of the two most abundant breeding Terns in Guinea-Bissau and Guinea, Caspian and West African Royal Tern, based on analysis of pellets. In doing this, we present here data on the diet of the potentially new species, the West African Royal Tern (but see Dunn 1972, Veen et al. 2018). We further compare two methods for quantifying the diet of both Terns, one based on the examination of all hard structures (e.g. otoliths, vertebrae, scales) and another one based only on otoliths, as their performances can vary substantially (e.g. Granadeiro and Silva 2000, Alonso et al. 2013). Finally, based on our data and a literature review, we discuss the dietary segregation and foraging ecology of these two taxa.

Methods

Study area

Fieldwork was carried out in five islands in the Bijagós archipelago, Guinea-Bissau, and one island in Guinea (Naufrage, see Figure 1). Besides important breeding populations of these two Tern species, during the boreal winter the region holds internationally significant numbers of other Tern species that come from Europe and North Africa (del Hoyo et al. 1996, van Roomen et al. 2015, Veen et al. 2015).

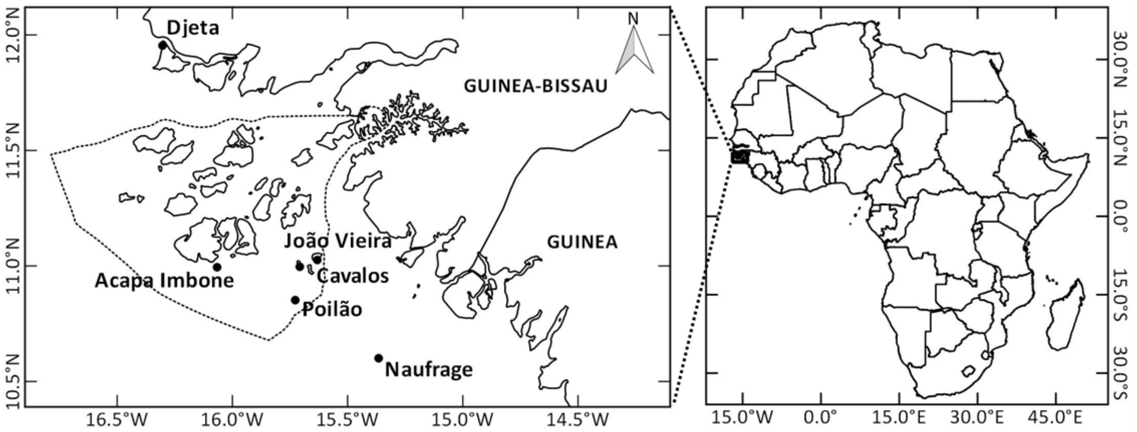

Figure 1 - Study area with the sampled sites marked with points, five of which in Guinea-Bissau (Djeta, João Vieira, Cavalos, Poilão and Acapa Imbone) and one in Guinea (Naufrage); dashed line delimits the Bijagós Archipelago Biosphere Reserve, Guinea-Bissau; zoomed in from the African continent map

Sample collection and laboratory processing

Pellets were collected from 2013 to 2015. Pellets from Naufrage, Acapa Imbone and Djeta (Figure 1) were collected in the breeding colonies when most of the birds were still incubating. We never collected pellets in areas with chicks, therefore pellets correspond to the diet of adult birds. Pellets of Royal Tern collected in Poilão, Cavalos and Poilão (Figure 1) were collected from roosts without the presence of Caspian Tern, therefore we were sure they correspond to Royal Terns.

Entire pellets were stored separately in plastic bags for examination in the laboratory. Samples were then sorted under binocular microscope, and all relevant structures (e.g. fish bones, dentaries, otoliths and scales) were stored dry, and identified to the lowest taxonomic level by comparison with our own reference material, consisting of an extensive collection of fish species from Guinea-Bissau collected during the course of this study. The number of fish in each pellet was estimated from the largest number of similar-sized/shaped pair structures (e.g. otoliths) or from the number of unpaired remains (e.g. diagnostic vertebrae).

Data analysis

To describe the presence and importance of each prey taxon in the diet of Terns we calculated the frequency of occurrence (FO%) as the percentage of pellets containing a given prey taxon and numerical frequency (N%) as the percentage of each prey item in relation to total number of prey items found. However, as pellets contained a low mean number of prey individuals (1.63 ± 0.77 (SD) in Caspian Tern and 1.67 ± 0.82 (SD) in Royal Tern), we present only FO% as it provides the most robust measure of diet composition (Baker et al. 2014). Data expressed as numerical frequencies were very similar to data calculated as frequency of occurrence, so analyses were only based the former (but see Supplementary material, Table S1, S2 and S3). We present the results at the species, family and prey domain level (based on the information from each species from the literature). The domain of each prey taxon was categorized as: *pelagic* – mainly marine species, living from surface to 1000 m depth; *benthopelagic* – mainly marine species, living near the bottom as well as in midwaters or near the surface; *benthic* – mainly marine species, that live on or near the bottom; *euryhaline* – species that are more often found on continental aquatic systems such as rivers and lakes, despite having salinity tolerance to enter and live in the ocean; and *freshwater* - as species that are only found on continental aquatic systems (Fischer et al. 1981, Froese and Pauly 2017). Moreover, we categorized each prey taxon (also based on published sources), into *coastal* – pelagic species living over the continental shelf or *offshore* – species occurring mostly on open ocean, beyond the continental shelf. Finally, prey were categorized as *schooling* - species that frequently form schools or *solitary* (Fischer et al. 1981, Froese and Pauly 2017). As samples from Djeta and Naufrages were collected from only one visit and these islands are relatively close to the Bijagós Archipelago (less than 50 km from the north and south limit respectively), we grouped data from all sites (but see Supplementary material, Table S1 and S2 for more detailed information).

We further compared the diet of the two Terns using the Shannon Wiener diversity index (Brower et al. 1998) based on the numerical frequency at species level, following the equation:

$$H' = -\sum pi \ \log_e pi \ ,$$

where *pi* is the proportion of individuals from the species *i* in relation to all individuals found. To avoid any bias in comparing diversity indexes of predators based on different samples sizes (i.e., on different number of pellets), we calculated rarefied diversity indexes for each Tern by repeatedly resampling (with reposition) a similar number of pellets (N = 140, corresponding to the smallest sample in our dataset, obtained from Royal Tern). Resampling was carried out 1 000 times for each predator, and we present the median of these diversity indexes, as well as the confidence intervals, calculated by the percentile method (i.e., as the 0.025 and 0.975 quantiles of, Efron 1981). Taxa that occurred only once in the diet of both Terns together were excluded from the analysis.

In order to examine the similarity in the diet of Terns among the different sites and between the two species, we performed permutational multivariate analysis of variance (PERMANOVA). We tested for differences between years for Caspian Tern (year as main factor), for differences between seasons for Royal Tern (season as main factor) and for differences between Tern species from the same site and season (species as main factor). We did not test for differences between sites for Royal Terns since two of the sites were sampled in just one day, which may bias the results (but see Supplementary material, Table S1 for detailed results from each site). PERMANOVA were carried out with adonis function in the vegan R package with Bray-Curtis similarities on prey presence/absence data, using 999 permutations (Anderson 2001, R Core Team 2017). As several prey items were only identified to the family level (hence excluding items not identified), PERMANOVA was conducted at this taxonomic level. Taxa that occurred only once in the pooled sample of the two Terns were excluded from the analyses above.

To evaluate the differences in prey size consumed by both terns, we calculated an allometric relationship between vertebrae width and fish length, using a linear regression. This model was calculated from measurements of the atlas vertebrae and body size from eight specimens of Madeiran sardinella (*Sardinella maderensis*) from our reference collection and is represented by the equation: *Total length (mm) = 67.77 (+- 0.85)* × *atlas width (mm)* + *6.94 (+-2.08)*, (r^2= 0.999, $F_{1, 6}$ = 6403, P < 0.001), (Supplementary material, Figure S1). This equation was used to estimate the size of fish preyed upon by Terns using the measurements of intact atlas vertebrae found in pellets (eroded bones were not used for size estimation). Measurements of the atlas in pellets and in our reference collection were made under a binocular microscope fitted with an eye-piece reticule, to the nearest 0.02 mm. Differences in size of *S. maderensis* consumed by Terns were tested using ANOVA. Means are presented ± standard deviation.

In order to understand the differences in the use of otoliths alone as opposed to the use of all hard structures (such as otoliths, vertebrae and other fish bones) in prey identification, we compared the FO% obtained with our results using each method for both Tern species.

We also conducted a literature review of the diet of Caspian and Royal Terns, which is mostly from American populations. We present a list of prey that had a frequency of occurrence / numeric frequency greater than 20%, in order to eliminate less relevant prey thus facilitating comparison among different sites.

Results

We collected a total of 152 pellets for Caspian Tern and 141 for Royal Tern from 2013 to 2015 in four islands of the Bijagós Archipelago, one island off the north coast of Guinea-Bissau (Djeta) and one island off the north of Guinea (Naufrage; Figure 1, Table 1).

Table 1 - Total number of pellets of Caspian Tern and Royal Tern collected (N) in each study site and season from 2013 to 2015 in Guinea-Bissau (Bijagós Archipelago and Djeta) and Guinea (Naufrage)

Tern	N	Site	Season
Caspian	52	Bijagós Archipelago (Acapa Imbone)	Dry 2013/2014
Caspian	100	Bijagós Archipelago (Acapa Imbone and João Vieira)	Dry 2014/2015
Royal	36	Bijagós Archipelago (João Vieira and Poilão)	Dry 2014/2015
Royal	18	Djeta	Dry 2014/2015
Royal	50	Naufrage	Dry 2014/2015
Royal	36	Bijagós Archipelago (Poilão)	Rainy 2013
Royal	1	Bijagós Archipelago (Cavalos)	Rainy 2015

Fish were present in all pellets examined (N = 293). The most common prey families were small pelagic, Clupeidae and Pristigasteridae. The most important prey (FO% greater than 20%) were *Sardinella* spp. (*Sardinella* n.i. and *Sardinella maderensis*) for Caspian Tern, and *Sardinella* spp. (*Sardinella* n.i.) and *Ilisha africana* for West African Royal Tern (Table 2). Pelagic fish were present in more than 80% and 90% of pellets, whereas benthopelagic fish were present in less than 40% and 25%, in Caspian and Royal Terns, respectively (Table 2). Benthic fish were virtually absent from pellets. Concerning the schooling / solitary behaviour of the prey, 74% of the fish prey identified in the diet of Caspian Tern frequently form schools and 26% are usually solitary. In the diet of in the diet of West African Royal Tern, 63% of fish prey identified frequently form schools and 37% are usually solitary (Table 2; Supplementary material, Table S1 and S2 for more detailed information).

Table 2 - Frequency of occurrence (FO%) of prey items in pellets of Caspian Tern and Royal Tern collected from 2013 to 2015 in Guinea-Bissau and Guinea, using all hard structures in prey identification by prey item domain, family and species (or lowest taxonomic level identified). Sample sizes (N) represent the total number of pellets analysed. Prey are categorized as schooling (¥) or solitary (§)

Domain	Family	Species	Caspian Tern FO% (N=152)	Royal Tern FO% (N=141)
FISH				
Pelagic			**80.3**	**93.6**
	Carangidae		2.6	2.8
		Hemicaranx bicolor §	0.7	0.7
		Carangidae n.i. ¥	2.0	2.1
	Clupeidae		72.4	68.8
		Sardinella n.i. ¥	40.1	51.8
		Sardinella aurita ¥	3.3	1.4
		Sardinella maderensis ¥	25.0	14.9
		Ethmalosa fimbriata ¥	3.3	0
		Clupeidae n.i. ¥	1.3	0.7
	Hemiramphidae	Hemiramphidae n.i. ¥	5.9	2.1
	Pristigasteridae	*Ilisha africana* ¥	9.9	32.6
	Scombridae		0.7	1.4
		Scomberomorus tritor ¥	0.7	0.0
		Scomber colias ¥	0.0	1.4
Benthopelagic			**39.5**	**24.8**
	Ariidae	*Carlarius* n.i. §	0	0.7
	Gerreidae		7.2	0.7
		Eucinostomus melanopterus ¥	2	0.7
		Gerres nigri ¥	3.3	0.0
		Gerreidae n.i. ¥	2.0	0.0
	Haemulidae		7.9	5.7
		Pomadasys n.i. ¥	1.3	1.4
		Haemulidae n.i. ¥	6.6	4.3
	Mugilidae		9.2	0.0
		Liza n.i. ¥	0.7	0.0
		Mugilidae n.i. ¥	8.6	0.0

	Polynemidae	*Galeoides decadactylus* ¥	13.2	11.3
	Sciaenidae		4.6	7.8
		Pseudotolithus elongatus §	2.0	2.8
		Pseudotolithus typus §	0.0	0.7
		Pseudotolithus n.i. §	0.7	1.4
		Pteroscion peli §	0.7	2.8
		Sciaenidae n.i. §	1.3	0.0
	Serranidae	*Epinephelus* n.i. §	0.7	0.0
Benthic	Paralichthyidae	*Citharichthys stampflii* §	**0.0**	**1.4**
Unidentified fish			7.2	2.1
CRUSTACEAN				
Benthic	Decapoda	Crab n.i.	0.7	0.7

There were significant differences in Caspian Tern diet between years (PERMANOVA, $F_{1,148} = 2.801$, $r^2 = 0.019$, $P = 0.04$). Concerning Royal Tern there were no differences between seasons (rainy 2013 / dry 2014) in the Bijagós Archipelago ($F_{1,70} = 1.45$, $r^2 = 0.020$, $P = 0.23$). When comparing the diet of the two Terns only using samples from the same area, season and year (Bijagós, dry season 2014), the differences between Royal and Caspian Terns were significant ($F_{1,201} = 7.45$, $r^2 = 0.036$, $P < 0.01$).

Caspian Tern showed a more diverse diet (Shannon Wiener diversity index: Caspian Tern, mean = 2.18, CI = [2.17, 2.18], Royal Tern, mean = 1.77, CI = [1.76, 1.77]).

Concerning the prey size, the *S. maderensis* preyed upon by Caspian Tern were significantly larger than the ones preyed upon by Royal Tern (ANOVA, $F_{1,57} = 44.99$, $P < 0.001$), with a total mean length of 238 ± 28.9 mm (ranging from 184.5 to 311.9 mm) and 177 ± 36.8 mm (ranging from 132.3 to 244.1 mm), respectively.

The use of otoliths alone (as opposed to using all hard structures) when assessing the diet of both Terns severely underestimated the FO of all fish families found in pellets (Figure 2), and also provided a biased portrait of the relative abundance of each taxon. In fact, using otoliths only, Clupeidae were completely absent from Caspian Tern diet and suggested only ca. 5% FO in West African Royal Tern diet (as compared with almost 70% in both species when using all hard structures). The percentage of unidentified fish would increase from ca. 7% to ca. 90% in both Tern species, since only 21% of Caspian Tern pellets and 28% of West African Royal Tern pellets contained otoliths (see Supplementary material, Table S3 for more detail).

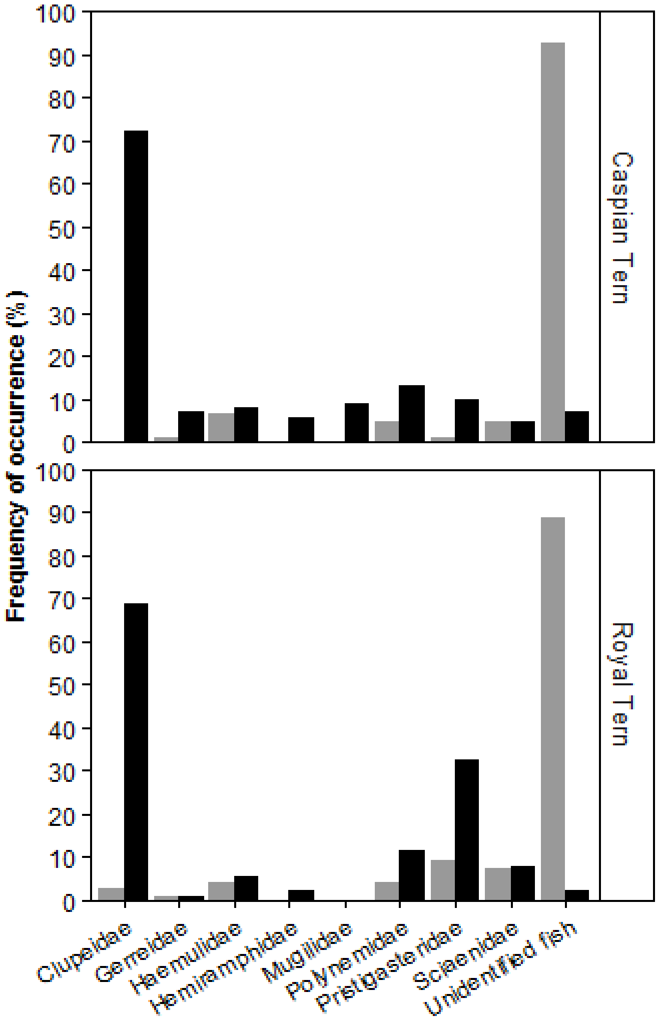

Figure 2 - Frequency of occurrence (%) of prey families (with an occurrence greater than 5% at least for one of the Tern species), identified based only on otoliths (grey) and all hard structures (black) from the pellets of Caspian Tern (N = 152) and Royal Tern (N = 141) collected from 2013 to 2015 in Guinea-Bissau and Guinea

The most important prey found in the literature for Caspian Tern and Royal Tern are presented in Table 3. In the case of Caspian Tern all information concerns American populations. In the case of Royal Tern, most studies are also from American populations (corresponding to *T. m. maximus*) and only two studies from Africa, from Ghana, Sierra Leone and Mauritania (corresponding to *T.*

m. albididorsalis; Dunn 1972, Veen et al. 2018). In terms of prey domains in Caspian Tern 45% of the prey taxa were pelagic, 15% benthopelagic, 5% benthic and 35% euryhaline. Moreover 60% of prey taxa were coastal and 40% offshore; 55% of prey frequently form schools and 45% were solitary prey taxa. For Royal Tern, in terms of prey domains 57% of the prey taxa were pelagic, 31% benthopelagic, 11% benthic and no euryhaline prey were identified. Besides that, 89% of the prey taxa were coastal and 11% were offshore; 66% of prey frequently form schools while 34% were solitary prey (Table 3). Most of the studies were based on direct observation (during foraging or prey delivery to the chicks), (Sirdevan 1996, Quintana and Yorio 1997, McGinnis and Emslie 2001, Collis et al. 2002, Roby et al. 2002, Thompson et al. 2002, Wambach and Emslie 2003, Aygen and Emslie 2006, Gatto and Yorio 2009), or based on the identification of fish remains and all hard parts (Buckley and Buckley 1971, Dunn 1972, Koli and Soikkeli 1974, Baltz et al. 1979, Liechty et al. 2013) and only two based on the identification of otoliths (and gastroliths of crayfish) from pellets (Parkin 1998, Favero et al. 2000).

Table 3 - Compilation of most frequent prey items (occurrence or numerical frequency greater than 20%) described in the literature for Caspian Tern and Royal Tern by class, domain, family and species prey (or lowest taxonomic level identified); Royal Tern information are from *Thalasseus maximus maximus*, except data from Ghana, Sierra Leone and Mauritania that are from *T. m. albididorsalis*. Data Sources are indicated by numbers ([1] Parkin 1998, [2] Buckley and Buckley 1971, [3] Dunn 1972, [4] Aygen and Emslie 2006, [5] Brewer et al. 1991, [6] Sirdevan 1996, [7] Wambach and Emslie 2003, [8] Roby et al. 2002, [9] del Hoyo et al. 1996, [10] McGinnis and Emslie 2001, [11] Liechty et al. 2013, [12] Favero et al. 2000, [13] Thompson et al. 2002, [14] Quintana and Yorio 1997, [15] Koli and Soikkeli 1974, [16] Baltz et al. 1979, [17] Collis et al. 2002, [18] Gatto and Yorio 2009, [19] Veen et al. 2018). Prey are categorized as coastal (¶) or offshore (£), as well as as schooling (¥) or solitary (§)

Class	Domain	Family	Species	Caspian Tern	Royal Tern
Actinopterygii					
	Pelagic	Atherinopsidae	*Atherinops affinis*[1] ¶ ¥	USA, California	-
			Menidia n.i.[2] ¶ ¥	-	USA, Virginia
			Odontesthes argentinensis[12, 18] ¶ §	-	Argentina, Buenos Aires
		Carangidae	*Chloroscombrus crysurus*[3] ¶ §	-	Ghana
			Caranx n.i.[2] ¶ ¥	-	USA, Virginia

		Carangidae n.i. [10] ¶ ¥	-	USA, North Carolina
	Clupeidae	*Alosa* n.i. [4; 5; 6; 7] ¶ ¥	USA, Michigan	USA, Virginia; USA, North Carolina
		Alosa pseudoharengus [5; 6] ¶ ¥	USA, Michigan	-
		Brevoortia n.i. [2] ¶ ¥	-	USA, Virginia
		Brevoortia tyrannus [4; 7] ¶ ¥	-	USA, Virginia; USA, North Carolina
		Clupea pallasi [8; 13] ¶ ¥	USA, Washington	-
		Opisthonema oglinum [4] ¶ ¥	-	USA, Virginia
		Sardinella maderensis [3] ¶ ¥	-	Sierra Leone
		Sardinops sagax [8; 9] ¶ ¥	USA, Washington	USA, Michigan
		Sprattus fuegensis [14] ¶ ¥	-	Argentina, Punta Léon
		Clupeidae n.i. [10, 15] ¶ ¥	Brändö, Finland	USA, North Carolina
	Engraulidae	*Anchoa hepsetus* [4] ¶ ¥	-	USA, Virginia
		Anchoa mitchilli [4; 11] ¶ ¥	-	USA, Virginia; USA, Louisiana
		Anchoviella n.i. [2] ¶ ¥	-	USA, Virginia
		Engraulis anchoita [12; 14, 18] ¶ ¥	-	Argentina, Buenos Aires; Argentina, Punta Léon
		Engraulis mordax [16] ¶ ¥	USA, California	-
		Engraulidae n.i. [8, 10] ¶ ¥	USA, Washington	USA, North Carolina
	Osmeridae	*Osmerus mordax* [5] ¶ ¥	USA, Michigan	-
	Scombridae	Scombridae n.i. [10] ¶ ¥	-	USA, North Carolina
Benthopelagic	Anguillidae	*Anguilla* n.i. [2] £ §	-	USA, Virginia
	Carangidae	*Selene setapinnis* [3] ¶ ¥	-	Ghana
		Trachinotus n.i. [3] ¶ ¥	-	Ghana
	Embiotocidae	*Cymatogaster aggregata* [1; 16] ¶ ¥	USA, California	-
	Ephippidae	*Ephippus goreensis* [3] ¶ §	-	Ghana
	Haemulidae	*Brachydeuterus auritus* [3] ¶ §	-	Sierra Leone

		Mugilidae	Mugilidae n.i. [3, 10 ,19] ¶ ¥	Mauritania	Sierra Leone; USA, North Carolina
		Osmeridae	*Hypomesus pretiosus* [13] ¶ ¥	USA, Washington	-
		Sciaenidae	*Genyonemus lineatus* [1] £ §	USA, California	-
			Micropogonias undulates [11] ¶ §	-	USA, Louisiana; USA, Virginia
			Paralonchurus brasiliensis [12] ¶	-	Argentina, Buenos Aires
			Sciaenidae n.i. [7; 11] §	-	USA, Louisiana; USA, North Carolina
		Sparidae	Sparidae n.i. [10, 19] ¶ §	-	USA, North Carolina; Mauritania
	Benthic	Batrachoididae	*Opsanus* n.i. [2] ¶ §	-	USA, Virginia
		Cottidae	*Leptocottus armatus* [1] ¶ §	USA, California	-
		Fundulidae	*Fundulus* n.i. [2] ¶ ¥	-	USA, Virginia
		Pleuronectidae	Pleuronectidae n.i. [2] £ §	-	USA, Virginia
		Syngnathidae	*Syngnathus* n.i. [2] £ §	-	USA, Virginia
	Euryhaline	Cyprinidae	*Rutilus rutilus* [15] £ §	Brändö, Finland	-
		Percidae	*Perca flavescens* [5] £ §	USA, Michigan	-
			Perca fluviatilis [15] £ §	Brändö, Finland	-
		Salmonidae	*Oncorhynchus* n.i. [13; 17] £ §	USA, Washington	-
			Oncorhynchus mykiss [8] £ §	USA, Washington	-
			Oncorhynchus tshawytscha [8] £ §	USA, Washington	-
			Oncorhynchus kisutch [8] £ §	USA, Washington	-
Cephalopoda					
	Pelagic	Loliginidae	*Loligo* n.i. [2]	-	USA, Virginia
Malacostraca					
	Benthopelagic	Crangonidae	*Crangon* n.i. [2]	-	USA, Virginia
	Freshwater	Cambaridae	*Procambarus clarkii* [1]	USA, California	-

Discussion

We present the first report of the diet of Caspian and West African Royal Terns from West Africa based on pellets collected at six different islands and four different periods from Guinea-Bissau and Guinea. Our study shows that clupeids, and particularly *Sardinella* spp. (mostly *S. maderensis*) are the most important prey in the diet of both Tern species. This finding highlights the importance of *S. maderensis* for the Bijagós Archipelago region and agrees with the suggestion of a wasp-waist ecosystem (Rice 1995; Correia et al. 2017). In fact, sardinella is also the most important prey to predatory pelagic fishes in the study area (Correia et al. 2017).

Our results show that pelagic prey fishes are present in more than 80% of the pellets of both Terns, with Clupeidae and Pristigasteridae being the most important prey families (Table 2). These two families are very abundant in the region and support significant regional fisheries (Lafrance 1994, Polidoro et al. 2016).

We found statistically significant differences between years in the diet of Caspian Tern, mostly related with the FO of less abundant species, but the overall diet composition seems broadly similar (see Supplementary material, Table S1). In fact, the most abundant prey family (i.e. Clupeidae) showed a frequency of occurrence greater that 70% in both years, and pelagic species were present in almost 80% of the samples in both years. This Tern species is opportunistic, so changes in diet can be related with variation in prey availability. Nevertheless, most of the prey taxa were found in the samples of both years. Conversely, we did not find differences between seasons in the diet of West African Royal Tern. Despite some reported differences in fish composition between dry and rainy seasons in the Bijagós marine ecosystem (Pennober 1999, Lafrance 1994), the similarity in the diet of Terns between seasons seems to support the idea of a prevalence of the dominant fish species over the seasons. In fact, predatory pelagic fishes in the archipelago, also did not show differences in diet between seasons (Correia et al. 2017), which strengthens this idea.

We found significant differences between Tern species, which might be related to a greater diversity of prey in Caspian Terns. Caspian Terns forage more inshore, where they can capture benthopelagic fishes, usually associated with sandy bottoms and shallow waters (e.g. Gerreidae, Mugilidae; Table 2). Moreover, Caspian Terns being larger than Royal Terns (~20% larger in wingspan and up to 60% larger in body mass) are thus able to capture larger prey, as suggested from our data on prey size. West African Royal Tern seems to prefer to forage offshore, as we rarely observed them foraging near the shore or in shallow waters. By comparing our results with the literature review we can find differences between the two Royal Tern subspecies concerning foraging habitats. *Thalasseus maximus albididorsalis* forages preferentially offshore opposed to *T. m. maximus* that forages preferentially near the shore (Sidervan 1996, Parkin 1998, McGinnis and Emslie 2001).

The fact that in our study area both Terns prey on abundant schooling fish species and only few species comprise the majority of their diet agrees with what is described for the American populations of these two species (Koli and Soikkeli 1974, Baltz et al. 1979, Parkin 1998, Aygen and Emslie 2006). Both species are described as opportunistic foragers and are capable of adjusting their foraging behaviour with ecosystem changes, being both able to switch their diet when changing between different geographical areas and seasons according to prey availability. As small pelagic fishes are patchily distributed, even more so in tropical waters (Longhurst and Pauly 1987), seabirds may reduce search effort by observing the foraging behaviour of other seabirds or other marine predators as cues to the presence of schools of prey (Fauchald 2009, Thiebault et al. 2016, Veit and Harrison 2017).

Marine fishery discards may represent up to 20% of the global marine fishery catches (Zeller et al. 2018) and many seabirds, including Terns, have been observed feeding on them (Oro and Ruiz 1997, Walter and Becker 1997, Valeiras 2003). Little information is available for Caspian and Royal Terns concerning this behaviour. Yet, there are reports of both species taking advantage of fishery discards (Blaber et al. 1995, Yorio and Caille 1999, Wickliffe and Jodice 2010) or else suspected to use discards by the high consumption of demersal species (Liechty et al. 2013). We do not have any evidence from our study site Terns are dependent on discards for feeding as their diet consists mostly of abundant pelagic coastal fishes, as opposed to benthic / demersal prey usually consumed when seabirds associate with fisheries discards (e.g. Blaber et al. 1995). Nevertheless, specific information about discards in our study area is still lacking, where most of the discarded groups are unidentified (Zeller et al. 2018).

Our results show that the use of otoliths alone, as opposed to the use of all hard parts in prey identification, severely underestimates the occurrence of species with fragile and small otoliths, such as clupeids and other small pelagics (Figure 2). Clupeidae otoliths were only found in four samples, but other types of remains (mainly vertebrae) were very common. Clearly, to avoid misleading results, diet studies in this and similar systems cannot rely on otoliths only for identification. We strongly recommend the combination of otoliths, vertebrae, scales and dentary, as well as other hard distinctive parts, in the identification of Tern prey (see also Alonso et al. 2013).

S. maderensis, one of the most abundant clupeids in the study area (Lafrance 1994), is currently classified as Vulnerable according to the IUCN (Polidoro et al. 2016). Moreover, the most important commercial clupeids in the region are considered to be overfished (i.e. *Ethmalosa fimbriata*, *Sardina pilchardus* and *S. maderensis*). Changes in pelagic fish communities as a result of overfishing and large-scale changes in nesting habitat (e.g. due to sea-level rise) may strongly influence the distribution and abundance of Caspian and West African Royal Tern populations. This study supports the idea that the Bijagós marine ecosystem is strongly dependent on one (or perhaps very few) small pelagic fish species, which makes it especially sensitive if these species face strong declines. Our results underline the relevance of an ecosystem-based management of fisheries, which has to take into account target fish species, but also local livelihoods and other components of the ecosystem, such as predatory fishes and seabirds.

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Supplementary material

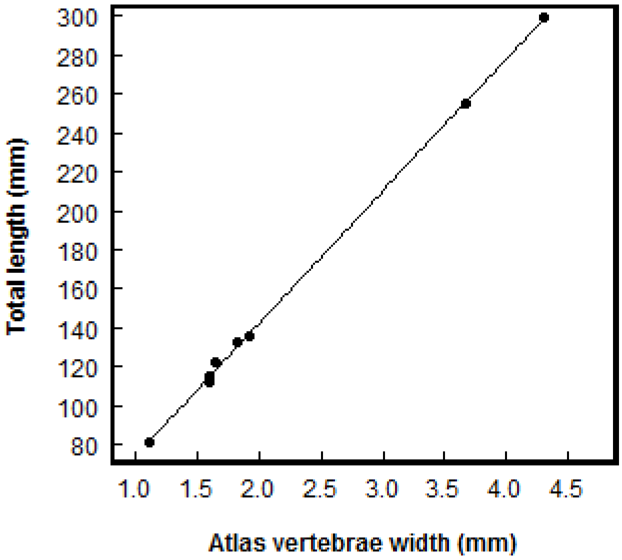

Figure S1 - Relationship between total length (mm) and atlas vertebrae width (mm) in Madeiran sardinella, calculated from eight fish specimens from our reference collection of fishes collected in Guinea-Bissau. Line represents linear regression: Total length (mm) = 67.77 (+- 0.85) × atlas width (mm) + 6.94 (+-2.08), ($F_{1, 6}$ = 6403, r^2 = 0.999, $P < 0.001$)

Table S1 - Frequency of occurrence (FO%) of prey items in pellets of Caspian Tern and Royal Tern by prey domain, family species (or lowest taxonomic level identified) and site. Samples collected from 2013 to 2015 in Guinea-Bissau and Guinea. Sample sizes (*N*) represent the total number of pellets analysed. n.i. - not identified

			Caspian Tern		**Royal Tern**		
Domain	**Family**	**Species**	**Bijagós 2013 FO% (N=52)**	**Bijagós 2014 FO% (N=100)**	**Bijagós FO% (N=73)**	**Djeta FO% (N=18)**	**Naufrage FO% (N=50)**
FISH							
Pelagic			**78.8**	**81.0**	**97.3**	**88.9**	**90.0**
	Carangidae		5.8	1.0	4.1	0.0	2.0
		Hemicaranx bicolor §	1.9	0.0	1.4	0.0	0.0
		Carangidae n.i. ¥	0.0	1.0	2.7	0.0	2.0
	Clupeidae		75.0	71.0	86.3	5.6	67.4
		Sardinella n.i. ¥	67.3	26.0	67.1	5.6	46.0
		Sardinella aurita ¥	0.0	5.0	0.0	0.0	4.0
		Sardinella maderensis ¥	7.7	34.0	17.8	0.0	16.0
		Ethmalosa fimbriata ¥	0.0	5.0	0.0	0.0	0.0
		Clupeidae n.i. ¥	0.0	2.0	1.4	0.0	0.0
	Hemiramphidae	Hemiramphidae n.i. ¥	0.0	9.0	4.1		
	Pristigasteridae	*Ilisha africana* ¥	5.8	12.0	16.4	83.3	38.0
	Scombridae		1.9	0.0	2.7	0.0	0.0
		Scomberomorus tritor ¥	1.9	0.0	0.0	0.0	0.0
		Scomber colias ¥	0.0	0.0	2.7	0.0	0.0
Benthopelagic			**36.5**	**41.0**	**21.9**	**27.8**	**28.0**
	Ariidae	*Carlarius* n.i. §	0.0	0.0	0.0	5.6	0.0
	Gerreidae		3.8	9.0	0.0	0.0	2.0
		Eucinostomus melanopterus ¥	0.0	3.0	0.0	0.0	2.0
		Gerres nigri ¥	1.9	4.0	0.0	0.0	0.0
		Gerreidae n.i. ¥	1.9	2.0	0.0	0.0	0.0
	Haemulidae		17.3	3.0	8.2	5.6	2.0
		Pomadasys n.i. ¥	1.9	1.0	1.4	5.6	0.0
		Haemulidae n.i. ¥	15.4	2.0	6.8	0.0	2.0
	Mugilidae		1.9	13.0	0.0	0.0	0.0
		Liza n.i. ¥	0.0	1.0	0.0	0.0	0.0
		Mugilidae n.i. ¥	1.9	12.0	0.0	0.0	0.0
	Polynemidae	*Galeoides decadactylus* ¥	11.5	14.0	8.2	5.6	18.0
	Sciaenidae		1.9	6.0	5.5	16.7	8.0
		Pseudotolithus elongatus §	0.0	3.0	2.7	11.1	0.0
		Pseudotolithus typus §	0.0	0.0	0.0	5.6	0.0
		Pseudotolithus n.i. §	1.9	0.0	0.0	0.0	4.0
		Pteroscion peli §	0.0	1.0	2.7	0.0	4.0
		Sciaenidae n.i. §	0.0	2.0	0.0	0.0	0.0
	Serranidae	*Epinephelus* n.i. §	1.9	0.0	0.0	0.0	0.0
Benthic	Paralichthyidae	*Citharichthys stampflii* §	**0.0**	**0.0**	**1.4**	**5.6**	**0.0**
Unidentified fish			11.5	5.0	2.7	5.6	0.0
CRUSTACEAN							
	Decapoda	Crab n.i.	1.9	0.0	0.0	0.0	2.0

Table S2 - Numerical frequency (N%) of prey items in pellets of Caspian Tern and Royal Tern by prey domain, family species (or lowest taxonomic level identified) and site. Samples collected from 2013 to 2015 in Guinea-Bissau and Guinea. Sample sizes (*N*) represent the total number of prey individuals analysed. n.i. - not identified. Prey are categorized as schooling (¥) or solitary (§).

			Caspian Tern		**Royal Tern**		
			Bijagós 2013	**Bijagós 2014**	**Bijagós**	**Djeta**	**Naufrage**
Domain	**Family**	**Species**	**N% (N=88)**	**N% (N=169)**	**N% (N=126)**	**N% (N=24)**	**N% (N=91)**
FISH							
Pelagic			**65.9**	**68.0**	**84.1**	**66.7**	**82.4**
	Carangidae		3.4	0.6	2.4	0.0	1.1
		Hemicaranx bicolor §	1.1	0.0	0.8	0.0	0.0
		Carangidae n.i. ¥	2.3	0.6	1.6	0.0	1.1
	Clupeidae		58.0	53.3	65.9	4.2	59.3
		Sardinella n.i. ¥	52.3	18.9	50.8	4.2	39.6
		Sardinella aurita ¥	0.0	3.6	0.0	0.0	4.4
		Sardinella maderensis ¥	5.7	26.6	14.3	0.0	15.4
		Ethmalosa fimbriata ¥	0.0	3.0	0.0	0.0	0.0
		Clupeidae n.i. ¥	0.0	1.2	0.8	0.0	0.0
	Hemiramphidae	Hemiramphidae n.i. ¥	0.0	5.3	2.4	0.0	0.0
	Pristigasteridae	*Ilisha africana* ¥	3.4	8.9	11.9	62.5	22.0
	Scombridae		1.1	0.0	1.6	0.0	0.0
		Scomberomorus tritor ¥	1.1	0.0	0.0	0.0	0.0
		Scomber colias ¥	0.0	0.0	1.6	0.0	0.0
Benthopelagic			**26.1**	**29.0**	**57.1**	**25.0**	**16.5**
	Ariidae	*Carlarius* n.i. §	0.0	0.0	0.0	0.0	0.0
	Gerreidae		2.3	5.3	0.0	0.0	1.1
		Eucinostomus melanopterus ¥	0.0	1.8	0.0	0.0	1.1
		Gerres nigri ¥	1.1	2.4	0.0	0.0	0.0
		Gerreidae n.i. ¥	1.1	1.2	0.0	0.0	0.0
	Haemulidae		11.4	2.4	4.8	4.2	1.1
		Pomadasys n.i. ¥	1.1	1.2	0.8	4.2	0.0
		Haemulidae n.i. ¥	10.2	1.2	4.0	0.0	1.1
	Mugilidae		2.3	8.9	0.0	0.0	0.0
		Liza n.i. ¥	0.0	0.6	0.0	0.0	0.0
		Mugilidae n.i. ¥	2.3	8.3	0.0	0.0	0.0
	Polynemidae	*Galeoides decadactylus* ¥	8.0	8.9	5.6	4.2	9.9
	Sciaenidae		1.1	3.6	3.2	12.5	4.4
		Pseudotolithus elongatus §	0.0	1.8	1.6	8.3	0.0
		Pseudotolithus typus §	0.0	0.0	0.0	4.2	0.0
		Pseudotolithus n.i. §	1.1	0.0	0.0	0.0	2.2
		Pteroscion peli §	0.0	0.6	1.6	0.0	2.2
		Sciaenidae n.i. §	0.0	1.2	0.0	0.0	0.0
	Serranidae	Epinephelus n.i. §	1.1	0.0	0.0	0.0	0.0
Benthic	Paralichthyidae	*Citharichthys stampflii* §	**0.0**	**0.0**	**0.8**	**4.2**	**0.0**
Unidentified fish			6.8	3.0	1.6	4.2	0.0
CRUSTACEAN							
	Decapoda	Crab n.i.	1.1	0.0	0.0	0.0	1.1

Table S3 - Frequency of occurrence (FO%) and numerical frequency (N%) of prey items in pellets of Caspian Tern and Royal Tern by prey domain, family species (or lowest taxonomic level identified) using only otoliths in prey identification. Samples collected from 2013 to 2015 in Guinea-Bissau and Guinea. Sample sizes (*N*) represent the total number of pellets analysed (in FO%) and total number of prey individuals analysed (on N%). n.i. - not identified. Prey are categorized as schooling (¥) or solitary (§)

			Caspian Tern		**Royal Tern**	
Domain	**Family**	**Species**	**FO% (N=152)**	**N% (N=257)**	**FO% (N=141)**	**N% (N=241)**
Pelagic			**1.3**	1.2	**11.3**	7.1
	Clupeidae	Clupeidae n.i. ¥	0	0	2.8	1.7
	Pristigasteridae	*Ilisha africana*	1.3	1.2	9.2	5.4
Benthopelagic			**17.8**	11.7	**16.3**	10
	Ariidae	*Carlarius* n.i. ¥	0	0	0.7	0.4
	Gerreidae		1.3		0.7	
		Eucinostomus melanopterus ¥	0.7	0.4	0.7	0.4
		Gerres nigri ¥	0.7	0.4	0	0
	Haemulidae	*Pomadasys* n.i. ¥	0.7	0.8	0	0
		Haemulidae n.i. ¥	5.9	3.9	4.3	2.5
	Mugilidae	*Liza* n.i. ¥	1.3	0.8	0	0
	Polynemidae	*Galeoides decadactylus* ¥	4.6	2.7	4.3	2.5
	Sciaenidae		4.6	2.7	7.1	4.1
		Pseudotolithus elongates §	2	1.2	2.1	1.2
		Pseudotolithus n.i. §	0.7	0.4	1.4	0.8
		Pseudotolithus typus §	0	0	0.7	0.4
		Pteroscion peli §	0.7	0.4	2.8	1.7
		Sciaenidae n.i. §	1.3	0.8	0	0
	Unidentified fish		92.8	86.8	88.7	83

CHAPTER 6

Trophic interactions between migratory seabirds, predatory fishes and small pelagics in West Africa

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CHAPTER 6

Trophic interactions between migratory seabirds, predatory fishes and small pelagics in West Africa

Abstract

Competition, predation and facilitation shape the structure of a community. Yet facilitative behaviour is still poorly studied, especially in marine ecosystems. Here we studied the diet and foraging behaviour of five Afro-Palaearctic migratory seabirds during their wintering period in West Africa, focusing on their facilitative associations with predatory fishes. We used next-generation sequencing to describe and compare the diet of seabirds, employing DNA metabarcoding on the identification of prey remains from their droppings. This was the first time this method was used for studying tern feeding ecology. Our results showed a high diet overlap between all seabirds studied, which was mostly due to the high frequency of occurrence (over 60%) of one dominant species: *Sardinella maderensis*, the most important prey species all-round. The subsurface marine predators identified in associations were Crevalle jack (*Caranx hippos*) and West African Spanish mackerel (*Scomberomorus tritor*). These two predatory fishes also rely on *Sardinella maderensis* as their most frequent prey in the Bijagós Archipelago. There were marked inter-specific differences in foraging behaviour of terns. Their degree of reliance on subsurface marine predators as facilitators for feeding varied greatly, ranging from completely independent (Little tern *Sternula albifrons*) to near-obligatory (Black tern *Chlidonias niger*). The different feeding techniques, degree of association use and spatial segregation may explain the co-existence of five tern species wintering together and preying mostly on the same fish species. Declines both in predatory fishes and small pelagics are likely to impact the long-distance migrant seabirds studied here.

Keywords: Predator–prey interaction, tern, Next-generation sequencing, DNA metabarcoding, sympatric predators, facilitated foraging

Introduction

Predator-prey and predator-predator interactions play an essential role in ecosystem functioning and structure (Sih et al. 1998, Petchey 2000, Duffy et al. 2007, Schmitz 2007). Predation can alter the dynamics of prey populations (e.g. Heinlein et al. 2010), while prey abundance can in turn influence the feeding rates, growth and reproductive success of predators (Furness and Tasker 2000, Piatt et al. 2007). The interactions between different predators can lead to competition or to facilitation. The latter occurs when different taxa associate together, improving prey detection or increasing prey availability (Charnov et al. 1976, Stachowicz 2001, Bruno et al. 2003). Predation, competition and facilitation combined influence the coexistence or exclusion of species in a community (Pianka 1974, Sih et al. 1998, Begon et al. 2006, Goyert et al. 2014).

Seabirds often associate with subsurface marine predators to feed (Balance and Pitman 1999). These associations have been mostly studied in the open ocean, with tunas and cetaceans being the most common subsurface facilitators to above-water predators (Veit and Harrison 2017). While it can be observed in most marine environments, facilitation seems to be more important in tropical regions (Balance and Pitman 1999, Veit and Harrison 2017). This may be due to the lower productivity of these regions when compared to temperate and polar ones. Additionally, marine tropical regions are expected to have their resources more patchily distributed and a higher number of large predatory fish (Longhurst and Pauly 1987, Ballance and Pitman 1999). All of these features may enhance associations between seabirds and subsurface marine predators (Ballance and Pitman 1999, Veit and Harrison 2017). However, current knowledge is based on studies conducted mostly offshore, and virtually nothing is known about such phenomena in tropical shallow coastal waters, where the suit of seabirds and predatory fishes is different.

There is a growing concern over the rapid declines observed in Afro-Palaearctic migratory birds (Vickery et al. 2014, Bairlein 2016). In seabird populations, such declines may be linked to the depletion of fishery resources as well as the direct mortality caused by fishing gear (Tasker et al.

2000, Barbraud and Weimerskirch 2003, Gremillet et al. 2015). Fluctuations in the availability of both prey and subsurface marine predators that facilitate foraging are likely to influence seabird abundance and distribution (Ballance and Pitman 1999, Furness and Tasker 2000). Even though the Eastern Central Atlantic region is highly productive due to an upwelling system influenced by the Canary current (Bakun 1996, Tandstad et al. 2014, Valdés and Déniz-González 2015), most of its pelagic fish stocks are considered either fully fished or overfished (FAO 2016). Considerable declines in subsurface marine top predators, as well as small pelagics, have been observed in recent years (Belhabib et al. 2016, Polidoro et al. 2017).

Many seabird populations are migratory, and little is known about their predatory behaviour and competitive interactions when they are away from the breeding grounds. Diet studies of bird species in wintering quarters tend to be more challenging, since most seabirds are only central-place foragers during breeding season. During the non-breeding season, birds are harder to catch and sample, and some can spend all wintering season offshore (e.g. Dias et al. 2015). Yet conditions experienced at the nonbreeding grounds affect survival, and subsequent migration and breeding success. Therefore, understanding wintering habits is essential for the conservation of migratory birds (Marra et al. 1998, Norris et al. 2004, Szostek and Becker 2015).

Detailed diet information is needed for understanding community ecology and thus applying successful conservation actions in any ecosystem (Barrett et al. 2007). The diet of seabirds can be used as an indicator of the health of marine ecosystems (Furness and Camphuysen 1997), as it may reflect shifts in prey abundance (Montevecchi 1993). DNA-based methods to study diet have rapidly evolved and proven to be powerful in detecting prey at species level (Pompanon et al. 2012). DNA metabarcoding techniques applied on prey identification from droppings allow the identification of a multitude of prey per sample and offer the possibility of being used in a completely non-invasive way (e.g. McInnes et al. 2017).

Here we present an insight into the diet and feeding ecology of some of the most abundant Afro-Palearctic migratory tern species wintering in West Africa (Cramp 1985, del Hoyo et al. 1996, Dodman and Sá 2005), namely Little Tern (*Sternula albifrons*), Sandwich Tern (*Thalasseus sandvicensis*), Lesser Crested Tern (*Thalasseus bengalensis*), Common Tern (*Sterna hirundo*) and Black Tern (*Chlidonias niger*). We used DNA metabarcoding techniques to obtain for the first time information on the diet of these five seabirds during their wintering season. Focal observations were performed to further describe and compare feeding habits, with special focus on the associations with subsurface marine predators as facilitators.

Methods

Study site

Fieldwork was carried out in the João Vieira and Poilão Marine National Park (hereafter JVPMNP), situated in the southeast of the Bijagós Archipelago, Guinea-Bissau (10.95°N, -15.75°W; Figure 1). The JVPMNP consists of four islands and two islets and an extensive area of sea, summing up to a total of 495 km^2, of which only 17 km^2 are in the terrestrial domain. It is characterized by shallow waters, usually not exceeding a depth of 20 m, with several sand banks, few of which are permanently exposed.

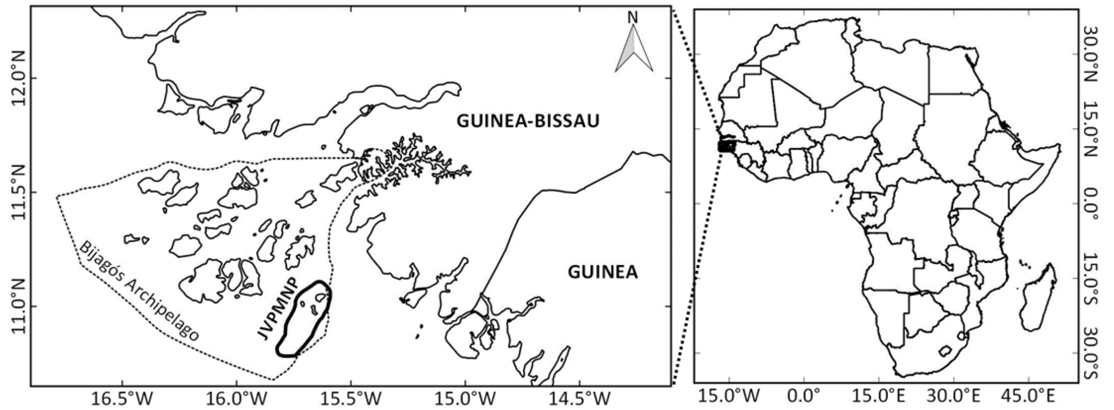

Figure 1- Location of the João Vieira and Poilão Marine National Park (JVPMNP), delimited by solid line in bold; dashed line delimits the Bijagós Archipelago Biosphere Reserve, Guinea-Bissau, zoomed in from the African continent map

Foraging behaviour

The fieldwork was carried out during two wintering seasons, 2014/2015 and 2015/2016. We performed observations of at-sea foraging behaviour on the most abundant wintering tern species in the study area: Little Tern (*Sternula albifrons*), Sandwich Tern (*Thalasseus sandvicensis*), Lesser Crested Tern (*Thalasseus bengalensis*), Common Tern (*Sterna hirundo*) and Black Tern (*Chlidonias niger*), (Table 1). Despite the likewise high abundance of Caspian (*Hydroprogne caspia*) and Royal (*Thalasseus maximus*) terns in the coast of Guinea-Bissau, they were rarely observed foraging in the study area and thus these two species were not included in this study. All observations were carried out from the coast. Individual terns were randomly chosen and observed until they stopped foraging or became too distant for an accurate observation. Individuals were observed up to a maximum of 15 minutes. We only considered birds displaying foraging behaviour.

All observations were performed with binoculars. For each observation we recorded: time elapsed, focal tern species, number of feeding attempts performed (with and without association with predatory fishes), whether terns were in flock or not, number of birds of each species in the flock, and distance to the shore of the last feeding attempt. In observations where the bird was foraging alone and entered a flock or vice versa, we categorised it from the behaviour that was dominant in terms of time in that particular observation. We categorized each feeding attempt as: plunge dive (PD) – a vertical plunge which usually involves submerging the entire body in water; dive to surface (DS) - a vertical plunge without fully submerging the body in the water; dipping (D) – occurs when birds flies lower over the water dipping down the surface of water or just below it.

The association with predatory fishes was classified on a four-point scale as: 0 – no association, 1 – when we were hardly able to recognize that predatory fishes were feeding near the surface, with only occasional turbulence or fins on the water surface; 2 - when the activity of predatory fishes could be easily seen through regular, but not constant signs on the water surface; 3 – when constant turbulence was seen (water appeared as “boiling”), with regular sightings of fins and occasional jumps out of the water by predatory fishes and/or by the small pelagics.

For each focal bird we calculated the number of feeding attempts per minute during the observation period. For each observation we calculated: the percentage of each dive type and the percentage of feeding attempts performed in association. We excluded observation bouts with mixed activity (i.e. where some feeding attempts were performed in association and other without association with predatory fishes) when comparing behaviours with and without associations.

We tested for differences among species in foraging distance from the shore with an ANOVA, followed by a post-hoc Tukey test. To test the effect of the intensity of association and species on the number of individuals that constituted the flocks, we performed a Generalised linear model (GLM), assuming a Poisson error distribution (using a log link function). In order to test for differences in the frequency of feeding attempts among species in the presence and absence of interactions, we performed a two-way ANOVA.

Table 1 – Total number of focal individuals observed (N) foraging in the João Vieira and Poilão Marine National Park from November 2014 to September 2016

Tern	N
Little Tern	50
Sandwich Tern	362
Lesser Crested Tern	43
Common Tern	183
Black Tern	88

Molecular analysis

In order to study the diet of seabirds, we collected their droppings from the sand at daytime roost sites from two wintering seasons, 2014/2015 and 2015/2016 (Table 2). Samples were stored in absolute alcohol immediately after collection, and upon return to the lab were kept refrigerated until further analysis. Next-generation sequencing (NGS) approach was used so that a multitude of DNA fragments per dietary sample was amplified, sequenced, and assigned to the respective prey species (DNA metabarcoding), (Pompanon et al. 2012).

Table 2 – Total number of dropping samples analysed (N) for DNA metabarcoding prey identification by tern species, collected in the João Vieira and Poilão Marine National Park from December 2014 to September 2015

Tern	N
Little Tern	23
Sandwich Tern	77
Lesser Crested Tern	9
Common Tern	31
Black Tern	9

Blood or tissue samples of the 5 target tern species were also collected in order to create reference sequences for designing tern specific amplification and blocking primers. DNA from these samples was extracted using DNeasy Blood and Tissue Extraction Kit (QIAGEN) following the standard protocol. We amplified tern DNA using 16S primers Chord_16S_F and Chord_16S_R (Deagle et al. 2009). PCR reactions were carried in volumes of 10 µL, comprised of 5uL of QIAGEN Multiplex PCR Master Mix, with 0.3 µL of each 10 pM amplification primer, and 1 µL of DNA extract. PCR cycling conditions consisted of 15 min of initial denaturing at 95°C, followed by 35 cycles of denaturing at 94°C for 30 s, annealing at 52°C for 90 s, extension at 72°C for 90 s, and a final extension of 10 min at 72°C. Amplicons were sent for Sanger sequencing at Macrogen, Inc (Amsterdam, Netherlands). We then built an alignment consisting of the 5 target tern species, as well as some expected prey fishes, and designed tern specific amplification primers (Tern_16S_F – 5'-GTGGAACTTAAAAATYAGCRGCC-3'; Tern_16S_R – 5'-GCTGTTATCCCTGGGGTAGC-3'), as well as a tern specific blocking primer (Tern_blocking_chord_16S – 5'-CCCTGTGGAACTTAAAAATCAGCRGCCACT-3SpC3-3').

In order to identify prey present in pellets we extracted DNA from one pellet per individual using the Stool DNA Isolation Kit (Norgen Biotek Corporation) following the manufacturer's protocol. Samples were extracted in batches of 10 plus a negative control, in which no sample was added, distributed in 96-well plates, and kept in a freezer at -20ºC until further use. We amplified prey DNA using the same chordate 16S primers as the ones used for the reference collection (Deagle et al. 2009), modified to contain Illumina adaptors and a small identification barcode. In order to reduce the amplification of predator DNA relative to prey DNA, we used the designed tern specific blocking primer. PCR reactions were carried in volumes of 10 µL, comprised of 5uL of QIAGEN Multiplex PCR Master Mix, with 0.3 µL of each 10 pM amplification primer, 0.3 µL of 100pM blocking primer, and 1 µL of DNA extract. Each DNA plate was amplified with amplification primers containing different barcodes, allowing for multiple plates to be pooled while maintaining the individuality of samples. Cycling conditions used initial denaturing at 95 °C for 15 min, followed by 35 cycles of denaturing at 95 °C for 30 s, annealing at 45 °C for 30 s and extension at 72 °C for 30 s, with a final extension at 72 °C for 10 min. Amplification success was checked by visually inspecting 2 µL of each PCR product on a 2% agarose gel. Library preparation followed the manufacturer's protocol for metagenomic sequencing (Illumina). PCR products were purified using ExoSAP-IT (Thermo Fisher Scientific), quantified using PicoGreen (Promega), diluted to 10 ng/µL and pooled into a single plate. Illumina indexes containing 96 unique barcode combinations were added to the clean PCR products using Nextera XT primers (Illumina), allowing the identification of each individually amplified product. Indexed PCR products were purified using Agencourt AMPure XP beads (Beckman Coulter), quantified using Nanodrop, diluted to 10nM and pooled. Finally, the library was quantified using qPCR (KAPA Library Quant Kit qPCR Mix, Bio-Rad iCycler), diluted to 4nM, and sequenced in a MiSeq desktop sequencer (Illumina).

In order to be sure of the identity of the scat we subsequently amplified the tern DNA from each pellet sample using the designed tern specific 16S primers. PCR reactions and conditions were the same as for diet, except that no blocking primer was added. Amplicons were sequenced in the Centre for Molecular Analysis (CTM, Porto, Portugal) using an automated DNA sequencer (ABI PRISM 3130 XL).

Bioinformatics

We used OBITools (Boyer et al. 2016) for general sequence processing. Shortly, paired-end reads were aligned and assigned to samples, barcodes and primers were removed, and sequences were collapsed into haplotypes. Singletons were removed, as well as sequences smaller than 100 bp. The remaining haplotypes went through 'obiclean', a method that removes haplotypes differing 1 bp from each other, if one has a higher read count than the other in every sample. From each PCR, we further removed haplotypes representing less than 1% of the total number of reads and those containing stop codons. We then compared the haplotypes retained against known sequences within the NCBI database (www.blast.ncbi.nlm.nih.gov). Haplotypes that best matched the same species were collapsed into a single taxon unit.

Diet data analysis

To describe the presence and importance of each prey taxon in the diet of each tern species we calculated the frequency of occurrence (FO%) as the percentage of droppings containing a given prey taxon.

The overlap between tern diets was measured by calculating Horn-Morisita similarity index on numerical frequency data (Morisita 1959, Horn 1966):

$$C_{jk} = \frac{2\sum_i x_{ij} x_{ik}}{\sum_i x_{ij} \sum_i x_{ik} (X_j + X_k)},$$

where x_{ij} is the number of individuals of prey *i* in the feeding regime of the predator *j*; x_{ik} is the number of individuals of prey *i* in the feeding regime of the predator *k*;

$$X_j = \frac{\sum_i x_{ij}^2}{\left(\sum_i x_{ij}\right)^2} \text{ and } X_k = \frac{\sum_i x_{ik}^2}{\left(\sum_i x_{ik}\right)^2}.$$

This index varies from 0, when the feeding regimes are completely distinct, to 1, when they are identical and a significant diet overlap can be considered when the index is greater than 0.6

(Langton 1982). This index was calculated based on prey items identified to the lowest possible taxonomic level. DNA metabarcoding does not provide information concerning the number of individuals present in each dropping, and therefore each prey taxa occurrence counted as one individual.

We used published data from local predatory fish (Crevalle jack *Caranx hippos*, Guinean barracuda *Sphyraena afra* and West African Spanish mackerel *Scomberomorus tritor*, Correia et al. 2017) and two tern species (Caspian Tern *Hydroprogne caspia* and Royal Tern *Thalasseus maximus*, Correia et al. submitted) along with data from the present study to calculate the diet overlap among these ten predators from the Bijagós Archipelago. The overlap was measured with Horn-Morisita similarity index, as shown above (Morisita 1959, Horn 1966). We calculated the similarity index using family-level data for fish prey items and using class-level for non-fish prey. To standardize the data from the different methods used for studying the predators diet (stomach contents and pellets macroscopic identification of prey and DNA metabarcoding from droppings), we used the occurrence of each prey taxa as its numerical frequency (Supplementary material, Table S1). Statistical analyses were carried out using the software R (R Core Team 2018).

Results

Facilitative behaviour

In regards to the all focal individuals observed, Little, Sandwich and Lesser Crested terns were mostly observed foraging alone (only 12%, 9% and 12% of the observations were from birds foraging in flocks, respectively), while Common and Black Terns were mostly observed foraging in flocks (54% and 89% of the observations, respectively). From the 87 different foraging flocks observed, 41% were mixed flocks and 59% were single species flocks. Common and Black terns were very frequent flock members, either together or in single-species flocks. Sandwich terns were also frequently seen in single-species or with other species (Table 3).

Table 3 – Percentage of each flock composition for 87 flocks observed in the João Vieira and Poilão Marine National Park, ● species present in the flock

Flock type	Little Tern	Sandwich Tern	Lesser Crested Tern	Common Tern	Black Tern	Royal Tern	Percentage (%)
Mixed species				●	●		29
		●		●			2
	●	●					2
		●				●	2
		●		●	●		2
		●	●	●	●		1
		●	●				1
			●			●	1
Single species				●			28
		●					17
					●		9
	●						5

The techniques used for foraging were quite diverse amongst tern species. Little tern and Sandwich Tern performed mostly plunge dives. Common tern mostly dives to surface and dipping, and Black tern and Lesser Crested tern Lesser Crested tern mostly dipping (Table 4).

Table 4 – Feeding techniques used by different tern species (mean % ± standard error); N – total number of focal individuals observed

	Little Tern (N=46)	Sandwich Tern (N= 278)	Lesser Crested Tern (N=34)	Common Tern (N=108)	Black Tern (N=42)
Plunge dive	88.4 ± 4.7	68.5 ± 2.6	12.1 ± 5.5	21.4 ± 3.6	2.4 ± 2.6
Dive to surface	6.5 ± 3.7	18.5 ± 2.1	37.5 ± 7.2	40.5 ± 4.5	3.6 ± 2.6
Dipping	5.1 ± 3.1	13.1 ± 1.9	50.4 ± 7.7	38.1 ± 1.9	94.0 ± 3.5

Black terns foraged on average farther from the shore while Little tern foraged on average near from the shore when in comparison with the other species (Table 5). These differences among species were statistically significant (ANOVA: $F_{4,\,384} = 19.74$, $P < 0.001$). Black Tern foraged significantly at a greater distance from the shore than all the other species (Tukey HSD test $P < 0.001$). While between the remaining species the differences were not significant.

Table 5 - Mean distance from the shore (m) of the last feeding attempt (± standard error) by species; N – total number of focal individuals observed

	Little Tern (N=40)	Sandwich Tern (N=175)	Lesser Crested Tern (N=27)	Common Tern (N=104)	Black Tern (N=42)
Distance from shore (m)	14.7 ± 2.1	18.1 ± 3.3	18.1 ± 5.6	30.2 ± 10.0	403.0 ± 111.1

The level of association between terns and underwater predators varied amongst species, ranging from Black terns, which spent 89% of their foraging activity in association with predatory fishes, to Little terns, which were never observed in association (Figure 2). Terns were observed in association with Crevalle jack (*Caranx hippos*) and West African Spanish mackerel (*Scomberomorus tritor*) (identified while fish jumped out of the water).

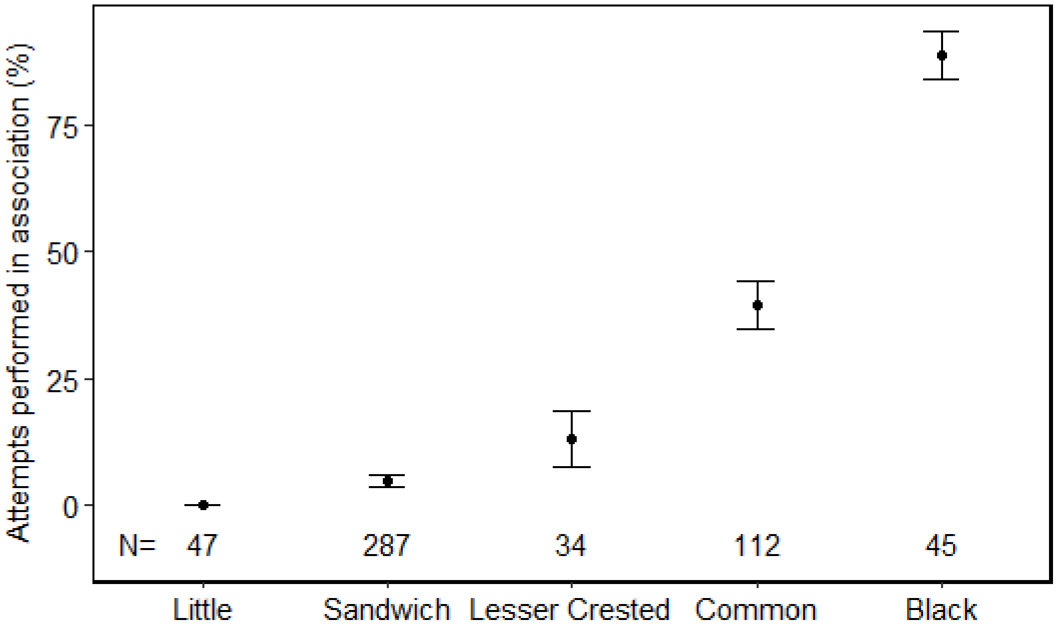

Figure 2 – Mean percentage (± standard error) of feeding attempts performed by each species in association with predatory fishes, N – number of focal individuals observed

On average, the size of the flocks associated with predatory fishes (75.2 ± 7.9 (SE) birds, in 129 focal observations) was ca. 1.7 times larger than that recorded in the absence of association (43.5 ± 6.5 (SE) birds, in 92 focal observations). We performed a GLM to test the effect of the intensity of the association and species on the number of individuals of each species in the flock. We excluded Little Tern and Lesser Crested Tern from this analysis since they were never observed in flocks and in association or without association, respectively (Figure 3). Flock size was significantly greater the more intense the association, after accounting for the effect of the species (GLM poisson, effect of levels of interaction: $X^2 = 1769$, df = 3, $P < 0.001$)

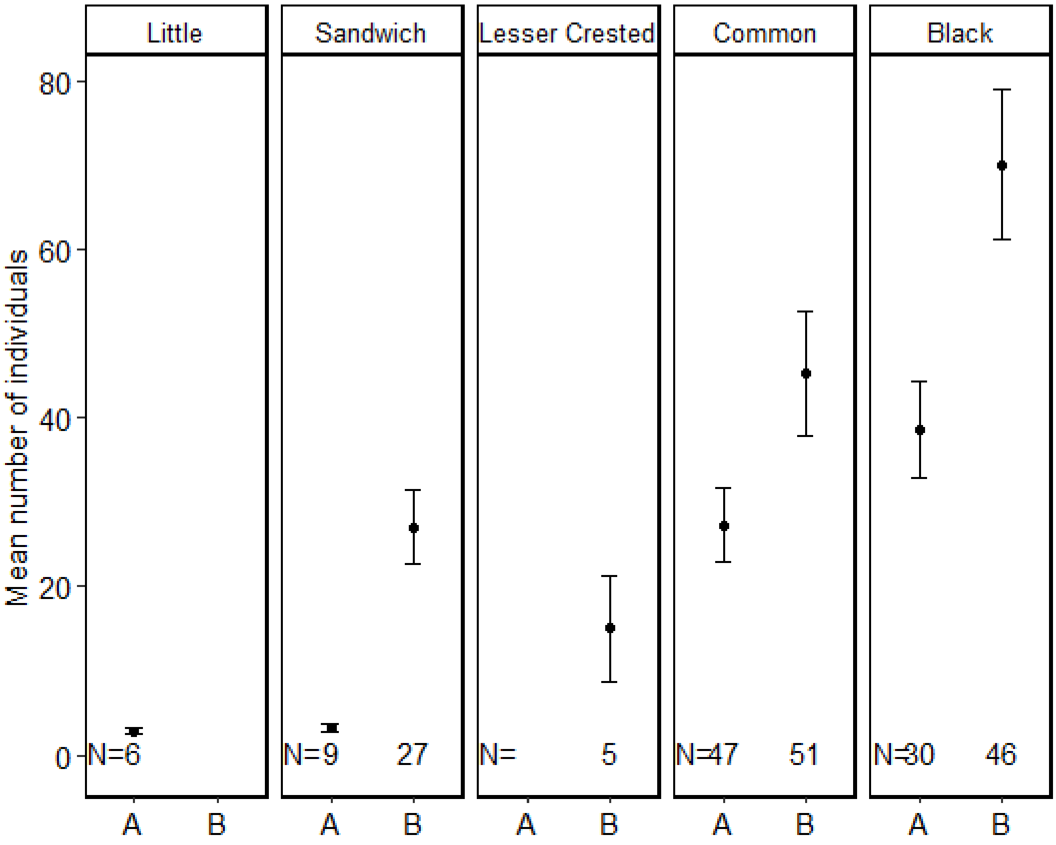

Figure 3 –Mean number of individuals (± Standard Error) of each species in flocks foraging without association (A) or in association with predatory fishes (B), N – number of focal individuals observed

A two-way ANOVA was conducted to test the effect of association with predatory fishes and tern species on the number of feeding attempts per minute. We excluded Little Tern because this species was never observed in association (Figure 4). The number of attempts was significantly higher when birds were in association with predatory fishes ($F_{1, 655} = 244.8$, $P < 0.001$, Figure 4). There were no significant differences between species ($F_{3, 655} = 0.46$, $P = 0.71$), (Figure 4).

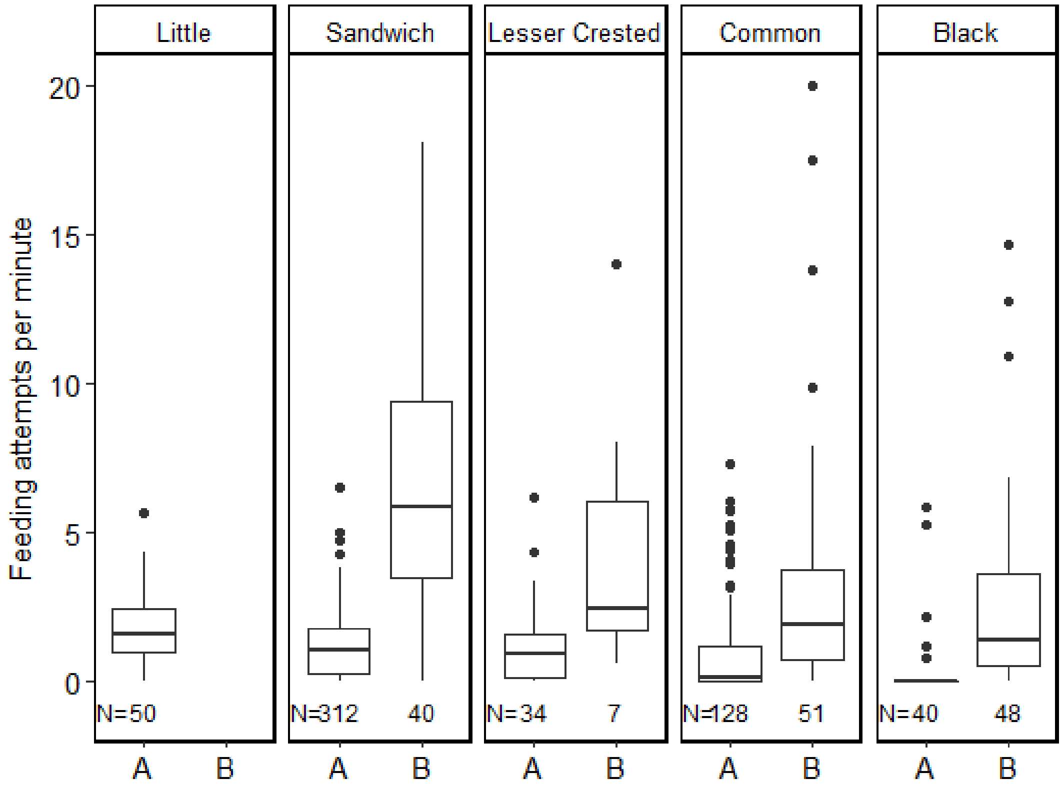

Figure 4 - Number of feeding attempts performed per minute when all the time was spent without association (A) or all the time was spent in association with predatory fishes (B), N – number of focal individuals observed

Diet / DNA metabarcoding

A total of 32 different prey taxa were identified in the diet of terns, including one from Gastropoda, two from Hexanauplia and nine from Malacostraca and 20 from Actinopterygii classes (Table 6). There was a dominance of Clupeidae in the diet of all tern species. *Sardinella maderensis* stands out as the prey species with higher frequency of occurrence for all seabirds. Within the Clupeidae, *Sardinella aurita* is also a frequent prey, mostly for Sandwich and Lesser Crested terns. Copepods (*Subeucalanus pileatus*) were present in the diet of all species (Table 6).

Table 6 – Frequency of occurrence (%) of prey items based on identification from droppings using DNA metabarcoding; Teleostei 1 and Teleostei 2 are two distinct species of non-identified Teleostei; N – number of droppings

Phylum / Subphylum	**Class**	**Family**	**Prey identified**	**Little Tern N=23**	**Sandwich Tern N=77**	**Lesser Crested Tern N=9**	**Common Tern N=31**	**Black Tern N=9**
CHORDATA / VERTEBRATA								
	Actinopterygii			**100**	**100**	**100**	**100**	**100**
		Jacks (Carangidae)	*Chloroscombrus chrysurus*	0	1	0	0	0
		Herrings, Sardines, Sardinellas, Shads (Clupeidae)	(total)	100	100	78	97	100
			Ethmalosa fimbriata	9	5	11	16	0
			Sardinella aurita	4	36	44	6	0
			Sardinella maderensis	96	90	67	97	100
		Anchovies (Engraulidae)	*Engraulis encrasicolus*	17	4	0	0	0
		Flyingfishes (Exocoetidae)	Exocoetidae	4	0	11	0	0
		Grunts (Haemulidae)	(total)	0	1	11	6	22
			Haemulidae	0	1	0	3	0
			Plectorhinchus sp.	0	0	0	3	0
			Pomadasys sp.	0	0	11	0	0
		Halfbeaks (Hemiramphidae)	(total)	4	0	11	3	11
			Hemiramphidae	4	0	0	3	11
			Hemiramphus brasiliensis	0	0	11	0	0
		Snake eels (Ophichthidae)	*Myrophis vafer*	0	1	0	0	0
		Pristigasterids (Pristigasteridae)	*Ilisha africa*	0	6	0	6	0
		Drums, Croaakers (Sciaenidae)	Sciaenidae	0	1	0	0	0
		Mackerels, tunas, bonitos (Scombridae)	(total)	4	4	0	3	22
			Scomber colias	0	4	0	0	0
			Scomberomorus tritor	4	0	0	3	22
		Barracudas (Sphyraenidae)	Sphyraenidae	0	1	0	0	0
		Cutlassfishes (Trichiuridae)	*Trichiurus lepturus*	0	0	0	3	0
		n.i.	Teleostei 1	4	4	22	3	11
			Teleostei 2	0	0	0	6	0
ARTHROPODA / CRUSTACEA				**9**	**12**	**11**	**13**	**33**
	Hexanauplia			**9**	**3**	**11**	**6**	**22**

		Copepods (Centropagidae)	Centropagidae	4	1	0	0	11
		Copepods (Subeucalanidae)	*Subeucalanus pileatus*	9	1	11	6	11
	Malacostraca			**0**	**9**	**11**	**13**	**11**
		Crabs (Menippidae)	*Menippe nodifrons*	0	1	0	0	0
		Crabs (Ocypodidae)	*Uca tangeri*	0	1	0	10	11
		Crabs (Panopeidae)	*Panopeus africanus*	0	1	0	0	0
		Crabs (Portunidae)		0	1	0	3	0
			Callinectes sp.	0	1	0	0	0
			Portunidae	0	0	0	3	0
		Shrimps (Penaeidae)		0	4	11	0	0
			Farfantepenaeus sp.	0	3	0	0	0
			Melicertus kerathurus	0	1	11	0	0
		Shrimps (Sicyoniidae)	*Sicyonia carinata*	0	0	0	0	11
		Mud shrimps (Upogebiidae)	*Upogebia* sp.	0	0	0	6	11
MOLLUSCA								
	Gastropoda			**4**	**0**	**0**	**0**	**0**
		Snails (Assimineidae)	*Assiminea* sp.	4	0	0	0	0

Diet overlap

The Horn-Morisita index showed a significant diet overlap between all tern species, with results ranging from 0.74 to 0.96 (Table 7). Furthermore, when comparing the diet overlap between all the three predatory fishes and seven seabirds from the study area, there was a significant overlap between all species, ranging from 0.71 to 0.98 (Supplementary material, Table S1).

Table 7 – Horn-Morisita index calculated at the lowest taxonomic level of identified prey, N – number of different individuals sampled

	Black Tern (N=9)	Common Tern (N=31)	Little Tern (N=23)	Lesser Crested Tern (N=9)
Common Tern	0.94			
Little Tern	0.93	0.96		
Lesser Crested Tern	0.74	0.78	0.76	
Sandwich Tern (N=77)	0.87	0.93	0.92	0.87

Discussion

This pioneering study on the feeding ecology of long-distance migratory seabirds wintering in West Africa has revealed several key-features of its coastal marine community. Different species showed contrasting levels of association with predatory fishes (jacks and mackerels) with Black and Common terns showing a heavy reliance on these associations. The association with predatory fishes facilitated the formation of larger foraging flocks and higher diving/dipping activity. The entire community relies predominantly on small pelagic Clupeidae, and most particularly on *Sardinella maderensis*.

Facilitative behavior

We studied the associations between seabirds and subsurface marine predators in the Eastern Central Atlantic in shallow marine areas (mostly < 10m). Previous studies performed in open waters have found these associations to be more common with larger marine predators (e.g cetaceans, seals, tunas) in all regions of the globe (Harrison and Seki 1987, Harrison et al. 1991, Camphuysen and Webb 1999, Veit and Harrison 2017). Our results showed however that smaller predatory species, including jacks and Spanish mackerels, can be of great importance to seabirds too. Similar inshore associations of seabirds with jacks and smaller scombrids had only been documented in the tropical Pacific (Harrison and Seki 1987).

Our results showed that all tern species gathered in larger flocks and performed significantly more feeding attempts when in association with predatory fishes, which may increase their feeding success (Thiebault et al. 2016). However, there were differences in the degree of use of these associations among tern species. The species that associated less with predatory fishes, the Little tern, was also the one that foraged mostly near the shore. On the other hand, the two species that foraged farther seaward, the Black and Common terns, showed a higher dependency on associations to feed. These results suggest that the use of associations influences the distribution of seabird species. At the same time, the ability to forage offshore may enhance seabird engagement in associations (Au and Pitman 1988, Schreiber and Burger 2002).

Flocks of seabirds were usually larger when the birds were associated with predatory fishes. Additionally, the more intense the association was, the higher the number of individuals of all tern species present. These tern species may be using a local enhancement mechanism, looking for cues for the presence of other predators (either shoals of predatory fishes or flocks of seabirds), rather than looking directly for prey (Thiebault et al. 2014, Tremblay et al. 2014).

Two species of predatory fishes (Crevalle jack and West African Spanish mackerel) were identified in association with the terns. Both are abundant in the Bijagós Archipelago and presented a high diet overlap with the seabirds studied here (see Supplementary material, Table S1; Correia et al. 2017, Correia et al. submitted). These fishes feed actively near the surface (Kwei 1978, Collette and Nauen 1983, Paugy et al. 2003) on large schools of small pelagic fishes, thus making large quantities of fish accessible to terns.

Crevalle jack and West African Spanish mackerel are caught for commercial and recreational purposes. Their catches have recently started to decline as a result of fishery intensification (Collette and Nauen 1983, Froese and Pauly 2018). The high level of illegal, unreported and unregulated fishing in the region may further threaten the populations of these species at a regional level (Belhabib et al. 2015, Doumbouya et al. 2017, Intchama et al. 2018).

Our results suggest that facilitative behaviour may have a strong influence on the distribution of species and possibly on their foraging efficiency (Ballance and Pitman 1999, Thiebault et al. 2016, Miller et al. 2018), thereby being an important factor for structuring the marine community in our study area. Population decline of predatory fishes like jacks and mackerels, with which seabirds associate, is likely to decrease foraging opportunities for seabirds and lead to a change in their distribution. Faced with less foraging opportunities, competition between seabirds may increase leading to lower levels of foraging success. Changes in the populations of predatory fishes should affect to a greater extent the seabird species that are more dependent on the associations, such as Black and Common terns. However, the other tern species studied here (with the exception of Little terns) may suffer as well, given that they too seem to benefit from the associations.

We believe that the use of associations by the different species is likely to be underestimated and that their relevance for the foraging behaviour of seabirds may be even greater than our results suggest. This is in part because the associations occurred mostly offshore and all our observations were performed from land (small islands). Additionally, the presence of predatory fishes might have occasionally gone unnoticed if they were totally submerged and not causing any visible turbulence on the water surface, particularly when observations were conducted from some distance.

Diet/ diet overlap

Most available information about the diet of the tern species studied here refers to their breeding grounds (e.g. Courtens et al. 2017). Data from diet in their wintering quarters is scarce (but see Dunn 1972, Cramp 1985, Piersma & Ntiamoa-Baidu 1995, Bugoni and Vooren 2004), particularly in West Africa and especially for the Lesser Crested tern and the Little tern.

Our study is the first to address the diet of seabirds from the Laridae family using DNA metabarcoding techniques and the first to apply them on migratory birds in their wintering quarters. Most of the previous studies on this bird family were conducted through the macroscopic identification of pellets (e.g. Bugoni and Vooren 2004). Yet these traditional methods presented serious limitations (like the severe underestimation of species with small otoliths; e.g. Alonso et al. 2013) particularly when applied outside the breeding season. Since different tern species roost together in the winter, it is often virtually impossible to link the samples collected to particular species. By using DNA metabarcoding techniques we were able to overcome this issue, as this method allowed us to identify the prey species present in the droppings as well as the corresponding tern species. Moreover, all droppings were collected directly from the ground in a completely non-invasive way to the birds.

Since the DNA metabarcoding method does not distinguish between prey caught live or dead, we were unable to determine whether the detection of invertebrates, such as copepods, resulted from direct predation, secondary prey amplification (a consequence of a predator consuming a prey which has just fed on another prey) or scavenging (Sheppard et al. 2005). However, the former limitation does not affect our main conclusions, given that our results showed a clear preference for Clupeiformes (such as Clupeidae, Pristigasteridae and Engraulidae) as the main prey group for all tern species. Moreover, the presence of non-fish prey varied between tern species, leading us to suspect that at least some of these prey were targeted. This is more evident in Black terns, which showed the highest frequency of occurrence of crustaceans, despite the small sample size. Further studies using primers to target invertebrates will be needed to confirm their importance in the wintering diet of terns.

The inter-specific differences in distribution (distance from the shore) of species while foraging, influenced by the degree of use of associations and preferred feeding techniques of each species, indicates some degree of spatial segregation. Furthermore, morphological differences between tern species may segregate them according to size and type of prey they capture. Very similar species like the Sandwich and Lesser Crested terns (in terms of body and bill size; Cramp 1985, del Hoyo et al. 1996) mostly used different techniques to capture prey. Little and Black terns look quite different yet are rather similar in terms of bill size and total body length (Cramp 1985, del Hoyo et al. 1996). The latter two species predominantly used different feeding techniques and while Black terns foraged almost exclusively in association with predatory fishes, Little terns were never observed in these associations. Common terns presented a broader behaviour in terms of feeding techniques as well as in the degree of association with predatory fishes. All these differences in foraging behaviour can contribute for the coexistence of these species in the same area with limited competition.

We observed a high diet overlap between ten marine predators (three predatory fishes and seven seabirds) coexisting in the Bijagós Archipelago (Supplementary material, Table S1). However, differences in the realized niches of competing species on limiting resources are predicted by ecological theory (Schoener 1983). When resources are abundant we may expect a greater interspecific niche overlap (Schoener 1982, Wiens 1993, Newton 1998, Weimerskirch et al. 2009). The high diet overlap observed can thus be related with the high availability of the main prey (*Sardinella maderensis*) in the region (Lafrance 1994, Valdés and Déniz-González 2015). We highlight the importance of *Sardinella maderensis* as prey species for the marine community of the Bijagós archipelago, which strengthens the suggestion of a wasp-waist structure for its ecosystem (Correia et al. 2017). *Sardinella maderensis* is a key species in the ecosystem and may control the population dynamics of the upper and lower trophic levels (Rice 1995).

Increasing pressure on local marine resources, caused by the expansion of fishermen from neighbouring countries in recent years, is a matter of concern for marine conservation in Guinea-Bissau (Kyle 2009, Njock and Westlund 2010, Binet et al. 2012). Marine resources are extremely valuable for human populations as the main protein source and one of the most important government revenues in the country (Dia and Bedingar 2001, Kyle 2009). Therefore, the importance of fish resources for the maintenance of seabird populations is far from being the only concern regarding their management. Nevertheless, our study clearly shows that a broad view of the marine ecosystem is needed for the management of the Bijagós Archipelago. The relevance of positive interactions between species from different taxa (predatory fishes and seabirds), as well as within the same group, strengthens the need for ecosystem-based approaches for its successful conservation (Katsanevakis et al. 2011). We stress here that maintaining sustainable levels of abundance of both prey and predatory fishes is fundamental for the conservation of long-distance migratory seabirds in the African-Eurasian migratory flyway.

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Supplementary material

Table S1 - Horn-Morisita overlap index between ten species of marine predators of the Bijagós Archipelago, using data from predatory fish (Correia et al. 2017) and terns (Correia et al. submitted, present study), calculated at the prey family level for fish and to the prey class level for non-fish; non-identified prey were excluded, N – number of individuals sampled

	Crevalle jack N=118	Caspian Tern N=152	Black Tern N=9	Royal Tern N=141	West African Spanish mackerel N=119	Guinean barracuda N=75	Common Tern N=31	Little Tern N=23	Lesser Crested Tern N = 9
Caspian Tern	0.98								
Black Tern	0.90	0.89							
Royal Tern	0.90	0.94	0.82						
West African Spanish mackerel	0.85	0.86	0.82	0.79					
Guinean barracuda	0.92	0.93	0.83	0.82	0.71				
Common Tern	0.94	0.94	0.95	0.89	0.93	0.83			
Little Tern	0.91	0.92	0.90	0.85	0.93	0.81	0.96		
Lesser Crested Tern	0.91	0.90	0.91	0.82	0.80	0.86	0.93	0.89	
Sandwich Tern N=77	0.93	0.93	0.91	0.88	0.97	0.80	0.98	0.98	0.88

CHAPTER 7

General discussion

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General discussion

Understanding trophic interactions provides important insight into the effect that different species in an ecosystem may have on the abundance and distribution of each other. In the scope of this thesis, trophic relationships are explored beyond the traditional predator-prey links, and also address the facilitative links between under- and above-water predators in the pelagic environment. In many coastal areas worldwide, particularly in the tropical and sub-tropical regions, the health of the seabird community is tightly linked with that of the local fish predators, that facilitate the access to prey that is patchily distributed and frequently outside the reach of seabirds. For that reason, it has become increasingly relevant to study these interactions in order to ensure and integrated and effective management and conservation of ecosystems. This thesis contributes to a better understanding of trophic interactions between predatory fish, seabirds and their prey, in a poorly studied yet biodiversity-rich ecosystem, recognised for its conservation value for several migratory and resident species – the Bijagós Archipelago (e.g. Dodman and Sá 2005, Catry et al. 2009a, Auliya et al. 2012).

Small pelagic fish community

In our study area the most common species of small coastal pelagic fishes in the João Vieira and Poilão Marine National Park belonged to the Clupeidae, Haemulidae and Gerreidae families, with *Sardinella maderensis* (Clupeidae) being clearly the dominant species. The composition of the fish community remained fairly similar throughout the year, although fish abundance varied between years and was overall lower during the rainy season. This difference may be related with latitudinal and longitudinal migratory movements (Chapter 1).

While investigating the structure and dynamics of the fish community, I also developed length–weight relationship for six fish species. This type of data allows for example for estimating the biomass consumed by seabirds from hard remains such as otoliths and vertebrae, that can be used to derive the size of prey. Moreover, such relationships enable for comparisons between populations of different areas and seasons, and can deliver important information concerning the overall condition of fish stocks. We reported original equations for three species, and improved the existing data for three other species (Chapter 2).

Diet and foraging behaviour of marine predators

The three most abundant pelagic predatory fishes (Crevalle jack, West African Spanish mackerel and Guinean barracuda) together with seven tern species (Caspian, Royal, Little, Sandwich, Lesser Crested, Common and Black terns) based their diet mostly on clupeids and consequently showed a very high diet overlap (Chapter 3, 4, 5). Although *Sardinella maderensis* was the most frequent species in the diet of all predators, differences in size of prey consumed, in spatial segregation of predators and in their foraging behaviour probably explain the co-occurrence of these marine predators. The co-existence of so many species preying on the same species without any major evidence for competitive exclusion is also probably made possible by the high local availability of small pelagic fishes, especially of *Sardinella maderensis*.

The level of associations with predatory fishes varied greatly among seabird species. Black and Common terns showed a high dependence on these associations whereas Sandwich and Lesser Crested terns showed a lower reliance on associations, and Little terns never used these associations. All species involved in associations seemed to benefit by associating with subsurface predators since they all performed more feeding attempts when in their presence. Moreover, the species relying more on associations foraged farther from the shore, indicating that these associations influence the distribution of seabirds. Therefore, declines in populations of predatory fishes, such as jacks and Spanish mackerels, are likely to decrease foraging opportunities for seabirds and their foraging success, affecting the structure of the marine community of the Bijagós Archipelago.

Even though conditions experienced during the non-breeding season are known to affect the survival, migration and the subsequent breeding success of migratory birds, information about the ecology of the seabird species studied here in their wintering quarters was largely missing.

Methods for diet studies

Detailed information about the diet and trophic interactions of upper trophic marine predators may give information about the state of their prey and the environmental conditions of the ecosystem (Furness and Camphuysen 1997, Montevecchi 1993). In this work, we were seeking detailed information on prey to assess which species sustain the community of marine predators in the Bijagós Archipelago. Diverse methods can be used in diet studies, such as the analysis of fatty acid signatures, the analysis of stable isotope ratios, observations of feeding events and the use of digital photography in prey-carrying seabirds (e.g. Barrett et al. 2007, Gaglio et al. 2017). However, while the first two methods aforementioned do not allow for identification of prey to the species level, the latter two were not applicable to this study due to logistical reasons. We therefore used a combination of traditional and molecular methods to identify prey to the species level with greatest certainty. These included the macroscopic identification of hard remains in the stomach contents of predatory fishes and in seabird pellets, as well as DNA metabarcoding techniques for genetically identifying prey in seabird droppings with a high taxonomic resolution.

For the successful identification of hard remains, we generated our own reference collection of fish bones and otoliths from 28 different species from study area. The macroscopic identification of prey can be applied to a large number of samples at a low cost, and provides both presence/absence data and the numerical frequency of prey. In the case of predatory fishes, we angled fishes from the shore and from boats to collect the stomach contents of predatory fishes. For the two breeding tern species studied, Caspian and Royal terns, we visited their colonies and collected pellet samples. Since both tern species group separately within mixed colonies, we were able to allocate each pellet to its specific species.

During the wintering season, however, tern species tend to roost together in beaches, therefore making it impossible to collect samples and accurately match them with the right predator. By genetically analysing droppings for identifying both seabird species and their prey, we were able to gain detailed information about the diet of all tern species without capturing or otherwise disturbing any birds, which would have been extremely difficult to achieve through any other method. Next generation sequencing techniques are evolving rapidly and becoming cheaper, therefore being increasingly popular in diet studies (e.g. Deiner et al. 2017). Even though some fish species from West Africa are not yet featured in the NCBI database (www.blast.ncbi.nlm.nih.gov), which may be a limitation for successfully identifying some prey to the species level, this drawback will most likely to be quickly resolved.

This was the first detailed study on the diet of these ten predator species in West Africa. It was also the first to use DNA metabarcoding techniques to describe the diet of migratory birds in their wintering grounds, and also on Laridae species.

Ecosystem structure

Sardinella maderensis was by far the most abundant coastal small pelagic fish, as well as the most frequent prey species for all marine predators studied. Based on these results, we proposed a *wasp-waist* ecosystem structure for the Bijagós Archipelago, with *Sardinella maderensis* as the key central species. In a *wasp-waist* ecosystem, a midtrophic-level small pelagic fish is expected to exert a considerable control of trophic dynamics. This small pelagic represents the link between the higher trophic level species, exerting a bottom-up control on its predators and a top-down control on plankton (Rice 1995).

This work also indicated that the distribution of some seabird species is to a large extent influenced that of predatory fish. Therefore, we stress the need for community-based studies focusing on different taxa groups to obtain a more complete view of the functioning of the ecosystem.

Conservation implications

This thesis emphasised the importance of considering trophic interactions between different species to ensure a sustainable use of marine resources. It provided evidence that *Sardinella maderensis* is highly relevant for the sustainability of the marine ecosystem of Guinea-Bissau, in addition to its already recognized importance for West Africa fisheries (Polidoro et al. 2016). The collapse of *Sardinella maderensis* stocks (and of other clupeid species) would impact the marine ecosystem of the Bijagós Archipelago as a whole, and consequently its human communities. Furthermore, this thesis suggested that the presence of predatory fishes is fundamental for the foraging success of seabirds. Population declines of predatory fishes like jacks and Spanish mackerels, with which seabirds associate, are very likely to decrease foraging opportunities and success for seabirds and lead to changes in their distribution and perhaps in their numbers.

The importance of the Bijagós Archipelago for the species that occur there goes far beyond the limits of its small area. The archipelago holds large numbers of migratory species with global distributions and the conditions they experience there have an impact on their migration, survival and reproductive success (e.g. Patrício et al. 2017). The marine ecosystem of the Bijagós is also extremely valuable for local human communities, who live in one of the poorest countries in the world and greatly rely on its natural resources to survive (Dia and Bedingar 2001, UNDP 2016).

Future research

The monitoring of populational trends of small pelagic and predatory fishes in Guinea-Bissau would be particularly relevant in helping to predict and prevent major ecosystem changes, particularly in face of the current drastic declines in fishery resources. Detailed information about fisheries catches, such as, species, abundance and size of individuals, are imperative to understand the stocks state (Pauly and Zeller 2016) and in Guinea-Bissau are particularly poorly documented (Belhabib and Pauly 2015). Additionally, information on the main reproductive season of predatory fishes and of *Sardinella maderensis* in Guinea-Bissau would further provide basal information for fishing management actions. Furthermore, the frequent occurrence of Chondrichthyes species suggests that the Bijagós Archipelago plays an essential role for the conservation of this rapid declining group (e.g. Baum et al. 2003, Ferretti et al. 2010), (Chapter 1).

In regards to seabirds, the performance of regular surveys of nesting populations and their breeding success would further contribute to a better understanding of their conservation status, since Guinea-Bissau holds significant numbers of breeding pairs. Regular and accurate counts of wintering populations, which are lacking for all species, would also be of utmost importance for controlling changes in seabird abundance.

Furthermore, more detailed information about the associations between terns and predatory fish may be important to understand the spatial predictability of these associations as well as total time spent feeding on these events, which could be studied by tracking birds (e.g. GPS devices). Tagging birds would also allow to better understand the offshore areas used by these species and relate that with fishery fleet distribution and potential fisheries discards, which would be useful for management purposes (Votier et al. 2004, Karpouzi et al 2007, Catry et al. 2009b).

In tropical areas the abundance of seabirds may be related to the abundance of subsurface marine predators that facilitate their feeding, as the most numerous seabird species seem to be the ones relying the most on these associations (Balance and Pitman 1999). Therefore, obtain information over the years about seabird abundance and predatory fish abundance (e.g. from landings), would allow to test the relationship between seabird and predatory fish abundance, and potentially use seabirds as indicators of predatory fish abundance (Jaquemet et al. 2014).

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