Vol. 622: 177–189, 2019
https://doi.org/10.3354/meps13022

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 18

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

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ABSTRACT: Competition, predation and facilitation shape community structure. Yet facilitative behaviour is poorly studied, especially in marine ecosystems. We investigated the diet and foraging behaviour of 5 Afro-Palaearctic migratory seabirds during their non-breeding period in West Africa, focussing on their facilitative associations with predatory fishes. We used next-generation sequencing to describe the diet of 5 tern species, employing DNA metabarcoding for the identification of prey from droppings. This is the first time this method has been used for studying the diet of non-breeding migratory seabirds. Our results showed a high diet overlap among all seabirds, mostly due to the dominance of a single prey species, *Sardinella maderensis* (with a mean frequency of occurrence of 90% in tern diets). The subsurface marine predators identified in association with terns were crevalle jack *Caranx hippos* and West African Spanish mackerel *Scomberomorus tritor*, 2 predatory fishes which also rely on *Sardinella maderensis* as their most frequent prey in the study area, the Bijagós Archipelago. There were marked inter-specific differences in the reliance of terns on subsurface marine predators as facilitators, ranging from completely independent (little tern *Sternula albifrons*) to near-obligatory (black tern *Chlidonias niger*). The varied feeding strategies and small-scale spatial segregation may explain the co-existence of the 5 tern species during the non-breeding period, preying mostly on the same clupeids. Declines both in predatory fishes and in *Sardinella maderensis* and other clupeids are likely to impact the long-distance migrant seabirds studied here, calling for integrated management of fisheries in these coastal ecosystems.

KEY WORDS: Predator–prey interaction · Tern · Next-generation sequencing · DNA metabarcoding · Sympatric predators · Facilitated foraging

1. 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. Begon et al. 2006, Heinlein et al. 2010), while prey abundance can in turn influence the feeding rates, growth and reproductive success of predators (Furness & Tasker 2000, Piatt et al. 2007). The interactions between different predators can lead to competition or to facilitation. The

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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 communities (Pianka 1974, Sih et al. 1998, Begon et al. 2006, Goyert 2014).

Seabirds often associate with subsurface marine predators to feed (Ballance & 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 & Harrison 2017). While it can be observed in most marine environments, facilitation seems to be more important in tropical regions (Ballance & Pitman 1999, Veit & Harrison 2017). This may be due to the lower productivity of these regions when compared to temperate and polar areas. Additionally, marine tropical regions are expected to have more patchily distributed resources and a higher number of large predatory fish (Longhurst & Pauly 1987, Ballance & Pitman 1999). All of these features may enhance associations between seabirds and subsurface marine predators (Ballance & Pitman 1999, Veit & Harrison 2017). However, current knowledge is based on studies conducted mostly offshore, and little is known about such phenomena in tropical shallow coastal waters, where the suite 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 & Weimerskirch 2003, Gremillet et al. 2015). Fluctuations in the availability of prey and of subsurface marine predators that facilitate foraging are also likely to influence seabird abundance and distribution (Ballance & Pitman 1999, Furness & Tasker 2000). Even though the Eastern Central Atlantic region is relatively productive due to an upwelling system influenced by the Canary current (Bakun 1996, Tandstad et al. 2014, Valdés & 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 West Africa 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 non-breeding quarters are much more challenging, since most seabirds are only central-place foragers during the breeding season. During the non-breeding season, birds are harder to catch and sample, and some can spend the non-breeding season offshore (e.g. Dias et al. 2015). Yet conditions experienced at the non-breeding grounds affect survival and subsequent migration and breeding success through carry-over effects. Therefore, understanding non-breeding habits is a prerequisite for the conservation of migratory birds (Marra et al. 1998, Norris et al. 2004, Szostek & 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 & 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 the species level (Pompanon et al. 2012). DNA metabarcoding techniques applied to prey identification from droppings allow the identification of a multitude of prey per sample and offer the possibility of being used in a non-invasive way (e.g. McInnes et al. 2017).

Here we present data on the diet and feeding ecology of Afro-Palaearctic migratory tern species that spend their non-breeding period in West Africa (Cramp 1985, del Hoyo et al. 1996), specifically little tern *Sternula albifrons*, Sandwich tern *Thalasseus sandvicensis*, lesser crested tern *T. bengalensis*, common tern *Sterna hirundo* and black tern *Chlidonias niger*. We used DNA metabarcoding techniques to obtain information on the diet of these 5 seabird species during their non-breeding season. Focal observations were also performed to further describe and compare feeding habits, with special focus on the associations with subsurface marine predators as facilitators.

2. MATERIALS AND METHODS

2.1. 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; Fig. 1). The JVPMNP consists of 4 islands and 2 islets and an extensive area of sea, covering a total of 495 km^2, of which

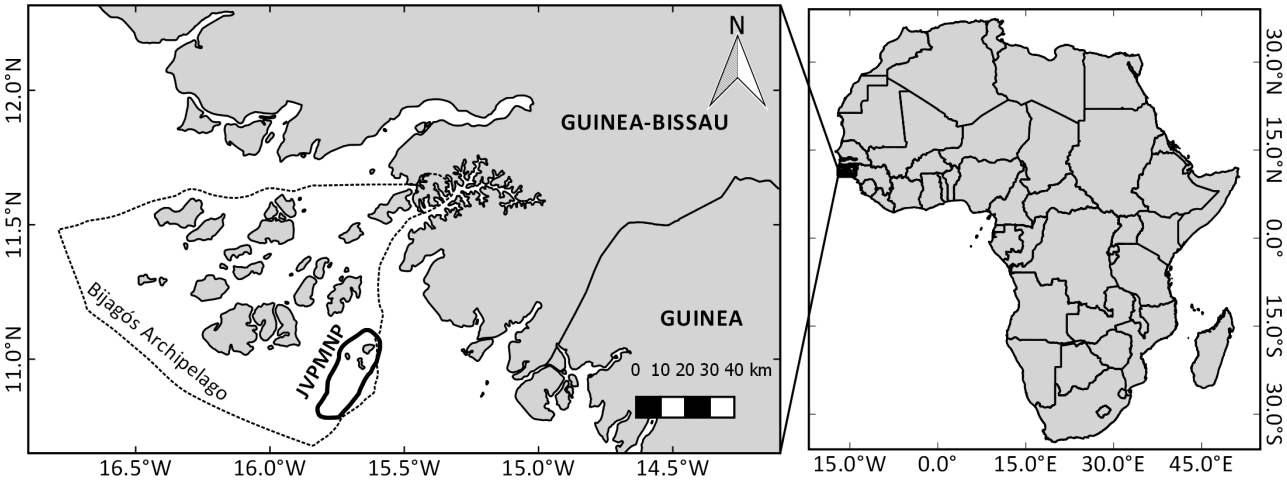

Fig. 1. Location of the João Vieira and Poilão Marine National Park (JVPMNP), delimited by the solid black line; the dashed line delimits the Bijagós Archipelago Biosphere Reserve, Guinea-Bissau, zoomed in from the African continent map

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.

2.2. Foraging behaviour

The fieldwork was carried out during 2 non-breeding seasons (August–April, del Hoyo et al. 1996) in 2014/2015 and 2015/2016. We performed observations of at-sea foraging behaviour on the most abundant non-breeding tern species in the study area: little, Sandwich, lesser crested, common and black terns. All observations were carried out from land, from all 4 islands of the JVPMNP. Individual terns were randomly chosen and observed until they stopped foraging or became too distant (more than 3000 m) for an accurate observation. Prior to the study, we trained and tested our accuracy in measuring distances on land, with the confirmation of a range finder; moreover, to avoid bias, all distances were assessed by the same observer (E. Correia). We assume that our distance estimates have a maximum error of 10%. Individuals were observed up to a maximum of 15 min. We only considered birds displaying foraging behaviour, i.e. birds actively searching for prey (e.g. frequently looking down, hovering or flying in a limited area) as opposed to birds simply commuting, i.e. flying in a straight line at constant speed without looking down.

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 a flock or not (we considered a flock when 2 or more birds were foraging together within a distance of 50 m), number of birds of each species in the flock and distance to the shore of the last dive. In observations where the bird was foraging alone and entered a flock or vice versa, we categorised it based on the behaviour that was dominant in terms of time in that particular observation. We categorised each feeding attempt as: plunge dive, a vertical plunge which usually involves submerging the entire body in water; dive to the surface, a vertical plunge without fully submerging the body in the water; and dipping, when birds fly lower over the water, dipping down to the surface of the water or just below it. For some observations, it was not possible to record all of the above behaviours; therefore, the sample size may vary depending on the analysis (for the total number of individuals observed, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m622p177_supp.pdf).

The association with subsurface marine predators was classified on a 4-point scale as: 0, no association; 1, we were scarcely able to recognize that subsurface marine predators were feeding near the surface, with only occasional turbulence or fins on the water surface; 2, when the activity of subsurface marine predators could be easily seen through regular, but not constant, signs on the water surface; 3, when constant turbulence was seen (water appeared to be 'boiling'), with regular sightings of fins and occasional jumps out of the water by subsurface marine predators and/or by small pelagics.

For each bird observed, we calculated the number of feeding attempts per minute; the percentage of feeding attempts performed in association with fish; and the percentage of each dive type performed. We excluded observation bouts with mixed activity (i.e. where some feeding attempts were performed in association, and others without association, with subsurface marine predators) when comparing behaviours with and without associations.

We tested for differences among species in foraging distance from the shore with Kruskal-Wallis tests (since the residuals did not show a normal distribution), followed by Dunn tests. 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). Since the dependent variable consisted of counts of birds, we assumed a Poisson error distribution and used 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 2-way ANOVA on log (x+1)-transformed data (to avoid non-normality).

2.3. Molecular analysis

In order to study the diet of seabirds, we collected fresh droppings from the sand at daytime roost sites in 2 non-breeding seasons, 2014/2015 and 2015/2016, from all 4 islands in the JVPMNP. As roosting locations often changed within a given island, we regularly walked along the beaches until we were able to find them. Therefore, samples were collected from several different places around the study islands. We collected droppings separated at least by 1 m from each other, to avoid collecting more than one dropping from the same individual. Samples were stored in absolute alcohol immediately after collection, and upon return to the lab were kept refrigerated until further analysis. Next-generation sequencing was used so that many DNA fragments per dropping were amplified, sequenced and assigned to the respective prey species (DNA metabarcoding) (Pompanon et al. 2012).

Tern-specific blocking primers were used to reduce the amplification of predator DNA relative to prey DNA. In order to create reference sequences for designing these specific blocking primers, we amplified DNA from blood or tissue samples of the 5 target tern species provided to us (see the Acknowledgements). DNA from these samples was extracted using a DNeasy Blood and Tissue Extraction Kit (Qiagen) following the standard protocol. We amplified tern DNA using the 16S primers Chord_16S_F and Chord_16S_R (Deagle et al. 2009). PCR reactions were carried in volumes of 10 µl, comprised of 5 µl 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′-GTG GAA CTT AAA AAT YAG CRG CC-3′; Tern_16S_R: 5′-GCT GTT ATC CCT GGG GTA GC-3′), as well as a tern-specific blocking primer (Tern_blocking_chord_16S: 5′-CCC TGT GGA ACT TAA AAA TCA GCR GCC ACT-3SpC3-3′).

In order to identify prey present in droppings, we extracted DNA from 1 dropping per individual using the Stool DNA Isolation Kit (Norgen Biotek) 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 –20°C 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. PCR reactions were carried in volumes of 10 µl, comprised of 5 µl of Qiagen Multiplex PCR Master Mix, with 0.3 µl of each 10 pM amplification primer, 0.3 µl of 100 pM 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^{-1} 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 10 nM and pooled. Finally, the library was quantified using qPCR (KAPA Library Quant Kit qPCR Mix, Bio-Rad iCycler), diluted to 4 nM, and sequenced in a MiSeq desktop sequencer (Illumina).

To be sure of the identity of the droppings, 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 at the Centre for Molecular Analysis (CTM, Porto, Portugal) using an automated DNA sequencer (ABI PRISM 3130 XL).

2.4. Bioinformatics

We used OBITools (Boyer et al. 2016) for sequence processing. In brief, 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 from each other by 1 bp, 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 identified the haplotypes retained through comparison of each to known sequences within the NCBI database (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Haplotypes that best matched the same species were collapsed into a single taxon unit.

2.5. Diet data analysis

The occurrence of each prey taxon in the diet of terns was described with the frequency of occurrence as the percentage of droppings containing a given prey taxon.

We calculated the Horn-Morisita similarity index on frequency data (Morisita 1959, Horn 1966; Eq. 1) to measure the overlap between the diets of terns:

$$C_{jk} = \frac{2\sum_i x_{ij} x_{ik}}{\sum_i x_{ij} \sum_i x_{ik} \left(X_j + X_k\right)} \quad (1)$$

where x_{ij} is the number of individuals of prey i in the feeding regime of predator j (Eq. 2); x_{ik} is the number of individuals of prey i in the feeding regime of predator k (Eq. 3);

$$X_j = \frac{\sum_i x_{ij}^2}{\left(\sum_i x_{ij}\right)^2} \quad (2)$$

$$X_k = \frac{\sum_i x_{ik}^2}{\left(\sum_i x_{ik}\right)^2} \quad (3)$$

The Horn-Morisita index varies from 0, when the diets are completely distinct, to 1, when they are identical; a significant diet overlap can be considered when the index is greater than 0.6 (Langton 1982). This index was calculated based on the lowest possible taxonomic level of prey identified. DNA metabarcoding does not provide information concerning the number of individuals present in each dropping, and therefore the occurrence of each prey taxon counted as one individual.

We used recently published data from Guinea-Bissau concerning the diet of predatory fish (crevalle jack *Caranx hippos*, Guinean barracuda *Sphyraena afra* and West African Spanish mackerel *Scomberomorus tritor*), assessed from macroscopic identification of stomach contents (Correia et al. 2017) and the diet of 2 tern species (Caspian tern *Hydroprogne caspia* and royal tern *Thalasseus maximus*), assessed from macroscopic identification of prey contents in pellets (Correia et al. 2018) along with data from the present study to calculate the diet overlap among these 10 predators. All 10 species of terns and fishes are amongst the most abundant coastal pelagic marine predators that forage in the Bijagós Archipelago. The overlap was also measured with the Horn-Morisita similarity index, as explained above. 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 diet of predators (macroscopic identification of prey in stomach contents and pellets, and DNA metabarcoding from droppings), we used the occurrence of each prey taxon as its numerical frequency (Table S3). Statistical analyses were carried out using the software R (R Core Team 2018).

3. RESULTS

3.1. Facilitative behaviour

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). Of 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 1).

The techniques used for foraging were quite diverse amongst the tern species (Table 2). Little and Sandwich terns performed mostly plunge dives. Common terns were mostly observed diving to the surface and dipping, and black and lesser crested terns were mostly observed dipping (Table 2). Black terns foraged on average farther from shore while little terns tended to forage closer to the shore relative to other species, but no differences were found among the other species (ANOVA: $F_{4,384} = 19.74$, $p < 0.001$, and Tukey HSD test $p < 0.001$, Table 3).

The level of association between terns and underwater predators varied amongst species, ranging from a strong association in black terns, which spent 89% of their foraging activity in association with subsurface marine predators, to no association at all in little terns (Fig. 2). Terns were observed in association with crevalle jack and West African Spanish mackerel (identified while fish jumped out of the water, and also during non-systematic fishing sessions from shore and from boats).

On average, the size of the flocks associated with predatory fishes (mean ± SE: 75.2 ± 7.9 birds, in 129 focal observations) was ca. 1.7 times larger than that recorded in the absence of association (43.5 ± 6.5 birds, in 92 focal observations). Flock size was significantly greater the more intense the association, after accounting for the effect of species (GLM Poisson, effect of levels of association: $\chi^2 = 7169$, df = 1, $p < 0.001$). Little and lesser crested terns were excluded from this analysis since they were never observed in flocks and in association or without association, respectively (Fig. 3).

The number of feeding attempts per minute was significantly higher when birds were in association with subsurface marine predators (2-way ANOVA: $F_{1,655} = 240.9$, $p < 0.001$, Fig. 4). There were significant differences among species ($F_{3,655} = 4.6$, $p = 0.004$), (Fig. 4). Little terns were excluded from this analysis because this species was never observed in association (Fig. 4).

Table 1. Percentage of each flock composition for 87 flocks observed in the Bijagós Archipelago, Guinea-Bissau from 2014 to 2016. +: species present in the flock

Flock type	Little tern	Sandwich tern	Lesser crested tern	Common tern	Black tern	Royal tern	Percentage (%)
Mixed				+	+		29
		+		+			2
	+	+					2
		+				+	2
		+		+	+		2
		+	+	+	+		1
		+	+				1
			+			+	1
Single species				+			28
		+					17
					+		9
	+						5

3.2. Diet and DNA metabarcoding

A total of 32 different prey taxa were identified in the diet of terns,

Table 2. Feeding techniques used by different tern species (mean ± SE %); N: total number of focal individuals observed in the Bijagós Archipelago, Guinea-Bissau from 2014 to 2016

	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 ± 3.55

Table 3. Mean ± SE distance from the shore (m) of the last feeding attempt by species; N: total number of focal individuals observed in the Bijagós Archipelago, Guinea-Bissau from 2014 to 2016

	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

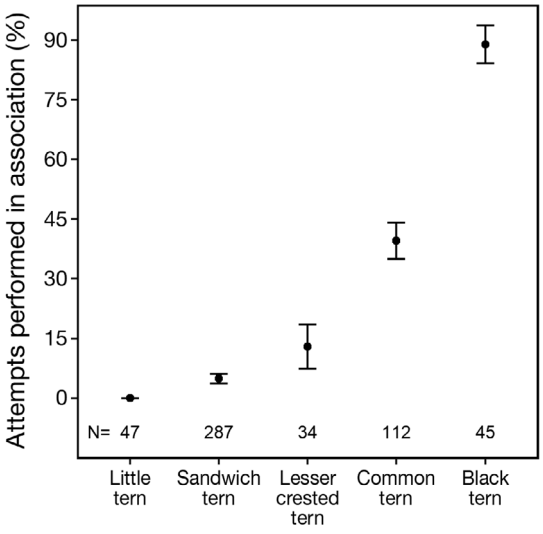

Fig. 2. Mean ± SE percentage of feeding attempts performed by each species in association with predatory fishes; N: number of focal individuals observed in the Bijagós Archipelago, Guinea-Bissau from 2014 to 2016

including 1 from Gastropoda, 2 from Hexanauplia, 9 from Malacostraca and 20 from Actinopterygii (Table 4). The diets of all tern species were dominated by Clupeidae, with *Sardinella maderensis* standing out as the prey species with the highest frequency of occurrence for all seabirds. Within the Clupeidae, *S. aurita* was also a frequent prey item, mostly for Sandwich and lesser crested terns. Copepods (*Subeucalanus pileatus*) were present in the droppings of all species (Table 4). All identified taxa have distributions known to include the study area and are known to occur in habitats similar to the study area. Negative controls did not show any indication of amplification.

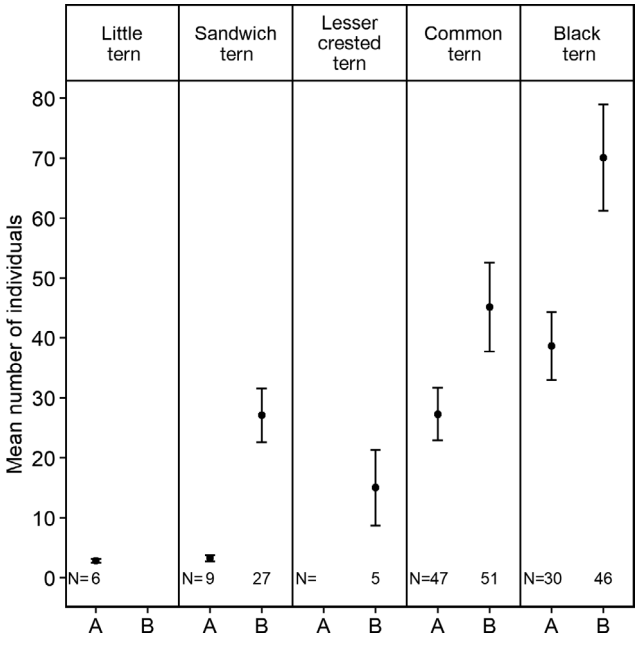

Fig. 3. Mean ± SE number of individuals of each species of tern in flocks foraging without association (A) or in association with predatory fishes (B). N: number of focal individuals observed in the Bijagós Archipelago, Guinea-Bissau from 2014 to 2016

3.3. Diet overlap

The Horn-Morisita index suggested a significant diet overlap between all tern species, with results ranging from 0.74 to 0.96 (Table S2). Furthermore, there was also a significant diet overlap between all the 3 predatory fishes and 7 seabirds from the study area (values ranging from 0.71 to 0.98), with predatory fishes and terns not segregating in separate groups (Fig. 5; Table S3).

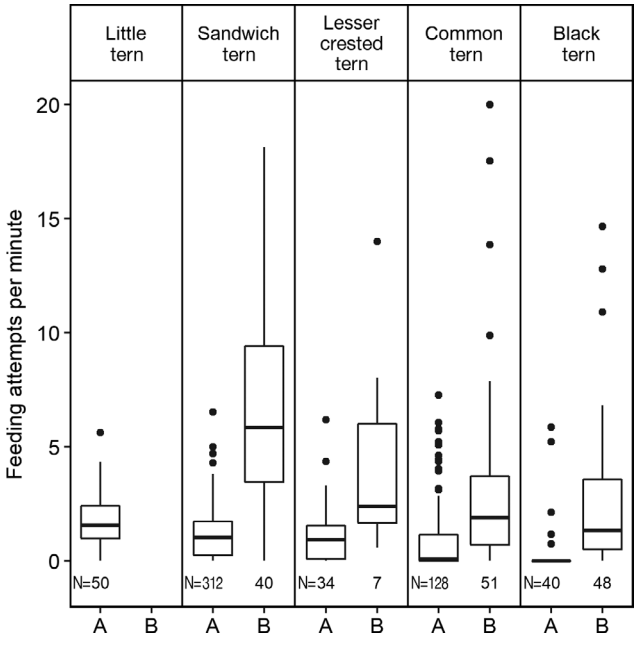

Fig. 4. Number of feeding attempts performed per minute when all the time was spent without association (A) or all the time was spent in association with predatory fishes (B). N: number of focal individuals observed in the Bijagós Archipelago, Guinea-Bissau from 2014 to 2016; boxes correspond to the interquartile range; line above box ends at the largest value within 1.5 times the interquartile range above the 75th percentile and below the box ends at the smallest value within 1.5 times interquartile range below 25th percentile; dots correspond to values between 1.5 and 3 times the interquartile range beyond the end of the box

Table 4. Frequency of occurrence (%) of prey items based on identification from tern droppings using DNA metabarcoding; Teleostei 1 and Teleostei 2 are 2 distinct species of non-identified Teleostei; N: number of droppings collected in the Bijagós Archipelago, Guinea-Bissau from 2014 to 2015

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	22
	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, croakers (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
Unidentified	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

4. DISCUSSION

This study on the feeding ecology of long-distance migratory seabirds during their non-breeding period in West Africa has revealed several key features of this coastal marine community. Different species displayed contrasting levels of association with subsurface marine predators (jacks and mackerels), with black and common terns showing a heavy reliance on these associations. The association with subsur-

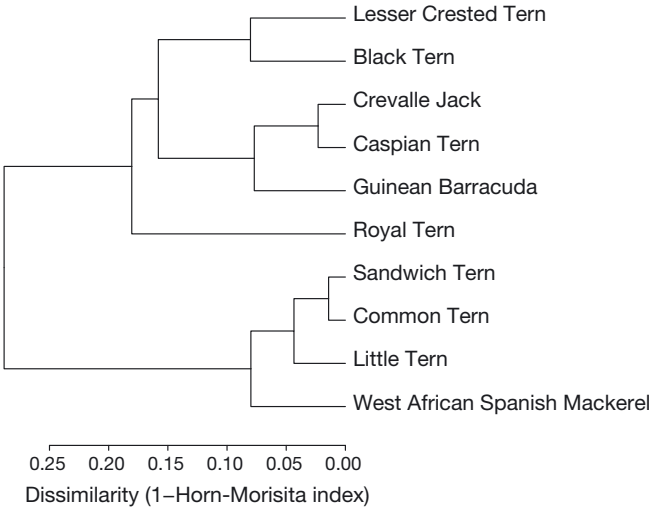

Fig. 5. Cluster analysis of diet dissimilarity (calculated as the distance metrics obtained substracting Horn-Morisita indices from 1) between 3 predatory fish (crevalle jack, Guinean barracuda, West African Spanish mackerel) and 7 tern species (Caspian, royal, little, Sandwich, lesser crested, common, black), calculated to the prey family level for fish and to the prey class level for non-fish; non-identified prey were excluded (data were collected in Guinea-Bissau and Guinea from 2013 to 2016, extracted from Correia et al. 2017, 2018 and the present study)

face marine predators facilitated the formation of larger foraging flocks and higher diving/dipping activity. The entire community, including 7 species of seabirds and the most abundant predatory fishes, relies predominantly on small pelagic Clupeidae, particularly on *Sardinella maderensis*.

4.1. Facilitative behaviour

We studied the associations between seabirds and subsurface marine predators in the Eastern Central Atlantic in shallow marine areas (mostly <10 m). Previous studies carried out 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 & Seki 1987, Harrison et al. 1991, Camphuysen & Webb 1999, Veit & Harrison 2017). However, our results showed that smaller predatory species, including jacks and mackerels, can also be of great importance to seabirds. Similar inshore associations of seabirds with jacks and smaller scombrids had only been documented in the tropical Pacific (Harrison & Seki 1987).

Our results showed that all tern species gathered in larger flocks and performed significantly more feeding attempts when in association with subsurface marine predators, which probably increased 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 subsurface marine predators, the little tern, was also the one that foraged mostly near shore. On the other hand, the 2 species that foraged farther offshore, black and common terns, showed a higher use of 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 & Pitman 1988, Schreiber & Burger 2002).

Flocks of seabirds were usually larger when the birds were associated with subsurface marine predators. 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 subsurface marine predators (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 (Table S3). These fishes feed actively near the surface (Kwei 1978, Collette & Nauen 1983, Paugy et al. 2003), preying on large schools of small pelagic fishes, thus making large quantities of fish accessible at the surface. Our results suggest that facilitative associations may have a strong influence on the distribution of species and possibly on their foraging efficiency (Ballance & Pitman 1999, Thiebault et al. 2016, Miller et al. 2018), thereby being an important factor for spatially structuring the marine community in our study area.

We believe that the use of associations by the different species is likely to be underestimated. This is in part because the associations occurred mostly offshore and all of our observations were performed from land (small islands). Additionally, the presence of subsurface marine predators 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. Hence, the importance of associations with subsurface marine predators for the foraging behaviour of seabirds may be even greater than our results suggest.

4.2. Diet and 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 on diet in their non-breeding quarters are scarce (but see Dunn 1972, Cramp 1985, Piersma & Ntiamoa-Baidu 1995, Bugoni & Vooren 2004), particularly in West Africa and especially for lesser crested and little terns.

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 to migratory birds in their non-breeding habitats. Most of the previous studies on this bird family were conducted through the macroscopic identification of pellets (e.g. Bugoni & Vooren 2004). Yet these traditional methods present limitations (like the severe underestimation of species with small otoliths; e.g. Alonso et al. 2013) particularly when applied outside of the breeding season. Also, since different tern species roost together in the winter, it is often virtually impossible to unequivocally link the samples collected to a particular species. DNA metabarcoding of pellets or scats is a useful alternative or complementary method to assess seabird diet (Deagle et al. 2007, Bowser et al. 2013, McInnes et al. 2017). The fact that it does not require hard identifiable prey fragments to be present and that it allows a very high taxonomic resolution has revolutionized how ecologists can study trophic interactions. Although the technique does not allow for prey biomass to be quantified, it does give an estimate of consumption frequency. Furthermore, by using molecular methods, we could also identify the corresponding predator species, thus allowing for samples to be collected non-invasively, directly from the ground, while avoiding the problem of species misassignment.

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). Considering that the presence of invertebrates varied between tern species and that during the non-breeding season these species may consume marine invertebrates (e.g. common terns, Blokpoel et al. 1989), we assumed 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. Nonetheless, our results showed a clear preference for Clupeiformes (such as Clupeidae, Pristigasteridae and Engraulidae) as the main prey group for all tern species.

The inter-specific differences in (1) distribution (distance from the shore) while foraging, (2) degree of use of associations and (3) preferred feeding techniques may contribute to the ecological segregation of the various tern species. Furthermore, morphological differences between terns may further 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 (mostly plunge diving and dipping, respectively). Little and black terns are also similar in terms of bill and body length (corresponding to the length from tip of bill to tip of tail; Cramp 1985, del Hoyo et al. 1996) but the 2 species predominantly used different feeding techniques, and while black terns foraged almost exclusively in association with subsurface marine predators, 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 subsurface marine predators, which fits well with its generalist habits across its vast geographic range. The inter-specific differences in foraging behaviour can alleviate competition and contribute to the coexistence of these species in the same area.

Differences in the realized niches of competing species on limiting resources are predicted by ecological theory (Schoener 1983), but when resources are abundant, we may expect a greater interspecific niche overlap (Schoener 1982, Wiens 1993, Newton 1998, Weimerskirch et al. 2009). We observed a high diet overlap between 10 marine predators (3 predatory fishes and 7 seabirds) coexisting in the Bijagós Archipelago (Table S3). The high diet overlap observed can thus be related to the high availability of the main prey (*Sardinella maderensis*) in the region (Lafrance 1994, Valdés & Déniz-González 2015). We highlight the importance of *S. maderensis* as a key species in the trophic dynamics of the marine community of the Bijagós Archipelago. The dominance of one or a few species of small pelagics (e.g. clupeids) that control the population dynamics of the upper and lower trophic levels was already described in other upwelling and coastal areas, and points to a wasp-waist ecosystem structure (Rice 1995, Bakun 1996, Cury et al. 2000, Atkinson et al. 2014). Our results strengthen the suggestion of this type of structure for the marine ecosystem of the Bijagós archipelago, with *S. maderensis* as the central key species (Correia et al. 2017).

4.3. Management implications

Increasing pressure on local marine resources, caused by the expansion of the activity of fishermen from neighbouring countries in recent years, is a matter of concern for marine conservation in Guinea-Bissau (Kyle 2009, Njock & Westlund 2010, Binet et al. 2012). Particularly in the case of crevalle jack and West African Spanish mackerel, both caught for commercial and recreational purposes, catches have started to decline as a result of fishery intensification (Collette & Nauen 1983, Froese & Pauly 2018). Moreover, the high level of illegal, unreported and unregulated fishing in the region may further threaten the populations of these fish species at a regional level (Belhabib et al. 2015, Doumbouya et al. 2017, Intchama et al. 2018).

Population decline of predatory fishes like jacks and mackerels is likely to decrease foraging opportunities for seabirds and lead to a change in their distribution (e.g. Veit & Harrison 2017). Faced with fewer 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.

Marine resources are extremely valuable as the main protein source for many human coastal communities and one of the most important sources of revenue in the region (Dia & 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 highlights that a broad view of the marine ecosystem is needed for the management of the Bijagós Archipelago and beyond. 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 (clupeids) and predatory fishes is also necessary for the conservation of long-distance migratory seabirds in the African–Eurasian migratory flyway.

Acknowledgements. This work was supported by the MAVA Foundation through a project granted to IBAP (Guinea-Bissau) – 'La recherche participative au service de la conservation de la biodiversité du Parc National Marin de João Vieira-Poilão (Archipel des Bijagós)'. We thank Camilo Carneiro, Joana Romero, Mohamed Henriques and Maria Alho for the help in fieldwork; Silke Wapp for valuable help in the laboratory; the park wardens, whose field knowledge was very useful; Madalena Boto for the manuscript revision; and Yvonne Verkuil, Jan van der Winden, Afonso Rocha, Nicola Bacetti, Adriano De Faveri, Sandra Bouwhuis and Peter H. Becker for providing biological samples of terns. Fundação para a Ciência e a Tecnologia (FCT Portugal) provided additional financial support through the strategic project MARE-UID/MAR/04292/2019 granted to MARE and project IF/00502/2013/CP1186/CT0003; FCT/MEC through national funds and the co-funding by FEDER, within the PT2020 Partnership agreement and Compete 2020 granted to CESAM (UID/AMB/50017). PD/BD/52594/2014 was granted to E.C. by the FCT.

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Editorial responsibility: Elliott Hazen, Pacific Grove, California, USA

Submitted: November 7, 2018; Accepted: June 4, 2019
Proofs received from author(s): July 11, 2019