FORAGING NORTHERN GANNETS *MORUS BASSANUS* SHOW NEAR-HORIZONTAL PLUNGE DIVES IN THE SHALLOWS OF BANC D'ARGUIN, MAURITANIA

THEUNIS PIERSMA[1,2,3*], LUC G. G. DE MONTE[1], EL-HACEN M. EL-HACEN[2,4], AMADOU ABDARAHMANE SALL[5], & TIM OORTWIJN[1,2]

[1]*Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, and Utrecht University, Texel, The Netherlands *(theunis.piersma@nioz.nl)*

[2]*BirdEyes, Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, University of Groningen, Leeuwarden, The Netherlands*

[3]*Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands*

[4]*Parc National du Banc d'Arguin, Tevragh Zeina, Nouakchott, Islamic Republic of Mauritania*

[5]*Institut Mauritanien de Recherches Océanographiques et des Pêches (IMROP), Nouadhibou, Islamic Republic of Mauritania*

Received 23 January 2026, accepted 6 April 2026

ABSTRACT

Piersma, T., de Monte, L. G. G, El-Hacen, E.-H. M., Sall, A. A., & Oortwijn, T. (2026). Foraging Northern Gannets *Morus bassanus* show near-horizontal plunge dives in the shallows of Banc d'Arguin, Mauritania. *Marine Ornithology*, *54*(2), 351–356. http://doi.org/10.5038/2074-1235.54.2.1708

The numbers of Northern Gannets *Morus bassanus* of all age classes within sight of the shores of the Iwik Peninsula, in the Parc National du Banc d'Arguin, have increased from nil to being rather common since 2022. At the same time, the local numbers of another bird that feeds on schooling fish, the Great Cormorant *Phalacrocorax carbo lucidus*, have exploded, indicating the presence of large local stocks of suitable prey. In this paper, we describe the plunge diving of gannets in the channels between exposed intertidal mudflats, including their participation in multi-species feeding flocks that also include cormorants and Great White Pelicans *Pelecanus onocrotalus*. We also describe a previously unreported foraging method used in still, shallow waters over seagrass beds (< 1 m deep): low-angle (near-horizontal), torpedo-like plunges just below the surface across distances up to 10 m.

Key words: multi-species feeding association, intertidal mudflats, inshore, pelagic fish, piscivores, seabirds, Sulidae, West Africa

INTRODUCTION

In his massive, 1,012-page tome on the behaviour of the gannets and boobies of the world, J. Bryan Nelson (Nelson, 1978) spent very few words on their foraging and food. The maps of potential fish prey across the North Sea indicate that this was not for lack of interest. It must reflect a lack of opportunity, as most of the lives of non-breeding Northern Gannets *Morus bassanus*—and all their foraging—play out on the open sea, beyond the visual reach of shore-bound researchers. Indeed, in a monograph published 32 years later, Nelson (2002) extensively discussed their offshore foraging.

Things have changed ever since observers on seagoing vessels started to systematically map seabirds at sea using standardized methods (Ainley et al., 2012; Camphuysen, 2011). And whilst these observers at sea were at it, researchers began to put increasingly sophisticated electronic tags on breeding gannets to follow individuals away from the colonies (e.g., Warwick-Evans et al., 2016). The tagging studies revealed how breeding females dive differently and feed farther offshore on longer foraging trips than the similar-looking males (Cleasby et al., 2015); how underwater wingbeats extend the depth and duration of plunge dives (Garthe et al., 2000; Ropert-Coudert et al., 2009); how plunge diving styles are associated with the presence of various kinds of pelagic fish (d'Entremont et al., 2022, 2023; Garthe et al., 2011); and the tight relationships between foraging efforts, breeding success, and fish abundance (Cohen et al., 2014). The tags even revealed that individual gannets consistently "roll" to either the left or the right side during plunge diving (Bennison et al., 2023). Using GPS data loggers, Wells et al. (2016) showed that in northern Bass Strait, Australia, breeding Australasian Gannets *M. serrator*, especially males, plunge dived in inshore waters with a depth of only 10 m, in addition to their well-known deep-water foraging.

Northern Gannets breeding in the North Atlantic spend their early years and the non-breeding seasons, when adult, along the Atlantic seaboard of southwestern Europe and, especially, northwest Africa (Atkins et al., 2025), with incursions into the Mediterranean as well (Foster, 2023). As winter visitors to the Atlantic Ocean of northwest Africa, especially the Canary Current upwelling zone, the largest numbers are found on the Mauritanian shelf precisely during the months when the coastal observations reported here were made (Camphuysen, 2022). For Mauritanian waters alone, Camphuysen et al. (2013) estimated the presence of 325,000 gannets, or *ca*. 30% of the world population. In a synthesis of the distribution of seabirds at sea across the southern Canary Current along the coast of Mauritania, Camphuysen (2022) showed that Northern Gannets mostly occurred in waters

over the continental shelf, with a decline in densities across the shelf break towards the deep ocean.

Indeed, in early 1980, when Altenburg et al. (1982) crisscrossed the full extent of the Parc National du Banc d'Arguin (PNBA; see Fig. 1)—i.e., the region inshore of the one mapped by Camphuysen (2022)—only 30 Northern Gannets were seen, and these were many kilometres away from the shore, in the vicinity of the city of Nouadhibou. During annual winter returns to the Banc d'Arguin by our team starting in 2002, Northern Gannets in low numbers (one to 15 birds) have been a regular sight in the open water between the village of Iwik and the island of Tidra, the latter of which is still 20–30 km away from off-shelf, deeper waters (unpublished observations). From 2022 on, however, numbers have been increasing, with tens of gannets encountered during crossings from Iwik to Tidra. Still, it was quite rare to see gannets from the shore. In this paper, we summarize our observations from 2022, 2024, and 2025 of Northern Gannets as nearshore foragers.

STUDY AREA AND METHODS

The observations reported here were collected in February 2022, December 2024, and November 2025, on or quite close to the Iwik Peninsula (19°53′N, 16°18′W), in the heart of the PNBA (Fig. 1). The PNBA is the largest marine protected area in Africa, with an area of 12,000 km^2. Half of the protected area is covered by shallow (< 20 m) Atlantic waters, bordered on parts of the Sahara side by *ca.* 450 km^2 of intertidal flats covered mostly with seagrass (Campredon, 2000; El-Hacen et al., 2024; Folmer et al., 2012; Oudman et al., 2020; van der Heide et al., 2012; Wolff & Smit, 1990; Fig. 1). The shallow waters have a slightly higher salinity than ocean water and a much lower turbidity than is typical of intertidal systems, even of the waters that cover the seagrass-covered mudflats during flood and ebb. Secchi disc depths typically measure 3–8 m or even more (Sevrin-Reyssac, 1993; personal observation by the authors).

During annual three-week shorebird demography research campaigns from 2002 to 2025 (see El-Hacen et al., 2024), five to eight observers spent most of the daylight hours in the field, watching waterbirds on all shorelines around the Iwik Peninsula (Fig. 1), with occasional forays further west and east. The observations in 2024–2025, after the 20 years of reports from the shore with no gannets, were remarkable for their singularity and novelty.

RESULTS

On 12 February 2022, PNBA wardens observed > 900 gannets between the island of Kiaone and Cape Tafarit (Cap Tafarit, in French) on the mainland (Site 1, Fig. 1B). They were plunge diving into relatively shallow water (< 20 m) in the company of tens of

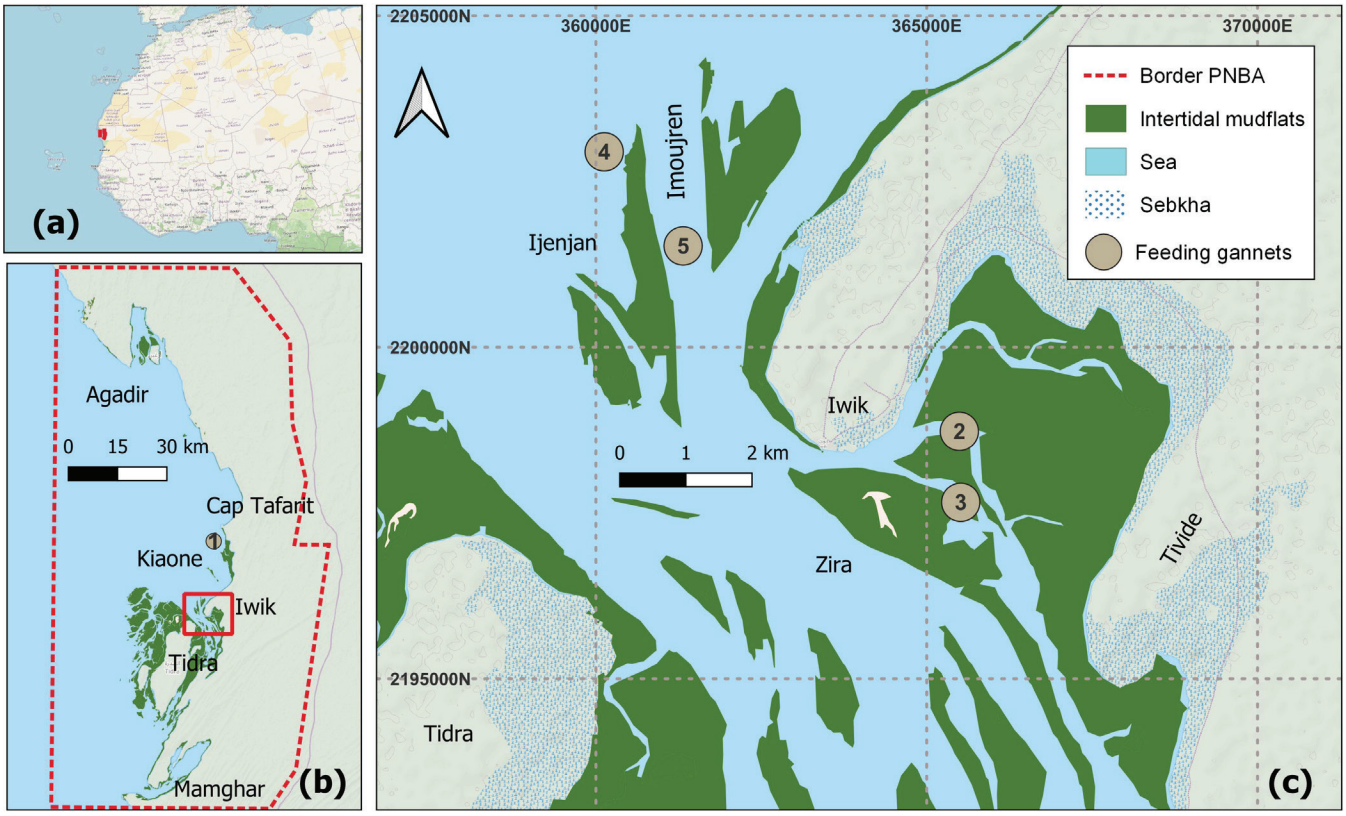


Fig. 1. (A) Location of the Parc National du Banc d'Arguin (PNBA), Mauritania, on the West African coastline, in red. (B) Map of the PNBA (within red-dashed border) showing the main coastal habitats, including the intertidal areas in green. (C) Map indicating sites where shallow-water-feeding Northern Gannets (*Morus bassanus*) were seen in 2022, 2024, and 2025 (numbered circles); geographic coordinates indicated using UTM Zone 28N. Sebkhas are hypersaline flats characterized by episodic flooding and subsequent evaporation, resulting in salt-encrusted soils with a lack of vegetation.

bottlenose dolphins *Tursiops truncatus*. The scene lasted at least 15 min, but then the aggregation of dolphins and gannets moved farther away from the coast, out of sight.

In the early morning of 09 December 2024, during an outgoing tide, one of the authors (LGGdM) witnessed 50 Northern Gannets plunge diving in a channel between exposed intertidal flats (Site 2, Fig. 1C)—a "feeding frenzy" also involving tens of Great White Pelicans *Pelecanus onocrotalus* and Great Cormorants *Phalacrocorax carbo lucidus* (previously known as White-breasted Cormorants *Phalacrocorax lucidus*). Then, during incoming tide on 21 November 2025, TO noticed 30–40 gannets in a neighbouring channel (Site 3, Fig. 1C), apparently resting on the water (Fig. 2) after an earlier foraging session.

On 25 November 2025, just after noon, as the tide turned and water started to cover the lowest-lying intertidal flats, TP noticed *ca*. 30 gannets circling at low heights just northwest of Ijenjan (Site 4, Fig. 1C). As the tide line crept up the mudflats, the gannets ended their circling after a low approach, diving at shallow angles (< 5°–10°, so, near horizontally), then "torpedoing" for another 10 m just below the water surface. As they sped along, the gannets even created bow waves before resurfacing. We could not determine whether these were real "pursuits" of fish with the gannets using their wings (e.g., Garthe et al., 2000), although it seemed likely. These near-horizontal dives occurred in water that likely was < 1 m deep, as it was in an area where the surface was flat, without waves. The water was being "captured" by the waving leaves of the freshly flooded seagrass meadow.

On 27 November 2025, again with an incoming tide, TO counted at least 230 gannets over the channel between the nearshore mudflats of Ijenjan and Imoujren (Site 5, Fig. 1C). Some individuals showed a different diving behaviour, in this case a low, slow approach, interrupted by a one-wingbeat stop to reach *ca*. 2 m above the water surface before a shallow plunge. During all these observations, the great variation in plumages, from the very dark of young of the year to the fully white of adults (Nelson, 1978), suggested that gannets of all ages were participating in this near-intertidal foraging.

DISCUSSION

The "feeding frenzy" of Northern Gannets, Great Cormorants, and Great White Pelicans observed in a gully close to Iwik on 09 December 2024 and the observation of gannets foraging with dolphins in February 2022 seem to be clear examples of what Camphuysen and Webb (1999) called multi-species feeding associations (MSFAs). MSFAs indicate local patches of forage fish, with the different predators capitalizing in different ways—and some of them facilitating co-occurring predators as a result of their chasing.

The increasing numbers of Northern Gannets close to Iwik Peninsula in recent years has occurred along with a surge in the numbers of Great Cormorants. The local counts jumped from the usual "less than 100" in the Iwik area (El-Hacen et al., 2024) to the 7,000 cormorants counted on 04 December 2024 and 9,700 counted on 17 November 2025. The presence of pelicans suggests that fish shoals were close to the surface, perhaps driven upward by the cormorants (van Eerden & van Rijn, 2021; van Eerden & Voslamber, 1995). The horizontal dives over a freshly submerged seagrass bed, with the depth of the overlying clear water < 1 m deep, took place in the absence of other foraging species. In this case, the shoals of fish would have been contained by the seagrass meadow.

Most likely, these cormorants, and the gannets too, concentrated in the inshore areas of Banc d'Arguin to forage on high densities of small schooling fish. In recent years, we have noticed more surface activity of shoals, with small fish jumping out of the water in the hundreds or thousands. Consultation with local fishermen and boat captains revealed that three species make up most of the fish involved. The two most common (both species with lengths < 20 cm) are the blackchin tilapia *Sarotherodon melanotheron* (an endemic West African cichlid adapted to saline waters) and the sargo, or common white seabream, *Diplodus sargus*. And certainly, in November 2025, many relatively small (25–30 cm) flathead grey mullet, or yellow mullet, *Mugil cephalus* were present (as part of their seasonal migration). Over the last two decades, the stocks of some of the first two fish species have increased within the PNBA, perhaps in response to the overfishing of possibly competing commercial bony fish (Lemrabott et al., 2023, 2024). Of course, there could also be downstream effects of the industrial overfishing occurring offshore and/or the overfishing of the predators of pelagic fish (Camphuysen, 2022; Lemrabott et al., 2025; Leurs et al., 2021; Meissa & Gascual, 2015).

In their reviews of feeding methods of seabirds, Ashmole (1971) and Ainley (1977) did not describe the near-horizontal plunge dives described here. This behaviour does occur among Blue-footed Boobies *Sula nebouxii* foraging in the shallows of the Gulf of California (D. Ainley, personal communication, 2025). Focussing on Northern Gannets, Camphuysen (2011) distinguished (1) deep plunging (headlong plunge dive into the sea; bird disappears below surface) and (2) shallow plunging (headlong plunge dive into the sea; bird remains visible at surface). In addition, Camphuysen recorded pelican-like "scooping" of fish from the sea surface by swimming gannets in short-lived MSFAs developing over lesser sand-eel *Ammodytes marinus* schools. In these cases, the fish were driven towards the surface by auks or small cetaceans. Note that gannets entered these MSFAs in deep waters of the mid-ocean by diving at low angles from low height (Camphuysen 2011). Thus, although there are reports of gannets entering inshore areas (notably Wells et al., 2016), the "horizontal dives" in water with a depth of < 1 m reported here appear to represent a hitherto undescribed foraging technique and feeding habitat of Northern Gannets. We hope that in the future this behaviour can be linked to signals from suitably tagged (see e.g., Garthe et al., 2000; Machovsky-Capuska et al., 2012) individuals that use the PNBA during the non-breeding season.

ACKNOWLEDGEMENTS

We thank the administration of the Parc National du Banc d'Arguin (PNBA) for permissions, logistic arrangements, and all kinds of administrative help; NIOZ for its ongoing financial support of the annual shorebird demographic efforts; Anne Dekinga and Job ten Horn for leading the expeditionary work; and our other colleagues during the 2024 and 2025 campaigns for great companionship and support. Kees Camphuysen provided enthusiastic expert feedback on drafts. We are also grateful for the help of reviewers and the editor.



Fig. 2. A group of Northern Gannets (*Morus bassanus*) resting on the surface of a channel between exposed intertidal flats between the islet of Zira (from where the photos were taken) and a mainland area called Tivide (Fig. 1C) on the coast of Mauritania on 21 November 2025. The Greater Flamingoes *Phoenicopterus roseus* in the foreground call attention to the shallow layer of water on the seagrass-covered mudflats; a line of shorebirds is on the distant shore. Note the jumping flathead grey mullet *Mugil cephalus* in the foreground of (A) and the gannets taking off in flight in both panels. Photo credit: Tim Oortwijn

REFERENCES

Ainley, D. G. (1977). Feeding methods in seabirds: A comparison of polar and tropical communities in the eastern Pacific Ocean. In G. A. Llano (Ed.), *Adaptations within Antarctic ecosystems* (pp. 669–685). Gulf Publishing Co.

Ainley, D. G., Ribic, C. A., & Woehler, E. J. (2012). Adding the ocean to the study of seabirds: A brief history of at-sea seabird research. *Marine Ecology Progress Series*, *451*, 231–243. https://www.jstor.org/stable/24875933

Altenburg, W., Engelmoer, M., Mes, R., & Piersma, T. (1982). *Wintering waders on the Banc d'Arguin, Mauritania: Report of the Netherlands Ornithological Mauritanian Expedition 1980* (Wadden Sea Working Group communication No. 006). Stichting Veth tot Steun aan Waddenonderzoek.

Ashmole, N. P. (1971). Sea bird ecology and the marine environment. In D. S. Farner & J. R. King (Eds.), *Avian biology* (Vol. 1, pp. 223–286). Academic Press.

Atkins, K. M., Pereira, J. M., Morgan, G., Morgan, L., Mitchell, C., Bearhop, S., Sherley, R. B., & Votier, S. C. (2025). Gannets wintering in the Canary Current and Iberian Coast feed primarily on pelagic fishes and co-occur with trawl and fixed gear fisheries. *Marine Ecology Progress Series*, *765*, 85–100. https://doi.org/10.3354/meps14898

Bennison, A., Clark, B. L., Votier, S. C., Quinn, J. L., Darby, J., & Jessopp, M. (2023). Handedness and individual roll-angle specialism when plunge diving in the Northern Gannet. *Biology Letters*, *19*(9), Article 20230287. https://doi.org/10.1098/rsbl.2023.0287

Camphuysen, C. J. (2011). Northern Gannets in the North Sea: Foraging distribution and feeding techniques around the Bass Rock. *British Birds*, *104*, 60–76.

Camphuysen, C. J. (2022). *Seabirds and other charismatic megafauna in offshore habitats off NW Africa: GTA Ecological Vulnerability Analysis* (NIOZ Report 2022-03). Royal Netherlands Institute for Sea Research. https://doi.org/10.25850/nioz/7b.b.md

Camphuysen, C. J., van Spanje, T. M., Verdaat, H., Kloff, S., & El Moustapha, A. O. M. (2013). *Ship-based seabird and marine mammal surveys off Mauritania, Nov-Dec 2012: Cruise report*. Royal Netherlands Institute for Sea Research. https://edepot.wur.nl/249785

Camphuysen, C. J., & Webb, A. (1999). Multi-species feeding associations in North Sea seabirds: Jointly exploiting a patchy environment. *Ardea*, *87*(2), 177–198.

Campredon, P. (2000). *Between the Sahara and the Atlantic: Banc d'Arguin National Park, Mauritania*. Fondation Internationale du Banc d'Arguin.

Cleasby, I. R., Wakefield, E, D., Bodey, T. W., Davies, R. D., Patrick, S. C., Newton, J., Votier, S. C., Bearhop, S., & Hamer, K. C. (2015). Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Marine Ecology Progress Series*, *518*, 1–12. https://doi.org/10.3354/meps11112

Cohen, L. A., Pichegru, L., Grémillet, D., Coetzee, J., Upfold, L., & Ryan, P. G. (2014). Changes in prey availability impact the foraging behaviour and fitness of Cape Gannets over a decade. *Marine Ecology Progress Series*, *505*, 281–293. https://doi.org/10.3354/meps10762

d'Entremont, K. J. N., Davoren, G. K., Walsh, C. J., Wilhelm, S. I., & Montevecchi, W. A. (2022). Intra- and inter-annual shifts in foraging tactics by parental Northern Gannets *Morus bassanus* indicate changing prey fields. *Marine Ecology Progress Series*, *698*, 155–170. https://doi.org/10.3354/meps14164

d'Entremont, K. J. N., Pratte, I., Gjerdrum, C., Wong, S. N. P., & Montevecchi, W.A. (2023). Quantifying inter-annual variability on the space-use of parental Northern Gannets (*Morus bassanus*) in pursuit of different prey types. *PLOS One*, *18*(7), Article e0288650. https://doi.org/10.1371/journal.pone.0288650

El-Hacen, E.-H. M., ten Horn, J., Dekinga, A., Loos, B., & Piersma, T. (2024). Two decades of change in nonbreeding population sizes of shorebirds and other waterbirds in the Iwik area of Parc National du Banc d'Arguin, Mauritania. *Wader Study*, *131*(2), 112–121. https://doi.org/10.18194/ws.00343

Folmer, E. O., van der Geest, M., Jansen, E., Olff, H., Anderson, T. M., Piersma, T., & van Gils, J. A. (2012). Seagrass–sediment feedback: An exploration using a non-recursive structural equation model. Ecosystems, *15*, 1380–1393. https://doi.org/10.1007/s10021-012-9591-6

Foster, C. (2023). *Cry of the wild: Eight animals under siege*. Penguin Random House.

Garthe, S., Benvenuti, S., & Montevecchi, W. A. (2000). Pursuit plunging by northern gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). *Proceedings of the Royal Society B*, *267*(1454), 1717–1722. https://doi.org/10.1098/rspb.2000.1200

Garthe, S., Montevecchi, W. A., & Davoren, G. K. (2011). Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. *Limnology and Oceanography*, *56*(3), 802–812. https://www.jstor.org/stable/10.2307/26955094

Lemrabott, S. Y. C., El-Hacen, E.-H. M., Piersma, T., Sall, A. A., Sidina, E., Mahmoud, L. Y. A., Olff, H., & van Leeuwen, A. (2023). Twenty years of monitoring reveal overfishing of bony fish stocks in the coastal national park Banc d'Arguin, in Mauritania. *Aquatic Conservation*, *33*(8), 833–844. https://doi.org/10.1002/aqc.3948

Lemrabott, S. Y. C., van Leeuwen, A., Leurs, G., El-Hacen, E.-H. M., Piersma, T., Sall, A. A., Sidina, E., Yarba, L. & Olff, H. (2025). Overfishing of threatened bycatch species in a Marine Protected Area: The elasmobranchs of Banc d'Arguin, Mauritania. *Fisheries Management and Ecology*, *32*(4), 97–106. https://doi.org/10.1111/fme.12786

Lemrabott, S. Y. C., van Leeuwen, A., Piersma, T., Braham, C.-B., Ball, A. C., Araujo, A., Olff, H., & El-Hacen, E.-H. M. (2024). The chronology of overfishing in a remote West-African coastal ecosystem. *Ecology and Society*, *29*(1), Article 9. https://doi.org/10.5751/ES-13902-290109

Leurs, G., van der Reijden, K. J., Cheikhna Lemrabott, S. Y., Barry, I., Nonque, D. M., Olff, H., Ledo Pontes, S., Regalla, A., & Govers, L. L. (2021.) Industrial fishing near West African marine protected areas and its potential effects on mobile marine predators. *Frontiers in Marine Science*, *8*, Article 602917. https://doi.org/10.3389/fmars.2021.602917

Machovsky-Capuska, G. E., Howland, H. C., Raubenheimer, D., Vaughn-Hirshorn, R., Würsig, B., Hauber, M. E., & Katzir, G. (2012). Visual accommodation and active pursuit of prey underwater in a plunge-diving bird: The Australasian gannet. *Proceedings of the Royal Society B*, *279*(1745), 4118–4125. https://doi.org/10.1098/rspb.2012.1519

Meissa, B., & Gascuel, D. (2015). Overfishing of marine resources: Some lessons from the assessment of demersal stocks off Mauritania. *ICES Journal of Marine Science*, *72*(2), 414–427. https://doi.org/10.1093/icesjms/fsu144

Nelson, J. B. (1978). *The Sulidae: Gannets and boobies*. Oxford University Press.

Nelson, J. B. (2002). *The Atlantic gannet*. Fenix Books.

Oudman, T., Schekkerman, H., Kidee, A., van Roomen, M., Camara, M., Smit, C., ten Horn, J., Piersma, T., & El-Hacen, E.-H. M. (2020). Changes in the waterbird community of the Parc National du Banc d'Arguin, Mauritania, 1980–2017. *Bird Conservation International*, *30*(4), 618–633. https://doi.org/10.1017/S0959270919000431

Ropert-Coudert, Y., Daunt, F., Kato, A., Ryan, P. G., Lewis, S., Kobayashi, K., Mori, Y., Grémillet, D., & Wanless, S. (2009). Underwater wingbeats extend depth and duration of plunge dives in northern gannets *Morus bassanus*. *Journal of Avian Biology*, *40*(4), 380–387. https://doi.org/10.1111/j.1600-048X.2008.04592.x

Sevrin-Reyssac, J. (1993) Hydrology and underwater climate of the Banc d'Arguin, Mauritania: A review. *Hydrobiologia*, *258*, 1–8. https://doi.org/10.1007/bf00006181

van der Heide, T., Govers, L. L., de Fouw, J., Olff, H., van der Geest, M., van Katwijk, M. M., Piersma, T., van de Koppel, J., Silliman, B. R., Smolders, A. J. P., & van Gils, J. A. (2012). A three-stage symbiosis forms the foundation of seagrass ecosystems. *Science*, *336*(6087), 1432–1434. https://doi.org/10.1126/science.1219973

van Eerden, M. R., & van Rijn, S. (2021). Social hierarchy within communal foraging flocks of Great Cormorants *Phalacrocorax carbo* as reflected by differences in prey composition and food intake at the roost. *Ardea*, *109*(3), 549–563. https://doi.org/10.5253/arde.v109i2.a23

van Eerden, M. R., & Voslamber, B. (1995). Mass fishing by Cormorants *Phalacrocorax carbo sinensis* at Lake Ijsselmeer, The Netherlands: A recent and successful adaptation to a turbid environment. *Ardea*, *83*(1), 199–212. http://ardea.nou.nu/ardea_search3.php?key=nummer&keyin=83&k2=1

Warwick-Evans, V., Atkinson, P. W., Arnould, J. P. Y., Gauvain, R., Soanes, L., Robinson, L. A., & Green, J. A. (2016). Changes in behaviour drive inter-annual variability in the at-sea distribution of northern gannets. *Marine Biology*, *163*, Article 156. https://doi.org/10.1007/s00227-016-2922-y

Wells, M. R., Angel, L. P., & Arnould, J. P. Y. (2016). Habitat-specific foraging strategies in Australasian Gannets. *Biology Open*, *5*(7), 921–927. https://doi.org/10.1242/bio.018085

Wolff, W. J., & Smit, C. J. (1990). The Banc d'Arguin, Mauritania, as an environment for coastal birds. *Ardea*, *78*, 17–38.