

Long-term changes in seagrass and benthos at Banc d'Arguin, Mauritania, the premier intertidal system along the East Atlantic Flyway

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ARTICLE INFO

Article history:

Received 5 March 2020

Received in revised form 9 November 2020

Accepted 9 November 2020

Keywords:

Benthic secondary production
Community shift
Macrozoobenthic communities
Sahel drought

ABSTRACT

The benthic communities of soft-sediment intertidal ecosystems trophically underpin the migration of birds and fish. Within the East Atlantic Flyway, along the coast of West-Africa, the intertidal mudflats of Banc d'Arguin, Mauritania, host over 2 million migratory waterbirds. Despite the protected status of the Banc d'Arguin, geographical remoteness and seemingly benign human exploitation, we show that large changes have taken place in the intertidal benthic macrofauna across an interval of 28 years. We compared the results of two comparable and spatially comprehensive large-scale benthic surveys in 1986 and 2014. Over this time, the benthos changed from a diverse community to one dominated by a few species of bivalve, with a loss of polychaete worms. The change was associated with a twofold increase in the seagrass cover. Our results suggest that the intertidal habitats of Banc d'Arguin have altered markedly over the last three decades and the estimated benthic secondary production has decreased by a factor of four. These shifts in community structure and production may have contributed to declines in some benthivorous migratory shorebirds.

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1. Introduction

Due to human development and activities, over the last 100 years the world has lost 64–71% of its wetland habitats (Davidson, 2014). As a result, seasonal long-distance migratory shorebirds which rely on these wetland habitats during the nonbreeding season (van de Kam et al., 2004; Mathot et al., 2018) have to rely on the 30% remaining habitats. Recently, further wetland losses have led to further declines, especially in coastal-living shorebirds across the world (Conklin et al., 2014; van Roomen et al., 2015). The cause of these declines has been mostly attributed to habitat loss and modification (Kraan et al.,

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2009; Ma et al., 2014; Piersma et al., 2016; Zhang et al., 2018) directly affecting the survival of wintering waterbirds and the food 'fuelling' long distance migrations (e.g., Rakhimberdiev et al., 2018). In addition to the loss of habitat, the suitability of coastal wetlands as feeding areas for shorebirds can be expected to vary due to other causes, such as catastrophic storms (Delany et al., 2009; van Roomen et al., 2015; Oudman et al., 2019), long-term climatic cycles, and internal species-environment feedbacks (van Gils et al., 2016; Correll et al., 2017). Further, migratory birds depend on series of sites at every stage of their annual migration. Thus, the current global loss of natural habitat may be removing some of these key sites along the global flyways, and decreasing the quality of their habitats (Galbraith et al., 2005; Piersma, 2006, 2007).

The Parc National du Banc d'Arguin in Mauritania is a key wintering and staging area for shorebirds along the East Atlantic Flyway (Altenburg et al., 1982; Wolff and Smit, 1990; Delany et al., 2009; Oudman et al., 2019). The park is by far the largest and the most important wintering and staging habitat along the Sahara coast, but is quite isolated, with the nearest comparable habitat in West Africa (in the Bijagós Archipelago, Guinea-Bissau) 1000 km towards the south. The discrepancy between the low abundance of benthic prey (Piersma, 1982; Wolff et al., 1993a) and the large number of shorebird predators (Altenburg et al., 1982) has attracted scientific interest, especially since some wintering shorebird species at Banc d'Arguin have shown serious population declines. Further, the main primary producer of the Banc d'Arguin, the dwarf eelgrass *Zostera noltei* (van der Zee et al., 2016; Wolff et al., 1993b), has shown tremendous variations in cover over the last few decades (Littaye and Sidi Cheikh, 2018).

In the Sahel and Saharan West Africa, rainfall is subject to many-decadal cycles (Ahmedou et al., 2008; Shanahan et al., 2009; Zwartz et al., 2009). Between 1970 and 1995, the region went through a severe drought (the 'great drought'), with rainfall reaching the lowest levels in 1984 (Hoerling et al., 2006). The resulting expansion of the Sahara desert had large implications for westward dust transport, with impacts even noticeable in the Caribbean (Hoerling et al., 2006). Recently, the rainfall of the Sahel showed an increase indicating a steady recovery toward pre-drought levels (Bichet and Diedhiou, 2018; Diawara et al., 2016). The 'great drought' likely affected the coastal systems of West Africa too, with distress to intertidal seagrass meadows at Banc d'Arguin through sedimentation and desiccation (de Fouw et al., 2016). Desiccation degrades seagrass through leaf dehydration (Leuschner et al., 1998). Sedimentation could kill seagrass (1) directly by inducing anoxia and light limitation (Bradley and Stolt, 2006; Han et al., 2012; Hirst et al., 2017) or (2) indirectly by elevating seagrass patches (Bos et al., 2007) and thus increase their air-exposure time, which make them more vulnerable to drought and heat stress (Suykerbuyk et al., 2018; Unsworth et al., 2012). Given the stark differences in macrozoobenthic communities between seagrass and non-seagrass covered intertidal flats (Honkoop et al., 2008; Bouma et al., 2009), we expected cascading impacts on the food and abundance of wintering shorebirds (van Gils et al., 2009, 2013, 2016).

In this study, we provide evidence of temporal change in the intertidal benthic macrofauna and seagrass cover of the Banc d'Arguin ecosystem. We combined a comparison between a large-scale historical benthic survey (1986; closely following the "great drought") and a recent survey (2014; "usual drought") with an analysis of seagrass cover from satellite images. Further, we identified the most important biophysical correlates of benthic composition (seagrass traits, sediment characteristics and wave exposure) at the landscape-scale. Finally, we discuss the implications of the change in benthic community structure on secondary productivity for shorebirds.

2. Materials and methods

The study was conducted at Parc National du Banc d'Arguin, Mauritania (Fig. 1). The Banc d'Arguin intertidal flats cover 453 km² (calculation based on Murray et al., 2019), of which 80% is covered with seagrasses, mainly *Zostera noltei* (Altenburg et al., 1983; Wolff and Smit, 1990; Folmer et al., 2012). The seagrass beds of the area, including *Z. noltei*, maintain their aboveground component year-round (El-Hacen et al., 2018) as opposed to the more northern ecotypes that lose their leaves in winter (Vermaat and Verhagen, 1996). The area borders the Sahara and not affected by rivers (Wolff et al., 1993b) nor human-waste discharges.

2.1. Macrofauna surveys

Based on the survey by Wolff and associates in Feb–Apr 1986 (Wolff et al., 1993a; Wijnsma et al., 1999) and our survey in Feb 2014, we compared quantitative data on benthic macrofauna between the two years. The first survey (hereafter: 'historical') provided the single available comparison to the most 'recent' one. The historic survey was done 2-years after the driest year of the great drought, whereas the recent one was done during a period of normal rainfall. To minimise the seasonal confounding factor in both benthic abundances and biomasses (see Ahmedou Salem et al., 2014; Wolff and Michaelis, 2008), the two surveys were performed at the same time of the year (Feb–Apr). Samples from both surveys were taken during low tide.

Although we copied the survey route around Tidra, the absence of precise GPS locations for the historic survey and a detailed navigation map for the sampling points, in many cases hindered visiting the exact locations. The spatial confounding factor was minimised by covering the same general geographical area of the core intertidal system of PNBA (Fig. 1a). The sampling locations of the historical survey were chosen randomly and so were our sampling sites. In preparation for the recent survey, the map of the historical survey was georeferenced in ArcMap and the approximate GPS coordinates of the historical stations were loaded into a navigation device (Trimble Yuma® 2, USA) used to find the sites. In total, 60 mudflats, of which 40 were from the historical survey, were selected around the island of Tidra, but only 40 of them could be reached with the modes of transport and time available. On each mudflat, two stations were chosen along an elevation gradient. The

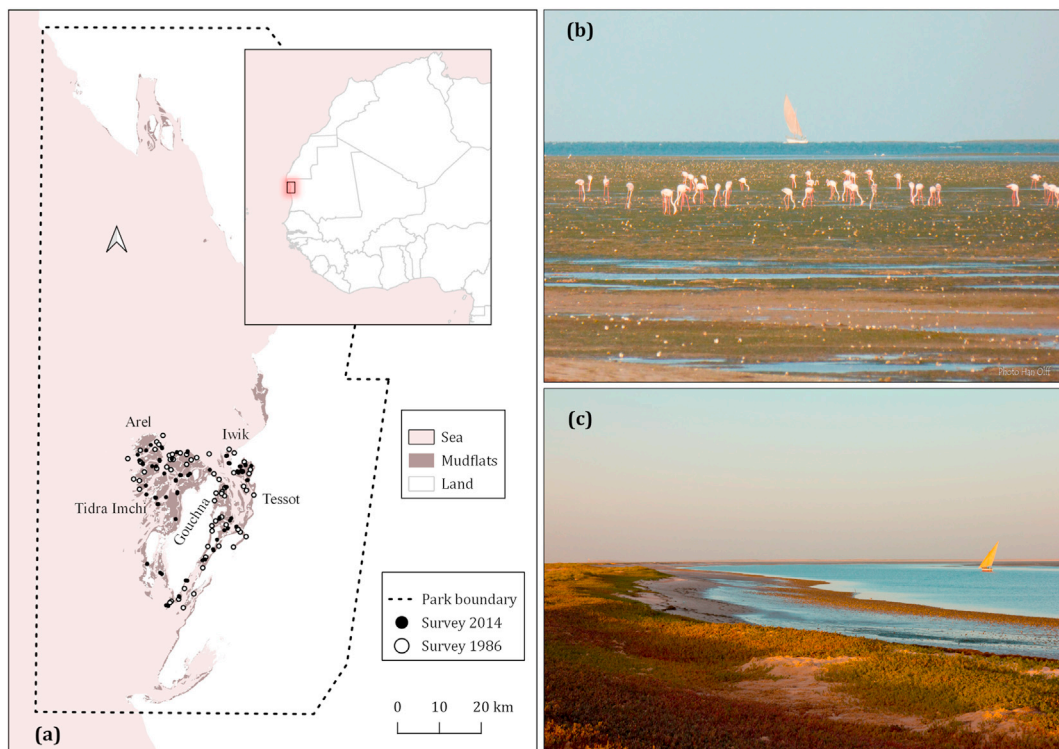


Fig. 1. (a) Map of sample locations in the core intertidal flats of Banc d'Arguin, Mauritania. Samples were collected over two surveys, indicated by open symbols for 1986 and by black dots for 2014 survey. Names indicate places where data loggers were positioned. (b) Photo showing a typical exposed mudflat at low tide, and (c) a typical shoreline flat. Photos by Han Olff and Jeroen Onrust.

selection along the elevation gradient was done to account for the lack of habitat descriptions in the historical survey, and to cover the most prevailing habitat types (i.e., low, mostly dense seagrass vs. high, mostly sparse seagrass or bare sediment). At every station, a PVC frame was thrown randomly and its landing position was selected for sampling. Sebckhas, salt barren flats above the high-tide marks, and subtidal stations were not considered in our survey. The Baie d'Arguin and Baie de St. Jean areas were not visited due to remoteness and their relatively small intertidal areas.

A total of 60 historical stations and 40 recent stations located around Tidra were judged compatible and thus used for the benthic community comparison (Fig. 1a). In the historical survey five cores (10-cm diameter, to a depth of 30 cm, covering 0.039 m²) were collected, pooled together (Wolff et al., 1993a), and sieved through a 0.6-mm mesh to represent a sampled station. In the recent survey two larger cores (15-cm in diameter, to a depth of 30 cm, covering 0.035 m²) were collected, pooled together, and sieved through 1-mm mesh to represent a sampling station. All samples were washed fresh and sieved on the spot with the sea water. We note that the use of different mesh sizes in both surveys is expected to affect the comparison, especially density, as the older survey with smaller mesh would have yielded more small bivalves and polychaetes than the recent one.

Samples of both surveys were sorted in 'laboratory tents' in the field, mostly the same day of collection or sometimes the next morning if the low tide occurred late in the afternoon. In both surveys sorted samples were preserved in 5% formalin, and then brought to The Netherlands for further analyses. In the laboratory, specimens were identified and weighed in a similar way. All specimens were identified to the species level in the historical survey while worms were only identified to family level in the recent survey. For this reason, the community comparison was done at the family level. Identification of specimens in the recent survey was based on a field benthic guide developed from the extensive list published in the historical survey (Wijnsma et al., 1999; Wolff et al., 1993a), and with the aid of the guides by Ardovini and Cossignani (2004) and Hayward and Ryland (1995). Ash-free dry mass (AFDM) was measured at taxon level per sample by drying to a constant weight at 60 °C for at least two days and then incinerated at 560 °C for 2 h. The West African bloody cockle *Senilia senilis* was subject to a separate sampling scheme in the historical survey (Wolff et al., 1993a), an effort not repeated here. Hence, bloody cockles were not included in this comparison. However, the individuals that were retrieved in the coring of 2014 were used in assessing the effect of environmental variables on benthic community structure.

To be able to make an integrated assessment of the differences in macrobenthic community between the two years, an integrator with trophic relevance, we computed annual macrofaunal somatic productivity (production/biomass: P/B, yr⁻¹) and secondary production (P, KJ m⁻² yr⁻¹) on the basis of the taxonomic data and general taxon and size relationships using a recent empirical artificial neural network model (Brey, 2012), see Appendix1 and Fig. S1 for details).

2.2. Seagrass cover change: NDVI calculation

To investigate overall changes in seagrass cover, Google Earth Engine (GEE) platform was used to obtain Normalized Difference Vegetation Index (NDVI) from 1986 to 2014 (<https://earthengine.google.com>). The entire Landsat 8-Day composites available from the study region were considered ("LANDSAT/LT05/C01/T1_8DAY_NDVI", "LANDSAT/LE7_L1T_8DAY_NDVI", and "LANDSAT/LC8_L1T_8DAY_NDVI"). Prior to the NDVI computation in GEE, all available scenes were first inspected for tide levels and atmospheric conditions over the intertidal zone of Banc d'Arguin using LandsatLook Viewer (<https://landsatlook.usgs.gov/>), and only low-tide scenes without cloud cover were selected for further analyses. To investigate the small-scale effect of seagrass cover on benthic communities, NDVI values were computed within a square buffer of 3600 m² (84.85 m diagonal) around each station. The buffer was large enough (4 pixels) to capture the errors resulting from the accuracy of the points, yet small enough to maintain the average habitat type around the sampling points. NDVIs were calculated in ESRI Geographic Information System (ArcMap 10.4) from 30-m spatial resolution Landsat images (scenes: 12/Jan/1985, Jan-1987, Oct-2013, and 12/Nov/2014) provided by U.S. Geological Survey (USGS). Selected scenes had little cloud cover (<0.5%) and were subjected to an atmospheric correction following (Vuolo et al., 2015; Young et al., 2017) prior NDVI calculation. The use of NDVI index from Landsat imagery has proven to be adequate and represent seagrass conditions in our study area (de Fouw et al., 2016; Folmer et al., 2012; Littaye and Sidi Cheikh, 2018).

2.3. Benthic community structure and environmental descriptors

Correlations between benthic community structure and the most prevailing local biotic (i.e., seagrass) and abiotic (i.e., sediment & wave action) properties were assessed for the recent survey. At each benthos-sampling point, a 15-cm diameter core and two 35.34 cm⁻³ volumetric syringes were collected to characterise seagrass and sediment properties, respectively (Bouma et al., 2009). Seagrass below- and aboveground dry biomasses (dried until constant weight at 70 °C for 48 h) were determined per core (Turner et al., 1999). Leaf and internode (first ten rhizomes) lengths were measured on three fresh intact shoot-rhizomes (Kiswara et al., 2009; Nicastrò and Bishop, 2013). Leaf area (LA) was estimated on photos taken from the intact shoots with the freely available ImageJ software. Seagrass percentage cover of each sampling point was visually estimated. Seagrass carbon (%C), nitrogen (%N), $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ contents were determined with an elemental analyser (Type NA 1500 Carlo Erbo Termo Fisher Science, USA), coupled to a spectrometer (Thermo Finnigan Delta Plus, USA). Total phosphorus (%P), iron (%Fe), and aluminium (%Al) in leaf tissue was measured on an inductivity-coupled-plasma emission spectrophotometer (ICP) (Spectroflame, Spectro Inc), after digestion of dried material with nitric acid and hydrogen peroxide. Sediment characteristics such as median grain size (D50) and organic matter content (OM, loss of ignition at 500 °C) were determined for each sampling point. Wave exposure at each site was calculated with the open source software Wave Exposure Model (WEMo, Malhotra and Fonseca 2007) developed by NOAA and is implemented in ESRI ArcGIS 9.3. WEMo incorporates bathymetry, wind, fetch lengths, and shoreline morphology to calculate relative wave energy (J m⁻¹).

2.4. Statistical analyses

All statistical analyses below were performed in R software (version 3.4.3, R Development Core Team, 2017). Differences in taxon' density and biomass between the historical and recent surveys were tested with t-tests. Linear regressions were used to assess changes of seagrass cover (NDVI) over time. The relationships between NDVI and the density of the different benthic taxa in both surveys were assessed with linear regressions. Data were transformed accordingly to meet normality assumptions.

Biophysical (seagrass traits, sediment characteristics, and wave exposure) variables that were measured in 2014 (Table S1) were analysed simultaneously to identify which were important in affecting the benthic composition at the landscape-scale. Conditional Inference Tree (CIT) an extension of 'random forest' approach (Breiman, 2001) was used to reduce the number of predictors and identify the most important factors influencing the benthic community composition (see Appendix 2 for more details). The explanatory variables used for CIT analysis include taxon abundance, seagrass cover, leaf %N, leaf %P, seagrass above-to-belowground biomass, leaf length, internode length, relative wave energy, sediment organic matter content, and sediment median grain size. The outcome of the analysis (Fig. A2) identified seagrass traits (cover, internode length, and leaf % N) as the most influential environmental factors, thus were subjected to further analysis. Bray-Curtis index of dissimilarity matrix (Hellinger transformed data) was computed to examine patterns in species compositions along seagrass cover gradient. Dissimilarities were visualised with a non-metric multidimensional scaling (NMDS) in 'vegan' package (Oksanen et al., 2016).

3. Results

3.1. Macrofauna surveys

In 2014, bivalves (without bloody cockles) and polychaete worms represented 80.5% and 11.5% of the total density of macrozoobenthic animals and 77.5 and 17% of their total biomass, respectively. The bivalves *Loripes orbiculatus*, *Abra* sp., *Dosinia* sp., *Diplodonta diaphana* and polychaete worms, together accounted for more than 86% of the total density and 81% of

total AFDM. Bivalve biomass and density were significantly higher in the recent survey than in the one of 1986 (biomass: Fig. 2a, $t(98) = -7.58, P < 0.001$; density: Fig. 2b, $t(98) = -4.23, P < 0.001$). Gastropod biomass and density were significantly lower in 2014 than in 1986 (biomass: Fig. 2a, $t(98) = 4.12, P < 0.001$; density: Fig. 2b, $t(98) = 2.42, P = 0.02$). The biomass and density of polychaete worms were also significantly lower in the recent survey than in the historical one (biomass: Fig. 2a, $t(98) = 7.88, P < 0.001$; density: Fig. 2b, $t(98) = 3.6, P < 0.001$). Finally, both secondary production (P/B) and productivity (P) were significantly lower in the recent survey than in the historical one (Fig. A1; P/B: $t(98) = 4.5, P < 0.001$; P: $t(98) = 8.72, P < 0.001$).

3.2. Seagrass cover and macrofauna densities

Across the study area, the NDVI values of the intertidal flats of Banc d'Arguin have shown a significant increase from 1986 to 2014 ($F_{1,15} = 5.5, R^2 = 0.29, P = 0.03$, Fig. 3). NDVI significantly predicted bivalve densities for the historical ($R^2 = 0.1, P < 0.01$, solid line in Fig. 4a) and recent surveys ($R^2 = 0.3, P < 0.01$, dashed line in Fig. 4a). NDVI did not significantly predict gastropod densities neither for the historical survey nor for the recent one ($P > 0.05$, Fig. 4b). Polychaete densities, on the other hand, were only significantly predicted by NDVI in the historical ($R^2 = 0.1, P < 0.05$, solid line in Fig. 4c) survey but not the recent one ($P > 0.05$, dashed line in Fig. 4c).

3.3. Benthic community structure and environmental descriptors

In the conditional inference trees (CIT) models, the variables most strongly associated with macrobenthic total abundance were seagrass rhizome internode length, leaf %N, and seagrass cover (Fig. S2). Differences in species composition along seagrass cover gradients were fairly represented by a two-dimensional NMDS ordination (stress = 0.17). The seagrass cover gradient was significantly correlated with the species composition in NMDS space (Fig. 5). Common species tended to group in few clusters in ordination space: (1) a few species occupying only very dense seagrass beds (*Tellina* sp., *Nassarius* sp.); (2) a larger group of species present at more intermediate cover (*Abra* sp., *Loripes orbiculatus*, *Prunum amygdala*, *Diplodonta diaphana*, and *Mesalia* sp.); (3) a group of species occurring especially in sparser seagrass habitats (*Dosinia* sp., Isopoda, Polychaeta, and *Bulla adansoni*); and (4) one species associated mostly with bare habitat (*Senilia senilis*).

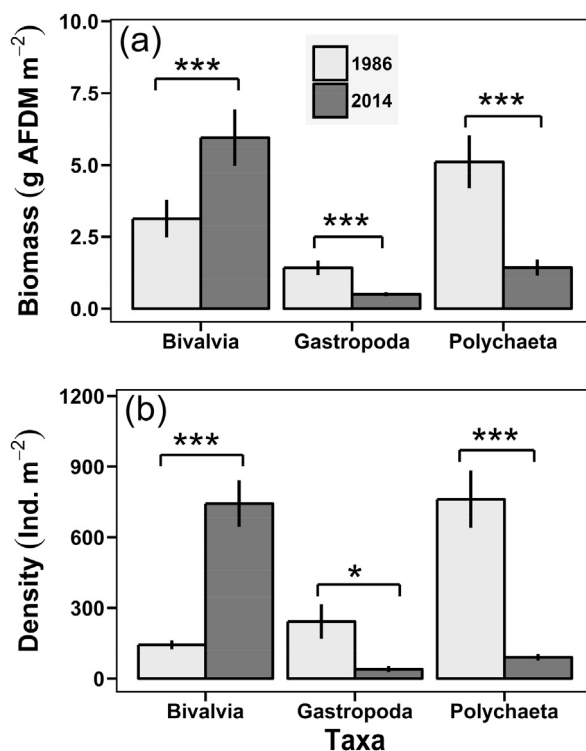


Fig. 2. Comparisons of the mean (\pm standard error) biomass (a) and density (b) of the most important benthic taxa in 1986 and 2014. The African bloody cockle *Senilia senilis* was not included in the analyses. Comparisons between the two periods were performed using *t*-test (Significant difference levels, ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$).

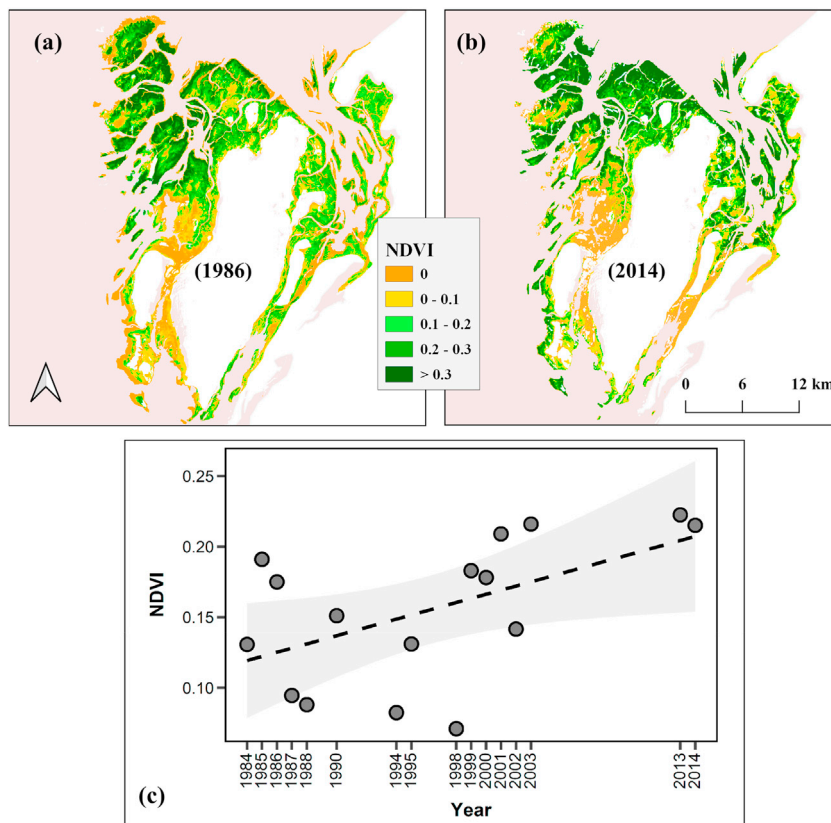


Fig. 3. (a) and (b) show Maps of changes in NDVI across the Banc d'Arguin in Jan. 1986 (a) and in Nov. 2014 (b). Maps were created based on Landsat imagery (NASA, scenes of December 11, 1986 and November 25, 2014) provided by USGS at: <http://earthexplorer.usgs.gov/>. (c) Changes of median NDVI values over time in Banc d'Arguin intertidal flats. Shaded area shows the 95% CI.

4. Discussion

We found evidence for a major shift in benthic community composition of the Banc d'Arguin intertidal flats over the last decades, a shift from polychaete worms to bivalves. The shift was associated with an increase in seagrass cover. Historically, polychaete worms were the most important taxonomic group in term of biomass and diversity (Piersma 1982; Gillet 1990; Wolff et al., 1993a). However, in the recent survey, polychaetes were no longer abundant and less numerous than molluscs, in accord with the findings at a single site near Iwik in 2012 (Ahmedou Salem et al., 2014). This negative relationship between seagrass cover and the abundance of polychaete worms, especially tube-building ones, has been shown before in intertidal soft-sediment systems (Barnes, 2019; Cardoso et al., 2004; Eklöf et al., 2015; Lundquist et al., 2018). For instance, in South Africa's premier seagrass site (Knysna Estuary) it has been found that the abundance of polychaetes increased from <50% to >90% of the total benthic community after the loss of *Z. capensis* beds (Barnes, 2019). For Arcachon Bay, France, Boström et al. (2002) reported little change to the benthic community following the disappearance of *Z. noltei*. Many bivalve species, on the other hand, seem to benefit from seagrass cover as it increases their survival and provides a refuge for the settlement of spat (Boström et al., 2002; Irlandi, 1997).

The use of different mesh sizes to sieve the historical (0.6 mm) and recent (1 mm) samples had likely contributed to the observed changes in benthic community structure. Several studies have compared the effect of sieving with different mesh sizes, mostly 0.5 mm vs. 1 mm, on macrobenthic community structure and some of them concluded that the use of different mesh-sizes affected the results (Bachelet, 1990; Couto et al., 2010; Rodrigues et al., 2007; Tanaka and Leite, 1998; Valença and Dos Santos, 2013). At the same time, other studies suggested that the use of 1 mm sieves resulted in a similar macrobenthic community structure compared to the use of 0.5 mm sieves (Barba et al., 2008; Hemery et al., 2017; James et al., 1995; Souza and Barros, 2015; Thompson et al., 2003). The common finding is that amongst the descriptors of macrobenthic communities, biomass is the least affected simply because the small animals retained by 0.5 mm sieves contribute disproportionately little (Gage et al., 2002; Morin et al., 2004; Rodrigues et al., 2007; Valença and Dos Santos, 2013). Another general finding is that polychaete densities decrease with increasing mesh size, as they have a tendency to actively escape through the mesh (Bachelet, 1990; Gage et al., 2002; James et al., 1995; Souza and Barros, 2015). Thus, it is likely that part of the decrease in

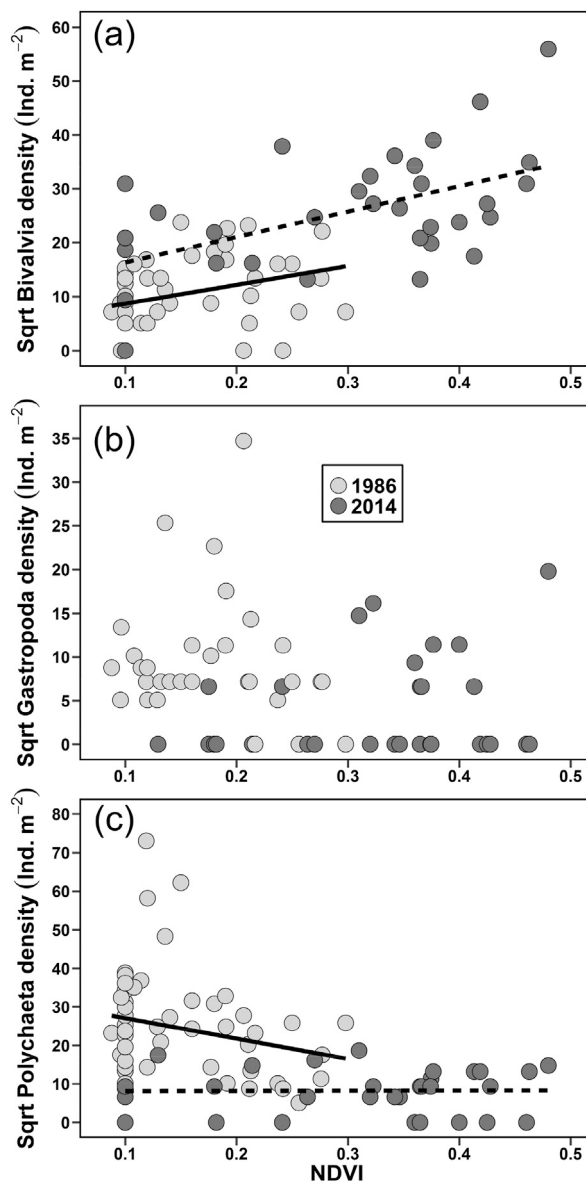


Fig. 4. Relationships of normalized difference vegetation index (NDVI) and the square-root densities of (a) bivalves, (b) gastropods and (c) polychaete collected from Banc d'Arguin in 1986 (light grey dots with solid lines) and in 2014 (dark grey dots with dashed lines). African bloody cockle *Senilia senilis* was not included in the analysis.

polychaete densities in the recent survey was caused by the use of a coarser mesh, but it is unlikely that this explains the decrease over time in their total biomass.

The increase in bivalve abundance was due to two species, *Loripes orbiculatus* and *Abra* sp. The lucinid bivalve *Loripes orbiculatus*, the most abundant species, aids the functioning of seagrass beds by nitrogen fixing (Petersen et al., 2016) and the uptake of hydrogen-sulphide, which is toxic to both seagrass and birds (van der Heide et al., 2012; van Gils et al., 2013). The second most important species for bivalve-eating shorebirds, *Dosinia* sp. (Onrust et al., 2013; van Gils et al., 2013), showed first a marked increase between 1980s (Piersma, 1982; Wolff et al., 1993a) and 2008 (Honkoop et al., 2008), followed by a marked decrease since then (see Table 1). However, the cause of the observed dynamic of *Dosinia* is not clear and merits further research. A recent study by van der Geest et al. (2019) found that *Dosinia* mostly inhabited seagrass covered areas, thus *Dosinia* would have been expected to have increased along with the increase in seagrass cover. Possibly, *Dosinia* (a filter feeder) is now outcompeted for food by *Loripes*, a facultative mixotroph that could require energy from different sources (van der Heide et al., 2012; van der Geest et al., 2014). In addition, the giant bloody cockle, another filter feeder known to contribute the most to molluscan biomass, has shown a tremendous increase in density since the 1980s (Honkoop et al., 2008; Wijnsma

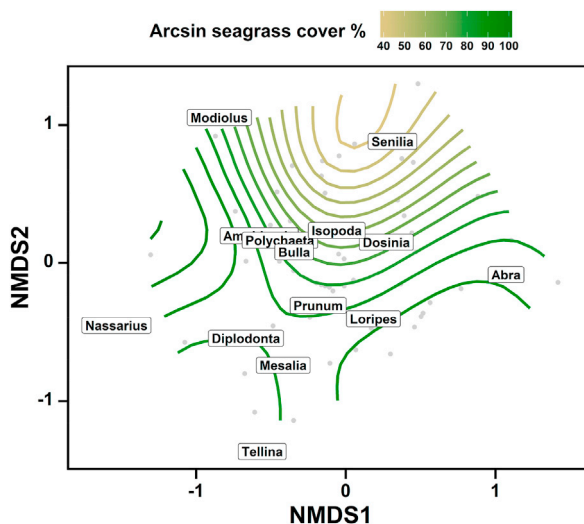


Fig. 5. Non-metric multidimensional scaling (NMDS) ordinations showing the Bray–Curtis dissimilarity scores of the most abundant benthic species (indicated by their genus names) along seagrass cover gradients.

Table 1
Composition of the density (individuals m⁻¹) and biomass (g AFDM m⁻²) of the main benthic taxa in the Banc d’Arguin between 1986 and 2014.

Taxon	1986		2014	
	Density	AFDM	Density	AFDM
Bivalvia				
<i>Abra tenuis</i>	56.9	0.0775	122.6	0.7317
<i>Diplodonta diaphana</i>	0.7	0.06	14.3	0.1448
<i>Dosinia</i> sp.	0.6	0.0669	29.1	0.6123
<i>Loricipes lacteus</i>	90.5	2.6002	451.6	3.9872
<i>Modiolus</i> sp.	0	0	5.9	0.0991
<i>Tellina</i> sp.	1.1	0.0002	5.9	0.0770
Others	23.2	0.1	41.1	0.9653
Total Bivalvia	173.4	2.9	670.5	6.6173
Gastropoda				
<i>Bulla adansoni</i>	1.1	0.0168	8.3	0.1018
<i>Columbella rustica</i>	8.5	0.2339	3.4	0.0873
<i>Mesalia mesal</i>	0	0	3.6	0.0622
<i>Nassarius</i> sp.	6.7	0.0393	5.9	0.0118
<i>Prunum amygdala</i>	3.9	0.0425	10.7	0.0911
Others	222.1	1.6	9.5	0.0738
Total Gastropoda	242.3	1.9	41.4	0.4280
Crustacea				
Amphipoda	47.0		3.6	0.0094
Isopoda	78.9		16.6	0.0764
Total Crustacea	145.0	0.1	20.2	0.0858
Annelida				
Total Polychaeta	788.7	3.9	97.3	1.4352

et al., 1999) and could also possibly outcompete *Dosinia* for suspended food material. Competition for food and space is common among benthic organisms that use similar resources and/or occupy the same ecological niche, and has been shown to significantly reduce some benthic populations (Galimany et al., 2017; Reise et al., 2017; Strayer and Malcom, 2018; Thielges, 2005). Further, the effect of the observed increase in *Senilia* population on the functioning of seagrass beds in Banc d'Arguin, especially mollusc assemblages, remains to be properly evaluated.

The observed increase in seagrass cover at Banc d'Arguin was not caused by humans dredging intertidal areas or removing seagrass in other ways (e.g., Piersma et al., 2001; Kraan et al., 2007). We suggest that the changes are a function of dust and sediment dynamics (de Fouw et al., 2016). The Sahelian drought caused huge losses of terrestrial vegetation cover (Niang et al., 2008; Zwarts et al., 2018). As a consequence, the frequency and intensity of dust storms increased during the peak of the drought years (Goudie and Middleton, 1992; Prospero and Lamb, 2003). Sediment deposition may cause seagrass mortality either directly through burial (Han et al., 2012; Hirst et al., 2017), or indirectly through adverse conditions such as anoxia (Brodersen et al., 2017) and desiccation (de Fouw et al., 2016). We propose that as a result of increasing dust storms, sediment deposition and desiccation, the seagrass beds in Banc d'Arguin experienced severe die-backs during the Sahel drought years. The future projection of the Sahel climate predicts an increase in drought and temperature (James and Washington, 2013), which is most likely going to decrease seagrass cover through heat waves and sediment dynamic (de Fouw et al., 2016; El-Hacen et al., 2018; Han et al., 2012) and subsequently alter the benthic community (Honkoop et al., 2008).

An emergent question is how such changes would affect benthic 'food' production for shorebirds (Table S2). Although estimates of P/B based on empirical models should be interpreted with caution as they are based on the means rather than on thorough long-term population dynamic assessments (size frequency, growth rate, and mortality) (Cusson and Bourget, 2005), we calculated that the change in benthic composition would have been accompanied by a reduction in estimated secondary production (P/B) by a factor four (Fig. A1). The reduction in P/B is not due to a reduction in the total standing stock of benthic biomass but rather an increase in bivalves compared to polychaetes (Fig. 2a). The large and slow-growing taxa (and this includes molluscs and echinoderms) show low P/B ratios (Mistri and Ceccherelli, 1994; Cusson and Bourget, 2005). The estimated P/B values presented here are in accordance with those found along the East Atlantic Flyway, with various studies showing P:B ratios to vary from 0.15 to 1.6 y^{-1} (see Asmus and Asmus 1985; Arias and Drake 1994; Bolam et al., 2010; Fuhrmann et al., 2015; Degen et al., 2016; Paar et al., 2016). Thus, our estimated historical P/B values (~2) are among the highest along the East Atlantic Flyway, while the recent values rank among the lowest (~0.5).

The suggested decrease in secondary production adds concern for the shorebirds (Table S2) that even during the times of the historical survey were shown to be able to deplete the early winter benthic food (Engelmoer et al., 1984; Wolff et al., 2009; Wolff and Michaelis, 2008). To sustain the high densities of consumers, the area was presumed to have a benthic community of species with particularly high P/B ratios (Altenburg et al., 1982). The historical P/B estimation is indeed consistent with this notion, but the recent estimation suggests that it no longer fits. This could explain why several shorebird species (Table S2) are now in serious decline (van Gils et al., 2013; van Roomen et al., 2015; Oudman et al., 2019). In addition to ongoing changes at the breeding grounds (i.e., the advancing snow melt probably affecting insect emergence and food conditions for chicks, van Gils et al., 2016; Rakhimberdiev et al., 2018), our results showed that shorebirds may have been under pressure in the wintering grounds through changes in food supplies.

Author contributions

EME, TP, and HO conceived the idea and the entire team performed the study. MASC and EME conducted the NDVI analyses. EME and HO analysed the data. EME and TP led the writing of the manuscript with important contributions from TB. All authors contributed critically to the manuscript draft and gave final approval for publication.

Funding

This work was funded by a PhD scholarship from MAVA Foundation, Switzerland [grant numbers 12/126, 2013].

Data availability

Data supporting the findings of this study are available from the authors and will be made archived and publicly available in the University of Groningen Research Data Repository (<http://www.rug.nl/research/gelifes/research/data-management/repository?lang=en>).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the managers of Parc National du Banc d'Arguin for granting us permission to conduct our study and to use the research vessel 'Théodore Monod'. We extend our sincere thanks to the scientific coordinator Lemhaba Yarba, the boat captain Mohamed Salem El Hadi and the skipper Mohamed Cheddad. We are grateful to the local team for their help in the field: Sall Amadou Abderahmane, Mamadou Ba Abdoul and Mohamed Brahim. We are particularly indebted to Wim Wolff, who paved the way for our survey and shared his historical data with us. Furthermore, we thank Sander Holthuijsen and Lennart van IJzerloo for their lab work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01364>.

References

- Ahmedou, O.C.A., Yasuda, H., Wang, K., Hattori, K., 2008. Characteristics of precipitation in northern Mauritania and its links with sea surface temperature. *J. Arid Environ.* 72, 2243–2250.
- Ahmedou Salem, M.V., van der Geest, M., Piersma, T., Saoud, Y., van Gils, J.A., 2014. Seasonal changes in mollusc abundance in a tropical intertidal ecosystem, Banc d'Arguin (Mauritania): testing the 'depletion by shorebirds' hypothesis. *Estuar. Coast Shelf Sci.* 136, 26–34.
- Altenburg, W., Engelmoer, M., Mes, R., Piersma, T., 1983. Recensement des limicoles et autres oiseaux aquatiques au Banc d'Arguin. Mauritania. Gerfaut 73, 243–264.
- Altenburg, W., Engelmoer, M., Mes, R., Piersma, T., 1982. Wintering Waders at the Banc d'Arguin, Mauritania, Report of the Netherlands Ornithological Expedition 1980. Stichting Veth tot Steun aan Waddenonderzoek, Leiden, The Netherlands. Leiden.
- Ardovini, R., Cossignani, T., 2004. West African Seashells. Museo Malacologico Piccino, Cupra Marittima, Italy.
- Arias, A., Drake, P., 1994. Structure and production of the benthic macroinvertebrate community in a shallow lagoon in the Bay of Cadiz. *Mar. Ecol. Prog. Ser.* 115, 151–167. <https://doi.org/10.3354/meps115151>.
- Asmus, H., Asmus, R., 1985. The importance of grazing food chain for energy flow and production in three intertidal sand bottom communities of the northern Wadden Sea. *Helgol. Meeresunters.* 39, 273–301. <https://doi.org/10.1007/BF01992775>.
- Bachelet, G., 1990. The choice of a sieving mesh size in the quantitative assessment of marine macrobenthos: a necessary compromise between aims and constraints. *Mar. Environ. Res.* 30, 21–35. [https://doi.org/10.1016/0141-1136\(90\)90008-C](https://doi.org/10.1016/0141-1136(90)90008-C).
- Barba, B., Larrañaga, A., Otermin, A., Basaguren, A., Pozo, J., 2008. The effect of sieve mesh size on the description of macroinvertebrate communities. *Limnética* 29, 211–220.
- Barnes, R.S.K., 2019. Context dependency in the effect of *Ulva*-induced loss of seagrass cover on estuarine macrobenthic abundance and biodiversity. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29, 163–174. <https://doi.org/10.1002/aqc.2977>.
- Bichet, A., Diedhiou, A., 2018. West African Sahel has become wetter during the last 30 years, but dry spells are shorter and more frequent. *Clim. Res.* 75, 155–162. <https://doi.org/10.3354/cr01515>.
- Bolam, S.G., Barrio-Frojan, C.R.S., Eggleton, J.D., 2010. Macrofaunal production along the UK continental shelf. *J. Sea Res.* 64, 166–179. <https://doi.org/10.1016/j.seares.2010.02.003>.
- Bos, A.R., Bouma, T.J., de Kort, G.L.J., van Katwijk, M.M., 2007. Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. *Estuar. Coast Shelf Sci.* 74, 344–348. <https://doi.org/10.1016/j.ecss.2007.04.006>.
- Boström, C., Bonsdorff, E., Kangas, P., Norkko, A., 2002. Long-term changes of a brackish-water eelgrass (*Zostera marina* L.) community indicate effects of coastal eutrophication. *Estuar. Coast Shelf Sci.* 55, 795–804. <https://doi.org/10.1006/ecss.2001.0943>.
- Bouma, T.J., Ortells, V., Ysebaert, T., 2009. Comparing biodiversity effects among ecosystem engineers of contrasting strength: macrofauna diversity in *Zostera noltii* and *Spartina anglica* vegetations. *Helgol. Mar. Res.* 63, 3–18. <https://doi.org/10.1007/s10152-008-0133-8>.
- Bradley, M.P., Stolt, M.H., 2006. Landscape-level seagrass-sediment relations in a coastal lagoon. *Aquat. Bot.* 84, 121–128.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45, 5–32.
- Brey, T., 2012. A multi-parameter artificial neural network model to estimate macrobenthic invertebrate productivity and production. *Limnol Oceanogr. Methods* 10, 581–589.
- Brodersen, K.E., Hammer, K.J., Schrammeyer, V., Floytrup, A., Rasheed, M.A., Ralph, P.J., Kühl, M., Pedersen, O., 2017. Sediment resuspension and deposition on seagrass leaves impedes internal plant aeration and promotes phytotoxic H₂S intrusion. *Front. Plant Sci.* 8, 1–13. <https://doi.org/10.3389/fpls.2017.00657>.
- Cardoso, P.G., Pardal, M.A., Lillebø, A.L., Ferreira, S.M., Raffaelli, D., Marques, J.C., 2004. Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. *J. Exp. Mar. Biol. Ecol.* 302, 233–248. <https://doi.org/10.1016/j.jembe.2003.10.014>.
- Conklin, J.R., Verkuil, Y.I., Smith, B.R., 2014. Prioritizing Migratory Shorebirds for Conservation Action on the East-Asian Australian Flyway. WWF-Hong Kong.
- Correll, M.D., Wiest, W.A., Hodgman, T.P., Shriver, W.G., Elphick, C.S., McGill, B.J., O'Brien, K.M., Olsen, B.J., 2017. Predictors of specialist avifaunal decline in coastal marshes. *Conserv. Biol.* 31, 172–182. <https://doi.org/10.1111/cobi.12797>.
- Couto, T., Patrício, J., Neto, J.M., Ceia, F.R., Franco, J., Marques, J.C., 2010. The influence of mesh size in environmental quality assessment of estuarine macrobenthic communities. *Ecol. Indic.* 10, 1162–1173. <https://doi.org/10.1016/j.ecolind.2010.03.019>.
- Cusson, M., Bourget, E., 2005. Global patterns of macroinvertebrate production in marine benthic habitats. *Mar. Ecol. Prog. Ser.* 297, 1–14. <https://doi.org/10.3354/meps297001>.
- Davidson, N.C., 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. *Mar. Freshw. Res.* 65, 934. <https://doi.org/10.1007/MF14173>.
- de Fouw, J., Govers, L.L., van de Koppel, J., van Belzen, J., Dorigo, W., Sidi Cheikh, M.A., Christianen, M.J.A., van der Reijden, K.J., van der Geest, M., Piersma, T., Smolders, A.J.P., Olf, H., Lamers, L.P.M., van Gils, J.A., van der Heide, T., 2016. Drought, mutualism breakdown, and landscape-scale degradation of seagrass beds. *Curr. Biol.* 26, 1051–1056.
- Degen, R., Jørgensen, L., Ljubin, P., Ellingsen, I., Pehlke, H., Brey, T., 2016. Patterns and drivers of megabenthic secondary production on the Barents Sea shelf. *Mar. Ecol. Prog. Ser.* 546, 1–16. <https://doi.org/10.3354/meps11662>.
- Delany, S., Scott, D.A., Dodman, T., Stroud, D.A., 2009. An Atlas of Wader Populations in Africa and Western Eurasia. Wetlands International, Wageningen.
- Diawara, A., Tachibana, Y., Oshima, K., Nishikawa, H., Ando, Y., 2016. Synchrony of trend shifts in Sahel boreal summer rainfall and global oceanic evaporation, 1950–2012. *Hydrol. Earth Syst. Sci.* 20, 3789–3798. <https://doi.org/10.5194/hess-20-3789-2016>.
- Eklöf, J.S., Donadi, S., van der Heide, T., van der Zee, E.M., Eriksson, B.K., 2015. Effects of antagonistic ecosystem engineers on macrofauna communities in a patchy, intertidal mudflat landscape. *J. Sea Res.* 97, 56–65. <https://doi.org/10.1016/j.seares.2014.12.003>.
- El-Hacen, E.-H.M., Bouma, T.J., Fivash, G.S., Sall, A.A., Piersma, T., Olf, H., Govers, L.L., 2018. Evidence for 'critical slowing down' in seagrass: a stress gradient experiment at the southern limit of its range. *Sci. Rep.* 8, 17263. <https://doi.org/10.1038/s41598-018-34977-5>.

- Engelmoer, M., Piersma, T., Altenburg, W., Mes, R., 1984. The Banc d'Arguin (Mauritania). In: Coastal Waders and Wildfowl in Winter. Cambridge University Press, Cambridge, pp. 293–310.
- Folmer, E.O., van der Geest, M., Jansen, E., Olff, H., Anderson, M., Piersma, T., van Gils, J.A., 2012. Seagrass–sediment feedback: an exploration using a non-recursive structural equation model. *Ecosystems* 15, 1380–1393.
- Fuhrmann, M.M., Pedersen, T., Ramasco, V., Nilssen, E.M., 2015. Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab. *J. Sea Res.* 106, 1–13. <https://doi.org/10.1016/j.seares.2015.09.003>.
- Gage, J.D., Hughes, D., Vecino, J.G., 2002. Sieve size influence in estimating biomass, abundance and diversity in samples of deep-sea macrobenthos. *Mar. Ecol. Prog. Ser.* 225, 97–107.
- Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B., Page, G., 2005. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. *Waterbirds* 25, 173–183.
- Galimany, E., Freeman, C., Lunt, J., Domingos, A., Sacks, P., Walters, L., 2017. Eeding competition between the native oyster *Crassostrea virginica* and the invasive mussel *Mytella charruana*. *Mar. Ecol. Prog. Ser.* 564, 57–66. <https://doi.org/10.3354/meps11976>.
- Gillet, P., 1990. Note sur les annélides polychètes du Banc d'Arguin (Mauritanie) et description de *Marphysa mauritanica* n.sp. *Beaufortia* 40, 73–84.
- Goudie, A.S., Middleton, N.J., 1992. The changing frequency of dust storms through time. *Climatic Change* 20, 197–225. <https://doi.org/10.1007/BF00139839>.
- Han, Q., Bouma, T., Brun, F., Suykerbuyk, W., van Katwijk, M., 2012. Resilience of *Zostera noltii* to burial or erosion disturbances. *Mar. Ecol. Prog. Ser.* 449, 133–143. <https://doi.org/10.3354/meps09532>.
- Hayward, P.J., Ryland, J.S., 1995. *Handbook of the Marine Fauna of North-West Europe*. Oxford University Press.
- Hemery, L.G., Politano, K.K., Henkel, S.K., 2017. Assessing differences in macrofaunal assemblages as a factor of sieve mesh size, distance between samples, and time of sampling. *Environ. Monit. Assess.* 189 <https://doi.org/10.1007/s10661-017-6127-8>.
- Hirst, A.J., McGain, S., Jenkins, G.P., 2017. The impact of burial on the survival and recovery of the subtidal seagrass *Zostera nigricaulis*. *Aquat. Bot.* 142, 10–15. <https://doi.org/10.1016/j.aquabot.2017.06.001>.
- Hoerling, M., Hurrell, J., Eischeid, J., Phillips, A., Hoerling, M., Hurrell, J., Eischeid, J., Phillips, A., 2006. Detection and attribution of twentieth-century northern and southern African rainfall change. *J. Clim.* 19, 3989–4008. <https://doi.org/10.1175/JCLI3842.1>.
- Honkoop, P.J.C., Berghuis, E.M., Holthuijsen, S., Lavaleye, M.S.S., Piersma, T., 2008. Molluscan assemblages of seagrass-covered and bare intertidal flats on the Banc d'Arguin, Mauritania, in relation to characteristics of sediment and organic matter. *J. Sea Res.* 60, 255–263. <https://doi.org/10.1016/j.seares.2008.07.005>.
- Irlandi, E.A., 1997. Seagrass patch size and survivorship of an infaunal bivalve. *Oikos* 78, 511–518. <https://doi.org/10.2307/3545612>.
- James, R., Lincoln Smith, M., Fairweather, P., 1995. Sieve mesh-size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. *Mar. Ecol. Prog. Ser.* 118, 187–198. <https://doi.org/10.3354/meps118187>.
- James, R., Washington, R., 2013. Changes in African temperature and precipitation associated with degrees of global warming. *Climatic Change* 117, 859–872. <https://doi.org/10.1007/s10584-012-0581-7>.
- Kiswara, W., Behnke, N., van Avesaath, P., Huiskes, A.H.L., Erfteimeijer, P.L.A., Bouma, T.J., 2009. Root architecture of six tropical seagrass species, growing in three contrasting habitats in Indonesian waters. *Aquat. Bot.* 90, 235–245. <https://doi.org/10.1016/j.aquabot.2008.10.005>.
- Kraan, C., Piersma, T., Dekinga, A., Koolhaas, A., van der Meer, J., 2007. Dredging for edible cockles (*Cerastoderma edule*) on intertidal flats: short-term consequences of Fisher patch-choice decisions for target and non-target benthic fauna. *ICES J. Mar. Sci.* 64, 1735–1742. <https://doi.org/10.1093/icesjms/fsm153>.
- Kraan, C., van Gils, J.A., Spaans, B., Dekinga, A., Bijleveld, A.I., van Roopen, M., Kleefstra, R., Piersma, T., 2009. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *J. Anim. Ecol.* 78, 1259–1268. <https://doi.org/10.1111/j.1365-2656.2009.01564.x>.
- Leuschner, C., Landwehr, S., Mehlig, U., 1998. Limitation of carbon assimilation of intertidal *Zostera noltii* and *Z. marina* by desiccation at low tide. *Aquat. Bot.* 62, 171–176. [https://doi.org/10.1016/S0304-3770\(98\)00091-6](https://doi.org/10.1016/S0304-3770(98)00091-6).
- Littaye, A., Sidi Cheikh, M.A., 2018. New insights in seagrass mortality patches at the Arguin Bank in the perspectives of climate change. *J. Earth Sci. Climatic Change* 9, 1–6. <https://doi.org/10.4172/2157-7617.1000445>.
- Lundquist, C.J., Jones, T.C., Parkes, S.M., Bulmer, R.H., 2018. Changes in benthic community structure and sediment characteristics after natural recolonisation of the seagrass *Zostera muelleri*. *Sci. Rep.* 8, 1–9. <https://doi.org/10.1038/s41598-018-31398-2>.
- Ma, Z., Melville, D.S., Liu, J., Chen, Y., Yang, H., Ren, W., Zhang, Z., Piersma, T., Li, B., 2014. Rethinking China's new great wall. *Science* (80- 346), 912–914. <https://doi.org/10.1126/science.1257258>.
- Malhotra, A., Fonseca, M.S., 2007. WEMo (Wave Exposure Model): Formulation, Procedures and Validation. NOAA Technical Memorandum NOS NCCOS, p. #65.
- Mathot, K.J., Piersma, T., Elnor, R.W., 2018. Shorebirds as integrators and indicators of mudflat ecology. In: Beninger, P.G. (Ed.), *Mudflat Ecology, Aquatic Ecology Series 7*. Springer Nature, Cham, pp. 309–338.
- Mistri, M., Ceccherelli, V., 1994. Growth and secondary production of the Mediterranean gorgonian *Paramuricea clavata*. *Mar. Ecol. Prog. Ser.* 103, 291–296. <https://doi.org/10.3354/meps103291>.
- Morin, A., Stephenson, J., Strike, J., Solimini, A.G., 2004. Sieve retention probabilities of stream benthic invertebrates. *J. North Am. Benthol. Soc.* 23, 383–391. [https://doi.org/10.1899/0887-3593\(2004\)023<0383:SRPOSB>2.0.CO;2](https://doi.org/10.1899/0887-3593(2004)023<0383:SRPOSB>2.0.CO;2).
- Murray, N.J., Phinn, S.R., DeWitt, M., Ferrari, R., Johnston, R., Lyons, M.B., Clinton, N., Thau, D., Fuller, R.A., 2019. The global distribution and trajectory of tidal flats. *Nature* 565, 222–225. <https://doi.org/10.1038/s41586-018-0805-8>.
- Niang, A.J., Ozer, A., Ozer, P., 2008. Fifty years of landscape evolution in Southwestern Mauritania by means of aerial photos. *J. Arid Environ.* 72, 97–107. <https://doi.org/10.1016/j.jaridenv.2007.04.009>.
- Nicastro, A., Bishop, M.J., 2013. Effects of tidal inundation on benthic macrofauna associated with the eelgrass *Zostera muelleri*. *Estuar. Coast Shelf Sci.* 117, 238–247. <https://doi.org/10.1016/j.ecss.2012.11.011>.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. Vegan: community ecology package. <http://cran.r-project.org/package=vegan>.
- Onrust, J., de Fouw, J., Oudman, T., van der Geest, M., Piersma, T., van Gils, J.A., 2013. Red knot diet reconstruction revisited: context dependence revealed by experiments at Banc d'Arguin, Mauritania. *Hous. Theor. Soc.* 60, 298–307. <https://doi.org/10.1080/00063657.2013.811213>.
- Oudman, T., Schekkerman, H., Kidee, A., van Roopen, M., Camara, M., Smit, C., ten Horn, J., Piersma, T., El-Hacen, M.E.-H., 2020. Changes in the waterbird community of the Parc National du Banc d'Arguin, Mauritania, 1980–2017. *Bird Conserv. Int.* 1–16. <https://doi.org/10.1017/S0959270919000431>.
- Paar, M., Voronkov, A., Hop, H., Brey, T., Bartsch, I., Schwanitz, M., Wiencke, C., Lebreton, B., Asmus, R., Asmus, H., 2016. Temporal shift in biomass and production of macrozoobenthos in the macroalgal belt at Hansneset, Kongsfjorden, after 15 years. *Polar Biol.* 39, 2065–2076. <https://doi.org/10.1007/s00300-015-1760-6>.
- Petersen, J.M., Kemper, A., Gruber-Vodicka, H., Cardini, U., van der Geest, M., Kleiner, M., Bulgheresi, S., Mußmann, M., Herbold, C., Seah, B.K.B., Antony, C.P., Liu, D., Belitz, A., Weber, M., 2016. Chemosynthetic symbionts of marine invertebrate animals are capable of nitrogen fixation. *Nat. Microbiol.* 2, 1–11. <https://doi.org/10.1038/nmicrobiol.2016.195>.
- Piersma, T., 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *J. Ornithol.* 148, 45–59. <https://doi.org/10.1007/s10336-007-0240-3>.
- Piersma, T., 2006. Migration in the balance: tight ecological margins and the changing fortunes of shorebird populations. In: Boere, G.C., Galbraith, C.A., Stroud, D.A. (Eds.), *Waterbirds Around the World*. The Stationary Office, Edinburgh, UK, pp. 74–80.

- Piersma, T., 1982. Macrobenthic fauna of the intertidal flats. Wintering Waders Banc d'Arguin, Mauritania. Rep. Netherlands Ornithol. Mauritanian Exped. 49–66.
- Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R., Essink, K., Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *J. Appl. Ecol.* 38, 976–990. <https://doi.org/10.1046/j.1365-2664.2001.00652.x>.
- Piersma, T., Lok, T., Chen, Y., Hassell, C.J., Yang, H.-Y., Boyle, A., Slaymaker, M., Chan, Y.-C., Melville, D.S., Zhang, Z.-W., Ma, Z., 2016. Simultaneous declines in summer survival of three shorebird species signals a Flyway at risk. *J. Appl. Ecol.* 53, 479–490.
- Prospero, J.M., Lamb, P.J., 2003. African droughts and dust transport to the Caribbean: climate change implications. *Science* (80-.) 302, 1024–1027. <https://doi.org/10.1126/science.1089915>.
- Rakhimberdiev, E., Duijns, S., Karagicheva, J., Camphuysen, C.J., Castricum, V., Dekinga, A., Dekker, R., Gavrilov, A., ten Horn, J., Jukema, J., Saveliev, A., Soloviev, M., Tibbitts, T.L., van Gils, J.A., Piersma, T., 2018. Fuelling conditions at staging sites can mitigate Arctic warming effects in a migratory bird. *Nat. Commun.* 9, 4263.
- Reise, K., Buschbaum, C., Büttger, H., Wegner, K.M., 2017. Invading oysters and native mussels: from hostile takeover to compatible bedfellows. *Ecosphere* 8, e01949. <https://doi.org/10.1002/ecs2.1949>.
- Rodrigues, A.M., Meireles, S., Pereira, T., Quintino, V., 2007. Spatial heterogeneity recognition in estuarine intertidal benthic macrofaunal communities: influence of sieve mesh-size and sampling depth. *Hydrobiologia* 587, 37–50. <https://doi.org/10.1007/s10750-007-0684-8>.
- Shanahan, T.M., Overpeck, J.T., Anchukaitis, K.J., Beck, J.W., Cole, J.E., Dettman, D.L., Peck, J.A., Scholz, C.A., King, J.W., 2009. Atlantic forcing of persistent drought in West Africa. *Science* 324, 377–380. <https://doi.org/10.1126/science.1166352>.
- Souza, G.B.G., Barros, F., 2015. Analysis of sampling methods of estuarine benthic macrofaunal assemblages: sampling gear, mesh size, and taxonomic resolution. *Hydrobiologia* 743, 157–174. <https://doi.org/10.1007/s10750-014-2033-z>.
- Strayer, D.L., Malcom, H.M., 2018. Long-term responses of native bivalves (Unionidae and Sphaeriidae) to a *Dreissena* invasion. *Freshw. Sci.* 37, 697–711. <https://doi.org/10.1086/700571>.
- Suykerbuyk, W., Govers, L.L., van Oven, W.G., Giesen, K., Giesen, W.B.J.T., de Jong, D.J., Bouma, T.J., van Katwijk, M.M., 2018. Living in the intertidal: desiccation and shading reduce seagrass growth, but high salinity or population of origin have no additional effect. *PeerJ* 37, e5234. <https://doi.org/10.7717/peerj.5234>.
- Tanaka, M.O., Leite, F.P.P., 1998. The effect of sieve mesh size on the abundance and composition of macrophyte-associated macrofaunal assemblages. *Hydrobiologia* 389, 21–28. <https://doi.org/10.1023/A:1003589404593>.
- Thieltges, D.W., 2005. Impact of an invader: epizootic American slipper limpet *Crepidula fornicata* reduces survival and growth in European mussels. *Mar. Ecol. Prog. Ser.* 286, 13–19. <https://doi.org/10.3354/meps286013>.
- Thompson, B.W., Riddle, M.J., Stark, J.S., 2003. Cost-efficient methods for marine pollution monitoring at Casey Station, East Antarctica: the choice of sieve mesh-size and taxonomic resolution. *Mar. Pollut. Bull.* 46, 232–243. [https://doi.org/10.1016/S0025-326X\(02\)00366-1](https://doi.org/10.1016/S0025-326X(02)00366-1).
- Turner, S.J., Hewitt, J.E., Wilkinson, M.R., Morrissy, D.J., Thrush, S.F., Cummings, V.J., Funnell, G.A., 1999. Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. *Estuaries* 22, 1016–1032. <https://doi.org/10.2307/1353080>.
- Unsworth, R.K.F., Rasheed, M.A., Chartrand, K.M., Roelofs, A.J., 2012. Solar radiation and tidal exposure as environmental drivers of *Enhalus acoroides* dominated seagrass meadows. *PLoS One* 7, e34133. <https://doi.org/10.1371/journal.pone.0034133>.
- Valença, A.P.M.C., Dos Santos, P.J.P., 2013. Macrobenthic community structure in tropical estuaries: the effect of sieve mesh-size and sampling depth on estimated abundance, biomass and composition. *J. Mar. Biol. Assoc. U. K.* 93, 1441–1456. <https://doi.org/10.1017/S0025315413000039>.
- van de Kam, J., Ens, B.J., Piersma, T., Zwarts, L., 2004. *Shorebirds: an Illustrated Behavioural Ecology*. KNNV Publishers, Utrecht.
- van der Geest, M., Sall, A., Ely, S., Nauta, R., van Gils, J., Piersma, T., 2014. Nutritional and reproductive strategies in a chemosymbiotic bivalve living in a tropical intertidal seagrass bed. *Mar. Ecol. Prog. Ser.* 501, 113–126. <https://doi.org/10.3354/meps10702>.
- van der Geest, M., van der Lely, J., van Gils, J., Piersma, T., Lok, T., 2019. Density-dependent growth of bivalves dominating the intertidal zone of Banc d'Arguin, Mauritania: importance of feeding mode, habitat and season. *Mar. Ecol. Prog. Ser.* 610, 51–63. <https://doi.org/10.3354/meps12851>.
- van der Heide, T., Govers, L.L., de Fouw, J., Olf, 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* (80-.) 336, 1432–1434.
- van der Zee, E.M., Angelini, C., Govers, L.L., Christianen, M.J.A., Altieri, A.H., van der Reijden, K.J., Silliman, B.R., van de Koppel, J., van der Geest, M., van Gils, J.A., van der Veer, H.W., Piersma, T., de Ruiter, P.C., Olf, H., van der Heide, T., 2016. How habitat-modifying organisms structure the food web of two coastal ecosystems. *Proc. R. Soc. B* 283, 20152326. <https://doi.org/10.1098/rspb.2015.2326>.
- van Gils, J.A., Lisovski, S., Lok, T., Meissner, W., Ożarowska, A., de Fouw, J., Rakhimberdiev, E., Soloviev, M.Y., Piersma, T., Klaassen, M., 2016. Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science* 352, 819–821. <https://doi.org/10.1126/science.aad6351>.
- van Gils, J.A., van der Geest, M., Kraan, C., Folmer, E.O., Jansen, E.J., Piersma, T., 2009. Hoe de draagkracht van de Waddenzee vogelaantallen op de Banc d'Arguin beperkt. (How the carrying capacity of the Wadden Sea regulates the number of wintering waders at Banc d'Arguin). *Limosa* 82, 134–140.
- van Gils, J.A., van der Geest, M., Leyrer, J., Oudman, T., Lok, T., Onrust, J., de Fouw, J., van der Heide, T., van den Hout, P.J., Spaans, B., Dekinga, A., Brugge, M., Piersma, T., 2013. Toxin constraint explains diet choice, survival and population dynamics in a molluscivore shorebird. *Proc. R. Soc. Lond. B Biol. Sci.* 280, 20130861.
- van Roomen, M., Nagy, S., Foppen, R., Dodman, T., Citegetse, G., Ndiaye, A., 2015. Status of Coastal Waterbird Populations in the East Atlantic Flyway. With Special Attention to Flyway Populations Making Use of the Wadden Sea (Programme Rich Wadden Sea, Leeuwarden, The Netherlands, Sovon, Nijmegen, The Netherlands, Wetlands International, Wageningen, The Netherlands, BirdLife International, Cambridge, United Kingdom & Common Wadden Sea Secretariat, Wilhelmshaven, Germany).
- Vermaat, J.E., Verhagen, F.C.A., 1996. Seasonal variation in the intertidal seagrass *Zostera noltii* Hornem.: coupling demographic and physiological patterns. *Aquat. Bot.* 52, 259–281.
- Vuolo, F., Mattiuzzi, M., Atzberger, C., 2015. Comparison of the Landsat surface reflectance climate data record (CDR) and manually atmospherically corrected data in a semi-arid European study area. *Int. J. Appl. Earth Obs. Geoinf.* 42, 1–10. <https://doi.org/10.1016/j.jag.2015.05.003>.
- Wijnsma, G., Wolff, W.J., Meijboom, A., Duiven, P., De Vlas, J., 1999. Species richness and distribution of benthic tidal flat fauna of the Banc d'Arguin, Mauritania. *Oceanol. Acta* 22, 233–243. [https://doi.org/10.1016/S0399-1784\(99\)80048-6](https://doi.org/10.1016/S0399-1784(99)80048-6).
- Wolff, W.J., Duiven, A.G., Duiven, P., Esselink, P., Gueye, A., Meijboom, A., Moerland, G., Zegers, J., 1993a. Biomass of macrobenthic tidal flat fauna of the Banc d'Arguin, Mauritania. *Hydrobiologia* 258, 151–163. <https://doi.org/10.1007/BF00006193>.
- Wolff, W.J., Michaelis, H., 2008. Do shorebirds graze down zoobenthic biomass at the Banc d'Arguin tidal flats in Mauritania? *Estuar. Coast Shelf Sci.* 79, 491–495. <https://doi.org/10.1016/j.ecss.2008.04.025>.
- Wolff, W.J., Smit, C.J., 1990. The Banc d'Arguin, Mauritania, as an environment for coastal birds. *Ardea* 78, 17–38.
- Wolff, W.J., van der Land, J., Nienhuis, P.H., de Wilde, P.A.W.J., 1993b. The functioning of the ecosystem of the Banc d'Arguin, Mauritania: a review. *Hydrobiologia* 258, 211–222.
- Wolff, W.J., van Etten, J.P.C., Hiddink, J.G., Montserrat, F., Schaffmeister, B.E., Vonk, J.A., de Vries, A.B., 2009. Predation on the benthic fauna of the tidal flats of the Banc d'Arguin, Mauritania. In: Symoens, J.-J. (Ed.), *Coastal Ecosystems of West Africa. Biological Diversity – Resources – Conservation*, pp. 43–59. Brussels.
- Young, N.E., Anderson, R.S., Chignell, S.M., Vorster, A.G., Lawrence, R., Evangelista, P.H., 2017. A survival guide to Landsat preprocessing. *Ecology* 98, 920–932. <https://doi.org/10.1002/ecy.1730>.

- Zhang, S.-D., Ma, Z., Choi, C.-Y., Peng, H.-B., Bai, Q.-Q., Liu, W.-L., Tan, K., Melville, D.S., He, P., Chan, Y.-C., van Gils, J.A., Piersma, T., 2018. Persistent use of a shorebird staging site in the Yellow Sea despite severe declines in food resources implies a lack of alternatives. *Bird. Conserv. Int.* 28, 1–15. <https://doi.org/10.1017/S0959270917000430>.
- Zwarts, L., Bijlsma, R.G., van der Kamp, J., 2018. Large decline of birds in Sahelian rangelands due to loss of woody cover and soil seed bank. *J. Arid Environ.* 155, 1–15. <https://doi.org/10.1016/j.JARIDENV.2018.01.013>.
- Zwarts, L., Bijlsma, R.G., van der Kamp, J., Wymenga, E., 2009. Living on the edge: wetlands and birds in a changing Sahel. *Mar. Technol. Soc. J.* <https://doi.org/10.4031/002533206787353088>.