Journal of Sea Research 60 (2008) 255–263

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Molluscan assemblages of seagrass-covered and bare intertidal flats on the Banc d'Arguin, Mauritania, in relation to characteristics of sediment and organic matter

Pieter J.C. Honkoop [a,*], Eilke M. Berghuis [a], Sander Holthuijsen [a], Marc S.S. Lavaleye [a], Theunis Piersma [a,b]

[a] Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands
[b] Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

ARTICLE INFO

Article history:
Received 22 May 2008
Received in revised form 29 July 2008
Accepted 31 July 2008
Available online 5 August 2008

Keywords:
Molluscs
Seagrass
Zostera noltii
Sediment
Phytopigments
Benthic Assemblages
Mauritania
West Africa

ABSTRACT

The Banc d'Arguin, a non-estuarine area of shallows and intertidal flats off the tropical Saharan coast of Mauritania, is characterised by extensive intertidal and subtidal seagrass beds. We examined the characteristics of intertidal seagrass (*Zostera noltii*) meadows and bare areas in terms of the presence and abundance of molluscs (gastropods and bivalves). To explain observed differences between molluscan assemblages in seagrass and bare patches, some aspects of the feeding habitat (top-5 mm of the sediment) and of food (organic materials) of molluscs were examined. The novelty of this study is that phytopigments were measured and identified to assess source and level of decay (freshness) of organic material in the sediment and to study their importance as an explanatory variable for the distribution of molluscs. Over an area of 36 km^2 of intertidal flats, at 12 sites, paired comparisons were made between seagrass-covered and nearby bare patches. Within seagrass meadows, dry mass of living seagrass was large and amounted to 180± 10 g AFDM m^{-2} (range 75–240). Containing twice the amount of silt per unit dry sediment mass, seagrass sediments were muddier than bare areas; the relative amount of organic material was also larger. The total number of species of bivalves and gastropods amounted to 27, 14 of which were found only in seagrass areas, 4 only in bare and 9 in both types of habitat. Among the three numerically most abundant species, the bivalves *Anadara senilis*, *Dosinia hepatica* and *Loripes lacteus*, the first was numerically most abundant in bare and the other two in seagrass-covered areas. Bare intertidal areas had greater mean total biomass of molluscs (80.5 g AFDM m^{-2}) than seagrass meadows (30.0 g AFDM m^{-2}). In both habitats, the bulk of the biomass was made up by *A. senilis*. Excluding this species, bare mudflats contained on average only 3.1 g AFDM m^{-2} and seagrass meadows 6.9 g AFDM m^{-2}. As compared to previous surveys in 1980–1986, the biomass of *A. senilis* had increased almost 10-fold and *D. hepatica*, previously found in very small numbers, had become the most numerous species. However, the total biomass excluding that of *A. senilis* was similar. Concentrations of phytopigments were similar to those observed at temperate mudflats, indicating that the Banc d'Arguin might not be as oligotrophic as previously thought. Per unit of dry sediment mass, smaller amounts of phytopigments were found in bare than in seagrass areas. Per unit of dry organic material, bare sediments contained most (fresh) phytopigments. This suggests that in seagrass-covered meadows the organic material is more degraded than in bare sediments. Overall, the composition of phytopigments, quite surprisingly, indicated a benthic-diatom-dominated trophic system. Multivariate statistics revealed that patterns of zoobenthic assemblages were correlated with patterns of a combination of four environmental parameters: grain size of the sediment, amount of fresh phytopigments and amounts of leaves and roots of seagrass.

1. Introduction

The Banc d'Arguin, at the western edge of the Sahara, is a large shallow area along the coast of Mauritania. It includes 500 km^2 of intertidal flats with no freshwater inflow from rivers. The entire area of the tropical intertidal mudflats is part of a well-protected national park with little human impact so far (Wolff, 2005). Seagrass *Zostera noltii* grows at about 85% of the intertidal flats (Wolff and Smit, 1990). Previous studies have suggested that the intertidal area of the Banc d'Arguin receives little or no input of nutrients from the oceanic upwelling 100 km offshore (Sevrin-Reyssac, 1993). In addition, there is no evidence for offshore transport of seagrass material (Berghuis et al., 1993). This suggests that the inshore parts of the Banc d'Arguin are isolated and nutrient-limited with slow rates of primary production by phytoplankton and microphytobenthos (Wolff et al., 1993b; Michaelis and Wolff, 2001). This may explain the relatively small standing stocks of benthic invertebrates, 7.6–17.0 g ash-free dry mass (AFDM) per m^2 (Piersma, 1982; Wolff et al., 1993a). These values are at

* Corresponding author. Tel.: +31 222 369300; fax: +31 222 369674.
E-mail address: phonkoop@nioz.nl (P.J.C. Honkoop).

1385-1101/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.seares.2008.07.005

the lower end of the range of values reported for intertidal areas in general (Michaelis and Wolff, 2001), where biomass values up to 100 g AFDM m^{-2} are no exception (Heip, 1995).

Seagrass meadows are particularly important habitats for ecological and economic reasons (Costanza et al., 1997) as they, generally, sustain a more diverse and abundant benthic fauna than other intertidal habitats (Orth et al., 1984; Heck et al., 1989; Edgar et al., 1994; Boström and Bonsdorff, 1997; Sheridan, 1997; Siebert and Branch, 2005, 2007). This is because seagrass meadows provide food and shelter, trap and recycle nutrients and stabilise the seabed (Larkum et al., 2006). Earlier studies on the Banc d'Arguin (Wolff et al., 1993a; Wijnsma et al., 1999) confirm that more invertebrate species occur in seagrass meadows than in bare habitat. However, the seagrass-covered areas had smaller zoobenthic biomass than bare areas, as a consequence of the prevalence of the large bivalve *Anadara senilis* in bare areas (Wolff et al., 1993a; Wijnsma et al., 1999; Michaelis and Wolff, 2001).

Although seagrass systems have large standing stocks of primary products, *i.e.* seagrass material, and a fast rate of primary production (Mateo et al., 2006), the products are hardly directly usable by benthic invertebrates. This is shown by stable isotope measurements; benthic invertebrates living in seagrass areas show a distinct algal isotopic signature (Dauby, 1989; Dauby, 1995; Loneragan et al., 1997; Yamamuro, 1999; Lepoint et al., 2000; Davenport and Bax, 2002). Fresh and degraded seagrass is poor food for the following reasons (1) Due to leaking of cell materials during the initial phases of degradation, the remaining material is deficient of inorganic nutrients, particularly N and P, making it less suitable as food (Harrison, 1989), (2) the remaining material is rich in breakdown-limiting phenolic compounds (Godshalk and Wetzel, 1978), refractory polysaccharides and lignin, and (3) as a consequence of the large amounts of organic material in the sediment and high bacterial activity, the benthic environment becomes anoxic, further reducing the rate of breakdown of organic material.

Despite the supposedly oligotrophic nature of the Banc d'Arguin and the poor quality of seagrass as a source of food for zoobenthos, the area is world-famous for its large numbers of (zoobenthos-eating) waterbirds (Smit and Piersma, 1989; Wolff and Smit, 1990). How can it be explained that the relatively small amounts of benthic invertebrates can sustain all these birds? Maybe, the waters are not as oligotropic as expected and primary production of benthic and pelagic algae may be larger than expected. Secondly, a substantial part of the zoobenthos may be able to utilise seagrass as a source of food. In particular, members of the bivalve family Lucinidae are highly specialised in using breakdown products of seagrass (Allen, 1958) and can occur in large densities (see references and data in Johnson et al., 2002).

The first aim of the present study was to quantify differences between seagrass habitat and bare habitat quantitatively and in greater detail than before. To establish the relative richness of zoobenthos in seagrass meadows, we made paired comparisons between the macrobenthic molluscan fauna in seagrass and adjacent bare habitats. Based on earlier work at the Banc d'Arguin (see above) it was predicted that the number of molluscan species was larger and the biomass smaller in seagrass than in bare habitats. The second aim was to find evidence for the importance of phytoplankton or microphytobenthos in the organic material as food for zoobenthos, assuming that fresh alga are an important source of food for many (if not most) molluscs (Page et al., 1992). We, therefore, studied the source and quality of the organic material in sediment. To do this, phytopigments were identified, concentrations determined and the ratio between fresh pigments and their breakdown products used as a measure of the quality of organic material as food for molluscs (Boon and Duineveld, 1996). Due to the accumulation of degradation products of seagrass (see above) it was predicted that the concentration of fresh (algal-derived) pigments in the sediment would be smaller in seagrass meadows than in bare patches. As different green plants have different pigments (Jeffrey and Vesk, 1997), the phytopigment signature can be used to establish the source of organic matter, and thus examine the possible contribution of algae in the food chain. Because seagrass beds trap silt and clay, fine sediments are often associated with a large species abundance (Gray, 1974), and sediment particles can be a major part of ingested materials (particularly for deposit-feeders and scavengers), the importance of sediment grain size as an explanatory variable for patterns in molluscan distribution was also estimated.

2. Material and methods

2.1. Fieldwork and laboratory assays

Our study was carried out in the vicinity of the Scientific Station maintained by the Parc National du Banc d'Arguin (PNBA) at Iwik (19° 52.42′ N, 16° 18.50′ W) between 30 Nov and 14 Dec 2004. As elsewhere on the Banc d'Arguin, near Iwik dense seagrass beds, mainly *Z. noltii*, cover most of the intertidal flats. Sampling locations were spread over an area of about 36 km^2 (Fig. 1) to obtain a representative coverage. At each location (one individual tidal flat) two bare sites and two sites covered in seagrass were selected such that the distance between each bare patch and the nearest seagrass site was always less than 50 m. In this way, five locations resulted in ten bare-seagrass pairs. Data from these 10 pairs (open dots in Fig. 1) were used for the permutational multivariate analysis of variance (see below). In addition, two more locations were visited where only one bare-seagrass pair could be sampled. Finally, one bare and one seagrass site at different locations were sampled (Fig. 1). In total, 13 bare and 13 seagrass sites were sampled, of which 12 bare sites were statistically paired with 12 seagrass sites and analysed accordingly (see below).

To describe patterns in the molluscan fauna in seagrass and bare habitats, three cores per site (internal diameter of 152 mm, thus covering 0.018 m^2) were taken to a depth of 30 cm. The content of each core was sieved through a 1-mm sieve and in the laboratory all (epi) benthic animals were separated from the matrix of seagrass remains

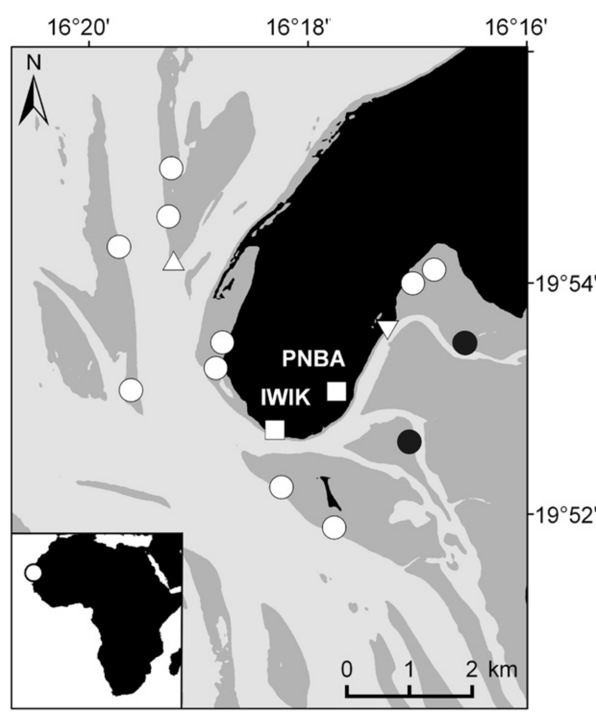

Fig. 1. Position of the sampling sites. The circles represent the sites where paired samples were taken in bare and seagrass areas. Data from the open circles were used in the permutational multivariate ANOVA. For other pairwise comparisons, data from the closed circles were also included. The up and down triangles represent a single seagrass and a single bare site, respectively, and the squares represent the location of the town of Iwik and of the scientific research station of Parc National du Banc d'Arguin (PNBA). Black = land, dark grey = intertidal area, light grey = subtidal area.