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Seasonal changes in mollusc abundance in a tropical intertidal ecosystem, Banc d'Arguin (Mauritania): Testing the 'depletion by shorebirds' hypothesis[☆,☆☆]

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ABSTRACT

At temperate latitudes densities and biomass of intertidal molluscs tend to be strongly seasonal. Here we provide a comparative study on seasonality of bivalves and gastropods in the tropical intertidal seagrass-covered soft sediment environment of Banc d'Arguin, Mauritania (20°N, 16°W). In this system, benthivorous shorebirds exert considerable predation pressure with strong seasonal variations. It has been proposed that during the period when (adult) shorebirds are absent (May–August) benthic biomass would be able to recover, but a first test was inconclusive. Over a full year (March 2011–February 2012), each month we sampled benthic invertebrates at sixteen permanent sites. The total of 3763 specimens comprised 20 species, representing eight orders and 19 families. Bivalves were much more common than gastropods. The bivalve *Loripes lucinalis* dominated the assemblage throughout the year (58% of total number), followed by *Dosinia isocardia* (10%), *Senilia senilis* (8%) and the gastropod *Gibbula umbilicalis* (6%). Average biomass amounted to 32 g AFDM/m^2, of which the large West-African bloody cockle *Senilia* made up three-quarter, *Loripes* 16%, *Gibbula* 2% and *Dosinia* 1%. Across the 20 species, lowest densities were reached in late spring (May) and summer (Aug.), whereas highest densities occurred in autumn (Oct.). The lowest overall density of 676 specimens/m^2 in August more than doubled to a peak density of 1538 specimens/m^2 in October, most of the increase being due to strong recruitment in both *Loripes* (densities increasing from 322 specimens/m^2 in Sept. to 785 specimens/m^2 in Oct.) and *Dosinia* (densities increasing from 18 specimens/m^2 in Aug. to 265 specimens/m^2 in Sept.). Our results suggest that by the time the feathered molluscivore predators returned in high numbers to Banc d'Arguin (after their summer breeding season in the Arctic), benthic animals were at a peak. In order to quantitatively understand the seasonal changes in mollusc abundance, we build upon a recently published optimal diet model in which the most abundant molluscivore shorebird, the red knot (*Calidris canutus*), could choose between *Loripes* and *Dosinia*. Observed changes in densities of these two bivalves closely match depletion trajectories predicted by the model. We conclude that molluscivore shorebirds are able to deplete their food stocks in the course of their 'winter' in a tropical intertidal area.

1. Introduction

It is well established that benthic invertebrates living in temperate intertidal soft-sediment systems show pronounced seasonality in density and biomass (Beukema, 1974; Zwarts et al., 1992; Zwarts and Wanink, 1993; Urra et al., 2013). In the tropics, temperature fluctuations are less pronounced, and this may also be true for the seasonal changes in food availability for benthic invertebrates (Sastry, 1979; Alongi, 1990; Lubet, 1994; Mandal and Harkantra, 2013). This could lead to tropical intertidal benthic communities remaining rather stable throughout the year

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[☆] Ahmedou Salem et al.: Seasonal changes in a tropical bivalve community.

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(Piersma, 1982; Wolff, 1991; Dittmann, 2000), even in regions with distinct rainy and dry seasons (Silva et al., 2011). However, benthic invertebrates are the food of consumers such as crabs, shrimp, fish and shorebirds (van de Kam et al., 2004). The shorebird component of this predator community is highly seasonal by virtue of the fact that shorebirds breed in northern areas from which they migrate south to winter in coastal wetlands, e.g. along the coasts of West-Africa (van de Kam et al., 2004; Piersma, 2007). This would result in strongly seasonal predation pressure (Wolff and Michaelis, 2008).

Such seasonality in predation pressure could be strong in Banc d'Arguin (Mauritania, West-Africa), which is an area of over 10,000 km^2 of shallow inshore waters bordering the Sahara (Wolff et al., 1993a). This area has received protection from human over-exploitation by the establishment in 1976 of the Parc National du Banc d'Arguin (PNBA). PNBA is one of the most important waterbird areas on the West-African coastline, hosting over two million wintering shorebirds (Engelmoer et al., 1984; Smit and Piersma, 1989; Ens et al., 1990; Zwarts et al., 1990, 1998), of which the red knot *Calidris canutus* is by far the most numerous molluscivore (230,000–300,000 individuals), followed by the much less abundant oystercatcher *Haematopus ostralegus* (5000–8000 individuals; Zwarts et al., 1998; Hagemeijer et al., 2004; Diawara and Overdijk, 2007). More than $^3/_4$ of the intertidal flats at Banc d'Arguin are covered by seagrass beds (Wolff and Smit, 1990), which, compared to bare flats, support the highest densities of shorebirds (Altenburg et al., 1982). This is for good reasons, since seagrass habitat is among the most productive and richest of shallow marine habitats, both locally (Honkoop et al., 2008) as well as globally (Duarte and Chiscano, 1999).

During the first studies of shorebirds and benthos of the Banc d'Arguin in 1980, the high ratio of birds to standing benthic biomass, in comparison with ratios found elsewhere in intertidal soft-sediment areas, were unexpected (Altenburg et al., 1982; Engelmoer et al., 1984). The high ratio implied high secondary production, but also suggested that shorebirds would be able to substantially reduce the standing stocks of benthos in the course of the main season of predation, i.e. from September through April. Wolff and Michaelis (2008) tested this by comparing the benthic biomass sampled across an extensive area in September 1988 (i.e. at the start of a shorebird migration season) with the standing stocks in February–March 1986 (i.e. at the end). The lack of difference between the two values may be explained either by an absence of depletion of benthos during the season of shorebird predation, or because of differences between years obliterated the measurement of the proposed effect. Here we provide a stronger test of the seasonal depletion hypothesis by examining monthly changes over a full year in a seagrass bed, intensively used by shorebirds, in a nearshore site of the Banc d'Arguin. As molluscs are by far the largest component of the intertidal benthic community of Banc d'Arguin (e.g. Piersma, 1982; Wolff et al., 1993a; Michaelis and Wolff, 2001), and since molluscivorous shorebirds, especially red knots, are very numerous, we limited our study to bivalves and gastropods.

2. Material and methods

2.1. Study area

This study was carried out from the PBNA Scientific Station at Iwik Peninsula on a nearshore area of dense seagrass beds (mainly *Zostera noltii* Hornem.), locally known as Abelgh Eiznaya (Fig. 1; see also Leyrer et al., 2006). 16 stations were chosen randomly within a 200-m radius from a central point (19°53.40′N, 16°18.50′W), which were sampled at monthly intervals from March 2011 to February 2012. About 1/3 of the stations was located in dense seagrass

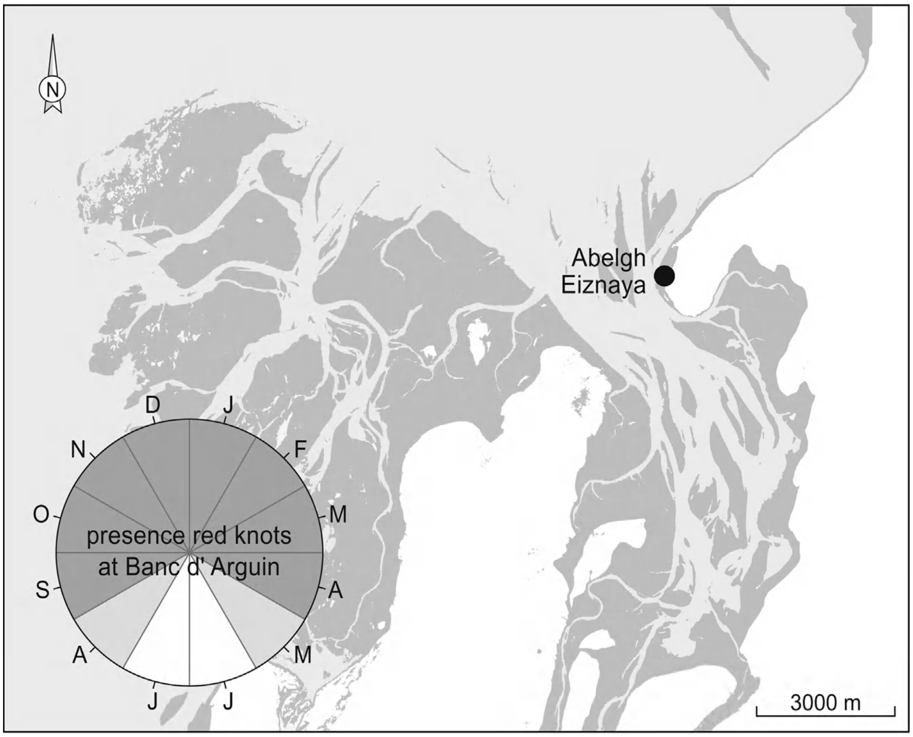

Fig. 1. Map of the Banc d'Arguin, with tidal flats given in dark grey, ocean in light grey and land in white. Black dot indicates the centre of our study area, Abelgh Eiznaya. Scale bar is expressed in metres. The pie indicates the presence of red knots in Banc d'Arguin (both adults and young birds present during September–April; adults are leaving and arriving in May and August, respectively; only young birds present during June–July). Note that the sampling area of Wolff and Michaelis (2008) was much larger than ours and covered roughly all tidal flats plotted in this map.

habitat, 1/3 in intermediate seagrass and 1/3 in bare habitat, with fine (median grain size ~50 μm), intermediate (~100 μm) and coarse sediment texture (~150 μm), respectively (Folmer et al., 2012). Tidal regime is the usual M2 type, also known as the 'principal lunar semi-diurnal' type, with an average amplitude of 1.61 m (Wolff and Smit, 1990). Meteorological measurements at a site 65 km south of the study area (at Nouamghar; http://www.accuweather.com/fr/mr/nouamghar/1112585/month/1112585?) showed monthly variations in minimal (15.0–25.7 °C) and maximal (29.0–37.8 °C) daily air temperatures during our study period, with the minimum in February and maximum in October. Most rain fell in August (27 mm vs. 3 mm/month on average).

2.2. Field sampling and laboratory analyses

Each month at each station we took a single sample down to a depth of 20 cm using a core with a 15 cm diameter. In order to determine whether prey were within reach of the 3.5 cm long bill of red knots (Zwarts et al., 1992), we separately sieved the top layer (0–4 cm) from the bottom layer (4–20 cm), using a 1-mm meshed sieve. The material remaining on the sieve was put in separate labelled plastic bags and frozen within a few hours after sampling. Over subsequent days all fleshed bivalves and gastropods were sorted from the debris of dead shells and seagrass material. Specimens were identified to species level, their lengths were measured to the nearest 0.1 mm, and they were then fixed in buffered formaldehyde (4%). Subsequently (May 2012), the biomass of the most abundant species (*Diplodonta circularis*, *Dosinia isocardia*, *Gibbula umbilicalis*, *Loripes lucinalis*, *Mesalia mesal*, *Modiolus* sp., *Petricolaria gracilis*, *Senilia senilis*, and *Tellina distorta*) was determined in the laboratory at NIOZ as ash-free dry mass (AFDM). In order to do so, specimens were dried at 60 °C for at least 48 h and were afterwards incinerated at 560 °C for 2 h (bivalves without shells, gastropods with shells).

2.3. Depletion model

We used an existing optimal diet model that has been developed for the most abundant molluscivore shorebird present in our study area, the red knot (van Gils et al., 2013). Red knots ingest their prey whole, and hence prey that have a circumference larger than their gape cannot be ingested (Zwarts and Blomert, 1992). Most mollusc species found at Banc d'Arguin do not grow very large and therefore large fractions are ingestible for red knots (Piersma et al., 1993).

We only modelled the depletion of *Loripes lucinalis* and *Dosinia isocardia* and left out all the other mollusc species. This is because *Loripes* and *Dosinia* are the two most abundant molluscs in the system. The third most abundant mollusc, *Senilia senilis*, is a thick-shelled bivalve which grows to heights of 80 mm and is therefore almost entirely unavailable to red knots (Wolff et al., 1987). Our focus on *Loripes* and *Dosinia* only is also justified because these two species together represent 80% of the molluscs consumed by red knots at Banc d'Arguin (van Gils et al., 2012; Onrust et al., 2013; van Gils et al., 2013).

Even though *Loripes* is by far the most abundant bivalve and has a very thin shell, it is not the most preferred prey of the two (van Gils et al., 2012; van Gils et al., 2013; Oudman et al., submitted for publication). Recent evidence suggests that this is due to the specialized metabolism of *Loripes* that lives in symbiosis with chemoautotrophic bacteria inside its gill structures (Herry et al., 1989). Feeding experiments with captive red knots showed that they develop diarrhoea, dehydrate and lose appetite when on a monospecific diet of *Loripes* (Oudman et al., submitted for publication). The depletion model used here takes account of the long-term maximum intake rate that red knots can sustain when foraging on *Loripes*. This model, called the Toxin Digestive Rate Model (TDRM), not only explained diet choice differences between years, it also explained most of the variation in annual survival rates in an 8-yr study of red knot demographics (van Gils et al., 2013). The model is an extension of the so-called Digestive Rate Model (DRM) that explained diet choice in red knots feeding on non-toxic prey (van Gils et al., 2005a) and we refer to van Gils et al. (van Gils et al., 2013) for its full mathematical details; here we will only introduce the basics.

According to Holling's functional response model (Holling, 1959), energy intake rate Y on two prey types (labelled 1 and 2) is given by:

$$Y = \frac{p_1 a_1 N_1 e_1 + p_2 a_2 N_2 e_2}{1 + p_1 a_1 N_1 h_1 + p_2 a_2 N_2 h_2} \tag{1}$$

where p is the acceptance probability upon encounter, a is searching efficiency, N is available numerical prey density, e is energy value and h is handling time for respectively prey type 1 and 2. Under some circumstances Y can be maximized by not accepting every prey that is encountered. Diet selection models make predictions about the values of p_1 and p_2 in order to maximize Y.

The classical diet model (Stephens and Krebs, 1986), sometimes called the contingency model (CM), ranks prey types on the basis of profitability, i.e. $e_1/h_1 > e_2/h_2$. A forager should only accept prey type 1 ($p_1 = 1$) and neglect prey type 2 ($p_2 = 0$) when the energy intake rate on prey type 1 alone exceeds the profitability of type 2, i.e. when:

$$\frac{a_1 N_1 e_1}{1 + a_1 N_1 h_1} > \frac{e_2}{h_2} \tag{2}$$

If not, it should accept both prey types in its diet ($p_1 = 1$; $p_2 = 1$).

The CM ignores digestive processing constraints, which real-world foragers often face, especially the ones such as molluscivores feeding on bulky prey. The digestive rate model (DRM), developed by Hirakawa (1995) and successfully applied to red knots (van Gils et al., 2005a; van Gils et al., 2005b; Kraan et al., 2009; Quaintenne et al., 2010), does take account of such a constraint. Defining k as a prey type's indigestible bulk mass, ballast intake rate X is defined as:

$$X = \frac{p_1 a_1 N_1 k_1 + p_2 a_2 N_2 k_2}{1 + p_1 a_1 N_1 h_1 + p_2 a_2 N_2 h_2} \tag{3}$$

Defining c as the maximum rate at which bulky material can be processed by a forager's digestive system, the following condition should always be met:

$$X \le c \tag{4}$$

The optimal solution for p_1 and p_2 can either be found graphically or analytically and we refer to the original paper by Hirakawa (1995) or to the first application in red knots by van Gils et al. (2005a).

Finally, the TDRM not only takes account of a constraint on processing bulky food, it also includes a maximally tolerable toxin intake rate. Defining s as a prey type's toxin content, toxin intake rate Z is given by:

$$Z = \frac{p_1 a_1 N_1 s_1 + p_2 a_2 N_2 s_2}{1 + p_1 a_1 N_1 h_1 + p_2 a_2 N_2 h_2} \tag{5}$$

Defining q as the maximally tolerable toxin intake rate, the following condition should always be met:

$$Z \le q \tag{6}$$

Parameters used (Table 1) are as in van Gils et al. (van Gils et al., 2013), except for energy values e and ballast masses k, which are

Table 1
Overview of the parameters used in the depletion model.

Parameter	Definition	Value	Unit	Source(s)
a_L	Searching efficiency on *Loripes*	4	cm^2/s	1, 2
a_D	Searching efficiency on *Dosinia*	4	cm^2/s	1, 2
c	Max. digestive processing rate	5	mg DM_{shell}/s	3
e_L	Energy value *Loripes*	5.91	mg $AFDM_{flesh}$	4
e_D	Energy value *Dosinia*	2.68	mg $AFDM_{flesh}$	4
h_L	Handling time *Loripes*	1	s	1, 2
h_D	Handling time *Dosinia*	1	s	1, 2
k_L	Ballast mass *Loripes*	41.56	mg DM_{shell}	4
k_D	Ballast mass *Dosinia*	34.31	mg DM_{shell}	4
q	Max. tolerable toxin intake rate	0.1	mg $AFDM_{flesh}/s$	5
s_L	Toxin contents *Loripes*	e_L	mg $AFDM_{flesh}$	5
s_D	Toxin contents *Dosinia*	0	mg $AFDM_{flesh}$	5

Sources: 1 de Fouw et al. (in preparation); 2 Piersma et al. (1995); 3 van Gils et al. (2003); 4 this study; 5 Oudman et al. (submitted for publication).

estimated in the current study. These parameters, in combination with the relatively low densities of *Dosinia* found in this study (see Results below), simplify the mathematics of the TRDM. Namely, on all monthly average densities of *Loripes* and *Dosinia* found in this study, red knots would never face a digestive constraint c but always a toxin constraint q (using Eqs. S8–S9 in van Gils et al. (2013) reveals that for the current parameter settings digestive constraint c occurs above 365 available *Dosinia*/m^2, while toxin constraint q is reached above 49 available *Loripes*/m^2). This implies that all available *Dosinia* can be accepted ($p_D = 1$), while only a proportion of the available *Loripes* can be accepted (i.e. $p_L < 1$ as long as densities are above 49 specimens/m^2). This latter proportion p_L can be calculated by assuming a toxin intake rate that is maximally tolerable, i.e.:

$$Z = q \tag{7}$$

Since only *Loripes* is toxic ($s_L = e_L$) and *Dosinia* is not ($s_D = 0$), and since $p_D = 1$, this can be written as:

$$\frac{p_L a_L N_L s_L}{1 + p_L a_L N_L h_L + a_D N_D h_D} = q \tag{8}$$

Rewriting this, p_L equals:

$$p_L = \frac{q(1 + a_D N_D h_D)}{a_L N_L (s_L - q h_L)} \tag{9}$$

Since depletion is expressed as changes in prey *numbers*, we need to calculate the *numerical* intake rate R given by Holling's functional response, which on *Loripes* equals (with p_D falling out since it equals 1):

$$R_L = \frac{p_L a_L N_L}{1 + p_L a_L N_L h_L + a_D N_D h_D} \tag{10}$$

Along the same lines, numerical intake rate R_D on *Dosinia* equals:

$$R_D = \frac{a_D N_D}{1 + p_L a_L N_L h_L + a_D N_D h_D} \tag{11}$$

Substituting Eq. (9) into Eqs. (10) and (11), respectively, gives:

$$R_L = \frac{q}{s_L} \tag{12}$$

$$R_D = \frac{a_D N_D (s_L - h_L q)}{s_L (1 + a_D N_D h_D)} \tag{13}$$

These numerical intake rates are multiplied by the red knot feeding time per m^2 (expressed as V) for our Abelgh Eiznaya study area. The average red knot feeding density of 18.3 birds/ha was derived from unpublished observations of feeding red knots carried out in March 2007 and February 2008 over two and four days, respectively (van Gils, van der Geest & Folmer, unpubl. data). Unfortunately, we have no detailed counts available during the period of sampling benthos (March 2011–February 2012), but the fact that we did not find a difference between the 2007 and the 2008 counts (Welch Two Sample t-test, $t = -0.34$, df = 3.11, $P = 0.75$), suggests that inter-annual variations in red knot numbers are negligible for our purpose. Nevertheless, we will explore the sensitivity of our results with respect to V, the more so because red knot densities at Abelgh Eiznaya tend to be higher than the average for Banc d'Arguin (Altenburg et al., 1982; van Gils et al., 2009). Assuming a daily feeding period of 14 h (Altenburg et al., 1982; van Gils et al., 2005b; Leyrer et al., 2006) gives an estimated V of $1.07 \cdot 10^{-3}$ feeding seconds per m^2 per second between mid-October and the end of May (i.e. 92.3 feeding seconds per m^2 per day). Since 1-yr old red knots stay at Banc d'Arguin during summer (June–August), we assumed a predation pressure V that is only 7% of the value during October–May (van Dijk et al., 1990). The model predicts the depletion from mid-October to mid-August, using the densities observed in October as starting values, with available densities updated for depletion per step length Δt of 1 s in the following way for *Loripes* and *Dosinia*, respectively:

$$N_{L,\,t} = N_{L,\,t-1} - R_L V \tag{14}$$

$$N_{D,\,t} = N_{D,\,t-1} - R_D V \tag{15}$$

Next, *unavailable* densities are added to *available* densities in order to arrive at *total* densities at time t (where unavailable densities are the unavailable densities measured in starting month October, being 222.82 and 31.83 m^{-2} for *Loripes* (>4 cm depth) and *Dosinia* (depth > 4 cm, length ≥ 13.2 mm), respectively).

2.4. Statistics

All statistics and graphs were carried out in R (R Development Core Team, 2013), including the GAM models that were used to smooth seasonal trends in numerical densities (using package mgcv; Wood, 2006). In these GAMs we added month as a non-parametrically smoothed function and sampling station as a parametrically estimated parameter.

3. Results

From 192 cores collected during the whole study period, a total of 3,763 mollusc specimens were retrieved. These comprised 20 species (Table 2) and represented eight orders and 19 families. Bivalves occurred in higher densities than gastropods, with nine bivalve species representing 88% of all specimens. Overall, the lucinid *Loripes lucinalis* dominated the assemblage (58% of all specimens), followed by the venerid *Dosinia isocardia* (10%) and the arcid *Senilia senilis* (8%).

The overall average biomass of the mollusc community amounted to 32 g AFDM/m^2, of which the West-African bloody cockle *Senilia* made up three-quarter (Fig. 2). Highest biomass densities were reached in February and July, and lowest in May (Fig. 2A). The contribution of *Senilia* was lowest in March–May, reaching a peak in the relative contribution of about 85% to overall biomass in February, June and July (Fig. 2B). On average, *Loripes* contributed 19%, a percentage that reached a minimum in July (9.6%) and a maximum in March (34.6%; Fig. 2B). Across the 20 species (Table 2), lowest densities were reached in late spring (May)

Table 2
List of all mollusc species encountered (ordered alphabetically), with density and biomass during the month(s) with the lowest and highest numerical densities.

Species	Lowest density month(s)			Highest density month(s)		
	Month(s)	Density (m^{-2})	Biomass (g AFDM/m^2)	Month(s)	Density (m^{-2})	Biomass (g AFDM/m^2)
Bivalvia						
Abra tenuis	5, 9–12	0.0	0.00	6	81.3	0.12
Diplodonta circularis	2	10.6	0.21	6	95.5	0.13
Dosinia isocardia	8	17.7	0.12	9	265.3	0.75
Loripes lucinalis	9	321.8	2.88	3	838.2	7.69
Modiolus sp.	3–4	0.0	0.00	7	148.5	0.55
Paphia dura	1–4, 6–12	0.00	0.00	5	7.1	0.59
Petricolaria gracilis	3	17.7	0.15	10	53.1	0.37
Senilia senilis	7	49.5	37.14	11	116.7	23.61
Tellina distorta	11	7.1	0.02	3	84.9	0.09
Gastropoda						
Bittium reticulatum	2, 5–6, 8–11	0.0	0.00	12	212.2	0.70
Bulla adansoni	2, 6, 8	0.0	0.00	5	31.8	0.24
Clavatula bimarginata	1, 3, 5–7, 9	0.0	0.00	11	7.1	0.44
Columbella rustica	1, 3–12	0.0	0.00	2	3.5	0.01
Crepidula sp.	1, 3–11	0.0	0.00	12	3.5	0.02
Gibberula sp.	3–5, 7–8	0.0	0.00	10	35.4	0.07
Gibbula umbilicalis	4	0.0	0.00	10	159.2	1.94
Hydrobia ulvae	1–2, 4–5, 7–12	0.0	0.00	3	3.5	0.00
Mesalia mesal	3	0.0	0.00	11	70.7	1.10
Nassarius pfeifferi	1–6, 8–12	0.0	0.00	7	10.6	0.10
Prunum amygdalum	2, 4–6, 11	0.0	0.00	10	7.1	0.08
Total	8	675.5	25.57	10	1538.5	30.50

and summer (Aug), whereas highest densities occurred in autumn (Oct).

Reflecting strong recruitment (as evidenced by the sudden occurrence of small, 2–6 mm long specimens in the samples), *Loripes* increased in density from 322 specimens/m^2 in September to 785 specimens/m^2 in October (Fig. 3A). Similarly, *Dosinia* increased from 18 specimens/m^2 in August to 265 specimens/m^2 in September (Fig. 3B), and *Senilia* increased from 50 specimens/m^2 in July to 117 specimens/m^2 in November (Fig. 3C). Two other bivalves that showed peak numbers in summer: *Modiolus* sp. (maximum of 149 specimens/m^2 in July; Fig. 3D) and *Diplodonta circularis*, (maximum 95 specimens/m^2 in June; Fig. 3E), while *Tellina distorta* peaked in spring (maximum 85 specimens/m^2 in March; Fig. 3F) and *Petricolaria gracilis* in autumn (maximum 53 specimens/m^2 in October). The semelid *Abra tenuis* was found in several months but always in low densities that were too low to be able to detect clear seasonal variation. The venerid *Paphia dura* was encountered in May only.

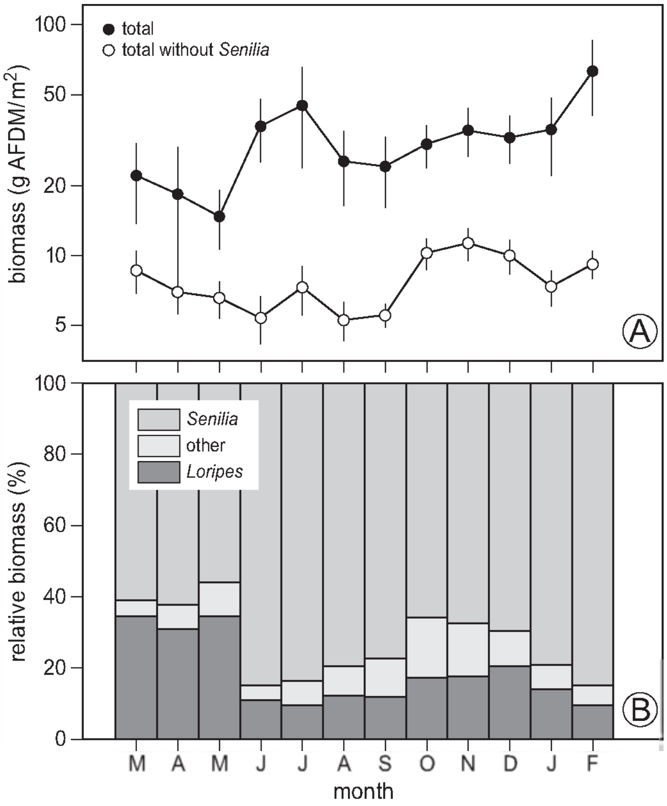

Fig. 2. Seasonal changes in (A) total and total without *Senilia* biomass and in (B) community composition (in biomass terms) of molluscs at Abelgh Eiznaya, Banc d'Arguin, Mauritania, from March 2011 to February 2012.

Numerically, the gastropods represented 12% of the assemblage, with the trochid *Gibbula umbilicalis* (6%) being the only one common enough for us to detect seasonal fluctuations in their numbers (reaching its maximum density in October; Fig. 3G). The turritelid *Mesalia mesal* and the small snail *Bittium reticulatum* contributed 2% each, while the other gastropods contributed even less (<1% each; in decreasing order of abundance: *Gibberula* sp., *Bulla adansoni*, *Clavatula bimarginata*, *Prunum amygdalum*, *Nassarius pfeifferi*, *Columbella rustica*, *Crepidula* sp. and *Hydrobia ulvae*; Table 2).

The depletion model qualitatively matched the pattern of change observed in *Dosinia* and *Loripes* densities (Fig. 4). The initial fivefold decline in *Dosinia* densities (Oct–Mar), followed by a nearly twofold decline in *Loripes* density (Mar–Aug), strongly suggests that predation is the main driver behind these changes, especially predation by molluscivorous red knots which should initially consume thicker-shelled *Dosinia* at a higher rate than the thinner-shelled but poisonous *Loripes*. In other words, the relative contribution of *Loripes* to the red knot's diet should gradually increase as *Dosinia* stocks become depleted, and this is indeed what the benthos data seem to suggest. Testing for the goodness of fit of the data (Oct–Aug) with the depletion model revealed that observed densities do not differ from predicted densities, nor in *Loripes* (log$_{10}$(observed density) $= 0.61 + 0.81 \times$ log$_{10}$(predicted density), $R^2 = 0.65$, $F_{1,9} = 16.7$, $P = 0.003$; intercept does not differ from 0 ($P = 0.29$); slope does not differ from 1 ($P = 0.35$)), neither in *Dosinia* (log$_{10}$(observed density) $= 0.62 + 0.75 \times$ log$_{10}$(predicted

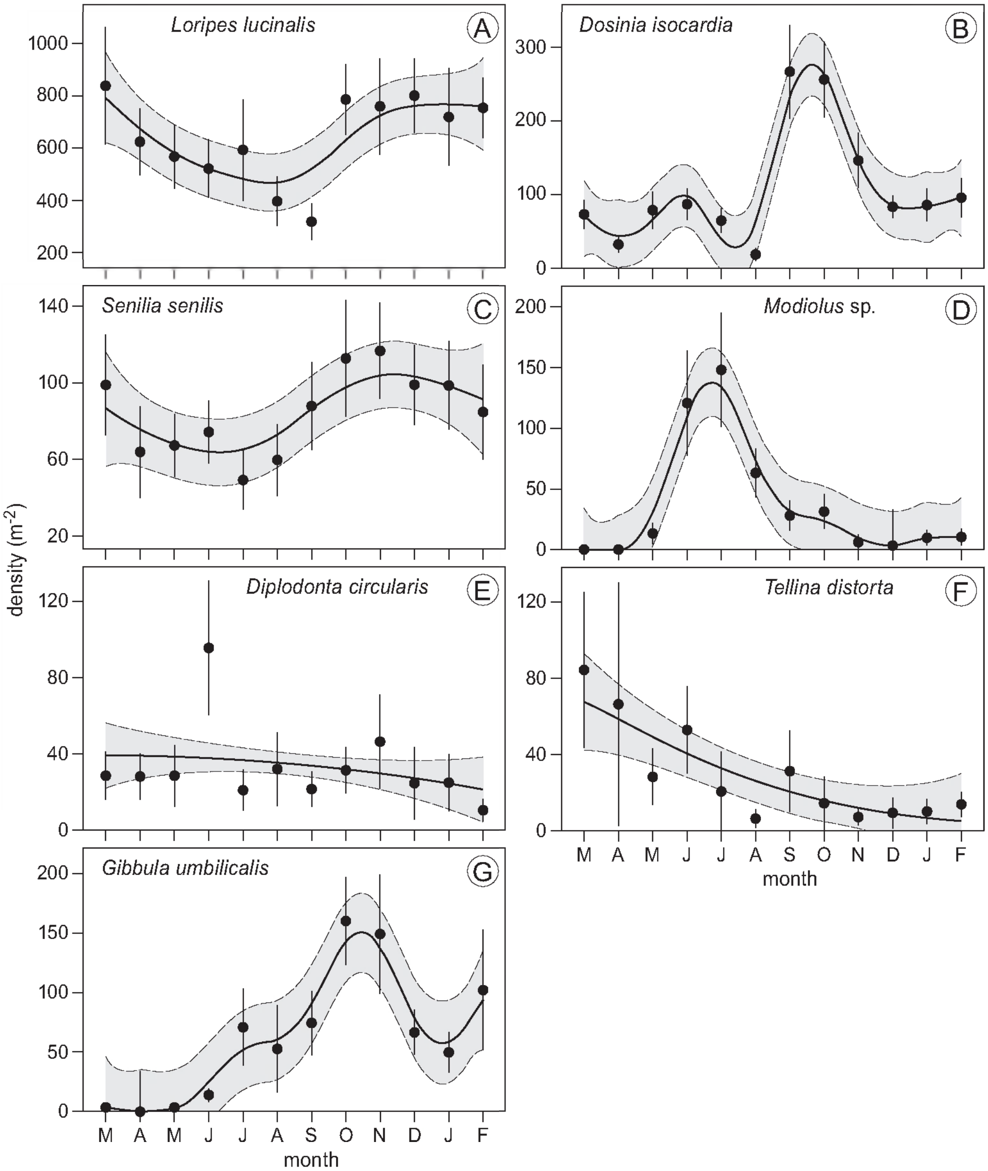

Fig. 3. Seasonal changes in the densities of the seven most common mollusc species at Abelgh Eiznaya, Banc d'Arguin, Mauritania, from March 2011 to February 2012. Dots give means, bars give SE and smoothed lines give GAM fit (solid line) ± 2 SE (dashed lines).

density), $R^2 = 0.54$, $F_{1,9} = 10.5$, $P = 0.01$; intercept does not differ from 0 ($P = 0.15$); slope does not differ from 1 ($P = 0.30$)). These results remained unaffected when we carried out a sensitivity analysis by varying predation pressure V by ±10% (V reduced by 10%: intercepts do not differ from 0 ($P = 0.70$ and 0.15 for *Loripes* and *Dosinia*, respectively), slopes do not differ from 1 ($P = 0.76$ and $P = 0.29$); V increased by 10%: intercepts do not differ from 0 ($P = 0.09$ and 0.15), slopes do not differ from 1 ($P = 0.12$ and $P = 0.32$)).

4. Discussion

In the present study, most (73%) of the mollusc biomass was contributed by *Senilia senilis*. Its relative share lies in the range of 63–85% found earlier for the entire intertidal Banc d'Arguin (Piersma, 1982; Wolff et al., 1993a; selecting molluscs only in these studies). However, its absolute value (24.1 AFDM g/m^2) exceeds previous estimates that ranged from 4.7 to 8.1 g AFDM/m^2 (Piersma, 1982; Wolff et al., 1993a). Biomass densities of the other two abundant bivalves, *Loripes lucinalis* and *Dosinia isocardia*, are also higher than estimates made for the 1980s (5.2 *vs.* 2.6 g AFDM/m^2 in *Loripes* and 0.3 *vs.* 0.1 g AFDM/m^2 in *Dosinia*; Wolff et al., 1993a). However, note that sampling in the 1980s covered an area of about 30,000 ha, while our study area was restricted to about 50 ha only (Fig. 1). Hence, we cannot be conclusive about these differences.

Although numerous benthic studies have now been carried out on the Banc d'Arguin tidal flats (Piersma, 1982; Wolff et al., 1987, 1993a,b; Michaelis and Wolff, 2001; Wolff and Montserrat, 2005; Honkoop et al., 2008; Wolff and Michaelis, 2008; van Gils et al., 2012), this is the first full-year survey of numerical changes in the molluscan assemblages in Banc d'Arguin. However, such year-round studies on seasonality are rare (Beukema, 1974; Wolff and de Wolf, 1977; Dittmann, 2002; de Goeij et al., 2003).

Mollusc biomass and numbers in our study showed considerable seasonal variation. Highest abundances occurred in the autumn and winter months and lowest in spring and summer, with a doubling of total abundance from August to October (Table 2).

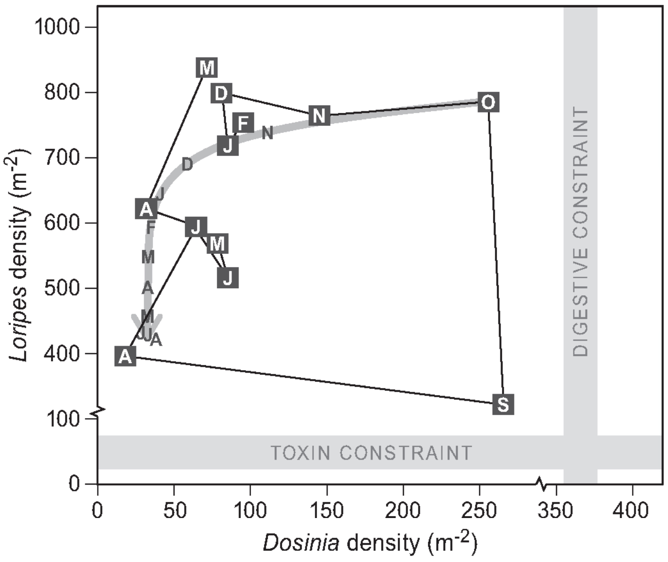

Fig. 4. Biplot of the observed density changes in the two bivalves *Loripes lucinalis* and *Dosinia isocardia* at Abelgh Eiznaya, Banc d'Arguin, Mauritania, from March 2011 to February 2012. Grey line gives the predicted depletion due to predation by red knots from mid-October to mid-August, taking October densities as starting values. Letters on the grey line denote months in the simulation. Vertical and horizontal bars give critical densities above which molluscivorous red knots face a digestive and a toxin constraint, respectively. At these critical densities red knots achieve an intake rate that the birds can just sustain in the long run when it comes to digestive processing and tolerating the toxin load (for details how these critical densities are derived we refer to van Gils et al., 2013). Given the densities found in this study, red knots would only face their toxin constraint and not their digestive constraint.

During the autumn months (September and October), the increase in abundance and species richness of molluscs has been generally related to recruitment events (Hodgson, 2010; van der Geest et al., submitted for publication). This also seems to be the case in our study, as can for example be inferred from the fact that the doubling of total abundance from August to October is accompanied by an increase in total biomass of 19% only. The marginal biomass declines during summer (Jul–Sep; Fig. 2A) are most likely due to high temperatures leading to desiccation (Alongi, 1990) and oxygen-limitation (Ferguson et al., 2013).

In contrast, the steep declines in densities, observed between autumn and spring, are most likely caused by intense predation by shorebirds spending their non-breeding season in large numbers at Banc d'Arguin (and in smaller numbers by young birds during summer; van Dijk et al., 1990). In fact, the observed reduction in biomass (36%; excluding *Senilia*; Fig. 2A) and numbers (45%; again excluding *Senilia*) between October and May parallels the calculations carried out on the basis of shorebird numbers and their energy budgets for tropical intertidal areas (p. 228 in van de Kam et al., 2004). Our findings differed to those of Wolff and Michaelis (2008), who did not find a difference in benthic biomass between autumn and spring. However, as admitted by these authors, their design did not allow discerning between an effect of season and an effect of year, since their autumn sampling was carried out in a different year (1988) than the spring sampling (1986). Furthermore, their comparison included three species of *available* bivalves only. Interestingly, among these three bivalve species, it was *Dosinia* that declined the steepest in their study (by 64%), a result that is in line with our depletion-by-red-knots model.

Finally it is of note that predation takes place on individual prey and hence it may be better to compare numerical densities rather than biomass densities. As predation may lead to competitive release among prey, it may lead to higher *per capita* biomasses and/or growth rates among surviving prey (Gurevitch et al., 2000). As a consequence, total biomass may even increase after predation (de Roos et al., 2007; Schröder et al., 2009). More to the point and being an example of release of *inter*specific competition, it has recently been shown that *Loripes* grows faster when *Dosinia* becomes depleted, presumably because *Loripes* is mixotrophic and also relies partly on the same resources as suspension-feeding *Dosinia* (van Gils et al., 2012; van der Geest et al., submitted for publication). Note that other predators than shorebirds, notably fish, may have also played a role in diminishing mollusc densities. However, although most fish species observed on the tidal flats at high tide feed on benthic fauna (Wolff et al., 2005), our two focal prey species, *Loripes* and *Dosinia*, do not seem to be important as prey species for fish (W.J. Wolff, pers. comm.). Shrimp, another potential predator of molluscs, are also commonly found at the Banc d'Arguin tidal flats (Schaffmeister et al., 2006). However, the size classes fed upon by shrimp are smaller than the size classes considered here (Andresen et al., 2013). Most crabs that occur at Banc d'Arguin are deposit-feeding *Uca* sp. (Wolff et al., 1993a).

More detailed study on the most important avian molluscivore in our study system, the red knot, allows us to explain differences in the seasonal timing of depletion of several species of molluscs. Red knots account for 80% of all predation on molluscs by vertebrates (van Gils et al., 2012), which justifies our focus on this predator of molluscan invertebrates. It has been shown elsewhere that the most important prey for red knots in Banc d'Arguin is *Dosinia* and not the much thinner shelled *Loripes* (van Gils et al., 2012, 2013). Since red knots can only sustain an intake rate of only 0.1 mg AFDM/s on diarrhoea-inducing *Loripes* (Oudman et al., submitted for publication), the depletion rates on this species are relatively low (Fig. 4). Upon arrival from their breeding grounds, red knots in October have the luxury to consume *Dosinia* at a relatively high rate (because of a high *Dosinia* density) and add *Loripes* at a relatively low but constant rate of 0.1 mg AFDM/s. However, by the time that most available *Dosinia* have been depleted (and other small but less abundant non-toxic bivalves), in the second half of winter (Fig. 4), the relative contribution of *Loripes* to the red knot diet increases (but still at the absolute rate of 0.1 mg AFDM/s) and peaks during spring/summer. This seasonal diet shift mimics differences in diet composition between years. In years that *Dosinia* is relatively poor, red knots include relatively much *Loripes* in their diet (65%), while in rich *Dosinia* years the proportion of *Loripes* in the diet levels out to around 20% (Onrust et al., 2013; van Gils et al., 2013).

This deterioration of feeding conditions for molluscivorous shorebirds may explain why fuelling rates of red knots at Banc d'Arguin are relatively low (Piersma et al., 2005). With an intake rate of at most 0.1 mg AFDM/s on *Loripes* only, red knots may find it difficult achieving an intake rate of at least 0.2 mg AFDM/s, which is the required level for fuelling at the Banc d'Arguin (van Gils et al., 2009). Thus, carrying capacity of tropical intertidal ecosystems for migratory shorebirds may be set by the spring food densities that remain after a long winter of intense predation by shorebirds exerted on molluscs.

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