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Trophic cascade induced by molluscivore predator alters pore water biogeochemistry via competitive release of prey

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Abstract Effects of predation may cascade down the food web. By alleviating interspecific competition among prey, predators may promote biodiversity, but the precise mechanisms of how predators alter competition have remained elusive. Here we report on a predator-exclosure experiment carried out in a tropical intertidal ecosystem, providing evidence for a three-level trophic cascade induced by predation by molluscivore red knots (*Calidris canutus*) that affects pore water biogeochemistry. In the exclosures, the knots' favorite prey (*Dosinia isocardia*) became dominant and reduced the individual growth rate in an alternative prey (*Loripes lucinalis*). *Dosinia*, a suspension-feeder, consumes suspended particulate organic matter (POM), whereas *Loripes* is facultative mixotroph, partly living on metabolites produced by sulfur-oxidizing chemoautotrophic bacteria, but also consuming suspended POM. Reduced sulfide concentrations in the exclosures suggest that without predation on *Dosinia*, stronger competition for suspended POM forces *Loripes* to rely on energy produced by endosymbiotic bacteria, thus leading to an enhanced uptake of sulfide from the surrounding pore water. As sulfide is toxic to most organisms, this competition-induced diet shift by *Loripes* may detoxify the environment, which in turn may facilitate other species. The inference that predators affect the toxicity of their environment via a multi-level trophic cascade is novel, but we believe it may be a general phenomenon in detritus-based ecosystems.

Key words: Bivalves, exclosure, facilitation, growth rate, hydrogen sulfide, interspecific competition, predation, seagrass, shorebirds, top-down effect, toxicity, trophic cascade.

INTRODUCTION

In the current biodiversity crisis, predators have often been the ones disappearing first (Byrnes et al. 2007): they are lowest in number (Purvis et al. 2000) and most sensitive to habitat fragmentation (Srivastava et al. 2008), but are nevertheless overfished (Myers and Worm 2003) and overhunted (Johnson et al. 2007). As predators often play key roles in the structuring and organisation of ecological communities (Chase et al. 2002), species loss may accelerate after the highest trophic levels in a food web have disappeared (Duffy 2003, Estes et al. 2011). Therefore, in order to predict future shifts in food webs, it is critical to get a better understanding of the cascading top-down role that predators play in ecosystems (Heithaus et al. 2008, Terborgh and Estes 2010).

Although predation is detrimental for those prey individuals being killed, predation may be beneficial for the surviving individuals. This is because, by reducing the number of prey, predators may alleviate the competition for space and resources among those prey individuals that remain. Under some conditions, such predator-mediated competitive release may promote species-coexistence (Paine 1966), but negative or no effects of predation on prey species-coexistence have also been claimed (Chase et al. 2002). Much depends on whether the prey compete for the same resources, whether they are able to exploit alternative resources under stringent competition, and whether they are fed upon by generalist or specialist predators or by predators using an intermediate strategy.

The extinction of one of two competing prey species can best be prevented by predators that are neither full specialists nor full generalists, but rather exhibit some intermediate form of polyphagy (Vandermeer and Pascual 2006). This matches earlier conclusions that predators switching diet promote prey coexistence (Murdoch 1969). More generally, it can be stated that *adaptive* behaviour by predators enhances the stability in systems where otherwise one prey

species outcompetes another (Fryxell and Lundberg 1997). By contrast, unless there are as many specialist predator species as there are competing prey species, fully specialized predators cannot maintain prey coexistence in a bistable competitive system (Schreiber 1997). On the opposite side of the spectrum, generalist predators that show no preference for one species over the other can under no condition stabilize a two-species bistable system (Hutson and Vickers 1983). This is because generalist predation leads to apparent competition between two prey species, meaning that the increase in one prey species enhances the predation pressure on the other prey by supporting a larger predator density, which eventually could lead to extinction of the latter prey species – even if prey do not compete for the same resources (Holt and Lawton 1994).

For a prey facing competitive exclusion there is one way out: it should switch to alternative resources. Thus, if prey coexistence is maintained by predation, and if those predators are removed from the system, we may expect the competitively weaker prey to switch resources (provided it has the machinery to do so). Though generalist-specialist competition has since long puzzled ecologists (see review by Abrams 2006), the impact of predation on this form of competition has barely received empirical attention. Furthermore, and this holds in general for predator-mediated coexistence, rather little empirical work has been performed on the actual mechanisms at the level of the *individual* prey (Gurevitch et al. 2000). There are some well-known examples of how predators affect the abundances of their prey *and* the prey's resources (Estes and Palmisano 1974, Ripple and Beschta 2004), but how such three-level trophic cascades feedback into the *performance* of individual prey remains to be investigated.

In this paper we try to contribute by testing for the effects of predation on bivalves by a molluscivore shorebird, the red knot (*Calidris canutus canutus*). We do so in a large-scale field experiment in a tropical intertidal ecosystem, Banc d'Arguin (Mauritania), which is the main wintering area for this subspecies of red knot (Piersma 2007). In this area, two species stand out

as the most abundant and most suitable prey for red knot. These are *Dosinia isocardia* (Dunker, 1845), a specialist suspension-feeding venerid bivalve and *Loripes lucinalis* (Lamarck, 1818), a lucinid bivalve which is believed to suspension-feed, but which, to a large extent, obtains its nutrition through a symbiosis with chemoautotrophic bacteria living inside its gills (Johnson et al. 1994). These bacteria obtain their energy by oxidizing sulfide (H_2S), which is produced by sulfate reducers during anaerobic degradation of organic matter. In seagrass beds, the dominant and preferred habitat for red knots in our study area (Altenburg et al. 1982), these two species together make up 72% of all molluscs, 79% of all bivalves and even 85% of all ingestible bivalves (Honkoop et al. 2008). Based on the total number of shorebirds wintering at Banc d'Arguin (Zwarts et al. 1998), their diets and their energy requirements, red knots should be responsible for about 80% of all mollusc-consumption by vertebrate predators in Banc d'Arguin. Over a period of a full year, we locally excluded knots from their prey using exclosures. Besides measuring the effects of predation on biomass densities of both prey, we quantified the effects on growth rate in *Loripes* and on changes in one of its resources, sulfide. The depletion trajectories of these two bivalve species can tell us whether red knots are generalist or specialist predators on these prey.

Are red knots specialist or generalist predators?

In general, plotting so-called 'depletion trajectories' enables exploring the diet strategy applied by the predator (Brown and Mitchell 1989) (Fig. 1). In a simple one-predator two-prey system, a specialist predator will only feed on a single prey (type 1) and deplete its densities towards a critical, so-called giving-up density (GUD; horizontal line in Fig. 1a) (Brown 1988).

By contrast, a generalist will feed on both prey species and will give up feeding at a certain combination of both prey densities (diagonal line in Fig. 1b)¹ (Holt and Kotler 1987).

In this framework, regressions of GUD against initial prey density (IPD) should be diagnostic for the diet strategy applied by the predator (Fig. 2). Considering the specialist predator and the prey that it specializes on, GUD will be constant and independent of IPD above a certain IPD (Fig. 2a), whereas GUD and IPD will be similar in the prey type that it ignores (Fig. 2b). Hence, there will be no relation between the GUD on prey type 1 and the GUD on prey type 2 (Fig. 2c; comparable to Fig. 1a). By contrast, in the generalist predator there will be much variation in the GUD on prey type 1 (Fig. 2d) as well as on type 2 (Fig. 2e), variation that is unrelated to a prey type's IPD. GUDs on prey type 1 will relate negatively to the GUDs on prey 2 (Fig. 2f; comparable to Fig. 1b).

On the basis of functional response parameters and quitting harvest rates (QHR) we can predict GUDs for both an imaginary specialist knot and a generalist knot. Red knots obey Holling's type II functional response (Piersma et al. 1995). By rearranging this well-known equation, we arrive at the GUD (#/m²) on the prey that the specialist knot feeds on:

$$\text{GUD} = \frac{\text{QHR}}{ea - \text{QHR}ah} \quad (1),$$

where e is the average energy contents per available prey, a is searching efficiency and h is handling time. Rearranging Holling's type II on two prey types (Brown and Mitchell 1989), we see that in the generalist knot, the GUD on *Dosinia* (GUD_D) depends on the GUD on *Loripes* (GUD_L) (and *vice versa*):

$$\text{GUD}_D = \frac{\text{QHR}}{e_D a - \text{QHR}ah} - \frac{\text{GUD}_L(e_L a - \text{QHR}ah)}{e_D a - \text{QHR}ah} \quad (2),$$

¹ Note that intermediate strategies, not considered here, do exist. For example, predators can switch from being specialist to becoming a generalist, a strategy coined 'the expanding specialist' (Heller 1980).

with e_D and e_L representing the average energy contents per available prey of respectively *Dosinia* and *Loripes* and assuming a and h to be similar in both species. On the basis of direct measurements on metabolic rates of actively foraging red knots (Piersma et al. 2003) and daily foraging times (van Gils et al. 2007), it has been estimated that knots feeding in Banc d'Arguin require a minimum intake rate of 0.2 mg ash-free dry mass (AFDM_{flesh}) per second in order to maintain a balanced energy budget (van Gils et al. 2009), which we will take as QHR. Functional response parameters for red knots feeding in seagrass habitat have recently been quantified experimentally (de Fouw & van Gils, unpubl. data): $a = 4 \text{ cm}^2/\text{s}$, $h = 1 \text{ s}$. Estimates for e_D and e_L were derived from benthic sampling results presented below (respectively 2.57 and 7.28 mg AFDM_{flesh}). As these are GUDs on the *available* part of the food supply, we need to correct for the fraction available (0.73 in *Dosinia* and 0.70 in *Loripes*; derived from benthic sampling results presented below) to get to *total* GUDs. Next, in order to express the total *numerical* GUDs as total *biomass* GUDs we need to take account the average AFDM_{flesh} per prey (equivalent to e_L in *Loripes* and 2.95 mg in *Dosinia* which is slightly larger than e_D as some size classes of *Dosinia* are too large to be ingested).

MATERIALS AND METHODS

Exclosures

In October 2009, we placed 112 exclosures, equally divided over 7 tidal flats in the vicinity of the scientific station of Parc National du Banc d'Arguin (PNBA) at Iwik (19° 53.0' N; 16° 17.7' W). Each exclosure consisted of 8 PVC-poles (0.5 m long), which were inserted vertically in the sediment (to a depth of 0.4 m) and aligned in a square of 1 m². A nylon rope was pulled through a hole in the top of each pole and acted as a 10-cm high fence. Such a simple construction has provided effective in the past in keeping out shorebirds from small-scale plots

(van Gils et al. 2003). About half of the exclosures (N = 57) did not survive the whole year until the end of the experiment. Sometimes exclosure poles were washed out by the tide, or crabs had made burrow structures around the poles resulting in a large puddle inside the exclosure. These exclosures (and their paired controls) were removed from further analyses.

Prey density

In October 2010, we sampled bivalve densities in order to study the effects of predation on prey density. One sample was taken in the middle of each exclosure, and one paired sample (the control) was taken outside each exclosure, 2.5 m away from the exclosure sample (random direction). Within the framework of depletion trajectories presented above (Fig. 2), we consider exploited prey densities in the controls as giving-up densities and unexploited prey densities in the exclosures as ‘initial’ prey densities, even though the latter cannot be considered as *true* initial densities at the time exclosures were placed. Dispersal, recruitment and non-predatory mortality may have changed the densities within the exclosures throughout the year. However, assuming similar changes have also taken place in the controls (i.e. assuming those changes to be density-independent), our approach to study effects of predation by comparing exclosures with their paired controls seems valid.

Each benthic sample constituted a sediment core (ø 15 cm), taken to a depth of 20 cm and sieved over a 1-mm mesh. The upper 4 cm was sieved separately from the rest of the core in order to distinguish accessible from inaccessible prey (red knots have bills of about 3.5 cm long). Top and bottom samples were also used to collect *Loripes* individuals that were calcein-stained to estimate growth rate (details given below). In the laboratory, we measured lengths (to nearest 0.1 mm) of all individuals and AFDM_{flesh} of a subset of individuals. The latter was done by separating flesh from shell and drying it for three days at 60 °C. Next, dried flesh was weighed

(to nearest 0.1 mg) and incinerated for 5 hours at 550 °C, subsequently ash mass was determined (to nearest 0.1 mg). The resulting AFDM_{flesh}[g]-length[mm] relationships (*Dosinia*: AFDM_{flesh} = $10^{-5.05}L^{3.07}$, N = 166, R² = 0.96, P < 0.001; *Loripes*: AFDM_{flesh} = $10^{-4.73}L^{2.96}$, N = 191, R² = 0.95, P < 0.001) were used to predict AFDM_{flesh} for the remaining individuals that were not incinerated, which enabled us to express species-specific total biomass densities (i.e. top and bottom layer pooled).

Prey growth rate

We used the technique of calcein staining to determine bivalve growth rates (van der Geest et al. 2011). Calcein is a fluorescent marker that bivalves incorporate into their shells upon ingestion and can be made visual by illuminating the shell with UV light under a fluorescence microscope. Growth can then be determined as the maximum growth axis between the calcein mark at the exterior of the shell (i.e. the calcareous layer deposited when calcein was administered) and the ventral margin (i.e. the latest calcareous layer, deposited just before collecting the bivalve). The technique was validated for *Loripes lucinalis* (van der Geest et al. 2011), to which we refer for further details (note that in this paper *L. lucinalis* is called *L. lacteus*; recent taxonomic insights have led to this nomenclature change; R. von Cosel, pers. comm.).

Calcein was administered in October 2009, at the moment exclosures were placed. During low tide, a PVC ring (ø 30 cm, height 15 cm) was pushed 10 cm into the sediment in each exclosure and its control. This ‘basin’ was then filled up by 0.5 l of calcein solution (containing 0.1 g calcein). As the next high tide would flush the solution, we again filled up the basin next day with a similar solution in order to make sure that the bivalves were exposed long enough to the marker. Next day PVC rings were removed. One year later, in October 2010,

samples of the calcein-stained individuals were collected by taking one core inside and one core outside the enclosure, exactly at the spot where calcein was administered the year before (the middle point between two short PVC sticks placed 1.5 m apart marked the control spot). These samples were also used to estimate prey densities (explained above).

Previously we showed that about 35% of all *Loripes* individuals treated with a similar concentration of calcein as we used has a clear, measurable calcein mark when recollected three months after marking (van der Geest et al. 2011). Unfortunately, and for yet unknown reasons, no clear measurable calcein marks could be detected in *Dosinia* shells. Hence, we have no estimates of growth rates for this species.

We fitted Von Bertalanffy's growth function to our data, a commonly used equation when modeling indeterminate bivalve growth. In this function, growth rate $\frac{dH_t}{dt}$ declines with an increase in size H_t in the following way:

$$\frac{dH_t}{dt} = k (H_{\infty} - H_t) \quad (3),$$

where H_{∞} is the mean maximum size and k is the growth constant. For each individual *Loripes* we estimated k by defining $\frac{dH_t}{dt}$ as the difference in shell height between 2010 and 2009, H_t as shell height in 2009 and H_{∞} as 11 mm (van der Geest & van Gils, unpubl. data). As there is some individual variation around H_{∞} we performed a sensitivity analysis with respect to the value of H_{∞} . To deal with pseudoreplication (due to having multiple *Loripes* per enclosure) we used a linear mixed-effect model with a random intercepts for each enclosure-control pair using the *nlme* package in *R*. We selected only those pairs of which we had growth estimates from both the enclosure and its control (N = 10 pairs).

At the end of the experiment, October 2010, we determined pore water sulfide concentrations in the exclosures and their controls. We collected pore water samples at three different depths (0-4 cm, 4-8 cm, 8-12 cm), using 60 ml vacuum syringes connected to ceramic moisture samplers (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). Total pore water sulfide concentrations (4 ml) were measured immediately, after returning at the field station, with a mixture of 50% sample and 50% Sulfide Anti-Oxidation Buffer (SAOB), using an ion-specific silver-sulfide electrode (following Lamers et al. 1998). Sulfide measurements were only carried out on a random subset of exclosures and their paired controls ($N_{\text{pairs}} = 21$; we could only import a limited amount of SAOB into Mauritania).

Faecal analysis

In order to confirm the degree of diet specialization by red knots we collected samples of their faecal droppings. This was done at onset of the exclosure experiment, i.e. October 2009. In total, we collected 17 dropping samples (more or less equally divided over the 7 tidal flats), each consisting of 40 droppings on average ($SE = 3$), which were stored in the freezer. Back in The Netherlands, samples were dried for 3 days at 60 °C, subsequently we determined dry mass DM_{drop} of those fragments that retained on a 300- μm sieve, separately for both species (Dekinga and Piersma 1993). Next, heights of all intact hinges were measured in order to reconstruct species-specific consumed size distributions, enabling us to calculate the species-specific average dry shell mass $\overline{DM_{\text{shell}}}$ of a consumed prey (Dekinga and Piersma 1993). For this purpose we used regression coefficients of $DM_{\text{shell}}[\text{g}]-\text{length}[\text{mm}]$ relationships that were determined on specimens collected in Banc d'Arguin in January 2011 (*Dosinia*: $DM_{\text{shell}} = 10^{-3.43} L^{2.63}$, $N = 124$, $R^2 = 0.96$, $P < 0.001$; *Loripes*: $DM_{\text{shell}} = 10^{-4.19} L^{3.25}$, $N = 119$, $R^2 = 0.96$, $P < 0.001$; Onrust *et al.* unpubl. data). In a recent calibration study on red knots it was shown that

about 65% of the ingested DM_{shell} is found back as DM_{drop} , both for *Dosinia* as well as for *Loripes* (Onrust *et al.*, unpubl. data). Therefore, N_{diet} , the number of prey items per species per sample is given by $DM_{\text{drop}} / (0.65 \cdot \overline{DM_{\text{shell}}})$.

At the same time, in order to relate diet composition resulting from the faecal analysis to available food stocks at that time, we collected benthic samples. In total, we collected 224 samples, of which half were taken just next to each enclosure (at a distance of 1 m), while the other half was taken at a distance of 25-100 m away from each enclosure. We used the same methodology as described above. We used only prey items that were both accessible and ingestible to calculate $N_{\text{available}}$, the average number of available prey items per species per sample per tidal flat (all *Loripes* size classes are ingestible, while only *Dosinia* < 13.2 mm can be ingested (based on Zwarts and Blomert 1992)).

We applied Ivlev's index (I) to express prey preference (Jacobs 1974). For a given prey species, it compares its relative fraction in the diet F_{diet} with its relative fraction in the available food supply $F_{\text{available}}$ in the following manner: $I = (F_{\text{diet}} - F_{\text{available}}) / (F_{\text{diet}} + F_{\text{available}})$. Hence, I ranges from -1 to 1, with $I > 0$ indicating preference and $I < 0$ indicating aversion. Taking *Dosinia* (D) as an example, its contribution to the diet $F_{\text{diet},D}$ relative to *Loripes* (L) is given by: $N_{\text{diet},D} / (N_{\text{diet},D} + N_{\text{diet},L})$. Similarly, $F_{\text{available},D}$, the relative contribution of *Dosinia* to the available food supply equals $N_{\text{available},D} / (N_{\text{available},D} + N_{\text{available},L})$. Diet and availability data were linked at the level of tidal flats.

RESULTS

Depletion trajectories

There was a weak but significant relationship between the total *Dosinia* densities in the controls (i.e. the GUDs) and the total *Dosinia* densities in the enclosures (i.e. the IPDs; Fig. 2g; y

= $0.66 + 0.12x$, $F_{1,53} = 4.71$, $P < 0.05$). However, in addition to good feeding sites this analysis included poor feeding sites containing few prey attractive to red knots. After excluding sites at which exclosure densities were below the predicted specialist GUD of 0.85 g/m^2 , the correlation between GUD and IPD disappeared ($y = 0.80 + 0.09x$, $F_{1,27} = 1.06$, $P = 0.31$). Leaving out the non-significant slope from this latter model yields an intercept that is larger than 0 (estimate \pm SE = 1.13 ± 0.21 , $P < 0.001$), which suggests that *Dosinia* densities were depleted to a constant, non-zero GUD (cf. Fig. 2a). This intercept does not differ from the predicted specialist GUD ($t = 1.37$, $P = 0.18$).

There was a strong and significant correlation between the total *Loripes* densities in the controls (i.e. the GUDs) and the total *Loripes* densities in the exclosures (i.e. the IPDs; Fig. 2h; $y = 1.42 + 0.76x$, $F_{1,53} = 89.59$, $P < 0.001$). The slope of this relationship was significantly lower than 1 ($F_{1,53} = 9.10$, $P < 0.005$), but not when forcing it to go through the origin ($F_{1,54} = 1.06$, $P = 0.31$). The correlation remained significant, even when selecting only data for which densities in the exclosure exceeded the predicted specialist GUD of 0.73 g/m^2 ($y = 0.51 + 0.85x$, $F_{1,20} = 62.38$, $P < 0.001$). This result suggests that predation on *Loripes* was marginal (cf. Fig. 2b).

The slope of the regression between the total densities in the controls (GUDs) of *Dosinia* and those of *Loripes* did not differ from 0 (Fig. 2i; $y = 0.93 - 0.01x$, $F_{1,53} = 0.07$, $P = 0.79$), which corroborates the prediction for a specialist predator on *Dosinia* (Fig. 2c) and refutes the prediction for a generalist predator (Fig. 2f).

Faecal analysis

Comparing the relative proportions of *Dosinia* and *Loripes* in the diet with those available in the field yielded a clear result (Fig. 3). *Dosinia* was much preferred over *Loripes* ($t = 6.5$, $df = 15$, $P < 0.001$), with the Ivlev index for *Dosinia* being larger than 0 ($t = 7.0$, $df = 15$, $P <$

0.001), indicating a significant preference and an Ivlev index being smaller than 0 for *Loripes* ($t = -3.4$, $df = 16$, $P < 0.005$), indicating a significant aversion. Note, however, that the Ivlev index for *Dosinia* is smaller than 1 ($t = -3.6$, $df = 15$, $P < 0.005$), while it is larger than -1 for *Loripes* ($t = 18.0$, $df = 16$, $P < 0.001$); this indicates that *Loripes* was not entirely ignored by red knots during the experiment.

Prey growth rate

Loripes grew 12% faster in the controls than in the exclosures (Fig. 4; $k_{\text{control}} = 0.66$, $k_{\text{exclosure}} = 0.58$, $t = 2.89$, $P < 0.005$, $N_{\text{pairs}} = 10$, $N_{\text{Loripes}} = 105$). The significance of this outcome was insensitive to the assumed value of H_{∞} across a wide range of values for H_{∞} (8.7-30.2 mm), reaching much beyond the natural range of H_{∞} (10-12 mm; van der Geest & van Gils, unpubl. data).

Sulfide

Sulfide concentrations of the pore water were lower in the exclosures than in the controls, but only so in the deepest layer of 8-12 cm. Here, concentrations were reduced by 70% (Fig. 5; $N_{\text{pairs}} = 21$). A linear mixed-effect model with random intercepts showed the following depth-dependent estimates for \log_{10} -transformed $\text{H}_2\text{S}_{\text{exclosure}}/\text{H}_2\text{S}_{\text{control}}$ ratios: 0-4 cm: 0.01 ($t = 0.04$, $P = 0.97$); 4-8 cm: 0.14 ($t = 0.58$, $P = 0.57$); 8-12 cm: -0.51 ($t = -2.11$, $P < 0.05$). It is the deepest layer that had the highest natural sulfide concentrations (288.8 μM vs. 98.4 μM in the 4-8 cm layer and 17.6 μM in the 0-4 cm layer; estimated by random-intercept mixed-effect model on controls only).

DISCUSSION

In our study, red knots showed a strong preference for *Dosinia* over *Loripes* (Figs. 2-3). In fact, on the basis of the exclosure results alone, we may conclude that knots behaved as specialists, largely ignoring *Loripes* and depleting *Dosinia* to a constant giving-up density. The fact that the observed GUD on *Dosinia* matched with the predicted GUD when feeding on *Dosinia* only ($0.85 \text{ g AFDM}_{\text{flesh}} \text{ m}^{-2}$), strongly supports the idea that red knots almost fully relied on *Dosinia* as their food source. Only at the beginning of our experiment, in October 2009, it seems that *Loripes* featured more in the diet of knots. This suggestion is based on the results of the dropping analyses, in which the Ivlev index on *Loripes* is significantly above -1 (Fig. 3). A value of -1 means full ignorance; the observed mean of -0.16 (SE = 0.05) suggests aversion but not full ignorance. Most likely, knots had to include *Loripes* in their diet in 2009 as *Dosinia* was then much less abundant, occurring in densities below the minimal GUD (mean \pm SE = $0.5 \pm 0.1 \text{ g AFDM}_{\text{flesh}} \text{ m}^{-2}$, N = 112, which represents only those sites where resampled in 2010), than one year later, in October 2010 ($1.2 \pm 0.1 \text{ g AFDM}_{\text{flesh}} \text{ m}^{-2}$, N = 112). Overall, by taking also the dropping analyses into account, we may conclude that knots behave as so-called ‘expanding specialists’ (Heller 1980), meaning that that they do accept alternative prey such as *Loripes* in times of scarcity of their favorite prey *Dosinia* (van Gils et al. submitted).

Initially, the preference of *Dosinia* over *Loripes* came as quite a surprise to us. Relative to their shell mass *Dosinia* contains 2-3 times less meat than *Loripes* (using regression equations given earlier for $\text{AFDM}_{\text{flesh}}$ and DM_{shell}), and it is well-established that red knots prefer prey with high meat/shell ratios (van Gils et al. 2005). Only recently have we been able to grasp the knot’s aversion for this energy-rich prey. Feeding trials showed that captive red knots offered a mono-specific diet of *Loripes* developed diarrhea and were less eager to continue eating (Oudman et al. submitted). Due to the sulfur-based metabolism in *Loripes* it is very likely that the diarrhea is due to a sulfide-release in the knot’s digestive tract once *Loripes*-meat is being digested. It has

been shown that pigs *Sus domesticus* develop diarrhea and lose weight when on a sulfide-rich diet (Wetterau et al. 1964). Furthermore, shallow-water fishes and crabs deterred feeding when offered prey which were collected in sulfide-rich deep-sea hydrothermal vents, presumably due to the high sulfide concentrations inside these prey (Kicklighter et al. 2004).

In spite of a relatively low predation pressure on *Loripes*, we did find an effect of predation on this species: *Loripes* experiencing predation grew faster than those without predation (Fig. 4). Possibly, *Loripes* benefited from the depletion of *Dosinia* stocks, which would imply some sort of competition between *Loripes* and *Dosinia*. Even though *Loripes*' principle source of energy stems from the oxidation of sulfide by endosymbiotic bacteria living inside its gills, mixotrophy has been observed in *L. lucinalis* (Johnson et al. 1994) and in other members of the Lucinidae family (Duplessis et al. 2004, Dufour and Felbeck 2006), especially during periods of gonad development (Le Pennec et al. 1995). In general, lucinids do have a functional, though reduced, digestive system (Allen 1958) in which particles of phytoplanktonic origin have been found (Le Pennec et al. 1988), suggesting the ability for this family to be mixotrophic. Possibly, *Loripes* relies on diatoms and suspended particulate organic matter (POM) when pore water sulfide concentrations are low. *Vice versa*, when suspended POM availability declines, *Loripes* needs to rely more and more on sulfide. We propose that the latter mechanism explains our results: by excluding knots, *Dosinia* was able to flourish, increase in numbers and use much of the available suspended POM. Hence, *Loripes* experienced reduced food intake, leading to retarded growth, which it could partly compensate by increase its use of sulfide, hence the observed decline in pore water sulfide concentrations inside the exclosures (Fig. 5). This proposed mechanism can be captured in a simple Holling type II functional response model on two resources, as exemplified in Figure 6. There is ample evidence for interspecific competition among suspension-feeding bivalves (e.g. Peterson and Black 1987,

Jonsson et al. 2005). Especially when flow velocities of the water column are low, suspension-feeders can deplete their own and their neighbors' resources on the small scale of centimeters (Herman et al. 1999). Dense seagrass meadows in particular are able to strongly attenuate currents and waves (Larkum et al. 2006), which makes the competition for suspended POM at the seagrass-covered tidal flats of Banc d'Arguin very probable. Consistent with this point of view, a recent analysis of 8 consecutive years of benthos sampling in our study area showed a suggestive negative correlation between densities of *Loripes* and *Dosinia* (Pearson's $r = -0.79$, $P < 0.05$, $N = 8$; van Gils et al. submitted).

Alternatively, the lower sulfide concentration inside the exclosures may be enhanced by the bioturbation caused by high *Dosinia* densities. It is known that suspension- and deposit-feeding leads to bioturbation, such as recently shown in a closely related species, *Dosinia discus* (Gingras et al. 2008). However, if this was the mechanism behind the sulfide decline, then we would have expected this decline to be strongest in the top 4 cm layer in which most suspension-feeding *Dosinia* live (70-80%; this study). In contrast, we only saw changes in the deepest, sulfide-richest layer (Fig. 5), an observation that matches well with the mechanism proposed in the previous paragraph.

However, with *Loripes* being the most likely reason for the changes in the deepest layer, one would expect *Loripes* in the exclosures to have moved to this sulfide-richest layer. This was not the case (percentage of individuals that lived in top-4 cm layer: 70% in controls vs. 73% in exclosures, $t = 0.50$, $P > 0.6$, based on the 48 out of 55 exclosure-control pairs that contained *Loripes*). However, lucinids and closely related thyasirids are able to 'mine' sulfide from deep anaerobic sulfide-rich sediment layers using their superextensile foot (up to 30 times the length of their shell; Dufour and Felbeck 2003). In this way, *Loripes* is able to exploit sufficient sulfide

while at the same time remaining relatively close to the sediment surface, which makes it easier to take up enough oxygen and compete for the remaining suspended POM with *Dosinia*.

Whatever the precise mechanism, the exclusion of molluscivore predators seems to cascade down to the level of pore water biogeochemistry by reducing sulfide concentrations. Three-level trophic cascades have been found before in coastal marine ecosystems, starting with the seminal paper by Estes and Palmisano (1974), then coined cascades by Paine (1980), and recently reviewed by Terborgh and Estes (2010) and Estes et al. (2011), the latter including top-down effects on biogeochemical cycles. The finding that predators affect the biogeochemical cycle of sulfide appears novel. Yet, it may be a general phenomenon in detritus-based ecosystems where sulfide is produced by the anaerobic decomposition of organic material. Though the exclusion of knots works out negatively for *Loripes*, as reflected by reduced shell growth rates, it may be beneficial to other organisms as high sulfide concentrations are known to be toxic to both plants and animals (Bagarinao 1992). However, this short-term effect of excluding predation by shorebirds may juxtapose long-term effects. In the absence of predation, the lower *Loripes* growth rates may lead to hampered reproduction in *Loripes*, eventually leading to a *Loripes* population decline and extinction – a form of competitive exclusion due to an overall increase in predation-free *Dosinia*. This will likely have the opposite effect to pore water biogeochemistry, leading to increased levels of sulfide as there would be no *Loripes* present to keep sulfide concentrations low. This would hamper most organisms living in the seagrass-covered tidal flats, including the seagrass itself. For example, a recent indoor experiment showed that seagrass grew better in the presence of *Loripes* due to *Loripes* reducing sulfide concentrations (van der Heide *et al.* submitted). Molluscivore shorebird populations are in steep decline worldwide (Piersma 2007, Delany et al. 2009). Often this is due to habitat loss at their temperate-zone stopovers, and not so much due to situations at their southern wintering grounds

(van Gils et al. 2009, Kraan et al. 2010). Thus, by affecting shorebird numbers in the temperate zone, we may affect the ecosystem state in relatively pristine and untouched tropical wintering grounds. We realize this scenario is hypothetical and we hope that it remains this way.

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- 579
580

[Figure captions:]

FIG. 1. (a) Specialist predators only feed on a single prey type and will deplete it down (arrows) to a fixed giving-up density GUD (horizontal line). (b) By contrast, generalist predators feed on multiple prey types, in the present case two. Both prey types will be depleted down to a combination of GUDs (diagonal line), depending on the initial prey densities (dots; which are equivalent to those in (a)). Depletion trajectories are straight whenever searching efficiencies are similar on both prey types. Grey lines are drawn to guide the eye. Note that in generalist predation, higher initial prey densities in one prey type will lead to lower GUDs in the other prey type; a short-term form of apparent competition (Holt and Kotler 1987).

FIG. 2. (a) A specialist predator will deplete prey type 1 down to a fixed GUD_1 , leaving patches unexploited when $IPD_1 < GUD_1$. (b) It will not feed upon prey type 2, hence $GUD_2 = IPD_2$. (c) Therefore, GUD_1 is constant and independent of GUD_2 . (d) A generalist predator will feed on both types and hence GUD_1 is not constant but depends on the density of prey type 2. (e) Likewise, GUD_2 depends on the density of prey type 1. (f) Therefore, GUD_1 and GUD_2 co-vary negatively in the generalist predator. (g) GUDs on *Dosinia* (biomass densities in controls) were low and constant relative to IPDs (biomass densities in exclosures); (h) GUDs on *Loripes* were not different from IPDs; (i) GUDs on *Dosinia* densities were not correlated with GUDs on *Loripes*.

FIG. 3. Diet selectivity at the onset of the exclosure experiment, October 2009, by means of faecal analyses. There was a clear preference for *Dosinia* (Ivlev index > 0) and a clear aversion of *Loripes* (Ivlev index < 0).

605

606 FIG. 4. *Loripes* grew faster in the controls than in the exclosures, as shown here by boxplots of
607 individual Von Bertalanffy's growth constants k .

608

609 FIG. 5. Sulfide concentrations were lower in the exclosures than in the controls, but only so in
610 the sulfide-richest deepest layer (8-12 cm). Plotted are means \pm SE of the ratio between sulfide in
611 the exclosure and in the paired control, with the dashed line representing the prediction of no
612 difference between exclosure and control.

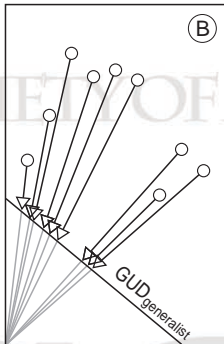
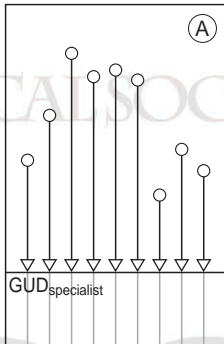
613

614 FIG. 6. Possible mechanism of how *Loripes* may experience hampered growth in the absence of
615 predation on *Dosinia*. Without predation, *Dosinia* densities will be higher, and hence suspended
616 POM availability will be lower. Assuming that in *Loripes* the consumption of suspended POM is
617 mutually exclusive with the utilization of sulfide, the absolute use of sulfide will increase when
618 suspended POM availability decreases, although total consumption rate (suspended POM and
619 sulfide), and hence growth rate, will decline.

SPECIALIST

GENERALIST

density prey type 1

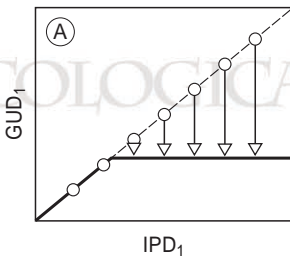
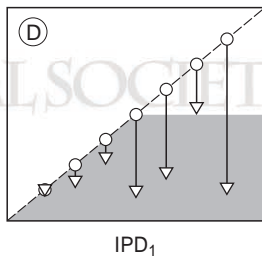
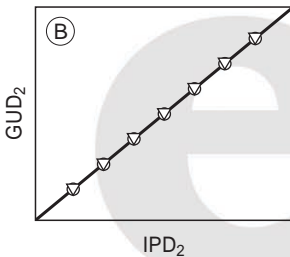
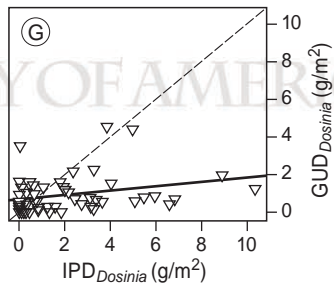
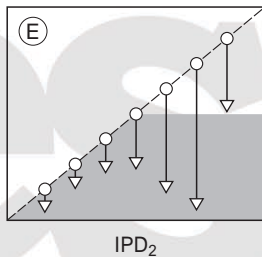
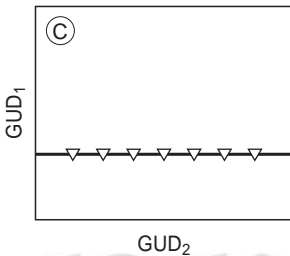
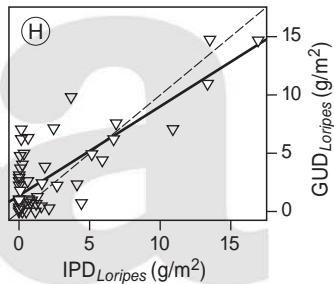
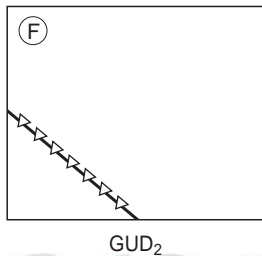


density prey type 2

SPECIALIST

GENERALIST

DATA

 IPD_1  IPD_1  IPD_2  IPD_2  GUD_2  GUD_2 