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Food web consequences of an evolutionary arms race: molluscs subject to crab predation on intertidal mudflats in Oman are unavailable to shorebirds

Roeland A. Bom[1,2*], Jimmy de Fouw[1,3,4], Raymond H. G. Klaassen[4,5], Theunis Piersma[1,6], Marc S. S. Lavaleye[1], Bruno J. Ens[4,7], Thomas Oudman[1], Jan A. van Gils[1]

1 Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

2 Remote Sensing and GIS Center, Sultan Qaboos University, P.O. Box 33, Al Khod PC 123, Oman

3 *Department of Aquatic Ecology and Environmental Biology, Institute for Water and Wetland Research, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands*

4 Foundation Working Group International Waterbird and Wetland Research (WIWO). P.O. Box 6521, 6503 GA Nijmegen, The Netherlands

5 Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, P.O. Box 11103, 9700 CC Groningen. The Netherlands & Dutch Montagu's Harrier Foundation, P.O. Box 46, 9679 ZG, Scheemda, The Netherlands

6 Chair in Global Flyway Ecology, Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

7 Sovon Dutch Centre for Field Ornithology, Sovon-Texel, P.O. Box 59, 1790 AB Den Burg (Texel), The Netherlands

***Corresponding author**

Email address: Roeland.Bom@nioz.nl

Telephone: 0031222369541

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Abstract

Aim: Molluscivorous shorebirds supposedly developed their present wintering distribution after the last ice age. Currently, molluscivorous shorebirds are abundant on almost all shores of the world, except for those in the Indo-West Pacific (IWP). Long before shorebirds arrived on the scene, molluscan prey in the IWP evolved strong anti-predation traits in a prolonged evolutionary arms race with durophagous predators including brachyuran crabs. Here, we investigate whether the absence of molluscivorous shorebirds from a site in Oman can be explained by the molluscan community being too well defended.

Location: The intertidal mudflats of Barr Al Hikman, Oman.

Methods: Based on samples from 282 locations across the intertidal area the standing stock of the macrozoobenthic community was investigated. By measuring anti-predation traits (burrowing depth, size and strength of armour), the fraction of molluscs available to molluscivorous shorebirds was calculated.

Results: Molluscs dominated the macrozoobenthic community at Barr Al Hikman. However, less than 17% of the total molluscan biomass was available to shorebirds. Most molluscs were unavailable either because of their hard-to-crush shells, or because they lived too deep in the sediment. Repair scars and direct observations confirmed crab predation on molluscs. Although standing stock densities of the Barr Al Hikman molluscs were of the same order of magnitude as at intertidal mudflat areas where molluscivorous shorebirds are abundant, the molluscan biomass available to shorebirds was distinctly lower at Barr Al Hikman.

Main conclusions: The established strong molluscan anti-predation traits against crabs precludes molluscan exploitation by shorebirds at Barr Al Hikman. This study exemplifies that dispersal of ‘novel’ predators is hampered in areas where native predators and prey exhibit strongly developed attack and defence mechanisms, and highlights that evolutionary arms races can have consequences for the global distribution of species.

INTRODUCTION

Marine molluscs have evolved their defence mechanisms under the selective pressure imposed by durophagous (shell-destroying) predators (Vermeij 1977a). Fossil records show the long evolutionary time over which this took place. During this period, molluscs strengthened their shell armour by increasing their shell thickness, and by the development of spines, ribs and/or nodules. At the same time, durophagous predators became better shell crushers, peelers, drillers and/or splitters (Vermeij 1976, 1977b, 1978, 1987). These observations led to the seminal idea that molluscan prey and durophagous predators have been, and currently are, engaged in an evolutionary arms race in which molluscs continuously evolve their defence mechanisms to adapt to their durophagous predators, which (in turn) continuously evolve their attack mechanisms (Vermeij, 1994; Dietl & Kelley, 2002).

Evolutionary arms races between molluscs and durophagous predators are most notable in tropical oceans, probably because higher ambient temperatures enabled higher calcification rates in molluscs, and more metabolic activity in durophagous predators (Vermeij, 1977b; Zipser & Vermeij, 1978). Within the tropical oceans, the Indo-West Pacific (IWP) has been recognized as an area where evolutionary arms races have been especially intense. Specifically, in the IWP molluscs have the hardest to crush shells, and durophagous crabs and fishes have the strongest claws and the strongest shell-crushing abilities (Vermeij, 1976, 1977b, 1987, 1989; Palmer, 1979). It has been hypothesized that the evolutionary arms race between molluscs and their predators in the IWP has prospered from a long history of co-evolution and escalation, low extinction rates, high nutrient availability, and high environmental stability (Vermeij, 1974, 1978, 1987; Roff & Zacharias, 2011; Kosloski & Allmon, 2015).

Although molluscs dominate many of the intertidal macrozoobenthic communities in the IWP (Piersma *et al.*, 1993a; Keijl *et al.*, 1998; Purwoko & Wolff, 2008; Fig. 1), these same intertidal mudflats lack a substantial number of molluscivorous shorebirds (Piersma, 2006; Fig. 1). Many of world's molluscivorous shorebirds are long-distance migrants, travelling between arctic and boreal breeding areas and temperate and tropical wintering grounds. The IWP is well within the flight range of the breeding areas of several molluscivorous shorebirds, including Eurasian oystercatcher (*Haematopus ostralegus,* hereafter: oystercatcher), great knot (*Calidris tenuirostris*) and red knot (*Calidris canutus*). However, most oystercatchers and great knots migrate to areas outside the IWP (Delany *et al.,* 2009; Conklin *et al.,* 2014), while red knots are absent from the IWP (Piersma, 2007), except for one area in northwest Australia (Tulp & de Goeij, 1994; Conklin *et al.,* 2014).

The fossil record shows that molluscs and the first durophagous predators, including crabs and fishes, developed their defence and attack mechanisms during the Mesozoic Marine Revolution in the Jurassic or earliest Cretaceous (Vermeij, 1977a, 1987; Walker & Brett, 2002; Harper, 2003; Dietl & Vega, 2008; Fig. 2). Shorebirds (Charadriiformes) appeared during the late Cretaceous between 79 and 102 Mya. Lineages of the currently known molluscivorous shorebirds diverged from other Charadriiformes lineages around 20 Mya (Paton *et al.*, 2003; Baker *et al.*, 2007; Fig. 2), whereas the current migratory flyways (Fig. 1) were established after the last Ice Ages, about 20 kyr (Buehler & Baker 2005; Buehler *et al.* 2006; Fig. 2). With the molluscan anti-predation traits evolving before the appearance of molluscivorous shorebirds, it could be that the relative scarcity of molluscivorous shorebirds within the IWP is a consequence of relatively intense and long-lasting evolutionary arms races in the IWP – arms races that have rendered the heavily defended molluscs unavailable to shorebirds.

Here, we investigate whether the absence of molluscivorous shorebirds from the intertidal mudflats of Barr Al Hikman in the Sultanate of Oman (Fig. 1, site 1) can be explained by molluscs being too well defended, because they have been, and remain subject to durophagous predation. We compare our results with molluscan communities on intertidal sites where molluscivorous shorebirds are abundant, and use these results to make inferences about the IWP as a whole.

MATERIALS AND METHODS

Study Area

Barr Al Hikman (20.6° N, 58.4° E) is a peninsula of approximately 900 km², located in the central-eastern Sultanate of Oman (Fig. 3a) and bordering the Arabian Sea. Seaward of the coastline an area of about 190 km^2 of intertidal mudflats is divided into three subareas: Shannah, Khawr Barr Al Hikman, and Filim (Fig. 3b, c). Over 400,000 nonbreeding shorebirds visit the area in winter (de Fouw *et al.* 2017), making it one of the most important wintering sites for shorebirds in the IWP (Delany *et al.,* 2009; Conklin *et al.* 2014). The oystercatcher and the great knot are the only molluscivorous shorebirds in the area. In 2008 their midwinter numbers were estimated at 3,900 and 360 respectively (de Fouw *et al.* 2017, Appendix S1), thus comprising about 1% of the shorebird population at Barr Al Hikman. The area is relatively pristine, with only a few local industries, including salt mining and some, mainly offshore, fisheries. There is no harvesting of shellfish in the area.

Macrozoobenthos standing stock assessment

The standing stock of the macrozoobenthic community, the potential food source for shorebirds, was sampled in January 2008 at 282 sampling stations (Fig. 3c, d). These stations were arranged in nine 250-m grids across the three subareas (Fig. 3c, d). Each grid comprised four rows perpendicular to the coastline. On the mudflat at Filim, one grid was limited to one row and another to two rows (Fig. 3c). Grids were aligned perpendicular to the coastline because variation within macrozoobenthic communities is often related to tidal height

(Honkoop *et al.,* 2006). The chosen inter-sampling distance of 250 m reflects the trade-off between spatial resolution and logistic feasibility. No additionally randomly located stations were sampled (as suggested by Bijleveld *et al.* 2011 and applied by Compton *et al.* 2013), because the aim of the study was not to extrapolate density estimates to unsampled locations. The chosen design of a fixed inter-sampling distance would give a biased estimation of the macrozoobenthic densities if the macrozoobenthic distributions were to show patterns at a regular distance as well (250 m in this case). However, earlier work at intertidal mudflats shows that such a pattern is unlikely to exist (Kraan *et al.* 2009).

All 282 sampling points were visited on foot during low tide. A sample consisted of a single sediment core with a diameter of 12.7 cm. The core was divided into an upper (0 – 4 cm) and a lower layer (4 – 20 cm, see below for explanation). These layers were separately sieved through a 1-mm mesh. Samples were brought to a field laboratory, where they were stored at relatively low temperatures. Next, within two days after collection, macrozoobenthic animals (i.e. all benthic animals larger than 1 mm in size) were sorted out and stored in a 6% borax-buffered formaldehyde solution. Later, at NIOZ, each organism was identified to taxonomic levels ranging from phylum to species. Taxonomic names are in accordance with those listed in the World Register of Marine Species (WoRMS, http://www.marinespecies.org/).

Each organism was measured to the nearest 0.1 mm. From a subsample, biomass expressed as ash-free dry mass (AFDM) was obtained by drying the samples at 55°C for a minimum of 72 hours, followed by incineration at 560°C for 5 hours. Prior to incineration, the bivalves' shells were separated from their soft tissue to make sure only flesh and no calcium carbonate was burned. Gastropods and crustaceans were incinerated without separating soft tissue from shell or exoskeleton. As applied by van Gils *et al.* (2005a), it is assumed that 12.5% of organic matter resided in the hard parts of gastropods and hermit crabs (living in the shells of gastropods), and 30% in crustaceans other than hermit crabs. The relation between AFDM and shell length was fitted with non-linear regression models using the software program R (R Development Core Team, 2013) with the package *nlme* (Pinheiro *et al.*, 2011). The *varPower* function was used to correct for the variance in biomass that increased with size. Significant regression models were derived for 18 species (see Table 1 for molluscs) which were used to predict AFDM for 4,885 specimen. For species for which no significant regression model could be derived (due to low sample size), a direct measure of AFDM was used if available (864 individuals), and species-specific average AFDM values otherwise (198 individuals).

The average overall (i.e. for the entire intertidal area) numerical density (# m^{-2}) and biomass density (g AFDM m^{-2}) was calculated by statistically weighting the contribution of each grid to the average according to the size of the area that it represents. The standard deviations of these means were also calculated by statistically weighting each grid according to its size. The size of the area that each grid represents was calculated with Voronoi polygons using QGIS (QGIS Development Team 2013).

Anti-predation traits

Predation opportunities for shorebirds on molluscs are hampered by anti-predation traits in molluscs. Such anti-predation traits include: (1) burrowing depth (Zwarts & Wanink, 1993), (2) size (Zwarts & Wanink, 1993), and (3) shell armour (Piersma *et al.*, 1993b). The extent to which anti-predation traits actually affect predation opportunities for shorebirds depends on the size and foraging method of a given shorebird species. In this study, the oystercatcher, the great knot and the red knot were taken as reference species as these are well-studied species, and which are abundant on intertidal mudflats outside of the IWP. The available biomass was calculated for each species separately as the fraction of the molluscan biomass that is accessible, ingestible and breakable.

Burrowing depth

When probing the mud, shorebirds can only access molluscs that are buried within the reach of their bill. Oystercatchers can probe to a depth of 9 cm (Sarychev & Mischenko, 2014), great knots to 4.5 cm (Tulp & de Goeij, 1994), and red knots to 4 cm (Zwarts & Blomert, 1992). Burrowing depth of bivalves was measured in two ways. During the sampling campaign in 2008 the core was divided into two layers (0 – 4 cm and 4 – 20 cm) to distinguish the accessible from inaccessible food for red knots (Zwarts & Wanink, 1993). To quantify the accessible and inaccessible part for great knots and oystercatchers, five sampling stations at the east coast of Shannah were visited again in April 2010. At each sampling point, a sediment sample was taken and then cut into transverse slices of 1 cm. From these samples, the exact burrowing depth of each encountered bivalve was measured to the nearest cm (Piersma *et al.*, 1993a). The average percentage biomass density of bivalves found per 1 cm slice was then calculated. Gastropods were always found in the top 4 cm of the sediment.

Size

Great knots and red knots swallow their molluscan (bivalves and gastropods) prey whole. A mollusc can only be ingested up to a certain size, as indicated by its circumference (Zwarts & Blomert, 1992). By and large, great knots can ingest roundly-shaped bivalves up to 28 mm across and more elongated bivalves with a shell length up to 36 mm (Tulp & de Goeij, 1994). Red knots can ingest roundly-shaped bivalves up to 16 mm across and more elongated bivalves with a shell length up to 29 mm (Zwarts & Blomert, 1992; Tulp & de Goeij, 1994). At Barr Al Hikman all bivalves above 16 mm appeared to be roundly-shaped venerids to which the for great knots and red knots ingestible limits of respectively 28 mm and 16 mm can be applied. Whether a gastropod can be ingested by great knots and red knots depends both on the size and shape of the gastropod. Most likely, elongated gastropods can be swallowed more easily than rounded ones. Oystercatchers do not face constraints on size as they open the molluscs (they eat bivalves only) with their bill (Swennen, 1990).

The length of each sampled organism was measured to the nearest 0.1 mm. From these measurements, the percentages of molluscs were calculated that are within the above mentioned ingestion thresholds for great knots and red knots, respectively.

Breaking force

After swallowing, great knots and red knots crush their molluscan prey in their gizzard. Red knots can generate forces up to 40 N in their gizzard (Piersma *et al.*, 1993b, note that in this paper breaking force was erroneously expressed two orders of magnitude too low), which is taken as the border between breakable and non-breakable prey items (thereby ignoring the possibility that the slightly larger great knot can generate somewhat higher forces within their larger gizzards). To quantify the strength of the molluscan shell armour, the forces needed to break the shells of the abundant mollusc species were measured with an Instron-like breaking-force device described by Buschbaum *et al.* (2007). The breaking force device works by placing a mollusc between two plates on top of a weighing scale, after which the pressure on the upper plate is gently increased with a thread spindle until the shell crushes. Molluscivorous shorebirds crush shells in a similar way (Piersma *et al.*, 1993b). The lower plate is connected to a balance which measures the maximum exerted weight to crush a shell. After calibration, this measure can be converted to a measure of force (to the nearest 0.1 N) (Buschbaum *et al.*, 2007).

Breaking force was measured in alcohol-preserved molluscs, collected alive in March 2015 and crushed a month later. Alcohol-stored bivalves require the same forces to crush as freshly collected ones (Yang *et al*., 2013). Breaking force was measured for the 10 most abundant (in terms of biomass density) molluscs, except for the tellinid *Jitlada arsinoensis*, the trochid *Priotrochus kotschyi* and the venerid *Marcia recens,* for which the samples did not contain enough specimens. To predict the breaking force for each sampled mollusc, the relation between break force and shell length was fitted with non-linear regression models, similar to the biomass-length regression models. For the gastropods *Mitrella blanda* and *Salinator fragilis* the linear regression was not significant, but the linear model was (Table 1). Neither linear nor non-linear regressions were significant for *Cerithium scabridum,* and hence the species-specific mean was used. For *J. arsinoensis* the regression model of the similar *Nitidotellina* cf. *valtonis* was used, and for *M. recens* the regression model of the similar *Callista umbonella*.

Repair scars

A widely used way to assess if a molluscan community is subject to crab predation is to check molluscs for repair scars, which they form after unsuccessful peeling or crushing by crabs (Vermeij 1993; Cadée *et al.,* 1997). Here, the eight most abundant molluscs found at Barr Al Hikman were checked for repair scars. Molluscs were collected alive in January 2009 and checked for repair scars under a microscope. The repair frequency was defined as the number of individuals having at least one repair divided by the total number of inspected molluscs (Cadée *et al.,* 1997).

RESULTS

Standing stock

A total of 5,947 macrozoobenthic specimens were collected, which yielded 64 distinct taxa of which 27 were identified to species level (Appendix S2). Table 2 presents the numerical density (individuals per m^2) and the biomass density (g AFDM/m^2) per taxonomic group for the entire sampled area (see Appendix S2 for AFDM measures per taxon and per sub-area). The average numerical density for the total area was 1,768 animals per m^2 and the biomass density was 19.7 g AFDM per m^2. More than 99% of the numerical and biomass densities were comprised of gastropods, bivalves, crustaceans, and polychaetes, with gastropods (64%) and bivalves (25%) dominating the biomass. Crustaceans (5%) and polychaetes (5%) were less abundant. At the species level, three species clearly stood out in terms of biomass density: the gastropods *Pirenella arabica* and *Cerithium scabridum* (Fig. 4a) and the bivalve *Pillucina fischeriana* contributed 44%, 16% and 18% to the total biomass density, respectively. Numerical density was dominated by *P. fischeriana* with 40% (Appendix S2). In 10% of the samples, no benthic organisms were found (Fig. 3). Table 1 presents the biomass densities of the most abundant molluscs.

Anti-predation traits and food availability for shorebirds

Burrowing depth

In the samples taken in 2008, 75% of the bivalve biomass was found in the bottom layer (Table 1). Sampling in April 2010 confirmed this result. Fig. 5a shows the results of the 2010 sampling, with the average percentage of bivalve biomass density plotted against the burrowing depth. Lines show the maximum depth to which molluscivorous shorebirds have access. Based on the samples collected in 2010, oystercatchers, great knots and red knots can access 61%, 35% and 25% of the bivalve biomass, respectively.

Size

In total, 90% of the bivalve biomass was found in shells smaller than 28 mm and 65% of the biomass in shells smaller than 16 mm (Table 1, Fig. 5b). All gastropods were smaller than 30 mm (Fig. 6a, Table 1). All abundant gastropods (Table 1) were found to be elongated, meaning that most likely all gastropods were ingestible by great knots and red knots.

Breaking force

16% of the total molluscan biomass was breakable (< 40 N). 51% of the total bivalve biomass was breakable (Fig. 5c, Table 1) and less than 1% of the gastropod biomass (Fig. 6b, Table 1).

Total available biomass density

For oystercatchers, the available molluscan biomass density (all accessible bivalves) was 3.0 g AFDM/m^2 (63% of the total bivalve biomass density and 17% of the total molluscan biomass density). For great knots, the available molluscs is comprised of all bivalves and gastropods that are accessible, ingestible and breakable. As 1% of the total gastropod biomass (12.71 g AFDM/m^2) was breakable, and as all gastropods were accessible and ingestible to great knots, the available gastropod biomass density equals 0.1 g AFDM/m^2. For bivalves, out of the total bivalve biomass (4.95 g AFDM/m^2), 35% was accessible, 90% ingestible, and 51% breakable. This means that the available bivalve biomass density was 0.8 g AFDM/m^2 (16% of the total bivalve biomass density, thereby ignoring a potential size-depth relation). Thus, the total available molluscan biomass density for great knots was 0.9 g AFDM/m^2 (4% of the total molluscan biomass density). The same calculation for red knots arrives at an available gastropod biomass density of 0.1 g AFDM/m^2, and an available bivalve biomass density of 0.4 g AFDM/m^2 (8% of the total bivalve biomass density). Thus, the total available molluscan biomass density for red knots was 0.5 g AFDM/m^2 (3% of the total molluscan biomass density).

Repair scars

Repair scars were observed in all checked species of gastropods (Table 1, Fig. 4b). Between species, the repair frequency varied between 4 and 26%. All scars were interpreted as jagged "can-opener" breaks which crossed growth lines, which was most likely the result of predation attempts by crabs (Vermeij, 1978, 1993; Cadée *et al.,* 1997), except for one borehole scar in a specimen of *C. scabridum*. One specimen of *P. arabica* had two repair scars, all the others had either one or zero. No repair scars were observed in bivalves.

DISCUSSION

Molluscan communities of intertidal mudflats compared

The macrozoobenthic community of Barr Al Hikman was dominated by molluscs, comprising 89 % of the total biomass density (64% gastropods, 25% bivalves). However, most of this potential food source was unavailable to molluscivorous shorebirds. Predation opportunities for shorebirds on gastropods were hampered by the shell armours of gastropods: only 1% of the total gastropod biomass was breakable (Fig. 6). Also bivalves were largely unavailable to shorebirds, mainly because they were either too deeply burrowed or too hard to break: for great knots and red knots 16% and 8% of the total bivalve biomass density was available, respectively. Conversely, for oystercatchers, that open bivalves before ingestion, 63 % of the total bivalve biomass density was available.

A comparison of the available molluscan biomass on intertidal areas around the world (at least for those for which detailed data were available) shows that Barr Al Hikman has the lowest average density of molluscs available to red knots (Fig. 1 & Fig. 7, Table 3, Appendix 3). Without discounting the unavailable prey, the average total density of molluscs at Barr Al Hikman was close to the average total density values of molluscs measured at other intertidal mudflats (Piersma *et al.*, 1993a; Dittmann, 2002; Table 3), meaning that there is little available molluscan biomass density because molluscs at Barr Al Hikman are relatively well defended. A direct comparison of the anti-predation traits in molluscs confirms this: The bivalves at Barr Al Hikman were among the hardest measured (Appendix S3) and the fraction of bivalves that was in the upper 4 cm of the sediment in Barr Al Hikman was among the lowest reported for any intertidal area (Table 3).

The data in Table 3 does not allow to compare the intra-site variation, which is known to exists in biomass densities (Beukema, 1976), prey sizes and burrowing depths (Zwarts & Wanink, 1993), and may cause the actual average mollusc densities to differ slightly from our estimates (Table 3). Yet, the estimated differences are so strong that they augment the idea that molluscivorous shorebirds are nearly absent from Barr Al Hikman because molluscs at this site are relatively well defended.

It is of particular interest to further investigate the absence of red knots from Barr Al Hikman. Currently, red knots breed on the Taimyr Peninsula, Russia, due north of Barr Al Hikman. After breeding, these red knots do not migrate to Barr Al Hikman (6,000 km from the breeding areas), but fly much further, mainly to the Banc d'Arguin in Mauritania (more than 9000 km; see Fig. 1; Piersma 2007). The intertidal mudflats of Banc d'Arguin are at the same latitude as Barr Al Hikman, meaning that climatic conditions cannot explain why red knots skip Barr Al Hikman. At both sites, species of the venerid and lucinid families are the most abundant bivalves; at Banc d'Arguin these bivalves are the main prey for red knots (van Gils *et al.* 2016). A comparison of the anti-predation traits in both families shows that bivalves were better defended at Barr Al Hikman (Fig. 7, Table 3, Banc d'Arguin data from Piersma *et al.* 1993a; Yang *et al.*2013; see Appendix S4 for accompanying statistics). As a consequence, the available molluscan biomass density at Barr Al Hikman was only 15% of that at Banc d’Arguin (Table 3). This again points to food availability as the reason for red knots to skip Barr Al Hikman, and head to Banc d’Arguin instead.

Molluscs at Barr Al Hikman subject to durophagous predation

It can be expected that the molluscs at Barr Al Hikman have been and are subject to strong predation pressure, as molluscs will only show costly morphological and behavioural defences when they are exposed to strong predation pressure. This is the case both on an evolutionary timescale (Dietl & Kelley, 2002; Bijleveld *et al*. 2015) and on the level of individual development (Appleton & Palmer, 1988; Zaklan & Ydenberg, 1997; Griffiths & Richardson, 2006). Several durophagous predators occur in Oman, including crabs, fishes, lobsters, stomatopods, starfish, sea anemones, gastropods and birds (Randall, 1995; Khorov, 2012; de Fouw *et al.* 2017). The established strong anti-predation traits could have evolved in response to either of them (Vermeij 1977a, Gregory *et al.*, 1979; Gray *et al.*, 1997). However, considering the usual trade-off with food intake, prey are not expected to evolve costly morphological or avoidance defences when predation risk is low (de Goeij & Luttikhuizen, 1998, Dietl & Kelley, 2002). Therefore, it is unlikely that the observed anti-predation mechanisms evolved in response to the few molluscivorous shorebirds that are around. It is more likely that they have evolved in response to brachyuran crabs and molluscivorous fish (sharks and rays), as both are abundant in the waters of Oman (Randall, 1995; Khorov, 2012). Repair scars were found in all gastropods species, providing evidence that molluscs at Barr Al Hikman are subject to crab predation (Table 1, Figure 4). Abundant crabs in Barr Al Hikman, including the giant mangrove crab (*Scylla serrata*) and the blue swimming crab (*Portunus segnis*), are known to feed on the heavily armoured *Cerithidea* and *Pirenella* gastropods (Wu & Shin, 1997, pers. obs. RAB). As no repair scars were found in bivalves, it remains unknown whether bivalves are currently exposed to crab predation or whether they simply never survive predation attempts (Leighton 2002). Given that bivalves are easier to break than gastropods (Figs. 5 & 6), it is possible that crabs will always succeed in breaking their shell armour. Fish do not leave marks on the shells of neither bivalves nor gastropods after a failed breaking attempt (Vermeij 1993). Further study, perhaps on shattered shell remains, must show the potential extent of mollusc predation by fish at Barr Al Hikman.

Indo-West Pacific

Vermeij (1976, 1977b, 1978) exclusively used data collected from rocky shores to show that molluscs in the IWP are relatively well defended, apparently due to a prolonged and intense arms race with durophagous predators. Our study shows that these findings can now be extended to at least one intertidal mudflat area. It remains to be seen whether molluscs at other intertidal mudflat areas in the IWP are similarly well-defended (for sites in the IWP where molluscs are abundant, see Piersma *et al.*, 1993a; Keijl *et al.*, 1998; Purwoko & Wolff, 2008; Fig. 1, sites 4, 9, 10, 11). North-West Australia's mudflats are the only intertidal mudflat areas in the IWP where mollusc anti-predation traits have been measured (Fig 1, site 4, Table 3). These are also the only intertidal areas in the entire IWP where molluscivorous shorebirds are abundant (Tulp & de Goeij, 1994; Conklin *et al.,* 2014), perhaps because the bivalves found at these sites are an exception to the rule that molluscs in the IWP are difficult to break. Indeed, although bivalves were found relatively deeply burrowed (Tulp & de Goeij, 1994), shell-mass data suggested that the bivalves in this area were relatively easy to break (van Gils *et al*. 2005b). Again this is in accordance with the idea that that the distribution of molluscivorous shorebirds in IWP can be explained by the strength of the defence mechanisms of the local molluscan communities.

Concluding remarks

Whether dispersing organisms can persist in regions beyond their native range largely depends on their attack and defence mechanisms relative to the traits found in their new communities (Vermeij, 1978). Thus, it is unlikely that novel predators will successfully disperse to areas where predators and prey exhibit strongly developed attack and defence mechanisms due to an evolutionary arms race (Vermeij, 1978). This explains why molluscivorous shorebirds are nearly absent from Barr Al Hikman: exploitation of molluscs by shorebirds at Barr Al Hikman may be precluded by molluscan anti-predation traits that were established long before the dispersal of modern shorebirds along the world's shorelines (Fig. 2). We conclude that our study is a novel illustration of Vermeij's (1978, 1987) proposition that evolutionary arms races can have consequences for food-web structure and for the global distribution of species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1: Shorebirds at Barr al Hikman

Appendix S2: Macrozoobenthic densities per taxon

Appendix S3: Break force-length relation for different bivalve prey

Appendix S4: Statistics accompanying Fig. 7.

Data Accessibility

Data is available upon request

BIOSKETCH

The research team of Prof Piersma and Dr van Gils studies how the numbers and distribution of migratory shorebirds are influenced by the intertidal resource landscape, predators, climate and the historical-genetic background, globally and locally. The team combines experiments, precise field observations and the latest tracking technology to understand processes that underlie the distribution and movements of shorebirds. An overarching aim is to understand how shorebirds are able to annually migrate through seemingly very different environments, which, modified by human activities, are currently changing at an unprecedented rate.

Author contributions: RAB, JdF., RHGK, TP, BJE, and JAvG. conceived the ideas; RAB, JdF, RHGK, ML, TO, and JAvG collected the data; RAB and TO analysed the data; and RAB and TP led the writing.

Editor: Alistair Crame

TABLES AND FIGURES

Table 1. Information on the most abundant molluscs found at Barr Al Hikman.

Species with family	**biomass density g AFDM/m^2 (±SD)**	**% < 16 mm**	**% < 28 mm**	**% in top 4 cm**	**% <40 N**	**non-linear model $Y = aX^b$ Y = AFDM (g) X = length (mm)**		**non-linear model $Y = aX^b$ Y = breaking force (N) X = length (mm)**		**Repair scars**	
						a	**b**	**a**	**b**	**n**	**% scars**
Bivalves											
Callista umbonella (Veneridae)	0.34 (± 1.07)	0	0	0	0	0.012	2.81**	3.55	1.32**		
Jitlada arsinoensis (Tellinidae)	0.16 (± 0.35)	100	100	24	100	0.034	2.23**			16	0
Marcia recens (Veneridae)	0.43 (± 0.54)	0	2	98	1	0.016	2.74**	3.55	1.32**	6	0
Nitidotellina cf. *valtonis* (Tellinidae)	0.07(± 0.09)	100	100	87	100	0.011	2.63**	0.16	1.50*		
Pelecyora ceylonica (Veneridae)	0.29 (± 0.42)	10	100	57	10	0.005	2.98**	0.07	2.33*	5	0
Pillucina fischeriana (Lucinidae)	3.62 (± 3.88)	100	100	17	72	0.005	3.38**	1.72	1.40**	64	0
Gastropods											
Cerithium scabridum (Cerithiidae)[1]	3.22 (± 2.55)	40	100	100	0	0.029	2.39**	378.58	0	39	21
Mitrella blanda (Columbellidae)[2]	0.09 (± 0.11)	100	100	100	0	0.032	2.27**	0.02	17.90**	6	17
Nassarius persicus (Nassariidae)	0.47 (± 0.24)	71	100	100	0	0.064	2.26**	0.15	1.13**	23	4
Pirenella arabica (Potamididae)	8.58 (± 4.42)	13	100	100	1	0.002	3.55**	0.36	2.33**	68	11
Priotrochuss kotschyi (Trochidae)	0.14 (± 0.14)	100	100	100	?	0.266	1.92**				
Salinator fragilis (Amphibolidae)[2]	0.04 (± 0.07)	100	100	100	100	0.027	2.68**	-4.73	1.09*		

[1] break force - length model was not significant, average values used instead

[2] break force - length model was not significant, linear model ($Y = a + bX$) used instead

** $p < 0.001$ * $p < 0.05$

Table 2. Average numerical density and biomass density (±SD) for the taxonomical macrozoobenthic groups at Barr Al Hikman.

Group	Taxonomic level	Numerical density (#/m²)	Biomass density (g AFDM/m²)
all benthos		1767.79 (± 975.81)	19.72 (± 8.70)
Anthozoa	class	3.02(± 4.03)	0.01 (± 0.02)
Bivalvia	class	787.20(± 701.77)	4.95 (± 3.56)
Crustacea	subphylum	259.57 (± 218.03)	0.99 (± 0.79)
Echinodermata	phylum	0.81 (± 1.62)	0.01 (± 0.02)
Gastropoda	class	476.89 (± 384.79)	12.71 (± 7.14)
Insecta	class	8.43 (± 21.54)	0 (± 0)
Plathyhelminthes	phylum	2.97 (± 1.91)	0.01 (± 0.01)
Polychaeta	class	226.91 (± 136.62)	1.00 (± 0.66)
Priapulida	class	1.20 (± 1.78)	0.03 (± 0.09)
Scaphopoda	class	0.80 (± 1.81)	0 (± 0)

Table 3. Total molluscan biomass and available molluscan biomass for red knots on a number of wintering and stopover sites and information on the most abundant (potential) prey items. In Alaska (USA), information was collected for the rock sandpiper (*Calidris ptilocnemis*), which is a similar sized molluscivorous shorebird as the red knot. Based on their size and abundance, *Pillucina fischeriana* and *Pelecyora ceylonica* can be regarded as the most likely candidate prey for red knots at Barr Al Hikman.

#	country	area	total molluscan biomass density (g AFDM/m^2)	available biomass (g AFDM/m^2)	most abundant (potential) molluscan prey items	% small molluscs in upper 4 cm	% breakable small molluscs	Reference
1	Oman	Barr Al Hikman	17.7	0.5	*Pillucina fischeriana* *Pelecyora ceylonica*	17% 57%	58% 100%	this study
2	Mauritania	Banc d' Arguin	4.8	3.4	*Loripes orbiculatus* *Pelecyora isocardia*	44% 49%	100% 100%	Piersma *et al.*, 1993a
3	China	Bohai Bay	4.5	> 3.2	*Potamocorbula laevis*	100%	100%	Yang *et al.,* 2013
4	Australia	Roebuck Bay	13.9	5.7	*Anodomia omissa,* Macoma sp, *Quadrans pristis*	all ~30%	*	Tulp & de Goeij, 1994
5	Netherlands	Wadden Sea	19.7	3.0	*Limecola balthica* *Cerastoderma edule*	> 95% 100%	100% 100%	Piersma *et al.*, 1993a
6	Argentina	Río Grande	>36	20.4	*Darina solenoides,* Mytilidae sp	all 100%	*	Escudero *et al.*, 2012
7	Argentina	San Antonio Oeste	23 – 117	10.9	*Brachidontes rodriguezi*	100%	*	González *et al.*, 1996
8	United States	Alaska	11.4	11.4	*Limecola balthica*	100%	100%	Ruthrauff 2014 & unpublished

*based on bivalve shell mass it can be expected that all these molluscs are breakable (van Gils *et al.*, 2005b).

Figure Legends

Figure 1. World map (Robinson projection) showing the IWP biogeographical area and the major shorebird flyways. The numbers refer to sites that are mentioned in the text: 1) Barr Al Hikman, Oman, our study site, 2) Banc d'Arguin, Mauritania, 3) Bohai Bay, China, 4) Roebuck Bay, Australia, 5) Wadden Sea, the Netherlands, 6) Río Grande, Argentina, 7) San Antonio Oeste, Argentina, 8) Alaska, United States of America, 9) Khor Dubai, United Arabian Emirates, 10) Java, Indonesia, 11) Sumatra, Indonesia.

Figure 2. Timescale indicating the estimated species divergence times and events relevant to this study. References to events are mentioned in the text.

Figure 3. (a) Oman with Barr Al Hikman highlighted. (b) Barr al Hikman. (c) Subsection Filim with macrozoobenthic biomass densities (g AFDM/m²) at each sampling station. (d) Sampling stations in subsections Khawr and Shannah. Maps c and d are on the same scale. Open points indicate sampling stations where no living benthos was found. Blue points indicate biomass density lower than the mean biomass density, and orange points indicate biomass density higher than mean.

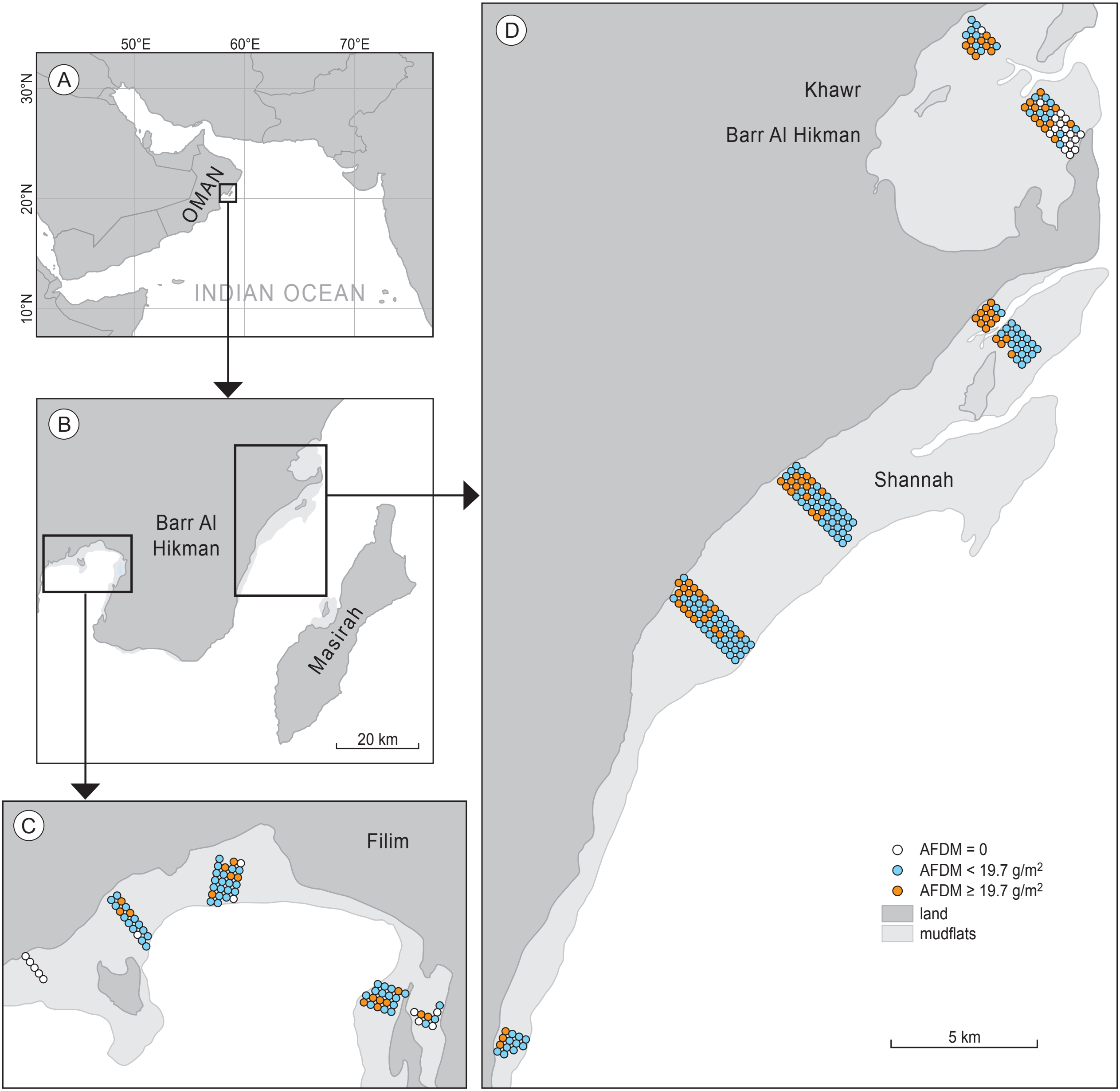
Figure 4. (a) A typical view on the intertidal mudflats of Barr al Hikman with high abundance of the thick-shelled *Cerithidea* and *Pirenella* gastropods about 30 mm long. Photo by JdF. (b) Repair scars in three gastropods. From left to right: *P. arabica*, *C. scabridum*, *Nassarius persicus.* Photo by Maaike Ebbinge.

Figure 5. Frequency distributions of three anti-predation mechanisms in bivalves at Barr Al Hikman on the basis of biomass. (a) Frequency distribution of burrowing depth (note the

reverse y-axis) with dashed lines indicating the maximum depth at which three molluscivorous shorebird species can probe. (b) Frequency distribution for length. Dashed lines shows which bivalves can be swallowed by red knots and great knots. (c) Frequency distribution of breaking force. The dashed line indicates the border between breakable and non-breakable bivalves.

Figure 6. Frequency distributions of two anti-predation mechanisms in gastropods at Barr Al Hikman on the basis of biomass. (a) Frequency distribution of bivalve length. (b) Frequency distribution of breaking force. The dashed line indicates the border between breakable and non-breakable gastropods.

Figure 7. Histograms of three anti-predation traits measured in the venerid *Pelecyora isocardia* and lucinid *Loripes orbiculatus* at Banc d'Arguin and the venerid *P. ceylonica* and the lucinid *P. fischeriana* at Barr Al Hikman. (a) The average burrowing depth relative to the biomass density (note the reverse y-axis), with lines indicating the depth to which red knots (upper), great knots (middle) and oystercatchers (lower) can probe. (b) Length relative to biomass with lines indicating which size is ingestible/non-ingestible by great knots (upper) and red knots (lower). (c) Breaking force relative to the biomass density with a dashed line indicates which bivalves are breakable and non-breakable for shorebirds. Data for Banc d'Arguin was obtained by Piersma *et al.* 1993a and Yang *et al.,* 2013. Data for Barr Al Hikman was collected in this study. Depth distributions for *P. ceylonica* are based on samples collected in 2008 and for *P. fischeriana* based on samples collected in 2010 (see Methods).


A
50°E
60°E
70°E
30°N
20°N
10°N
OMAN
INDIAN OCEAN
B
Barr Al Hikman
Masirah
20 km
C
Filim
D
Khawr
Barr Al Hikman
Shannah
○ AFDM = 0
● AFDM < 19.7 g/m²
● AFDM ≥ 19.7 g/m²
land
mudflats
5 km


A
10 cm
B

Journal of Biogeography

SUPPORTING INFORMATION

Food web consequences of an evolutionary arms race: invertebrates subject to crab predation on intertidal mudflats in Oman are unavailable to shorebirds

Roeland A. Bom[1,2*], Jimmy de Fouw[1,3], Raymond H. G. Klaassen[3,4], Theunis Piersma[1,5],
Marc S. S. Lavaleye[1], Bruno J. Ens[3,6], Thomas Oudman[1], Jan A. van Gils[1]

Appendix S1

Number of shorebirds present in Barr al Hikman in January 2008 (unpublished data JdF). The last 5 columns give the main diet as observed for each shorebirds species (unpublished data, BJE). A distinction is made between crabs and crustaceans other than crabs.

		diet				
species	number	bivalves	crustaceans	crabs	gastropods	polychaetes
bar-tailed godwit	65,300		+	+		+
broad-billed sandpiper	200		+	+		+
crab plover	6,900			+		
curlew sandpiper	37,800		+	+		+
dunlin	84,500		+			+
eurasian curlew	7,100			+		+
great knot	400	+		+		
greater sandplover	2,800		+	+		+
greenshank	500					
grey plover	2,200			+		+
kentish plover	2,100			+		
lesser sandplover	35,700		+	+		+
little stint	12,000		+			
marsh sandpiper	100					
oystercatcher	3,900	+		+		+
redshank	34,500		+			
ringed plover	100		+			+
ruddy turnstone	5,700					
sanderling	3,100		+	+		+
terek sandpiper	700			+		
whimbrel	700					
Total	306,300					

APPENDIX S2

Numerical density (#/m²) and biomass density (g AFDM/m²) for all identified species (or the level to which identification was possible). Averages values ± standard errors (between grid variance) are shown for the entire area and for the three sub-areas Filim, Khawr and Shannah. For Khawr no standard error is given as in this sub-area one grid was sampled.

		total		**Filim**		**Khawr**		**Shannah**	
Species	**taxonomic level**	**numerical**	**biomass**	**numerical**	**biomass**	**numerical**	**biomass**	**numerical**	**biomass**
ANTHOZOA									
Actiniaria spp	order	3.02±4.03	0.01±0.02	1.21±1.66	0.01±0.02	1.44	0	4.96±4.96	0.02±0.03
BIVALVIA									
Arcuatula senhousia	species	0.53±0.94	0	0.58±1.45	0	1.44	0	0	0
Bivalvia sp.	class	0.11±0.52	0	0	0	0	0	0.38±0.76	0
Callista umbonella	species	1.26±3.10	0.34±1.07	3.10±0.92	0.92±2.06	1.44	0.31	0	0
Cardiolucina semperiana	species	0.18±0.52	0	0	0	0	0	0.38±76	0
Diplodonta crebristriata	species	0.42±0.74	0	0	0	0	0	0.90±0.88	0
Jitlada arsinoensis	species	36.01±88.74	0.16±0.35	92.51±163.37	0.38±0.64	1.44	0.02	21.87±25.82	0.12±0.13
Laternula anatina	species	0.37±0.68	0.03±0.05	0	0	1.44	0.11	0	0
Marcia recens	species	5.53±4.54	0.43±0.54	4.17±4.26	0.01±0.02	11.48	1.22	3.01±1.99	0.24±0.26
Nitidotellina cf *valtonis*	genus	16.75±30.54	0.07±0.09	42.08±51.61	0.09±0.14	0	0	11.1±5.69	0.09±0.08
Ostreidae sp.	family	0.75±1.36	0.01±0.01	0	0	2.87	0.03	0	0
Pelecyora ceylonica	species	17.59±22.23	0.29±0.42	10.19±22.85	0.32±0.81	47.36	0.49	5.36±3.42	0.15±0.07
Pillucina fischeriana	species	706.14±732.40	3.62±3.88	44.56±50.44	0.22±0.27	218.16	0.87	1370.06±450.85	7.17±2.29
Pinguitellina cf. *pinguis*	genus	0.32±1.46	0	0	0	0	0	0.68±2.25	0
Pinguitellina pinguis	species	0.24±0.62	0	0	0	0	0	0.52±0.87	0
Tivela mulawana	species	0.56±1.35	0	0.92±2.20	0	0	0	0.67±1.21	0
CRUSTACEA									
Amphipoda sp.	order	188.01±210.25	0.25±0.30	0	0	22.96	0.03	391.41±67.76	0.53±0.17

Anomura sp.	Infraorder	39.71±37.04	0.42±0.46	62.6±67.62	0.50±0.83	22.96	0.18	35.51±12.43	0.50±±0.29
Astacidea sp.	Infraorder	5.11±8.03	0.10±0.18	1.21±1.66	0	1.44	0	9.46±10.61	0.20±0.22
Brachyura sp.	Infraorder	1.43±3.28	0±0.01	1.16±2.91	0±0.01	0	0	2.39±4.40	0.01±0.01
Caridea sp.	Infraorder	0.31±0.84	0	0	0	0	0	0.67±1.21	0
Isopoda sp.	order	2.4±4.48	0	0	0	0	0	5.16±5.57	0
Leucosiidae sp.	family	4.94±4.58	0.03±0.02	6.68±7.44	0.04±0.03	1.44	0.01	5.86±2.83	0.03±0.02
Macrophthalmus grandidieri	species	0.24±0.62	0	0	0	0	0	0.52±0.87	0
Macrophthalmus laevis	species	0.33±0.99	0	1.21±1.66	0.01±0.01	0	0	0	0
Macrophthalmus sulcatus	species	4.38±7.69	0.11±0.19	12.2±11.23	0.30±0.28	0	0	2.19±2.21	0.07±0.07
Maxillopoda sp.	class	0.37±0.68	0	0	0	1.44	0	0	0
Mysida sp.	order	4.54±6.99	0.01±0.01	2.43±3.32	0.02±0.02	0	0	8.33±8.82	0.1±0.01
Pinnotheridae sp.	family	1.16±3.00	0.01±0.04	4.22±4.58	0.05±0.05	0	0	0	0
Portunidae sp.	family	1.81±3.15	0.01±0.01	0.92±2.20	0.01±0.01	0	0	3.36±3.97	0.01±0.02
Scopimera sp.	genus	3.58±6.55	0.04±0.06	8.50±11.63	0.08±0.11	2.87	0.06	1.06±1.15	0.01±0.01
Xanthidae sp.	family	1.23±2.20	0.01±0.01	3.35±3.09	0.02±0.02	0	0	0.67±1.21	0
ECHINODERMATA									
Holothuroidea sp.	class	0.81±1.62	0.01±0.02	0	0	0	0	1.73±2.20	0.02±0.03
GASTROPODA									
Aticulastrum cylindricum	species	1.05±1.22	0.02±0.02	0.92±2.20	0.01±0.02	1.44	0.01	0.90±0.88	0.03±0.03
Bulla ampulla	species	0.42±0.74	0.02±0.06	0	0	0	0	0.9±0.88	0.05±0.08
Cerithium scabridum	species	194.78±177.56	3.22±2.56	40.05±49.12	0.81±0.92	361.69	5.13	193.24±193.00	3.58±2.89
Crepidula sp	genus	1.25±3.38	0	0	0	0	0	2.68±4.85	0
Gastropoda sp.	class	1.37±1.88	0.05±0.08	0.58±1.45	0.02±0.05	0	0	2.61±1.91	0.10±0.09
Littoraria intermedia	species	1.48±1.78	0.03±0.05	0	0	1.44	0.02	2.38±2.25	0.06±0.08
Mitrella blanda	species	9.57±8.62	0.09±0.12	12.2±15.91	0.12±0.23	5.74	0.05	10.15±4.91	0.10±0.04
Nassarius persicus	species	25.95±12.82	0.47±0.24	15.77±16.15	0.26±0.28	35.88	0.54	26.43±10.17	0.55±0.21
Nerita textilis	species	1.06±1.42	0.02±0.02	0	0	2.87	0.05	0.67±1.21	0.01±0.02
Oliva bulbosa	species	0.66±1.26	0.04±0.08	0	0	0	0	1.42±1.59	0.10±0.10

Opisthobranchia sp.	infraclass	0.84±1.48	0	0	0	0	0	1.81±1.77	0
Pirenella arabica	species	162.66±185.23	8.39±4.42	70.44±66.60	4.56±4.20	443.5	11.19	60.53±43.94	9.01±4.53
Pirenella / Cerithium	genus	66.06±73.88	0.19±0.22	23.1±24.12	0.03±0.03	147.83	0.38	45.86±78.95	0.18±0.27
Priotrochus kotschyi	species	6.30±9.75	0.14±0.14	1.21±1.66	0	7.18	0.17	8.83±14.43	0.20±0.17
Salinator fragilis	species	3.08±4.14	0.04±0.07	0	0	1.44	0.01	5.82±4.81	0.08±0.09
Umbonium eloiseae	species	0.36±1.04	0	0	0	0	0	0.77±1.51	0
Umbonium vestiarium	species	0.32±1.46	0	0	0	0	0	0.68±2.25	0
INSECTA									
insect larvae	class	8.43±21.54	0	0	0	0	0	18.12±30.52	0
PLATYHELMINTHES									
Platyhelminthes	phylum	2.97±1.91	0.01±0.01	3.01±3.03	0.01±0.01	2.87	0	3.01±1.99	0.01±0.01
POLYCHAETA									
Chaetopteridae sp.	family	15.99±18.36	0.23±0.29	21.77±20.23	0.31±0.32	4.31	0.04	19.09±21.68	0.28±0.34
Polychaeta sp.[1]	phylum	210.92±129.36	0.77±0.50	106.02±68.76	0.51±0.33	132.05	0.38	317.02±101.03	1.15±0.43
PRIAPULIDA									
Priapulida sp	class	1.2±1.78	0.03±0.09	1.21±1.66	0	0	0	1.86±2.17	0.07±0.13
SCAPHOPODA									
Dentalium octangulatum	species	0.80±1.81	0	0	0	0	0	1.71±2.48	0

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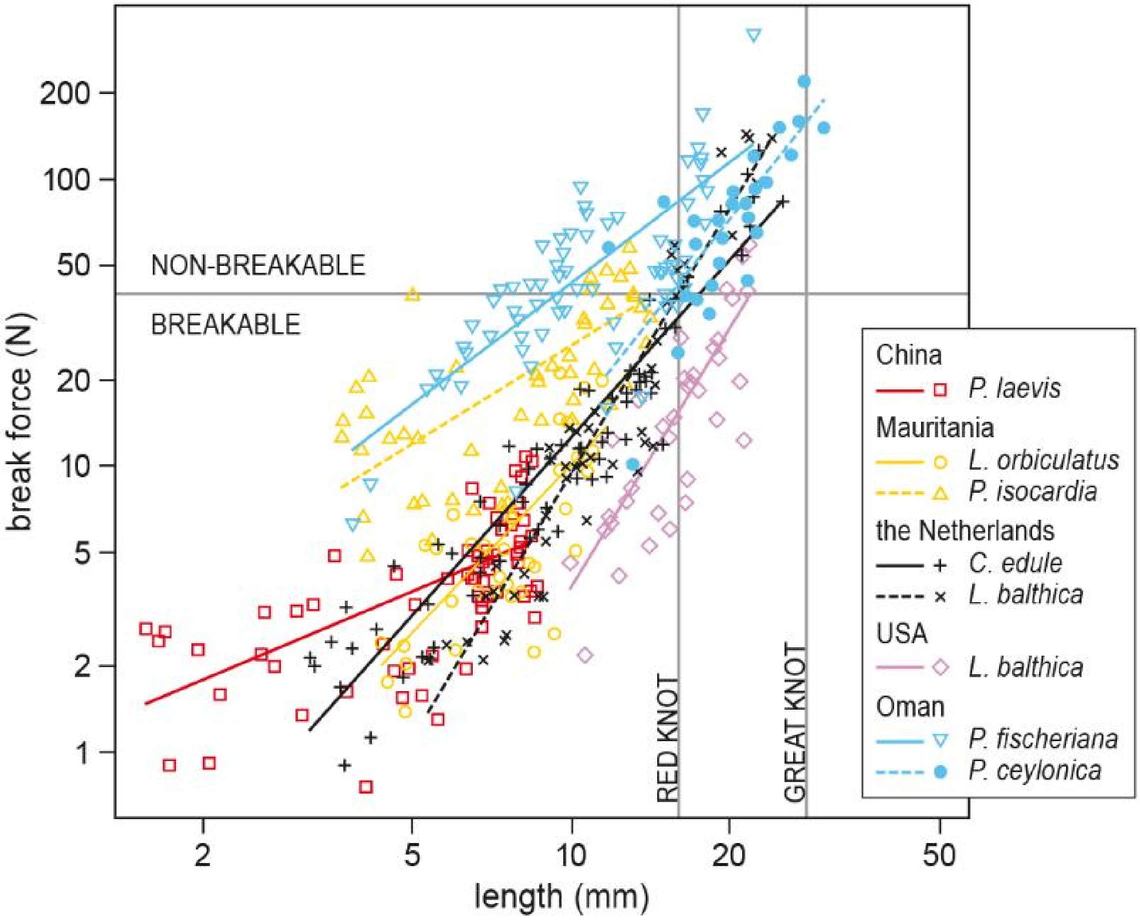
[1] Polychaetes of the families Capitellidae, Cirratulidae, Glyceridae, Maldanidae, Nereididae, Opheliidae, Orbiniidae, Palmyridae, Spionidae and Terebellidae were recognized in our samples, but not all polychaetes were identified to family level.

APPENDIX S3



Shell break force as a function of shell length in five bivalve species. Data on *Loripes orbiculatus*, *Pelecyora isocardia, Potamocorbula laevis, Limecola balthica* (Wadden Sea) and *Cerastoderma edule* was earlier published by Yang *et al.* 2013. Data on *Pillucina fischeriana* and *Pelecyora ceylonica* was collected for this study and data for *Limecola balthica* (Alaska) was unpublished. All data was collected by TO or RAB and obtained using the breakforce machine described in the methods. For further information on the species we refer to Table 3. Vertical lines indicate the maximum size that red knots and great knots can ingest and the horizontal line indicates the maximum break force red knots can generate in their gizzards.

APPENDIX S4

Results of the binomial proportions test comparing the proportion of biomass that is accessible and not accessible, ingestible and not ingestible, breakable and not breakable for the venerid *Pelecyora isocardia* (n = 38) and lucinid *Loripes orbiculatus* (n = 76) at Banc d'Arguin and the venerid *Pelecyora ceylonica* (n = 60) and the lucinid *Pillucina fischeriana* (n = 2918) at Barr Al Hikman. Data for Banc d'Arguin was obtained by Piersma *et al.* 1993a (with breakforce conversion according to the breakfore-length relationships obtained by Yang *et al.,* 2013). Data for Barr Al Hikman was collected in this study.

Group	anti-predation trait	Barr Al Hikman % < x	Banc d'Arguin % < x	p	χ^2	df
venerids	depth (x = 4 cm)	42	44	0.10135	0.75	1
lucinids	depth (x = 4 cm)	17	49	2.194e-06	22.417	1
venerids	length (x = 16 mm)	16	100	< 2.2e-16	192.31	1
lucinids	length (x = 16 mm)	96	100	0.414	0.66559	1
venerids	breakforce (x = 40 N)	16	100	< 2.2e-16	193.09	1
lucinids	breakforce (x = 40 N)	55	100	3.04e-07	26.225	1