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Growth and population structure of bloody cockles *Senilia senilis* at Banc d'Arguin and Bijagós with different environmental conditions and harvesting regimes

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ABSTRACT: In addition to density-dependent (i.e. food availability) and independent (i.e. abiotic gradients) forces, size-selective harvests of organisms often induce changes to their life history, demography, and reproduction. Shellfish are increasingly overexploited worldwide, and the effect of size-selective harvest on their populations is unclear. The African bloody cockle *Senilia senilis* is a dominant bivalve in most West African coastal systems, where it is an important source of protein. Here, we studied its population structure (abundance, biomass, and size) and life history traits (age, annual growth rate, and size for age) under contrasting harvesting conditions at the 2 largest intertidal systems in the region: the Bijagós archipelago in Guinea-Bissau (harvested) and Banc d'Arguin in Mauritania (unexploited). To account for local ecological context, we assessed environmental variables that could also affect the abundance and size of *S. senilis* at these sites. We found that the *S. senilis* population at Bijagós is significantly denser and older, with lower standing biomass and smaller-sized shells than the population from Banc d'Arguin. In Bijagós, the annual growth is 3-fold lower, and the size-for-age is half of that at Banc d'Arguin. At both sites, *S. senilis* densities and sizes were correlated with habitat quality indicators: mangrove and mudflat productivity at Bijagós and seagrass and sediment characteristics at Banc d'Arguin. The smaller-sized mature individuals, denser populations, and lower standing biomass at Bijagós compared to Banc d'Arguin are indications of considerable size-selection pressure at Bijagós.

KEY WORDS: Banc d'Arguin (Mauritania) · Bijagós archipelago · Exploitation · Shellfish · Size-selective harvesting

1. INTRODUCTION

With the worldwide collapses of many coastal important fish stocks, focus has shifted to harvesting

shellfish in many places (Lotze 2007). As a consequence, many shellfish populations are increasingly under pressure (Aswani et al. 2015, Blake & Ermgassen 2015, Escrivá et al. 2021), and there is an

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urgent need to understand its effect on these newly affected populations. For example, some of the most important shellfish populations along the Latin American Pacific coast, mangrove cockles *Anadara* spp., are now under heavy harvesting pressure throughout their distribution ranges (MacKenzie 2001). The effect of shellfish harvest on intertidal systems is a growing concept in marine biology and management around the world. In addition, the effect of size-selective harvesting on shellfish populations has been widely recognized over the last few decades (Buxton 1993, Grift et al. 2003, Pellowe & Leslie 2020).

Artisanal shellfish harvesting is a selective practice, as collectors tend to seek large-sized individuals, because they are the easiest to find and give the highest yield of protein per unit effort (Siegfried et al. 1994). Size-selective harvesting often causes changes in life history, demography, reproductive output, and even ecological interactions of targeted species (Fenberg & Roy 2008, Jimenez et al. 2015, Borges et al. 2015). The primary effect of size-selective harvesting is an overall decline in the number of individuals surviving to older ages and larger sizes. This removal of the oldest and largest individuals has been shown to cause negative effects on the size, growth, and survival of many fish species (Haug & Tjemsland 1986, Birkeland & Dayton 2005, Bubley et al. 2013). While harvest-induced biological changes have been well documented in fish (Baskett et al. 2005, de Roos et al. 2006), the effects are less established in shellfish populations.

The bloody cockle *Senilia senilis* (hereinafter '*Senilia*'; previously known as *Arca senilis* then as *Anadara senilis*) has been harvested by local communities along the West African coast since prehistoric times (Barousseau et al. 2007, Valdeyron & da Silva Domingos 2012, Hardy et al. 2016). Shell-middens of *Senilia* can be found all along the coast from northern Mauritania to the coast of Luanda (Angola) (Nicklès & Fischer-Piette 1950, Valdeyron & da Silva Domingos 2012, Lavaud et al. 2013, Hardy et al. 2016). Many of these shell-middens date back to the late Holocene period (~5000 yr BP) (Barousseau et al. 2010, Hardy et al. 2016). Although *Senilia* is no longer part of the diet of the northern coastal communities of West Africa (e.g. Mauritania), it is still an important source of protein for local communities in Guinea-Bissau (Regalla et al. 2013), and to a lesser extent in Senegal (Hardy et al. 2016), Sierra Leone (Okera 1976), Ivory Coast (Zabi & Le Loeuff 1994), and Ghana (Keeling et al. 2013).

Bloody cockles are the dominant mollusc species in many intertidal systems in West Africa, either in terms

of biomass or abundance (Nicklès & Fischer-Piette 1950, Zabi & Le Loeuff 1994, Honkoop et al. 2008, Meijer et al. 2021), and the species has very few natural enemies. Its large and extremely hard shell makes it unavailable as a food source for foraging shorebirds, with the exception of oystercatchers *Haematopus ostralegus* (Swennen 1990), which are not common in the region. The large muscled gastropods *Cymbium* spp. also feed on *Senilia*, although their predation pressure on bloody cockles at Banc d'Arguin has been estimated to be <1% of deaths yr⁻¹ (Wolff & Montserrat 2005). These predatory *Cymbium* have become an important part of the diet of many West African communities (Tittikpina et al. 2021) and are now likely under strong harvest pressure. In addition, bull rays *Aetomylaeus bovinus* and Lusitanian cownose rays *Rhinoptera marginata* appear to be capable of cracking the valves of *Senilia* with their muscled jaws (S. Y. C. Lemrabott unpubl. data). Traces of episodic cracking events of bloody cockles have been observed across both the Banc d'Arguin and Bijagós intertidal flats (authors' pers. obs.).

At Banc d'Arguin, Mauritania, bloody cockles are a dominant mollusc species in terms of biomass (Honkoop et al. 2008, Ahmedou Salem et al. 2014), and are not harvested. There are strong indications of an increase in biomass over the last 3 decades. The early biomass estimates of *Senilia* in the 1980s (Piersma 1982, Wolff et al. 1993a) have at least tripled according to the most recent estimates (Honkoop et al. 2008, Ahmedou Salem et al. 2014). In Banc d'Arguin, *Senilia* seems to have gained ground over the last 3 decades from polychaetes, gastropods, and other small bivalves such as *Dosinia* sp. that have all shown sharp declines (El-Hacen et al. 2020). However, the reason behind the increase in the population of *Senilia* in Banc d'Arguin is not yet understood. Wolff et al. (1987) hypothesised that *Senilia* settlement is favoured by brackish conditions (Debenay et al. 1994, Azzoug et al. 2012, Keeling et al. 2013). Indeed, the year-class distribution of *Senilia* correlated significantly with the discharge of the nearest river (as a proxy for rainfall) (Wolff et al. 1987). Thus, the observed increase in *Senilia* at Banc d'Arguin since the 1980s may have been caused by an increase in rainfall over the last 2 decades (Diawara et al. 2016, Bichet & Diedhiou 2018). Another reason for the increase in *Senilia* might be the ongoing overexploitation of their natural enemies such as bull and cownose rays (S. Y. C. Lemrabott et al. unpubl. data).

Similarly, *Senilia* also contributes the most to the molluscan biomass (50%) and density (15%) in the Bijagós archipelago, in Guinea-Bissau, followed by

Dosinia isocardia (Meijer et al. 2021). Unfortunately, no historical data are available for this area. The Bijagós intertidal system is dominated by mangrove forests bordering bare mudflats (Coelho et al. 2022), while seagrass beds dominate at Banc d'Arguin. Another large difference from Banc d'Arguin is the fact that *Senilia* are subjected to regular artisanal harvest by the women and children of the local indigenous fishing communities (Regalla et al. 2013). Bloody cockles are a major source of protein for the local communities of Bijagós and are considered a strategic resource (Regalla et al. 2013). Their dried meat is used in many local sacred ceremonial festivals and can be found in most food markets, providing a relatively cheap and abundant source of protein (E. M. El-Hacen pers. obs.). *Senilia* harvesting takes place at low tide, mostly with bare hands. Bloody cockles occur mainly in sandy habitats (Meijer et al. 2021), and hence they are easy to harvest compared to other desirable shellfish such as *Tagellus adansonii* (Regalla et al. 2013) that occur in muddier areas (Meijer et al. 2021).

The large difference in human harvesting pressure on *Senilia* in Bijagós and Banc d'Arguin is expected to affect the population structure and growth at both sites. The consistent removal of larger individuals by fishing communities in Bijagós should result in relatively younger and smaller-sized individuals compared to an unexploited area like Banc d'Arguin. Further, the annual growth rate is expected to be higher in the harvested zone due to the removal of larger individuals that usually compete for food resources. The sizes of *Senilia* in Ghana (Keeling et al. 2013) and Sierra Leon (Okera 1976) were larger in relatively unexploited lagoons than in sites subjected to greater human exploitation. In this study, we examined natural variability of *Senilia* density, biomass, size, age, annual growth rate, and size-for-age at landscape scales in West Africa's 2 largest intertidal systems: Banc d'Arguin in Mauritania (unharvested) and Bijagós archipelago in Guinea-Bissau (harvested). We further determined environmental factors that could affect the *Senilia* size and abundance at these 2 sites. Density-dependent competition for space and resources (e.g. food) and density-independent (e.g. environmental gradients) forces are also known to affect the growth and density of molluscs (Bertness 1999). As the intertidal system of Bijagós receives regular input of organic matter (OM) from the Geba River and the offshore upwelling system (Campredon & Catry 2018), we expected *Senilia* here to suffer less competition for food (better growth condition) compared to *Senilia* at Banc d'Arguin, a system which is isolated from the surrounding ecosystems (El-Hacen et al. 2022).

2. MATERIALS AND METHODS

2.1. Study sites

The first study site was located in the Parc National du Banc d'Arguin in Mauritania (Fig. 1), a UNESCO World Heritage Site characterised by extensive intertidal flats (453 km²) (El-Hacen et al. 2020), of which 80% are covered by eelgrass *Zostera noltei* (Wolff & Smit 1990). The Banc d'Arguin borders the Sahara and receives a considerable amount of dust every year (Goudie & Middleton 1992, Prospero & Lamb 2003). From the ocean side, the year-round active and rich upwelling of Cap Blanc is in close proximity (Steinfeldt et al. 2015) but has little effect on the inner intertidal flats of Banc d'Arguin (Sevrin-Reyssac 1993, Carlier et al. 2015, El-Hacen et al. 2019). There is a strong gradient in wave action and seagrass cover from the northernmost exposed zone toward the southern inner mudflats (El-Hacen et al. 2019, 2020). Salinity seems to follow the same gradient, with an average of 38‰ in the northern part, while the more isolated bays can reach up to 54‰ (ould Dedah 1993, Wolff et al. 1993b). Rainfall is extremely low (<50 mm yr⁻¹), and the area receives no regular freshwater runoff (Ahmedou et al. 2008).

The second study site was located in the Bijagós archipelago, a UNESCO Biosphere Reserve in Guinea-Bissau that includes 2 national parks (João Vieira and Orango) and the Urok community-based marine protected area. The biosphere reserve is characterised by extensive mudflats (~760 km²) which are mostly bare but fringed by the most extensive mangroves (650 km²) in Africa (Temudo & Cabral 2017). The mangroves of Bijagós are dominated by *Rhizophora* and *Avicennia* species (Altenburg & van Spanje 1989). The area receives high annual rainfall (2200 mm), combined with regular freshwater discharges from the Geba River (Fig. 1) (Campredon & Catry 2018). The intertidal benthic community of the area is influenced by the degree of connectivity to mangrove forests (area and distance to mangroves) (Meijer et al. 2021). There is an expected salinity gradient from the mouth of the Geba River toward the outer mudflats of the island of Orango (Campredon & Catry 2018) (Fig. 1).

2.2. *Senilia* sampling

At Banc d'Arguin, sampling took place in November 2016 at 63 intertidal locations around the island of Tidra with different seagrass cover and tidal

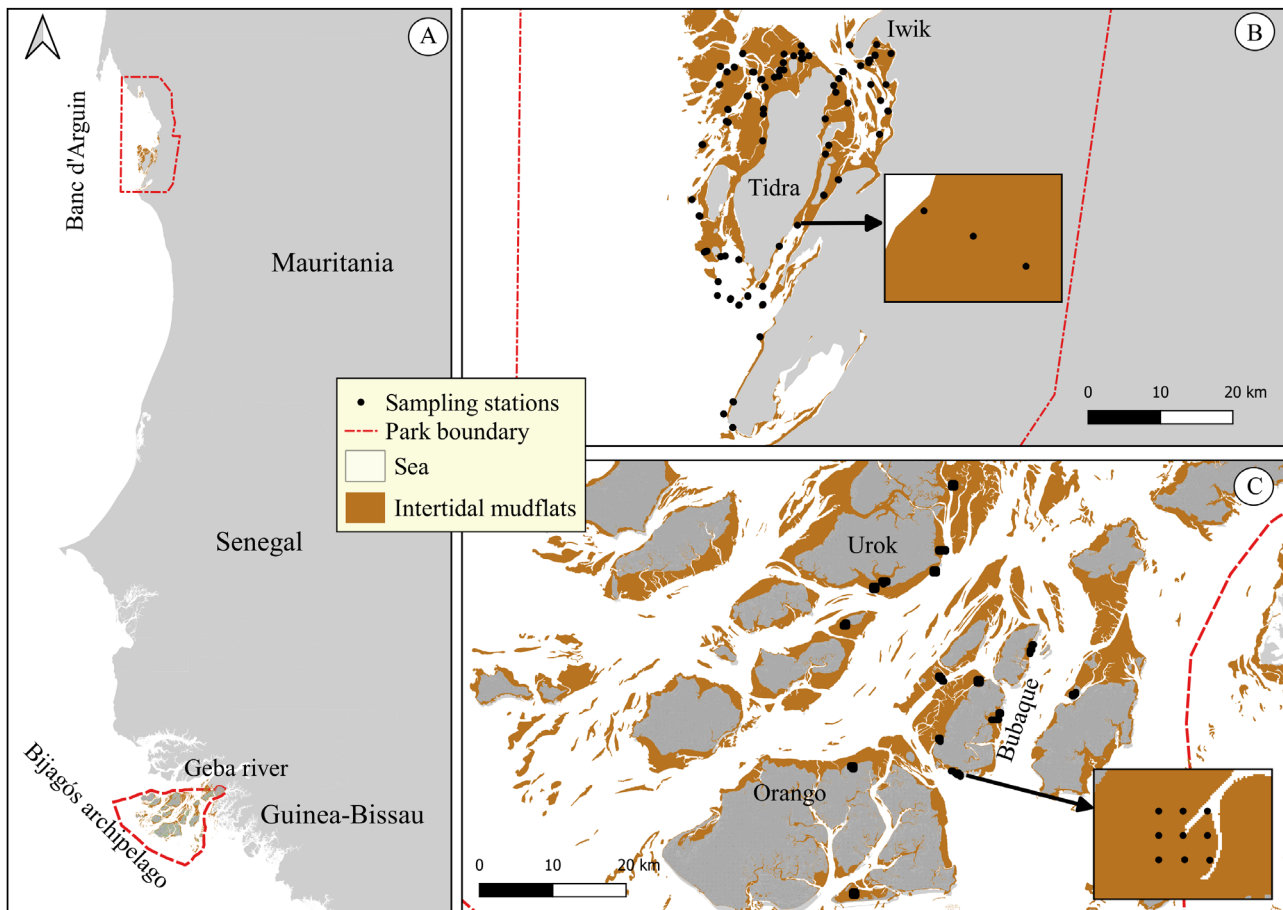


Fig. 1. (A) Study area in West Africa as well as the sampling sites in (B) Parc National du Banc d'Arguin in Mauritania and (C) Bijagós Biosphere reserve in Guinea-Bissau. Black dots: sampling locations at Banc d'Arguin ($n = 189$ quadrats along an elevation transects from 63 sites) and Bijagós ($n = 125$ quadrats from 250×250 m grids on 15 sites)

regimes (Fig. 1). Sites ranged from completely bare mud- or sandflats to areas densely covered with sea-grass, and from areas highly exposed to wave energy ($14\,940 \text{ J m}^{-1}$) to sheltered areas (45 J m^{-1}) (El-Hacen et al. 2019). At every site, 3 quadrats of 1×1 m each were selected randomly and all *Senilia* within the quadrats were collected by hand and brought back to the lab for measurements. The total lengths of all 4183 collected individuals were measured to the nearest 1 mm. Further, the growth marks of a subset of 415 individuals that represented collected age classes per quadrat were measured following the method of Wolff et al. (1987). The growth marks of *Senilia* have been suggested to be deposited on an annual basis in both Banc d'Arguin (Wolff et al. 1987, Lavaud et al. 2013) and sub-Saharan estuaries (Okera 1976, Debenay et al. 1994, Azzoug et al. 2012). The relationship between the length and ash-free dry mass (AFDM) of *Senilia* is well established in

Banc d'Arguin (Wolff et al. 1987) and thus was used to estimate AFDM per individual.

In the Bijagós, sampling took place in January–February 2019 in 125 plots spread across 15 different mudflats with great variability in geomorphology and connectivity with mangroves (Fig. 1). At each mudflat, 6–9 plots (250 m grid) were sampled by taking 3 quadrats of 0.3×0.3 m per plot (see Meijer et al. 2021). At each plot, *Senilia* was hand-sampled and measured in a manner similar to at Banc d'Arguin. In total, 1168 individuals were encountered and measured, of which 323 were used for growth mark analyses. The relationship between the dimensions of *Senilia* and its AFDM in Bijagós was estimated based on a previous large-scale benthic coring survey (Meijer et al. 2021), which resulted in a very strong linear relationship between AFDM and length. This relationship was used to estimate AFDM per individual.

2.3. Environmental descriptors

In Banc d'Arguin, the following environmental covariates were measured at each plot: seagrass cover (%), seagrass leaf length (mm), water temperature, and salinity. Seagrass cover was estimated visually for each quadrat. The shoot lengths were measured on 3 fresh intact leaf samples from each core to the nearest 0.1 mm. Salinity and temperature were measured with a portable handheld conductivity meter (VWR International, CO 310 M). In addition, wave energy (J m^{-1}), sediment grain size (μm), and OM content (%) were extracted from existing large-scale raster maps from the study area (El-Hacen et al. 2019) using QGIS software (v.3.4.1; QGIS Development Team 2019).

In the Bijagós, we measured the following environmental covariates: sediment grain size, OM content, mudflat productivity (NDVI, see below), mangrove connectivity index (MCI), and distance to river mouth (km). Grain size distribution was measured with laser diffraction using a Malvern particle size analyser (Mastersizer 2000). OM content was determined for each plot (10 g subsample) as weight loss on ignition for 4 h at 450°C. Mudflat productivity was estimated from a Sentinel-2 image (scenes from 16 December 2018) as the Normalised Difference Vegetation Index (NDVI; using red and infrared bands). MCI was calculated for each plot following the method of Meijer et al. (2021). Salinity measurements were not available for Bijagós; hence, we used the distance to the mouth of the Geba River as a proxy (Campredon & Catry 2018). The distance of each plot to the mouth of the Geba River was determined by calculating a proximity raster for each attribute in QGIS. Other water salinity estimates, however, were computed using a remote sensing oceanic model (see Text S1 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m710p071_supp.pdf) to get an idea of the magnitude difference in salinity conditions between the 2 sites.

2.4. Statistical analyses

We used a Student's *t*-test to assess the differences in shell length and age of *Senilia* between the populations at Banc d'Arguin and Bijagós. Analysis of covariance (ANCOVA) was used to determine whether *Senilia* growth was significantly different between the 2 sites (Banc d'Arguin and Bijagós), controlling for age classes. Stepwise multiple linear regressions were carried out, separately for each site, to assess the effects of environmental variables on the abundance and length of *Senilia*. Selection of environmental vari-

ables was based on prior knowledge of factors known to affect benthic communities per site (Honkoop et al. 2008, El-Hacen et al. 2020, Meijer et al. 2021). Initial models for Banc d'Arguin included wave energy, silt content (%), water salinity, and seagrass cover and leaf length. Sediment OM, grain size, and silt content showed strong collinearity (maximum variance inflation factor >2.5), and thus only silt content was retained in the analyses as it best predicted the response variables. The models for Bijagós included wave energy, sediment OM, mudflat productivity (via NDVI), MCI, and distance to river mouth (via salinity, suspended material). A backward elimination procedure was used to select the best fit model based on Akaike's information criterion. Normality and heteroscedasticity of the data were inspected visually on the residuals of the final models. We used an alpha level of 0.05 for all statistical tests. All statistical analyses were performed and graphics generated with the free software R v.4.0.2 (R Core Team 2020).

3. RESULTS

In Banc d'Arguin, the bloody cockle generally lives in an environment that is siltier, richer in OM, saltier, and colder compared to that in Bijagós (Table 1). The mean biomass of *Senilia* was 4-fold higher at Banc d'Arguin ($32.8 \pm 7.6 \text{ g AFDM m}^{-2}$; mean \pm SE) than in Bijagós ($8.3 \pm 1.3 \text{ g AFDM m}^{-2}$) (Fig. 2A; $t_{63} = 3.2$, $p = 0.002$). *Senilia* densities, on the other hand, were 2-fold higher in Bijagós ($35.2 \pm 5.3 \text{ ind. m}^{-2}$; mean \pm SE) than at Banc d'Arguin ($16.3 \pm 3.6 \text{ ind. m}^{-2}$) (Fig. 2B; $t_{63} = -2.9$, $p = 0.003$). Shell length, on average, was 2-fold larger in Banc d'Arguin ($57.1 \pm 2.3 \text{ mm}$; mean \pm SE) than in Bijagós ($25.5 \pm 1.9 \text{ mm}$) (Fig. 2C; $t_{1949} = 104$, $p < 0.001$). In addition, the average (\pm SE) age of

Table 1. Comparison of environmental variables relevant for *Senilia senilis* growth measured at both Parc National du Banc d'Arguin (Mauritania) and Bijagós Archipelago Biosphere Reserve (Guinea-Bissau). Salinity and temperature estimates were based on an oceanic model (The Hybrid Coordinate Ocean Model [HYCOM] v.2.2.; see Text S1 in the Supplement at www.int-res.com/articles/suppl/m710p071_supp.pdf). Values are mean \pm SE. D50: sediment median grain size; OM: organic matter

Source of variation	Banc d'Arguin	Bijagós
Sediment grain size (D50)	89.0 \pm 2.2	139.1 \pm 3.3
Sediment OM (%)	4.9 \pm 0.1	2.2 \pm 0.2
Salinity (PSU)	36.2 \pm 0.04	33.5 \pm 0.2
Water temperature (°C)	22.7 \pm 1.0	26.8 \pm 0.6

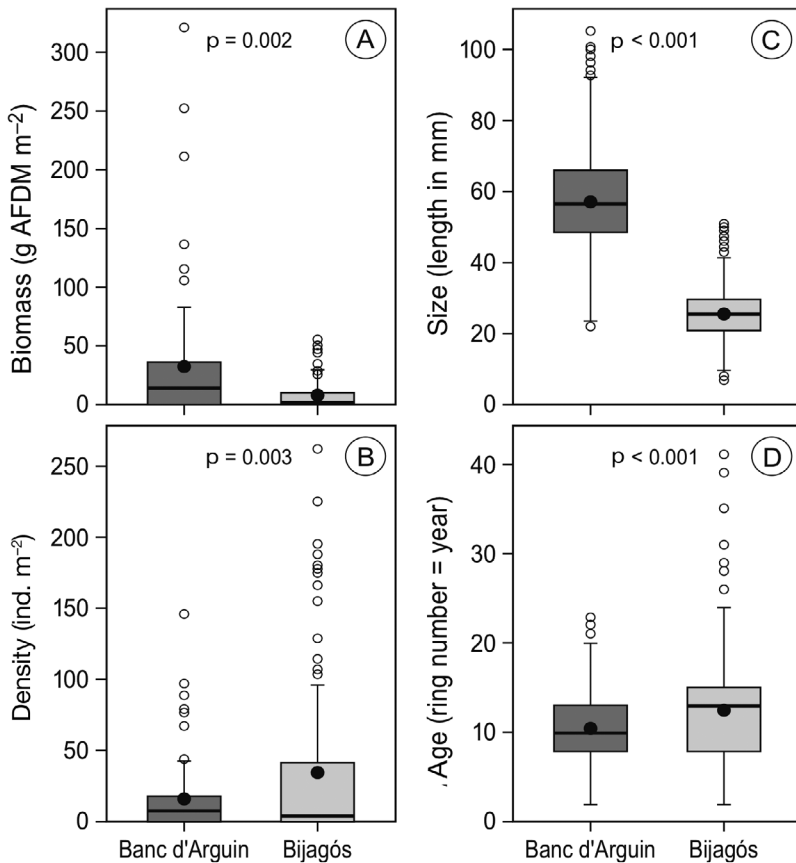


Fig. 2. Comparisons of the (A) mean biomass, (B) density, (C) size, and (D) age of the African bloody cockle *Senilia senilis* between Parc National du Banc d'Arguin (Mauritania) and Bijagós Biosphere Reserve (Guinea-Bissau). Comparisons between the 2 sites were performed using *t*-tests. AFDM: ash-free dry mass. The interquartile range of the box plot shows the middle 50% of the score, while the upper and the lower quartiles represent 25% of the scores each. The horizontal lines inside the interquartile show the median and the black dots the mean

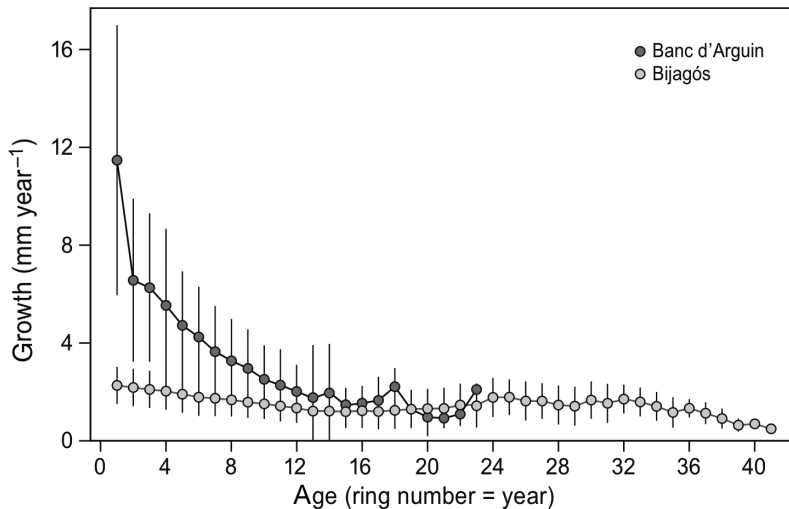


Fig. 3. Changes of mean (\pm SD) annual growth rate of African bloody cockles *Senilia senilis* over age from 2 populations: Parc National du Banc d'Arguin, Mauritania, and Bijagós Biosphere Reserve, Guinea-Bissau

Senilia from Banc d'Arguin (10.4 ± 0.2 yr; range: 1–23 yr) was 2 yr younger than the average of the population at Bijagós (12.6 ± 0.3 yr, range: 1–41 yr; Fig. 2D; $t_{322} = -5.7$, $p < 0.001$). In general, there were younger age-classes (1–6 yr) at Bijagós than at Banc d'Arguin (Fig. S2). Total biomass and density of *Senilia* were significantly predicted (Fig. S3) at both sites by easting geographical position (from offshore toward the mainland) but in opposite trends: at Banc d'Arguin, there was an increase in density and biomass towards the mainland, whereas in the Bijagós, these values increased westward (further from the coast) (Fig. S3).

Surprisingly, the average annual growth (mm) of *Senilia* was almost 3-fold (2.8 higher in Banc d'Arguin (4.8 ± 0.05 mm yr^{-1}) than in Bijagós (1.7 ± 0.01 mm yr^{-1}) (Fig. 3; $F_{1,61} = 10.8$, $p = 0.001$). This difference in annual growth rate of *Senilia* between the 2 sites was mainly due to the growth patterns of the young cohorts (up to 12 yr), as older individuals from both sites showed similar annual growth rates (Fig. 3). Further, size-for-age was 2-fold higher in the population at Banc d'Arguin than at Bijagós (Fig. 4). The size of individuals of a certain age is substantially smaller in the exploited Bijagós area than in the unharvested population at Banc d'Arguin (Fig. 4).

Stepwise multiple regression analyses revealed that at Banc d'Arguin, the abundance of *Senilia* was significantly predicted by seagrass cover (positively) and leaf length (negatively) (Table 2, Fig. 5), while shell length was only significantly predicted by sediment silt content (negatively) (Table 2, Fig. 5). The best models for Banc d'Arguin indicated that 29 and 39% of the variations in abundance and length, respectively, were explained by these environmental parameters (Table 2). At Bijagós, the abundance of *Senilia* was significantly predicted by MCI (positively) and marginally by sediment OM content (negatively) (Table 2, Fig. 5), while its length was significantly predicted by salinity (negatively) and marginally by mudflat NDVI (positively) (Table 2, Fig. 5). The best models for Bijagós indicated that

only 10 and 14% of the variations in abundance and length, respectively, were explained by these environmental parameters (Table 2).

4. DISCUSSION

We observed a lower biomass and denser population of *Senilia* comprised of smaller-sized, older individuals at the exploited site (Bijagós) compared with the unharvested site (Banc d'Arguin).

4.1. Uncertainties and limitations

Our study contains 2 uncertainties that should be interpreted with caution. The first is related to the growth marks of bloody cockle that we considered annual for both Banc d'Arguin and Bijagós, even though this needs to be empirically verified for the latter system. It is known that the growth marks of *Senilia* at Banc d'Arguin are deposited on an annual basis (Wolff et al. 1987, Lavaud et al. 2013). The Bijagós, however, ex-

Table 2. Final stepwise multiple linear regression models to assess the effects of environmental variables on the abundance and length of *Senilia senilis* at Parc National du Banc d'Arguin (Mauritania) and Bijagós Archipelago Biosphere Reserve (Guinea-Bissau). RWE: relative wave energy; OM: organic matter; MCI: mangrove connectivity index (see Meijer et al. 2021). Significant and marginally significant predictors ($\alpha = 0.05$) are shown in **bold**

Dependent variable	Parameter	Overall R ²	Coeff.	t	p
Banc d'Arguin					
<i>Senilia</i> abundance	Silt content	0.29	-0.42	-1.5	0.14
<i>Senilia</i> abundance	Salinity		-0.93	-0.72	0.47
<i>Senilia</i> abundance	Seagrass cover		0.35	2.93	0.005
<i>Senilia</i> abundance	Leaf length		-3.18	-3.1	0.003
<i>Senilia</i> length	RWE	0.39	-0.56	-1.1	0.32
<i>Senilia</i> length	Silt content		-6.1	-3.8	0.0007
<i>Senilia</i> length	Salinity		-4.5	-0.7	0.48
<i>Senilia</i> length	Seagrass cover		-0.77	-1.27	0.21
<i>Senilia</i> length	Leaf length		0.41	0.7	0.5
Bijagós Archipelago					
<i>Senilia</i> abundance	OM content	0.1	-1.45	-1.97	0.05
<i>Senilia</i> abundance	MCI		3.12	2.45	0.01
<i>Senilia</i> length	Mudflat productivity	0.14	17.2	1.9	0.06
<i>Senilia</i> length	Salinity		-1.6	-2.6	0.01

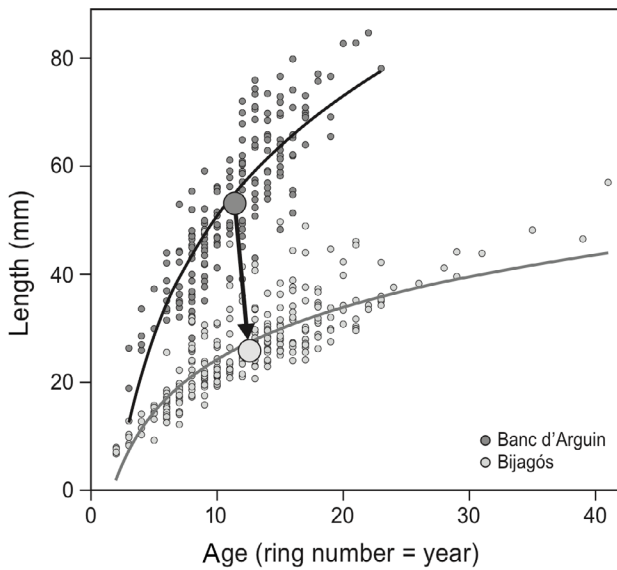


Fig. 4. Size-for-age distribution of 2 *Senilia senilis* populations under different human exploitation pressures: unharvested in Banc d'Arguin National Park (Mauritania) and harvested by locals in the Bijagós archipelago (Guinea-Bissau). Black arrow: schematic change in the centroid means of the 2 populations (n = 196 for Banc d'Arguin and n = 324 for Bijagós). With regular harvest, the size of older and matured individuals appears to become smaller compared to unharvested individuals

periences one rainy season that is warm and with low salinity and high turbidity, which is likely to cause a temporal reduction in shell growth followed by a growth mark deposition (Okera 1976). Similarly, it has been shown that the growth marks of *Senilia* are formed once a year in various sub-Saharan estuaries in Sierra Leone (Okera 1976) and Senegal (Debenay et al. 1994), including Delta du Saloum (Azzoug et al. 2012) in close proximity to Bijagós. These sub-Saharan tidal systems are fringed by mangroves and have many geomorphological similarities to Bijagós (Okera 1976, Azzoug et al. 2012). Nonetheless, weak growth marks are sometimes also deposited in response to irregular environmental stressors (Debenay et al. 1994). Thus, the number of annual growth marks reported here for Bijagós may have been slightly overestimated if the irregular weak marks occurred and were obvious enough to be counted.

The second uncertainty comes from using distance to the Geba River as a proxy for salinity. Obviously, the distance from the river mouth will also affect the amount of suspended organic material, turbidity, and anthropogenic contaminants. All these factors are known to affect the growth of bloody cockles. Thus, the variation in growth attributed to the distance to the Geba River is not exclusively related to salinity (see Section 4.3). Nevertheless, a remote sensing analysis of salinity indeed showed that *Senilia* is exposed to a more saline environment in Banc d'Arguin compared to Bijagós (Fig. S1). It seems that

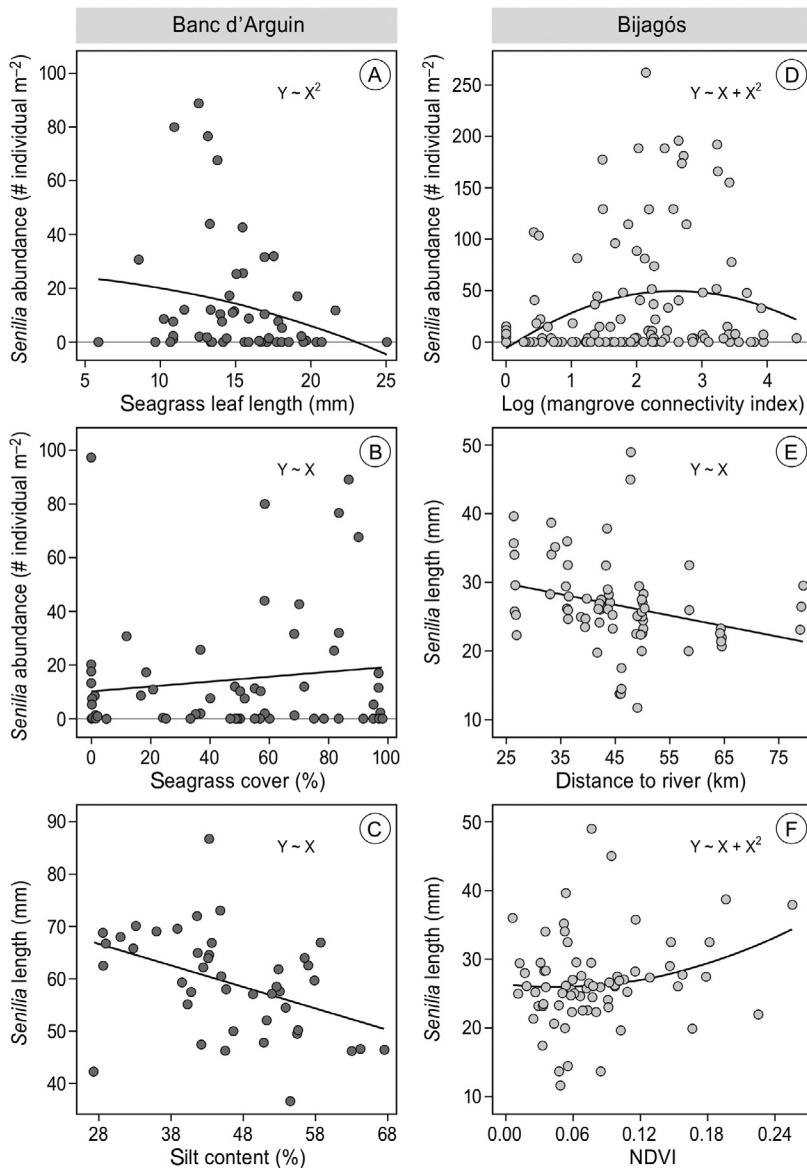


Fig. 5. Relationships between the abundance and length of the African bloody cockle *Senilia senilis* and the environmental variables that significantly predicted its distribution (Table 2) in (A,B,C) Banc d'Arguin and (D,E,F) Bijagós. (E) Distance to river is a proxy for salinity; (F) NDVI is a proxy for mudflat productivity

Senilia of Banc d'Arguin experience, on average, no seasonal change in salinity, while in Bijagós there is a clear seasonal trend with a peak just before the rainy season (Fig. S1). Nonetheless, the model showed only relatively small seasonal variation in salinity (~3 PSU) in Bijagós.

4.2. Recruitment

Senilia recruitment has been suggested to be controlled to a large extent by rainfall (Okera 1976, Wolff

et al. 1987), as the genus is believed to be of a brackish origin (see Wolff et al. 1987). This is important, as the Banc d'Arguin is a saline environment with no freshwater discharge, whereas the Bijagós archipelago is an active estuary that receives prominent river discharges. In our comparison, smaller size classes (0–10 mm) were more abundant in Bijagós than Banc d'Arguin, suggesting that recruitment was higher in the wetter than the latter drier site. This finding also agrees with earlier observations by Regalla et al. (2013), who found many small individuals (0–5 mm) in Bijagós (with regular rainfall), and by Wolff et al. (1987), who hardly encountered smaller individuals (0–10 mm) in a particularly dry string of years at Banc d'Arguin. Similarly, in Roebuck Bay, a dry region with seasonal rains, a bloody cockle species, *Anadara granosa*, recruited during the wet season (de Goeij et al. 2003). On this basis, we infer that recruitment of *Senilia* happens in Bijagós during each wet season, leading to denser populations, but only occasionally happens in Banc d'Arguin, i.e. when the irregular and scarce rainfall gives a window of opportunity (Ahmedou et al. 2008).

4.3. Growth

What can explain the immense difference in growth rates of *Senilia* between the 2 study sites, with shell lengths achieved at any age at Banc

d'Arguin being almost twice those at Bijagós? Let us first look at the resource base for *Senilia*, i.e. phytoplankton concentrations. For Banc d'Arguin, existing data are in disagreement, as Sevrin-Reyssac (1983) reported chlorophyll *a* (chl *a*) values ranging from 0.3–0.7 mg m⁻³, and values ranging from 0.1–1.7 mg m⁻³ in a separate study (Sevrin-Reyssac 1984), whereas along the edge of the Banc d'Arguin intertidal system, van Camp et al. (1991) reported values >20 mg m⁻³. In Bijagós, chl *a* values ranging from 1–9 mg m⁻³ (Berrit & Rehert 1977) and 0.42–5.15 mg m⁻³ (Diouf et al. 1994) were also reported. If we fol-

low Sevrin-Reyssac (1983,1984), chl *a* biomass at Banc d'Arguin would be lower than at Bijagós. This notion is supported by the reported phytoplankton production at Banc d'Arguin (41–164 mg C m⁻² d⁻¹; Sevrin-Reyssac 1977) and from the surrounding waters of Bijagós (555–1500 mg C m⁻² d⁻¹; Berrit & Rehert 1977, Amorim et al. 2004). However, growth rates and sizes of *Senilia* that we measured were substantially smaller in Bijagós than in Banc d'Arguin, indicating that factors other than food may have been the cause of the observed differences in growth.

In Bijagós, the density of *Senilia* was more controlled by mudflat productivity (NDVI and MCI) and distance to the Geba River. The positive relationship between *Senilia* density and mudflat productivity could be explained by an increase in food supply in productive areas compared to poorer sites, while the negative relationship between the density of *Senilia* and distance to the Geba River could result from either a decrease in suspended OM in the water column or a decrease in freshwater input. Increasing turbidity and suspended silt content in the water have a strong effect on the sizes and performance of feeding apparatus (gills and palps) of bivalves, and consequently their biological performance (growth and reproduction) (Payne et al. 1995, Ellis et al. 2002, Drent et al. 2004, Compton et al. 2008, Dutertre et al. 2009, 2017). Filter feeders usually have larger gill (pumping) to palp (sorting) ratios compared to deposit feeders (Compton et al. 2007). In addition, filter feeders seem to invest in larger gills at the expense of palps in clear and phytoplankton-poor waters, whereas in more turbid and silt-rich water they invest more in sorting palps than in pumping gills (Payne et al. 1995, Compton et al. 2008, Dutertre et al. 2009, 2017). In response to changing food conditions, bloody cockles *A. granosa* in northwest Australia appear to make such morphological adjustments (Compton et al. 2008). The observed decrease in *Senilia* sizes with increasing silt content in Banc d'Arguin is in line with this notion and thus could explain part of the observed decrease in abundance and biomass of *Senilia* toward the Geba river mouth in Bijagós. Another possibility is the increase in human harvesting pressure toward the mainland (Geba River).

As discussed above, low salinity (as a consequence of high rainfall) may trigger reproduction. However, it can also cause harm to already established cockles and reduce further growth if they have to close their valves to maintain blood osmolality and water balance (Rainer et al. 1979, Ivanovici et al. 1981, Mars-

den 2004, Wang et al. 2011, Verdelhos et al. 2015). Many closely related species to *S. senilis* (Arcidae family) respond to low salinity by closing their valves, which would reduce the energy available for growth and reproduction (Rainer et al. 1979, Ivanovici et al. 1981, Davenport & Wong 1986, Nieves-Soto et al. 2011, Mirzaei et al. 2017, Taylor et al. 2017). Low salinities can also increase calcification costs in cockles and significantly reduce shell growth (Sanders et al. 2018), as concentrations of Ca²⁺ and HCO⁻³ (elements needed for calcification) often decrease with salinity (Sanders et al. 2018, Sillanpää et al. 2020). Calcium-carbonate shells constitute most of the total mass of molluscs (Eklöf et al. 2017) that need a significant investment of their annual energy to build and maintain. Indeed, Keeling et al. (2013) found lower growth rates and smaller-sized *Senilia* in the hypersaline Muni lagoon in Ghana (~70‰) compared to the otherwise comparably low-saline lagoon at Benya (~17‰).

Pathogen and parasite infection may also reduce the growth rate and sizes of macrobenthic species, particularly sedentary filter feeders (O'Connell-Milne et al. 2016). For example, when exposed to parasite infection, European cockles *Cerastoderma edule* suffered from severe reduction in growth and even mortality (Desclaux et al. 2004). Blood cockles *A. granosa* may be infected by a number of parasites, including trematodes that could reduce growth (Uddin et al. 2011). West African bloody cockles also carry considerable numbers of pathogens, particularly in riverine estuaries (Sampson et al. 2020), that potentially could diminish their growth.

4.4. Population structure: the role of harvest

Density-dependent growth, an indicator of competition for resources, shapes many intertidal bivalve populations (Bertness 1999). Nevertheless, benthic filter feeders appear to experience less intense competition for food than deposit feeders, as they rely on the overlying phytoplankton supply for feeding instead of organic detritus in the vicinity (Levinton 1972). Indeed, previous empirical manipulation of *Senilia* densities in Banc d'Arguin did not result in noticeable intraspecific competition (van der Geest et al. 2019). However, the observed low growth rate in the relatively denser *Senilia* population in Bijagós may be an indication of density-dependent competition. The density of *Senilia* in Bijagós (35 ind. m⁻²) was double what we found in Banc d'Arguin (16 ind. m⁻²). The fact that the intertidal flats of Bijagós stock

denser populations of *Senilia* than Banc d'Arguin may seem surprising in view of the constant artisanal exploitation at Bijagós.

The most common effect of size-selective harvest in wild populations is the reduction in mean size, which will decrease the number of individuals reaching sexual maturity (Haug & Tjemsland 1986, Buxton 1993, Grift et al. 2003, Harris & Weisler 2017). Reduction in mean body size and age can decrease average reproductive output over the lifetime of organisms and negatively affect their long-term survival (Haug & Tjemsland 1986, Buxton 1993, Grift et al. 2003, Berkeley et al. 2004, Pellowe & Leslie 2020). Aswani et al. (2015) found that an area in the Solomon Islands with restricted cockle harvests had larger *A. granosa* individuals than exploited areas. In addition, the population of *Anadara* from the restricted area comprised greater numbers of sexually mature individuals and, thus, a greater potential for reproduction than in non-restricted areas (Aswani et al. 2015).

The combined increase in density with decreasing biomass and size is a sign of overexploitation in shellfish (reviewed by Harris & Weisler 2017). Unexploited mollusc populations tend to be dominated by larger and older individuals, which usually dominate in terms of biomass but not numbers (Ortega 1987, Lasiak & Field 1995, Roy et al. 2003, Jimenez et al. 2015, Harris & Weisler 2017). The consistent harvest of larger individuals by locals in Bijagós would result in relatively smaller-sized individuals compared to an unexploited area like Banc d'Arguin. In a year-round survey of *Senilia* in the Bijagós, at 3 sites with different exploitation pressures (intense, intermediate, and low), Regalla et al. (2013) showed that the intensity of the harvest was negatively associated with the maximum length class found: 50–55 mm in the minimally harvested site, 45–50 mm in the intermediate, and 40–45 mm in the intensely harvested site. Studies addressing the growth of *S. senilis* in Ghana (Keeling et al. 2013) and Sierra Leon (Okera 1976) also showed that individuals from relatively unexploited lagoons were larger than individuals from sites subjected to greater human exploitation. In addition, other Arcidae species occurring in other parts of the world are also vulnerable to overexploitation, which seems to negatively affect the standing stock biomass and length classes (McGraw et al. 2001, Stern-Pirlot & Wolff 2006, Shunula 2009). Thus, the striking differences observed in sizes and densities of *Senilia* between Banc d'Arguin and Bijagós fit established patterns of size in relation to human exploitation.

5. CONCLUSIONS

In this study, we compared the *Senilia senilis* population at the Bijagós archipelago (Guinea-Bissau), which is subjected to regular harvest by local communities, to the unharvested population at Banc d'Arguin (Mauritania). We found high densities of *Senilia* at Bijagós with individuals that were smaller-sized, slower-growing, and smaller at maturity compared to those at Banc d'Arguin. At both sites, *Senilia* densities and sizes were correlated with habitat quality indicators—mangrove connectivity and mudflat productivity at Bijagós and seagrass characteristics and sediment silt content at Banc d'Arguin. The sparse published data on *Senilia* diet (phytoplankton) suggests that the waters of Bijagós should offer more food for filter feeders than at Banc d'Arguin but that turbidity, salinity, and pathogens might reduce growth. Nonetheless, we propose that the observed smaller-sized mature individuals and denser population at Bijagós is likely shaped by size selection during human harvest. The *Senilia* population at Banc d'Arguin, on the other hand, seems to suffer most from an absence of recruitment. Apparently, it is difficult to establish new cohorts, but once established, they seem to grow well.

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