



Juvenile growth deficit as an early alert of cockle *Cerastoderma edule* mortality

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ABSTRACT: In the population dynamics of bi-phasic marine invertebrates, the fitness of one stage in the life of a cohort affects that of the following stage. This effect makes the prediction of the fate of a cohort challenging. We conducted a 22 yr monthly survey of a population of cockles *Cerastoderma edule* focussed on the juvenile stage. Two types of years were distinguished in terms of cohort longevity: a low-mortality group ('L') and a high-mortality group ('H'). The cockle shell lengths of the 0⁺ cohorts was higher in the L group, in August and September. A cohort could hereby confidently be assigned to the L or H group as soon as August. Maximum cockle abundance in the cohorts, parasite load, or date of recruitment did not discriminate the groups, while an early date for the peak of the 0⁺ cohort abundance could be related to the L group. The maximum air temperature and the chl *a* concentration in July were higher in the H group, whereas the minimum salinity during the month of September was slightly lower in the H group of years. Therefore, a juvenile shell length under a given threshold was identified as an early alert for a short lifespan of the cockle cohort. This long-term analysis contributes to the deeper understanding of the population dynamics of bi-phasic invertebrates. The success of juveniles is not solely related to the intensity of recruitment or mortality by predation, but could also be linked to their fitness, their growth rates appearing as a proxy.

KEY WORDS: *Cerastoderma edule* · Growth · Mortality · Juvenile · Cohort

1. INTRODUCTION

The fate of bi-phasic marine invertebrate populations is a major concern in the study of population dynamics (Feller et al. 1992, Beukema & Dekker 2020). When deciphering the life cycle of these species, an important aspect is to understand how each stage of the cycle can have a significant impact on the following stage(s), a process called the 'cascade effect'. Moreover, these relationships are not only quantitative. For example, a high adult biomass is not always a guarantee of good juvenile recruitment, and intense recruitment does not necessarily lead to a high number of adults. This reflects the complexity of the stock-recruitment relationship (Beukema et al. 2010, Bohn et al. 2013, Magalhães et al. 2016). A

peak in bivalve or polychaete planktonic larvae abundance may successfully predict the period of benthic recruitment, but its intensity (number of recruits per m²) is less foreseeable (Feller et al. 1992). Indeed, the fitness of each stage within the life cycle is important for a cohort lifespan and depends on biotic and abiotic factors. 'Carry-over effects' have been defined when environmental factors occurring during pre-metamorphic stages affect post-metamorphic stages in terms of fitness of both juveniles and adults. Carry-over effects can be divided into 2 periods: 'maternal effects', i.e. adult conditioning influences offspring quality, and 'latent effects', which describe the influence of offspring fitness on the subsequent fate of juveniles and adults (Pechenik 2006, Calado & Leal 2015). Several carry-over effect exam-

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ples concern bi-phasic invertebrates. When competent marine gastropod larvae (*Crepidula fornicata*) are reared under food-limited conditions, the resulting juveniles display reduced growth (Pechenik et al. 1996). Warm sea temperature and low phytoplankton concentration impact the echinoid planktonic larvae stage, which relies on phytoplankton as a source of food (Feehan et al. 2018); this has also been observed for planktonic larvae of certain crab species (e.g. *Carcinus maenas*) (Rey et al. 2016). Temperature and food availability are usually considered to be the most relevant factors shaping larval performance and survival (Rey et al. 2019). After recruitment, most species with benthic post-metamorphic stages undergo high mortality rates (Keough & Downes 1982, Gosselin & Qian 1997, Hunt & Scheibling 1997), with a particularly strong predation pressure (Mileikovsky 1974, Ejdung & Elmgren 1998). High growth performance subsequently becomes an efficient strategy to escape many predators (Reise 1978, 1985, Andresen et al. 2013), which again is closely related to food availability and temperature (Smaal et al. 1986, Laing et al. 1987, Dowd 1997, Smaal 1997). Furthermore, early life stages are also vulnerable to abiotic stress, particularly those of molluscs and echinoderms (Przeslawski et al. 2015).

In the present work, we ignored the carry-over effects and focussed on the post-recruitment period. We concentrated on the short temporal segment of bi-phasic life-cycle species spanning from recruitment to the first months of benthic life. Our biological model is one of the most prevalent bivalve species along north-eastern Atlantic coasts, the edible cockle *Cerastoderma edule*. The cockle provides numerous ecosystem services (Carss et al. 2020) and is a particularly important food resource (Kamermans & Smaal 2002, Fahy et al. 2005, Ferreira et al. 2007, Ponsero et al. 2009, Pronker et al. 2015). The cockle is also an important ecosystem engineer species (Goñi-Urriza et al. 1999, Ciutat et al. 2006, Rakotomalala et al. 2015, Cozzoli et al. 2020) and a dominant prey species for many shore birds (Norris et al. 1998, Beukema & Dekker 2006). Populations of cockles display large stock fluctuations with episodic mass mortality events (Beukema & Dekker 2005, 2020, Burdon et al. 2014). The origin of such mass mortality is sometimes related to diseases (Jonsson & André 1992, Thieltges 2006, Carrasco et al. 2011), but most of the time, these events are unpredictable and unexplained.

Banc d'Arguin (southwest France) is a well-documented area where cockles and their trematode parasites have been sampled monthly since 1998. Cockle density and biomass fluctuate, with a clear decline

occurring from 2012 to 2019 (Magalhães et al. 2016). Recently, Magalhães et al. (2016) showed that a recruitment failure would explain a short cohort lifespan. Indeed, when the recruitment density was <500 individuals (ind.) per m², the corresponding cohort did not survive for more than 4 mo. However, this prediction was tarnished by a few exceptions. In 2001, the cohort disappeared within 4 mo although a recruitment peak of 5051 ind. m⁻² was observed, and in 1998 the cohort survived for more than a year, with a recruitment peak of <200 ind. m⁻². These authors found that there were 2 kinds of cohorts: those that did not survive longer than 6 mo and those that lived for at least 1 yr and showed no strict relationship with recruitment intensity. Therefore, the early prediction of a 0⁺ cohort lifespan remains challenging and is of prime importance for stakeholders with regard to exploited species (Mahony et al. 2020).

Based on a 22 yr database, our objective was firstly to identify one or more population dynamics traits of early benthic life (maximum density, length at a given month, and growth rate) that would rapidly predict the fate of a cohort: (1) Maximum peak of recruitment (density) is an important factor to be tested. The density of the early stages of recruitment can determine the relative abundance of adults as long as the post-settlement mortality is not too severe (Beukema et al. 2010, Magalhães et al. 2016). (2) The date of occurrence of this recruitment peak and the shell length on a given date are also of importance due to the subtle relationship between the biology of cockles and environmental factors. For prey as well as suspension feeders, different shell lengths (and ages) promote different interactions with predators (Reise 1978, 1985, Sanchez-Salazar et al. 1987, Mascará & Seed 2000) and primary producers (Kang et al. 1999, Karlsson et al. 2003). Moreover, these interactions necessitate the spatial and temporal co-occurrence of the species (Sprung 2001, Strasser & Günther 2001, Dekker & Beukema 2014). (3) Finally, the individual growth rate is also a major parameter influencing population dynamics. Cockles display a strong phenotypic plasticity in terms of growth (Jensen 1992, de Montaudouin 1996), with individuals from the same shell length class displaying a shell length increment varying by a factor of up to 5 within a 10 mo monitoring period (de Montaudouin et al. 2012a). Such inter-individual variability has also been observed for spat of Manila clam *Ruditapes philippinarum* (Tamayo et al. 2011). A growth deficit can maintain cockles for a long time period within a length range that is particularly vulnerable to different factors such as predation (Reise 1985, Sanchez-

Salazar et al. 1987, Andresen et al. 2013) and parasitism (de Montaudouin et al. 2012b).

Secondly, we aimed to identify environmental factors discriminating the 2 categories of 0⁺ cohorts i.e. short-lived cohorts disappearing within 6 mo of benthic life or long-lived cohorts lasting for more than 1 yr: (1) Temperature influences cockle physiology (Ong et al. 2017) and, consequently, growth and survival (Sobral & Widdows 1997). Global warming could impact these variables either directly (metabolism) or indirectly (food availability, pathogens, and predator occurrence) (Beukema & Dekker 2005, 2020). The studied cockle population in Arguin is intertidal and withstands high summer temperatures. At this site, sediment temperature often reaches 32°C at low tide, while the maximum is 23°C at high tide (de Montaudouin et al. 2003). Thus, both air and water temperatures were analysed. However, we only selected the maximal values per month, as episodic heat waves during summer can have detrimental effects on benthic fauna (Pansch et al. 2018). (2) Cockles accommodate brackish and hyper-haline waters with salinity ranging from 11 to 45 (Rygg 1970). Considering that the usual range of salinity is narrow in Banc d'Arguin, i.e. 34 to 35 (Auby et al. 1999), a sudden low salinity event could affect cockle populations (Kater et al. 2006, Peteiro et al. 2018). This is why we focused on the minimal salinity values recorded each year between June and September. (3) Food limitation is commonly considered to be a major factor affecting growth (Smaal et al. 1986, Smaal 1997). In the present case, all the cockles were sampled at a similar tidal level, meaning that the effect of immersion time should not have been significant (de Montaudouin 1996, Navarro et al. 1998). In terms of food availability, the mean monthly chl *a* concentration, a proxy of phytoplankton concentration, was used rather than extreme values, as the concentrations were highly variable at the hourly scale and cockles can compensate for low or null ingestion periods (e.g. during low tide) with a high ingestion period at phytoplankton peaks (Ibarrola et al. 2000). (4) Several trematode parasite species use cockles as intermediate hosts (de Montaudouin et al. 2009). Juvenile cockles are not suitable hosts for trematodes using cockles as first intermediate hosts (sporocyst stage) (Magalhães et al. 2015, 2020). By contrast, very small cockles (ca. 2 mm) can be infected by trematodes as second intermediate hosts (metacercariae stage) (Wegeberg et al. 1999), which affects their growth (de Montaudouin et al. 2012a) and survival (Wegeberg & Jensen 1999). However, small cockles are usually characterized by low infec-

tion abundances (0 to 50 metacercariae per cockle) because they have only lived for a short time, display a low filtration rate (which is the main route of infestation), and provide little tissular space (Mouritsen et al. 2003, Desclaux et al. 2004, Gam et al. 2009). Arguin is known for its high diversity of trematodes in cockles (de Montaudouin et al. 2000, 2021), thus justifying the need to investigate trematode infection. (5) Finally, cockles represent prey for many predators, in particular crabs (Sanchez-Salazar et al. 1987, Romano et al. 2011), shrimp (Dekker & Beukema 2014), finfish (Reise 1977), and birds (Johnstone & Norris 2000, Stillman et al. 2005). Among these potential predators, the only available data in Banc d'Arguin concerned *Calidris canutus*, a sandpiper reputed to be a significant predator of juvenile cockles (Sturbois et al. 2015).

2. MATERIALS AND METHODS

The main strategy we used was to measure population dynamics traits and the biotic and abiotic factors influencing the cockle 0⁺ cohort and its environment, from recruitment (May and June) to December of the same year.

2.1. Study area and sampling

The sampled population of cockle *Cerastoderma edule* was situated in Banc d'Arguin (Fig. 1). This small sandy island is located at the entrance of Archon Bay, a 180 km² lagoon along the southwest Atlantic coast of France (44° 40' N, 1° 10' W). Banc d'Arguin is a National Reserve with semi-sheltered intertidal sandflats which occasionally harbour a population of cockles. The sediment is composed of sands with a median grain size of 330 µm (de Montaudouin & Lanceleur 2011). The salinity is rather constant (34 to 35), while the water temperature fluctuates between 9.5°C in winter and 21.5°C in summer. The temperature range in the sediment is wider and varies from -0.2 to 32°C. The tide is semi-diurnal, with a height of between 0.9 and 4.9 m (Gasiat 1989).

The macrobenthic intertidal fauna at Banc d'Arguin has been described previously (Bachelet & Dauvin 1993, Desclaux 2003, Do et al. 2011), as well as the community of trematode parasites in molluscs (de Montaudouin et al. 2000, Desclaux 2003, Gam et al. 2009, Do et al. 2011, Magalhães et al. 2015, 2020). Conversely, birds have been counted by the reserve

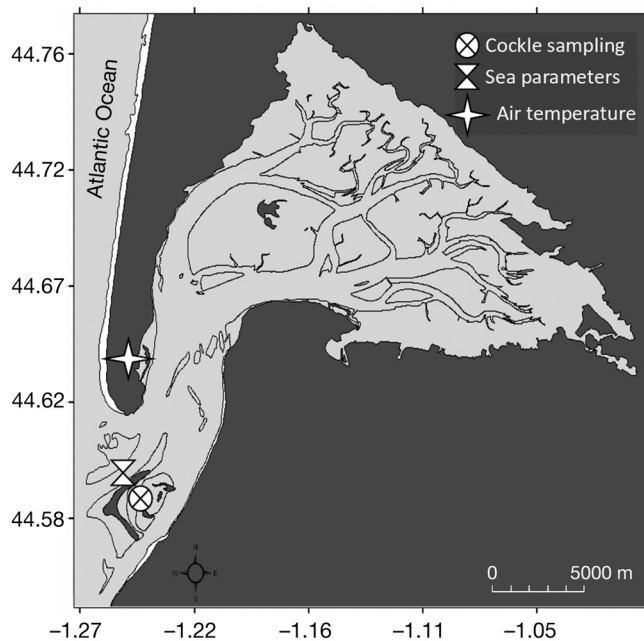


Fig. 1. Arcachon bay (France) and the different sampling areas

rangers but there are very few publications on this topic (Davant 1967, Campredon 1976).

From January 1998 to December 2019 (a period of 22 yr), cockles were collected every month at low tide using six 0.25 m² quadrats aligned along a 100 m transect parallel to the water border, between 0.5 and 2.0 m above low tide level. Samples were sieved with 1 mm mesh. Cockles were counted and every shell length was measured to the nearest lower mm with a vernier calliper.

2.2. Cohort analysis, recruitment and growth

Along the Banc d'Arguin, cockles were recruited from May to June (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m679p085_supp.pdf). The first step of this study was to identify 2 groups of years: the years during which the cockle cohort (0⁺) survived for at least for 1 yr (low-mortality years, L) and the years when the 0⁺ cohort disappeared before the month of November of the recruiting year (high-mortality years, H).

Monthly length–frequency histograms were analysed using the Bhattacharya method to discriminate the different cohorts present in the data set (Bhattacharya 1967). Each cohort was followed, when possible, for 1 yr (May 0⁺ to April 1⁺). To do so, the software package FISAT II (FAO-ICLARM stock as-

essment tool) was used (Gayanilo et al. 2005). Modal class progression analysis (MPA) identifies cohorts by decomposing the polymodal size distribution into its normal distribution components (Fig. S1). Cohorts were assumed to 'exist' when their density was ≥ 10 ind. m⁻² and to be single when the separation index was > 2 between 2 consecutive shell size classes (Gayanilo et al. 2005). In the present study, recruits were defined as the first individuals, after their settlement in the sediment, that were caught by a 1 mm mesh sieve.

The recruitment occurrence was defined when at least 2 juveniles per m² were sampled (corresponding to the date of occurrence). The first recruitment peak was defined when at least 10 juveniles per m² were sampled (corresponding to the date of recruitment). The dates were transformed into the number of days since January 1 of the studied year. Finally, the maximal 0⁺ cockle abundance derived from the cohort analysis, between May and September, was estimated.

The shell growth of recruits was calculated as the Absolute Growth Rate (AGR), which can adequately describe short segments of growth curves (especially for shell lengths) (Lugert et al. 2016): $AGR = (\text{final shell length} - \text{initial shell length}) / (\text{elapsed time})$.

2.3. Air and sea parameters

Air temperature was obtained by Météo France (<https://donneespubliques.meteofrance.fr/>) at a station situated 7 km from the cockle-sampling site in Banc d'Arguin (Fig. 1), where acquisition frequency is 1 value per min. Maximal daily temperature was selected and the mean of these 30 to 31 data points was calculated for each month between June and September, which was the critical period for cockle growth and survival.

The water temperature, salinity, and chl *a* concentration between June and September of each year were obtained from the ARCHYD program (<https://www.ifremer.fr/Recherche/Departements-scientifiques/Focus/Quadriges>). Their monitoring station was situated 1.5 km from the cockle sampling area (Fig. 1), in the same water mass (the external neritic water body). In this program, samples are usually collected on 4 different sampling dates, with 2 dates at low tide and 2 dates at high tide. The maximal sea temperature (°C) and the minimal salinity were extracted each month from these 4 different sampling dates. The mean chl *a* concentration (µg l⁻¹) was calculated per month based on these 4 different sampling dates.

2.4. Parasites

Trematodes were identified in the 0⁺ cockle cohort every month. However, in the present study, only July was selected because cockle shell length in the H (high-mortality) and L (low-mortality) years were still in the same range (4.6 vs. 7.6 mm, respectively). This prevented shell length from being a confounding factor, as infection is often positively related to shell size (de Montaudouin et al. 1998, 2005, Mouritsen et al. 2003, Thieltges & Reise 2006) and/or particularly sensitive to certain sizes (de Montaudouin et al. 2012b). Ten cockles per 0⁺ cohort were dissected each year in July, squeezed between 2 glass slides and observed under a stereomicroscope. Only the metacercariae stage was observed in juvenile cockles (Magalhães et al. 2015, 2020), which allowed us to calculate the mean parasite abundance (mean number of metacercariae per cockle) (Bush et al. 1997).

2.5. Predators (birds)

In spring and early summer, the only bird able to forage juvenile cockles in Banc d'Arguin is a sandpiper, the knot *Calidris canutus*. The National Reserve has collected data from regular monthly surveys since 1998. The rangers visit this offshore reserve on at least 1 day per month and record the highest number of birds counted during that day, or between different days of a given month when appropriate. The investigated area includes the whole reserve, approximately 43 km².

2.6. Data analysis

Our data set was composed of 26 independent variables (cockle average length, dates of recruitment, maximal abundance, temperatures, salinity, chl *a* concentration, trematode parasite abundance and prevalence, and sandpiper abundance) recorded over 22 yr. Each year was labelled as L for a low or H for a high mortality level.

The normality assumptions for the variables were evaluated with the Shapiro-Wilks test. The assumption of homoscedasticity between the L and H series was evaluated with the Fisher-Snedecor test. A large proportion of our series fitted neither the normality nor the homoscedasticity hypothesis, and the sample size was relatively low; therefore, rank-based non-parametric approaches were used.

An analysis of similarities (ANOSIM) was first applied to test for the possible statistical significance of dissimilarity matrices between the L and H groups in the complete set of data ($p = 0.008$). Non-metric dimensional scaling (NMDS) was carried out on the data set with a 'Canberra' dissimilarity matrix. Our data were relatively heterogeneous, and Canberra dissimilarity, which treats species pairs more equally than Bray-Curtis dissimilarity, assigns weights according to the species abundance. The ordination solution dimension was 2 (the mortality factor is either H or L). The significance of the NMDS fitted vectors was assessed using the permutation of environmental variables with envfit.

Statistical analyses were performed with R (version 4.04) (R Core Team 2021). The vegan (Oksanen et al. 2020), GGally (Schloerke et al. 2021), ggplot2 (Wickham 2016), and ggrepel (Slowikowski 2021) packages were also used for NMDS and plotting the data.

In order to estimate the probability (from 0 to 1) of a year belonging to a low mortality year (L) according to the mean shell length of cockles (cohort 0⁺) in August and September, logistic regressions were fitted using a generalized linear model and the following equation model:

$$Probability = \frac{1}{1 + e^{-(a+b \times L)}} \quad (1)$$

where L is the mean cockle shell length (mm), and a and b are constants.

All hypothesis tests were conducted with a probability (alpha) of 5%.

3. RESULTS

NMDS discriminated the 2 groups of years, L and H, with a stress of 0.13 (Fig. 2). The structuring factors were the median shell lengths in July, August, and September; the minimum salinity in September; the chl *a* concentration in July; and the date of the 0⁺ cockle abundance peak (Table 1).

3.1. Cohort mortality

Two groups of years were defined from cohort abundance monitoring: one set of 9 years when the 0⁺ cockle cohort survived for at least 1 yr (L, for low-mortality years: 1998, 2000, 2003–2004, 2006–2007, 2009–2011), and another set of 13 years when the 0⁺ cockle cohort collapsed before the month of November of their first year (H, for high-

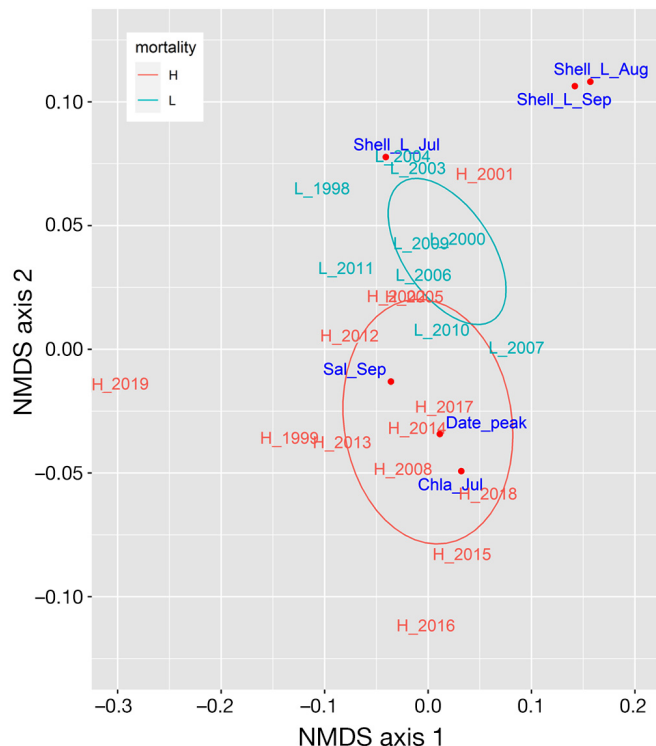


Fig. 2. NMDS separating years of low mortality (starting with 'L_') from years of high mortality (starting with 'H_'). Significant explicative factors (Table 1) are named: Shell_L_month: median cockle shell length for a given month; Date_peak: median date of the abundance peak for juvenile cockles; Sal_Sep: median minimum weekly salinity in September; Chla_Jul: median chl *a* concentration in July. Stress = 0.13

mortality years: 1999, 2001–2002, 2005, 2008, 2012–2019) (Figs. 3 & 4). Belonging to a group of years did not depend on the cockle abundance during the maximum peak of the cohort ($p > 0.05$) (Table 1) which ranged between 111 ind. m^{-2} in 2008 and 5051 ind. m^{-2} in 2001, both years belonging to the H group. However, the chance of success of the 0^+ cohort was higher when this abundance peak occurred earlier in the year, since the median date was June 30 for L (ranging from April 12 to July 11) and July 8 for H (ranging from June 2 to July 22) (Table 1) ($p < 0.05$). In 2001, the peak of 0^+ cockles was the highest ever observed, although this was a H year. This is partly why 2001 was separated from the other H years in the NMDS (Fig. 2). In the 1998 cohort, a sudden increase in cockle abundance in January 1999 was related to sediment migration and heavy rain during a winter storm, gathering more cockles in the sampling area (Fig. 3).

3.2. Cohort growth

The 2 distinct sets of years (L and H) corresponded to 2 different sets of growth curves (Figs. 5 & 6). In June, both groups of cohorts had a similar median shell length i.e. 2.8 and 3.1 mm, respectively (Table 1). After this, there was a deficit of growth in the H group, with smaller shell lengths in July (4.6 vs. 7.3 mm in L) and particularly in August (5.5 vs. 12.8 mm) and September (6.9 vs. 16.4 mm) (Fig. 6, Table 1). Between July and September, the AGR was 4.3 times higher for the L group ($33 \mu m d^{-1}$) than the H group ($142 \mu m d^{-1}$). In August, the probability of belonging to the L group increased with mean shell length of the 0^+ cohort, following a logistic regression ($p < 0.05$, $R^2 = 0.70$) (Fig. 7a). When the mean shell length of the 0^+ cohort reached 12 mm, the probability of surviving beyond December was 80 %, and was close to 100 % if the size reached 15 mm. In September, the probability of belonging to the L group also increased with mean shell length of the 0^+ cohort, following a logistic regression ($p < 0.05$, $R^2 = 0.58$) (Fig. 7b). When the mean shell length of the 0^+ cohort reached 16 mm, the probability of surviving beyond December was 80 %, and was close to 95 % if the size reached 19 mm. The differences in AGR were independent of the recruitment date (median = May 19) ($p > 0.05$) (Table 1).

Apart from the high maximum peak of the H cohort in 2001 (see Section 3.1.), this year is separated from the other H years because the median cockle shell length in August was rather high for this group (12.1 mm, while the median for the H group was 5.5 mm).

3.3. Environmental parameters

The monitoring period extended each year from June to September. The median monthly maximum air temperature ranged between 23.7°C in June and 25.8°C in August (Table 1). The hottest month was July 2006 (28.7°C) (see Fig. S2 in the Supplement). In July, the monthly maximum air temperature was 1.8°C higher during the H years (26.0 vs. 24.2°C in the L years, $p = 0.053$), with the last 8 years presenting temperatures higher than 25°C and all qualifying as H years (Table 1, Fig. S2). The median monthly maximum sea temperature ranged between 20.0°C in June and 22.4°C in August, with similar values for L and H years (Table 1). The hottest month was July 2013 (25.7°C) (Fig. S3). The median monthly minimum salinity ranged between 33.1 in June and 34.1 in August and September. In September, this factor

Table 1. Comparison of the 2 groups of years, i.e. L for low-mortality years (N = 9) and H for high-mortality years (N = 13), for different population dynamics parameters and environmental variables. Determination coefficient (R^2) and p-value (p) from NMDS analysis are provided. Significant results are shown in **bold** (p < 0.05)

Parameter	Unit	Month	Median (L vs. H)	R^2	p
Maximum cockle density ('0 ⁺ peak')	ind. m ⁻²		724 > 355	0.27	0.073
Date of 0 ⁺ occurrence			1 May < 13 May	0.01	0.942
Date of recruitment			13 May < 21 May	0.10	0.395
Date of '0⁺ peak'			30 Jun < 8 Jul	0.45	0.008
Shell length	mm	Jun	2.8 < 3.1	0.03	0.721
		Jul	7.3 > 4.6	0.43	0.003
		Aug	12.8 > 5.5	0.70	0.001
		Sep	16.4 > 6.9	0.49	0.002
Maximum air temperature	°C	Jun	23.6 < 23.9	0.07	0.513
		Jul	24.2 < 26.0	0.25	0.053
		Aug	25.8 < 25.9	0.01	0.732
		Sep	24.0 > 23.5	0.03	0.866
Maximum sea temperature	°C	Jun	20.0 = 20.0	0.13	0.269
		Jul	22.1 < 22.3	0.11	0.344
		Aug	22.4 > 22.2	0.02	0.847
		Sep	20.6 < 21.0	0.05	0.603
Minimum salinity		Jun	33.6 > 32.3	0.18	0.150
		Jul	33.8 > 33.2	0.15	0.175
		Aug	34.2 > 33.8	0.14	0.216
		Sep	34.2 > 34.0	0.28	0.042
Chl a	µg l ⁻¹	Jun	1.88 > 1.81	0.17	0.177
		Jul	1.51 < 1.71	0.34	0.026
		Aug	1.28 < 1.49	0.16	0.181
		Sep	1.66 < 1.98	0.03	0.728
Parasite abundance	Metacercariae per cockle	Jul	1.6 > 0.7	0.09	0.362
Predator abundance	Birds per month	Jun	38 > 4	0.20	0.099

contributed to the difference between the L and H groups (Fig. 2, Table 1). However, the low R^2 value indicated that the variance in cockle mortality could moderately be explained by the variance in salinity (p < 0.05). H years were systemically less salty than L years, this difference decreasing from June (1.3) to September (0.2) (Fig. S4). The median monthly concentration of chl a ranged between 1.47 µg l⁻¹ in August and 1.84 µg l⁻¹ in June. In July, the variance in cockle mortality explained 33% of the chl a variance (p < 0.05) (Table 1, Fig. S5).

3.4. Parasites and predators (birds)

For trematode parasites, the median number of trematode metacercariae in cockles was low and similar between the L and H years, with a median of 1.3

metacercariae per cockle in July between 1998 and 2019 (Table 1). The maximum mean parasite abundance occurred in July 2018, with 14.2 metacercariae per cockle (Fig. S6).

The *Calidris canutus* abundance in June fluctuated between 0 and 270 (in 2004). It became rare in July until the upcoming spring. The median numbers of *C. canutus* in June were similar between the L and the H years (Table 1, Fig. S7).

4. DISCUSSION

This study focused on the first 4 mo of cockle benthic life (summer time) in order to identify environmental drivers or population dynamics traits that could predict the lifespan of a given cohort. For the assessment of some ecological issues related to ecosystem changes, monitoring is the only way to obtain meaningful results, as demonstrated by the 50 yr monitoring of intertidal areas in the Wadden Sea (Beukema & Dekker 2020). During our 22 yr monthly survey, 2 contrasting groups of years were identified: the years when the 0⁺ cohort did not survive beyond October of the recruiting year and the years when this cohort lasted for at least 1 yr. Departing from a similar shell length in June, the

stunted growth of juveniles between July and September was a clear sign of the upcoming disappearance of the 0⁺ cohort and can be used as an early alert for cockle population decline. The critical threshold values of shell length in August and September beyond which the probability of low mortality is low is certainly a local value, but the existence of such a threshold should be verified in other ecosystems.

The median weekly maximum sea temperature was similar between both groups of years. By contrast, the monthly median daily maximum air temperatures in July were higher in the H years (but p = 0.053). This trend, as well as the fact that the last 8 years (2012 to 2019) belonged to the H group, are arguments in favour of a positive relationship between mortality and global warming. The cockle is particularly sensitive to summer heat waves. In the

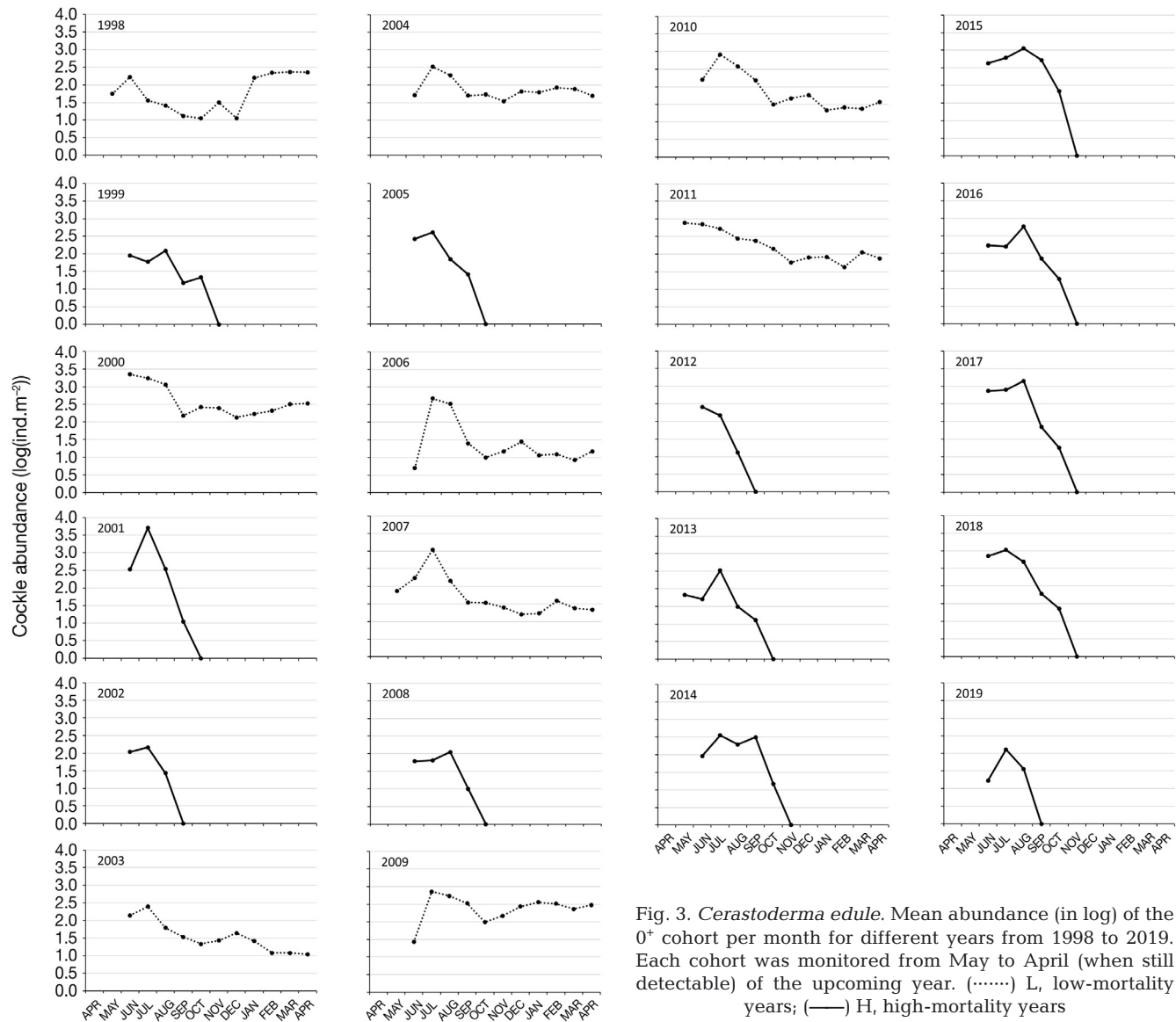


Fig. 3. *Cerastoderma edule*. Mean abundance (in log) of the 0^+ cohort per month for different years from 1998 to 2019. Each cohort was monitored from May to April (when still detectable) of the upcoming year. (.....) L, low-mortality years; (—) H, high-mortality years

scenario where these heat waves increase in intensity and frequency, cockle populations have been identified to be particularly at risk due to the temperature effect on burrowing, scope for growth, and survivorship (Domínguez et al. 2021). However, cockles can support daily and seasonal temperature variations that are buffered in an oceanic site such as Arguin, even though the sediment temperature at low tide can easily rise above 30°C during summer (de Montaudouin et al. 2003). Also, an effect of trophic resource is possible. For example, in the Manila clam *Ruditapes philippinarum* from a subarctic lagoon in Japan, shell growth in culture was significantly stimulated by an above ambient temperature, in interaction with trophic resource availability (Yoon et al. 2013). Arcachon Bay is known as a mesotrophic

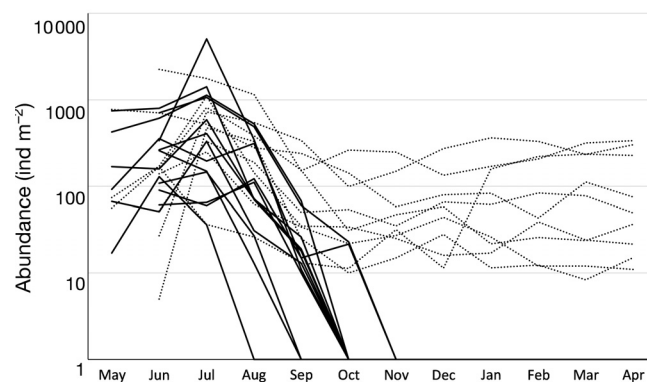


Fig. 4. *Cerastoderma edule*. Mean abundance of the 0^+ cohort per month for different years from 1998 to 2019. (.....) L, 9 low-mortality years; (—) H, 13 high-mortality years

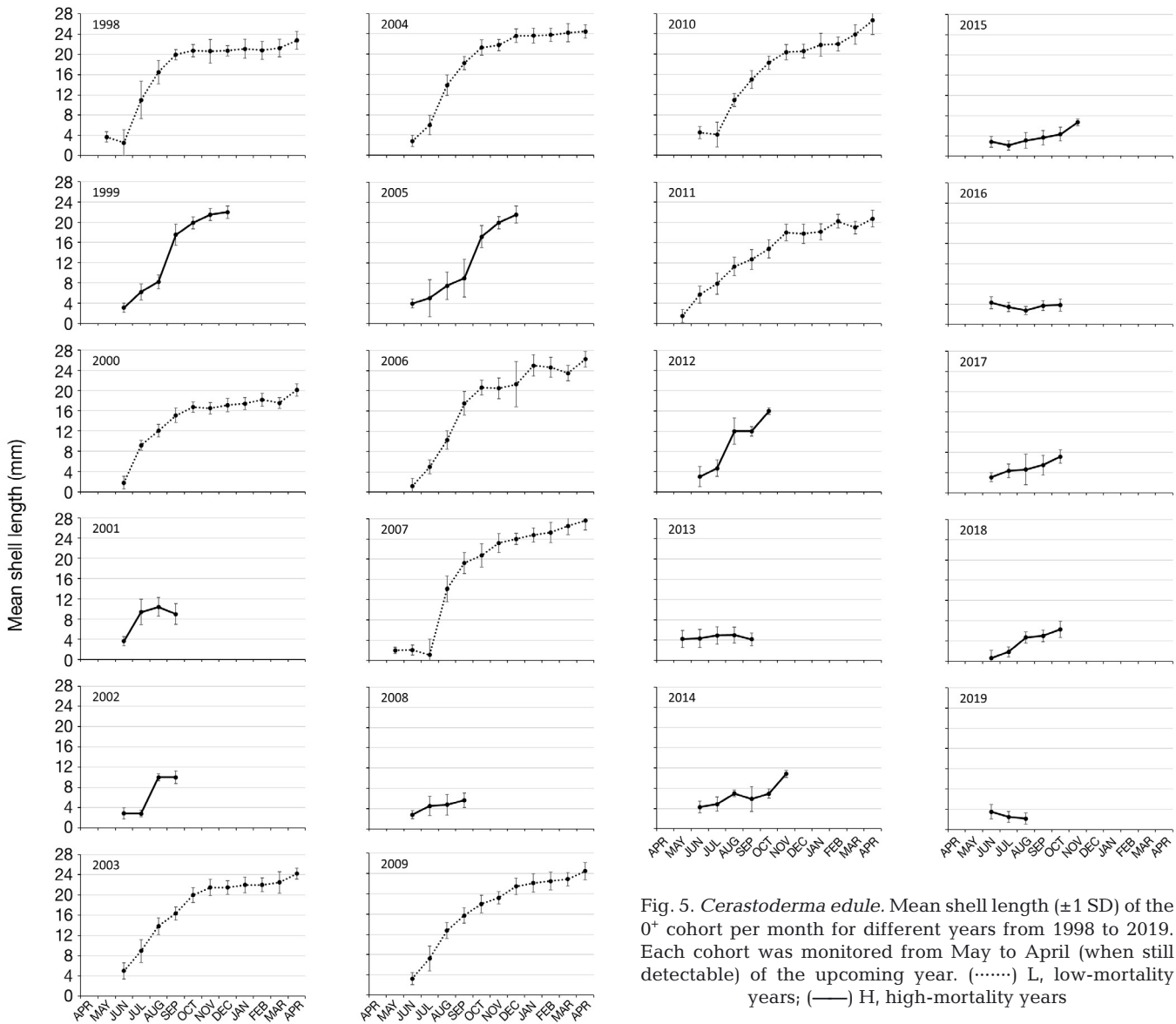


Fig. 5. *Cerastoderma edule*. Mean shell length (± 1 SD) of the 0⁺ cohort per month for different years from 1998 to 2019. Each cohort was monitored from May to April (when still detectable) of the upcoming year. (.....) L, low-mortality years; (—) H, high-mortality years

lagoon with an annual chl *a* concentration of approximately $2 \mu\text{g l}^{-1}$ (Glé 2007). Food availability is a major factor controlling suspension-feeder growth. In *Mytilus edulis*, phytoplankton depletion is closely related to bivalve performance and shell growth in particular (Filgueira et al. 2014). The trophic resource can also be microphytobenthos (Kang et al. 2006), as for the clams *Ruditapes* spp., with current driving microphytobenthos resuspension (Sobral & Widdows 2000, Abe et al. 2015). The diversity of potential trophic resources can make it difficult to correlate chl *a* concentration and bivalve growth (Jung et al. 2019). This was particularly the case in July, when the concentration was higher in years of high mortality (and stunted growth). In the present study, chl *a* (median value of 4 samples per month), a proxy

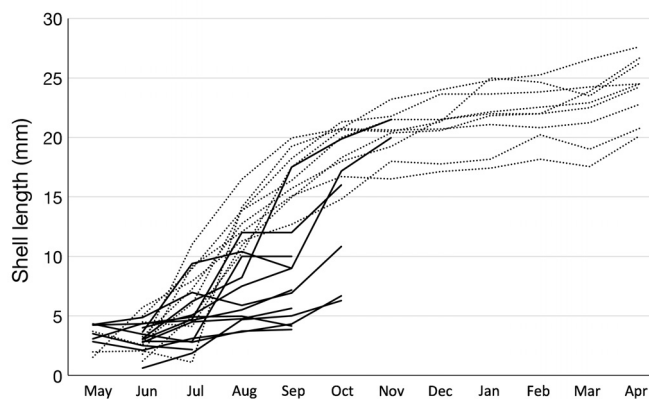


Fig. 6. *Cerastoderma edule*. Mean shell length of 0⁺ cohort per month for different years from 1998 to 2019. (.....) L, 9 low-mortality years; (—) H, 13 high-mortality years

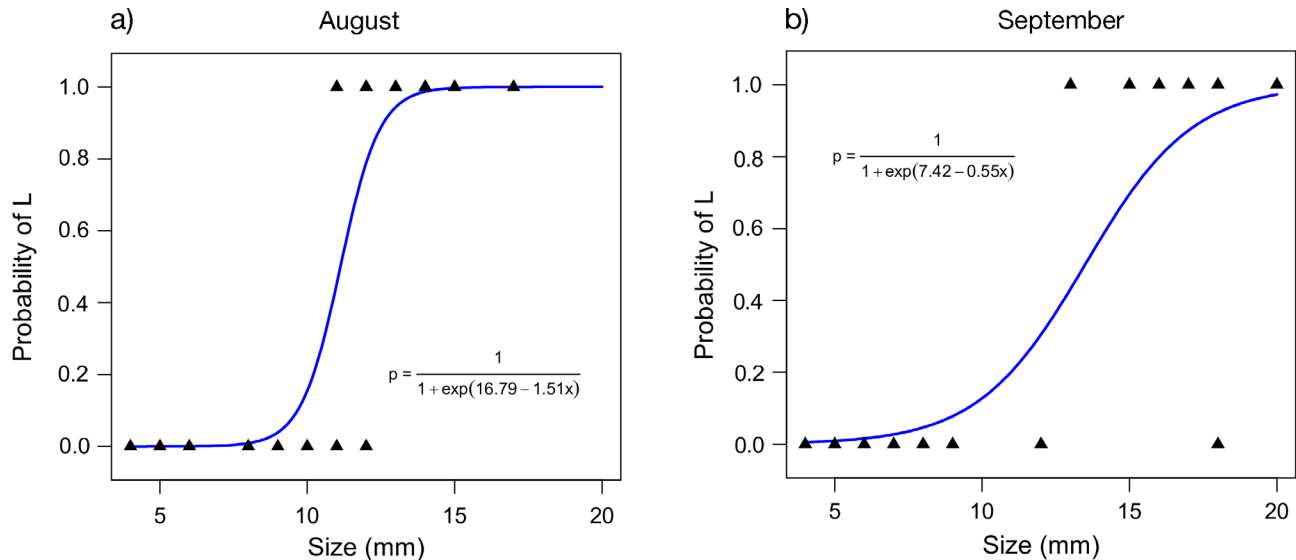


Fig. 7. *Cerastoderma edule*. Logistic regression describing the probability of a 0^+ cockle cohort belonging to the low-mortality group (L) according to mean shell length (in mm) reached (a) in August and (b) in September. Each triangle represents one or more year(s)

for primary production, was very similar in both year groups (except in July) and could not explain the growth difference. The concentrations were rather low throughout the whole sampled period but were characteristic of Arcachon Bay (Glé 2007) and known as a possible cause of the generalized low growth rates of bivalves in this lagoon (de Montaudouin et al. 2016). Food limitation can also be caused by prolonged emersion, which is a major driver of suspension-feeder growth. Apart from some exceptions (Kamermans et al. 1992), cockle growth is slower at the upper tidal level due to the shorter immersion time and lower food availability (Richardson et al. 1980, Peterson & Black 1987, 1988, Jensen 1992, de Montaudouin 1996). In our study, however, cockles were always sampled at the same tidal level. Moreover, in many suspension-feeding molluscs, not only the quantity but also the quality of food may affect growth performance. This is the case for the northern quahog *Mercenaria mercenaria* and the eastern oyster *Crassostrea virginica* in Peconic estuary (NY, USA), whose growth rates are often correlated with the density of specific cells or quality of seston rather than bulk measures of the global phytoplankton (Wall et al. 2013)

The minimum salinity in Banc d'Arguin was highest in August. September was the only summer month for which the median weekly minimum salinity was different between both groups of years. The cockle has been reported in very different salinity contexts, from estuaries, where seasonal differences in salinity can reach 16, to bays, where this differ-

ence is less than 4 (Correia et al. 2020), as in Banc d'Arguin. Indeed, cockles in Banc d'Arguin could be poorly acclimated to a salinity deficit and particularly sensitive in the H years. However, the most significant deficit occurred in September, which is too late to influence juvenile cockle growth. Our salinity sampling frequency was certainly too low to detect short and extreme events (4 samples per month), but it is noteworthy that the sampling site is far from the rivers and that the influence of the Atlantic Ocean prevents high salinity fluctuations. The infection by trematodes was a good candidate to explain the differences in cockle growth and cohort mortality. In adult cockles, a 23 % growth deficit due to the trematode *Himasthla interrupta* has been calculated (de Montaudouin et al. 2012a). A similar growth deficit has been observed in other trematode-infected bivalves, such as *Austrovenus stutchburyi* (O'Connell-Milne et al. 2016) and *Mytilus edulis* (Bakhmet et al. 2017). However, this effect was possibly the result of interactions with other unidentified factors, because no effect of *H. interrupta* on cockle growth was observed experimentally (Wegeberg & Jensen 2003). In the present study, the abundance of metacercariae was normally low due to the young age and small size of the cockles and did not display any significant difference between both groups of years. Finally, size-dependent predation could have been responsible for the apparent deficit of growth, which would be related to the predation of the larger individuals. In the bay of Saint-Brieuc, out of 1001 collected droppings, 66 % contained remains of *Cerastoderma*

edule, meaning that this bivalve is a favourite prey (Sturbois et al. 2015). However, *Calidris canutus* forage shell lengths ranging from 9 to 15 mm (Dekinga & Piersma 1993) and were certainly less interested in smaller cockles, which dominated in the H years. Our results suggest that *C. canutus* were not responsible for the depletion of the young cockle stock in the H years.

In the future, beyond the analysis of these factors one by one, the effects of their interactions should be studied because the environment is under multifactorial control and organisms undergo not one but several sources of stress (de Montaudouin et al. 2010, Paul-Pont et al. 2010). A meta-analysis has shown that synergistic interactions of different stressors are dominant amongst marine bi-phasic invertebrates and that molluscs and echinoderms are particularly vulnerable to abiotic stress (Przeslawski et al. 2015). For example, the effect of parasites on their host (infectivity, mortality) can be modulated by temperature (Marcogliese 2001, Thieltges & Rick 2006) and oxygen content (Marcogliese 2001). Studying the effect of salinity, temperature, and pH on cockle biochemical performance, Magalhães et al. (2018) observed higher biochemical alterations in parasitized cockles exposed to all experimental stressful conditions of extreme salinity, temperature, and acidity (pH).

In conclusion, slow individual shell growth in the first months of benthic life appears to be a sign of the low probability of cohort survival. This finding precludes the notion that high mortality could only be related to a sudden and brutal event such as sediment burial, predation, or fishing/poaching, suggesting that it is rather the conclusion of a fitness deficit. Among other factors that could be tested, pollutants and diseases could explain bad fitness and stunted growth. Oyster farming is present in Arguin and the quality of the water is regularly monitored, with no particular worry regarding pollutants, including microbiological and phytotoxin contamination (IFREMER 2017). On the other hand, the present study was restricted to trematodes, although cockles in the Banc d'Arguin and elsewhere can be affected by many other infectious diseases, including disseminated neoplasia (Le Grand et al. 2010, Longshaw & Malham 2013, Díaz et al. 2016, de Montaudouin et al. 2021).

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