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 a cohort's life affects the fitness of the following stage, from the planktonic larval stage to the adult stage. This cascading effect, also called the carry-over effect, makes the prediction of a cohort's fate challenging. We conducted a 22-year monthly survey of a population of cockles *Cerastoderma edule* in a single station of Banc d'Arguin (France) and focussed on the first months of their benthic life. On each sampling occasion, cockles were counted and measured and their trematode burden was estimated by dissection. Cockle cohorts recruited in the period May–June, and cohorts were identified and monitored using the Bhattacharya method. Two types of years were clearly distinguished in terms of cohort longevity: a low-mortality group ("L") gathering 9 years during which the 0^+ cohort survived for at least 12 months and a high-mortality group ("H") composed of 13 years during which the 0^+ cohort disappeared before its first month of November. When comparing both types of years, the median cockle shell lengths were similar in June. By contrast, in the month of July and more particularly August and September, the 0^+ cohort's median shell length was higher in the

"L" group than in the "H" group. Following this result, a cohort could hereby confidently be assigned to the "L" or "H" group as soon as August and more robustly by September. Intrinsic factors such as maximum cockle abundance in the cohorts, parasite load, and date of recruitment did not discriminate the groups, while an early date for the peak of the 0^+ cohort's abundance could be related to the "L" group. The median values of environmental factors that could also potentially discriminate these two groups of years were collected weekly and extracted from institutional databases, namely air and water maximum temperature, minimum salinity, mean Chl *a* concentration, and maximum number of avian predators (sandpipers). The maximum air temperature as well as the mean 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 than in the "L" group of years.

Therefore, a juvenile shell length under a given threshold (in August and/or in September) was identified as an early alert for a short lifespan of the cockle cohort. This long-term analysis contributes to the deeper understanding of bi-phasic invertebrates' population dynamics, in particular during their early benthic life. The success of juveniles during this period is clearly not solely related to the intensity of recruitment or mortality by predation, but could also be linked to the fitness of these juveniles, 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 occuring during pre-metamorphic stages affect post-metamorphic stages in terms of fitness of both juveniles and adults. Carry-over effects can be divided into two 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 examples concern bi-phasic invertebrates. When competent marine gastropods 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 was also observed for planktonic larvae of certain crab species (*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 pressure of predation (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

1   stages are also vulnerable to abiotic stress, in particular molluscs and echinoderms (Przeslawski et al.

2   2015).

3   In the present work, we ignored the carry-over effects and focussed on the post-recruitment period.

4   Indeed, we concentrated on the short temporal segment of bi-phasic life-cycle species spaning from

5   recruitment to the first months of benthic life. Our biological model is one of the most prevalent

6   bivalve species along north-eastern Atlantic coasts, the edible cockle *Cerastoderma edule*. The cockle

7   provides numerous ecosystem services (Carss et al. 2020) and is a particularly important food

8   resource (Kamermans & Smaal 2002, Fahy et al. 2005, Ferreira et al. 2007, Ponsero et al. 2009,

9   Pronker et al. 2015). The cockle is also an important ecosystem engineer species (Goñi-Urriza et al.

10   1999, Ciutat et al. 2006, Rakotomalala et al. 2015, Cozzoli et al. 2020) and a dominant prey species

11   for many shore birds (Norris et al. 1998, Beukema & Dekker 2006). Populations of cockles display

12   large stock fluctuations with episodic mass mortality events (Beukema & Dekker 2005, Burdon et al.

13   2014, Beukema & Dekker 2020). The origin of such mass mortality is sometimes related to diseases

14   (Jonsson & André 1992, Thieltges 2006, Carrasco et al. 2011) but most of the time these events are

15   unpredictable and unexplained.

16   Banc d'Arguin (South West of France) is a well-documented area where cockles and their trematode

17   parasites have been sampled monthly since 1998. Cockle density and biomass fluctuate, with a clear

18   decline occurring from 2012 to 2019 (Magalhães et al. 2016). Recently, Magalhães et al. (2016)

19   showed that a recruitment failure would explain a short cohort lifespan. Indeed, when the

20   recruitment density was < 500 ind.m^{-2}, the corresponding cohort could not survive for more than 4

21   months. However, this prediction was tarnished by a few exceptions. In 2001, the cohort

22   disappeared within 4 months although a peak of 5051 recruits.m^{-2} was observed, and in 1998 the

23   cohort survived for more than a year, with a peak of recruits of < 200 ind.m^{-2}. These authors

24   indicated that there were two kinds of cohorts: those that did not survive longer than 6 months and

25   those that lived at least one year and showed no strict relationship to recruitment intensity. Then,

26   the early prediction of a 0^{+} cohort lifespan remains challenging and is of prime importance for

27   stakeholders in regard to exploited species (Mahony et al. 2020).

1   Based on a 22-year database, our objective was firstly to identify one or more population dynamics

2   traits of early benthic life (maximum density, length at a given month, and growth rate) that would

3   rapidly predict the fate of a cohort: 1) Maximum peak of recruitment (density) is an important factor

4   to be tested. The density of the early stages of recruitment can determine the relative abundance of

5   adults as long as the post-settlement mortality is not too severe (Beukema et al. 2010, Magalhães et

6   al. 2016). 2) The date of occurrence of this recruitment peak and the shell length at a given date are

7   also at importance due to the subtle relationship between the biology of cockles and environmental

8   factors. For prey as well as suspension-feeders, different shell lengths (and ages) promote different

9   interactions with predators (Reise 1978, 1985, Sanchez-Salazar et al. 1987, Mascaró & Seed 2000)

10   and primary producers (Kang et al. 1999, Karlsson et al. 2003). Moreover, these interactions

11   necessitate the spatial and temporal co-occurrence of the species (Sprung 2001, Strasser & Günther

12   2001, Dekker & Beukema 2014). 3) Finally, the individual growth rate is also a major parameter

13   influencing population dynamics. Cockles display a strong phenotypic plasticity in terms of growth

14   (Jensen 1992, de Montaudouin 1996), with individuals from the same shell length class displaying a

15   shell length increment varying by a factor of up to 5 within a 10-month monitoring period (de

16   Montaudouin et al. 2012a). Such inter-individual variability was also observed for the spat of Manila

17   clam *Ruditapes philippinarum* (Tamayo et al. 2011). A deficit of growth can maintain cockles for a

18   long time period in a range of lengths that is particularly vulnerable to different factors such as

19   predation (Reise 1985, Sanchez-Salazar et al. 1987, Andresen et al. 2013) and parasitism (de

20   Montaudouin et al. 2012b).

21   Secondly, we aimed to identify environmental factors discriminating the two categories of 0^+ cohorts

22   *i.e.*, short-lived cohorts disappearing within 6 months of benthic life or long-lived cohorts lasting for

23   more than one year: 1) Temperature influences cockle physiology (Ong et al. 2017) and,

24   consequently, growth and survival (Sobral & Widdows 1997). Global warming could impact these

25   variables either directly (metabolism) or indirectly (food availability, pathogens, and predator

26   occurrence) (Beukema & Dekker 2005, Beukema & Dekker 2020). The studied cockle's population in

27   Arguin is intertidal and withstands high summer temperatures. In this site, sediment temperature

1   often reaches 32°C at low tide, while the maximum is 23°C at high tide (de Montaudouin et al. 2003).

2   Thus both air and water temperatures were analysed. However, we only selected the maximal values

3   per month, considering that during summer episodic heat waves can have detrimental effects on

4   benthic fauna (Pansch et al. 2018). 2) Cockles accommodate brackish and hyper-haline waters with

5   salinity ranging from 11 to 45 (Rygg 1970). Considering that the usual range of salinity is narrow in

6   Banc d'Arguin i.e., 34–35 (Auby et al. 1999), a sudden low salinity event could affect cockle

7   populations (Kater et al. 2006, Peteiro et al. 2018). This is why we focused on the minimal salinity

8   values recorded each year between June and September. 3) Food limitation is commonly considered

9   to be a major factor affecting growth (Smaal et al. 1986, Smaal 1997). In the present case, all the

10   cockles were sampled at a similar tidal level, meaning that the effect of immersion time should not

11   have been significant (de Montaudouin 1996, Navarro et al. 1998). In terms of food availability, the

12   mean of monthly Chl *a* concentration, proxy of phytoplankton concentration, was used rather than

13   extreme values, as these concentrations were highly variable at the hourly scale and cockles can

14   compensate for low or null ingestion periods (e.g., during low tide) with a high ingestion period at

15   phytoplankton peaks (Ibarrola et al. 2000). 4) Several trematode parasite species use cockles as

16   intermediate hosts (de Montaudouin et al. 2009). Juvenile cockles are not suitable hosts for

17   trematodes using cockles as first intermediate hosts (sporocyst stage) (Magalhães et al. 2015, 2020).

18   By contrast, very small cockles (ca. 2 mm) can be infected by trematodes as second intermediate

19   host (metacercariae stage) (Wegeberg et al. 1999), with effects on cockle growth (de Montaudouin

20   et al. 2012a) and survival (Wegeberg & Jensen 1999). However, small cockles are usually

21   characterized by low infection abundances (0–50 metacercariae per cockle) because they have yet

22   experienced a short life, display a low filtration rate (which is the main route of infestation), and

23   provide little tissular space (Mouritsen et al. 2003, Desclaux et al. 2004, Gam et al. 2009). Arguin is

24   known for its high diversity of trematodes in cockles (de Montaudouin et al. 2000, de Montaudouin

25   et al. 2021), thus justifying the need to investigate trematode infection. 5) Finally, cockles represent

26   prey for many predators, in particular, crabs (Sanchez-Salazar et al. 1987, Romano et al. 2011),

27   shrimp (Dekker & Beukema 2014), finfish (Reise 1977) and birds (Johnstone & Norris 2000, Stillman

1 et al. 2005). Among these potential predators, the only available data in Banc d'Arguin concerned

2 *Calidris canutus*, a sandpiper reputed to be a significant predator of juvenile cockles (Sturbois et al.

3 2015).

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6 ## 2. MATERIALS AND METHODS

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8 The main strategy we used was to measure population dynamics traits and the biotic and abiotic

9 factors influencing the cockle 0^+ cohort and its environment, from recruitment (May-June) to

10 December of the same year.

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13 ### 2.1. Study area and sampling

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15 The sampled population of cockle *Cerastoderma edule* was situated in Banc d'Arguin (Fig. 1). This

16 small sandy island is located at the entrance of Arcachon Bay, a 180-km² lagoon along the southwest

17 Atlantic coast of France (44°40'N,1°10'W). Banc d'Arguin is a National Reserve with semi-sheltered

18 intertidal sandflats which occasionally harbor a population of cockles. The sediment is composed of

19 sands with a median grain size of 330 µm (de Montaudouin & Lanceleur 2011). The salinity is rather

20 constant (34 to 35), while the water temperature fluctuates between 9.5 °C in winter and 21.5 °C in

21 summer. The temperature range in the sediment is wider and varies from -0.2 °C to 32 °C. The tide is

22 semidiurnal, with a height of between 0.9 and 4.9 m (Gassiat 1989).

23 The macrobenthic intertidal fauna at Banc d'Arguin has previously been described (Bachelet &

24 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, Magalhaes et al. 2020). Conversely, birds have been counted by the reserve rangers but there are very few publications on this topic (Davant 1967, Campredon 1976).

From January 1998 to December 2019 (a period of 22 years), 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 calliper.

2.2. Cohort analysis, recruitment and growth

Along the Banc d'Arguin, cockles were recruited from May to June (S1). The first step of this study was to identify two 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 analyzed using the Bhattacharya method to discriminate the different cohorts present in the data set (Bhattacharya 1967). Each cohort was followed, when possible, for one year (May 0^+ to April 1^+). To do so, the software package FISAT II (FAO-ICLARM stock assessment 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 (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 two 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.m^{-2} were sampled (corresponding to the date of occurrence). The first recruitment peak was defined when at least 10 juveniles.m^{-2} were sampled (corresponding to the date of recruitment). The dates were transformed into the number of days since January 1st 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 = [final shell length - initial shell length]/[elapsed time].

2.3. Air and sea parameters

Air temperature was obtained by Meteo France (https://donneespubliques.meteofrance.fr/) in a station situated 7 km from the cockle sampling site in Banc d'Arguin (Fig. 1) where acquisition frequency is one value per minute. Maximal daily temperature was selected and the mean of these 30–31 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://wwz.ifremer.fr/Recherche/Departements-scientifiques/Focus/Quadrige). 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 at 4 different sampling dates, with two dates at low tide and two 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 ($\mu g.L^{-1}$) was calculated per month based on these 4 different sampling dates.

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3   **2.4. Parasites**

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5   Trematodes were identified in the 0^+ cockle cohort every month. However, in the present study, July

6   only was selected because cockle shell length in the "H" (high-mortality) and "L" (low-mortality)

7   years were still in the same range (4.6 *vs.* 7.6 mm, respectively). This prevented shell length from

8   being a confounding factor, as infection is often positively related to shell size (de Montaudouin et al.

9   1998, Mouritsen et al. 2003, de Montaudouin et al. 2005, Thieltges & Reise 2006) and/or a

10 particularly sensitive to certain sizes (de Montaudouin et al. 2012b). Ten cockles per 0^+ cohort were

11 dissected each year in July, squeezed between two glass slides and observed under a

12 stereomicroscope. Only the metacercariae stage was observed in juvenile cockles (Magalhães et al.

13 2015, Magalhaes et al. 2020), which allows us to calculate the mean parasite abundance (mean

14 number of metacercariae per cockle) (Bush et al. 1997).

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17   **2.5. Predators (birds)**

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19 In spring and early summer, the only bird able to forage juvenile cockles in Banc d'Arguin is a

20 sandpiper, the knot (*Calidris canutus*). The National Reserve has collected data from regular monthly

21 surveys since 1998. The rangers visit this offshore reserve at least one day per month and retain the

22 highest number of birds counted during that day, or between different days of the given month

23 when appropriate. The investigated area includes the whole reserve, ca. 43 km².

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2 **2.6. Data analysis**

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4 Our data set was composed of 26 independent variables (the cockle average length, dates of

5 recruitment, maximal abundance, temperatures, salinity, Chl a concentration, trematode parasites

6 abundance and prevalence, and sandpiper abundance) recorded over 22 years. Each year was

7 labelled as "L" for a low or "H" for a high mortality level.

8 The normality assumptions for the variables were evaluated with Shapiro–Wilk test. The assumption

9 of homoscedasticity between the "L" and "H" series was evaluated with Fisher–Snedecor test. A large

10 proportion of our series fitted neither the normality nor the homoscedasticity hypothesis, and the

11 sample size was relatively low; therefore, rank-based non-parametric approaches were used.

12 An analysis of similarities (anosim) was first applied to test for the possible statistical significance of

13 dissimilarity matrices between the "L" and "H" groups in the complete set of data (p=0.008). Non-

14 metric dimensional scaling (NMDS) was carried out on the data set with a "Canberra" dissimilarity

15 matrix. Our data were relatively heterogenous, and Canberra dissimilarity, which treats species pairs

16 more equally than Bray–Curtis dissimilarity, assigns weights according to the species abundance. The

17 ordination solution dimension was 2 (the mortality factor is either "H" or "L"). The significance of the

18 NMDS fitted vectors was assessed using the permutation of environmental variables with envfit.

19 Statistical analyses were performed with R (version 4.04) (R Core Team 2021). The vegan (Oksanenet

20 al. 2020), GGally (Schloerke et al. 2021), ggplot2 (Wickham 2021), and ggrepel (Slowikowski 2021)

21 packages were also used for NMDS and plotting the data.

22 In order to estimate the probability (from 0 to 1) of a year belonging to a low mortality year ("L")

23 according to the mean shell length of cockles (cohort 0^+) in August and September, logistic

24 regressions were fitted using a generalized linear model and the following equation model:

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

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

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

3

4   **3.   RESULTS**

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6   NMDS discriminated the two groups of years, "L" and "H", with a stress of 0.13 (Fig. 2). The

7   structuring factors were the median shell lengths in July, August, and September; the minimum

8   salinity in September; the Chl *a* concentration in July; and the date of the 0^+ cockle peak of

9   abundance (Table 1).

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11

12   **3.1. Cohort mortality**

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14 Two groups of years were defined from cohort abundance monitoring: one set of 9 years when the 0^+

15 cockle cohort survived at least one year ("L", for low-mortality years: 1998, 2000, 2003–04, 2006–07,

16 2009–11), and another set of 13 years when the 0^+ cockle cohort collapsed before the month of

17 November of their first year ("H", for high-mortality years: 1999, 2001–02, 2005, 2008, 2012–19) (Fig.

18 3 and 4). Belonging to a group of years did not depend on the cockle abundance of the maximum

19 peak of the cohort (p>0.05) (Table 1) which ranged between 111 ind.m^{-2} in 2008 and 5051 ind.m^{-2} in

20 2001, both years belonging to the "H" group. However, the chance of success of the 0^+ cohort was

21 higher when this peak of abundance was sooner in the year, since the median date was June 30th for

22 "L" (ranging from April 12th to July11th) and July 8th for "H" (ranging from June 2nd to July22nd) (Table

23 1) (p<0.05). In 2001, the peak of 0^+ cockles was the highest ever observed but corresponded to a "H"

24 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 two distinct sets of years ("L" and "H") corresponded to two different sets of growth curves (Fig. 5 and 6). In June, both groups of cohorts had a similar median shell length i.e., 2.8 mm and 3.9 mm, respectively (Table 1). After this, there was a deficit of growth in the "H" group, with smaller shell lengths in July (4.6 mm vs. 7.3 mm in "L") and particularly in August (5.5 mm vs. 12.8 mm) and September (6.9 mm vs. 16.4 mm) (Figure 6, Table 1). Between July and September, the absolute growth rate (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 cockle 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 to survive beyond December was of 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 cockle 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 to survive beyond December was of 80%, and was close to 95% if the size reached 19 mm. The differences in AGR were independent of the recruitment date (median = May 19th) ($p>0.05$) (Table 1).

The year 2001, apart from the high maximum peak of this "H" cohort (see Section 3.1), 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) (S2). In July, monthly maximum air temperature was 1.8°C higher during the "H" years (26.0°C vs. 24.2°C the "L" years, p=0.053), the eight last years presenting temperatures higher than 25°C and all qualifying as "H" years (Table 1, 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) (S3). The median monthly minimum salinity ranged between 33.1 in June and 34.1 in August–September. This factor in September contributed to the difference between the "L" and "H" groups (Fig. 2, Table 1). However, the low R^2 value indicated that the variance of cockle mortality could moderately be explained by the variance of the salinity (p<0.05). "H" years were systemically less salty than "L" years, this difference decreasing from June (1.3) to September (0.2) (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 of cockle mortality explained 33% of the Chl a variance (p<0.05) (Table 1, 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.cockle^{-1} (S6).

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

4. DISCUSSION

This study focused on the first four months 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-year monthly survey, two contrasting groups of years were identified: the years when the 0^+ cohort could not survive beyond October of the recruiting year and the years when this cohort could last for at least one year. 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 eight last years (2012-2019) 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 scenario where these heat waves would increase in intensity and frequency, cockle populations have been identified particularly at risk due to temperature effect on burrowing, scope for growth and survivorship (Dominguez 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 overpass 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* of a subarctic lagoon in Japan, shell growth in culture was significantly stimulated by a warmer temperature than the ambient, in interaction with the trophic resource availability (Yoon et al. 2013). Arcachon Bay is known as a mesotrophic lagoon with an annual Chl *a* concentration of ca. 2 µg.L^{-1} (Glé 2007). Food availability is a major factor controlling suspension-feeder growth. In *Mytilus edulis*, phytoplankton depletion was 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), which was the case in July in particular, as the concentration was higher in the years of high mortality (and stunted growth). In the present study, Chl *a* (median value of four samples per month), a proxy for primary production, was very similar in both groups of years (except in July) and could not explain the growth difference. The values of concentration were rather low along 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 upper tidal level due to the lower immersion and 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 was the case for the northern quahog *Mercenaria mercenaria* and the eastern oyster *Crassostrea virginica* in Peconic estuary (NY, USA), whose growth rates were often correlated with the density of specific cells or quality of seston rather than bulk measures of the global phytoplankton (Wall et al. 2013)

1 The minimum salinity in Banc d'Arguin was highest in August. September was the only summer

2 month for which the median of weekly minimum salinity was different between both groups of

3 years. The cockle has been reported in very different contexts of salinity from estuaries, where

4 seasonal differences in salinity can reach 16, to bays, where this difference is less than 4 (Correia et

5 al. 2020), as in Banc d'Arguin. Indeed, cockles in Banc d'Arguin could be poorly acclimated to a

6 salinity deficit and particularly sensitive in the "H" years. However, the most significant deficit

7 occurred in September, which is too late to influence juvenile cockle growth. Our salinity's sampling

8 frequency was certainly too low to detect short and extreme events (4 samples per month) but it is

9 noteworthy that the sampling site is far from the rivers and that the influence of the Atlantic Ocean

10 prevents from high salinity fluctuations. The infection by trematodes was a good candidate to explain

11 the difference in cockle growth and cohort mortality. In adult cockles, a 23% growth deficit due to

12 the trematode *Himasthla interrupta* was calculated (de Montaudouin et al. 2012a). A similar growth

13 deficit was observed in other trematode-infected bivalves, such as *Austrovenus stuchburyi*

14 (O'Connell-Milne et al. 2016) and *Mytilus edulis* (Bakhmet et al. 2017). However, this effect was

15 possibly the result of interactions with other unidentified factors, because no effect of *H. interrupta*

16 on cockle growth was observed experimentally (Wegeberg & Jensen 2003). In the present study, the

17 abundance of metacercariae was normally low due to the young age and small size of the cockles and

18 did not display any significant difference between both groups of years. Finally, size-dependent

19 predation could have been responsible for the apparent deficit of growth, which would have been

20 related to the predation of the larger individuals. In the bay of Saint-Brieuc, out of 1001 collected

21 droppings, 66 % contained remains of *Cerastoderma edule*, meaning that this bivalve is a favorite

22 prey (Sturbois et al. 2015). However, *Calidris canutus* forage shell lengths ranging from 9 to 15 mm

23 (Dekinga & Piersma 1993) and were certainly less interested in smaller cockles, which dominated in

24 the "H" years. Our results suggest that *C. canutus* were not responsible for the depletion of the

25 young cockle stock in the "H" years.

26 In the future, beyond the analysis of these factors one by one, the effects of their interactions should

27 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 showed 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) showed that higher biochemical alterations were observed in parasitized cockles exposed to all experimental stressful conditions in terms 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 be only 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 can 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 (I.F.R.E.MER 2017). On the other hand, in terms of diseases, 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 (de Montaudouin et al. 2021).

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1 Table 1. Comparison of the two groups of years i.e., "L" for low-mortality years (N=9) and "H" for
2 high-mortality years (N=13) for different population dynamics parameters and environmental
3 variables. Determination coefficient (R^2) and p-value (p) from NMDS analysis are provided. Significant
4 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**
Air max 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	0.866
		Sep	24.0>23.5	0.03	0.732
Sea max 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
Min 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.cockle^{-1}	Jul	1.6>0.7	0.09	0.362
Predator abundance	birds.mo^{-1}	Jun	38>4	0.20	0.099

5
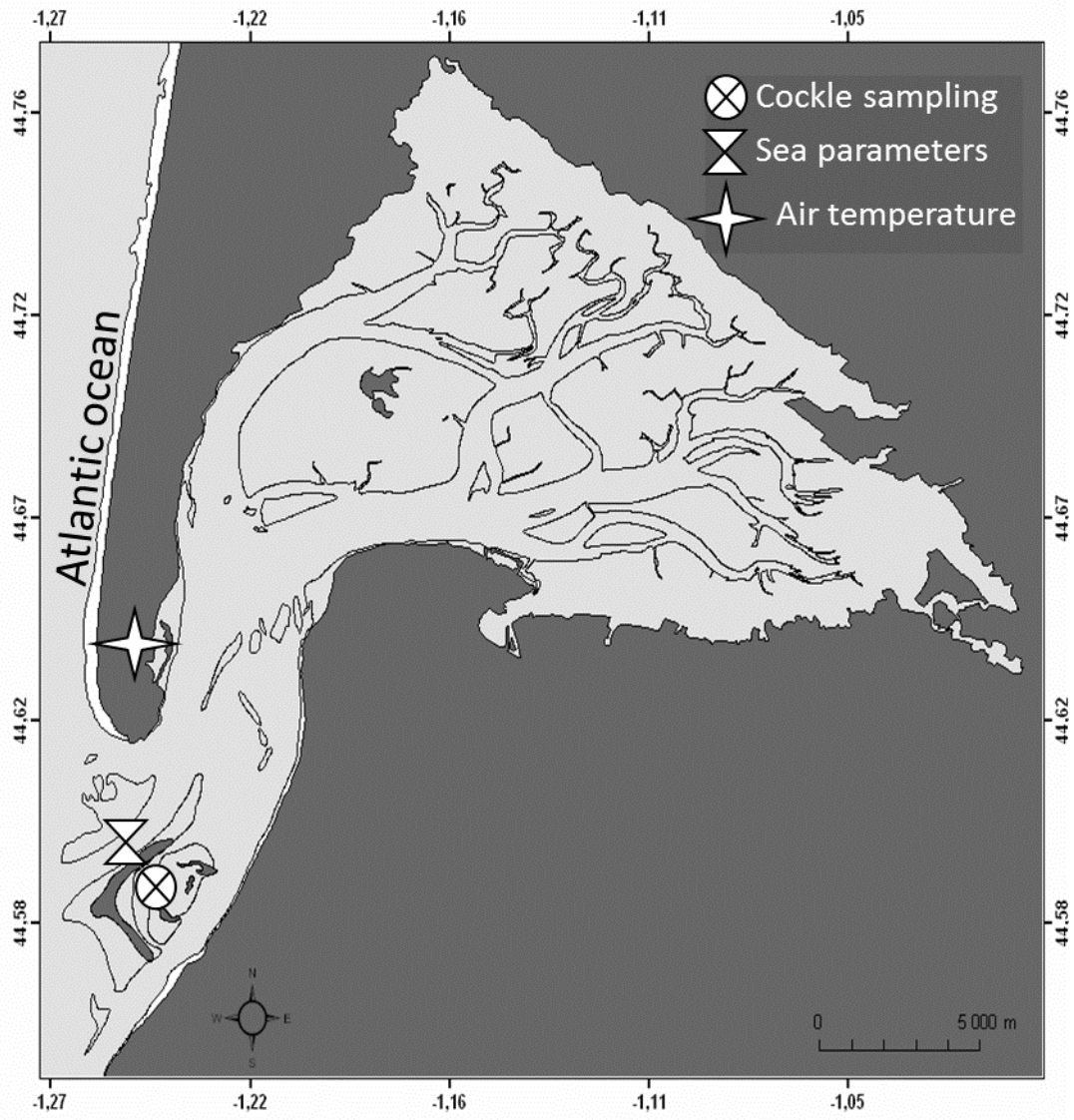
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2   Fig. 1. Arcachon bay (France) and the different sampling areas.

3

1
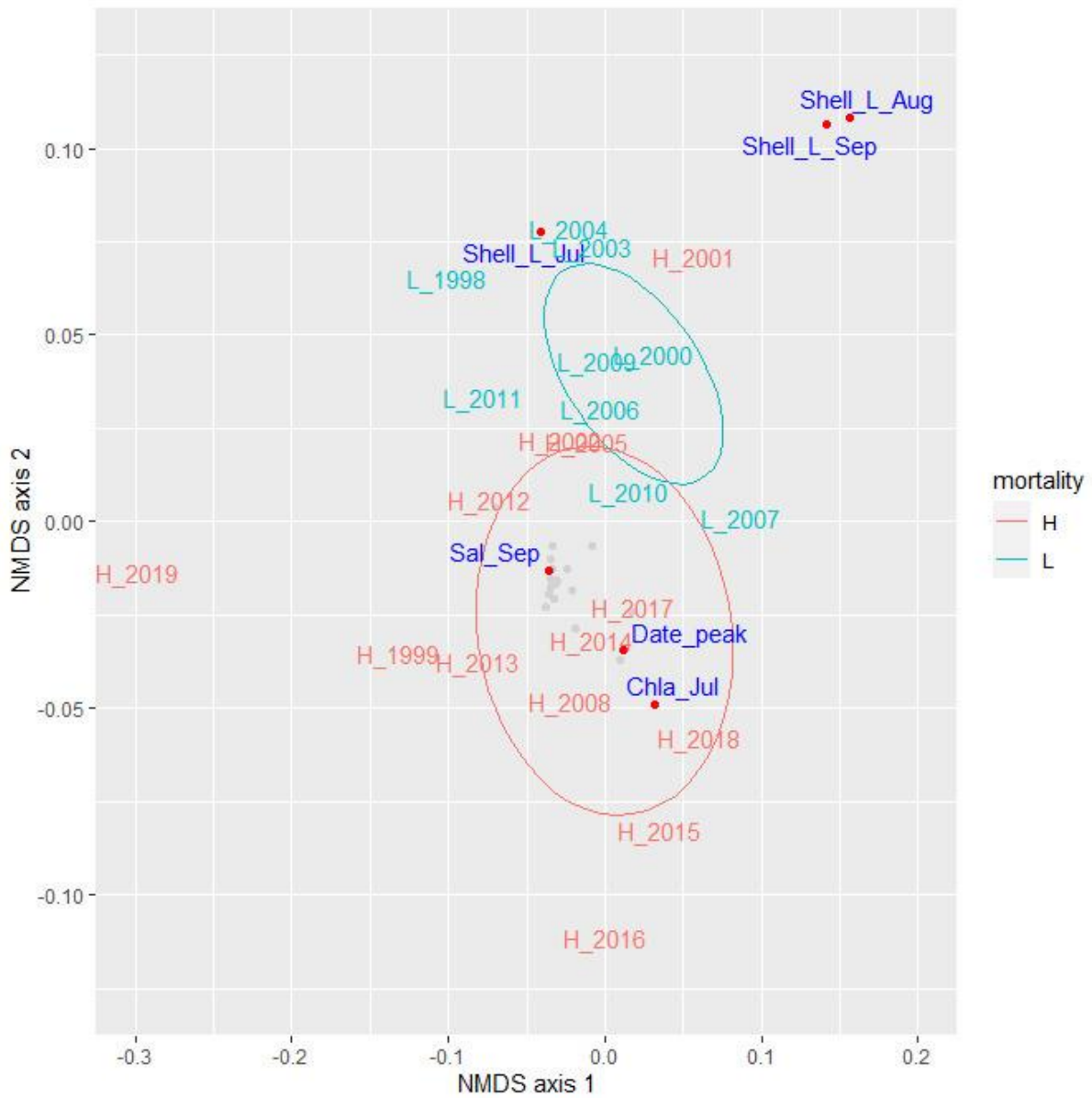
Fig. 2. NMDS separating years of low mortality (starting with "L-") from years of high mortality
(starting with "H-"). Significant explicative factors (Table 1) are named: "Shell_L_month" is the
median cockle shell length for a given month, "Date_peak" is the median date of the peak of
abundance of juvenile cockles, and "Sal_Sep" is the median minimum weekly salinity in September.
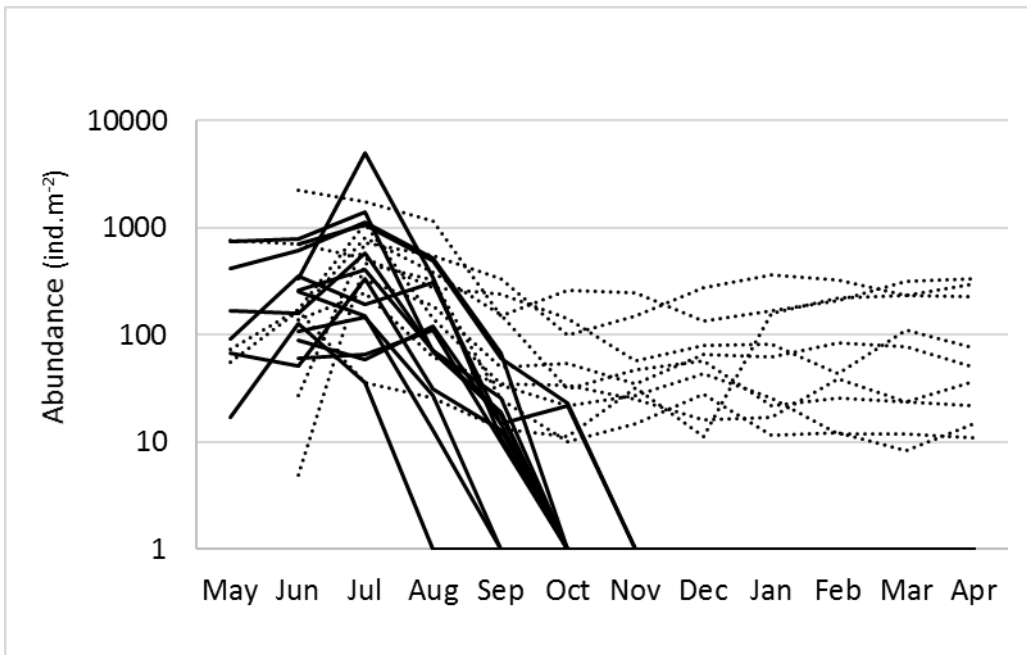Stress =0.13.
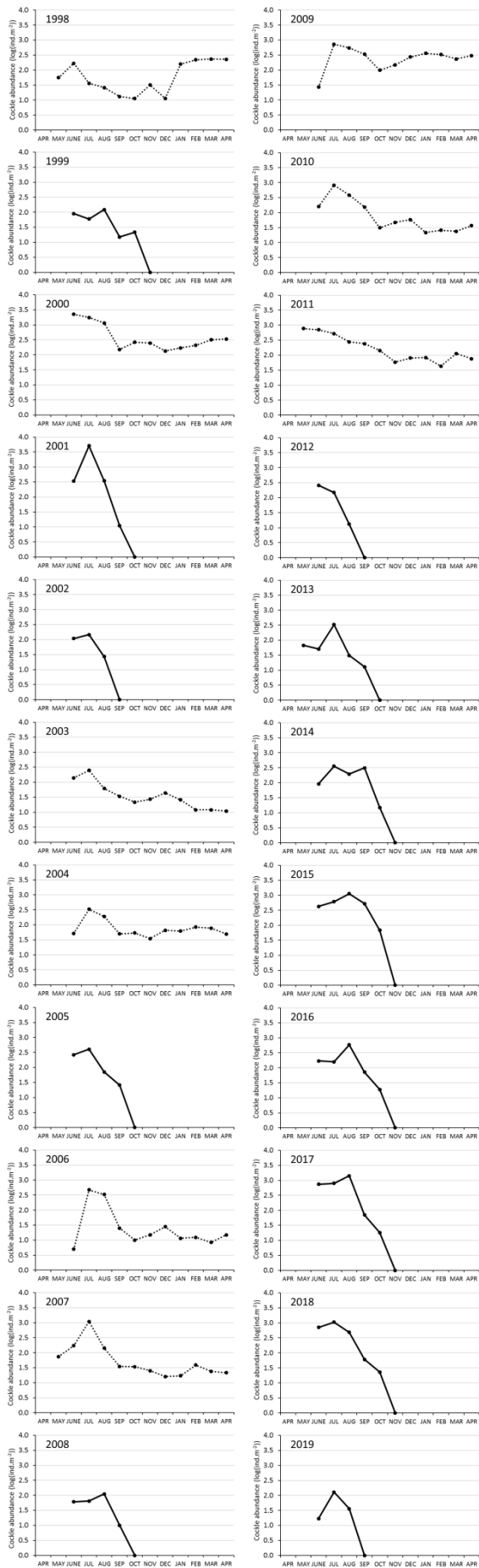
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2

1　Fig. 3. *Cerastoderma edule.* Mean abundance (in log) of the 0^+ cohort per month for different years

2　from 1998 to 2019. Each cohort was monitored from May to April (when still detectable) of the

3　upcoming year. Dashed lines: "L", low-mortality years; solid lines: "H", high-mortality years.
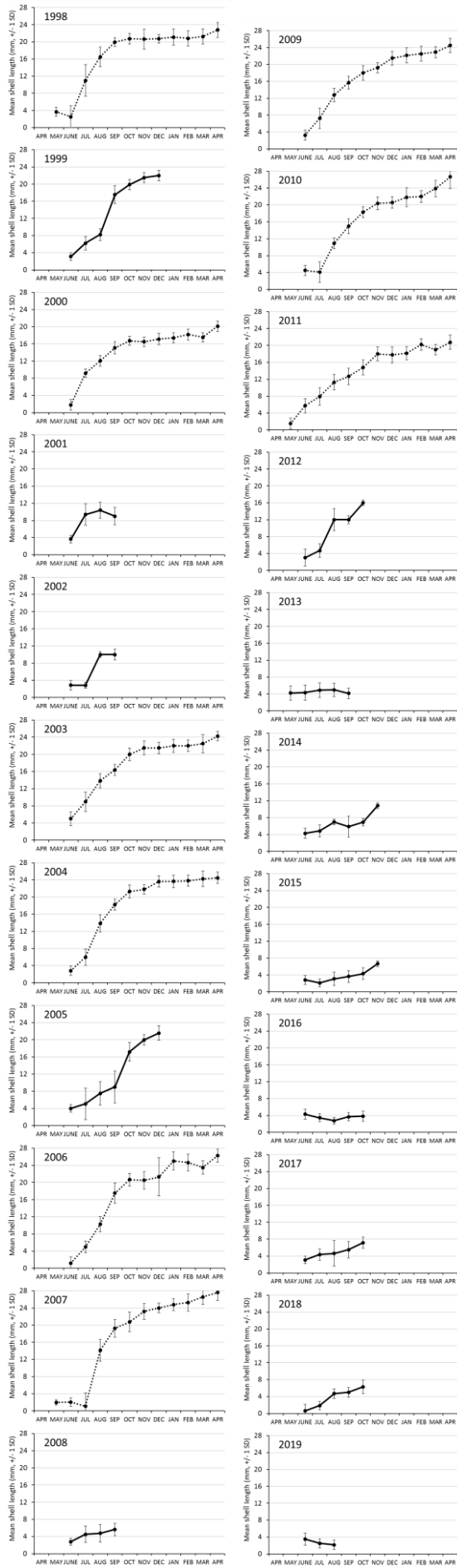
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4   Fig. 4. *Cerastoderma edule.* Mean abundance of the 0^+ cohort per month for different years from

5   1998 to 2019. Dashed lines: "L", nine low-mortality years; solid lines: "H", thirteen high-mortality
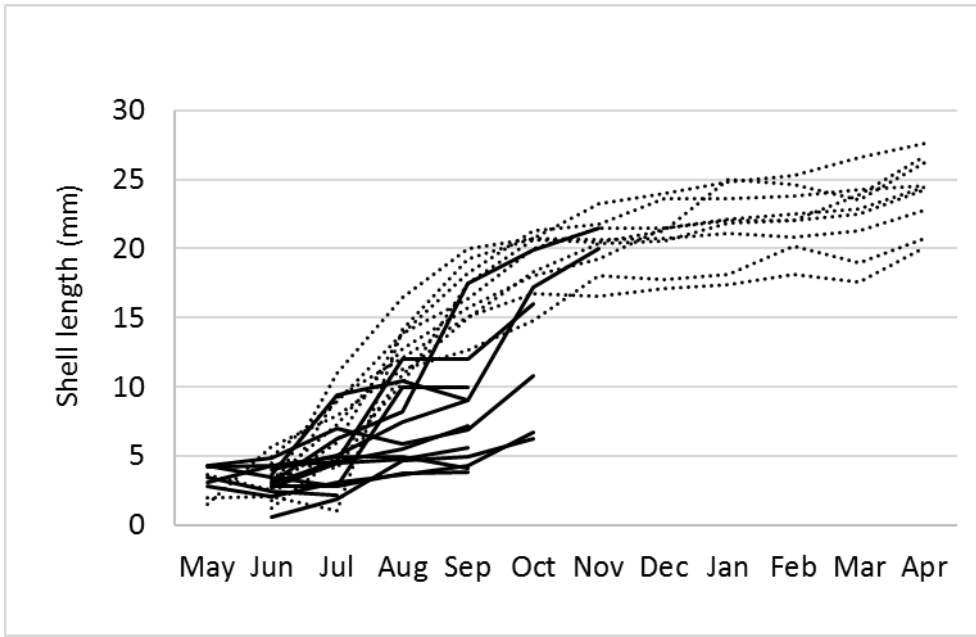
6   years.

7

1   Fig. 5. *Cerastoderma edule.* Mean shell length (+/- 1 standard deviation) of the 0^+ cohort per month

2   for different years from 1998 to 2019. Each cohort was monitored from May to April (when still

3   detectable) of the upcoming year. Dashed lines: "L", low-mortality years; solid lines: "H", high-
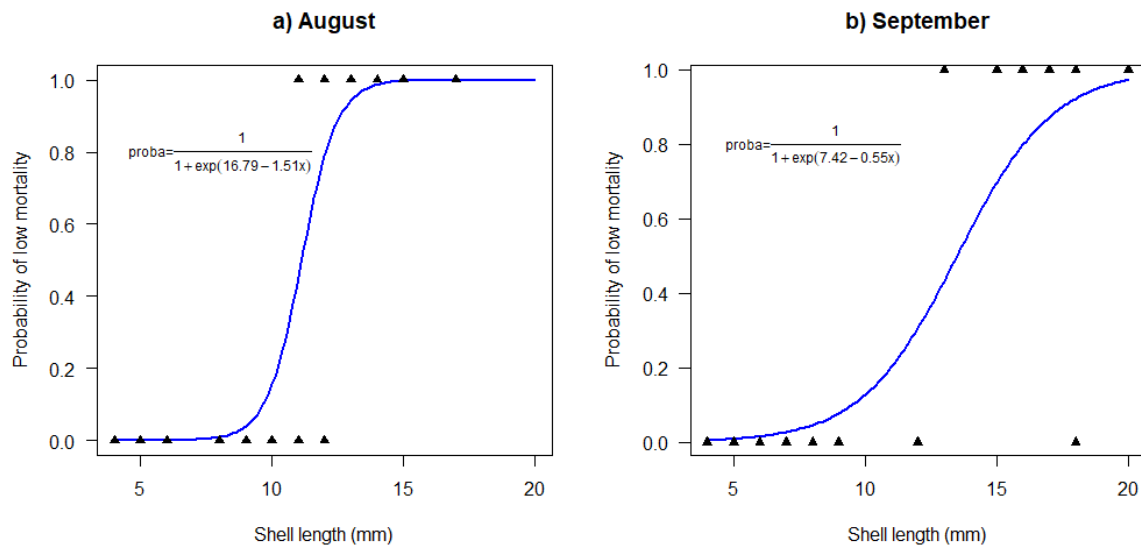
4   mortality years.

5

6

1

2

3 Fig. 6. *Cerastoderma edule.* Mean shell length of 0^+ cohort per month for different years from 1998

4 to 2019. Dashed lines: "L", nine low-mortality years; solid lines: "H", thirteen high-mortality years.

5

6

a) August

$$proba = \frac{1}{1 + \exp(16.79 - 1.51x)}$$

b) September

$$proba = \frac{1}{1 + \exp(7.42 - 0.55x)}$$

1

2   Fig. 7. *Cerastoderma edule.* Logistic regression describing the probability of a 0^+ cockle cohort to

3   belong to low mortality group ('L") according to mean shell length (in mm) reached in August (a) and

4   in September (b). Each triangle represented one or more year(s).