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Spatiotemporal variations of *Chlamys islandica* larval shell morphometry between 2000 and 2018 in a depleted coastal scallop fishing area

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ABSTRACT

Bivalves larval shell morphometry can provide valuable information on their planktonic (PI-Prodissoconch I) and early benthic life (PII). We examined spatial (at two scales: fishing sub-areas and exploited beds) and temporal variability (between 2000 and 2018) of PI and PII sizes among 424 Icelandic scallop juveniles (<10 mm total length) from the northern Gulf of St. Lawrence. PI and PII mean sizes were not different from juveniles collected inside or outside of exploited beds. For PI sizes, there were no temporal changes, but there was a difference between the two scallop fishing sub-areas, suggesting a disparity in egg size, origin or in broodstock physiological state. Regarding PII sizes, there was no difference between sub-areas, but PII sizes in 2003 and 2004 were significantly higher, likely related to differential larval growth or delayed metamorphosis associated to synergistic effects of environmental factors. Finally, this study demonstrates the possibility to accurately follow larval morphometry variations from small juvenile bivalve shells to track potential changes of recruitment success in order to sustainably manage stocks of commercial bivalve species.

1. Introduction

Considerable biological and ecological information relevant to recruitment, which is crucial in the determination of population dynamics (Thorson, 1950), can be derived from the examination of the embryonic or larval portion of molluscan shells (e.g., Jablonski and Lutz, 1983; Martel et al., 2014; Ockelmann, 1965). As the larval shell is a record of the growth and developmental history, it can be used to infer the mode of larval development (planktotrophic or lecithotrophic) as well as crucial parameters of larval ecology (Jablonski and Lutz, 1983; Lima and Lutz, 1990; Ockelmann, 1965).

In benthic-planktonic bivalves, the larval prodissoconch shell includes two distinct regions: prodissoconch I (PI) and prodissoconch II (PII) (Ockelmann, 1965). The punctate region of the PI is secreted by the shell gland and mantle epithelium generally within less than one day in most of species (Cragg, 2016 for a review). The success of this related lecithotrophic first phase depends on the amount of yolk reserves available from maternal input. Thus, PI size variations can provide information on egg quality and/or the physiological state of broodstocks during the maturation phase. This has already been demonstrated for pectinid species such as for *Argopecten purpuratus,* for which both quantity and quality of egg-derived energy reserves can be modified by alterations of adult diet, with cascading effects on the fate of early larval stages (Uriarte et al., 2004). For the Atlantic bay scallop (*Argopecten irradians*) and the Atlantic great scallop (*Pecten maximus*), larvae originating from larger than average eggs had a higher survival rate over the first two days of development (Kraeuter et al., 1982) and take less time to reach metamorphosis (Paulet et al., 1988). When moving into the motile veliger larva, the PI enlarges to form the PII that formed as the early D-shaped veliger feeds and develops within the plankton. Shell mineralization secretion is then different from PI as PII shell is secreted by the veliger's mantle edge. PII shell usually exhibits conspicuous close-set concentric or commarginal growth annuli, which contrasts with the more uniform punctate surface of PI (Ockelmann, 1965). As the planktonic veliger grows, a new shell is continuously added to PII until the larva is fully developed and physiologically competent for benthic settlement (Chanley and Andrews, 1971). After settlement and metamorphosis, when the veliger resorbs the velum and transforms into a juvenile (Veniot et al., 2003), the mantle initiates the secretion of the dissoconch (D) or adult shell form. This process also affects the shell structure by producing a distinct demarcation line between the shell of the veliger (PII) and that of the juvenile (dissoconch) (Martel et al.,

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1995). PII shell thus informs about size at metamorphosis, at the beginning of its benthic life, and can provide valuable post-facto information on the planktonic larval ecology. Many environmental processes may affect PII size such as changes in the flow-driven larval dispersal and retention (McGarvey et al., 1993), constraints of food supply, depth, salinity, but most importantly temperature (Cragg, 2016 for a review) and informs on the environmental conditions occurring during the larval planktonic development phase (e.g., Martel et al., 1995; Martel et al., 2014). Although previous studies on benthic molluscs with planktotrophic larval development already shown that PII size displays wide range of spatiotemporal variations within each species (Bayne, 1965; Coon et al., 1990; Lesoway and Page, 2008; Pechenik, 1990; Toupoint et al., 2012), the spatiotemporal patterns of such changes remain largely unexplored (Phillips and Gaines, 2002; Martel et al., 2014).

Recruitment processes are primordial in fisheries perspective in a view to manage sustainably stocks of commercially harvested species. This is especially true for scallops which are known to exhibit “boom and bust” trends in catch landings, a characteristic generally related to high, environmentally driven, recruitment variability (Chandrapavan et al., 2020). To better understand the recruitment magnitude in a given scallop fishing area, we examined the spatiotemporal recruitment dynamics of a commercially harvested scallop species, *Chlamys islandica*, from the northern Gulf of St. Lawrence where landings have sharply declined since the early-2000s (DFO, 2021). Little is known about *C. islandica* reproduction and recruitment in this area, except that adults show a rapid gonadal maturation during late spring, followed by a synchronous spawning occurring from late July to mid-August, potentially triggered by summer phytoplankton blooms (Arsenault and Himmelman, 1998). Therefore, we suggest that the skeletal record of the growth and developmental history morphology of the shell larvae of this pectinid species could be useful to understand spatiotemporal variability of recruitment success in our study area.

In this study, we examined inter-annual variability of the PI and PII sizes of *C. islandica* from 2000 to 2018 in two scallop fishing subareas (divided for management purpose) and inside or outside of scallop beds historically exploited by the fishery (Fig. 1). We hypothesized that the use of PI and PII larval measurements could be used as proxies to infer spatiotemporal variability of scallop recruitment, especially in this depleted stock on which very few studies were performed, and in a region without coastal environmental monitoring. First, we aim to determine the interannual range of variation of PI shell length within the two spatial scales previously mentioned (fishing subareas and historically exploited scallop beds) to identify potential changes in egg quality and/or in the physiological state of *C. islandica* broodstocks during the maturation phase. Second, we study the PII shell length spatiotemporal variability to determine if potential detected changes could originate from specific environmental conditions during the larval planktonic development phase of *C. islandica*. Third, we discuss the average PI/PII ratio derived from our study to infer *C. islandica* larval developmental mode and its relevance as an indicator of bivalve recruit quality. Finally, we evaluate the potential of using scallop larval growth marks (PI and PII) as indicators of recruitment success, information that could help assist with advice on stock health to management.

2. Materials and methods

2.1. Study area and Icelandic scallop fishery

This study was carried out in two scallop fishing subareas of Area 16 (16E and 16F) of the North Shore of the Gulf of St.-Lawrence, Quebec (Fig. 1). Area divisions are defined for management purposes and not driven by biological or environmental considerations. From the late 1980s to the mid-2000s, scallop landings on the North Shore (mainly 16E and 16F scallop fishing subareas) consistently accounted for more than 65% of total catches in Quebec (DFO, 2021). Since then, this proportion has dropped sharply due to the depletion of particular scallop beds and to socioeconomic circumstances that have been unfavourable to scallop fishery. In the subarea 16E, landings were generally greater than 50 tonnes (t) of meat prior to 1997, then decreased to levels below 16 t since 2013. In the subarea 16F, landings remain below 5 t per year since 2009 compared to levels higher than 25 t prior to 2007. The other spatial scale considered in the present study lie on *C. islandica* concentration areas (called “exploited scallop beds” hereafter) described as being known and commercially exploited historically and/or currently (grey polygons on Fig. 1). The mapping of these beds is based on several sources of information: research surveys (since 1977), exploratory fisheries (2000, 2001, 2003) and commercial fisheries (annually) (DFO, 2021; Trottier et al., 2017).

2.2. Field sampling of juveniles

Chlamys islandica juveniles were collected by dredging (rhombus-

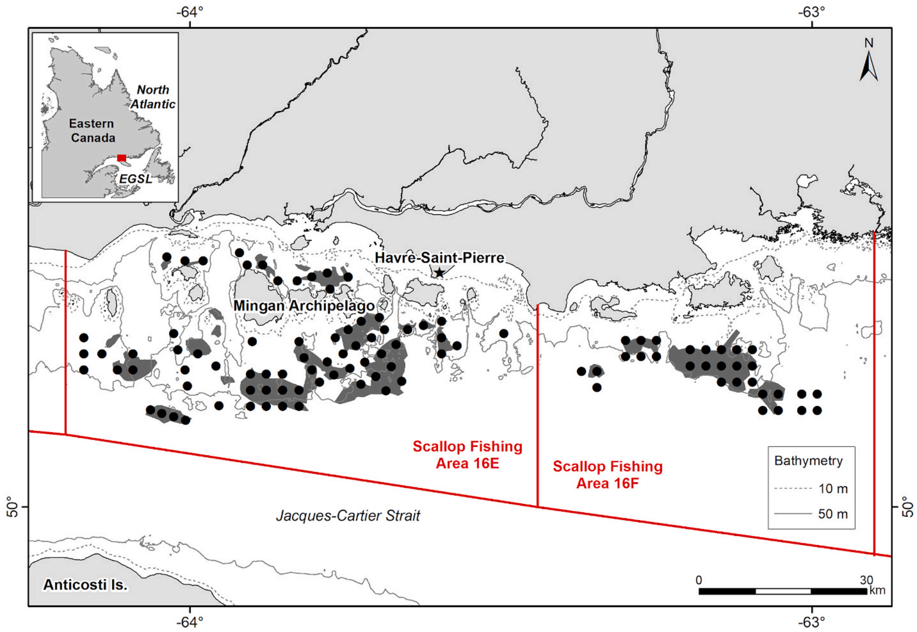

Fig. 1. Location of the study area. Top left inset: Map of the Estuary and Gulf of St. Lawrence (*EGSL*) showing the global position of our study area (red rectangle) in Eastern Canada. Main panel: Regional map of the Mingan Archipelago showing the scallop fishing subareas 16E and 16F, with black dots for the stations (n = 102) where *C. islandica* juveniles were collected from spring 2001 to 2019 (fall recruitment being from 2000 to 2018) and grey shaded polygons representing *C. islandica* commercially exploited (historically and/or currently) beds. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

shaped mesh = 20 mm) in May or June during scientific scallop surveys, operated by Fisheries and Oceans Canada (DFO). Although these scientific surveys have been conducted on a biennial basis since 1977, *C. islandica* juvenile shells have only been preserved in 2001–2002, 2004–2005, 2007–2008, 2010, 2012, 2014, 2016, 2018 and 2019. During each survey, a subsample (± 700 individuals/survey) representing all size classes up to 130 mm in shell height was used to establish size-at-age relationships. Age was determined from reading the bands on the upper/left valve of each sampled scallop and the two valves for juveniles were subsequently stored in the DFO-MLI mollusc research dry collection (DFO- Maurice Lamontagne Institute, Mont-Joli, QC). In this study, we selected all years with available juvenile shells (collected at sea during late spring) that recruited the fall before (mean total length = 8.85 mm ± 2.85 mm; N = 424). Mean depth (m) at which individuals were sampled was shallower in subarea 16E (42.6 ± 10.2 m; range 23–71 m) than 16F fishing subarea (52.7 ± 13.3 m; range 28–88 m). Although mesh size was larger than the juvenile length used in this study, sampling was obtained by the juvenile scallop behavior to settle in empty adult shells that provide a refuge from benthic predators, particularly from crabs (Arsenault and Himmelman, 1996a, 1996b).

2.3. Prodissoconch I and II measurements

The flatter/right valve of *C. islandica* juveniles was used for larval shell measurements (Dijkstra et al., 2009; Gruffydd, 1976) after a pre-treatment. Briefly, each valve was first ultrasonically cleaned during 30 s to remove organic matter and biofilm and then carefully brushed. We used a rectangular cuboid (1.5 × 1.5 × 15 cm) support (Fig. 2) coated with modelling clay (Fimo Effect ®) to position vertically all valves under the microscope with the umbo ridge parallel to the support upper edge (Fig. 2A).

Photos of shell umbos were taken (Fig. 2B) under reflected light using a “Keyence VHX-2000” digital microscope equipped with a “100-1000 x VH-Z100UR” objective, using depth composition function, under 800x magnification in High Dynamic Range (HDR) mode (vertical pitch = 4 μm). Prodissoconch I (PI) and Prodissoconch II (PII) length (Fig. 2B) were measured digitally to the nearest 0.01 μm using the “Keyence-VHX-2000-software”. As the growth mark corresponding to the first winter was difficult to identify on shells, we assumed that individuals recruited during the fall (y) prior to late spring sampling (y+1) when both PI and PII ending marks (corresponding to maximum PI and PII lengths) were not eroded (Fig. 2B). Since a large proportion of the juveniles were broken at the ventral margin, due to the small size of the analyzed shells stored for more than 20 years, we have not been able to study the dissoconch growth. However, PI and PII were well preserved for all samples analyzed.

2.4. Environmental data

The PI and PII length of a bivalve may be influenced by various environmental drivers. Thus, PI lengths were compared to juvenile collection depth, satellite-derived sea surface Chl *a* (May, June, July, August), sea surface (0–10 m) and bottom (30–40 m) temperature (March, June, August). Months were chosen as they occurred during *C. islandica* broodstock maturation phase which could affect PI sizes variation over years. PII lengths were compared in the same way to juvenile collection depth, satellite-derived sea surface Chl *a* (August, September), sea surface (0–10 m) and bottom (30–40 m) temperature (August, November). Months were chosen as they occurred during *C. islandica* larval pelagic development phase and could therefore affect PII sizes variation over years. These variables represent the set of environmental data available for the given period (2000–2018) and geographic area (16E and 16F scallop fishing subareas).

Satellite-derived Chl *a* data was extracted from sensors SeaWiFS (2000–2010) and MODIS Aqua (2002–2018) for the scallop fishing area from 2000 to 2018. Chl *a* concentration (mg/m^3) was estimated using the empirical orthogonal function method (Laliberté et al., 2018) specifically adapted for the St. Lawrence Estuary and Gulf waters. The dataset includes a 14-day product for sensors SeaWiFS (2000–2010) and MODISAqua (2002–2018), both with a spatial resolution of 1 km. The 14-day product was averaged temporally to a monthly resolution before being analyzed.

Surface (0–10 m) and bottom (30–40 m) temperatures (°C) were obtained by averaging the pixels in that depth range on temperature maps constructed from DFO-AZMP (Atlantic Zone Monitoring Program) surveys, as detailed in Tamdrari et al. (2012), and shown in Fig. 43 of Galbraith et al. (2019).

2.5. Data and statistical analysis

As the number of *C. islandica* sampled varies among sites and years, non-parametric permutational multivariate analyses of variance (PERMANOVA) were performed to test PI and PII length differences among years and scallop fishing subareas (16E and 16F) and their interaction (Site x Year) using the *adonis* function of the *vegan* package (9999 permutations). The same statistical procedure was used to test PI and PII length differences between the shells collected inside and outside the exploited scallop beds. We decided to test Site x Year and beds separately because we didn’t have enough replicates to test the Site x Bed x Year combination. Moreover, missing information about scallop sampling beds for 4 individuals enabled us to test the bed effect on 420 individuals versus 424 for the Site x Year. Variance homoscedasticity was verified for all groups by using a permutation test (*permutest.betadisper* function of the *vegan* package) which calculate the average distance of group members to the group spatial median in multivariate

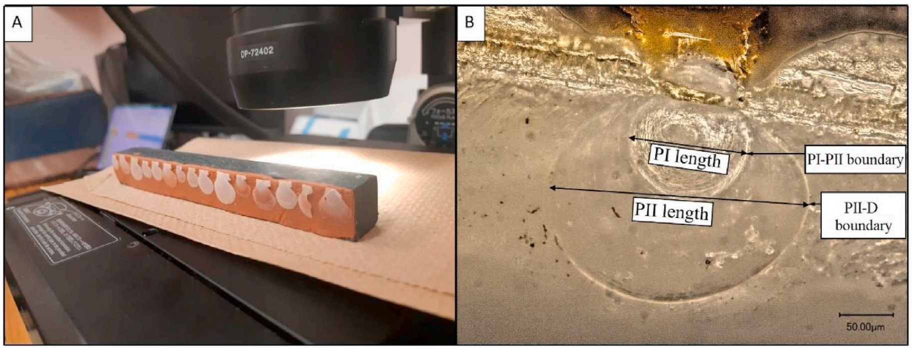

Fig. 2. Panel A: Rectangular cuboid (1.5 × 1.5 × 15 cm) support used to position and calibrate vertically the right valve under a Keyence digital microscope VHX-2000 (800x magnification). Panel B: Picture of a C. islandica juvenile larval shell with PI-PII and PII-D (Dissoconch) boundaries (growth marks) used to measure maximum PI and PII length.

space (Anderson et al., 2008). Pairwise comparisons for significant PERMANOVA results (*P*-value <0.05) were conducted and corrected for multiple testing using Benjamini-Hochberg false discovery rate (FDR) correction (Waite and Campbell, 2006), implemented in the “pairwise. adonis” wrapper function downloaded from https://github.com/pmartinezarbizu/pairwiseAdonis. Resemblance matrixes were calculated on Euclidean distances.

Correlations between temperature (surface and bottom), surface Chl *a*, juvenile collection depth and the PI or PII length were performed using Spearman’s rank correlation with a threshold of $\alpha < 0.05$. All data analyses were performed with R version 4.1.2 (www.r-project.org).

3. Results

3.1. Morphometric analysis of the prodissoconch I in time and space

There were no differences between PI length variances from 16E and 16F scallop fishing subareas (*P*-value = 0.23) and from inside and outside the exploited scallop beds (*P*-value = 0.94). However, PI length variances among years were different (*P*-value = 0.03) allowing us to conclude that variance homogeneity assumption has been violated. Mean *C. islandica* PI length ranged from 118.5 ± 2.6 (2015 in 16F scallop fishing subarea) to 123.6 ± 5.8 μm (2010 in 16E scallop fishing subarea) (Fig. 3) with differences between year (PERMANOVA; $Df^{year} = 11$, $Df^{total} = 423$, Pseudo-F = 2.03, *P*-value = 0.03) and fishing subareas/site ($Df^{site} = 1$, $Df^{total} = 423$, Pseudo-F = 9.88, *P*-value = 0.001) without any interaction ($Df^{year*site} = 7$, $Df^{total} = 423$, Pseudo-F = 1.20, *P*-value = 0.30). Thus, juveniles collected in 16F zone showed PI length *ca.* 2% lower than juveniles collected in 16E zone. However, no discriminations were found by the post-hoc PERMANOVA PI sizes comparisons between years when *P*-value were adjusted for multiple testing (overall PI mean: 121.48 ± 4.17 μm, N = 424). Moreover, the violation of variance homogeneity assumption of PI sizes among years demonstrates the existence of years with stable egg sizes and other ones with more variability. No significant differences were detected between PI length of juveniles collected from inside and outside the exploited scallop beds (PERMANOVA; $Df^{bed} = 1$, $Df^{total} = 419$, Pseudo-F = 0.15727, *P*-value = 0.6914). PI size frequency histograms for each year and scallop fishing subareas are available in supplementary information (Figs. S1 and S2). There were no significant correlations found between all available environmental variables tested and PI lengths (Fig. S3).

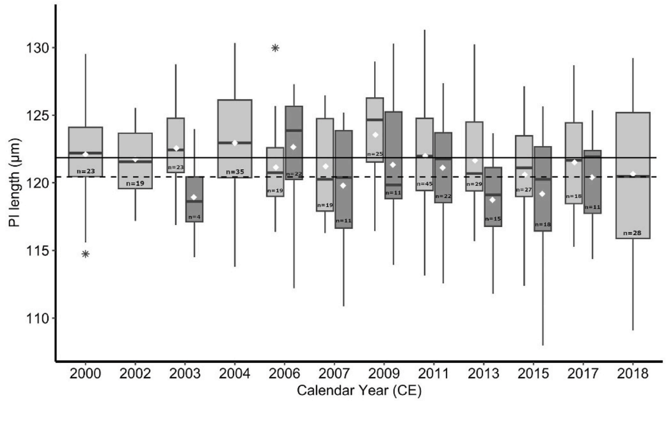

Fig. 3. Box-plots of C. islandica PI lengths for 16E (light grey) and 16F (dark grey) scallop fishing subareas over years of recruitment. The number of individuals (n) measured for each of the corresponding years are shown at the bottom of boxplots. Lower and upper box boundaries 25th and 75th percentiles, respectively, line inside box median, rhombus inside box mean, lower and upper error lines 10th and 90th percentiles, respectively, asterisks data falling outside 10th and 90th percentiles. Solid and dotted horizontal lines represent respectively mean PI length from the 16E (121.86 μm, n = 310) and 16F (120.44 μm, n = 114) scallop fishing areas.

3.2. Morphometric analysis of the prodissoconch II in time and space

There were no differences between PII length variances from 16E and 16F scallop fishing subareas (*P*-value = 0.82), from inside and outside the exploited scallop beds (*P*-value = 0.93) and among years (*P*-value = 0.15). Mean PII length ranged from 238.7 ± 7.7 (year 2001) to 248.6 ± 10.9 μm (year 2004) (Fig. 4) with differences (PERMANOVA) between PII length among years ($Df^{year} = 11$, $Df^{total} = 423$, Pseudo-F = 5.41, *P*-value = 0.0001). No differences were detected between PII length from 16E and 16F scallop fishing subareas ($Df^{site} = 1$, $Df^{total} = 423$, Pseudo-F = 0.5335, *P*-value = 0.4665) nor interaction ($Df^{year*site} = 7$, $Df^{total} = 423$, Pseudo-F = 1.46, *P*-value = 0.1756). Post-hoc PERMANOVA comparisons revealed that mean PII length in 2003 were larger than in 2000, 2011, 2013 and 2018 (Fig. 4) while 2004 PII mean length was about 5% larger than other years except for 2002 and 2003 (Fig. 4). Since there was no difference between PII lengths in 16E and 16F subareas, we elected to group the PII measurements from each site (Fig. 4) to enhance graphical representation clarity. No differences were detected between PII length from inside and outside the exploited scallop beds (PERMANOVA; $Df^{bed} = 1$, $Df^{total} = 419$, Pseudo-F = 0.15727, *P*-value = 0.6914). PII size frequency histograms for each year and scallop fishing subareas are available in supplementary information (Figs. S4 and S5). There were no correlations found between all available environmental variables tested and PII lengths (Fig. S6).

The PI/PII ratio varied between 0.47 and 0.51 with maximum standard deviation between site and/or year of 0.029 (overall PI/PII mean: 0.50 ± 0.02, N = 424).

4. Discussion

We had hypothesized that the use of PI and PII larval measurements could be used as proxies to infer spatiotemporal variability of *C. islandica* recruitment. We observed some spatial and also annual variability, suggesting potential differential recruitment processes. In context of scientific survey without possibility to measure settlement and recruitment success, index basis on PI and PII measurements could provide information on eggs quality and larval development.

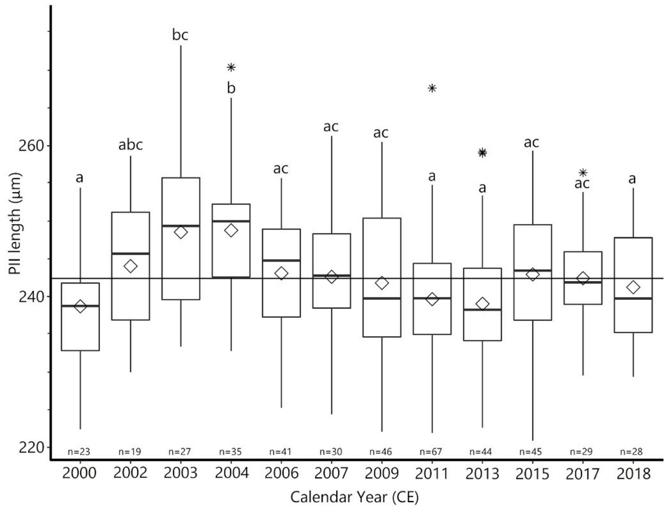

Fig. 4. Box-plot (see Fig. 3 caption for box-plot explanation) of PII lengths (16E and 16F pooled) over years of recruitment. The number of individuals (n) measured for each of the corresponding years are shown above the abscissa axis. Horizontal black line represents the global mean of PII sizes (242.43 μm, n = 424). Significant results of pairwise PERMANOVAs conducted among years are presented and letters indicate significant differences (p < 0.05).

4.1. PI variability indications: spatial difference but temporal stability in maternal investment

PI measurements, representing estimations of *C. islandica* egg size, of different larval cohorts are slightly different among the two scallop fishing subareas, with larger PI mean length in the 16E than in the 16F scallop fishing subareas. Gruffydd (1976) reported comparable mean PI sizes of 120 μm in *C. Islandica* from north area of Norway, very near to those observed in the present study. PI sizes have not been extensively studied in pectinid species (Cragg, 2016), and even less in *C. islandica*. However, in larval ecology, egg size or mass usually correlates positively with offspring performance and fitness, a phenomenon known as "the bigger the better" (Marshall et al., 2010). *In-situ* intraspecific variation in offspring size has mainly been associated with the maternal phenotype or the environment experienced by mothers during the maturation phase (Rollinson and Rowe, 2016). Thus, PI results from the present study seem to point out a slight difference between 16E and 16F scallop fishing subareas which could suggest existing differences within broodstock providing the larval supply in these two sites. Thus, adult females from 16E seem to invest more energy by egg than female from 16F. On the other hand, the absence of detectable interannual differences within the 12 studied years seems to indicate an overall stability over time. Moreover, no significant differences were detected between PI length of juveniles collected from inside and outside the commercially exploited scallop beds. This result suggests that the broodstock pool providing recruits in and out of the main commercially exploited scallop beds seem to be the same. However, our measurements come from individuals caught in late May/early June after their recruitment which occurred in the previous fall. This sampling method could therefore bias the PI measurements representativeness as measured individuals have already undergone a selection pressure during their pelagic life phase, their benthic metamorphosis and during their first winter spent on the seafloor. However, our results suggest that surviving juveniles after their first winter were individuals showing PI size over 108 μm at their settlement.

4.2. PII variability indications: spatial homogeneity but temporal differences

Measurements of size at benthic metamorphosis (mean PII length of *ca.* 242 μm) were similar between the two scallop fishing subareas and within juveniles collected from inside or outside the commercially exploited scallop beds. This finding suggests that environmental conditions experienced by *C. islandica* larvae during their pelagic development seem rather homogeneous for both of the examined spatial scales (fishing subareas and historically exploited scallop beds). Overall PII mean value reported in the present study are much smaller than the PII mean size of 305 μm reported in northern Norway by Gruffydd (1976). This difference can be explained through the fact that individuals measured by Gruffydd (1976) came from a fjord with low salinities which could have delayed benthic metamorphosis or modify their daily larval growth. In the present study, we observed a significant increase in size at metamorphosis in 2003 and 2004, which cannot be related to maternal investment in egg size since no significant temporal differences could be attributed to PI length. This difference in PII sizes in 2003 and 2004 seem to be related to the duration of *C. islandica* planktonic phase. Indeed, previous laboratory studies have shown that under similar food supply and seawater temperature conditions, the longer the veligers keep swimming and feeding in the water column, the larger they grow, and the larger their size at settlement (Pechenik et al., 1990). This delay has been extensively documented in laboratory studies dealing with culture of larval molluscs (Bayne, 1965; Coon et al., 1990; Pechenik, 1990; Pechenik et al., 1990; Pechenik et al., 1993; Lesoway and Page, 2008). The most accepted hypothesis explaining this delay of metamorphosis in molluscs larvae is related to suitable substrate availability for pediveliger, thus resulting in extended pelagic larval development (Bayne, 1965; Bayne, 1976; Pechenik et al., 1990; Bishop et al., 2006). This is especially true for *C. islandica* which pediveligers can settle repeatedly onto substratum and be resuspended in the water column, where they continue to swim and feed (Harvey et al., 1993, 1995). According to Harvey et al. (1993) in another region in Eastern Canada, *C. islandica* spat settle preferentially on the perisarcs of dead hydroids or on filamentous red algae. Unfortunately, we do not have any time series relating to the coverage and variability of these two epibiont species in the two scallop fishing subareas studied. However, available data on fishing effort in the study area indicates relative stability from 2000 to 2006, before decreasing from 2007 onwards (Fig. 4 in DFO, 2021). The lack of increasing trend in 2003 and 2004 of this fishing effort thus prevents us from linking clearly the larger PII sizes measured in those two years to a destruction of *C. islandica* settlement substratum through dredging.

An alternative hypothesis that may explain the observed differences in size at settlement of *C. islandica* in 2003 and 2004 should be related to environmental factors known to affect veliger sizes at the end of their planktonic life. Water salinity and temperature are the two most documented key variables for larval development (Helm and al. 2006). For salinity, Gruffydd (1976) demonstrated that survival of *C. islandica* veligers over a 24-h exposure period is slightly affected by low salinities up to 21 psμ, but markedly reduced under this value at 14 psμ, with 100% mortality at 7 psμ. However, salinity measurements (0–10 m and 30–40 m) from DFO-AZMP surveys extracted over the same time period and area of the present study (2000–2018) were excessively stable (mean salinity = 31.53 ± 0.69 psμ), well beyond the 21 psμ threshold reported by Gruffydd (1976). This finding tends to demonstrate that salinity is likely not a significant factor affecting *C. islandica* pelagic larval development in the two scallop fishing subareas investigated in the present study. More interestingly, low seawater temperature decreases larval growth and increases size at metamorphosis as reported for pectinid larvae (Cragg, 2016) and various marine bivalve species, including mussels (Bayne, 1965), oysters (Flores-Vergara et al., 2004) and clams (Lutz and Jablonski, 1978). Thus, seawater cooling leads to an increase in both larval duration and size at settlement (i.e., larger PII size). Unfortunately, data from field collections of larvae generally lack sufficient information about temperatures during larval development to permit detailed analysis of this correlation (Cragg, 2016). This is also the case in the present study where *in-situ* measured temperature data came from interpolations and were limited to a few months per year. Thus, the partial nature of the temperature dataset does not allow to totally rule out the possible influence of sea surface or bottom temperature on PII length interannual variations. However, by exploring regional seawater temperature data available in DFO reports, we noticed that a higher volume of cold and saline Labrador shelf water entering into the Gulf of St. Lawrence through the Strait of Belle Isle occurred in 2003–2004 (Fig. 35 in Galbraith et al., 2021). Interestingly, this cold-water of Labrador origin entering the Gulf during winter has previously been reported to affect Mingan Archipelago water properties several months later (Plourde and Therriault, 2004). This phenomenon could have increased the stratification in the 16E and 16F areas during these years. Effects of thermocline on larval settlement have previously been reported under laboratory conditions for *Argopecten irradians* (Daigle and Metaxas, 2011) and *Placopecten magellanicus* (Pearce et al., 2004). Therefore, *C. islandica* planktonic larvae vertical up and down movements may be constrained by thermoclines in the water column which may act as physical barriers. But we do not know whether the effects of temperature on larval distribution are due to a kinesis response to temperature level or to a direct effect of physical conditions on larval swimming (Cragg, 2016). Thus, significantly larger PII sizes in 2003 and 2004 could be related to delayed metamorphosis associated with colder bottom water temperatures, stronger stratification, changes in phytoplankton assemblages or to synergistic effects of these environmental parameters.

Factors such as water depth where planktotrophic veliger spend at least part of their developmental period have previously been linked to variability in PII size at settlement (Robertson, 1994; Martel et al., 2001). In the present study, we did not find any significant correlation between juvenile recruitment depth and PII lengths. Moreover, this seems to be confirmed by PERMANOVA's results as any differences in PII lengths were detected among 16E and 16F scallop fishing subareas areas despite a 10 m difference in average sampling depths.

Another environmental factor affecting pectinid larval shell growth rates is the effectiveness of feeding regimes and food (Cragg, 2016). *In situ*, pectinid larvae are able to survive several days without food (Salaün, 1994) and may resume normal growth once feeding conditions improve to build up a sufficient quantity of reserves to allow metamorphosis (Cragg, 2016). Therefore, throughout the pelagic stage, a temporal lack of food could increase PII size at metamorphosis, by delaying it. Exploration of interannual variability of satellite derived sea-surface Chl. *a* data, a proxy of algal biomass, during the *C. islandica* pelagic larval development phase (August, September) does not correlate to PII sizes over time. This is not surprising as pectinid larvae, during their pelagic development, seem mainly sensitive to their diet properties and especially to the quality of lipid provided as they are unable to synthesise sterols which are essential fatty acids for their larval development (Soudant et al., 1998). Thus, consumption of micro-algae promoting triacylglycerol accumulation have been identified to accelerate pelagic larval development and improve their metamorphosis success (Gagné et al., 2010; Pernet et al., 2006; Robert et al., 1999). Moreover, Toupoint et al. (2012) described a trophic settlement trigger based on the match between the presence of mussel larvae and high dietary essential fatty acids in the water column, which was correlated to a peak of picoeucaryotes in an Eastern Canadian coastal lagoon characterized by heterotrophic production. As substantial interannual changes in phytoplankton community composition have recently been reported (over the period 2013–2018) in the studied geographic area (Deblois et al., 2022), we may consider the hypothesis that phytoplankton community changes may have driven, at least in part, PII mean size interannual variations, especially in 2003 and 2004, despite the lack of data to validate that.

4.3. PI/PII ratios representative of a planktotrophic larval developmental mode species

High-resolution pictures of *C. islandica* larval shells obtained from the 16E and 16F scallop fishing subareas depict morphological features typical of marine bivalves with planktotrophic larval development, including two prodissoconch regions, PI and PII, as well as distinct PI-PII and PII-D boundaries (Fig. 2B). In planktotrophic larvae, the PII stage is much larger than the PI stage (Berkman et al., 1991). Based on this observation, Cragg (2016) presented examples of the scallop species PI/PII ratios ranging from 0.24 to 0.55 for planktotrophic and 0.87 to 0.98 for lecithotrophic larvae. Among pectinid species for which PI and PII data are available (Cragg, 2016), almost all display a ratio indicative of planktotrophy. This dominant larval developmental mode is mainly observable for species living in euphotic coastal waters like the Mingan Archipelago (Le Fouest et al., 2010). Whereas lecithotrophy may improve the chances of survival where suspended particulate food is limited (such as for abyssal species) or where the parental environment is extremely patchy (coral reefs or mid-ocean ridges) (Cragg, 2016). According to the evidence presented in this study, *C. islandica* recruited from 2000 to 2018 presented a mean PI/PII ratio of 0.50 indicative of a PII length twice longer than PI, that fit with planktotrophic developmental mode and could suggest good environmental and trophic condition for larval development. These PI/PII ratios calculated in this study are substantially higher than for *C. islandica* in Norway (*ca.* 0.39, Gruffydd, 1976) and in Iceland (*ca.* 0.40, Dijkstra et al., 2009). Differences between PI/PII from our study site and the same ratio from other localities are related to smaller PI (100 μm) in Iceland (Dijkstra et al., 2009) and to larger PII (305 μm) in Norway (Gruffydd, 1976). It therefore seems that the higher PI/PII ratios observed within our study area indicate that this region is a good location for this species, in fact it is the best Icelandic scallop fishing location in Quebec (DFO, 2021). Thus, we wanted to raise the interest of investigating the PI/PII ratio as an indicator of a good bivalve recruit as long as environmental factors are temporally stable.

4.4. Perspectives of using PI and PII in C. islandica fishery science advice and management

First of all, the present study demonstrates the possibility to accurately measure PI and PII lengths from small *C. islandica* juvenile shells (mean total length about 8.85 mm ± 2.85 mm) recruited during the fall preceding late spring field collection. In this regard, this work allowed us to gain insight about *C. islandica* larval ecology in the Mingan Archipelago over time and space and represents an essential premise to analyse potential effects of environmental changes in future research assessing scallop recruitment in the study area. However, the absence of juveniles recruited before 2000 in the DFO-MLI shell collection, makes it difficult to conclude on the importance of larval morphometry variations on the Icelandic scallop fishery crash in the early 2000s.

Prodissoconch I (PI length) results demonstrate a slight but significant difference among 16E and 16F scallop fishing subareas which could suggest existing differences in the broodstock sources providing the larval supply to these two subareas. This spatial difference could originate from scallop genetic diversity, differential food availability, or site quality. Further fine scale (among scallop beds) genetic studies should investigate this hypothesis (e.g., Lehnert et al., 2019) . In terms of temporal differences, the available *C. islandica* shell samples did not reveal significant interannual differences over the 12 studied years. This result may indicate an overall stability of *C. islandica* broodstocks physiological state during the female maturation phase and/or constant egg quality hatched over time. Future histological studies tracking broodstock maturation status and integrating high-frequency environmental monitoring on a fine spatial scale would allow a better understanding of this apparent temporal stability. It would be also relevant to test in a near future PI length differences on individuals collected just after their fall recruitment compared to later in late spring, to evaluate first winter selection pressure exerted on *C. islandica* recruits.

Measurements of size at metamorphosis (PII length) were not significantly different for both spatial scales (scallop fishing subareas, inside or outside of commercially exploited scallop beds). This finding could suggest that environmental conditions experienced by *C. islandica* larvae during their pelagic development phase were homogeneous within the study area, at least from 2000 to 2018. Regarding the temporal dimension, we observed a significant increase in PII size in years 2003 and 2004 which could be related to delayed metamorphosis or decreased larval growth rates probably associated with colder bottom water temperatures, stronger stratification, changes in phytoplankton assemblages or to synergistic effects of these environmental variables. Unfortunately, as it is often the case in studies using in situ larval-related, the lack of environmental measurements at appropriate scales did not allow a quantitative analysis of their impacts on *C. islandica* larval development. To allow a more comprehensive interpretation of morphometric variations in Icelandic scallop juvenile shells, future studies should include high frequency environmental monitoring and lipid analysis of live collected juveniles over time and from different scallop beds.

We hypothesized that the use of PI and PII larval measurements could be used as proxies to infer spatiotemporal variability of scallop recruitment, especially in the present context of a scientific survey without possibility to easily and accurately measure in situ settlement and recruitment success. We demonstrated that PI and PII measurements could provide valuable information on egg quality and larval development, respectively. However, PI and PII related-information only contribute to a part of the full recruitment success story. For example, PI and PII data do not provide information on larval supply quantity and post-larval mortality related to benthic predation which are also involved in Icelandic scallop recruitment success rate. Nevertheless the small PI and PII differences demonstrated in the present study, we suggest continuing the monitoring of PI and PII measurements in time and space in the Mingan Archipelago, especially in the current context of bottom-up ecosystem changes where the phytoplankton community structure and temporal dynamic have changed since the mid-2000's (Poitevin et al., 2022). Similar changes have been addressed in many other coastal marine ecosystems (Daufresne et al., 2009; Mousing et al., 2014; Agirbas et al., 2015; Pinckney et al., 2015; Correia-Martins et al., 2022), where the proportion of picophytoplankton in the phytoplankton community is increasing in response to global warming. As scallop gills are adapted to retain efficiently large particles (Rosa et al., 2018), increasing picophytoplankton abundance could potentially results in lower energetic accumulation by Icelandic scallops' adults and lower maternal transfer in eggs. Adult bivalves can assimilate small phytoplankton particles (Sonier et al., 2016), but the capture and retention efficiency being regulated by their gills morphology is largely lower (Rosa et al., 2018). For larvae, on one hand, their velum feeding organ is less selective than for adults (Bower and Meyer, 1990), suggesting that larval growth estimated by PII measurements could be less affected by phytoplankton changes than PI measures. On the other hand, as long-chain polyunsaturated essential fatty acids (EFAs) produced by phytoplankton are predicted to decrease due to ocean warming (Hixson and Arts, 2016; Colombo et al., 2017), impact on PII size could also be observed. Therefore, in the current context of climate and ecosystem changes, indicators of egg and larvae quality, respectively PI and PII sizes, can supplement current science advice information addressed for best management practices of scallop fisheries.

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CRediT authorship contribution statement

Pierre Poitevin: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Virginie Roy:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Gauthier Cervello:** Writing – review & editing, Validation, Software, Methodology, Formal analysis. **Frédéric Olivier:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Réjean Tremblay:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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