



Sexual dimorphism in shell growth of the oviparous boreal scallop *Swiftopecten swiftii* (Bivalvia: Pectinidae)

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ABSTRACT

A combined analysis of measurements of shell morphology and oxygen isotopic composition in shells of *Swiftopecten swiftii* (Bernardi, 1858) revealed that the step-like growth of commarginal ridges correspond to annual fluctuations in water temperature. The main role of these cyclically-formed ridges may be to enlarge the internal volume of the shell rapidly in time with gonad maturation. The sexual difference in shell width is correlated with the significantly larger size of the ovary in comparison with the testis; valves of the females had a more prominent bulge than those of the males. This type of dimorphism is very rare among bivalves and is the first example reported in the order Pectinoida. Results of detailed oxygen isotopic analysis in both sexes indicate that step-like commarginal ridge formation occurs in winter. In addition, a drastic change in the direction of growth was observed in the middle of December in the males and in November in the females. This is consistent with the possibility that the female needs a longer time to develop a larger gonad. We conclude that the sexual difference in energy invested in reproduction reflects the differential production of shell during the breeding season.

INTRODUCTION

In general, relatively few bivalves show morphological differences between males and females. With few exceptions, the known examples of bivalve sexual dimorphism are either of dwarf males, or of ovoviviparous species that nurse their young in the marsupium (e.g. Cox *et al.*, 1969; Voight, 2016). While numerous studies have documented sexual dimorphism in molluscan shell morphology, no research has focused on the mechanism of formation of sexually-differentiated shell morphology.

In this paper we report on sexual differences in valve morphology in the boreal sessile scallop *Swiftopecten swiftii* (Bernardi, 1858). *Swiftopecten swiftii* is a common cold-water epifaunal pectinid, distributed from Choshi in Chiba Prefecture, Japan, to the Pacific coast of Alaska, and from Gangwon-do, Korea, northward to the northern Sea of Japan. The habitat of this species is on rocky and gravel bottoms at depths shallower than 50 m (Sinelnikova, 1975; Volova & Scarlato, 1980; Min *et al.*, 2004; Hayami, 2017). This species is known to be gonochoric and to attain sexual maturity in its second year, as is also the case in *Mizuhopecten yessoensis*, which is distributed in similar geographic areas (Kosaka & Ito, 2006). *Swiftopecten swiftii* is characterized by a distinctive cyclic step-like accretionary growth of ridges on the shell, which we refer to as commarginal ridges (Fig. 1).

The aim of this study is to compare shell morphology and formation between males and females in *S. swiftii*, and to relate this to

gonadal development. Previous studies have regarded commarginal ridges in pectinoid bivalves as merely marking winter growth breaks. We performed a combined analysis of inner-volume measurement and oxygen-isotopic composition ($\delta^{18}\text{O}$) of shells to identify the depositional timing of the step-like growth of commarginal ridges in relation to annual water temperature fluctuation. In addition, more detailed records of $\delta^{18}\text{O}$ in the shells of both sexes were examined to clarify the mechanism underlying sexual differences in commarginal ridges.

MATERIAL AND METHODS

Material

Specimens of *Swiftopecten swiftii* were collected from Yubetsu, Hokkaido, Japan (44°17'24"N, 143°39'14"E) in the Sea of Okhotsk, and from Dolinsk, Sakhalin, Russia (47°56'27"N, 142°46'54"E). The specimens from Hokkaido were collected with a scallop-fishing net. The live specimens used for morphological analysis and shell microstructure observation were collected from Yubetsu at depths between 15 and 20 m, on 1 April 2016, and the specimens for isotopic analysis at a depth of 50 m on 2 May 2014. The dead specimen from Sakhalin used for isotopic analysis was collected by K. Ogasawara from a beach at Dolinsk on 7 August 2007; this specimen is preserved in the Graduate School of Life

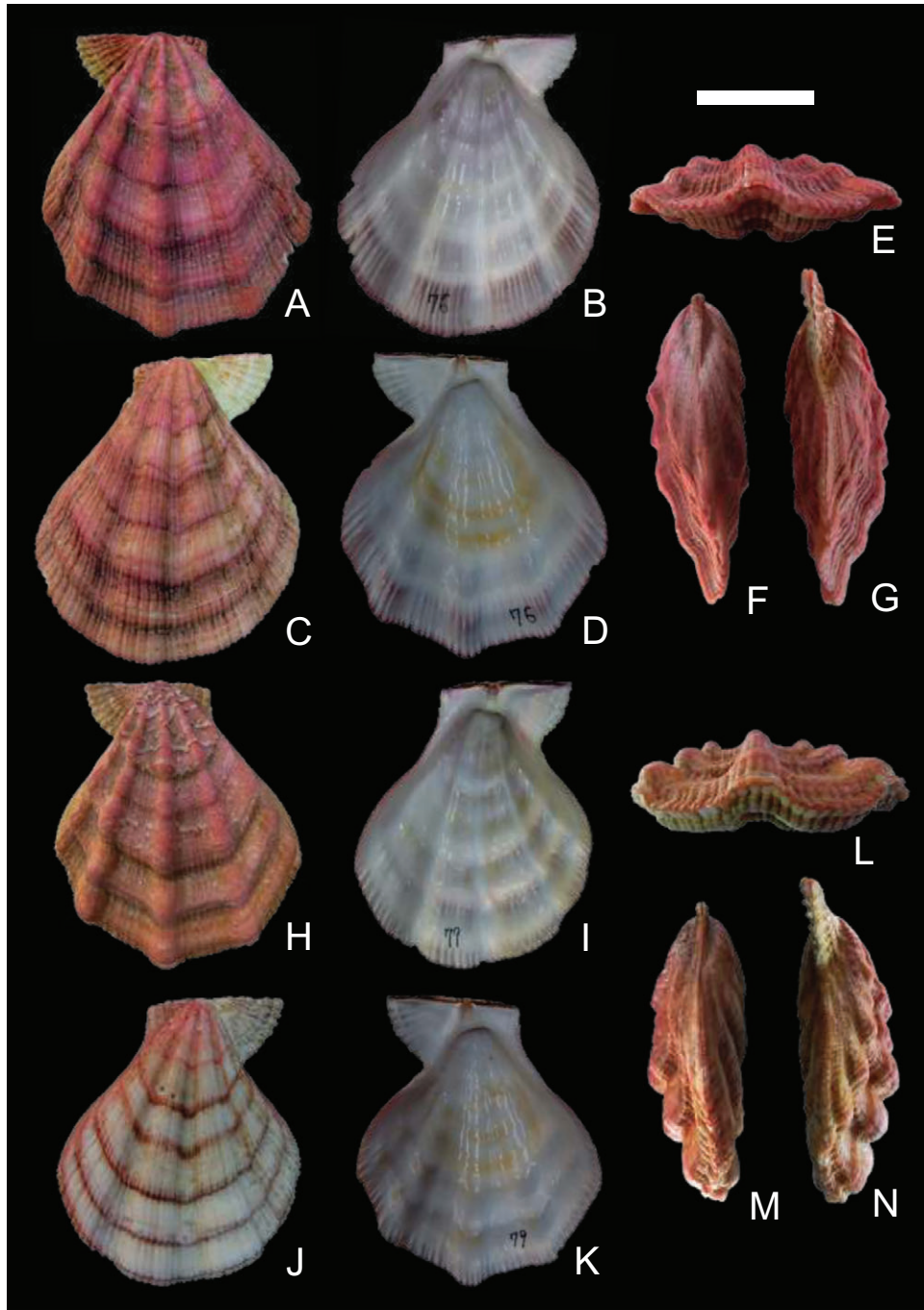


Figure 1. Male and female *Swiftopecten swiftii* from Yubetsu, Hokkaido, Japan, depth 50 m. **A–G. Male** (KSHS-R1-076). **H–N.** Female (KSHS-R1-079). **A, C, H, J.** Exterior view of right (**A, H**) and left (**C, J**) valves. **B, D, I, K.** Inner view of right and left valves. **E, L.** Ventral view of articulated valves. **F, G, M, N.** Posterior and anterior lateral views of articulated valves. Scale bar = 50 mm.

and Environmental Science, University of Tsukuba. All other specimens are preserved in Keio Senior High School (KSHS).

Morphological analyses

Shells and soft parts of 134 individuals from Yubetsu were measured, comprising 74 males and 60 females. Wet weight of gonad and total tissue were recorded with an electronic balance. Shell height and articulated width (Fig. 2) were measured with vernier callipers in four- to six-year-old individuals. The age of each

individual was determined based on the number of commarginal ridges, whose annual deposition were confirmed from oxygen-isotopic profiles. Discrimination between males and females was made on the basis of gonad colour, white to yellowish white for males and orange to reddish pink for females. The significance of differences in wet weight and size were tested statistically with a combination of *t*-test and Kolmogorov–Smirnov test; *P* values less than 0.05 were considered statically significant. The gonadal index (GI) was calculated, as a typical means of quantifying reproductive effort in scallops: $GI = [\text{gonadal mass (g)} / \text{total tissue mass (g)}] \cdot 100$.

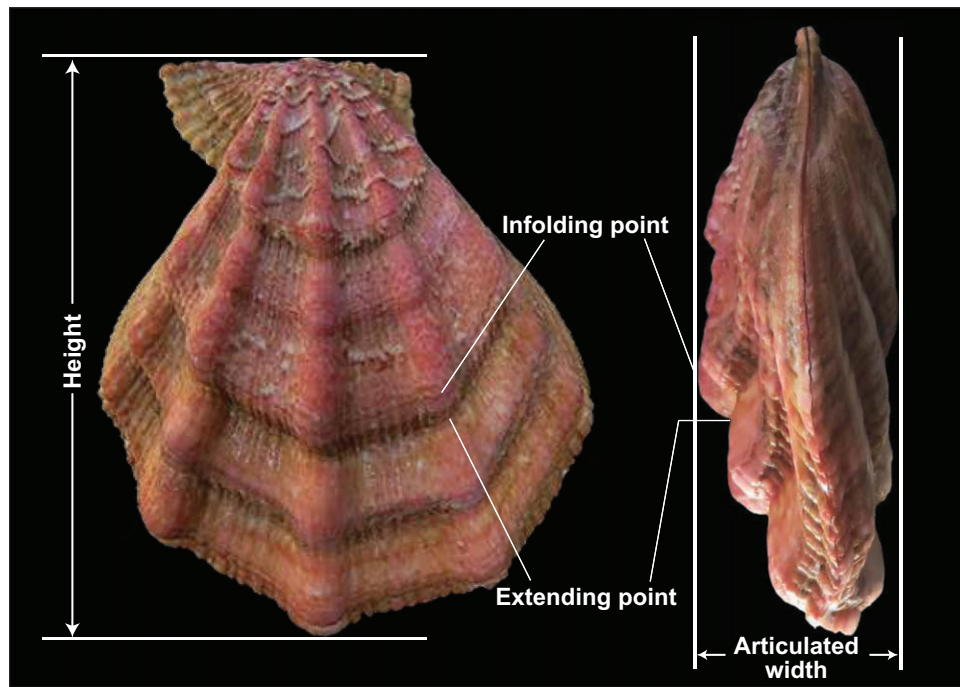


Figure 2. Morphological terminology for shell of *Swiftopecten swiftii*.

Shell microstructure

Distribution of shell layers and microgrowth lines were observed in order to reveal the growth pattern of the shells. A 4-mm thick section from each specimen was cut along the maximum growth axis, then ground, polished and stained with Mutvei's solution (Schöne *et al.*, 2005), and finally photographed with a digital microscope (Keyence VHX-2000). Then, each sample was coated with platinum–palladium for scanning electron microscopy (SEM; using microscope Keyence VHX-D510) to examine shell microstructure.

Carbon- and oxygen-isotopic analyses

To understand the functional morphological role of the peculiar step-like growth ribs in *S. swiftii*, we conducted stable isotopic analysis for carbon and oxygen ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively) of shells. A first set of analyses was performed to investigate seasonality in the growth patterns based on shell $\delta^{18}\text{O}$ as a temperature proxy, based on one dead shell from Dolinsk and another live-collected shell from Yubetsu. Shell powder samples were obtained along the maximum growth axis of the shell surface at 2.0–3.5 mm intervals, using a motor drill. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were measured with a mass spectrometer (IsoPrime, GV Instruments) housed at the Japan Agency for Marine–Earth Science and Technology. The measurements were used to reconstruct water temperatures from the $\delta^{18}\text{O}$ values and salinity data (J-DOSS, period covered: 2007–2015). Note that since sample collection depth of *S. swiftii* was deeper than 15 m, $\delta^{18}\text{O}$ values are likely to be mainly attributable to the inverse relationship with temperature, salinity remaining relatively constant.

In a second set of analyses, to understand the mechanisms underlying sexual differences in commarginal ridges, fluctuations in water temperature and timing of valve formation were compared in detail with shell-layer morphology and microgrowth patterns. This examination was based on one male and one female individual collected from Yubetsu. A motor drill was used to sample shell powder at 1.0-mm intervals from a cross-section cut along

the maximum growth axis, to reveal intra-annual cycles at the three- to four-year stages. $\delta^{18}\text{O}$ values in the obtained powder were measured using a continuous flow – isotope ratio mass spectrometer (Delta V plus, Thermo Fisher Scientific) equipped with an automated carbonate reaction device (GasBench II, Thermo Fisher Scientific) housed at the Atmosphere and Ocean Research Institute, the University of Tokyo. Detailed analytical settings have been reported elsewhere (Kubota *et al.*, 2017; Shirai *et al.*, 2018). Water temperature was estimated from the shell $\delta^{18}\text{O}$ values, using the equation given by Kim *et al.* (2007), for which seawater $\delta^{18}\text{O}$ values were inferred based on the salinity at each locality, based on the North Pacific salinity $-\delta^{18}\text{O}_{\text{water}}$ relationship reported by LeGrande & Schmidt (2011).

RESULTS

Male–female differences in gonad size and shell morphology

The 134 specimens, with shell heights ranging from 6.5 to 12.8 cm, were 55% males and 45% females (Fig. 1).

A comparison of males and females of the same shell size showed that the ovary was significantly larger than the testis (Fig. 3A). The average GI of the ovary was *c.* 1.34 times larger than that of the testis at the beginning of April. The GI of testis and ovary average *c.* 4.22 and 5.67 respectively (Fig. 3B). The null hypothesis of a normal distribution was not rejected for the gonad weight of males (Kolmogorov–Smirnov test $D = 0.05487$, $P = 0.6207$) or females ($D = 0.07156$, $P = 0.6654$). A *t*-test confirmed a significant difference between the mean gonad weights of males and females ($t = 19.452$, $df = 13.142$, $P = 1.165 \times 10^{-12}$).

With regard to shell morphology, the female valves had a more prominent bulge (expressed as a greater articulated width) than those of the males (Fig. 4). Again, the null hypothesis of a normal distribution was not rejected in either males ($D = 0.1013$, $P = 0.6712$) or females ($D = 0.1365$, $P = 0.7246$) and a *t*-test confirmed a significant difference between the sexes ($t = 23.165$, $df = 15.043$, $P = 1.051 \times 10^{-11}$).

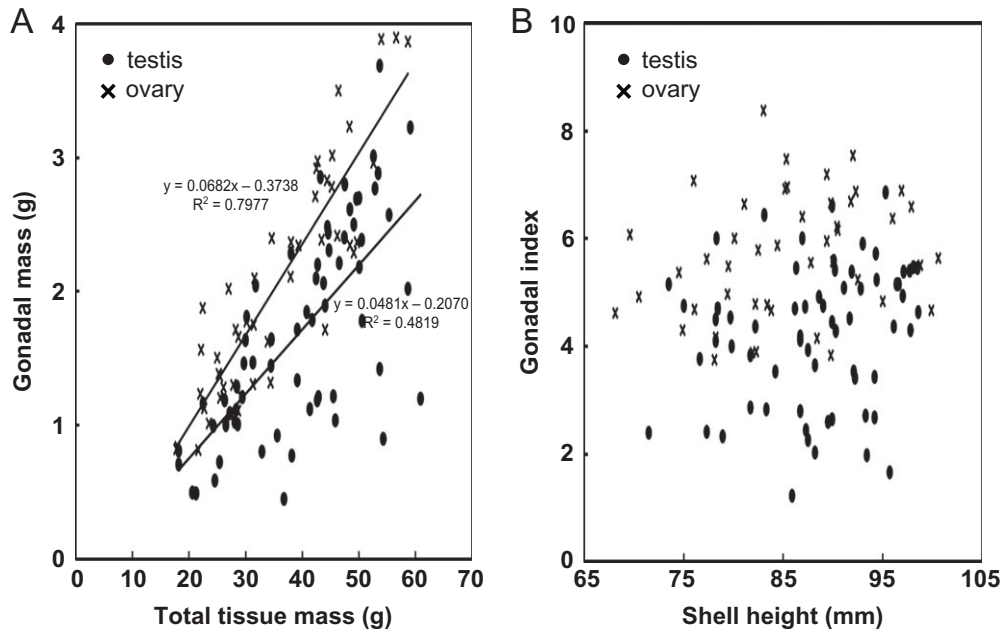


Figure 3. *Swiftopecten swiftii* from Yubetsu, Hokkaido, Japan, collected 1 April 2016. **A.** Gonadal mass in relation to total tissue mass for testis and ovary. **B.** Relation between gonadal index and shell height, for testis and ovary.

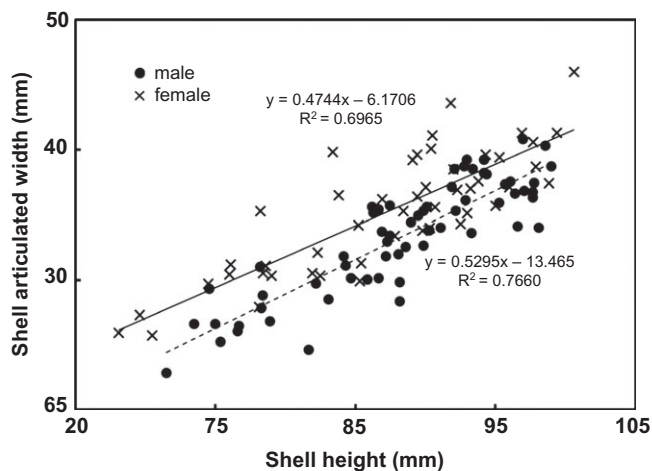


Figure 4. *Swiftopecten swiftii* from Yubetsu, Hokkaido, Japan, collected 1 April 2016. Regression of articulated shell width on shell height and width for males and females.

Shell layers and microstructure

The shell of *S. swiftii* consists of two layers, the outer layer (OL) and inner layer (IL), separated by the myostracal layer (ML). The OL and IL have a foliated structure (Fig. 5A, C), whereas the ML has a simple prismatic structure (Fig. 5B) with inclined angles of $c. 60^\circ$ against the OL and the IL (Fig. 5A–C). The patterns of growth lines differed between the OL and IL (Fig. 5D): the OL showed a periodic growth pattern characterized by alternating growth lines and increments, with a growth disturbance mark just before the infolding point (see Fig. 2 for definition); on the contrary, the IL showed no clear growth lines, since it grows towards the inside of the shell, not in the radial direction of increasing shell height.

Carbon and oxygen isotopic analyses

Intra-annual $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ profiles from commarginal ridges of two specimens (from Yubetsu and Dolinsk) are shown in Figure 6.

The $\delta^{18}\text{O}$ value of the shell is mainly controlled by ambient temperature and resulting $\delta^{18}\text{O}$ composition of sea water (e.g. Kim *et al.*, 2007). The shell $\delta^{18}\text{O}$ shows cyclical fluctuations, which can therefore be interpreted as being of annual periodicity. The number of cycles corresponds with the number of commarginal ridges, suggesting that these ridges formed annually. The valve edges become folded inwards after the $\delta^{18}\text{O}$ maxima (i.e. summer), then grow straight after the minima (i.e. winter). In other words, shell growth of *S. swiftii* has two stages: a length-expansion stage from summer to autumn and a volume-expansion stage from winter to spring. The two individuals from the two localities showed similar cyclical patterns in $\delta^{18}\text{O}$ profile and timing of commarginal ridge formation, although they presented different absolute values. Oxygen isotope composition was mainly between -0.5 and 2.5‰ (Fig. 6A) in the specimen from Yubetsu, and mainly between -1.5 and 2.0‰ in that from Dolinsk (Fig. 6B).

On the contrary, the fluctuation in $\delta^{13}\text{C}$ showed no clear seasonal periodicity. The specimen from Yubetsu showed $\delta^{13}\text{C}$ values mainly from -1.5 to 1.3‰ (Fig. 6A), whereas values from the specimen from Dolinsk ranged mainly between 0.0 and 2.5‰ (Fig. 6B).

The $\delta^{18}\text{O}$ profiles obtained from shell cross-sections provided more detailed comparison between growth timing and shell morphology (Fig. 7). Since these specimens were collected alive from Yubetsu, where a record of environmental temperature is available, comparison of reconstructed temperature from shell $\delta^{18}\text{O}$ (Fig. 7) and observed local temperature (Fig. 8) is possible—bearing in mind that the local temperature records are for the sea surface rather than the seafloor where the scallops lived. The *S. swiftii* specimens recorded water temperatures of 1 – 15°C and showed a sinusoidal cyclic pattern and no growth cessation during minimum temperatures.

Figure 7 shows differences in the positions of the extending points (Fig. 2), but producing maximal volumes at 10 – 12°C in both sexes. Based on annual water temperature (Fig. 8), we estimate that the volume inside the valves is maximized around July, which is the spawning season for this species (Kosaka & Ito, 2006). However, a comparison of the infolding points (Fig. 2) in shells of the two sexes shows that the shift to inward growth occurs at 4 – 6°C in the male (Fig. 7A) and 2 – 3°C in the female (Fig. 7B). These

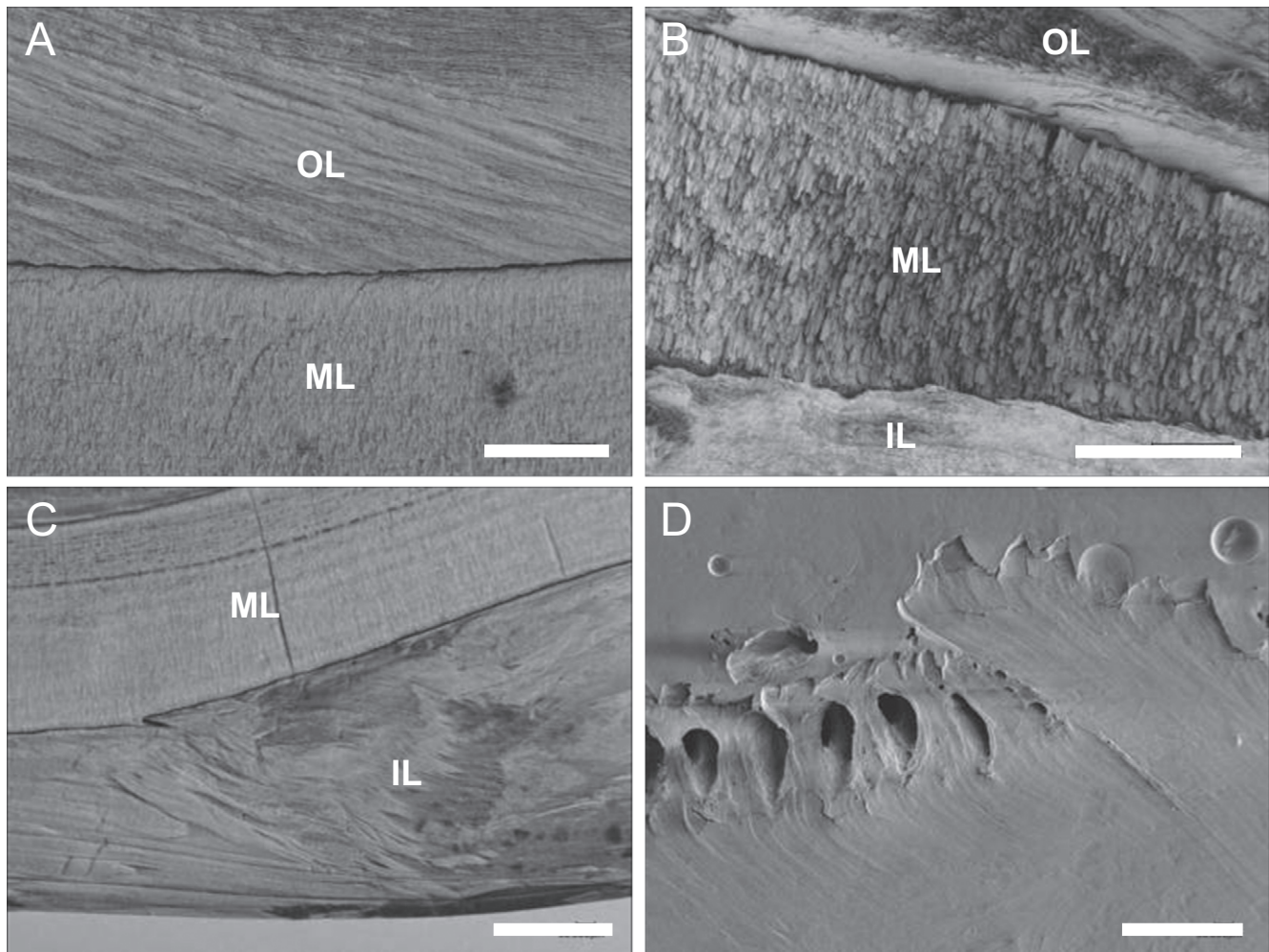


Figure 5. Shell microstructure of *Swiftopecten swiftii*. **A.** Outer layer, foliated structure. **B.** Myostracal layer, simple prismatic structure. **C.** Inner layer, foliated structure. **D.** Enlargement of infolding point. Abbreviations: IL, inner layer; OL, outer layer; ML, myostracal layer. Scale bars: **A** = 150 μm ; **B** = 100 μm ; **C** = 300 μm ; **D** = 300 μm .

temperatures correspond to the middle of December and the middle of November, respectively. Therefore, infolding in the female occurred approximately one month earlier than in the male.

DISCUSSION

Ecological significance of step-like commarginal ridges in Swiftopecten swiftii

Previously, the formation of commarginal ridges has been considered to be caused by pauses in shell growth (Habe, 1977) but, for pectinids, Takenaka & Hayami (1998) considered them instead to reflect reproductive cycles. Our study of shell geochemistry and microstructure has confirmed this for *Swiftopecten swiftii*. The commarginal ridges of this taxon are prominent steps, which are quite unique among bivalve shells—there being no other taxa showing such a great change in internal volume in a cyclical fashion (Yoshimura, 2017). In our study, oxygen-isotope data confirmed that the valves are folded inward from winter to spring and grow straight (i.e. increasing shell length) from summer to autumn. We have also shown that the commarginal ridges in *S. swiftii* are annual rings in the third year and later. In regard to this point, *S. swiftii* is known to start reproduction from its third year, the gonad first becoming mature from the winter of the third year (Kosaka &

Ito, 2006). Therefore, we consider that the commarginal ridges in *S. swiftii* are linked with its reproductive cycle.

Previous studies have suggested functions for various ‘ribs’ in bivalve shells from a functional-morphological viewpoint. For example, in many pectinid species, radial ribs may contribute to shell strength through reinforcement against bending stress (Hayami, 1994). Checa (2002) suggested that the oblique ribs on the shells of a few epibenthic bivalves (e.g. Mytilidae and Chamidae) might function in reinforcement of the margin. In another groups of pectinoideans, Hayami (1994) considered that internal ribs in *Amusium japonicum* have a similar function in maintaining shell strength and also that radial ribs enhance the occlusion of the valves. For other bivalve groups, the function of oblique ribs in burrowing was demonstrated quantitatively by Stanley (1975). The significance of ribs in burrowing bivalves was also discussed by Seilacher (1973) and Savazzi (1981). Divaricate ribs in *Solecurtus* represent another case of specialization, minimizing damage to the valve margins during burrowing by intercepting radial breaks (Checa, 1993). Ribs in bivalve shells thus play critical roles in reinforcement, occlusion or burrowing.

The relationship between shell formation and reproductive cycles in *S. swiftii* indicates a unique life-history strategy and provides a new functional perspective on shell morphology. Yoshimura (2017) conducted measurements of these step-like commarginal ridges and showed that the average ratio of growth increments (measured in

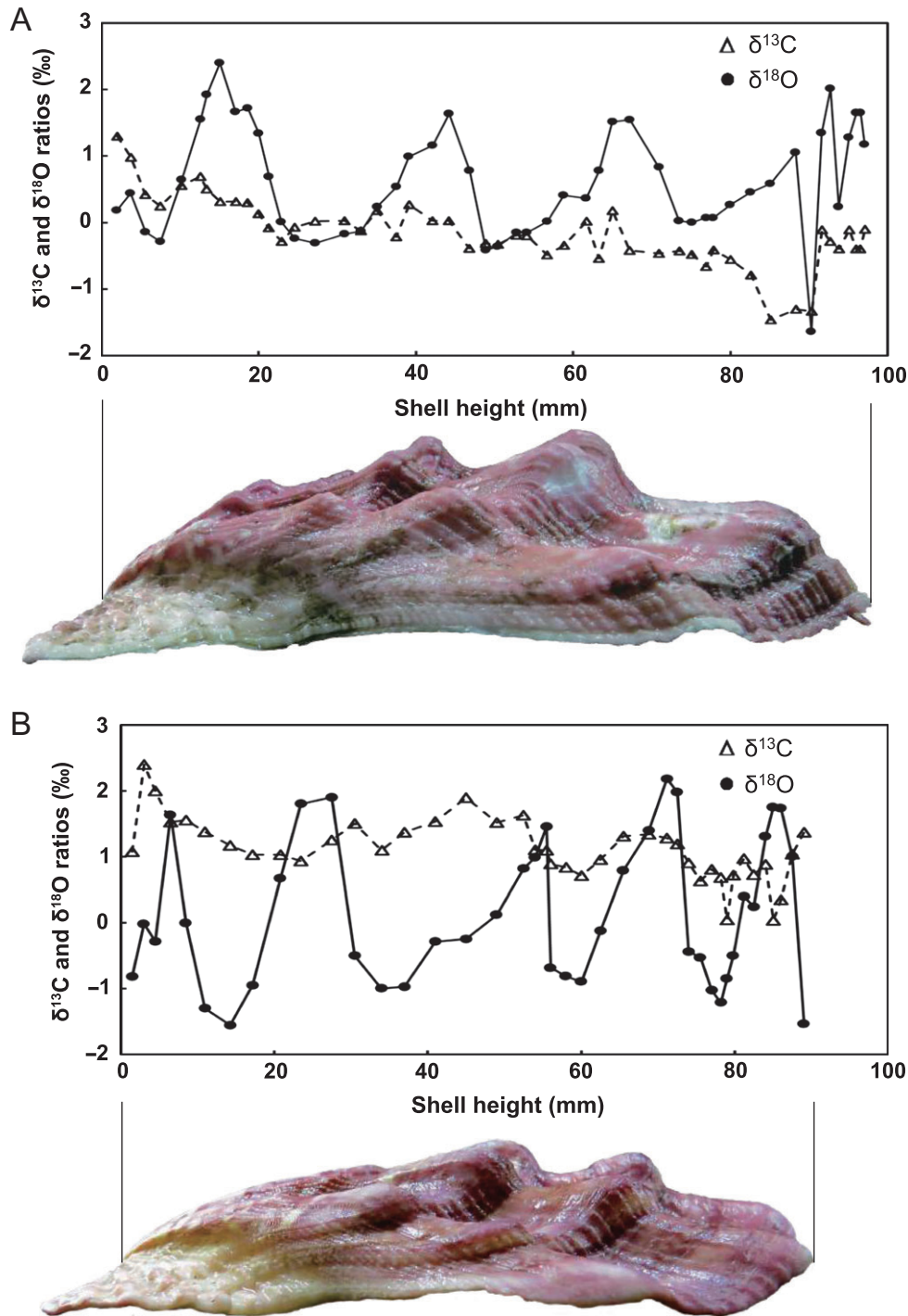


Figure 6. Carbon- and oxygen-isotopic analyses of *Swiftopecten swiftii*. **A.** Specimen from Yubetsu, Hokkaido, Japan. **B.** Specimen from Dolinsk, Sakhalin, Russia.

direction of growth, not as increase in shell height) during the extending and infolding phases (Fig. 2) is 3:1. Together with our oxygen-isotope profiles, this result indicates that linear shell growth in *S. swiftii* from summer to autumn is approximately three times larger than that from winter to spring. The swollen valves effectively enlarge the internal volume of the shell at a minimum production cost. This strategy is also consistent with that fact that the solubility of CaCO_3 is lower at higher water temperatures and that, therefore, the cost of calcification is then greater (Vermeij,

1987; Morse, Arvidson & Lutge, 2007). Jodrey & Wilbur (1955) studied shell growth in relation to metabolic seasonality. It is well known that the fluctuation of carbon isotopes reflects an individual's metabolism and phytoplankton intake (Wong & Sackett, 1978; Hayes, 1993). The carbon-isotope ratio in *S. swiftii* is high in summer and autumn, indicating higher metabolism. Hence, from the aspects of calcification costs, metabolism and nutrition, the life-history strategy of *S. swiftii* is optimized for shell production at high water temperatures from summer to autumn and for energy saving

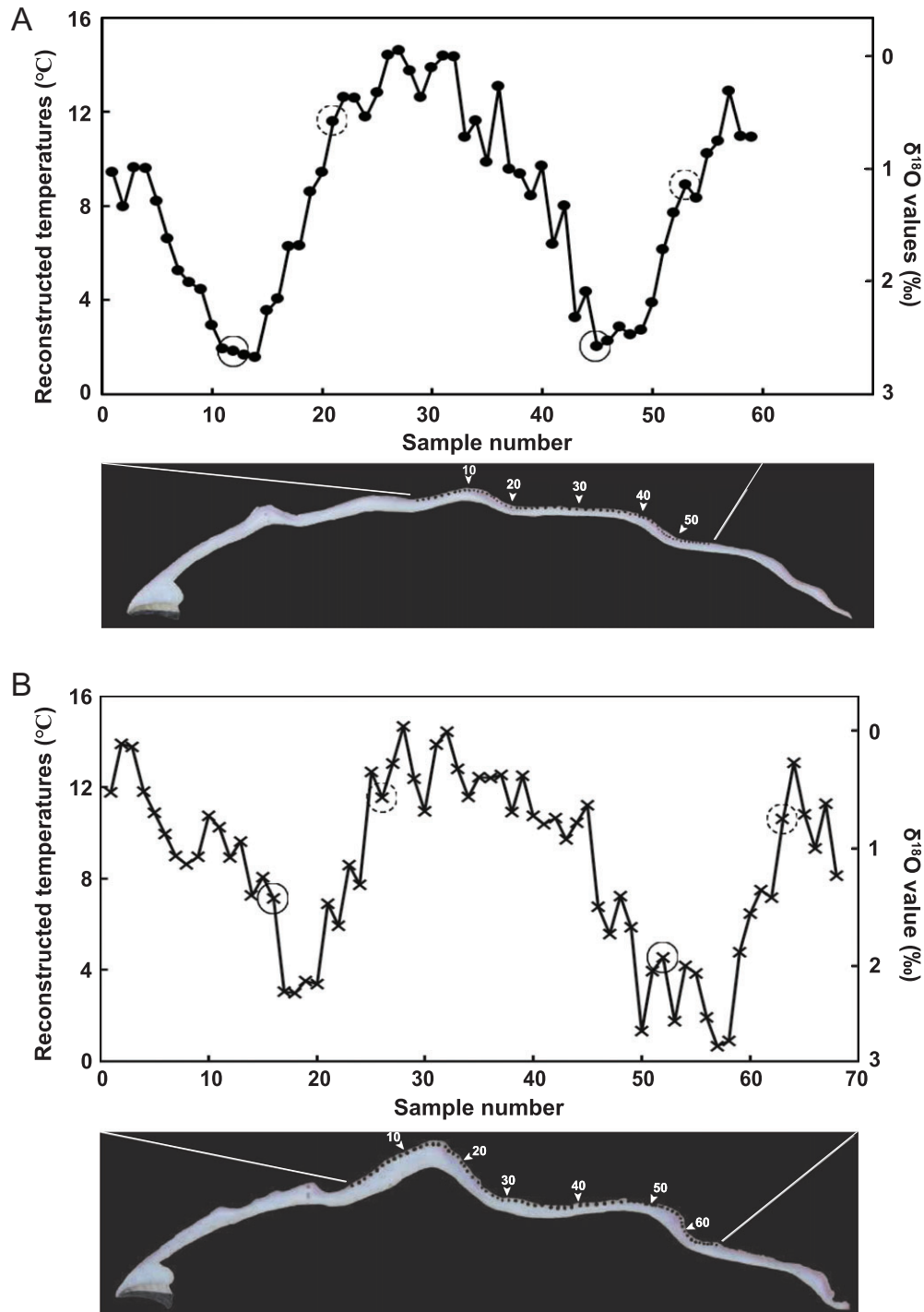


Figure 7. Comparison of detailed oxygen isotopic analyses between male and female *Swiftopecten swiftii* shells from Yubetsu, Hokkaido, Japan. Salinity data from Japan Oceanographic Data Center (J-DOSS). **A.** Male. **B.** Female. Solid and dotted circles correspond to infolding points and extending points, respectively (see Fig. 2).

at low water temperatures from winter to spring. Shumway & Parsons (2016) have discussed the trade-offs between energetic costs of reproduction and growth in pectinids.

Adaptive significance of sexually dimorphic commarginal ridges

We found that shell width was greater in females than males and also that female gonads are larger than male gonads, as a

proportion of total tissue mass. The significance of the sexual differences in shell growth, and hence internal volume, in *S. swiftii* is likely related to gonad maturation and reproductive cycles.

Notably, the timing of the extending points was similar in both sexes, resulting in maximum volumes for both sexes at the same time. This is consistent with the fact that both sexes spawn at the same time (Kosaka & Ito, 2006). On the other hand, the formation of the infolding points in the two examined specimens

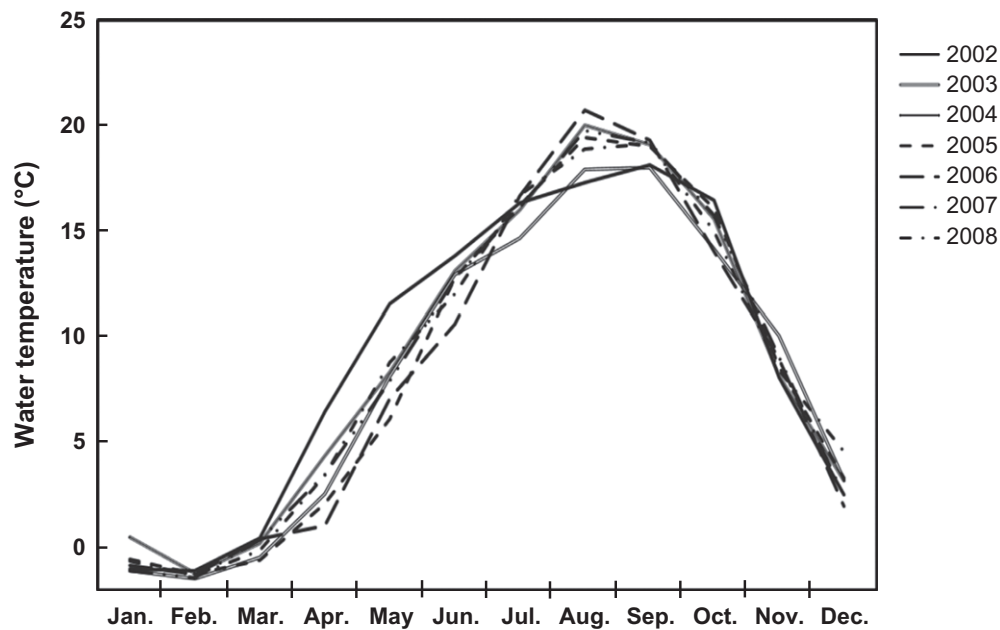


Figure 8. Seasonal fluctuation of water temperature in Monbetsu, Hokkaido, Japan (50 m depth).

indicated that the timing of the change in growth direction was one month earlier in the female than in the male. Assuming that the examined specimens were representative, this temporal difference together with the more developed commarginal ridges of females, is consistent with the likelihood that the female takes longer to develop a larger gonad than the male.

Known cases of sexual dimorphism in oviparous bivalves and other molluscs

Sexual dimorphism is not uncommon in molluscs. According to previous studies, dimorphism has been documented in shells of at least 140 species belonging to 50 families (see Supplementary Material). The taxonomic composition of this dimorphism is 72% Gastropoda (36 families), 20% Bivalvia (11 families), 6% Cephalopoda (2 families) and 2% Polyplacophora (1 family). Among the Bivalvia, 50% of the cases represent dwarf males and 37% are ovoviviparous species. *Swiftopecten swiftii* is the first case of shell sexual dimorphism in the order Pectinoidea.

Most cases of molluscan sexual dimorphism are found among gastropods conducting internal fertilization and cephalopods reproducing via copulation (e.g. Cazzaniga, 1990). It is generally expected that the female oviduct, being thicker than a male spermi duct, causes broader or larger shells in females. In Bivalvia, ovoviviparous species display exceptional sexual dimorphism related to brooding. The most spectacular cases are females of the carditids *Thecalia* and *Mineria*, which form a deep hollow space in their ventral margin to nurse their larvae (Cox *et al.*, 1969). Females of the Unionidae are known to have more bulging shells than males, to accommodate the ctenidial brood pouch for nursing their glochidia (e.g. Kotrla & James, 1987). Extreme size differences (dwarf males) are typical of the specialized group, Xylophagaidae (e.g. Turner & Yakovlev, 1983; Haga & Kase, 2013). In contrast to the above examples, *S. swiftii* is the first case of dimorphism identified in bivalves that practice external fertilization and lack parental care. In swimming pectinids, a swollen shell might affect swimming performance, but byssus-attaching species like *S. swiftii* do not have such a constraint, so that shell morphology can develop to maximize the size of the gonad at

reproduction, while growing normally during rest of the year. Sexual dimorphism in *S. swiftii* therefore represents an exceptional case of specialization in bivalves.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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