

OBSERVATIONS ON THE GROWTH OF THE SCULPTURED SHRIMP
SCLEROCRANGON BOREAS (DECAPODA: CARIDEA)

Bernard Sainte-Marie, Isabelle Bérubé, Sophie Brillon, and François Hazel

(BSM, correspondence; IB, SB) Direction des invertébrés et de la biologie expérimentale
(FH) Direction de la gestion des Océans

Institut Maurice-Lamontagne, Pêches et Océans Canada, C.P. 1000 Mont-Joli (Québec) G5H 3Z4, Canada

(BSM: Sainte-MarieB@dfo-mpo.gc.ca; IB: BérubéI@dfo-mpo.gc.ca; SB: BrillonS@dfo-mpo.gc.ca; FH: HazelF@dfo-mpo.gc.ca)

A B S T R A C T

Little is known of the growth of the sculptured shrimp *Sclerocrangon boreas*, a remarkable member of arctic and subarctic marine shelf communities. We determined the length-weight relationship, abdomen allometry, and size structure of shrimp in a population of the Gulf of Saint Lawrence, eastern Canada. We also reared shrimp for up to 3.5 years to measure their growth. The presence of very small immature females in the wild population indicates that the sculptured shrimp is not obligatorily a protandric hermaphrodite, if at all. Females grow faster, reach a greater size, and live longer than males. Males may be ≥ 4 years old at 17 mm cephalothorax length (CL) and females ≥ 6 years old at 29 mm CL. Ovigerous females have a broader abdomen with longer pleopod setae than similarly-sized immature females. After releasing their progeny, some females may molt and grow in length but revert to a condition of narrow abdomen and short pleopod setae, and then molt again to a condition of broad abdomen with long pleopod setae. This finding and demographic data suggest that some females are alternate-year spawners. Other females did not molt for ≥ 2 years and may spawn in successive years.

INTRODUCTION

The sculptured shrimp, *Sclerocrangon boreas* (Phipps, 1774), is a marine caridean of the family Crangonidae. It has a circumpolar range and is an arctic-boreal species (Heegaard, 1941; Butler, 1980; Squires, 1990). The sculptured shrimp may be found in water $\leq 8\text{--}11^\circ\text{C}$ on a variety of substrates, from fine mud to rock, although it appears to occur most frequently at $\leq 4^\circ\text{C}$ on sand, gravel or glacial till (Williams and Wigley, 1977; Klekowski and Węślawski, 1991; Bukin, 1992; Birkely and Gulliksen, 2003a). Temperature and sediment permitting, the sculptured shrimp distributes itself from the intertidal down to about 450 m (Heegaard, 1941; Klekowski and Węślawski, 1991). The sculptured shrimp may undergo seasonal bathymetric migrations, but reports conflict as to their direction/timing. Ingram (1979) indicated that shrimp move deeper in summer, and Bukin (1992) the contrary. The sculptured shrimp's diet consists mainly of polychaetes, gammaridean amphipods, mollusks, ophiuroids and, to a lesser degree, hydroids (Tabunkov and Chernysheva, 1985; Birkely and Gulliksen, 2003b). In turn, the sculptured shrimp is a common prey to cod (*Gadus* spp.), sculpins (*Myoxocephalus* spp.), snailfish (*Liparis gibbus*), beluga whale (*Delphinapterus leucas*), and seals (Sergeant, 1973; Falk-Petersen et al., 1988; Squires, 1990; Hjelset et al., 1999).

The sculptured shrimp is the largest of crangonids. Record sizes are 42 mm cephalothorax length (CL) from off Greenland (Ingram, 1979) and 145 mm total length from off the Koryak coast along the northwest Bering Sea (Bukin, 1992). Because of its large size and exquisite taste, the sculptured shrimp has attracted interest from the fishing industry (Ingram, 1979). However, exploratory fishing with various towed gear shows that the species is patchily distributed and never very abundant (Ingram, 1979; Hanson and Lanteigne, 1999). The highest reported catch rate, at 430 shrimp \cdot 1000

m^{-2} , comes from a 26-km² patch in the north Gulf of Saint Lawrence (Bernier and Poirier, 1981). However, average catch rate in this patch was substantially lower and more so in the day (7 shrimp \cdot 1000 m^{-2}) than at night (125 shrimp \cdot 1000 m^{-2}) suggesting that sculptured shrimp burrow during light hours (also see Butler, 1980). Maximum catch rate was 72 shrimp \cdot 1000 m^{-2} in the northwest Bering Sea (Bukin, 1992) and 66 shrimp \cdot 1000 m^{-2} in a Spitsbergen fjord (Birkely and Gulliksen, 2003a). The scattered distribution, low catch rate, and apparent scarcity of large (marketable) sculptured shrimp make profitable fishing unlikely (Bernier and Poirier, 1981). Alternatively, the possibility of culturing this species has been envisaged (Ingram, 1979; Miglav, 1992).

Little is known of the growth of sculptured shrimp. This species is considered to be univoltine with females spawning in the spring or summer (Ingram, 1979; Klekowski and Węślawski, 1991; Birkely and Gulliksen, 2003a). The large eggs are incubated on the female and development is almost direct: the two larval stages are passed under the mother's abdomen and last about 3–5 days altogether (Makarov, 1968; Ingram, 1979). The association between mother and young ceases about 9–12 months after oviposition, some time from April to July, after the larvae have molted to the juvenile stage (Ingram, 1979). Females reach a much larger size than males and this feature led some investigators to suggest that the sculptured shrimp is a protandric hermaphrodite (Bernier and Poirier, 1981), although this evidence alone is inconclusive. The presence in one population of putative intermediate sex forms and of large females with supposed vestigial male anatomical traits is additional support for protandry (Ingram, 1979). However, Birkely and Gulliksen (2003a) concluded that the sculptured shrimp is dioecious based on the existence of very small females. Ingram (1979) extrapolated laboratory growth data to the field and inferred

that the largest females in an Iceland fjord were ≥ 6 years old. Birkely and Gulliksen (2003a) concluded from modal analysis of size frequency distributions of sculptured shrimp in a Spitsbergen fjord that males lived < 2 years and that females lived for up to 4 years, but shrimp were much smaller there than in Iceland. Females may be semelparous (Birkely and Gulliksen, 2003a) or iteroparous and spawn annually (Squires, 1990) or in alternate years (Ingram, 1979).

As a contribution to the general biology of sculptured shrimp, we have examined allometric relationships and demography in populations of the northern Gulf of Saint Lawrence, eastern Canada. We also reared a broad size range of males and females and contrasted laboratory growth with natural growth inferred from size frequency distributions.

MATERIALS AND METHODS

Field Collections and Growth Study

A beam trawl was used to assess shrimp demography at two sites in the northern Gulf of Saint Lawrence: Baie Sainte-Marguerite (about 50°06'N, 66°35'W) on 10–11 May 2003 and off Havre Saint-Pierre (about 50°13'N, 63°36'W) on 10 July 2003. This beam trawl has a horizontal opening of 3 m, is fitted with heavy tickler chains to dislodge buried animals, and is towed at a speed of 2–2.5 knots. The stretched mesh size in the codend is 17 mm, but smaller shrimp are retained when the mesh becomes clogged. Trawl samples were taken during daytime from bottoms 15–40 m deep at a temperature of -0.5 to 3°C . The sampled depths cover the species' full bathymetric range at the two sites (Sainte-Marie, unpubl. data).

Shrimp were sexed according to the presence/absence of an appendix masculina on the second pleopod (Ingram, 1979) and we were careful of possible intermediate sex forms. A few smaller shrimp could not be sexed from external criteria and were recorded as 'unsexable'. We noted for females the degree of setation of the inner side of the distal part of the endopod of the second pleopod: (i) no setae, (ii) fringe of short setae, or (iii) fringe of long setae. Cephalothorax length (CL) and total length (TL) were measured from the posterior edge of the eye socket to the middle of the posterior margin of the cephalothorax and to the tip of the telson, respectively. Abdomen width (AW) was measured across the broadest part of the second abdomen segment. Length and width were measured to the nearest 0.01 mm with a vernier caliper. Wet weight was determined to the nearest 0.1 g after blotting intact specimens that were devoid of epizootes.

Shrimp for the laboratory growth study were collected with the beam trawl in Baie Sainte-Marguerite in May 1999 and July 2000. At the Maurice Lamontagne Institute, shrimp were housed in trays with a 31.5×39.0 cm ($= 0.123$ m²) bottom area and a water depth of 6.5 cm. Trays were subdivided by PVC opaque walls into sections each with a bottom area of 50 or 300 cm². Shrimp were reared singly in a small tray section when < 10 mm CL ($n = 23$) or in a large tray section when bigger ($n = 49$). The bottom and removable cover of the tray were fitted with 1-mm mesh. Each tray was embedded in a larger drawer, and the drawers were stacked in columns of eight drawers. The trays were continuously supplied with fresh seawater drawn from a depth of 17 m, at the upper limit of sculptured shrimp habitat, offshore of the Maurice Lamontagne Institute. Water entered the rear of the top drawer and flowed beneath the tray, moving up through the tray's bottom and out through its cover, before cascading down to the next drawer. The flow rate was set at $5-6 \cdot \text{L min}^{-1}$ to renew water in each tray about every 1.5 min. Temperature and salinity were usually recorded on a daily basis. Shrimp were fed excess thawed northern shrimp (*Pandalus borealis*) twice weekly. At the same time, trays were controlled to record molts or mortality. Shrimp exuviae or corpses were removed and their sex, CL and AW determined as above. Shrimp were reared for up to 3.5 years, during which temperature ranged from -0.1 to 11.5°C (mean = 5.0°C) and salinity from 24.2 to 32.5‰ (mean = 28.4‰), and therefore several successive molts were recorded for some individuals.

Data Analysis

Means and allometric scaling factors reported in text are accompanied by their standard error. For wild shrimp, we described relative growth of abdomen in reference to CL by linear regression of TL or AW on CL by

sex, after data were transformed to their natural logarithm as prescribed for allometric studies (Teissier, 1948; Hartnoll, 1978). A *t*-test was used to determine if the slope coefficient *b*, i.e., allometric scaling factor, departed significantly from one (= isometry). The allometry is negative when $b < 1$ and positive when $b > 1$ (Teissier, 1948; Hartnoll, 1978). Regression was also used to describe the relationship between wet weight and CL. Slopes of regressions were compared between sexes by analysis of covariance.

Mixture distribution analysis was performed using MIX (MacDonald and Pitcher, 1979) to resolve modes in CL frequency distributions of wild shrimp from Baie Sainte-Marguerite. This iterative analysis requires the input of reasonable initial parameters (number of modes, mean size and proportion of individuals per mode) based on visual inspection of size frequency distributions; various plausible combinations were tried and we retained the one providing the best fit (convergence) to observed CL frequency distribution based on a χ^2 test (MacDonald and Pitcher, 1979). Unsexable shrimp were included in analyses of both males and females.

Growth models were developed for laboratory shrimp by regression of molt increment (= postmolt CL less premolt CL) or intermolt (= days elapsed between first and second molt) on premolt CL. We used only the first molt increment and intermolt recorded for each individual to ensure independence of data and limit the possible negative effects of prolonged holding on growth (see Oh and Hartnoll, 2000).

RESULTS

Characteristics of Wild Sculptured Shrimp

The CL of the 562 sculptured shrimp caught in Baie Sainte-Marguerite in May 2003 ranged 5.6–10.3 mm for unsexable individuals, 6.1–19.8 mm for males, and 7.7–31.0 mm for females. Ovigerous females measured > 23.5 mm CL excepting one female of 16.7 mm CL. Of the 106 females > 23.5 mm CL, 37.7% were brooding and 6.6% more had just weaned their young judging from the appearance of their pleopods. Broods were usually a mix of ripe eggs and larvae, but in two cases the brood was comprised of recently extruded eggs. Off Havre Saint-Pierre, we collected a total of 229 sculptured shrimp in July 2003. No individual was unsexable and the CL range was 8.8–19.4 mm for males and 8.7–31.0 mm for females. Ovigerous females measured > 24.8 mm CL and of the 35 females above this threshold 31.4% were brooding recently extruded eggs and 5.7% more had just weaned their young. No intermediate sex form was found at either site.

The following analyses of wild shrimp focus on the larger Baie Sainte-Marguerite sample. Maximum wet weight was 10.2 g for males (Fig. 1A) and 43.3 g for females (Fig. 1B). Non-ovigerous females were conspicuously lighter than ovigerous females of similar CL (Fig. 1B), excepting one barren female with mature ovaries that was probably close to oviposition. The length–weight regressions for males and non-ovigerous females were significant (Fig. 1), but slopes differed between sexes ($F_{1,277} = 9.32$, $P = 0.002$). Females were increasingly heavier than males with growing CL.

Regressions of TL on CL were significant for both sexes (Fig. 2), but differed in slope ($F_{1,213} = 4.66$, $P = 0.032$). Total length scaled isometrically to CL in males ($b = 1.018 \pm 0.016$; $H_0: b = 1$; $t = 1.11$, $P > 0.2$), but negatively to CL in females ($b = 0.974 \pm 0.009$; $H_0: b = 1$; $t = -2.80$, $P < 0.01$). Thus as shrimp grew in size the ratio CL : TL remained constant in males but increased in females, i.e., the abdomen was relatively shorter in large than in small females.

The relationships of AW on CL are shown in Fig. 3. In females, the vertical scatter of AW increased abruptly at

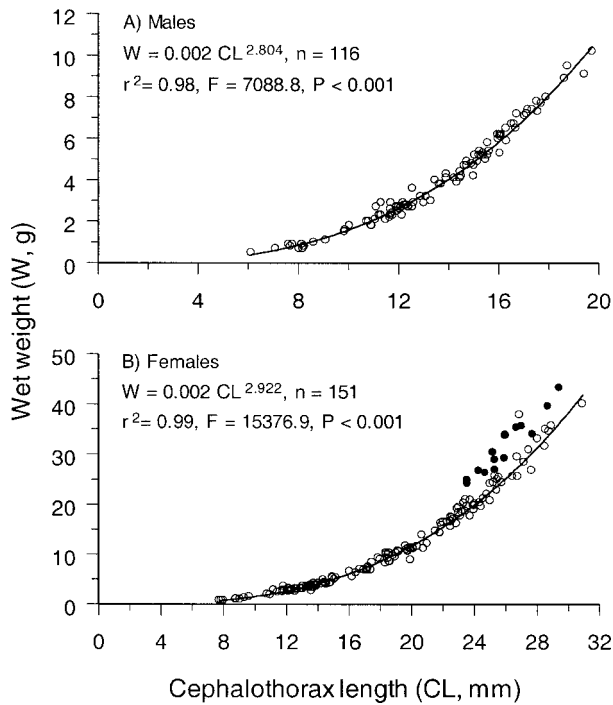


Fig. 1. Relationship of wet weight to cephalothorax length for (A) male and (B) female *Sclerocrangon boreas*. Brooding females represented by full circles are excluded from regression.

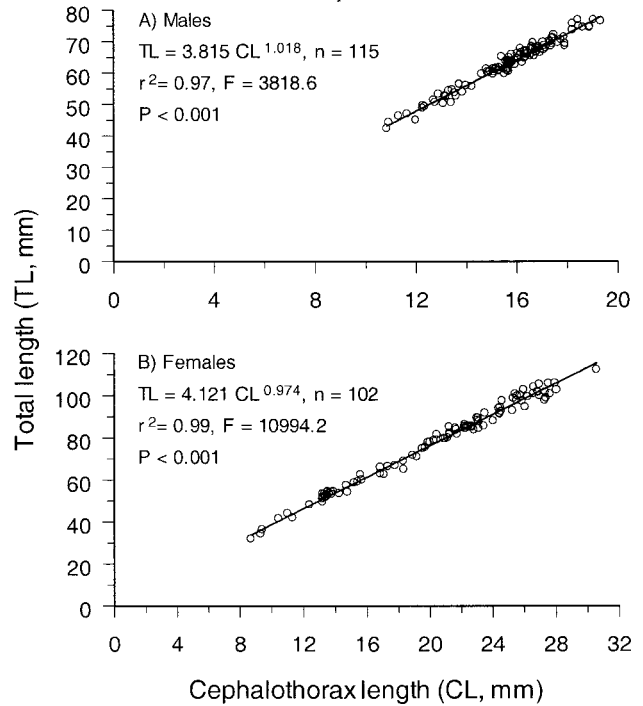


Fig. 2. Regression of total length on cephalothorax length for (A) male and (B) female *Sclerocrangon boreas*.

23.5 mm CL and this determined a second (upper) cloud of points representing females with an AW : CL ratio ≥ 1 . Ovigerous females all had long setae on the inner distal part of the endopod of pleopods, and all but two had an AW : CL ratio ≥ 1 . Exceptions were the small female of 16.7 mm CL and one of 26.7 mm CL (Fig. 3b). Among the 49 females with an AW : CL ratio ≥ 1 , 98.0% had long setae and 2.0% had short setae on the distal part of the pleopod's endopod. Among the 62 females ≥ 23.5 mm CL with an AW : CL ratio < 1 , 95.5% had short setae and 4.5% had long setae. Considering only shrimp < 23.5 mm CL, regressions of AW on CL were significant for both sexes (Fig. 3) but differed in slope ($F_{1,413} = 41.62, P < 0.001$). Abdomen width scaled negatively to CL in males ($b = 0.899 \pm 0.013; H_0: b = 1; t = -7.88, P < 0.001$), but isometrically to CL in females ($b = 1.007 \pm 0.011; H_0: b = 1; t = 0.62, P > 0.4$). Thus as shrimp grew in size the AW : CL ratio decreased in males, but remained constant in females until some point at which the abdomen suddenly broadened.

We resolved 4 modes of males ($\chi^2 = 6.81, df = 17, P = 0.986$) and 6 modes of females ($\chi^2 = 23.06, df = 30, P = 0.813$) in the CL frequency distributions of wild shrimp from Baie Sainte-Marguerite (Fig. 4). Several brooding females belonging to the last three modes had very heavy epibiosis (Fig. 5), but males usually carried no epizoites or only small spirorbid polychaetes. Percent mature females (ovigerous and post-ovigerous) by 1.5-mm CL class increased steeply at 24.0–25.5 mm CL and then oscillated around 50% (Fig. 4).

Growth of Sculptured Shrimp in the Laboratory

Molt increments in the laboratory were generally small, more so for males (Fig. 6A) than for females (Fig. 7A), and their relationship to premolt CL was dome-shaped. A two-

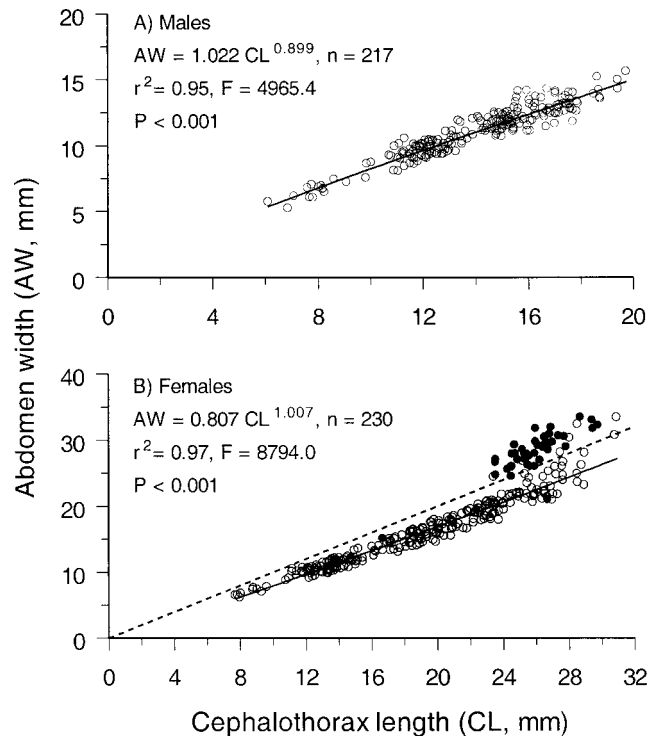


Fig. 3. Relationship of abdomen width to cephalothorax length (CL) for (A) male and (B) female *Sclerocrangon boreas*. Brooding females are represented by full circles. Shrimp ≥ 23.5 mm CL were excluded from regression. The dashed line represents an AW : CL ratio of 1.

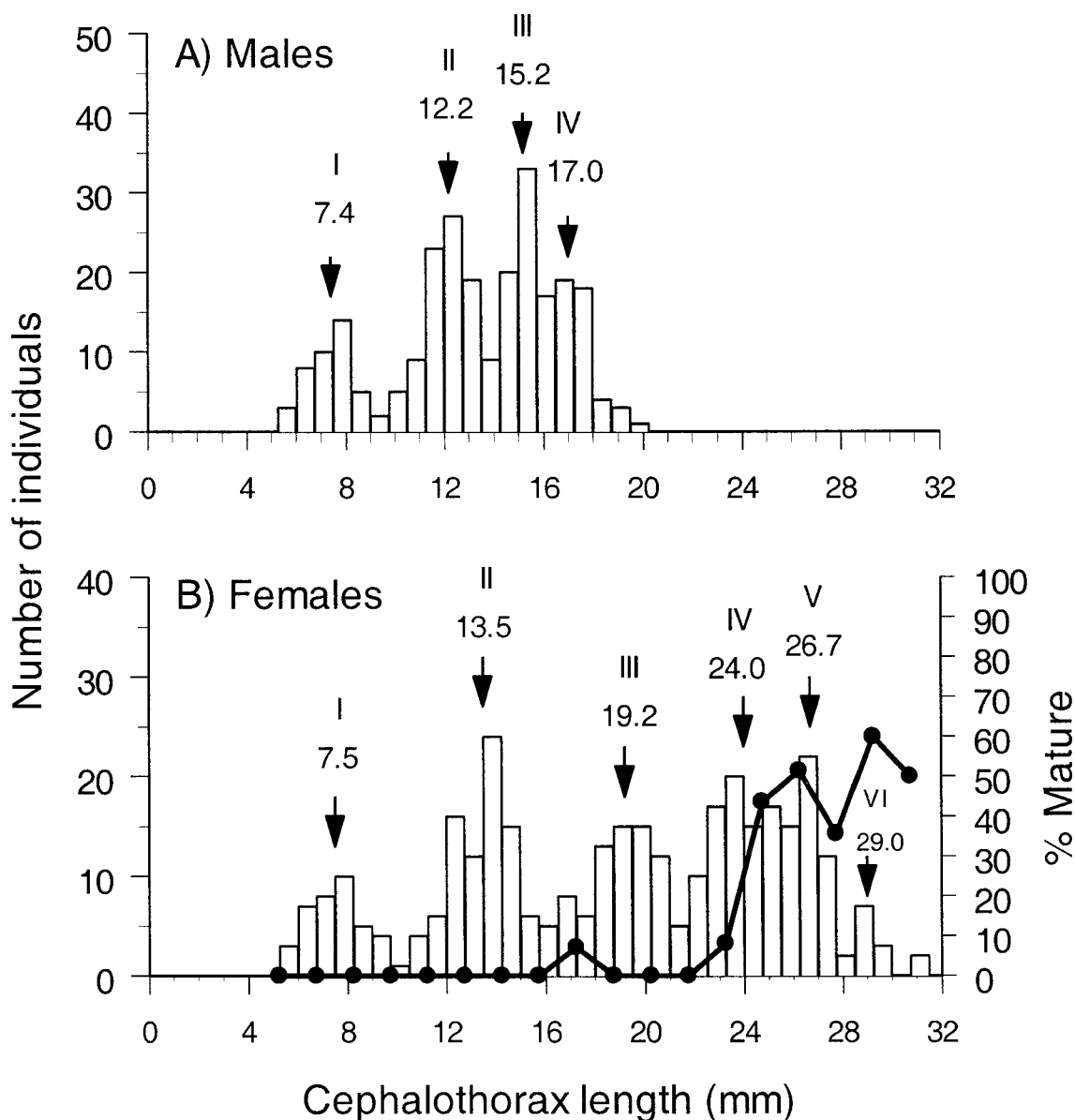


Fig. 4. Frequency distribution of cephalothorax length (CL) of (A) male and (B) female *Sclerocrangon boreas*. Size-classes are 0.75 mm and arrows, roman numerals and mean CL (mm) identify modes. Full black circles and line represent percent mature females by 1.5-mm CL class.

order polynomial regression model was fitted to molt increment vs premolt CL data (Figs. 6A and 7A). Based on this model and an initial size of 2.86 mm CL, representing the mean CL for juveniles separated from their mother in our study, males grow to 17 mm CL and females to 27 mm CL in 22 molts. The model predicts a maximum size of 19.6 mm CL for males and 27.7 mm CL for females after many additional molts. At the upper boundary of the 90% confidence interval (90% CI) for the predicted molt increment, males reach their maximum size of 19.8 mm CL in 14 molts and females reach 31.0 mm CL in just 13 molts.

The time between molts increased with shrimp size (Figs. 6B and 7B). Some of the largest shrimp had very long intermolts, up to 421 days for a male of 14.4 mm CL and 721 days for a female of 28.6 mm CL. Most of the females with a very long intermolt were ovigerous. However, for

both large males and females there was a distinct clustering of intermolt around 200 days. Intermolt values > 400 days were identified as outliers (Studentized residual > 2) in regression analysis. With these values excluded, an s-curve was adjusted satisfactorily to data (Figs. 6B and 7B). Based on this model, size-specific intermolt was similar for males and females and tended toward an asymptote of ≈ 200 days. Intermolt at the lower boundary of the 90% CI for predicted values was about half the average value at any given shrimp size.

Growth trajectories based on average molt increment and intermolt from our models produced age estimates of 7.5 years at 17 mm CL for males and 9.2 years at 27 mm CL for females (Fig. 8). Under the optimistic scenario of the upper and lower boundaries of the 90% CI for molt increment and intermolt, respectively, males could grow to 19.8 mm

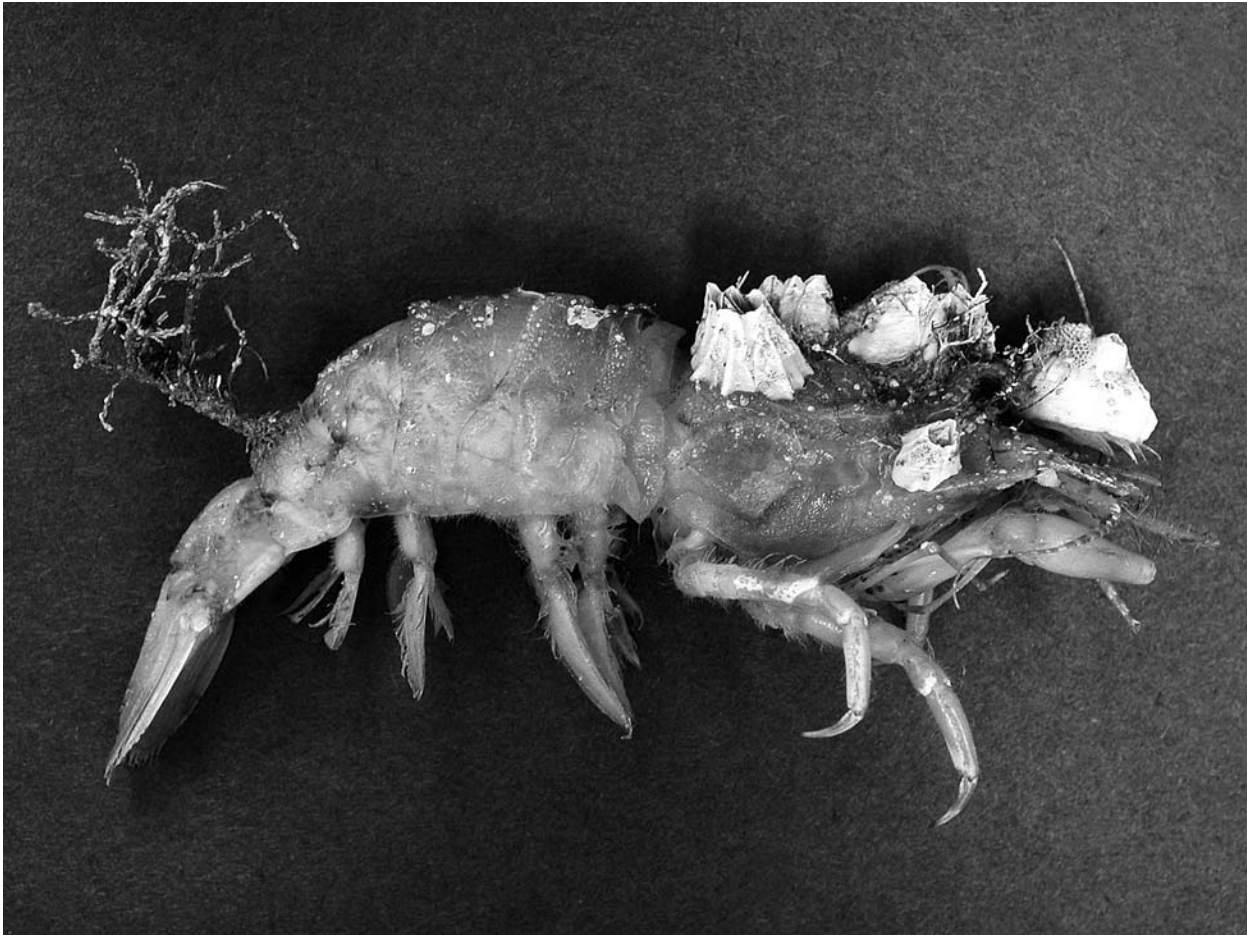


Fig. 5. Brooding female *Sclerocrangon boreas* of 25.8 mm cephalothorax length with heavy epibiosis. The female carries 6 barnacles, *Balanus balanus*, the largest of which is 16.1 mm in diameter at its base. One barnacle is hidden from view.

CL in 2.4 years and females to 31 mm CL in just 3 years (Fig. 8). Individual laboratory growth trajectories were consistent with or slightly faster than predictions of the average growth model. For example, one male grew from 6.9 to 11.9 mm CL in 6 molts over 1.4 years and another grew from 12.7 to 17.2 mm CL in 7 molts over 3 years. One female grew from 8.3 to 13.9 mm CL in 6 molts over 2.1 years, another from 13.5 to 22.0 mm CL in 7 molts over 2.4 years, and another from 19.1 to 26.3 mm CL in 6 molts over 2.8 years. No sex reversal was observed among the 21 males that initially measured ≥ 10 mm CL and that were reared through 3–7 molts.

Additional observations on female growth are noteworthy. Oviparous females molted within a few weeks of releasing their progeny or ≈ 6 –12 months later, but one female molted during the late stage of brood incubation. The AW : CL ratio of some females > 19.3 mm CL shifted from < 1 to ≥ 1 , and *vice versa*, over just one molt. Upward shifts ($n = 8$) averaged $+0.108 \pm 0.014$ units of AW : CL ratio and resulted from much larger positive growth of AW ($+12.7 \pm 1.2\%$) than of CL ($+1.4 \pm 0.6\%$). Downward shifts ($n = 11$) averaged 0.105 ± 0.012 units and resulted from negative growth of AW ($-7.2 \pm 1.0\%$) and positive growth of CL ($+3.1 \pm 1.0\%$). The setae on the distal part of the endopod of pleopods lengthened when the AW : CL

ratio surpassed 1 and usually shortened when it decreased to < 1 . Two females with an initial CL of 23.6 and 23.7 mm alternated between states of “narrow” and “broad” abdomen: sequences of AW : CL ratio were $1.09 \rightarrow 0.98 \rightarrow 1.06 \rightarrow 0.96$ and $0.92 \rightarrow 1.03 \rightarrow 0.96 \rightarrow 1.10$, respectively.

DISCUSSION

Sexual System

The nature of the sexual system of the sculptured shrimp remains uncertain. On one hand, Ingram (1979) concluded that the sculptured shrimp is a protandric hermaphrodite based on the finding that a few shrimp of 10–15 mm CL had second pleopod features intermediate between the male and female forms and that all of 30 examined females of 16–20 mm CL had a strand-like structure extending from the ovary to the base of the fifth pereopod, which he suggested was a vestigial vas deferens (also see Boddeke et al., 1991). Histology on the Arctic arigid *Argis dentata*, another crangonid shrimp, revealed that a similar strand-like structure in females was tubular and compatible with a degenerate vas deferens (Fr chet te et al., 1970). On the other hand, some observations suggest the sculptured shrimp is not a protandric hermaphrodite. First, we observed no sex reversal among

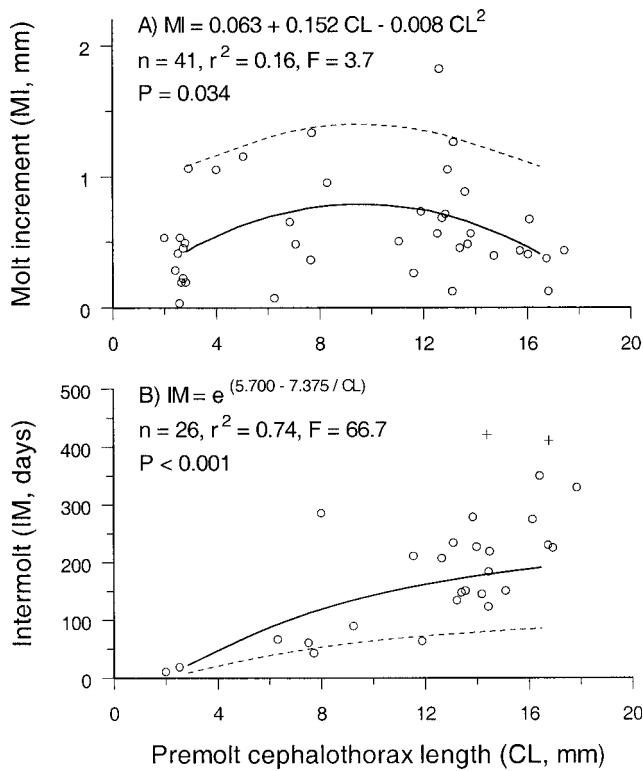


Fig. 6. Regression (full line) of (A) molt increment and (B) intermolt on premolt cephalothorax length for male *Sclerocrangon boreas* reared in the laboratory. The dashed line is the upper (pane A) or lower (pane B) boundary of the 90 % confidence interval on model predictions. Intermolt data marked by a plus sign were excluded from regression.

several males of ≥ 10 mm CL reared through several molts. However, this could be a laboratory artifact if sex reversal is controlled by environment or social interaction (see below) because we reared shrimp singly and in only one set of conditions. Second, a few very small (7–8 mm CL) immature females occurred in populations investigated by Ingram (1979) and Bernier and Poirier (1981), and they were relatively more numerous in populations studied by Birkely and Gulliksen (2003a) and us. These immature females were as small as the smallest recognizable males; therefore they indicate at the very least that the sculptured shrimp is not an obligate protandric hermaphrodite.

The seemingly conflicting interpretations of the sexual system of sculptured shrimp are not irreconcilable. Sex determination and reversal among the Crustacea may be flexible and can vary in response to temperature, photoperiod, diet, parasites, and/or sociosexual context (Ginsburger-Vogel and Charmiaux-Cotton, 1982; Juchault and Mocquard, 1989; Zupo, 2000; Chiba et al., 2003). Partial protandry combining sequential hermaphrodites, primary females and primary males was documented in the hippolid shrimp *Thor manningi* (Bauer, 1986). Facultative hermaphroditism exists in a variety of crustaceans (Brook et al., 1994; Rudolph, 1995) and the proportion of hermaphrodites in a population may vary among years/localities (for *C. crangon* as an example, compare Martens and Redant, 1986; Boddeke et al., 1991). The sculptured shrimp might exhibit similar flexibility of sexual development.

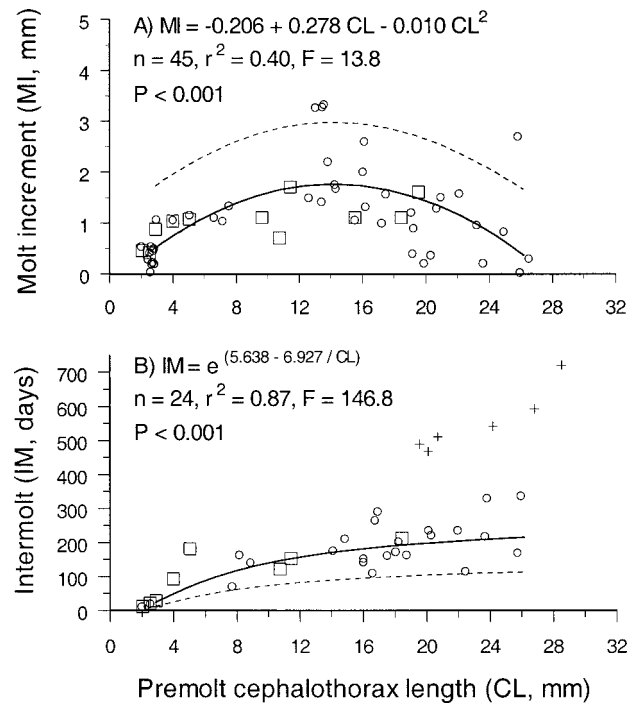


Fig. 7. Regression (full line) of (A) molt increment and (B) intermolt on premolt cephalothorax length for female *Sclerocrangon boreas* reared in the laboratory. The dashed line is the upper (pane A) or lower (pane B) boundary of the 90 % confidence interval on model predictions. Intermolt data marked by a plus sign were excluded from regression. Growth data from Ingram's (1979) "cold regime" treatment are overlaid on our data as open squares.

Growth

Growth of sculptured shrimp in the laboratory was previously documented for small unsexed shrimp and immature females < 22 mm CL by Ingram (1979). There, shrimp were reared under a naturalistic "cold" regime (mean = 6.3°C over one year, range of monthly averages: 3.0–10.0°C) and a "warm" regime (mean = 9.1°C, range: 3.5–14.0°C). Size-specific molt increment did not vary with temperature, whereas the intermolt was approximately 50% shorter and the mortality rate higher, in the warm than in the cold regime. Average growth data from Ingram's cold regime (his figures 38, 39, 40 and 41) are overlaid on our data in Fig. 7 to illustrate the consistency of findings between the two studies.

We infer from CL frequency distributions of sculptured shrimp in Baie Sainte-Marguerite that females live longer than males. The sculptured shrimp is a univoltine species (Ingram, 1979; Klekowski and Węstawski, 1991; Birkely and Gulliksen, 2003a) and the mean CL of the first mode in size frequency distributions (mode I: 7.4–7.5 mm CL) was about three times greater than the 2.0–2.9 mm mean CL (Ingram, 1979; this study) of juveniles just separated from their mother. From data in Ingram (1979) and our study, shrimp take about one year to grow from 2.5–3.0 mm to 6–8.5 mm CL. Therefore, because field sampling in Baie Sainte-Marguerite occurred toward the beginning of the April–July period of juvenile release, shrimp forming mode I were about 1-year old since leaving their mother. Each of the subsequent modes in the CL frequency distribution

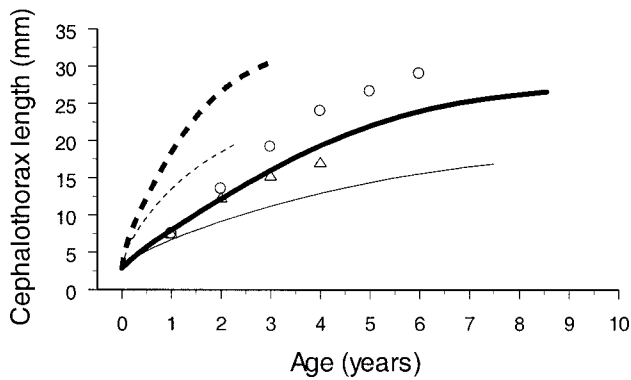


Fig. 8. Growth of male (thin lines and triangles) and female (heavy lines and circles) *Sclerocrangon boreas*. The full and dashed lines represent average and optimistic growth, respectively, derived from molt increment and intermolt data for laboratory-reared shrimp (see text and Figs. 6 and 7). Triangles and circles represent growth of wild males and females inferred from frequency distributions of cephalothorax length (see Fig. 4).

likely represents cumulative growth accrued through at least 2 (mode II), 3 (mode III), 4 (mode IV), 5 (mode V) and 6 (mode VI) years of life. Assuming dioecism, males probably require ≥ 4 years and females ≥ 6 years to reach their respective maximum size. This interpretation of age-at-size is similar to Ingram's (1979) for an Iceland population where shrimp became as large as in the Gulf of Saint Lawrence. However, Birkely and Gulliksen (2003a) detected only one mode for males (11.8 mm CL) and three for females (11.4, 18.3 and 21.7 mm CL) among sculptured shrimp from a Spitsbergen fjord sampled in May, corresponding roughly to our modes II, III and IV. The trawl used by Birkely and Gulliksen had a much coarser mesh (40 mm) than ours and we suspect that shrimp forming our mode I were missed. Moreover, in Spitsbergen shrimp did not reach sizes corresponding to our modes V and VI.

Female age-at-size is likely more variable and greater on average than is apparent from modal structure. Assuming dioecism, most females in the north Gulf of Saint Lawrence were probably aged 4 or 5 years at first maturity. The finding that females can shift between states of morphological maturity (broad abdomen, long pleopod setae) and immaturity (narrow abdomen, short setae), consistent with the observation that percent mature females in modes V and VI averaged 50%, strongly suggests alternate-year spawning/brooding. Alternate-year spawning was inferred for females of the sculptured shrimp (Ingram, 1979) and Antarctic crangonid *Notocrangon antarcticus* (Bluhm and Brey, 2001). Additionally, some female sculptured shrimp did not molt for a long time as evidenced by large epizoites on their carapace in this and other studies (MacGinitie, 1955; Zarenkov, 1970). Although growth of the barnacle *Balanus balanus* has not been documented, the related cold-water species *B. crenatus* and *B. hesperius* were 2–4 years old since settlement (Paul and Paul, 1986) at a similar size to the largest encrusting barnacle in our study. Thus some female sculptured shrimp stop molting or have > 1 year intermolts (as confirmed by our laboratory study) during which they might undergo successive-year spawning. Females of the American lobster *Homarus americanus* spawn in alternate or

successive years depending on female size and environmental conditions (Aiken and Waddy, 1980; Comeau and Savoie, 2002). The implication of alternate- or successive-year spawning is that the largest female sculptured shrimp at our study site could potentially be ≥ 8 –9 years old.

Even the largest male sculptured shrimp had clean carapaces or carried only small epizoites. This observation suggests that male intermolt is usually < 1 year or that males have a much higher mortality rate than females, as inferred for the sculptured shrimp (Birkely and Gulliksen, 2003a) and other crangonids (Krygier and Horton, 1975; Bluhm and Brey, 2001) under the assumption of dioecism. Alternately, this observation could betray protandry.

The laboratory observations and the analysis of CL frequency distributions indicate that female sculptured shrimp grow faster than males, at least in the first four years of life. A similar pattern was reported for other crangonids: *A. dentata* (Couture and Filteau, 1971), *C. crangon* (Oh et al., 1999), *C. septemspinosa* (Haefner, 1972), *C. nigricauda* and *C. franciscorum* (Krygier and Horton, 1975), *N. antarcticus* (Bluhm and Brey, 2001), and *Philocheirus trispinosus* (Labat, 1984). This pattern may be linked to the earlier onset of sexual maturity in males compared to females. Laboratory rearing demonstrated that the faster growth of females resulted primarily from larger molt increments, the intermolt being only slightly longer in males than in females in *C. crangon* (Oh and Hartnoll, 2000) or not different between males and females (this study).

The average growth trajectories derived from our laboratory study indicate that males and females are older and smaller at maximum size than inferred from CL frequency distributions of wild shrimp (Fig. 8). This discrepancy could be due to sub-optimal feeding conditions, which markedly reduce molt increment while moderately increasing intermolt in *C. crangon* (Oh and Hartnoll, 2000). For the sculptured shrimp, Ingram (1979) noted that food deprivation lengthened intermolt but did not comment on how it affected molt increment. The optimistic laboratory growth model derived by considering the upper and lower boundary of 90% CIs on predicted molt increment and intermolt, respectively, fully encompasses inferred growth in Baie Sainte-Marguerite (Fig. 8). This model can also suggest that an appropriate choice of temperature and food could reduce considerably the time required to rear sculptured shrimp to a marketable size.

Although the sculptured shrimp's "direct" development mode is clearly an asset for culturing, there remain several consequential knowledge gaps to be filled in preparation thereof. In particular, we must know if the sculptured shrimp is a facultative protandric hermaphrodite (implying that only the faster growing primary females should be cultured). We should also investigate the factors involved in female first maturity, because growth slows considerably after. Finally, in the perspective of mass cultures, information is needed on the putative cannibalistic habit of the species (see Ingram, 1979).

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