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ORIGINAL PAPER

Strong maternal effects and extreme heterogeneity of progeny development in the caridean shrimp *Sclerocrangon boreas* (Crangonidae)

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Abstract *Sclerocrangon boreas* is uncommon among marine coastal carideans in having a non-dispersing, abbreviated (2-stage) larval phase. We investigated the implications of this strategy in terms of fecundity, offspring provisioning and brood care in *S. boreas* from the St. Lawrence Gulf and Estuary in 2009–2010. Fecundity scaled positively to female body size but was low due to the production of large, lipid-rich eggs. Offspring size at all stages of development was positively related to female size. Larval traits and lipid dynamics indicate obligatory lecithotrophic development from hatching to juvenile. The larva becomes a juvenile on the mother and remains associated with her for sometime after. The co-occurrence of early egg stages among many juveniles in some clutches raises the possibility that maternal care of juveniles includes the provisioning of trophic eggs or eggs reclaimed from other females.

Introduction

Knowledge of maternal effects is important for understanding the ecology, biology and aquaculture potential of marine species. Maternal effects are varied and may include: offspring provisioning (size) which may be influenced by female size and nutritional condition, or season; mate choice; manipulation of offspring sex/phenotype in response to environmental stimuli; brood care; and selection of sites and times for offspring release. Maternal effects are major factors influencing population dynamics and evolutionary trajectories (Marshall and Keough 2008; Marshall et al. 2008).

Maternal investment patterns determine how the finite amount of energy devoted to gamete production is partitioned among reproductive events (clutches) and between the number and size of oocytes within individual clutches (Marshall and Keough 2008). Crustacean maternal investment patterns at the species level are largely constrained by phylogeny and habitat (e.g., Sainte-Marie 1991), whereas at the individual level they may be modified by local environmental (e.g., temperature) effects on physiological processes (e.g., maternal growth, oogenesis, embryogenesis) and maternal genotype and phenotype (e.g., size, age). With respect to phenotype, it is generally the case among crustaceans that larger females produce more eggs per clutch than smaller females (e.g., Hines 1982; Clarke 1993a). Larger females also may produce bigger and presumed better quality (i.e., better performing) offspring, at the expense of a proportional reduction of fecundity (size–number tradeoff) but with the possible return of greater offspring and/or maternal fitness (Marshall and Keough 2008; but see Marshall et al. 2010).

Marine crustacean eggs are in general relatively largest in species with abbreviated (advanced or direct) development (Rabalais and Gore 1985; Anger 2001; Bauer 2004). The larger egg size reflects larger nutrient (yolk) reserves which are essential for extended lecithotrophic development (Clarke 1993b; Graeve and Wehrtmann 2003; Thatje

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et al. 2004). Lipids are the main energetic reserve for embryos of all marine crustaceans, contributing at least 60% of the total energy used for development, but they also are important for metabolic processes and the formation of cellular membranes (Wehrtmann and Kattner 1998; Anger 2001; Figueiredo et al. 2008). The two major lipid components of embryos and larvae are triacylglycerol (TAG), a class of reserve lipids, and phospholipids which may have multiple roles (Clarke 1977; Heras et al. 2000; Graeve and Wehrtmann 2003). The change in proportions of TAG and phospholipids in successive offspring developmental stages can indicate at which stage offspring shift from lecithotrophy to exogenous feeding (Ouellet et al. 1992; Graeve and Wehrtmann 2003). Among invertebrates with direct development, moreover, the nutritional needs of emerging juveniles may be met temporarily by nurse eggs, sibling cannibalism or partial predation on maternal body parts (Perry and Roitberg 2006; Marshall et al. 2008).

The sculptured shrimp *Sclerocrangon boreas* (Phipps 1774) is a boreal-arctic species of the family Crangonidae. This large marine caridean may be found in coarse sediments from the intertidal down to 450 m depth (e.g., Squires 1990; Klekowski and Węsławski 1991; Bukin 1992). This species is gonochoric, but females become much larger and live longer than males (Birkely and Gulliksen 2003a; Sainte-Marie et al. 2006; Lacoursière-Roussel and Sainte-Marie 2009). Crangonids, and in particular *S. boreas*, are highly benthic and their grooming appendages and behaviors are usually not as well developed as in other caridean families (Bauer 2004). Consequently, female crangonids may accumulate epibioses on their carapace (illustrated for *S. boreas* in Sainte-Marie et al. 2006) and may host various worms and mollusks beneath their abdomen (e.g., Fontaine 1977; Miglavs et al. 1993).

There is little information on fecundity, offspring provisioning and brood care in *S. boreas*. Females spawn in the period April to August hundreds of large eggs that are reportedly incubated over winter (ca 1 year) beneath the abdomen (Ingram 1979; Klekowski and Węsławski 1991; Birkely and Gulliksen 2003a). Larval development of *S. boreas* is abbreviated to two, presumably lecithotrophic stages (one zoea and one "postlarva") which cling to the mother's pleopods with their subcheliform first pereiopods and hooked dactyls of pereiopods 2–5 (Makarov 1968; Ingram 1979; Haynes 1985). The zoea stage is ephemeral, while the postlarval stage may last for only 3–5 days (at 5°C) and separate from its mother before or at "metamorphosis" and transform to a juvenile on the bottom (Ingram 1979). However, juveniles have been found on females (Birkely and Gulliksen 2003a; Lacoursière-Roussel and Sainte-Marie 2009), so "metamorphosis" may possibly occur before offspring leave the female. Ingram (1979) found a positive relationship between egg number and diameter and female size in *S. boreas*, but noticed no difference in larval size between small and large females. Positive associations between egg diameter and female size in *S. boreas* reported in Lacoursière-Roussel and Sainte-Marie (2009) are inconclusive due to small sample size. These two last studies and Birkely and Gulliksen (2003a) casually remarked on the co-occurrence of at least two offspring developmental stages in *S. boreas* clutches.

This study explores aspects of maternal investment in *S. boreas*. We tested the hypothesis that maternal offspring size effects are apparent at every stage of progeny development, including larvae and juveniles. We also wanted to better characterize the female size–fecundity relationship, heterogeneity of progeny development within clutches, and site of transformation from postlarva to juvenile. Finally, we qualified and quantified the lipid classes present in progeny stages to confirm lecithotrophic development.

Materials and methods

Field collections and laboratory analyses

Sclerocrangon boreas were collected from two localities of the St. Lawrence Gulf and Estuary: Baie Sainte-Marguerite (BSM; ca. 50°06′N, 66°35′W) on 14–19 May 2009, and Bic Island (BIC; ca. 48°24′N, 68°50′W) on 15–16 October 2009 and 6–11 May 2010. A beam trawl with a 3-m wide horizontal opening and a codend lined with 17-mm netting was used to collect shrimp. We collected premature and brooding female *S. boreas* of the broadest size range possible for determination of fecundity, progeny size and lipid composition, and eventually genetic parentage analysis. Each trawl set lasted 2–5 min at a speed of 1.5–2.0 knots at depths between 15 and 35 m. Trawl contents were promptly sorted and brooding *S. boreas* females were placed into individual pots to minimize loss of progeny.

At BSM, 109 brooding females were preserved individually in 4% formalin ($n = 62$) or 100% ethanol ($n = 47$). Twenty-five premature females, recognizable by green ovaries showing through the cephalothorax exoskeleton, were preserved in 4% formalin. Uncertainty about our ability to discern developmental stage of eggs preserved in ethanol, a required preservation method for genetic paternity analyses, motivated the partitioning of brooding females between formalin and ethanol. However, subsequent examination revealed that we could distinguish egg developmental stages regardless of preservation method. At BIC, brooding females were collected in May and October and brought alive to the Maurice-Lamontagne Institute where their progeny was processed for lipid analyses within 2 weeks of capture.

In the laboratory, using a vernier caliper (±0.01 mm) we measured the cephalothorax length (CL) of brooding females from the posterior margin of the eye socket in straight line to the posterior margin of the cephalothorax. Progeny and any other organisms beneath the abdomen of females were removed, identified and counted. The progeny of brooding females was enumerated by developmental stage adapted from the classifications of Makarov (1968), Haynes (1985) and Lacoursière-Roussel and Sainte-Marie (2009):

Stage A egg has no eyespot and no other visible embryological structures, we did not determine whether the egg was fertilized or not;
Stage B egg (embryo) has small eyespots and other rudimentary embryological structures;
Stage C egg (embryo) has large eyespots and other well-developed embryological structures;
Stage 1 larva (called a zoea by Haynes 1985 and Anger 2001) has sessile eyes, no rostrum, a rounded and highly inflated cephalothorax, no or few setae on pereiopods and pleopods, and a rounded and poorly developed telson;
Stage 2 larva (called a postlarva by Makarov 1968 or a megalopa by Haynes 1985) has pedunculate eyes, a rostrum that extends beyond the eyes, an oval and slightly inflated cephalothorax, setae on pereiopods but not on pleopods, and a triangular and more developed telson but with uropods still undifferentiated;
Juvenile has a well-developed rostrum, an adult-like cephalothorax armature with a spiny dorsal keel, setae on pleopods and pereiopods, and well formed telson and uropods.

Additionally, we observed females with variable numbers of large white eggs, without eyespots or any other embryological feature, that did not fit in the continuum of egg developmental stages.

We measured the diameter of up to 6 eggs of each developmental stage and the CL and total length (TL, from the posterior margin of the eye or eye socket in straight line to the end of the telson) of up to 6 larvae or juveniles on all brooding females. Diameter was determined as the mean of the short and long axes of individual eggs. All measurements of progeny were done under an image capture system comprised of a binocular microscope matched to a computer with Image-Pro Plus 6.1 (Media Cybernetics Inc., Bethesda, MD, USA). For each brooding female, we calculated the mean size of progeny by developmental stage.

The 25 premature females were measured in CL. They were then dissected to extract the ovaries, which were separated into primary and secondary oocytes (see Lacoursière-Roussel and Sainte-Marie 2009). The whole wet mass of secondary oocytes and the wet mass of 3 aliquots of 10 haphazardly selected secondary oocytes were determined on a Mettler AE240 electronic microbalance (±0.01 mg). For each premature female, the average mass of one secondary oocyte was determined as the mean mass of the three aliquots divided by 10, and ovarian fecundity was estimated by dividing total secondary oocyte mass by the average mass of one secondary oocyte.

We analyzed lipid composition of every progeny stage on 20 females from BIC with 3 replicates by female of up to 5 eggs or 3 larvae or juveniles each. The extraction procedure was adapted from protocols of Bligh and Dyer (1959). Samples were stored at −80°C until they were used and all manipulations were done on ice. Each progeny replicate was homogenized in 1.5 mL of 0.9% NaOH solution. In a clean tube, 0.2 mL of homogenate and 0.03 mL of nonadecane were added to 0.75 mL of methanol : chloroform solution (2v : 1v), 0.5 mL of chloroform and 0.25 mL of Millipore water, and the mix was centrifuged at 4°C, 1,500*g* for 10 min. Nonadecane was used as an internal standard. In a clean tube, we placed 0.03 mL of replicate supernatant and evaporated the solvent under a nitrogen stream, and then resuspended the residue by adding 0.01 mL of chloroform: methanol solution (2v : 1v). The resulting sample was transferred to a SIII-Chromarod for lipid quantification using flame ionization detection with a model MK-III Iatroscan (Iatron Inc., Japan). One sample of each replicate was processed on a rod developing triacylglycerol (TAG), diacylglycerol (DAG), free fatty acids (FFA) and sterol, and another sample was processed on a rod developing the phospholipids (PH) phosphatidylcholine and phosphatidylethanolamine. Both rods were developed after a 30-min bath of hexane: diethyl ether: formic acid (82v : 2.5v : 0.045v) allowing separation of nonadecane. Then, the first rod was placed in hexane : diethyl ether : formic acid (55v : 30v : 0.075v) for 27 min to separate TAG, DAG, FFA and sterol, whereas the second rod was placed in acetone (85v) for 5 min and finally in methanol : chloroform : water (25v : 55v : 3v) for 45 min. The quantification in μg of each constituent was based on calibration curves constructed from solutions of standard neutral lipids (Ouellet et al. 1992). We measured on a Cahn C-31 micro balance (±0.1 μg) the wet and dry mass of 5 additional individuals of each progeny stage from each female; dry mass was obtained by oven-drying at 60°C for 24 h.

Data analysis

Normality of distribution and homogeneity of variance were verified and data were transformed if necessary. Mean values in text are reported with their standard error (SE). We used TL to describe larvae and juvenile size, because this metric has been reported more commonly in the literature, but we provide a predictive (least squares linear regression) for CL based on TL. Pearson correlation or

least squares regression was used to describe or test for significant relationships between fecundity or progeny size and female CL. For regressions between progeny and female size, model fits were better with the independent variable CL transformed to its reciprocal (CL^{-1}) than with no transformation or with other more common transformations (logarithmic) of independent and/or dependent variables, as assessed by coefficient of determination and distribution of residuals. Analysis of covariance (ANCOVA) was used to compare the regression models of ovarian and clutch fecundity, and of progeny size across the various progeny developmental stages, on female body size. We first tested for differences in slope by checking for a significant interaction between covariate (CL or CL^{-1}) and factor (developmental stage) and when there was none, we tested for differences in y-intercept.

Analyses of fecundity were performed only on females with clutches dominated by stage A, stage B or white eggs. Females with clutches dominated by stage C eggs were too few to be included in analyses. We used the numerically dominant egg stage on each female to characterize her clutch, but all eggs contributed to the fecundity count. Based on visual examination of scatterplots of fecundity against CL, we excluded females with <100 eggs because they clearly had lost many eggs before or during trawling and sorting. We did not consider fecundity relationships for larvae- or juvenile-dominated clutches because these stages are mobile and easily lost from the female abdomen during trawling and sorting.

Analysis of the relationship between progeny size and maternal CL was carried out only for progeny developmental stages represented by 2–6 measurements by female. We used ANCOVA to measure the effect of the preservation agent (ethanol or formalin) on diameter of the various egg stages and on TL of larvae and juveniles, with preservation agent and developmental stage as fixed factors and female CL or CL^{-1} as the covariate. The sizes of stage A eggs and of larvae and juveniles were independent of preservation agent; however, small conversion factors were necessary to make diameters of formalin- and ethanol-preserved stage B and C eggs comparable. Ethanol-equivalent diameter values are reported for these two developmental stages.

Results

Female size and clutch composition at BSM

Brooding females from BSM ranged from 21.0 to 31.5 mm CL and collectively featured all progeny developmental stages (Table 1). Notably, juveniles occurred on 37.6% of brooding females and on all but one brooding female with larvae (Table 1). The number of juveniles on individual females ranged from 4 to 87 (mean = 34.4). Larvae observed on females belonged to stage 2, except for one-stage 1 larva that was found with two-stage 2 larvae and many juveniles. For females carrying post-hatch progeny, the mean of proportional representation of stage 1 larva, stage 2 larva and juvenile by clutch was 0.1, 35.8 and 64.1%, respectively. Females with stage C eggs were uncommon due to the time of year.

Brooding females carried either of two types of clutches (Table 1). Homogeneous clutches occurred on 70.6% of brooding females and consisted of one or two consecutive progeny developmental stages; heterogeneous clutches occurred on 29.4% of brooding females and consisted of a group of early stage eggs mixed with a group of post-hatch stages, with one or more intervening development stages missing between the two groups. Homogeneous clutches were comprised of stage A, stage B or a mix of both egg types in 81.8% of cases, of a mix of stage B and C eggs or of only stage C eggs in 5.2% of cases, or of larvae and juveniles in the remaining 13.0% of cases (Table 1). Most heterogeneous clutches were combinations of stage B eggs, larvae and juveniles or a mix of stage A and B eggs with larvae and juveniles (46.9 and 28.1% of cases, respectively; Table 1). One heterogeneous clutch contained stage C eggs (Table 1). Excluding this last clutch, the overall mean contribution of progeny developmental stages to heterogeneous clutches was $1.5 \pm 0.5\%$ for stage A eggs, $6.0 \pm 1.0\%$ for stage B eggs, $32.2 \pm 4.2\%$ for larvae, and $60.3 \pm 3.8\%$ for juveniles. In no case did stage A or B eggs alone or altogether numerically dominate the progeny in heterogeneous clutches.

White eggs were found only in 19.7% of homogeneous clutches with stage A, B or C eggs (Table 1). The proportion of white eggs did not exceed 7.0% of all eggs in a clutch except in two females where it reached 78.4 and 85.1%. The presence of white eggs was apparently not related to the occurrence of alien species; many females that hosted other species did not carry white eggs. Alien hosts were found on 42.7% of all brooding females and included hirudineans (4.0%) or their eggs attached to the female's pleopods (36.0%), gastropod egg capsules (2.7%) and the gastropod *Tectura testudinalis* (1.3%).

Fecundity at BSM

Clutch fecundity (total number of eggs per clutch) was as high and as variable whether measured on female *S. boreas* with clutches predominated by stage A or stage B eggs (Fig. 1). The two females carrying mostly white eggs were also relatively fecund (Fig. 1). Regression analysis on all females in which stage A, stage B or white eggs predominated indicated that clutch fecundity increased significantly with female CL (Fig. 1). Ovarian fecundity (total number of

Table 1 Combinations of progeny developmental stages in clutches of *S. boreas* females in Baie Sainte-Marguerite during May 2009

Clutch type	Progeny stages in clutch					*n*	% Clutch type	% All clutches
	A	B	C	Larv	Juv			
Homogeneous ($n = 77$)	●					28 (2)	36.4	25.7
	●	●				5 (3)	6.5	4.6
		●				30 (7)	39.0	27.5
		●	●			3 (1)	3.9	2.8
			●			1 (0)	1.3	0.9
				●	●	10 (0)	13.0	9.2
Heterogeneous ($n = 32$)	●			●	●	3 (0)	9.4	2.8
	●				●	1 (0)	3.1	0.9
	●	●		●	●	9 (0)	28.1	8.3
	●	●			●	1 (0)	3.1	0.9
	●		●	●	●	1 (0)	3.1	0.9
		●		●	●	15 (0)	46.9	13.8
		●		●		1 (0)	3.1	0.9
		●			●	1 (0)	3.1	0.9
$\sum n$						109 (13)		

Clutches of single or consecutive developmental stages are classified as homogeneous and those with a mix of nonconsecutive developmental stages are classified as heterogeneous. Progeny stages are stage A, B and C eggs, larvae (Larv), and juvenile (Juv). Percent occurrence of progeny combinations is calculated relative to number of females within-clutch type (% clutch type, *n*) and overall (% all clutches, $\sum n$). The number of females with white eggs appears in parentheses under the column *n*

secondary oocytes) in premature females ranging 21.8–30.6 mm CL also increased significantly with female CL (Fig. 1). ANCOVA revealed no difference in slope between the regression of ovarian fecundity and clutch fecundity on CL (fecundity type × CL: $F_{(1,85)} = 0.13$, $P = 0.719$), but the y-intercepts were highly different ($F_{(1,86)} = 71.50$, $P < 0.001$). Adjusted mean clutch fecundity at 25.3 mm female CL was 292.6 ± 8.6 eggs, 46.8% less than the adjusted ovarian fecundity of 429.5 ± 13.7 secondary oocytes. This perceived difference between ovarian and clutch fecundity at size would be slightly increased by the intervening maturity (parturial) molt, because of weak albeit significant negative CL growth at that molt (Guay unpubl data).

Progeny size at BSM

The scatterplots of stage A, B and C egg diameter on female CL overlapped almost completely, but white eggs stood out as being of a much greater size than any other egg stage (Fig. 2a). The scatterplots of stage 2 larva and juvenile TL[1] on female CL had very little overlap (Fig. 2b). A positive relationship between progeny size and female CL was visually apparent in Fig. 2 for every stage except white

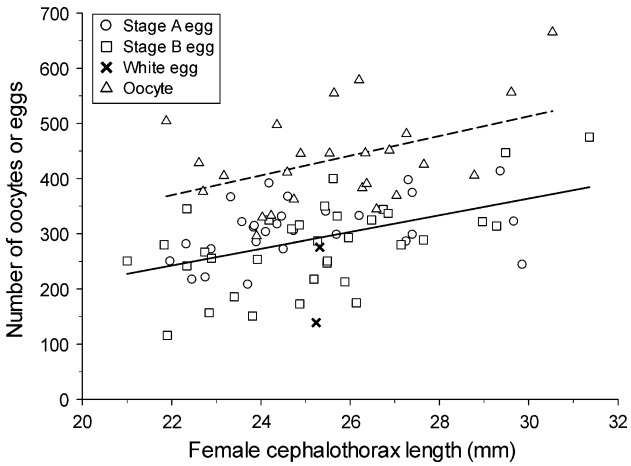

Fig. 1 *Sclerocrangon boreas* at Baie Sainte-Marguerite in May 2009. Scatterplots and regressions of ovarian fecundity (*O* number of secondary oocytes) and clutch fecundity (*E* number of eggs) on female cephalothorax length (CL, mm). Females are designated as carrying stage A, stage B or white eggs based on the stage that predominated in clutch. *Dashed line* $O = -22.708 + 17.848$ CL, $r^2 = 0.195$, $F_{1,23} = 5.555$, $P = 0.027$; *solid line* $E = -90.362 + 15.135$ CL, $r^2 = 0.226$, $F_{1,62} = 18.113$, $P < 0.001$

eggs. Regression analysis confirmed a significant relationship between progeny size and the reciprocal of female CL (CL^{-1}) for the stage A egg ($r^2 = 0.18$, $F_{1,35} = 7.83$, $P = 0.008$), stage B egg ($r^2 = 0.37$, $F_{1,54} = 31.06$, $P < 0.001$), stage 2 larva ($r^2 = 0.13$, $F_{1,37} = 5.59$, $P = 0.023$) and juvenile ($r^2 = 0.37$, $F_{1,38} = 22.08$, $P < 0.001$). However, the

[1] Progeny CL can be estimated for stage 2 larva by $CL = 0.740 + 0.218$ TL, $r^2 = 0.39$, $F_{1,211} = 135.68$, $P < 0.001$; for juvenile by $CL = -0.041 + 0.292$ TL, $r^2 = 0.56$, $F_{1,242} = 303.08$, $P < 0.001$.

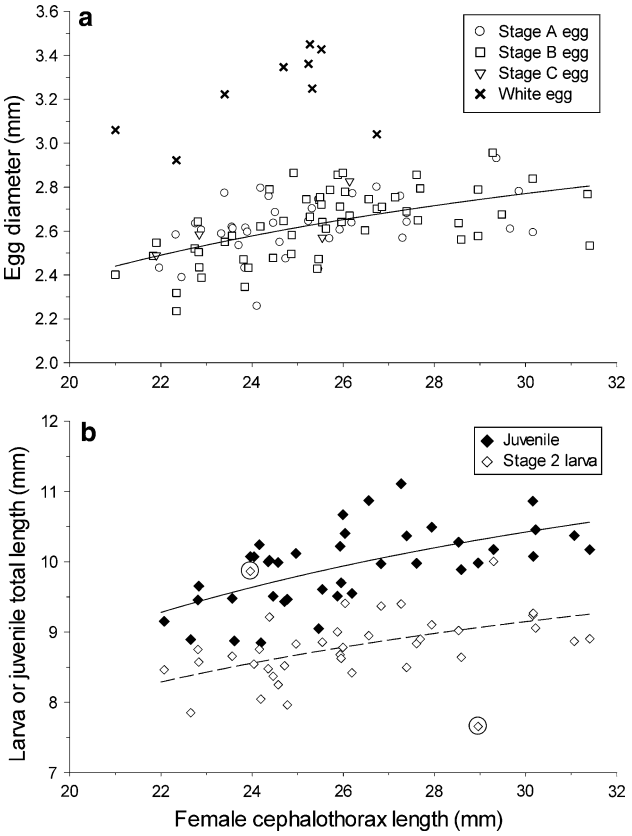

Fig. 2 *Sclerocrangon boreas* at Baie Sainte-Marguerite in May 2009. Mean diameter (D, mm) of stage A, B, C and white eggs (**a** *upper pane*) and total length (TL, mm) of stage 2 larva and juvenile (**b** *lower pane*) on female cephalothorax length (CL). Regression equations are $D = 3.5417–23.133\ CL^{-1}$, $r^2 = 0.297$, $F_{1,91} = 38.48$, $P < 0.001$ for stage A and B eggs together, $TL = 11.512–70.913\ CL^{-1}$, $r^2 = 0.335$, $F_{1,35} = 17.62$, $P < 0.001$ for the stage 2 larva (*dashed line*, excludes two outliers *circled* in graph) and $TL = 13.567–94.320\ CL^{-1}$, $r^2 = 0.367$, $F_{1,40} = 22.124$, $P < 0.001$ for the juvenile (*solid line*)

relationship between progeny size and female CL^{-1} was not significant for the few stage C ($r^2 = 0.57$, $F_{1,2} = 2.63$, $P = 0.247$) and white ($r^2 = 0.28$, $F_{1,7} = 2.75$, $P = 0.141$) eggs. In the case of the stage 2 larva, there were two conspicuous outliers (Studentized residual >3, Fig. 2b) that were confirmed to be real by remeasuring larvae and females. Excluding these two outliers considerably improved the TL-CL^{-1} relationship ($r^2 = 0.34$, $F_{1,35} = 17.62$, $P < 0.001$). The fact that progeny size was better related to CL^{-1} than to CL of female means that progeny size increases more steeply with increasing CL at small than at large maternal sizes. The mean wet mass of the secondary oocyte also increased with increasing female CL ($n = 14$, $r = 0.58$, $P = 0.028$; for females with total secondary oocyte mass >2 g).

ANCOVA on egg diameter with female CL^{-1} as the covariate revealed no significant difference in slope (stage × CL^{-1}: $F_{(1,89)} = 1.24$, $P = 0.269$) and in y-intercept ($F_{(1,90)} = 0.045$, $P = 0.833$) between stage A and B eggs (common regression for stage A and B eggs plotted in Fig. 2a). The adjusted mean diameter was 2.63 ± 0.02 mm for stage A eggs and 2.62 ± 0.02 mm for stage B eggs at 25.5 mm female CL; the arithmetic mean diameter was 2.62 ± 0.07 mm for stage C eggs and 3.23 ± 0.06 mm for white eggs. ANCOVA revealed no difference in the slope of the TL-CL^{-1} relationship between the stage 2 larva (outliers excluded) and the juvenile (stage × CL^{-1}: $F_{(1,73)} = 0.78$, $P = 0.379$), but the y-intercepts were different ($F_{(1,74)} = 156.18$, $P < 0.001$). The adjusted mean TL at 26.2 mm female CL was 8.78 ± 0.07 mm for the stage 2 larva and 9.93 ± 0.06 mm for the juvenile. Thus, the molt increment from the stage 2 larva to the juvenile was on average 13.1% of initial TL. The only stage 1 larva found in samples was 8.11 mm TL.

Coefficients of progeny size variation (CV = standard deviation divided by mean × 100) within clutches with 6 measurements by stage ranged 1.2–6.3% for stage A egg diameter (mean = 3.6%, $n = 31$ females), 1.4–6.5% for stage B egg diameter (3.8%, $n = 44$), 2.4–5.6% for stage C egg diameter (3.7%, $n = 4$), 2.1–6.3% for stage 2 larva TL (4.3%, $n = 31$), and 2.0–7.5% for juvenile TL (4.6%, $n = 40$). The within-clutch CV was independent of female CL ($P > 0.092$) for all progeny stages. The CV of progeny mean size among these same females was 6.2% for the stage A egg, 7.3% for the stage B egg, 6.0% for the stage C egg, 6.6% for the stage 2 larva, and 6.9% for the juvenile.

Progeny mass, water content and lipid composition at BIC

Sclerocrangon boreas females from BIC that were used for progeny lipid analysis ranged 20.1–29.4 mm CL. Stage A, B, C and white eggs came from females collected in October 2009; larvae and juveniles came from females collected in May 2010. From the stage A egg to the juvenile, progeny wet mass tripled whereas progeny dry mass declined by about 25% (Table 2). The mean percent water content of progeny (±SE of clutch means) increased continuously from 45.0 ± 0.8% for the stage A egg, 48.9 ± 1.1% for the stage B egg, 60.0 ± 1.4% for the stage C egg, and 82.2 ± 1.2% for hatched progeny (stage 1 and 2 larvae and juvenile combined). White eggs were conspicuously different from any of stage A to C eggs in having a larger wet mass and smaller dry mass (Table 2), yielding a high water content of 84.0%.

Stage A eggs were lipid-rich with total measured lipids representing on average 56.8% of egg dry mass (Table 2). The total lipid content of progeny declined continuously with development and was 69.6% less in the juvenile than in the stage A egg (Table 2). Moreover, the percent contribution of the various lipid classes to progeny total lipid content changed through development

Table 2 *Sclerocrangon boreas* at Bic Island in 2009–2010

Progeny stage (*n*)	Maternal CL (mm)	Progeny mass (mg ind^{-1})		Progeny lipid content (mg ind^{-1})					
		Wet mass	Dry mass	TAG	Sterol	PH	DAG	FFA	Total lipids
W (1)	23.2	14.96	2.39	0.491	0.070	0.000[a]	0.124	0.307	0.993
A (3)	21.4 ± 0.9	8.94 ± 1.33	4.91 ± 0.71	1.955 ± 0.250	0.063 ± 0.005	0.773 ± 0.047	0.000[a]	0.000[a]	2.791 ± 0.301
B (8)	23.6 ± 0.4	8.85 ± 0.41	4.51 ± 0.18	1.956 ± 0.123	0.067 ± 0.003	0.703 ± 0.09	0.000[a]	0.000[a]	2.725 ± 0.211
C (6)	22.9 ± 0.5	10.57 ± 0.63	4.21 ± 0.21	1.353 ± 0.094	0.062 ± 0.006	0.412 ± 0.031	0.000[a]	0.000[a]	1.827 ± 0.111
L1 (1)	23.6	12.43	2.79	1.392	0.070	0.189	0.000[a]	0.000[a]	1.651
L2 (4)	24.8 ± 1.6	21.66 ± 2.29	3.83 ± 0.41	0.981 ± 0.216	0.179 ± 0.039	0.456 ± 0.155	0.000[a]	0.000[a]	1.616 ± 0.099
Juv (1)	21.8	26.98	3.70	0.128	0.115	0.604	0.000[a]	0.000[a]	0.847

Maternal cephalothorax length (CL) and progeny individual (ind) wet and dry mass and lipid content by lipid class or overall (total measured lipids). Mean values with their standard error (SE) are shown when multiple mothers (clutches) were sampled (number of mothers, *n*, in parentheses). Progeny stages include white eggs (W), stage A, B and C eggs, stage 1 larva (L1), stage 2 larva (L2), and juvenile (Juv). Lipid classes are triacylglycerol (TAG), sterol, phospholipids (PH), diacylglycerol (DAG) and free fatty acids (FFA)

[a] Not detected

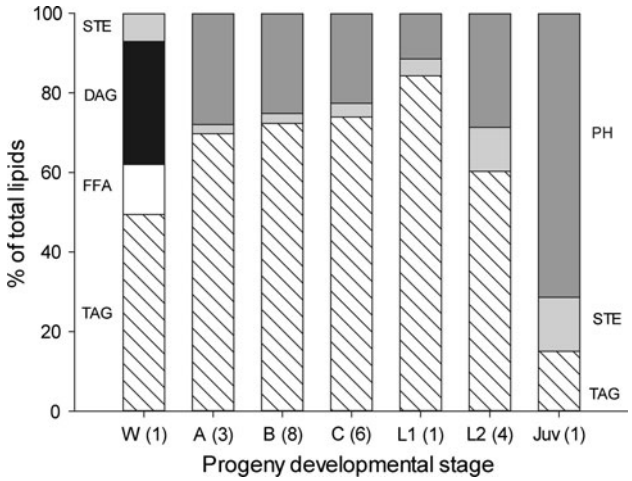

Fig. 3 *Sclerocrangon boreas* at Bic Islands in 2009–2010. Mean percent contribution of lipid classes to total lipids for each progeny developmental stage (W, white egg; A, stage A egg; B, stage B egg; C, stage C egg; L1, stage 1 larva; L2, stage 2 larva; Juv, juvenile). Lipid classes are triacylglycerol (TAG), diacylglycerol (DAG), free fatty acids (FFA), sterol (STE), phospholipids (PH). The number of sampled clutches is in *parentheses*

(Fig. 3). TAG represented 69.7% of all measured lipids in stage A eggs. From the stage A egg to the stage 1 larva, the proportion of TAG and sterol increased while the proportion of PH declined. From the stage 1 larva to the juvenile, the proportion of TAG decreased steeply while that of sterol and PH increased (changes were especially apparent in the juvenile). White eggs were uniquely different from other eggs and post-hatch progeny in containing DAG and FFA, which together accounted for 43.4% of all measured lipids, but no detectable amounts of PH (Table 2; Fig. 3).

Discussion

Progeny development and maternal care

Although every progeny developmental stage was observed on female *S. boreas* from BSM, the stage C egg and the stage 1 larva were uncommon because the first develops mostly during October–March (Ingram 1979; Sainte-Marie unpubl data) while the second may be of very short duration (Makarov 1968; Ingram 1979). Embryo and larval development were accompanied by a trend of increasing progeny wet mass (and linear dimension in later stages) and decreasing progeny dry mass as seen in other carideans (e.g., Wehrtmann and Kattner 1998; Oh and Hartnoll 1999; Li et al. 2011). The 45% water content of *S. boreas* stage A eggs is low compared to values recorded in early egg stages of other carideans, notably the boreal pandalid shrimp *Pandalus borealis* (58–61%, Brillon et al. 2005), the temperate crangonid shrimp *Crangon crangon* (68%, Pandian 1967), and 3 Antarctic species including the crangonid *Notocrangon antarcticus* (67%, Graeve and Wehrtmann 2003). However, the water content of recently hatched progeny does not differ markedly among *S. boreas* (82%), *P. borealis* (82–83%, Brillon et al. 2005) and *C. crangon* (87%, Pandian 1967). Water is thought to facilitate hatching, act as a buffer against temperature or salinity variation, and promote larva floatability (Pandian 1970). The last proposed advantage seems irrelevant to a benthic shrimp with no dispersive larvae. The decrease in *S. boreas* progeny dry mass and total lipid content with development reflects lipid use for metabolism and tissue growth (Heras et al. 2000; Morais et al. 2002; Sibert et al. 2004).

Larval features and lipid dynamics of *S. boreas* indicate an obligate lecithotrophic mode of development from hatching to first juvenile stage. Makarov (1968) reported

that both larval stages of *S. boreas* have incompletely developed feeding appendages and that the inflated cephalothorax of stage 1 and to a lesser degree of stage 2 larvae contains residual lipid reserves. In our study, the absolute quantity of TAG and the ratio TAG : PH declined from the stage 1 larva to the juvenile, indicating use of TAG for metabolism and growth as seen in some other decapod crustaceans with abbreviated larval or direct development (Heras et al. 2000; Anger 2001). The TAG–PH ratio of 60% : 29% in the *S. boreas* stage 2 larva was very high compared to the ratio in developing embryos of many other carideans and only in the *S. boreas* juvenile did the ratio reach a level (15% : 71%) rather comparable to that found in recently hatched larvae of carideans with a dispersive, planktotrophic larval phase (e.g., 3–5% : 80% in *P. borealis*, Ouellet et al. 1995). This suggests the onset of exogenous feeding at or soon after the molt to juvenile.

Lecithotrophic larval development in *S. boreas* is associated with exceptionally large eggs (stage A, 2.63 mm mean diameter or 9.53 mm^3) and lipid reserves at spawning (57% of egg dry mass). To our knowledge, among coastal marine carideans *S. boreas* is rivaled in egg size only by its congener *S. ferox* (2.50 mm, Zarenkov 1965).[2] However, several bathyal or abyssal carideans may also have relatively large eggs: for example *Sclerocrangon* congeners (2.86 and 2.97 mm, Zarenkov 1965), *Glyphocrangon alata* (2.81 mm, Quiroga and Soto 1997) and psalidopodids (2.70 and 3.00 mm, Chace and Holthuis 1978) among benthic species; and oplophorids and pasiphaeids (2.65–4.11 mm, Herring 1974)[2] among mesopelagic species. Many of these deep-dwelling species are assumed to have abbreviated development (Bauer 2004). Further, in *S. boreas* the relative contribution of measured lipids (i.e., fatty acids) to stage A egg mass (57% dry, 31% wet) exceeds by a factor of at least 2.5 times the levels reported for a suite of tropical to polar marine coastal carideans with planktotrophic larval stages, including *N. antarcticus* and *P. borealis* (reviewed in Graeve and Wehrtmann 2003), and is comparable only to values recorded in bathyal or deep-sea carideans with eggs exceeding 2 mm diameter (e.g., range 20–67% and mean 39% of egg wet mass, calculated from Herring 1974). Also, TAG represented a higher share (70%) of total measured lipids in *S. boreas* stage A eggs compared to recently spawned eggs of *N. antarcticus* (42%, Graeve and Wehrtmann 2003), *P. borealis* (39–41%, Brillon et al. 2005) and several other coastal marine carideans (e.g., 36–53%, Wehrtmann and Graeve 1998; Graeve and Wehrtmann 2003).

The frequency of occurrence and number of juveniles in *S. boreas* clutches were high enough to warrant the proposition that the stage 2 larva transforms to the first juvenile stage on the female, not on the bottom as suggested by Ingram (1979), and that the juvenile–mother association continues for some time after transformation. For how long might this association last? If one assumes that the probability of sampling a post-hatch progeny stage on a brooding female is directly related to the duration of that stage and or of its association with the mother, then the observed mean proportional representation of 36% stage 1 and 2 larvae and 64% juvenile in clutches at BSM would suggest that the juvenile–mother association can last longer than the assumed 3–5-day-long larval phase. *Sclerocrangon boreas* is the first marine caridean species reported to have maternal care of hatchlings extended to the juvenile stage; so far the only other caridean with this feature is the freshwater *Dugastella* (Cuesta et al. 2006; Huguet et al. 2011; Rodríguez and Cuesta 2011).

Heterogeneous progeny development within clutches

The widely disparate progeny developmental stages found in some *S. boreas* clutches is a seemingly rare feature reported to our knowledge only once before among decapod crustaceans (Torati and Mantelatto 2008). It is not uncommon to find some developmental heterogeneity within clutches of decapod crustaceans, due for example to differential oxygenation (Fernández et al. 2003). However, the co-occurrence of stage A or B eggs (the latter certainly fertilized) with larvae or juveniles in some *S. boreas* clutches requires other explanations because the two groups of progeny are in principle separated by several months of development (Ingram 1979; B. Sainte-Marie, unpubl data). Such a pattern could hypothetically arise from spawning of new eggs prior to release of the previous clutch, fostering of progeny reclaimed from another female, or excessively asynchronous progeny development.

The first hypothesis (H1) that spawning occurs prior to complete release of the previous clutch has been demonstrated in the hermit crab *Loxopagurus loxochelis*, where heterogeneous clutches were numerically dominated by recently extruded eggs (Torati and Mantelatto 2008). On first appraisal, H1 seems impossible for *S. boreas* because spawning in carideans is thought to always be preceded by a parturial molt and mating (Correa and Thiel 2003; Bauer 2004), during which the previous clutch would inevitably be lost. However, some large, brooding *S. boreas* females can exceptionally host heavy, apparently ≥2-years epibioses and one possible interpretation of this fact is that they spawn in successive years without molting (Sainte-Marie et al. 2006; Lacoursière-Roussel and Sainte-Marie 2009). Nevertheless, H1 does not seem to suit *S. boreas* because the general rule appears to be that females spawn only every other year, alternating 1 year of body growth with

[2] Cited diameters are the mean of egg width and length reported in each study; most studies did not indicate egg development stage and maternal size which both influence egg diameter.

1 year of spawning and egg incubation (Sainte-Marie et al. 2006; Lacoursière-Roussel and Sainte-Marie 2009). Furthermore, heterogeneous clutches were always numerically dominated by larvae or juveniles (this study) whereas early egg stages would be expected to dominate if the female spawned a new clutch into the old clutch. The second hypothesis (H2) of reclaiming progeny dropped from another female was demonstrated for example in the gammaridean amphipod *Apherusa jurinei* (Patterson et al. 2008). In this case, the female sometimes ate the reclaimed early stage eggs or introduced them into her incubating chamber (Patterson et al. 2008) where they might serve as food for her hatched progeny. While this hypothesis cannot immediately be excluded for *S. boreas*, under normal circumstances the shrimp's eggs are less likely to be dropped than those of amphipods because the former are attached to the pleopod setae by funiculi.

This leaves (H3) excessively asynchronous development of progeny from the same spawn as the most likely explanation for heterogeneous clutches in *S. boreas*. One intriguing possibility is that early stage eggs in heterogeneous clutches are trophic (nurse) eggs that are fertilized but programed to develop slowly or to stop developing at some point (e.g., Smith and Gibson 1999). The existence of trophic eggs has been proposed once before in malacostracans (Caine 1991) and in *S. boreas* they could serve the dual purpose of reducing cannibalism by juveniles on larvae (within-clutch sibling predation: Elgar and Crespi 1992; Perry and Roitberg 2006) while providing the female with more flexibility for choosing offspring release time and site. The third and second hypotheses are nonexclusive and represent forms of offspring provisioning that could increase offspring and maternal fitness. Resolving which of the three hypotheses is (are) valid will be possible through the use of molecular markers or mitochondrial DNA. Maternal alleles should be present in all progeny stages of heterogeneous clutches if H1 and H3 are true but only in larvae–juveniles if H2 is true, and the mix of paternal alleles should differ between eggs and larvae–juveniles if H1 and H2 are true.

White eggs occurred rather frequently and occasionally in large numbers in *S. boreas* clutches. These white eggs were relatively large compared to normally developing *S. boreas* embryos but in other respects appear similar to the relatively small, nonviable "chalky eggs" produced by some synalpheid shrimps. Chalky eggs have been hypothesized to be produced by females that are not fully mature or that are exposed to unusually cold waters (Felder 1982; Erdman and Blake 1987). In *S. boreas*, the high percentages of FFA and DAG, which are byproducts of lipid degradation (Ouellet et al. 1992; Brillon et al. 2005), indicate that white eggs are deteriorated. The presence of white eggs in *S. boreas* is unlikely to be related to female maturity status or cold water and it also seems unrelated to the presence of alien hosts. We hypothesize that white eggs are unfertilized ova (which can attach to pleopods in some carideans, Bauer 2004) or aborted early embryos because they occurred only in homogeneous clutches that contained stage A or B eggs. This hypothesis is consistent with laboratory observations of failed inseminations (Guay and Sainte-Marie unpubl data) implying that the mating or fertilization process is not failsafe—sperm limitation can occur—and/or that some mates are genetically incompatible. The fate of these white eggs is unknown. They were not found in clutches with late progeny stages, either because they were eliminated before or because they were consumed by juveniles (Perry and Roitberg 2006 discuss the use of sterile or aborted eggs as food).

Maternal fecundity and offspring size effects

Both ovarian and clutch fecundity scaled positively to female CL; however, we found a large (≈47%) difference between the two estimates indicating egg losses between spawning and preservation time. The difference between the two measures of fecundity may be explained by traumatic trawling and sorting procedures, although we took great steps to minimize such losses, and one or more natural processes including retention of oocytes, failure of eggs to adhere to pleopod setae, incomplete fertilization or genetic incompatibility, clutch abrasion due to burrowing, egg displacement with growing clutch volume, egg predators or parasites, alien hosts competing for space beneath the female, or maternal cannibalism (e.g., Fontaine 1977; Kuris 1991; Oh and Hartnoll 1999; Li et al. 2011). Regardless of the cause(s), such losses discredit any investigation of tradeoffs between egg number and size based on clutch fecundity; they also undermine estimates of reproductive output using clutch fecundity. Examination of relationships between secondary oocyte number and size would be more informative, conditional on the use of gravid females selected immediately before spawning (when secondary vitellogenesis is completed). Nevertheless, it is clear for *S. boreas* that production of large eggs occurs at the expense of reduced fecundity (Ingram 1979; Lacoursière-Roussel and Sainte-Marie 2009).

A positive size relationship in *S. boreas* between female and progeny was found at every well-sampled progeny developmental stage. The relationship was apparently not linear and was less pronounced at larger than at smaller female sizes. The impression that the gradient in maternal offspring size effects is more pronounced at smaller sizes would be reinforced for stage A and B eggs if diameters of similar eggs from females of 16–24 mm CL from the study of Ingram (1979; illustrated in Lacoursière-Roussel and Sainte-Marie 2009) were overlaid on our data. This pattern can suggest different anatomical constraints (see below)

and/or egg size–number and somatic–gonadic tradeoffs between small and large females. These findings are consistent with data in other polar and temperate marine carideans demonstrating a positive relationship between maternal size and egg size (Clarke 1993a). The linear (diameter or TL) variability of progeny size among females (CV > 6%) was higher than generally reported for decapod crustaceans (≤6%) but not unusually high for species with abbreviated (direct) development (both reviewed in Marshall and Keough 2008), although such comparisons must be treated with caution as they are generally not standardized for variability of female size.

Maternal offspring size effects are widely viewed as being adaptive by increasing offspring survival, and the offspring size–performance relationship is expected to be strongest in species with direct development (Marshall and Keough 2008). In our study, the ≈1.2-mm average difference in TL between juveniles produced by the smallest and largest *S. boreas* and the 2.4-mm maximum juvenile TL difference between females with the smallest and the largest juveniles, respectively represent the equivalent of about 1 and 2 juvenile molt increments (Sainte-Marie et al. 2006). This probably represents a substantial size advantage for a carnivorous species (Birkely and Gulliksen 2003b) in foraging and competition with siblings or conspecific juveniles. However, maternal fecundity and offspring size effects may be partly or fully conditioned by (nonadaptive) anatomical scaling constraints: eggs and offspring must fit within female reproductive structures. Such constraints are known to exist for example in brachyuran crabs (Hines 1982) and other arthropods (Fox and Czesak 2000).

In summary, *S. boreas* is characterized by exceptionally large and lipid-rich eggs that hatch into very large offspring. Development from hatching to juvenile occurs on the female and is fully lecithotrophic. Maternal care is apparently extended to the first juvenile stage. Strong maternal offspring size effects are apparent at every progeny developmental stage and result in substantial variability among females in progeny size. Future research should: (1) explore egg size–number tradeoffs through the use of gravid females, (2) test the hypotheses proposed to explain heterogeneous progeny development within clutches, (3) measure the duration and temporal flexibility of the mother–juvenile association in relation to intrinsic (e.g., offspring provisioning) and extrinsic (e.g., predators, habitat suitability) factors, and (4) evaluate the fitness benefits of maternal offspring size effects.

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