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Seasonal variations in larval biomass and biochemical composition of brown shrimp, *Crangon crangon* (Decapoda, Caridea), at hatching

Ángel Urzúa · Klaus Anger

Abstract The "brown shrimp", *Crangon crangon* (Linnaeus 1758), is a benthic key species in the North Sea ecosystem, supporting an intense commercial fishery. Its reproductive pattern is characterized by a continuous spawning season from mid-winter to early autumn. During this extended period, *C. crangon* shows significant seasonal variations in egg size and embryonic biomass, which may influence larval quality at hatching. In the present study, we quantified seasonal changes in dry weight (W) and chemical composition (CHN, protein and lipid) of newly hatched larvae of *C. crangon*. Our data revealed significant variations, with maximum biomass values at the beginning of the hatching season (February–March), a decrease throughout spring (April–May) and a minimum in summer (June–September). While all absolute values of biomass and biochemical constituents per larva showed highly significant differences between months ($P < 0.001$), CHN, protein and lipid concentrations (expressed as percentage values of dry weight) showed only marginally significant differences ($P < 0.05$). According to generalized additive models (GAM), key variables of embryonic development exerted significant effects on larval condition at hatching: The larval carbon content (C) was positively correlated with embryonic carbon content shortly after egg-laying ($r^2 = 0.60$; $P < 0.001$) and negatively with the average incubation temperature during the period of embryonic development ($r^2 = 0.35$; $P < 0.001$). Additionally, water temperature ($r^2 = 0.57$; $P < 0.001$) and food availability (phytoplankton C; $r^2 = 0.39$; $P < 0.001$) at the time of hatching were negatively correlated with larval C content at hatching. In conclusion, "winter larvae" hatching from larger "winter eggs" showed higher initial values of biomass compared to "summer larvae" originating from smaller "summer eggs". This indicates carry-over effects persisting from the embryonic to the larval phase. Since "winter larvae" are more likely exposed to poor nutritional conditions, intraspecific variability in larval biomass at hatching is interpreted as part of an adaptive reproductive strategy compensating for strong seasonality in plankton production and transitory periods of larval food limitation.

Keywords *Crangon crangon* · Eggs · Larvae · Biochemical composition · Seasonal variations · Carry-over effects · Southern North Sea · Food availability

Introduction

Marine organisms with a complex life cycle develop through a series of different ontogenetic stages including embryonic, larval, juvenile and adult phases, which are linked to each other (Giménez 2006; Podolsky and Moran 2006). In invertebrates and fish, variability in the density of adult populations has mainly been attributed to fluctuations in brood size and to variations in growth and mortality during earlier life-history stages (McCormick and Hoey 2004; Marshall and Keough 2006).

The environmental conditions experienced during the embryonic phase have been recognized as important factors influencing larval performance, and therefore, indirectly also later benthic life-history phases of marine invertebrates

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(Grosberg and Levitan 1992; Giménez 2010). In all pleo-cyemate decapod crustaceans, the eggs are carried under the abdomen of the females and thus experience the parental environmental conditions prevailing in the habitat. Newly laid eggs contain all the energy that is necessary for embryonic development (Jaeckle 1995), and therefore, the initial larval biomass depends on both these initial energy reserves and their subsequent utilization during embryogenesis (Anger 2001). Also, it is influenced by physico-chemical factors experienced during embryogenesis, for example, temperature (Wear 1974; Fischer et al. 2009), oxygen (Fernandez et al. 2006) and salinity (Giménez and Anger 2001), so that previous environmental conditions may also affect the larval capacity to face starvation during periods of planktonic food limitation (Paschke et al. 2004; Calado et al. 2007).

In the pelagic marine environment, crustacean larvae may seasonally be exposed to food limitation and temperature changes, and combined effects of both factors may influence their growth and development (Anger 2001). As an adaptation to seasonal variation in food availability, planktotrophic larvae may therefore seasonally vary in their energy content at hatching, showing enhanced endogenous reserves during periods of low plankton productivity (Anger 2001, 2006). In temperate and high-latitude marine invertebrates, this reproductive trait has been interpreted as an evolutionary adaptation to a mismatch between short seasonal periods of planktonic food availability and a prolonged larval development at low temperatures (e.g. Anger et al. 2003).

Environmental effects on sets of reproductive traits of organisms can have important consequences on populations. For a better understanding of the ecology of species with complex life cycles, we need to study how the various life-history phases are connected to each other. One important link is between the embryonic and the larval phase. In this context, the larval performance can be related to maternal input, conditions experienced during embryogenesis, and to environmental factors prevailing at hatching or thereafter (Giménez 2006). The combination of these pre- and post-hatching factors may explain larval survival and, consequently, affect also later phases of the life cycle (Roughgarden et al. 1988; Giménez 2010). Hence, the quality of early larval stages may be relevant not only for the settlement and recruitment success in the field (Pan et al. 2011), but also for aquaculture (Racotta et al. 2003) and fisheries management (Campos et al. 2009).

The subject of this study is the generally well studied and commercially important "brown shrimp", *Crangon crangon*. This species is very common and abundant in the shallow areas of the German Bight (Siegel et al. 2008), plays an important role in the energy transfer within marine food webs (Pihl and Rosenberg 1984; Campos et al. 2009) and sustains an important fishery with annual captures exceeding 35,000 tons (ICES 2010). The complex life cycle

of *C. crangon* comprises a benthic juvenile–adult and a pelagic larval phase (Tiews 1970; Hufnagl and Temming 2011), which are tightly linked (Daewel et al. 2011; Viegas et al. 2012). It is thus necessary to also investigate traits of the early life-history phases, which may influence the population dynamics.

The reproductive pattern of *C. crangon* is characterized by continuous egg-laying from mid-winter throughout spring, summer and early autumn. During this extended period, this species shows significant seasonal variations in size and biomass of newly laid eggs (Boddeke 1982; Urzúa et al. 2012). However, the question remains, whether seasonal variations in egg biomass directly translate to variations in larval quality at hatching, as suggested by studies of larval tolerance of food limitation (Paschke et al. 2004). We therefore explored relationships between previously published data of biomass and chemical composition of eggs (Urzúa et al. 2012), water temperature during embryogenesis (Wiltshire et al. 2010) and larval biomass at hatching, which may indicate "latent" or "carry-over effects" between successive early life-history phases (Harrison et al. 2011).

Materials and methods

The methodology used in this study is described only briefly, as it is largely the same as explained in details in a recent paper dealing exclusively with the embryonic phase of *C. crangon* (Urzúa et al. 2012).

Sampling and maintenance of ovigerous females

Throughout most of the reproductive season of *C. crangon* in 2009 (January–September), shrimps were periodically sampled from a population living in the lower Elbe estuary (54°03′–54°04′N; 8°18′–8°24′E; ca 13 m depth) employing bottom trawls of research vessel "Uthörn". Adult individuals were transferred to the Helgoland Marine Biological Station. No samples were taken in October–December due to unavailability of ship time. In the laboratory, ovigerous females ($n = 32$; 48–54 mm total body length) were isolated and placed in aerated flow-through seawater aquaria with similar temperatures and salinities as in the field, until newly hatched larvae were found in sieves (0.2 mm mesh size) receiving the overflowing water from the aquaria.

Total length (TL), dry weight (W), elemental composition (CHN) and proximate biochemical composition (total protein and lipid) of newly hatched larvae

Newly hatched larvae were taken in regular intervals (approximately monthly) for parallel determinations of

total length (TL), dry weight (W), elemental composition (contents of carbon, hydrogen and nitrogen; collectively CHN) and proximate biochemical composition (total protein and lipid), which were measured with standard techniques (for recent description of details, see Urzúa and Anger 2011; Urzúa et al. 2012). The energy content was estimated from biochemical data (Winberg 1971), because conversions from CHN data (Salonen et al. 1976) tend to underestimate the energy content more strongly than conversions from biochemical composition (Anger 2001; Urzúa et al. 2012).

Statistical analyses

Statistical analyses were performed with standard methods (Sokal and Rohlf 1995) using the statistics software packages STATISTICA 8 (StatSoft) and Brodgar 2.6.6. All tests were run on the 95 % confidence level ($P < 0.05$). Normality and homogeneity of variances were tested with Kolmogorov–Smirnov and Levene's tests, respectively. Data of seasonal variations in biomass and biochemical composition of newly hatched larvae were tested using a two-level nested ANOVA, with month as fixed factor and hatch (or female) as nested factor. Significant differences were analyzed with a multiple comparison test (Student–Newman–Keuls). Relationships between egg size and larval biomass at hatching were tested with regression analysis.

Generalized additive models (GAM)

We applied generalized additive models based on the R-mgcv function (Zuur et al. 2007) with various explanatory variables to determine, in a first step (GAM I), the influence of embryonic physiology (pre-hatching factors) on initial larval biomass. As a second step (GAM II), we evaluated relationships between larval quality and environmental parameters prevailing at the time of hatching (for more details, see Urzúa et al. 2012). Normality, outliers and collinearity were checked following Zuur et al. (2007).

Effects of pre-hatching factors (GAM I)

Data of initial egg biomass and mean temperature during the period of embryonic development were taken from Urzúa et al. (2012), and the effects of these factors on larval carbon content (used as a proxy for total organic matter) at hatching were tested with the following model:

$$Y_i = \alpha + f_1(\mathrm{EB}_i) + f_2(\mathrm{TE}_i) + \varepsilon_i \tag{1}$$

with Y = larval carbon (μg larva^{-1}), EB = initial egg biomass (C, μg egg^{-1}), TE = mean temperature during the

period of egg development (°C), α = intercept, $f_{1,2}$ = smoothing functions, ε = error term, i = observed data, σ^2 = variance, where $\varepsilon_i \sim n\,(0, \sigma^2)$.

Environmental conditions prevailing at the time of hatching (GAM II)

As explanatory variables, we included in this model the mean water temperature and phytoplankton carbon (as a proxy for food availability) measured through a fortnight period prior to the day of larval hatching (data from Wiltshire et al. 2010). The relationships between these environmental parameters and larval quality at hatching were explored with the equation:

$$Y_i = \alpha + f_1(\mathrm{TH}_i) + f_2(\mathrm{PB}_i) + \varepsilon_i \tag{2}$$

with Y = larval carbon (μg larva^{-1}), TH = mean temperature during a fortnight period prior to hatching (°C), PB = mean phytoplankton biomass during a fortnight period prior to hatching (mg C m^{-3}); other parameters as above (Eq. 1).

Results

Seasonal variations in offspring size and female energy investment in egg production

Measurements of egg volume (Urzúa et al. 2012) revealed significant differences between seasons, with higher average values observed in winter than in summer (44.3 ± 3.26 vs. 34.5 ± 1.66 mm$^3 \times 10^{-3}$; $F = 242.76$; $P < 0.05$). Corresponding with larger "winter eggs", larvae hatching in late winter and early spring were on average larger than those hatching in late spring and summer (total length, 2.80 ± 0.12 vs. 2.10 ± 0.06 mm; $F = 122.56$; $P < 0.05$).

While the average number of eggs produced per female was significantly lower in winter than in summer (1842 ± 86 vs. 2526 ± 108; $F = 82.94$; $P < 0.05$), the female energy investment in egg production (calculated as number of egg multiplied by the energy content per egg) did not show significant seasonal differences (1484 ± 86 vs. 1518 ± 44 J; $F = 1.22$; $P = 0.18$).

Seasonal variations in larval dry weight (W) and elemental composition (CHN) at hatching

Periodical samples of newly hatched larvae revealed that all values of biomass showed significant differences among months (Table 1). Maximal values were measured at the beginning of the larval hatching season in late winter (February–March), decreasing values during spring (April–May) and minimum values in summer (June–September)

Table 1 *Crangon crangon*, newly hatched larvae

Biomass parameters	Factor	SS	df	MS	F
W (µg)	Month	2303.63	7	329.09	297.69***
	Hatch (month)	209.89	24	8.75	7.91*
	Error	106.13	96	1.11	
	Total	2619.64	127		
C (µg)	Month	451.692	7	64.527	281.23***
	Hatch (month)	42.972	24	1.791	7.80*
	Error	22.027	96	0.229	
	Total	516.691	127		
N (µg)	Month	38.3862	7	5.4837	299.67***
	Hatch (month)	2.8055	24	0.1169	6.39*
	Error	1.7568	96	0.0183	
	Total	42.9484	127		
H (µg)	Month	14.0591	7	2.0084	363.88***
	Hatch (month)	1.0340	24	0.0431	7.81*
	Error	0.5299	96	0.0055	
	Total	15.6230	127		
Lipid (µg)	Month	8.1994	7	1.1713	323.39***
	Hatch (month)	0.6374	24	0.0266	7.33*
	Error	0.5795	160	0.0036	
	Total	9.4163	191		
Protein (µg)	Month	182.220	7	26.031	1011.6***
	Hatch (month)	2.697	24	0.112	4.4*
	Error	4.117	160	0.026	
	Total	189.034	191		
E (J)	Month	0.63117	7	0.090167	388.65***
	Hatch (month)	0.06995	24	0.002914	12.56*
	Error	0.03722	160	0.000232	
	Total	0.73834	191		
C (% W)	Month	56.5	7	8.1	10.8*
	Hatch (Month)	109.5	24	4.6	6.1*
	Error	72.1	96	0.8	
	Total	238.1	127		
N (% W)	Month	34.69	7	4.96	36.88*
	Hatch (month)	6.87	24	0.29	2.13*
	Error	12.90	96	0.13	
	Total	54.46	127		
H (% W)	Month	53.864	7	7.695	163.7**
	Hatch (month)	10.731	24	0.447	9.5*
	Error	4.512	96	0.047	
	Total	69.107	127		
C/N ratio	Month	0.970	7	0.139	14.8*
	Hatch (month)	0.809	24	0.034	3.6*
	Error	0.896	96	0.009	
	Total	2.675	127		
Lipid (% W)	Month	4.987	7	0.712	23.9*
	Hatch (month)	5.124	24	0.214	7.2*
	Error	4.765	160	0.030	
	Total	14.877	191		

Table 1 continued

Biomass parameters	Factor	SS	df	MS	F
Protein (% W)	Month	32.8	7	4.7	37*
	Hatch (month)	8.4	24	0.3	3*
	Error	20.3	160	0.1	
	Total	61.4	191		
E (J*mg W^{-1})	Month	30.00	7	4.29	15.8*
	Hatch (month)	31.23	24	1.30	4.81*
	Error	43.02	160	0.27	
	Total	104.25	191		

Two-level nested ANOVA evaluating differences in dry weight, elemental composition and proximate biochemical composition among months and hatches nested within months; interaction between these factors; biomass parameters: (W) dry weight, (C) contents of carbon, (N) nitrogen, (H) hydrogen, C/N ratio, lipid, protein and (E) energy; significant differences marked with *asterisks* (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

(Figs. 1, 3). Hence, larvae hatching during winter were heavier than those hatching in summer (Fig. 1a). Consistent with higher dry weight, "winter larvae" showed also higher contents of CHN per individual (Fig. 1b–d). Their average biomass reached twice the values recorded in "summer larvae" (11 vs. 6 µg C; 3 vs. 1.5 µg N; 1.8 vs. 1 µg H; cf. February vs. July) (Fig. 1).

While all absolute values of biomass per larva showed highly significant differences among months (all $P < 0.001$), values expressed in percent of dry weight showed only marginally significant differences ($P < 0.05$) (Table 1). For example, carbon and nitrogen (expressed in

% W) remained relatively stable at average levels of about 37 and 10 %, respectively (Fig. 2).

Seasonal variations in the proximate biochemical composition of larval biomass

The biochemical composition (total lipid and protein per larva) and energy content (J per larva, estimated from biochemical data) showed similar patterns as dry weight and elemental composition (Fig. 3). Again, a maximum level was found in February–March, with average values of about 1.3 µg lipid, 8 µg protein and 0.7 J per larva.
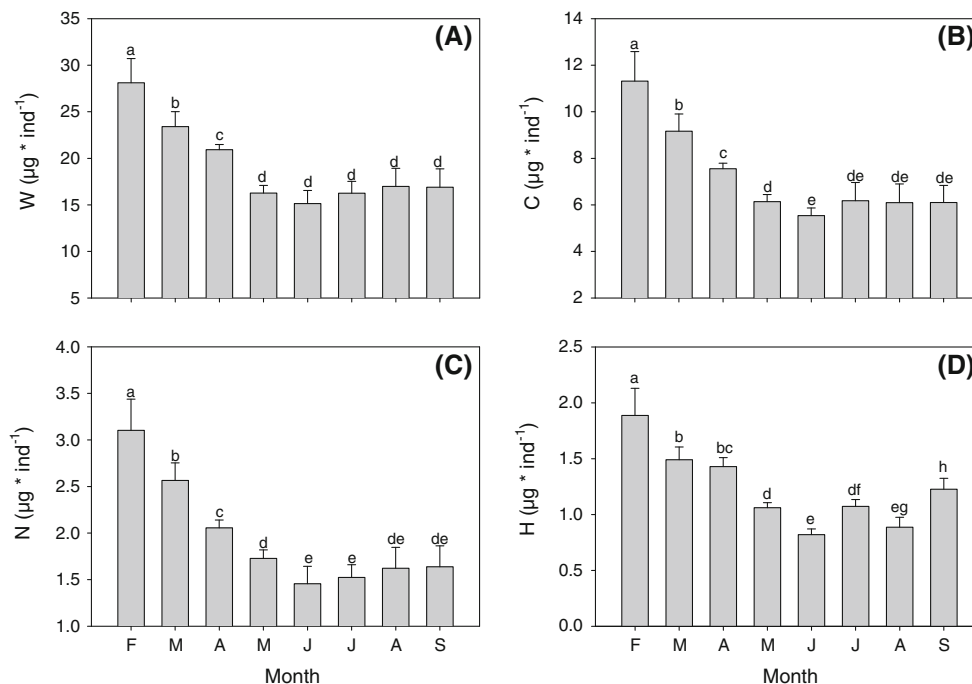
Fig. 1 *Crangon crangon*, newly hatched larvae. Seasonal variations in dry weight (W) and elemental composition (CHN): **a** dry weight, **b** carbon, **c** nitrogen and **d** hydrogen (all expressed in µg ind^{-1}); mean values ± SD. *Different lower case letters* indicate significant differences among months (after SNK test)
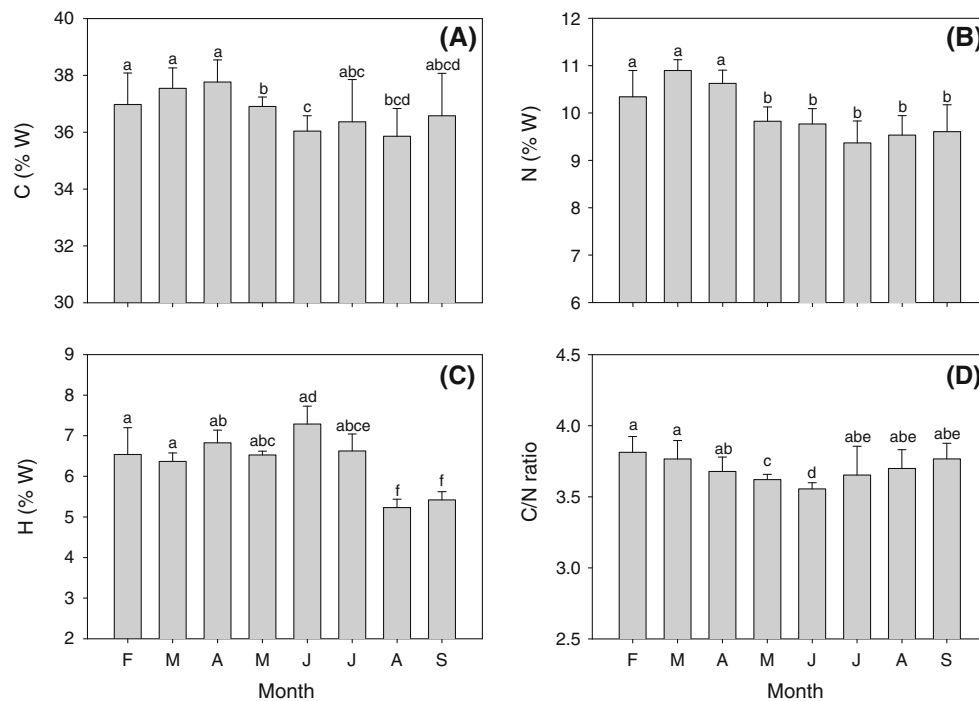
Fig. 2 *Crangon crangon*, newly hatched larvae. Seasonal variations in elemental composition: **a** carbon, **b** nitrogen and **c** hydrogen (all expressed in % of W); **d** C/N ratio; mean values ± SD. *Different* *lower case letters* indicate significant differences among months (after SNK test)

Decreasing levels were measured from April to June, with minimum values about 0.7 μg lipid, 5 μg protein and 0.45 J. A slight increase occurred subsequently between July and September, reaching values of about 0.8 μg lipid, 6 μg protein and 0.5 J (Fig. 3). All values of lipid, protein and energy content per larva differed significantly among months (all $P < 0.001$) (Table 1).

Compared to the absolute biomass values, the relative biochemical composition and energy content (expressed in % of W or J mg W^{-1}, respectively) showed only marginally significant seasonal variations throughout the reproductive period ($P < 0.05$) (Table 1), with average values of about 5.7 % lipid, 46 % protein and 18.5 J mg W^{-1} (Fig. 3).

Relationships between egg size and elemental composition of newly hatched larvae

The elemental composition (CHN) and energy content (E, estimated from biochemical data) of newly hatched larvae (values in μg or J per individual, respectively) were positively correlated with egg size ($r^2 = 0.71$, 0.73, 0.68 and 0.75 for C, N, H and E, respectively; all $P < 0.001$, Fig. 4). Seasonal variations in egg size are thus propagated to larval biomass at hatching, so that larvae hatching from larger "winter eggs" showed higher CHN and energy values than those hatching from smaller "summer eggs".

Effects of pre-hatching factors

According to generalized additive models (GAM) of multiple explanatory variables, a combination of key factors related to embryonic physiology exerted significant effects on the carbon content of newly hatched larvae. Based on the smoothing function of the GAM I model, the carbon content at hatching showed a highly significant positive relationship with initial egg biomass (data from Urzúa et al. 2012) and a negative relation with the average incubation temperature during the period of embryonic development (Fig. 5a, b; Table 2). About 60 % of the variation in the carbon content per larva can be explained by effects of seasonal variations in embryonic carbon, while the average incubation temperature contributed 35 % to the variation in the carbon content of newly hatched larvae (Fig. 5a, b).

Effects of environmental conditions prevailing at the time of hatching

The temperature (TH) and phytoplankton biomass (PB) prevailing at the time of hatching are significantly linked with initial larval quality (measured as C content). An additive model of multiple explanatory variables indicated that larval C showed highly significant negative correlations with both TH ($r^2 = 0.57$; $P < 0.001$) and PB ($r^2 = 0.39$; $P < 0.001$) measured at the time of hatching
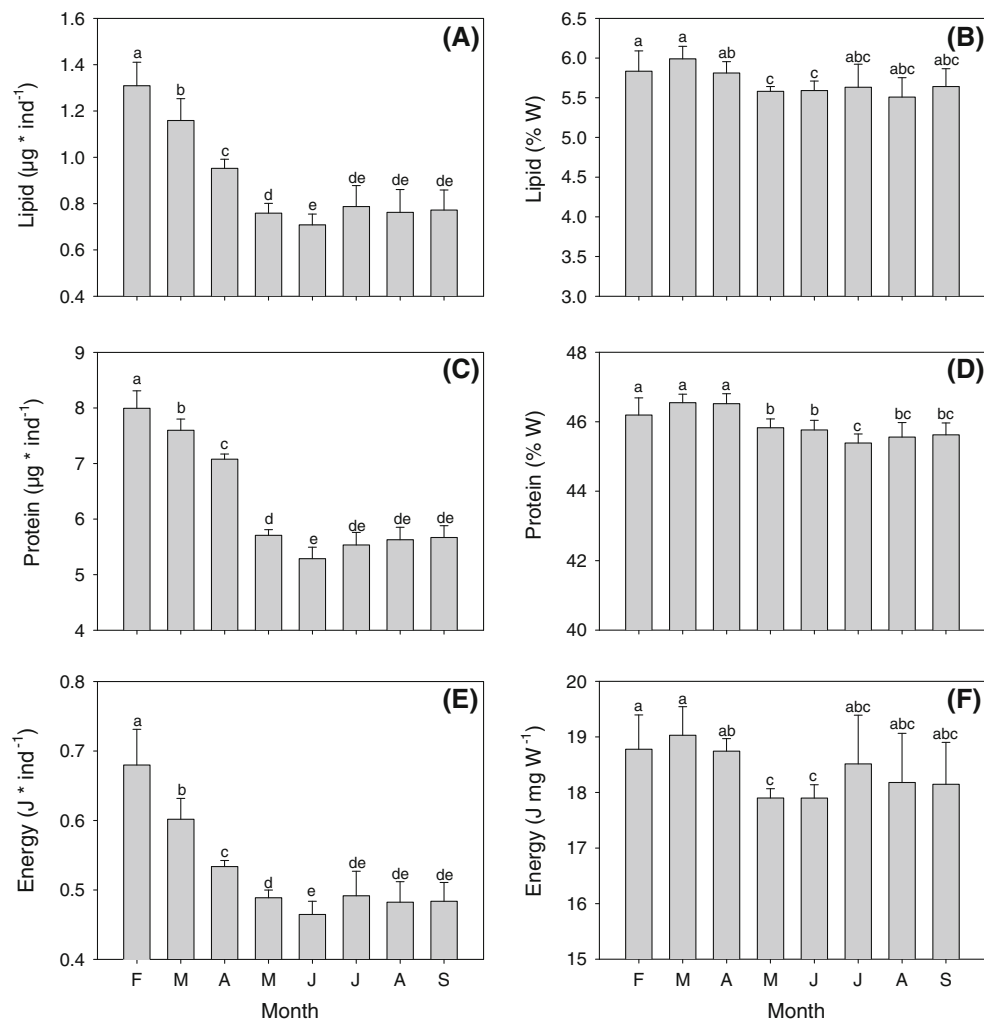
Fig. 3 *Crangon crangon*, newly hatched larvae. Seasonal variations in proximate biochemical composition: **a**, **b** lipid, expressed in μg ind^{-1} and % of W, respectively; **c**, **d** protein, expressed in μg ind^{-1} and % of W, respectively; **e**, **f** energy content (estimated from biochemical data), expressed in J ind^{-1} and J mg W^{-1}, respectively; mean values ± SD. *Different lower case letters* indicate significant differences among months (after SNK test)

(Table 2). According to the GAM II model, the smoothing function for larval quality showed a maximum level in winter (environmental conditions at the time of hatching: ca. 5 °C and 27 mg C m^{-3}·10; TH and PB, respectively), decreased gradually thereafter, reached a minimum in spring (ca. 10 °C and 38 mg C m^{-3}·10) and increased subsequently again in late summer (ca. 17 °C and 62 mg C m^{-3}·10) (Fig. 5c, d).
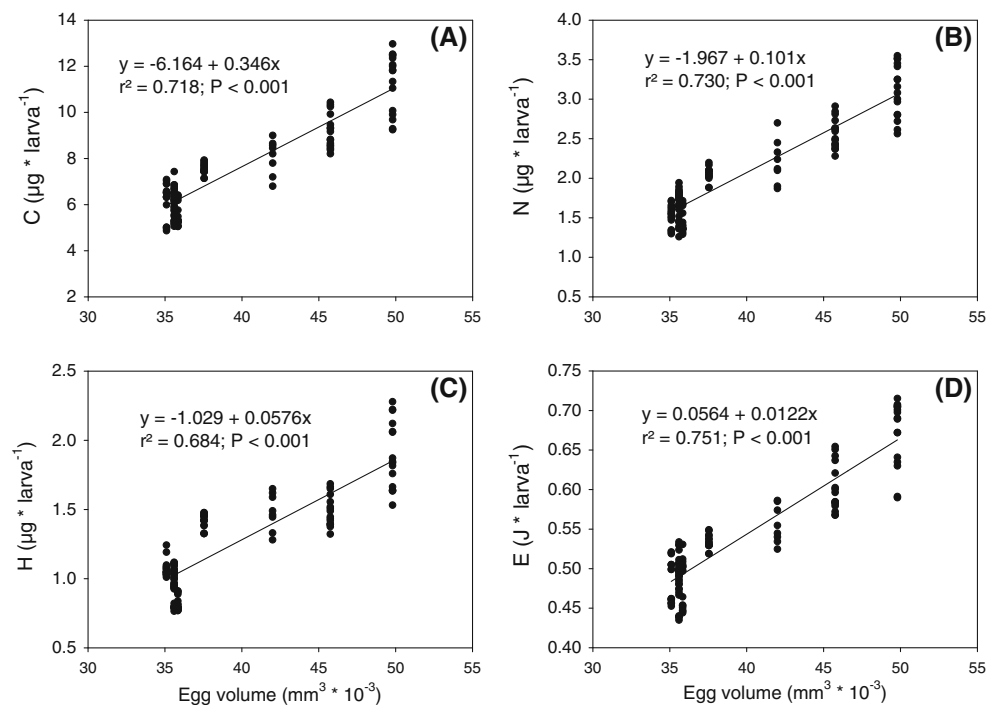
Discussion

In marine invertebrates with complex life cycles, the different life-history stages are closely linked to each other (Allen and Marshall 2010; Harrison et al. 2011). In the early stages of the life cycle of *C. crangon*, our results indicate that seasonal variations in egg size are translated to variations in larval biomass. We demonstrate here that larvae hatching from larger "winter eggs" show higher absolute values of elemental (CHN) and biochemical constituents (lipid, protein) than larvae hatching from smaller "summer eggs".

In crustaceans, larval traits at hatching are related to key variables associated with embryonic development (Giménez and Anger 2001; Webb et al. 2007). For example, the average egg incubation temperature exerts significant effects on the development time and bioenergetics of the embryo and influences the initial larval biomass at hatching (Paschke 1998; Fischer et al. 2009). In *C. crangon*, the initial larval biomass was negatively correlated with the incubation temperature during egg development. Compared to larvae hatching from eggs that had been incubated at cold winter temperatures, "summer larvae" showed lower values of biomass. While egg development is

Fig. 4 *Crangon crangon*, newly hatched larvae. Linear regression model evaluating relationship between egg size (volume) and elemental composition of newly hatched larvae: $y =$ **a** carbon, **b** nitrogen, **c** hydrogen and **d** energy content (all expressed in values per larva); $a =$ intercept, $b =$ slope; $r^2 =$ determination coefficient; $P =$ significance level; in all cases $n = 128$

(A) $y = -6.164 + 0.346x$; $r^2 = 0.718$; $P < 0.001$

(B) $y = -1.967 + 0.101x$; $r^2 = 0.730$; $P < 0.001$

(C) $y = -1.029 + 0.0576x$; $r^2 = 0.684$; $P < 0.001$

(D) $y = 0.0564 + 0.0122x$; $r^2 = 0.751$; $P < 0.001$

accelerated at higher temperatures, this may be at the cost of changes in metabolic efficiency (Kunisch and Anger 1984), leading to a reduction in initial larval biomass. This has been shown in various caridean shrimp species, for example, *Betaeus emarginatus* and *Pandalus borealis* (Wehrtmann and Lopez 2003; Brillon et al. 2005).

In order to evaluate the adaptive significance of intra-specific variation in egg size, we need to understand how differential traits may be carried over to later life-history stages. Most likely, an enhancement of larval biomass at hatching should improve larval survival under suboptimal food conditions. This may be influenced by genetic or maternal factors that are involved in the determination of larval quality (Palacios et al. 1998; Meidel et al. 1999).

In planktonic organisms living in environments with seasonal variations in productivity (food availability), parental organisms may assess the nutritional conditions that their offspring will likely encounter and adjust the energy investment per offspring accordingly (Fischer et al. 2011). According to the relationship between environmental conditions prevailing at hatching and larval biomass observed in our study, the smoothing function of GAM showed a maximum level in larval biomass during winter, a minimum in the late spring and another increase in late summer. High larval carbon content during late winter may improve the tolerance of fasting, when poor nutritional conditions coincide with prolonged duration of larval development at cold temperatures (Criales and Anger 1986; Paschke et al. 2004; Daewel et al. 2011). Hence, the production of larger "winter larvae" seems to be an adaptive

reproductive trait of *C. crangon*, allowing for an extension of the period of reproduction (Siegel et al. 2008; Urzúa et al. 2012), which is in most other decapod crustaceans in temperate regions restricted to late spring and summer (Anger 2001). At higher temperatures and planktonic food concentration, during late spring and summer (Wiltshire et al. 2008), smaller shrimp larvae hatch in the southern North Sea. This match between favorable conditions of food availability and high temperatures with larval peak abundance during spring–summer (Wehrtmann 1989) allows the larvae to exploit rich food resources and reach fast rates of growth and development (Temming and Damm 2002). In this way, our study confirms the hypotheses proposed by Paschke et al. (2004) and provides a chemical basis explaining the previously observed seasonal patterns in larval starvation resistance. Similar seasonal variations in offspring quality and environmental conditions prevailing at hatching have also been described in other aquatic crustacean species, for example in porcelain crab (Gebauer et al. 2010), marine copepods (Acheampong et al. 2011) and limnic cladocerans (Boersma 1997).

While the production of large larvae in winter is probably related mainly to low food availability, larger size could also play a role as a protection from predators (Morgan 1995). Predation is a major cause of larval mortality in *C. crangon* (e.g. Henderson et al. 2006), with various fish species being well-known predators (Tiews 1978). As large "winter larvae" show a prolonged planktonic development time, they are also exposed to a higher risk of predation. By contrast, smaller "summer larvae"

Fig. 5 *Crangon crangon*, newly hatched larvae. Smoothing function (*S*) obtained by generalized additive model (GAM) for larval carbon content (C, µg larva^{-1}) exploring the effects of pre-hatching factors [**a** initial egg biomass and **b** incubation temperature] and the environmental conditions prevailing at the time of hatching [**c** temperature and **d** phytoplankton biomass]. These plots allow evaluating the relationships between explanatory variables (*x*-axis) and adjusted residuals of dependent variable (carbon, *y*-axis). *Solid line* estimated smoothing function; *dotted lines* 95 % confidence intervals. Total variance is quantified by values of r^2, the significance of the smoothing function by values of *F* and *P*; *dots* represent mean values, in all cases *n* = 128. For statistical model and parameters, see Table 2
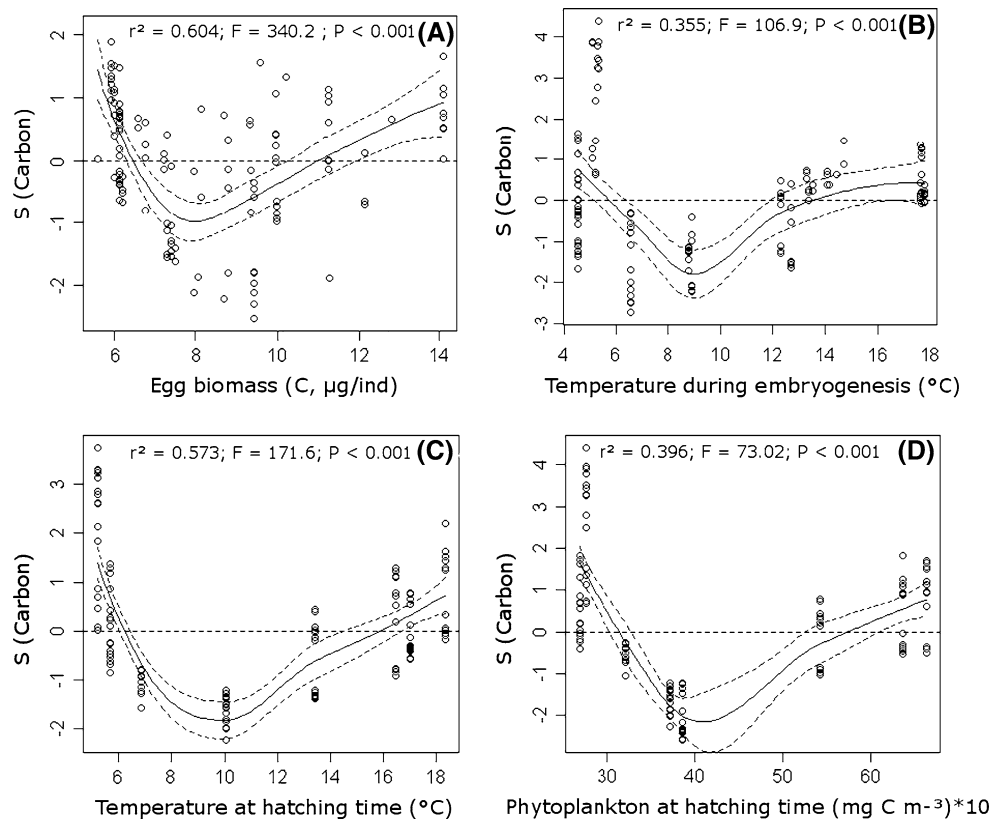
Table 2 *Crangon crangon*, newly hatched larvae

Parametric coefficients	Estimate	SE	*t* value	r^2	*P* value
Effects of pre-hatching factors					
Intercept	−3.332	0.58	−5.721	–	<0.001
Initial egg biomass	0.402	0.021	17.42	0.60	<0.001
Temperature during embryogenesis	−0.278	0.026	−10.34	0.35	<0.001
Environmental conditions					
Intercept	10.56	0.36	29.31	–	<0.001
Temperature prevailing at hatching time	−0.303	0.023	−13.1	0.57	<0.001
Phytoplankton prevailing at hatching time	−0.081	0.009	−8.545	0.39	<0.001

Additive model of various explanatory variables evaluating the effects of pre-hatching factors and environmental conditions prevailing at the time of hatching on larval condition; evaluated parameters, estimate, SE, *t* values, coefficients of determination (r^2), significance level (*P value*)

show faster rates of development and growth (Linck 1995; Criales and Anger 1986), which reduces the time of exposure to predation and other potential risks in the plankton, enhancing the chance of successful recruitment (Morgan 1995).

Crangon crangon produces fewer but larger "winter eggs" and a higher number of smaller "summer eggs" (Urzúa et al. 2012). In this context, the female energy investment in egg production did not show significant differences between winter and summer. In *C. crangon*, as well as other decapod crustaceans, total energy investment in embryo production is influenced by maternal traits such

as female size and abdominal space available for egg incubation (Ouellet and Plante 2004; Moland et al. 2010).

The reproductive traits of *C. crangon* may vary over latitudinal gradients within the large climatic range of distribution of this species (Tiews 1970; Campos and van der Veer 2008). In populations at lower latitudes (e.g. the west coast of Portugal, southwestern Europe), reproduction takes place only from late winter to early summer, with a main spawning and breeding season during spring (Marchand 1981; Viegas et al. 2012). The offspring there is smaller, and no seasonal variations in egg weight have been observed (Viegas et al. 2012). In the warmer and

seasonally less variable Mediterranean Sea, the brown shrimp shows a shorter breeding season, comprising only the coldest months from November to April (Gelin et al. 2000). In conclusion, strong seasonality in plankton production of temperate regions, such as the southern North Sea, may represent a selection factor favouring an evolution of seasonal variability in larval biomass. We suggest that this reproductive trait allows the brown shrimp to extend its reproductive period.

Besides seasonal, also interannual variability has been observed in the biomass of crustacean offspring (e.g. Shirley and Shirley 1989; Giménez 2010; Urzúa et al. 2012). In future investigations, it would thus be interesting, especially in the context of climate change, to further consider variability among year classes of eggs and larvae and their relationships with variations in environmental factors.

Our study shows that seasonal variations in egg biomass of *C. crangon* are propagated to similar patterns of variation in larval biomass at hatching, indicating "carry-over effects" from the embryonic to the larval phase. Future studies of temperate species including *C. crangon* should thus investigate whether seasonal variations in larval biomass are propagated also further into the juvenile phase (see Giménez 2006, 2010; Pechenik 2006). In brown shrimp, comparative studies of the influence of temperature and food conditions on development time, survival and growth of both "winter larvae" and "summer larvae" may reveal implications for the condition of benthic juveniles and adults and thus for the stability and production of an important marine fishery resource.

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