ORIGINAL ARTICLE

Seasonal variation in dry weight and elemental composition of the early developmental stages of *Petrolisthes laevigatus* (Guérin, 1835) (Decapoda: Porcellanidae) in the Seno de Reloncaví, southern Chile

P. Gebauer · K. Paschke · A. Barría · K. Anger

Abstract In the Seno de Reloncaví, southern Chile, seasonal changes in dry weight (DW) and elemental composition (CHN) were studied in embryo (initial embryonic stage), newly hatched zoeae, and newly settled megalopae of a porcelain crab, *Petrolisthes laevigatus*. Samples were taken throughout the seasons of egg laying (March-December), hatching (August-February), and settlement (October–February). Values of DW and CHN per embryo or larva, respectively, were consistently minimum in the middle of each season and maximum near its beginning and end. Patterns of seasonal variation in early embryonic biomass may thus be carried over to larvae at hatching and, possibly, to the settlement stage. Such carry-over effects may be selectively advantageous, as zoeae released at the beginning or near the end of the hatching season face conditions of poor planktonic food availability in combination with low winter temperatures or decreasing temperatures at the end of summer (enforcing long development duration). Hence, an enhanced female energy allocation into egg production may subsequently translate to enhanced yolk reserves remaining at hatching, allowing for a larval development under unfavourable winter conditions. In summer, by contrast, plankton productivity and temperatures are generally high, allowing for fast larval growth and development. This coincides with minimal biomass and energy contents both at hatching and settlement. In conclusion, our data suggest that seasonal patterns in the biomass of early developmental stages of *P. laevigatus* may reflect phenotypic variability as an adaptive response to predictable variations in environmental conditions, allowing this species to reproduce in temperate regions with marked seasonality in water temperature and plankton productivity.

Keywords Bioenergetic traits variability · Embryo · Larvae · Elemental composition · *Petrolisthes laevigatus* · Seasonal variability

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Introduction

Population demographics and dynamics of marine invertebrates are consequences of pre- and post-settlement processes (Connell 1985; Gaines and Rougharden 1985; Grosberg and Levitan 1992; Giménez 2004). Analysis of life-history traits is thus critical for an understanding of these aspects of population biology. Life-history patterns have generally been considered as adaptive, because they are subject to environmental pressures of evolutionary selection towards an optimization of the survival of progeny (Roff 1992; Stearns 1992; Levin and Bridges 1995). However, both physical and biological conditions can modify some traits, indicating phenotype plasticity (Pfennig et al. 2010). Intraspecific variations in various life-history traits have been found, for instance, in crustaceans and other marine invertebrates (Hines 1986a, b; Anger 2001, 2006). Among these intraspecifically variable traits, offspring size

has been considered as particularly important, because it affects developmental time, survival in the plankton, and the success of recruitment (Miner et al. 2005; Marshall and Keough 2006; Moran and McAlister 2009). Such variations in offspring size have been studied mainly across the latitudinal range of distribution of species, whose populations may live under different environmental conditions (Brante et al. 2004; Ouellet and Plante 2004; Rotllant et al. 2004; Bas et al. 2007; Lardies et al. 2010; Weiss et al. 2010).

Seasonal variations in environmental factors such as temperature and food supply have been identified, in general, as important causes of intrapopulational variability in reproductive traits of marine invertebrates (Ghiselin 1987). However, such variations have not extensively been studied in decapod crustaceans. Seasonal differences have been found, for instance, in the number and volume of anomuran and brachyuran crab eggs (Sampedro et al. 1997; Bas et al. 2007), in the elemental composition of shrimp and crab embryos (Paschke 1998; Bas et al. 2007; Urzúa et al. 2012) and in the biochemical composition of blue crab embryos (O'Leary Amsler and George 1984). Furthermore, seasonal variations have been identified in the nutritional vulnerability of first-stage larval shrimp (Crangon crangon; Paschke et al. 2004) and porcelain crab (Petrolisthes laevigatus; Gebauer et al. 2010).

The species P. laevigatus (Guérin 1835) is a filter-feeding crab that typically inhabits mid-upper rocky intertidal zones on the Pacific coast of South America. Its geographic range extends from the south of Peru (12°S) to southern Chile (46°S) (Retamal 1981). Near the southern limit of this range, in the Seno de Reloncaví (41°45′S, 72°20′W), females with early eggs are present from March to January–February, whereas final embryonic stages are mainly found between August and February (Gebauer et al. 2007). The embryonic development may last up to approximately five months (Gebauer et al. 2007). Female P. laevigatus are able to reproduce at least twice during each reproductive season (Gebauer, personal observation).

In southern-Central Chile, the eggs of P. laevigatus in an initial embryonic stage have a volume of about 0.23 mm^3 and a dry weight of ca 88 µg (Lardies and Wehrtmann 1996). The release of the larvae extends for 7 months, from August to February (Gebauer et al. 2007), with different cohorts showing differential nutritional vulnerability (Gebauer et al. 2010). The nutritional vulnerability index (NVI; Gebauer et al. 2010) fluctuates between 2.2 and 1.7 in August and October, respectively, indicating high values of point of reserve saturation and low values of point of no return, representing high dependence on food of early larval stage (Gebauer et al. 2010). The settlement period of this species extends over six months, from October to March, showing both inter- and intra-annual variations in settler abundance (Gebauer et al. 2007, 2011). Due to the

long duration of the periods of egg laying, larval hatching, and megalopal settlement, females and early developmental stages (embryos, zoeae, megalopae) face seasonally variable environmental conditions.

In a temperate environment, as Seno de Reloncaví, with marked seasonality in temperature, ranging between 4 °C (August) and 17 °C, (January) in the intertidal zone (Gebauer et al. 2007) or between 9 °C (July) and 17 °C (February) in the water column, while primary productivity fluctuates approximately between 1 mg C m^{-3} h^{-1} (winter) and 23–12 mg C m^{-3} h^{-1} (spring and fall) (Iriarte et al. 2007), the occurrence of embryos, early larvae, and settlers of P. laevigatus throughout extended periods raises the question whether these early developmental stages differ intra-annually in biomass, elemental composition, and/or quality (expressed in terms of energy content). If these aspects show variability, this might indicate an adaptive strategy to face the seasonally or latitudinally variable conditions.

Materials and methods

Throughout the periods of egg laying, hatching, and settlement, porcelain crabs (P. laevigatus) were regularly collected from the intertidal zone of Pelluhuín, Seno de Reloncaví, Chile (41°45′S, 72°20′W). Females with mature gonads were manually collected and transported to the laboratory, where they were kept in aquaria. These were placed in a water bath connected to an open system with circulating coastal seawater (9.5–15 °C, corresponding to field temperatures during the period of collection; constant 31 psu), together with males, remaining unfed for maximally five days, until eggs were laid (females were checked daily). Every month (from March to December), samples of embryos in initial stage (meaning less than 1 day of embryonic development) were removed from five females and prepared for later analyses (see below). In females, carapace length (CL) was measured, and all embryos were counted. For thirty embryos from each female, embryonic length and width were measured under a stereo microscope, and embryo volume was calculated (Valdés et al. 1991). These embryos were subsequently divided into five replicate samples for further determinations of dry weight (DW) and elemental composition (carbon, hydrogen, nitrogen; collectively CHN).

From August to February, females with embryos in a final stage of embryonic development were regularly collected from the same intertidal habitat. They were subsequently kept for maximally 5 days in individual aquaria without food (10–15 °C; field temperatures during the period of collection; constant 31 psu), until Zoea I larvae hatched. The water was changed daily and checked for the

presence of larvae. Thirty newly hatched larvae obtained from each of five females (carapace size measured as above) were divided in 5 replicate samples per female and stored frozen for later DW and CHN determinations.

From October to February, newly settled megalopae were collected monthly carefully with forceps from the intertidal zone (same habitat where the female with embryos were collected). In order to assure that megalopae collected for later determinations of DW and CHN had settled no more than 24 h before the day of collection, all megalopae were removed from the assigned collection areas (ca. 20 stones in average 700 cm² each), one day prior to the collection. Twenty-five megalopae divided into five replicates were used for the analyses. Previous to CHN sampling, the megalopae were identified according to Albornoz and Wehrtmann (1996) and maintained one day in filtered seawater (0.45 μm pore size) to allow them to empty the intestine.

All samples (embryos, Zoea I, megalopae) were washed with distilled water, frozen at −80 °C, lyophilized for 48 h, and stored at −80 °C for later determinations of DW and CHN. DW was measured on a Sartorius SC2 microbalance (precision 0.1 μg), CHN with standard techniques (Anger and Harms 1990) using an Elemental Vario Micro CHN analyser with Sulphanilamide as a standard.

Statistical analysis

To evaluate the effect of the factor season (month) on the measured variables in initial embryos, Zoea I, and megalopae, one-way ANOVA was applied. Tests for homogeneity of variance (Levene test) and normality (Kolmogorov–Smirnov test) were performed to check if the data set complied with the assumptions of parametrical tests; when the data did not meet these assumptions, differences among groups were assessed using a Kruskal–Wallis H test. Multiple comparisons were carried out with Student–Newman Keuls test (SNK) (Zar 1999). Differences with a probability of error $P < 0.05$ were considered as statistically significant.

Results

Embryo in an initial stage of development

The size of the females, from which embryos in an initial stage of development were sampled, fluctuated during the season of collection in a narrow range between 10.3 and 12.9 mm CL ($F = 1.28$, $P = 0.25$). Embryo dry weight (DW) and volume showed significant variations within the reproductive season (March–December) (Fig. 1a, b; $F = 6.06$, $P < 0.001$ and $F = 5.7$, $P < 0.001$, respectively). Highest values of embryo DW were found near the

beginning and the end of the reproductive season (90 ± 6 and 95 ± 4 μg, respectively; Fig. 1a), while a minimum was observed in August–September (transition winter–spring, 76 ± 5 μg). In general, significant differences were detected between the period August–September and the periods March–April (beginning) and October–December (end of the reproductive season; Fig. 1a). Seasonal variation in embryo volume showed a similar pattern as DW, ranging between 0.15 ± 0.02 mm³ (December) and 0.12 ± 0.02 mm³ (June), with smallest embryos observed in June and August (middle of the reproductive season; $P < 0.05$, multiple comparisons; Fig. 1b). Within the size range of females sampled in this study (10.3–12.9 mm CL), fecundity did not vary significantly during the season (471 ± 169 egg female⁻¹, $P > 0.62$). No relationship was observed between female size (within the size range sampled in this study) and embryo volume or DW.
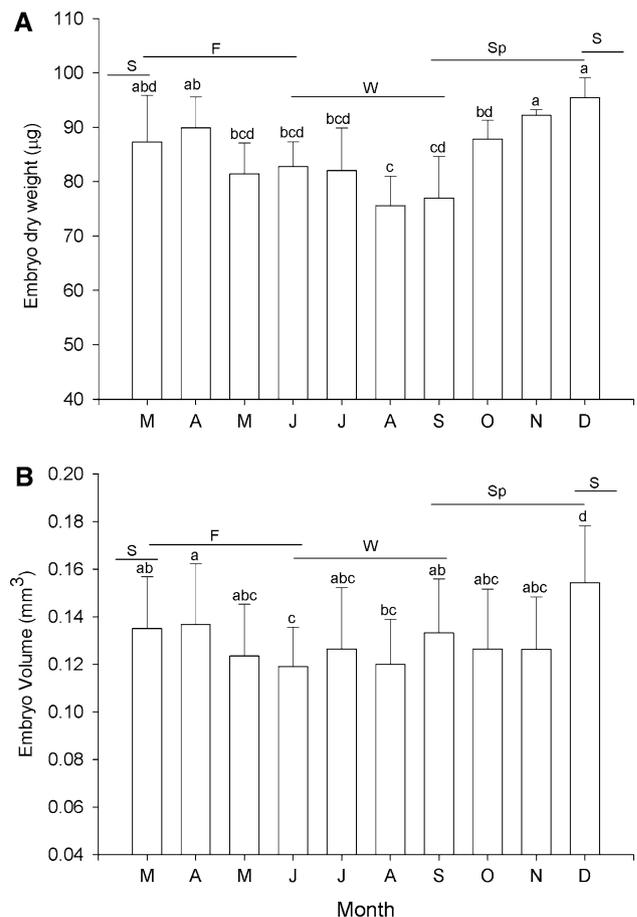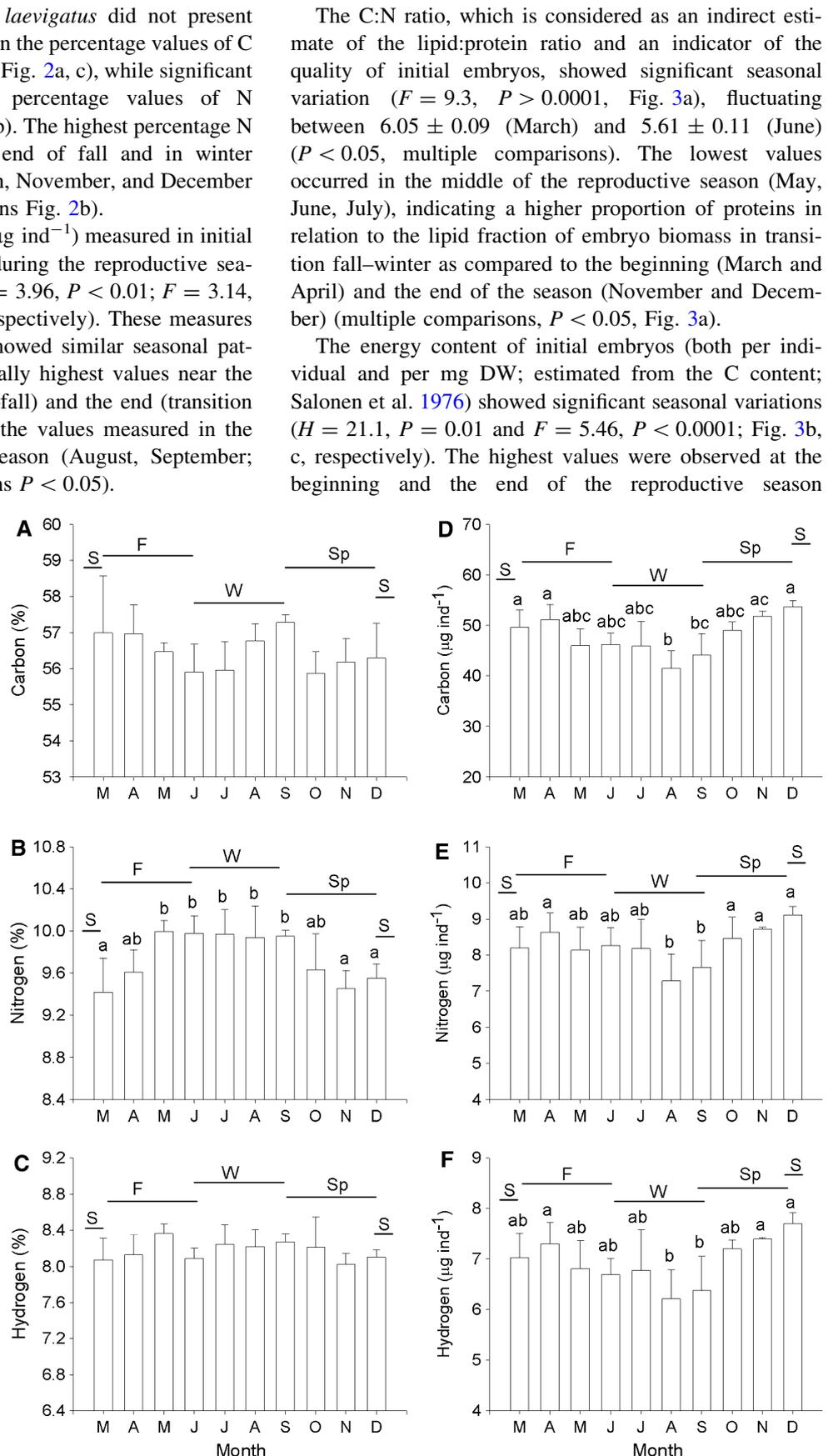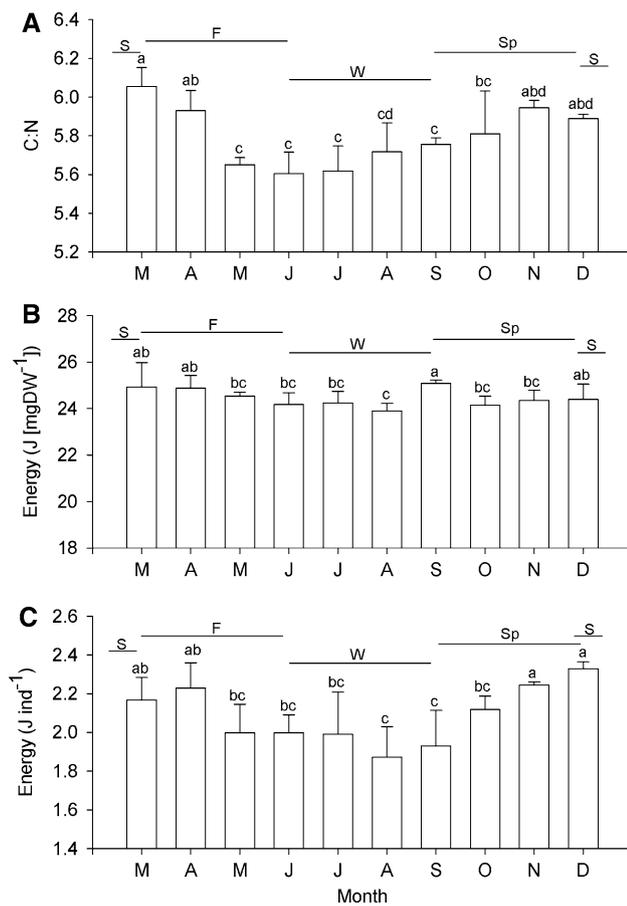

Fig. 1 *Petrolisthes laevigatus*, initial embryos during the reproductive season (2006) in the Seno de Reloncaví, Chile. **a** Dry weight (DW, μg ind⁻¹), **b** initial embryo volume (mm³); mean + SD. Differences among months are indicated by *different letters* over the columns, $P < 0.05$ based on multiple comparisons (Student–Newman Keuls test). *S* summer, *F* fall, *W* winter, and *Sp* spring

The initial embryos of *P. laevigatus* did not present significant seasonal variations in the percentage values of C and H (in % of DW; $P > 0.05$; Fig. 2a, c), while significant differences occurred in the percentage values of N ($F = 5.40$, $P < 0.0001$, Fig. 2b). The highest percentage N values were found near the end of fall and in winter (Fig. 2b), differing from March, November, and December ($P < 0.05$, multiple comparisons Fig. 2b).

The absolute CHN values (µg ind^{-1}) measured in initial embryos varied significantly during the reproductive season ($F = 5.69$, $P < 0.001$; $F = 3.96$, $P < 0.01$; $F = 3.14$, $P < 0.001$, in C, N, and H, respectively). These measures of organic embryo biomass showed similar seasonal patterns as total DW, with generally highest values near the beginning (transition summer–fall) and the end (transition spring–summer) compared to the values measured in the middle of the reproductive season (August, September; Fig. 2d–f, multiple comparisons $P < 0.05$).

The C:N ratio, which is considered as an indirect estimate of the lipid:protein ratio and an indicator of the quality of initial embryos, showed significant seasonal variation ($F = 9.3$, $P > 0.0001$, Fig. 3a), fluctuating between 6.05 ± 0.09 (March) and 5.61 ± 0.11 (June) ($P < 0.05$, multiple comparisons). The lowest values occurred in the middle of the reproductive season (May, June, July), indicating a higher proportion of proteins in relation to the lipid fraction of embryo biomass in transition fall–winter as compared to the beginning (March and April) and the end of the season (November and December) (multiple comparisons, $P < 0.05$, Fig. 3a).

The energy content of initial embryos (both per individual and per mg DW; estimated from the C content; Salonen et al. 1976) showed significant seasonal variations ($H = 21.1$, $P = 0.01$ and $F = 5.46$, $P < 0.0001$; Fig. 3b, c, respectively). The highest values were observed at the beginning and the end of the reproductive season

Fig. 2 *Petrolisthes laevigatus*, initial embryos during the reproductive season (2006) in the Seno de Reloncaví, Chile. Graphs **a–c** percentage contents of carbon (*C*), nitrogen (*N*), hydrogen (*H*) (all in % DW); **d–f** CHN contents per embryo (in µg ind^{-1}); mean + SD. For further explanations, see Fig. 1

Fig. 3 *Petrolisthes laevigatus*, initial embryos during the reproductive season (2006) in the Seno de Reloncaví, Chile. **a** C:N mass ratio; **b** mass-specific energy content (J [mg DW]$^{-1}$); **c** energy content per embryo (J ind^{-1}); mean + SD. For further explanations, see Fig. 1

$(2.17 \pm 0.12$ and 2.33 ± 0.03 J ind^{-1}, respectively), while a minimum occurred in the middle of the season (August and September), i.e. in late winter $(1.87 \pm 0.16$ J ind$^{-1})$ $(P < 0.05$, multiple comparisons, Fig. 3c).

Newly hatched Zoea I larvae (ZI)

The hatching season of *P. laevigatus* lasted in the Seno de Reloncaví from August to February. The size of the females from which we obtained newly hatched zoeae (ZI) fluctuated between 11.5 and 12.7 mm CL $(F = 1.33,$ $P = 0.27$). Larval dry weight (DW) at hatching showed significant seasonal variations $(F = 3.47, P < 0.01;$ Fig. 4a), with heaviest zoeae observed near the beginning and at the end of the season of larval release $(94.9 \pm 2.4$ and 88.9 ± 2.5 µg DW in late fall and summer, respectively) compared to those released in the middle of the hatching season (December) $(P < 0.05$, multiple comparisons). Likewise, the CHN content per larva (in µg ind^{-1}) varied significantly among sampling months $(F = 6.29,$ $P < 0.0001; F = 4.32, P < 0.01; F = 8.20, P < 0.0001;$

for C, N, and H, respectively; see Fig. 4b–d). The highest C and H values were found at the beginning and the end of the season (C: 33.7 ± 2.4 and 31.2 ± 1.3 µg ind^{-1}; H: 4.7 ± 0.27 and 4.5 ± 0.18 µg ind^{-1} in August and February, respectively), showing significant differences to December $(P < 0.05$, multiple comparisons). The N content of the ZI was maximum in August, at the beginning of the hatching season $(7.69 \pm 0.1$ µg ind^{-1}), decreasing by approximately 13 % in December (multiple comparisons, $P < 0.05$; Fig. 4c).

The percentage N values (in % of DW) also varied significantly during the season, fluctuating between 8.7 ± 0.2 % in September and 7.5 ± 0.5 % in February, respectively $(F = 3.25, P < 0.01;$ multiple comparison, $P < 0.05$). The percentage C and H values, by contrast, did not show significant seasonal variations, with average values of 35.9 ± 0.7 and 5.2 ± 0.2 %, respectively.

The C:N mass ratio measured in newly hatched zoeae was maximum near the end of the season, in February (4.69 ± 0.28), differing significantly from values measured in September, October, November, and December $(P < 0.05,$ a posteriori comparisons). This indicates a higher proportion of lipids in relation to the protein fraction (Fig. 4e). The energy content per newly hatched ZI (in J ind^{-1}, estimated from C data; Salonen et al. 1976) was ca 15 % higher near the beginning (August) compared to the middle of the season (November and December; $F = 5.16, P < 0.001$; multiple comparisons, $P < 0.05$; Fig. 4e). However, no significant seasonal variation was detected in the weight-specific energy content (average: 12.6 ± 0.3 J mg DW^{-1}).

Newly settled megalopa

The settlement season of *P. laevigatus* lasted in the Seno de Reloncaví from October to February. The dry weight (DW) of recently settled megalopae fluctuated seasonally between 741 ± 26 and 586 ± 26 µg ind^{-1} in October and December, respectively $(F = 40.3, P < 0.0001$; a posteriori comparisons $P < 0.05$; Fig. 5a). Similarly, the absolute (in µg ind^{-1}) as well as the percentage values of CHN (in % of DW) varied significantly during the settlement season. The highest values were generally found near the beginning and at the end of the settlement season showing, in general, significant differences to December (Fig. 5b–g). The C:N ratio decreased from October towards the transition spring–summer and increased in January $(F = 9.16,$ $P < 0.0002$; Fig. 6a). Again, this indicates seasonal variations in the proportions of lipid and protein in newly settled larvae, differing between November–December and October–January $(P < 0.05$, a posteriori comparisons, Fig. 6a). Also, the energy content (both expressed in J ind^{-1} and in J mg DW^{-1}) varied significantly throughout the settlement season $(F = 59.3, P = 0.0001; F = 17.3,$
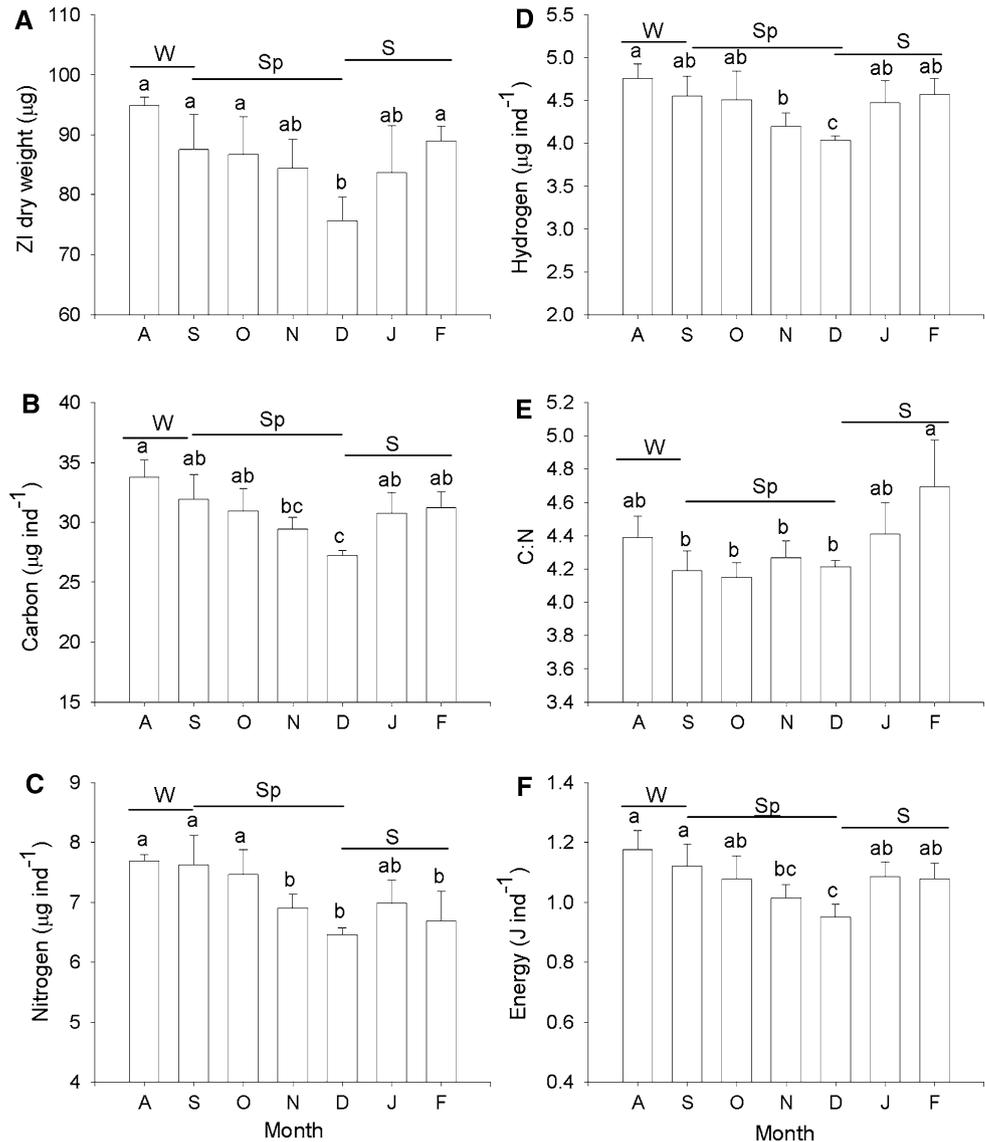
$P < 0.0001$, respectively; Fig. 6b, c). This seasonal pattern was similar to that described above for early embryos and newly hatched larvae. Settling megalopae contained in October and February about 44 and 22 %, respectively, more energy (in J ind^{-1}) than in December. The multiple comparisons revealed four groups according to their energetic content (J ind^{-1}), those settled in (a) October, (b) November, (c) December, and (d) January–February ($P < 0.05$, a posteriori comparisons).

Discussion

In the Seno de Reloncaví, near the southern limit of the geographic distribution range of *P. laevigatus*, various bioenergetic traits of early developmental stages (initial embryos, newly hatched Zoea I larvae, newly settled

megalopae) showed significant seasonal variations. In general, the elemental constituents C, H, and N (which are predominantly bound in the organic fraction of biomass) as well as the energy content (estimated from CHN data) of embryos and larvae were maximum near the beginning and the end of the respective seasons. Recurrent patterns of variability in bioenergetic traits may be considered as a strategy of this species, which may optimize larval survival and growth in a physically variable temperate environment, and ultimately, enhance the survival of progeny (see Hadfield and Strathmann 1996).

Since the embryonic stages are completely non-feeding, seasonal variations in biomass, chemical composition, and energy content of initial embryos may be considered as adaptive, if they later translate to maximum larval fitness (expressed as maximum larval energy content, allowing for reduced dependence on planktonic food), and if those
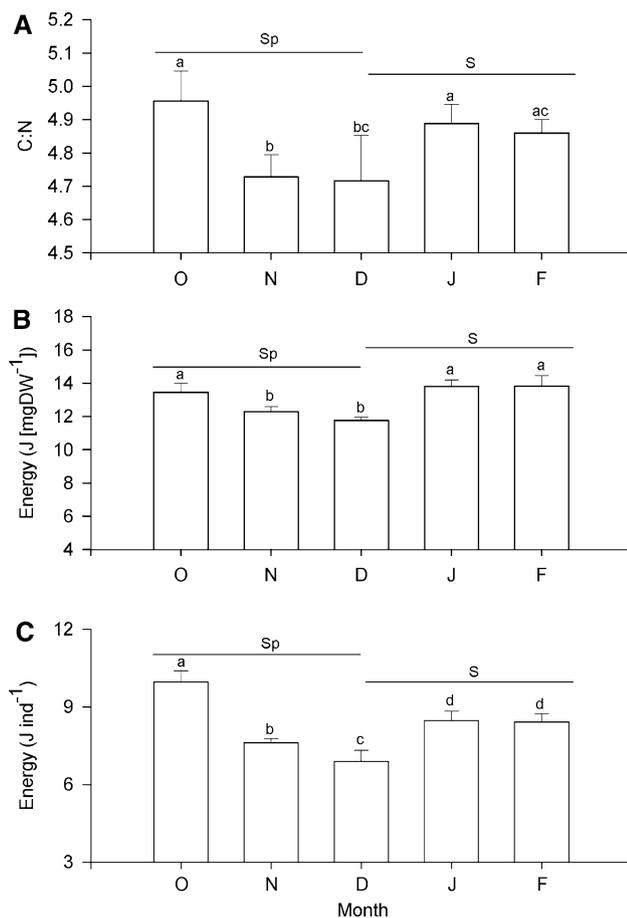
Fig. 5 *Petrolisthes laevigatus*, newly settled megalopae during the settlement season (2006–2007) in the Seno de Reloncaví. **a** Dry weight (µg ind^{-1}); **b–d** percentage contents of carbon, nitrogen, hydrogen (all in % DW); **e–g** CHN contents per megalopa (in µg ind^{-1}); mean + SD. For further explanations, see Fig. 1
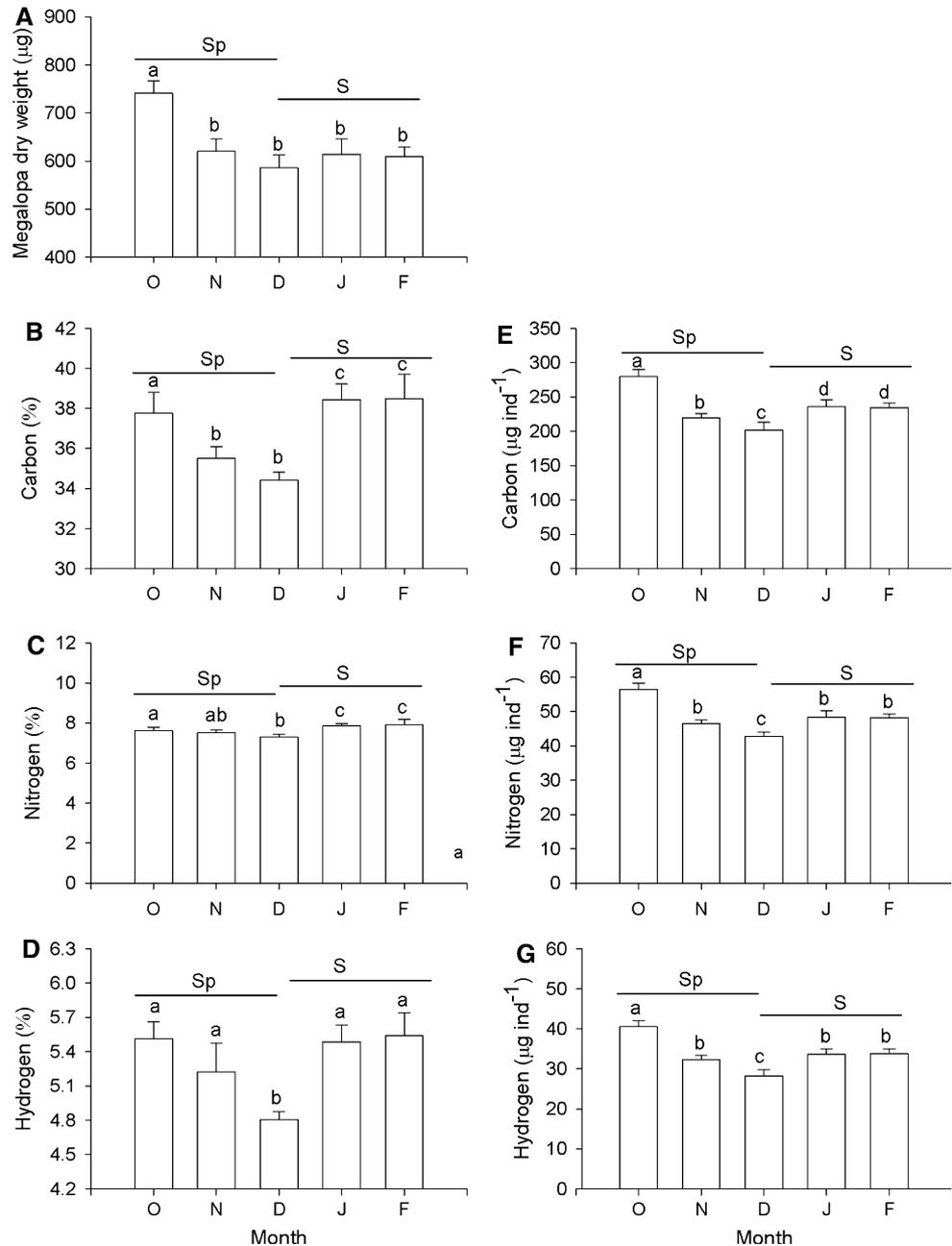
fitness maxima in the planktotrophic larval stages concur with a predictable pattern of exposure to adverse nutritional conditions. Our observations have shown that, due to temporal shifts in the seasons of egg laying, hatching, and settlement, the months of maximum biomass and energy content differ among these successive developmental stages. However, larger embryos (which also are heavier and richer in energy) tend to develop to heavier and fitter Zoea I larvae, and these may subsequently develop to heavier and fitter megalopae. These recurrent but seasonally shifting patterns in the initial biomass of embryos, newly hatched zoeae, and newly settled megalopae appear to indicate carry-over effects through successive life-

history stages (see Anger 2006; Bas et al. 2008; Harrison et al. 2011).

While carry-over effects are plausible for the relationship between embryo biomass and larval energy content at hatching, the condition of settling megalopae does not exclusively depend on previously stored energy reserves, but also on larval feeding and metabolic energy losses in the plankton. Moreover, the megalopa has access to both planktonic and benthic food sources, so that it may depend less on plankton productivity than the pelagic zoeae. In conclusion, there may be confounding effects of seasonal changes in feeding rates and metabolic energy losses occurring during larval development. The importance of

Fig. 6 *Petrolisthes laevigatus*, newly settled megalopae during the settlement season (2006–2007) in the Seno de Reloncaví, Chile. **a** C:N mass ratio; **b** mass-specific energy content (J [mg DW]$^{-1}$); **c** energy content per megalopa (J ind^{-1}); mean + SD. For further explanations, see Fig. 1

seasonal variation in the biomass of the megalopa stage at settlement remains thus to be further scrutinized in future studies, where metabolic parameters such as respiration and the activities of metabolic enzymes should also be considered (Meyer et al. 2002; Rotllant et al. 2010).

In order to evaluate the importance of seasonal variations in embryonic biomass, it must be ascertained if the timing of maximum larval fitness at hatching or at settlement coincides with an occurrence of trophic limitations or other environmental challenge. As all fjords in the South of Chile, the Seno de Reloncaví presents marked seasonality in primary productivity, with blooms in spring and fall (Palma and Silva 2004; Iriarte et al. 2007; Iriarte and González 2008; González et al. 2010), and temperature (Gebauer et al. 2007; Iriarte et al. 2007). Variations in bioenergetic traits of initial embryos observed in our study could thus be a consequence of seasonal variations either in the availability and conversion of benthic or planktonic food and, alternatively or additionally, in endogenously

controlled female energy investments in egg production. During winter, the availability of food for suspension feeders such as *P. laevigatus* is actually lower in the study area (Iriarte and González 2008; González et al. 2010), which may explain the production of eggs with a lower energy content in winter (Fig. 3). Better food availability in fall and spring (i.e. at the beginning and the end of the reproductive season) may thus allow the females to invest more energy per embryo, as observed in our study.

In addition to presumable effects of variable food availability in the benthos, there may also be endogenous factors influencing the energy allocation into egg production. Female *P. laevigatus* pass through at least two reproductive cycles during each season (Gebauer, personal observation), which also might contribute to a lower quality of embryos in the middle of the season due to reproductive exhaustion (see Palacios et al. 1999; Bas et al. 2007). However, poor embryonic quality should in this case be expected, but has not been observed, at the end of the season of egg production (December). This might be due to a compensating effect of greater availability of suspended food in spring and summer. Poor nutritional conditions in the benthos in winter may thus either cause directly a production of smaller eggs with less energy per embryo, or seasonal variation in food availability may serve as a triggers from the habitat, which could tune the endocrine control system involved in egg production (for recent review, see Nagaraju 2011). In the latter case, however, also other environmental variables, in particular, decreasing day length or low water temperatures may be perceived and used as environmental signals, alone or in combination with nutritional or further factors that are characteristic of winter conditions (Urzúa et al. 2012).

The variations in bioenergetic traits of newly hatched Zoea I larvae reflect those observed in the initial embryos and, possibly, variable utilization of metabolic substrates during embryonic development under different environmental conditions (see Giménez and Anger 2001). Our data suggest that variations in the bioenergetic traits of initial embryos are later carried over to first-stage larvae, leading to maximum biomass and energy values observed at the beginning of the hatching season (i.e. in winter). Although these newly hatched zoeae still are planktotrophic, displaying a high nutritional vulnerability (Gebauer et al. 2010), their enhanced energy content may allow them to develop also under unfavourable winter conditions with poor food availability in combination with low temperatures prevailing at the beginning of the hatching season. These adverse conditions prolong the duration of the Zoea I stage to about twice the time needed by larvae hatching with less energy in December (Gebauer et al. 2010).

Seasonal variations in reproductive traits have also been detected in the elemental composition and energy content

of eggs and first-stage larvae of various other decapod crustaceans such as shrimp (*Crangon crangon*; Boddeke 1982; Paschke et al. 2004; Urzúa et al. 2012; *Crangon* spp.; Kattner et al. 1994) and crab (*Neohelice granulata*; Bas et al. 2007). Heavier embryos and larvae with higher energy and C:N values were also in these species observed at the beginning of the seasons of egg laying and hatching, indicating an enhanced lipid content. These authors suggested that larvae presenting a greater biomass or energy content would be especially well adapted to survive and develop under unfavourable conditions, e.g. food limitation in combination with low temperatures, encountered especially at the beginning of the hatching season (Anger 2001; Giménez and Anger 2005; Gebauer et al. 2010).

In addition to the seasonal fluctuations in temperature and food supply mentioned above, also salinity varies in the study area, being particularly low in December (Gebauer 2004; Iriarte and González 2008), while the settlement rate of *P. laevigatus* is strongly reduced (Gebauer 2004; Gebauer et al. 2011). Hence, the relatively few megalopae that settle in the intertidal zone during this period may be exposed to conditions of low-salinity stress.

Seasonal variations in the elemental composition and energy content of recently settled megalopae of *P. laevigatus* may have significant consequences for the performance of the subsequent juvenile stages, especially in seasonally fluctuating environments like that of the Seno de Reloncaví. To understand the population dynamics of *P. laevigatus*, the real contribution to recruitment (number and quality) must be known for megalopae settling in different periods of the season. Studies on the supply-side ecology of barnacles in Nahart (Massachusetts) and fish in Barbados and Florida Keys have shown great variability in traits of settlers, leading to variations in settlement success as well as post-settlement growth and survival (Jarret 2003; Sponaugle and Grorud-Colvert 2006).

Connections between life-history characteristics in successive developmental phases have been documented in numerous marine invertebrate species, probably exerting a significant impact on population dynamics (Giménez 2004, 2006, 2010; Beckerman et al. 2002; Giménez et al. 2004; Marshall and Keough 2006; Allen and Marshall 2010). As Pechenik (2006) pointed out, "metamorphosis is not a new beginning". In *P. laevigatus*, seasonal patterns of variation in larval fitness prior to metamorphosis resemble variations observed already at larval hatching, and even those in early embryos soon after egg laying. It is thus possible that patterns observed in biomass and elemental composition of early embryos are transferred not only to the newly hatched Zoea I, but eventually also through metamorphosis to the early juvenile stages, similar as observed in a crab, *Neohelice granulata* (Giménez et al. 2004; Bas et al. 2008).

Seasonal variability in bioenergetic traits of the early developmental stages of *P. laevigatus* observed in our study suggest that seasonal variation may be an important trait of this species, enabling it to inhabit environments with marked seasonal variations in food availability and temperature, so that it also can occupy a wide geographic-climatic range, in which it is subject to differential environmental selection pressures. Finally, this study clearly shows that seasonal variability in life-history traits must be taken into account in future research on this and other comparable species living in temporally or spatially highly variable environments.

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