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Secondary production of *Arctodiaptomus salinus* in a shallow saline pond: comparison of methods

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ABSTRACT: Research on secondary production is important because it allows the formation of general theories of biological productivity, to elucidate material and energy transfers, and to detect the effects of perturbations on the ecosystem. These studies are widespread in marine systems, but are scarce in shallow saline endorheic ponds. However, the latter can be noteworthy because these wetlands characteristically have short trophic webs and, unlike the situation in marine systems, their relative isolation makes them ideal natural laboratories to track a single population and understand its secondary production and dynamics. To date there is no universally adopted method of estimating secondary production, and different methods usually produce different results. In order to contribute to the long debate about these methodologies, the growth rates of the different stages of the copepod *Arctodiaptomus salinus* from an endorheic pond were calculated by 2 different methods based on the moult rate method. In Method A the vital rates were estimated from laboratory observations, whereas in Method B they were estimated from a stage-dependent matrix model developed from time series of abundances observed in field. Method B reported more realistic and lower estimates than Method A, probably because the former took into account mortality, population growth rate and dormancy. Differences between the methods were lower when the population was closer to a steady state. However, since most populations in nature are not in a steady state, and mortality is not zero, we conclude that secondary production should be estimated from methods implemented with accurate demographic parameters obtained in the field.

KEY WORDS: Calanoida · Copepod · Growth rate · Matrix modelling · Secondary production · Shallow lake

INTRODUCTION

Copepods are the focus of many studies of secondary production, since they are an intermediate link between primary production and higher trophic levels. This research is widespread in marine systems (e.g. Beckman & Peterson 1986, Middlebrook & Roff 1986, Guerrero & Rodríguez 1994, Liang & Uye 1996, 1997, Guerrero & Rodríguez 1997, Guerrero et al. 1997, Calbet et al. 2000) because their higher trophic levels are made up of commercial fish. However, research is scarce in fishless systems without economic interest, such as endorheic shallow saline ponds. Studies of these systems can, nevertheless, be very informative since they are characterized by short trophic webs (Alcorlo 1999, Alcorlo et al. 2001) and in some ponds copepods suffer a low risk of predation (such as the pond in this study). In addition, unlike a marine system, the relative isolation of endorreic ponds makes them an ideal natural laboratory to track a single population's secondary production and dynamics throughout its lifecycle.

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Secondary production estimates are important because they allow the formation of general theories of biological productivity, elucidate the material and energy transfers and detect the effects of pollution and climate change (Downing 1984, Muxagata et al. 2012). However, to date there is no universally adopted method of estimating secondary production, and different methods usually produce different results (Middlebrook & Roff 1986, Morin et al. 1987, Gómez et al. 2012). This problem was emphasized by Hirst et al. (2005), who reported the different sources of errors of the most widespread method used in secondary production research, termed the moult rate method. One of the main errors pointed out by these authors is the assumption that stage duration and moult rate are equivalent; however this assumption is only true when there is zero mortality, no dormancy, and the population is steady state. In nature it is possible to find a population in a steady state and without dormancy, but zero mortality is not possible.

These and other limitations, such as difficulties in monitoring the same population over time, advection or indistinguishable cohorts (see Review by Runge & Roff 2000), means that most studies on secondary production are limited to egg production estimates (e.g. Beckman & Peterson 1986, Laabir et al. 1995, Poulet et al. 1995, Calbet et al. 2002), whereas estimates of *in situ* development and growth rates of nauplii and copepodites are less abundant (e.g. Calbet et al. 2000, Hirst et al. 2003, Sastri & Dower 2006). In contrast, we characterize and record all of the developmental stages of *Arctodiaptomus salinus* from an endorheic saline pond. The growth rates of the different stages were calculated by 2 different methods, based on the moult rate method or growth rate approach. In Method A the vital rates were estimated from laboratory observations, whereas in the Method B they were estimated from a stage-dependent matrix model developed from time series of abundances (Jiménez-Melero et al. 2013).

Arctodiaptomus salinus is an egg-carrying copepod which is very abundant in the arid, semiarid and endorehic regions of Spain (Alonso 1998) where it is often the main constituent of the zooplankton community (Zotina et al. 1999, Boronat Chirivella 2003). The site of this study, Laguna Honda, is a fishless shallow saline pond in eastern Andalusia, southern Spain, characterized by a marked year-on-year variability in both biotic and abiotic variables (Guerrero & Castro 1997, López-González et al. 1998). *A. salinus* is usually the highest level in Laguna Honda's trophic web, as no predators are normally detected in the water column. Our main objective was to estimate the secondary production of the *A. salinus* population. Specifically, we aimed to (1) study the seasonal variation of body size and biomass of the different developmental stages, (2) estimate the relative contribution of the different stages to the total biomass throughout the study period and (3) contribute to the debate about the methodologies applied for estimating secondary production by comparing 2 methods where vital rates were estimated by different approaches, one based on laboratory estimations and another based on field estimations.

MATERIALS AND METHODS

Study site and sampling

Laguna Honda (UTM: 30SVG992619) is a fishless, inland, saline pond (460 m a.s.l.) located in an endorheic zone in the Guadalquivir river catchment area (Andalusia, Spain). Its maximum depth is 3.16 m and its basin surface is 9 ha (Castro et al. 2003). The waters of Laguna Honda are saline chloride, with a predominance of sodium chloride (Cl-Na-Mg-SO_4 chemical subtype) (Castro 2004). The level and permanence of water is extremely variable, and this pond is characterized by a marked year-on-year variability to both biotic and abiotic variables (Guerrero & Castro 1997, López-González et al. 1998). Laguna Honda is recharged principally by groundwater inputs, but also through direct precipitation and surface runoff. Water losses are principally by evaporation, but also from infiltration (Andreo et al. 2008).

Environmental variables such as temperature, chlorophyll-*a* concentration (chl *a*), salinity and organic matter concentration (OM) were measured weekly. Temperature was measured with a Wissenschaftlich-Technische Werkstätten microprocessor meter (Weilheim). Water transparency was estimated with a Secchi disc. For salinity measurements, determined as total dissolved solids (TDS), 100 ml of pond water was filtered through a Whatman GF/C fibreglass filter and then dried at 105°C for at least 48 h. The same procedure was followed for measurements of total particulate matter, but a larger volume (between 0.3 and 4 l) was filtered for this analysis. Subsequently, the filter was weighed both before and after 1 h at 550°C to estimate its OM content (Hakanson & Jansson 1983). Chl *a*, corrected for phaeopigments, was determined by spectrophotometry after filtration of 0.5 to 6 l of pond water through a Whatman GF/C fibreglass filter and a 24 h cold-pigment extraction in 90% acetone (Lorenzen 1967).

Zooplankton was sampled weekly from 25 June to 8 December 2001 at a station placed in the deepest zone of Laguna Honda. A vertical haul was made over the entire water column with a plankton net of 40 µm mesh size and 25.5 cm diameter. Samples were preserved in buffered 4% formaldehyde pond water for estimating the stage structure, from egg to adult, and for body size measurements.

Body size and biomass

Length was measured bi-weekly on 20 to 30 ind. per stage and sex. For nauplii, overall length was measured. For copepodites and adults, prosome and urosome were measured separately in order to obtain both cephalothorax and overall lengths. Individuals were measured under a microscope connected through a television camera to an image analyzer (NIKON Digital Sight DS-U1).

Weight estimates were obtained from the length-weight regressions established by Saadi & Champeau (1994).

For nauplii and copepodites:

$$W = 0.723 \times e^{2.055 \times 10^{-3} \times L} \quad (1)$$

For adult males and non-ovigerous females:

$$W = 2.374 \times 10^{-7} \times L^{2.48} \quad (2)$$

For ovigerous females:

$$W = 2.822 \times e^{1.596 \times 10^{-3} \times L} \quad (3)$$

where W is µg of dry weight and L is the overall length in µm. When length measurements were not available for a particular date, the weight was calculated by interpolating the 2 length values obtained on the previous and the following dates. Finally, the biomass of a given stage was obtained by multiplying the abundance of this stage by the mean weight estimated from the respective length-weight regression.

Seasonal variation of *Arctodiaptomus salinus* body size and differences between sexes were tested by means of factorial ANOVA analyses. Copepodite lengths were log-transformed to meet the assumptions of parametric tests. Regression analyses were used to describe the relationship between mean body size and temperature. Potential differences between stages were tested with a homogeneity of slopes model. The relation of the different environmental variables to body size was tested with Pearson's correlation test. STATISTICA software was used in all analyses (StatSoft).

Post-embryonic development times

The relationship between temperature and the median development times (MDT) was predicted with the Bělehrádek function (Bělehrádek 1935):

$$\mathrm{MDT} = S(T - T_0)^{-b} \quad (4)$$

where T is the temperature, S is a constant determining the proportional response on the time or rate scale (McLaren 1995), T_0 or 'biological zero' places the curve on the arbitrary Celsius scale (McLaren 1995) and b is a curvature coefficient. Since only a small data set is available, a multiparameter equation is not reliable because different 'best fitted' functions can be obtained depending on the method of iteration or software used and on the values assigned to the parameters at the start of the exploration (Hillier & Lieberman 1986, Guerrero et al. 1994). This problem can be avoided by fixing one of the parameters. S cannot be fixed: since it determines the rate scale, it increases when MDT increases (McLaren 1995). T_0 cannot be fixed either because this variable might be different among different life stages. McLaren (1995) suggested that there is no *a priori* reason to expect differences in the 'shape' of temperature responses; therefore, here the constant b is fixed to 1.78. This value comes from Bělehrádek's function fitted with the median embryonic development times of *A. salinus* at 7 different temperatures (Jiménez-Melero et al. 2012). STATISTICA software (StatSoft) was used for Bělehrádek curve fitting analyses.

MDT values of the copepodite stages used for Bělehrádek's function estimations came from the Gamma Density Functions (GDF) previously estimated from lab data (Jiménez-Melero et al. 2007). For the naupliar stages, the GDF reported by Jiménez-Melero et al. (2007) could not be used since they were fitted for aggregated stages. For this reason, Bělehrádek functions describing the relationship between naupliar development times and temperature were estimated using the whole data set instead of the median values. Hence, Eq. (4) uses D (development time) instead of MDT.

Secondary production

The most commonly used method for measuring secondary production (PR) is the weight increment method which consists of multiplying the weight-specific growth rate of each developmental stage (g_i) by its biomass (B_i):

$$PR = \sum (g_i \times B_i) + g_F B_F \quad (5)$$

The first term of the equation corresponds to the somatic growth rate of the juvenile population from the N1 to C5 Stages, and the second term corresponds to the specific egg production rate by the females.

However, results are different depending on the method used to estimate g_i (Hirst et al. 2005). The most widespread method is:

$$g_{i\_A} = \ln\left(\frac{W_{i+1}}{W_i}\right) \times MR_i \quad (6)$$

where W_i is mean weight of Stage i, W_{i+1} is mean weight of Stage $i+1$, and MR_i is the moult rate (d^{-1}). In many cases the inverse of the stage duration is used instead of MR_i. However, stage duration and MR are only equivalent when there is zero mortality and the population is in steady state (Hirst et al. 2005). Hirst et al. (2005) also found another source of errors by using mean weights and proposed the following correction:

$$g_{i\_B} = \ln\left(\frac{W_{i\_\text{exit}}}{W_{i\_\text{entry}}}\right) \times MR_i \quad (7)$$

where W_{i_entry} and W_{i_exit} are arithmetic mean weights of animals entering and leaving Stage i.

In this study, 2 different approaches (Method A and Method B) were used to estimate weight-specific growth rate.

Method A

Method A applied Eq. (6): MR_i was considered to be equivalent to the inverse of the duration of the Stage i, which was calculated as the difference between the development time of the Stage $i+1$ and the development time of the Stage i. These development times were assumed to be dependent only on temperature, which allowed the use of Bělehrádek functions fitted with the development times previously observed in the lab (Jiménez-Melero et al. 2007, Jiménez-Melero et al. 2012).

In Method A, specific egg production rates were calculated by using the following equation:

$$g_F = \frac{W_{\text{eggs}}}{W_{\text{female}}} \times pem \quad (8)$$

where W_{eggs} is calculated by considering the weight of an individual egg multiplied by the average clutch size and pem is the inverse of the interclutch period calculated from Bělehrádek's function (see Jiménez-Melero et al. 2007). Egg weight was assumed to be equal to the weight of the first naupliar stage. Here the term B_F in Eq. (5) corresponds only to the biomass of the egg-carrying females.

Method B

Assumptions of stage duration and moult rate being equivalent when there is no mortality, no dormancy and a steady state population cannot be fulfilled. Hence, a second approach, hereafter called Method B, was performed by substituting into Eq. 7 the moult rates previously estimated by Jiménez-Melero et al. (2013) by means of an inverse method based on a matrix projection model (Fig. 1).

When individuals can be marked and followed over a period of time, the elements of a projection matrix can be determined directly. However, for copepod zooplankton these elements cannot be measured directly and an inverse method is necessary. In this study, we have time series of abundance data and we want to estimate the vital rates determining these abundances. Once these vital rates are known, a matrix projection model for complex life cycles (Caswell 2001) can be constructed. In this scenario, we applied the inverse method of Wood's quadratic programming method, which minimises quadratic forms subject to inequality constraints (Caswell 2001). A detailed description of this method can be found in Twombly (1994) and Caswell (2001). From the projection matrix we can estimate the finite population growth rate, which is a projection of the growth of the population if the environmental conditions were maintained indefinitely. For this reason the study period had to be divided into internally

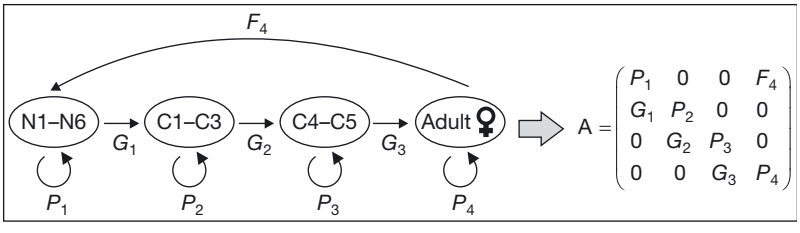

Fig. 1. *Arctodiaptomus salinus*. Life cycle graph: nodes represent the different stages aggregated in 4 groups. Males are not included into the model. P_i is the probability of survival and remaining in Stage i, G_i is the probability of surviving and moulting from Stage i to Stage $i+1$ and F_4 is the fertility of the females. The '0' elements are structural zeros, i.e. transitions that cannot occur in the life cycle of this species

consistent subperiods: a period of high temperatures denoted Period H from 25 June (day of the year, DOY 176) to 18 September (DOY 261), a period of moderate temperatures denoted Period M from 19 September to 12 November (DOY 316) and a Period L characterised by low temperatures from 13 November to 28 December (DOY 362). Details about this division can be found in Jiménez-Melero et al. (2013). Finally, a projection matrix was estimated for each sub-period.

In summary, in Method B we used the moult rates, denoted as G_i, listed in Table 2 of Jiménez-Melero et al. (2013). Since these rates were calculated from the abundances observed in the field, they take into account mortality, dormancy and the population growth rate. Note that in the chosen life cycle (Fig. 1), the different stages were aggregated in 4 groups; consequently W_{i_entry} in Eq. (7) corresponds to the mean weight of the first stage of the aggregated group and W_{i_exit} corresponds to the mean weight of the first stage of the next aggregated group.

In this method, female reproductive production was calculated by using the following equation:

$$g_F = \frac{W_{N1}}{W_{\mathrm{female}}} \times F_4 \quad (9)$$

F_4 represents the contribution of the females to Stages N1 to N6 and consequently represents the rate of nauplii recruitment rather than the egg production rate (i.e. hatching success and larval mortality are included in F_4). F_4 values used in Method B came from Table 2 in Jiménez-Melero et al. (2013). Since G_i and F_4 were estimated from aggregated stages the equation for secondary production in this approach can be written:

$$\begin{aligned} PR = {} & [G_{N1-N6} \times (B_{N1} + B_{N2} + B_{N3} + B_{N4} + B_{N5} + B_{N6})] + \\ & [G_{C1-C3} \times (B_{C1} + B_{C2} + B_{C3})] + \\ & [G_{C4-C5} \times (B_{C4} + B_{C5M} + B_{C5F})] + g_F \times B_F \end{aligned} \quad (10)$$

In both Method A and B, male reproductive production was assumed to be negligible.

RESULTS

Seasonal variation in body size

A factorial ANOVA analysis detected significant differences in both the size of individuals collected on different dates and between stages (for naupliar body size: $F_{73,2236}$ = 431.1876, $p < 0.001$; for copepodite body size: $F_{89,2649}$ = 1158.202, $p < 0.001$). Moreover, there was a significant interaction between sampling date and stage: body size of the different stages did not change uniformly throughout the study period ($p < 0.001$). The longest length occurred in the coldest months (Fig. 2). All the stages showed a negative relationship with temperature, and this relation was linear in most cases (Tables 1 & 2, Fig. 3).

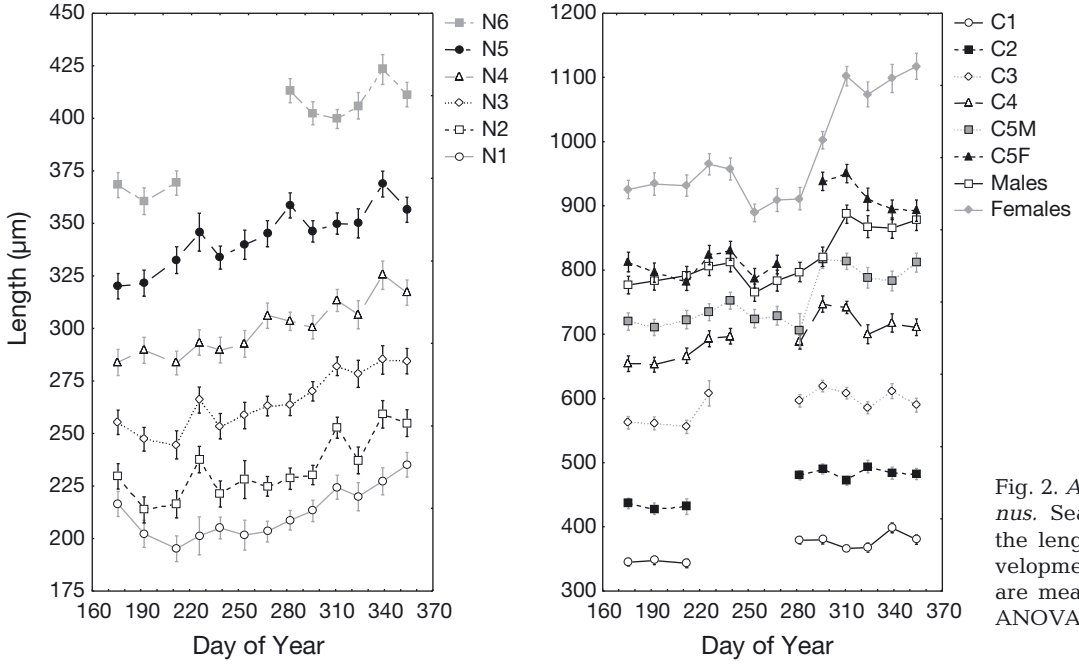

Fig. 2. *Arctodiaptomus salinus*. Seasonal variation in the length of different developmental stages: lengths are means from a factorial ANOVA model. Bars show CIs of 95%

The variation in body size over the temperatures range followed a similar pattern between the naupliar stages (Fig. 3) Indeed, a homogeneity-of-slopes model did not detect significant differences in the slopes of the regression lines ($F_{5,62}$ = 1.01, p = 0.422) . In contrast, the relationship between temperature and the cephalothorax length of the copepodites and adults was not similar at all stages. This relationship was linear in the C1, C2 and Adult Stages, polyno-

Table 1. *Arctodiaptomus salinus.* Parameter estimates (Estim.) for regressions of body size on temperature for each naupliar Stage N1 to N6 (see Fig. 3). For every regression the intercept (a) and coefficient of linear regression (b_1) are shown. Values of p < 0.01 are shown in **bold**

		Estim.	SE	*t*	p
N1	a	240.039	7.707	31.14	**<0.001**
	b_1	−1.296	0.385	−3.37	**0.012**
	R^2	0.564			
N2	a	269.799	9.033	29.87	**<0.001**
	b_1	−1.818	0.451	−4.03	**0.005**
	R^2	0.656			
N3	a	303.145	6.820	44.45	**<0.001**
	b_1	−1.888	0.340	−5.55	**<0.001**
	R^2	0.788			
N4	a	334.978	6.605	50.72	**<0.001**
	b_1	−1.734	0.330	−5.26	**0.001**
	R^2	0.769			
N5	a	379.294	9.194	41.25	**<0.001**
	b_1	−1.841	0.459	−4.01	**0.005**
	R^2	0.654			
N6	a	441.693	12.440	35.51	**<0.001**
	b_1	−2.505	0.621	−4.03	**0.005**
	R^2	0.656			

Table 2. *Arctodiaptomus salinus.* Parameter estimates (Estim.) for regressions of body size on temperature for each copepodite and adult stage (see Fig. 3). For every regression the intercept (a), the coefficient of linear regression (b_1) and the quadratic coefficient (b_2; only when a polynomial regression was adjusted) are shown. Values of p < 0.01 are shown in **bold**

		Estim.	SE	*t*	p
C1	a	403.506	11.105	36.34	**<0.001**
	b_1	−2.047	0.561	−3.65	**0.011**
	b_2				
	R^2	0.638			
C2	a	518.741	14.724	35.23	**<0.001**
	b_1	−2.957	0.743	−3.98	**0.007**
	b_2				
	R^2	0.6793			
C4	a	558.195	51.101	10.92	**<0.001**
	b_1	22.641	6.472	3.50	**0.017**
	b_2	−0.699	0.176	−3.97	**0.011**
	R^2	0.789			
C5M	a	660.547	60.591	10.90	**<0.001**
	b_1	20.557	7.673	2.68	**0.044**
	b_2	−0.680	0.209	−3.25	**0.023**
	R^2	0.799			
C5F	a	693.214	110.137	6.29	**0.002**
	b_1	31.427	13.948	2.25	0.074
	b_2	−1.012	0.380	−2.67	**0.045**
	R^2	0.681			
Male	a	927.694	20.080	46.20	**<0.001**
	b_1	−5.137	1.014	−5.07	**0.002**
	b_2				
	R^2	0.779			
Female	a	1200.999	31.311	38.36	**<0.001**
	b_1	−9.721	1.581	−6.15	**<0.001**
	b_2				
	R^2	0.840			

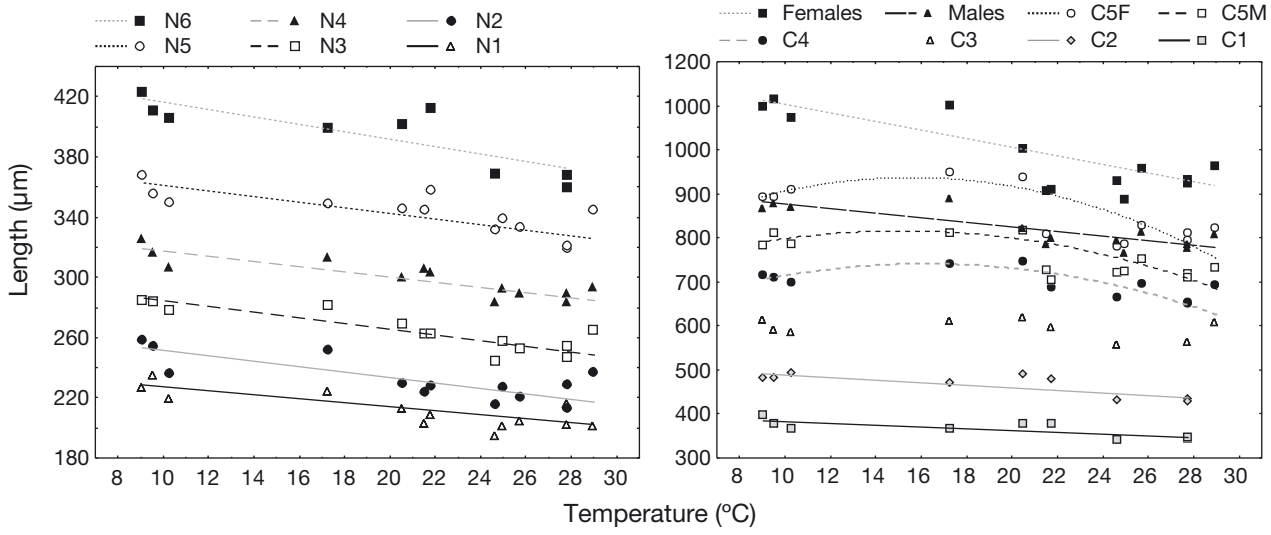

Fig. 3. *Arctodiaptomus salinus.* Body size of each developmental stage over a thermal gradient: lengths are means predicted by a factorial ANOVA. Lines represent statistically significant regressions (see Tables 1 & 2)

mial in the C4 and C5 Stages, and there was no significant relationship between temperature and C3 Stage (Table 2). Subsequent analyses showed that the slopes of the first group (C1, C2 and Adult Stages) were not homogeneous ($F_{3,36}$ = 7.272, p < 0.001), although no significant differences were detected between the slopes of C1 and C2 Stages ($F_{1,14}$ = 0.755, p = 0.400). Length changed with the temperature in a similar way in the 3 Stages C4, C5F and C5M: the coefficients of the 3 polynomial regressions were not significantly different (for linear coefficient: $F_{2,28}$ = 0.191, p = 0.828; for quadratic coefficient: $F_{2,28}$ = 0.190, p = 0.828).

Since body size can also be determined by food availability, Pearson correlations were performed in order to detect a potential relationship between length and chl *a*. No correlation was significant (p > 0.485). A potential relationship between body size and OM was also tested: these correlations were also not significant (p > 0.179). A positive correlation was found between total dissolved solids (TDS) and body size of adults and copepodites (r > 0.787, p < 0.020) whereas no correlation was found with naupliar body sizes (p > 0.153).

Females were larger than males in both C5 and Adult Stages and their sizes did not change in a similar way throughout the study period (Fig. 2; $F_{47,1414}$ = 203.3575, p < 0.001). There was a significant interaction between sampling date, stage and sex (p = 0.0054). In the case of females, the differences in size between the adult and C5 Stage were higher than in the case of males.

Biomass

Naupliar and earlier copepodites (Stages C1 and C2) showed higher levels of biomass during the second half of the study period, whereas the later copepodite stages showed greater biomass in the first half (Fig. 4). Biomass of adults was in general similar throughout the whole study period except for some outlying peaks (Fig. 5). Total biomass was

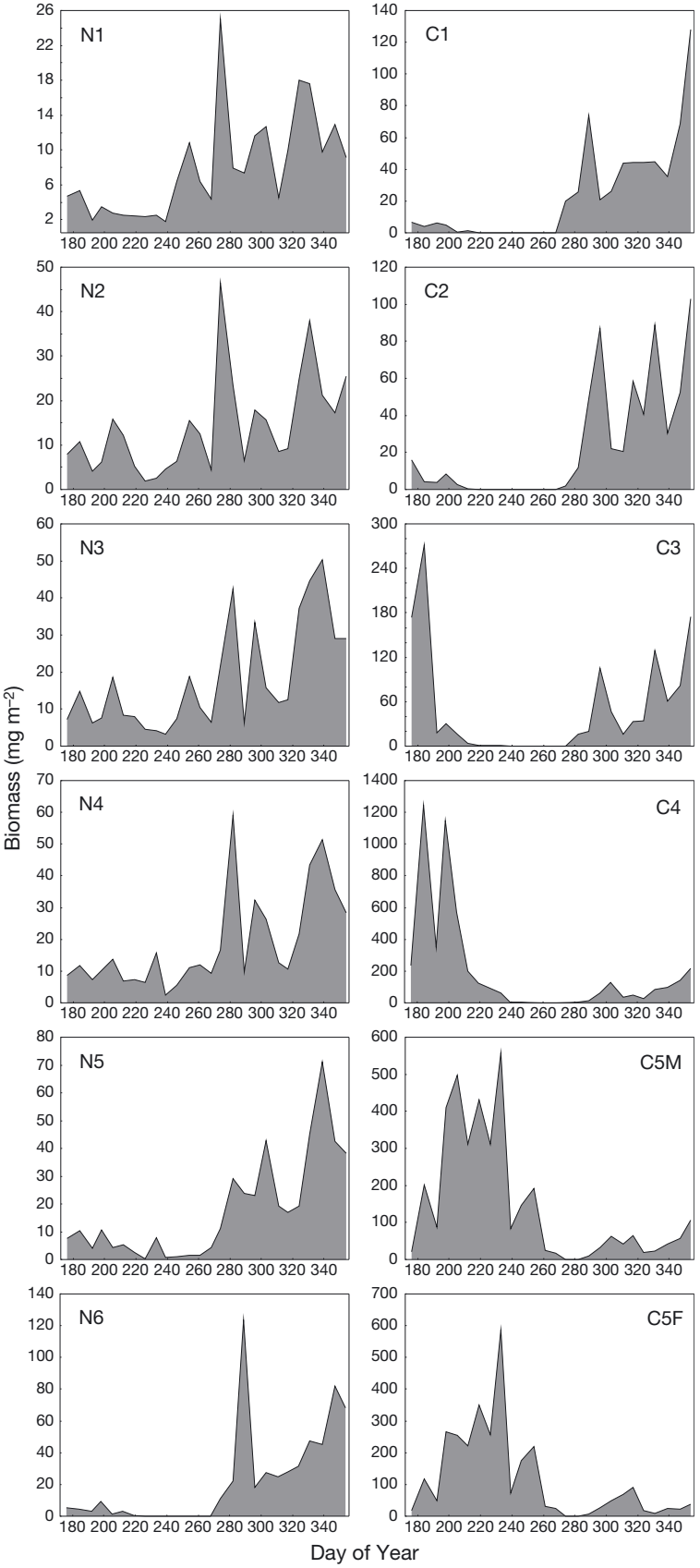

Fig. 4. *Arctodiaptomus salinus*. Seasonal biomass variation of the naupliar (N1 to N6) and copepodite (C1 to C5) Stages

15.42, 4.25 and 6.48 dw g m^{-2} during Periods H, M and L, respectively.

During Period H the later copepodite stages and adults represented >90% of the total biomass (Fig. 6). During the remaining months, naupliar and first copepodites (Stages C1 and C2) increased their contribution to the total biomass, and the Adult Stages were the ones that contributed most (Fig. 6).

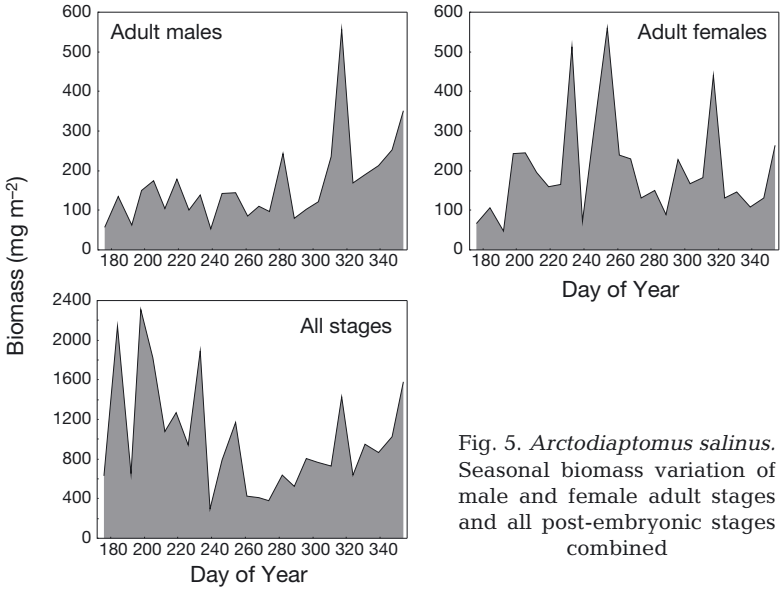

Fig. 5. *Arctodiaptomus salinus.* Seasonal biomass variation of male and female adult stages and all post-embryonic stages combined

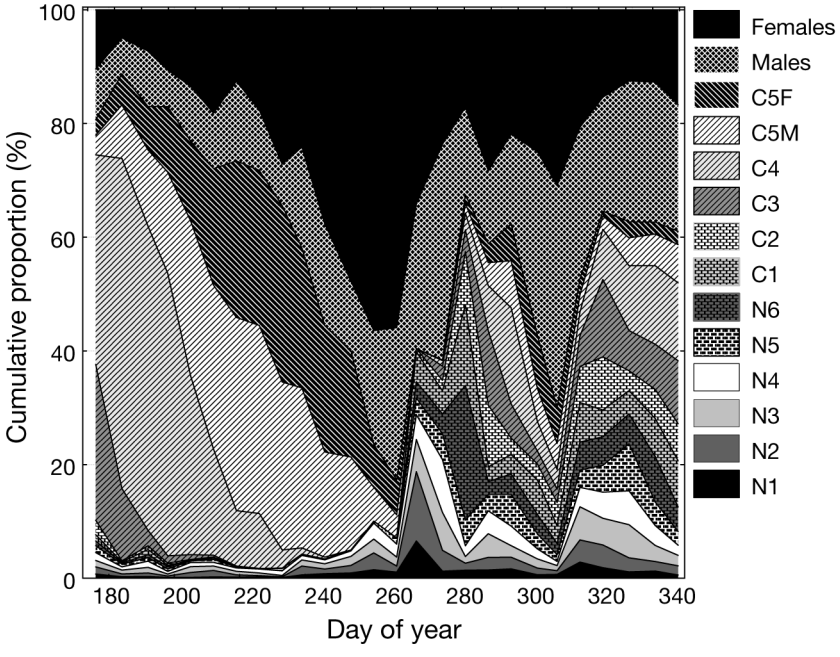

Fig. 6. *Arctodiaptomus salinus.* Relative contribution (%) of the different life stages to the total biomass (mg m^{-2}) throughout the study period

Secondary production

In Method A, MR_i is considered to be equivalent to the inverse of the duration of the Stage *i*, which is calculated as the difference between the development time of the Stage *i*+1 and the development time of the Stage *i*. Consequently, in order to know the development time of a given stage at any temperature, Bělehrádek functions were estimated for each stage (Table 3).

Method A computed higher values than Method B in general (Fig. 7). Differences were especially marked during Period H, where the production estimated by Method A was as much as 72 times larger than that estimated by Method B. In contrast, for the Periods L and M the production estimated by both methods was more similar (Fig. 7).

Mean total production (i.e. larval, juvenile and female reproductive production) estimated by Method A was 119.1, 33.7 and 24 mg m^{-2} day^{-1} for Periods H, M and L, respectively. Mean total production estimated by Method B was 7.6, 22.3 and 23.3 mg m^{-2} day^{-1} for Periods H, M and L, respectively.

DISCUSSION

Seasonal variation in body size

During the study period the body size of all the stages of *Arctodiaptomus salinus* decreased when temperature increased, and females were significantly larger than males. These patterns have been commonly observed among copepod species: for example *Pseudodiaptomus marinus* (Liang & Uye 1997), *Acartia clausi* (Leandro et al. 2006a) and *Acartia tonsa* (Leandro et al. 2006b). It is striking that this relationship is linear in all stages of *A. salinus* except in Stages C4 and C5. A plausible explanation might be that body size did not change over the dormant period of these stages (several weeks duration) (Jiménez-Melero et al. 2013), while the temperature did. The negative correlation of body size with tem-

Table 3. *Arctodiaptomus salinus.* Parameters of the Bělehrádek function describing the relationship between temperature (T) and development time (D) or median development time (MDT). T_0 (biological zero) places the curve on the arbitrary Celsius scale and S is a constant determining the proportional response on the time or rate scale. $R^2 > 0.96$ in all the stages

	Stage	S	T_0
$D = S \times (T–T_0)^{-1.78}$	N2	284.77	–6.01
	N3	622.04	–5.56
	N4	1034.61	–5.86
	N5	1444.70	–5.65
	N6	1902.36	–5.08
$MDT = S \times (T–T_0)^{-1.78}$	N4–N6	1 048.08	–6.00
	C1	2 439.77	–4.60
	C2	4 459.39	–7.59
	C3	5 901.77	–7.45
	C4	6 448.83	–5.42
	C5	7 196.26	–4.60
	Male	8 920.58	–5.15
	Female	8 616.226	–4.78

perature might have a physiological explanation, i.e. in the majority of ectotherm species, an increased temperature increases rate of growth and differentiation and thereby reduces the size at a given stage due to the imbalance between anabolic and catabolic reactions (Ray 1960, Leandro et al. 2006a). Hart (1990) suggested that males are smaller than females because they tend to develop faster in order to increase the probability of mating with receptive females. However, only at low temperatures (i.e. 10°C) did *A. salinus* males reach adulthood before females, whereas at 20 and 25°C both sexes reached adulthood at the same time (Jiménez-Melero et al. 2007). Leandro et al. (2006b) suggested that constraints on the minimum size of females may be imposed by the selective advantage of producing large numbers of eggs, as production increases with body size.

In addition to temperature, the body size of adult copepods can be determined by other environmental variables, such as available food, salinity or predation (see Uriarte & Villate 2006 and references therein). For example, the body size of *Arctodiaptomus salinus* adults showed a positive relationship with salinity. This pattern was also observed by Uriarte & Villate (2006) in *Acartia clausi* from different estuaries. These authors emphasized the importance of salinity in fluctuating environments where copepod viability requires both behavioural and physiological adaptations to shifting salinity (Fiksen & Giske 1995, Uriarte & Villate 2006). Smaller sizes at low salinities may be a physiological and ecological advantage, since the necessary extra energy for the osmorregulation is balanced by energy saving as consequence of low growth rate and low oxygen consumption (Miliou 1996, Uriarte & Villate 2006). In terms of available food, *A. salinus* size did not show any relationship with chl *a* and OM. This lack of relationship has also been observed in other studies (Leborgne et al. 1985, Hopcroft & Roff 1990, Uriarte & Villate 2006). Traditionally, *A. salinus* was considered to be detritivorous and herbivorous; however, Lapesa et al. (2004) found that it is also an active predator. Consequently chl *a* and OM may not be the best parameters to measure food availability for this species.

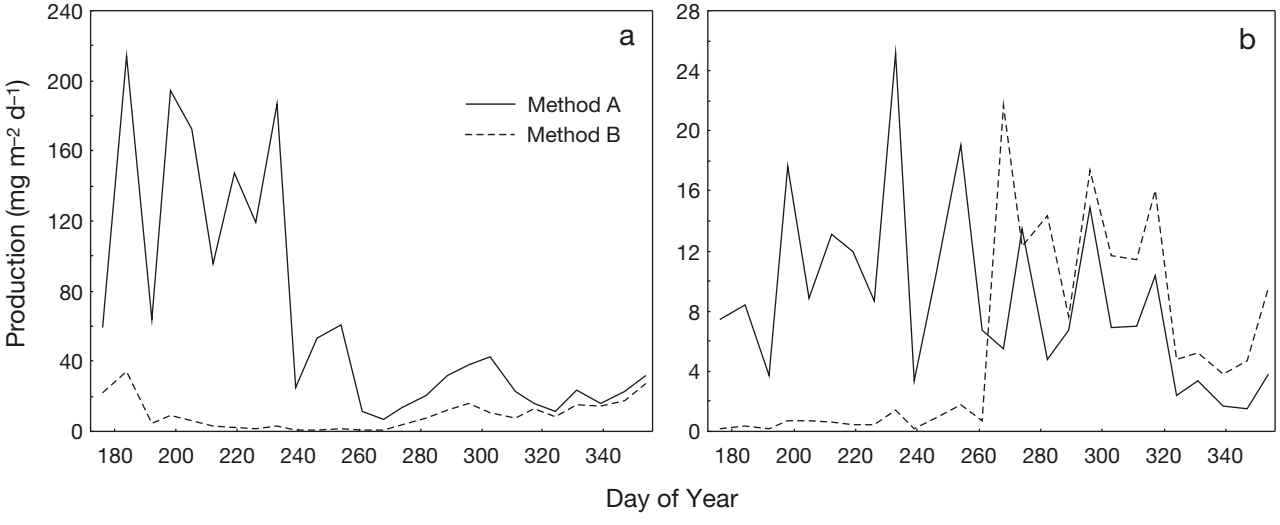

Fig. 7. *Arctodiaptomus salinus.* Production of (a) naupliar and copepodite Stages and (b) female reproductive production estimated by 2 different methods, Method A and Method B

Seasonal variation in biomass

Standing stock of *Arctodiaptomus salinus* ranged from 300 to 2308 mg m^{-2} and averaged 1006 mg m^{-2} ± 108 (mean ± SE), which are the same orders of magnitude or even higher than those reported in tropical and subtropical epicontinental copepods (Grass & Saint-Jean 1983, Mavuti 1994, Irvine & Waya 1999). Detailed standing stock data, including the different stages of development, are not common (Melão & Rocha 2004). However, in our study we document the contribution of every stage to the overall standing stock (Fig. 6). In general, the adult stage contributed the most to the total biomass. In contrast, the non-adult stages showed marked seasonal variability. In the period of high temperatures, the later copepodite stages were, along with the adults, those that most contributed to the total biomass, and the contribution of the earlier copepodite and naupliar stages were lower than 10%. Jiménez-Melero et al. (2013) suggested that this population over-summers by lying dormant during C4 and C5 Stages. Therefore, it is expected that the contribution of these stages to the overall biomass is important during this period. In the following months the differences between stages were not so marked, although the contribution to the total standing stock increased slightly with age (except for Stage C5). Similar to *A. salinus*, an 'active diapause' has been also observed in the egg-carrying copepod *Eudiaptomus graciloides,* which showed a summer delay in the development of the C4 and C5 Stages (Pasternak & Arashkevich 1999) and adult diapause in winter (Zeller et al. 2004).

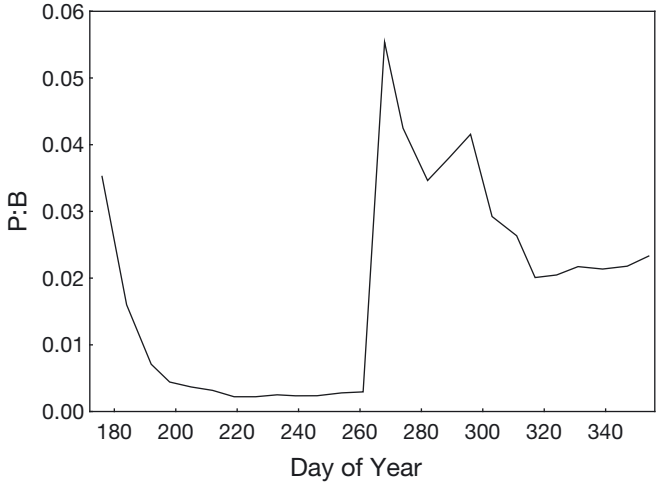

Fig. 8. *Arctodiaptomus salinus.* Seasonal variation of the production to biomass ratio P:B (production values estimated by Method B)

Despite the high production and biomass registered, the productivity and turnover rate was very low: P:B ratios (with production values from Method B) ranged from 0.002 to 0.055 (Fig. 8). These ratios showed no relationship to the temperature registered in the middle of the water column, whereas a polynomial convex relationship was found with the surface temperature (R^2 = 0.406, p = 0.001). Interestingly, the lowest P:B values were registered in the period of high temperatures, and the highest P:B values in the period with moderate temperatures. A strong and consistent correlation between water temperature and P:B index has been observed in previous studies (e.g. Shuter & Ing 1997). However, in these studies, this relationship was positive and linear whereas in this study this relation is non-linear. The low P:B observed at high temperatures might be due to increases in salinity with temperature because of evaporation. However, no relationship was found between P:B and salinity. Nevertheless, since salinity tolerance decreases when temperature increases (Kimmel & Bradley 2001, Hall & Burns 2002) a synergic effect might explain this result. P:B index also showed a positive significant relationship with the oxygen concentration (p = 0.007) although the explained variance was very low (R^2 = 0.233). However, no relationship was found with the remainder of the environmental variables tested.

The observed P:B ratios were very low compared with those of copepods from tropical and subtropical regions (see Grass & Saint-Jean 1983, Zoppi de Roa et al. 1998, Irvine & Waya 1999, Ara 2004, McClatchie et al. 2004, Melão & Rocha 2004) which, like Laguna Honda, experience high annual irradiance and water temperatures. On the other hand, these ratios were similar to (Shuter & Ing 1997) or lower than (e.g. Hay 1995) those recorded in many temperate regions. According to the observed P:B ratios, the total biomass of *Arctodiaptomus salinus* population in Laguna Honda would be replaced and renewed completely in 299 ± 145, 28 ± 7 and 45 ± 2 days (mean ± SD) during the Periods H, M and L, respectively. This is probably a reflection of the harsh environmental conditions during Period H inhibiting or stopping *A. salinus* production, resulting in the copepod spending summer in a dormant state. The low productivity in the following periods suggests, moreover, that this population is food limited. These results concur with the low clutch sizes observed over the study period (Jiménez-Melero et al. 2013) which were much lower that the clutch sizes observed in the laboratory under ad libitum conditions (Jiménez-Melero et al. 2012).

Seasonal secondary production: comparison of both methods

Hitherto there has been no universally adopted method for measuring secondary production. Several approaches have been applied (e.g. Hynes & Coleman 1968, Hamilton & Hynes 1969, Waters 1977, Rigler & Downing 1984, Kimmerer 1987, Roff et al. 1994, Poulet et al. 1995, Guerrero & Rodríguez 1997) but none is practical nor entirely satisfactory, and each leads to different results. In this study, the 2 methods differed both in absolute values and general trends. Consequently, the final conclusions could be completely different depending on the chosen method. For example, according to Method A, the most productive period is that of high temperatures (Period H) whereas Method B gave contrasting results. So, which is the more accurate method?

In Method A, development times were assumed to be dependent only on temperature. This assumption may tend to overestimate secondary production since factors other than temperature might have influenced development rates (Rey-Rassat et al. 2004). Moreover, Method A assumes that moulting rates are equivalent to the inverse of stage durations, which only happens when there is zero mortality, the population is in steady-state and there is no dormancy (Hirst et al. 2005). The stage durations used in this method were estimated as the moment in which surviving individuals, which were reared separately in the lab, moulted to the next stage (Jiménez-Melero et al. 2007). That is, dead individuals were not included in the estimation. Consequently, the moult rates used in Method A are probably greater than the moult rates occurring in the field where mortality is not zero. In this sense, Bi et al. (2011a) found that estimated development times are biased if based only on survivors. Individual variability on development can be also another error source when this method is applied (Bi et al. 2011a), although in this study individual variability was taken into account when development times were estimated (Jiménez-Melero et al. 2007).

On the other hand, dormancy in latter copepodite stages was observed in the field during Period H (Jiménez-Melero et al. 2013); therefore, moult rates with Method A are over-estimated again. Furthermore, it is noted that the population was not in a steady-state during this period, but rather it decreased (λ = 0.78) (Jiménez-Melero et al. 2013). Hence, we can conclude that, at least during Period H, secondary production is over-estimated when Method A is used: the production estimates are unrealistic since they are markedly higher than the copepod production rates recorded in tropical and subtropical regions (see Grass & Saint-Jean 1983, Mavuti 1994, Irvine & Waya 1999, Melão & Rocha 2004) — although these differences might also be due to the fact that these authors used other methods. In addition, Method A assumes that the interclutch periods are constant; however, recent studies have shown that this increases when females age (e.g. Devreker et al. 2009). Nevertheless, in the case of this *Arctodiaptomus salinus* population, no relationship between interclutch period and age, nor between clutch size and age, has been observed (Jiménez-Melero et al. 2012). Method A presents, moreover, other disadvantages as clearly shown by Hirst et al. (2005): besides the assumptions reported above, it only works when the durations of the Stages i and $i + 1$ are equal and the growth rates of both stages are also equal (which does not occur in *A. salinus*). In contrast, Method B was implemented with moult and recruitment rates estimated from field data and, therefore, it takes into account mortality, population growth rate, dormancy and other factors. However, it should be noted that not all are advantages in this method. Sampling errors in the time series data remains a major challenge for inverse algorithm, such as quadratic programming (Bi et al. 2011b). In some cases, the algorithm could not converge, requiring a more robust algorithm such as sequential quadratic programming (Bi et al. 2011b).

The importance of stage-specific mortality when studying or modeling the demography of copepods has been widely reported in the literature (e.g. Ohman & Wood 1995, Souissi & Ban 2001, Eiane & Ohman 2004, Bi et al. 2011a, 2011b) and the uncertainty inherent in estimating mortality in the field is one of the limitations in all modeling approaches. Due to the difficulties of estimating mortality rates from field data, most studies that aim to understand production in pelagic ecosystems have focused on the processes of recruitment by means of sophisticated models — but use very simple assumptions about loss terms such as mortality (Eiane & Ohman, 2004). On the other hand, the importance of population growth rate and dormancy when secondary production is being estimated has not been as widely reported in the literature as mortality (e.g. Hirst et al. 2005, Yebra et al. 2006). However, our results show that these factors are very important for an accurate estimation of secondary production. Indeed, outcomes of Methods A and B were very different in the Period H, when dormant stages were present and when the population was far from a steady-state (λ =

0.784). In contrast, the estimates of both models differed less when population growth rates were equal to 0.921 (Period M) and 1.054 (Period L) and when there were no dormant stages (Jiménez-Melero et al. 2013). Hence, as the population moved closer to a steady state, the differences between the methods became less pronounced.

In summary, since most populations in nature are not in a steady state, mortality is not zero, and diapausing stages are sometimes present in the population, secondary production should be estimated from methods such as those suggested by Bi et al. (2011a) or Jiménez-Melero et al. (2013). These methods use accurate demographic parameters previously obtained in the field, and not from laboratory observations. Our results show that dormancy and population growth rates that are not equal to 1 may be sources of error as important as mortality rates.

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