

Effects of temperature and food concentration on the survival, development and growth rates of naupliar stages of *Oithona davisae* (Copepoda, Cyclopoida)

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ABSTRACT: *Oithona* spp. are probably the most abundant and ubiquitous copepods in the world's oceans. However, knowledge of their development and growth rates is scarce compared to that of calanoid copepods. In the present laboratory study, we determined the survival, development and growth rates of the naupliar stages of *Oithona davisae* under different temperature regimes and food concentrations. Naupliar survival was reduced to approximately 60% at the lowest food concentration tested ($11 \mu\text{g C l}^{-1}$ after 7 d at 20°C). The development of *O. davisae* nauplii was equiproportional, but not isochronal. Food concentrations required for maximum development and growth rates were 56 and 87 $\mu\text{g C l}^{-1}$, respectively. The Q_{10} values for development and growth depended on the temperature range. *O. davisae* nauplii showed similar developmental times, but lower growth rates and food requirements than values reported in the literature for calanoid copepods. We suggest that these differences may help to explain the ubiquity of *Oithona* spp. in oceanic environments.

KEY WORDS: Nauplii · *Oithona davisae* · Growth · Development · Survival · Food · Temperature

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INTRODUCTION

Copepod nauplii are under-studied components of plankton communities, even though they are the most abundant metazoans on the planet (Björnberg 1986, Fryer 1986) and the main prey for many fish larvae of commercially important species (Last 1980). The lack of information about naupliar ecology is partially because they have been under-sampled by conventional methods, such as plankton nets of 200 μm mesh (Alcaraz 1977, Calbet et al. 2001, Gallienne & Robins 2001). With the use of appropriately sized plankton nets, nauplii have frequently been found to outnumber late copepodites and adults by several orders of magnitude (Calbet et al. 2001, Turner 2004). They can also sometimes represent a comparable or higher fraction of copepod biomass than older life stages (Castellani et al. 2007).

Knowledge of copepod life history, such as larval survival, development and growth rates, under different environmental conditions is essential to comprehending their population dynamics. Many field and

laboratory studies have shown that water temperature and food concentration are the most important environmental factors influencing development, growth and survival of copepods (see reviews by Huntley & Boyd 1984, Huntley & Lopez 1992, Hirst & Lampitt 1998, Hirst & Kiørboe 2002). However, most studies have focused on adults or late copepodites (Hart 1990, Hirst & Bunker 2003), while naupliar life stages have received less attention. Therefore, information about copepod naupliar ecophysiology is crucial in order to gain a better understanding of the role of zooplankton in marine biogenic fluxes. From an economic perspective, copepod nauplii are preferred and nutritious food sources for many farm-raised marine fish and shrimp larvae (Hernández-Molejón & Álvarez-Lajonchère 2003 and references therein). Therefore, knowledge about the food requirements and experimental conditions for optimal growth and production of nauplii in the laboratory may be useful for aquaculture operations.

Among marine planktonic copepods, the genus *Oithona* (Cyclopoida) is probably the most abundant

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and ubiquitous copepod in the world's oceans (Gallienne & Robins 2001). Nevertheless, knowledge about the biology and ecology of these small copepods is limited compared to the vast body of research devoted to larger calanoid copepods (Paffenhöfer 1993, Turner 2004). Information is available on *Oithona* spp. development and fecundity (Sabatini & Kiørboe 1994, Uye & Sano 1995, Peterson 2001, Castellani et al. 2005a). However, studies are scarce on growth rates of *Oithona* spp. nauplii as a function of environmental variables, such as food concentration and temperature (Sabatini & Kiørboe 1994, Hopcroft & Roff 1998). To partially fill this knowledge gap, we have examined the effects of temperature and food concentration on survival, development and growth rates of *Oithona davisae* nauplii in the laboratory. This species inhabits eutrophic embayments and may occasionally dominate the copepod community (Uye & Sano 1995). It is indigenous to western Pacific, coastal areas, but is also an invasive species along the United States west coast (Ferrari & Orsi 1984), southern Chilean coast (Hirakawa 1988) and the Spanish Mediterranean (Saiz et al. 2003).

MATERIALS AND METHODS

Experimental organisms. *Oithona davisae* specimens came from a continuous culture maintained in our laboratory since October 2000 (Saiz et al. 2003). Specifically, specimens were grown in 20 l methacrylate tanks at $20 \pm 1^\circ\text{C}$ in a room maintained at constant temperature and under a 12 h light:12 h dark cycle. Copepod cultures were fed ad libitum a suspension of the heterotrophic dinoflagellate *Oxyrrhis marina* (equivalent spherical diameter [ESD] = 15 μm). *O. marina* were fed the cryptophyte *Rhodomonas salina* (ESD = 8 μm). Prey sizes were measured by a Coulter Multisizer III particle counter (Beckman Coulter).

To obtain cohorts of nauplii, we removed adults (including egg-bearing females) from the stock culture with a 132 μm sieve and placed them in a new tank where they were fed *Oxyrrhis marina* ad libitum (i.e. >3000 cells ml^{-1} , equivalent to >660 $\mu\text{g C l}^{-1}$). Adults were removed with a 100 μm sieve after 20 h, and the hatched nauplii were transferred to a new tank. To isolate the dislodged egg sacs, we allowed them to settle for 2 h before siphoning the nauplii into new tanks.

Experimental design and general procedures. We examined the survival, development and growth of *Oithona davisae* naupliar life stages as they relate to food concentrations (i.e. food-effects experiment). A cohort of nauplii was split into aliquots of about 4000 nauplii each that were placed into 10 l methacrylate tanks containing *Oxyrrhis marina* suspensions at different concentrations (50, 200, 400, 600 and 1200 cells

ml^{-1} , equivalent to 11, 44, 88, 132 and 265 $\mu\text{g C l}^{-1}$, respectively). The *O. marina* volume was converted to C content using a conversion factor of 0.123 $\mu\text{g C } \mu\text{m}^{-3}$ provided by Pelegri et al. (1999). The *O. marina* cultures used in our experiments were not fed the day before use, to ensure that the dinoflagellate depleted all the *Rhodomonas salina* and that only *O. marina* was offered as prey. The absence of *R. salina* in stock bottles was verified with a Coulter Multisizer particle counter. Nauplii were incubated for 7 d at $20 \pm 1^\circ\text{C}$ in a temperature-controlled room under a 12 h light:12 h dark cycle. Time was measured relative to the starting time of incubations of egg-bearing females.

Food concentrations were checked daily using a Coulter Multisizer III particle counter. Variations in food concentrations between daily adjustments were frequently <20% and never exceeded 40% of the corresponding food level. Each experimental container was sampled every 24 h by filtering an aliquot of water through a 32 μm sieve. This isolated at least 200 individuals for subsequent counting, measuring and staging. Naupliar samples were preserved with Lugol's solution. The original water volume in the experimental containers was kept constant by daily adjustments with either fresh *Oxyrrhis marina* from stock cultures or alternatively by adding filtered (0.2 μm) seawater.

A second experiment was conducted to examine the influence of temperature on survival, development and growth of *Oithona davisae* naupliar stages (i.e. temperature-effects experiment). Five temperatures were tested (12, 16, 20, 24 and 28°C) under satiating food concentrations (>2000 cells ml^{-1}). Approximately 8000 nauplii from each temperature tested were placed in 2 l Pyrex glass bottles. These individuals were fed *Oxyrrhis marina* for 7 d under a 12 h light:12 h dark cycle. Temperatures were maintained at $\pm 0.2^\circ\text{C}$ of the desired temperature using water-baths controlled by thermoregulators. Daily food adjustments were made to maintain food satiation during the experiment. All other procedures were the same as those described for the food-effects experiment.

Body length–weight relationships. To estimate weight-specific growth rates (see below), we determined the body length–weight relationships of *Oithona davisae* nauplii and copepodites. Samples from naupliar cohorts were taken over the course of their development. These samples were concentrated using 37 and 60 μm sieves for nauplii and copepodites, respectively, and rinsed thoroughly in autoclaved and filtered (0.2 μm) seawater. Three aliquots containing 1000 individuals each were filtered onto pre-incinerated (450°C , 6 h) glass-fibre filters (GF/A grade), after which the filters were dried (60°C , 24 h) and stored in a vacuum desiccator (with silica gel) for further analysis of organic C and N content. Three additional ali-

quots of ~100 individuals per replicate) were fixed in a 4% borax-buffered formaldehyde solution for the counting of larvae and length determinations. The C and N content of the larvae were determined by a Perkin-Elmer 2400 CHN Elemental Analyzer. Total larvae per aliquot were counted with an inverted microscope (40× magnification). Body sizes (L , μm) of *O. davisae* larvae (copepodites: prosome length; nauplii: total length) were measured by capturing digital pictures of at least 50 individuals under a microscope (100× magnification) and using ImageJ software for quantitative analysis. Relationships between body weight (measured as C and N mass) and body size for both nauplii and copepodites were calculated by regression analysis.

Estimates of survival, development and growth rates. Larval survival (S) in each incubation container was estimated daily by subsampling as described above and applying the following calculation:

$$S_x (\%) = [(N_x \times V_{\text{tank}} / V_{\text{aliquot}} + N_R) / N_i] \times 100 \quad (1)$$

where N_x is the current number of live larvae estimated from the aliquot at Day x , N_R is the number of larvae removed on previous days, N_i is the number of initial larvae and V_{tank} and V_{aliquot} are the tank and aliquot volume, respectively.

Samples were counted using an inverted microscope at 40× magnification, and the developmental stages of at least 40 individuals per incubation container were determined with microscopy at 100× magnification according to Uchima (1979). Stage-specific median development time (MDT) and stage duration (SD) were calculated from observed changes in stage frequency over time (see Table 1 for terminology and definitions). The stage-specific MDT was calculated as the time required for 50% of the individual organisms in culture

to moult to the following stage (Landry 1983). The MDT for a given developmental stage was estimated by fitting a sigmoidal Hill function to the cumulative proportion of that stage over time:

$$y = a \times t^b / (\text{MDT}^b + t^b) \quad (2)$$

where y is the cumulative percentage of each stage, t is the time (d) since females were separated, a is the highest y -axis value (i.e. 100% when the entire cohort is in early developmental stages), MDT is the t value that produces 50% of the y -axis value and b is the shape coefficient.

Stage-specific development rates (D , d^{-1}) were calculated as the inverse of the MDT. The stage duration was estimated as the difference in MDT of 2 consecutive developmental stages. The equiproportional rule of copepods (i.e. the duration of a given life-history stage occupies a constant proportion of the total or egg developmental time regardless of temperature; Corkett 1984) was tested considering the proportion of time that each stage occupied with respect to the total naupliar development time (time between egg hatching and moult into the first copepodite stage [CI]).

For specific growth rate determinations, the body lengths of 50 random individuals from each cohort were measured daily, and their C weights were calculated by applying body size to C content relationships. Additionally, we measured 30 individuals per treatment at each developmental stage (from Nauplius Stage I to VI, NI to NVI) to estimate the effects of temperature and food concentration on naupliar body length. In all cases, body length was determined using ImageJ software, as mentioned previously. Weight-specific growth rates (G , d^{-1}) were calculated as the slope of regression lines relating the natural logarithm of C biomass to incubation time.

Table 1. Terminology and units

Symbol	Term	Unit	Explanation
MDT	Median developmental time	d	Time at which 50% of the larvae in the culture has moulted to the following stage
SD	Stage duration	d	Difference in MDT of 2 consecutive stages
D	Developmental rates	d^{-1}	Inverse of MDT
D_{max}	Maximum development rate	d^{-1}	From Ivlev's equation
W	Weight	ng	
L	Length	μm	
G	Specific growth rates	d^{-1}	
G_{max}	Maximum specific growth rates	d^{-1}	From Ivlev's equation
C	Food concentration	$\mu\text{g C l}^{-1}$	
C_D	Satiating food concentration for development	$\mu\text{g C l}^{-1}$	Food concentration required to achieve 95% of D_{max}
C_G	Satiating food concentration for growth	$\mu\text{g C l}^{-1}$	Food concentration required to achieve 95% of G_{max}

Temperature coefficient (Q_{10}) values for the temperature-effects experiment were calculated as:

$$Q_{10} = (M_2/M_1)^{10/(T_2 - T_1)} \quad (3)$$

where M_2 and M_1 are the rates of the studied process at temperatures T_2 and T_1 (°C), respectively.

All statistical analyses and regressions were conducted with SPSS 17.0 software. All curves were fitted by standard least-squares procedures using Sigma plot 9.0 software.

RESULTS

Elemental composition (C, N) of *Oithona davisae* nauplii and copepodites

The relationships between body weight (W , organic C and N) and body length (L , μm) of nauplii and copepodites are shown in Fig. 1A, B. The fitted equations were:

$$W (\text{ng C}) = 0.0021 \times L^{2.14}, r^2 = 0.96 \text{ for nauplii} \quad (4)$$

$$W (\text{ng N}) = 7.47 \times 10^{-6} \times L^{2.92}, r^2 = 0.98 \text{ for nauplii} \quad (5)$$

$$W (\text{ng C}) = 0.0318 \times L^{1.61}, r^2 = 0.94 \text{ for copepodites} \quad (6)$$

$$W (\text{ng N}) = 0.0091 \times L^{1.58}, r^2 = 0.99 \text{ for copepodites} \quad (7)$$

The C:N ratio decreased during larval development of *Oithona davisae* (Fig. 1C). Nauplii showed gradual decreases from 8.4 (NI to NII) to 5.4 (NV to NVI) in their C:N ratios with increasing age/size. In contrast, C:N ratios in copepodites varied only slightly between developmental stages, with an average value of 4.12. The relationship between the C:N ratio and body length (L , μm) of nauplii *O. davisae* is described by the equation (Fig. 1C):

$$\text{C:N} = 239 \times (1 + L)^{-0.74}, r^2 = 0.96 \quad (8)$$

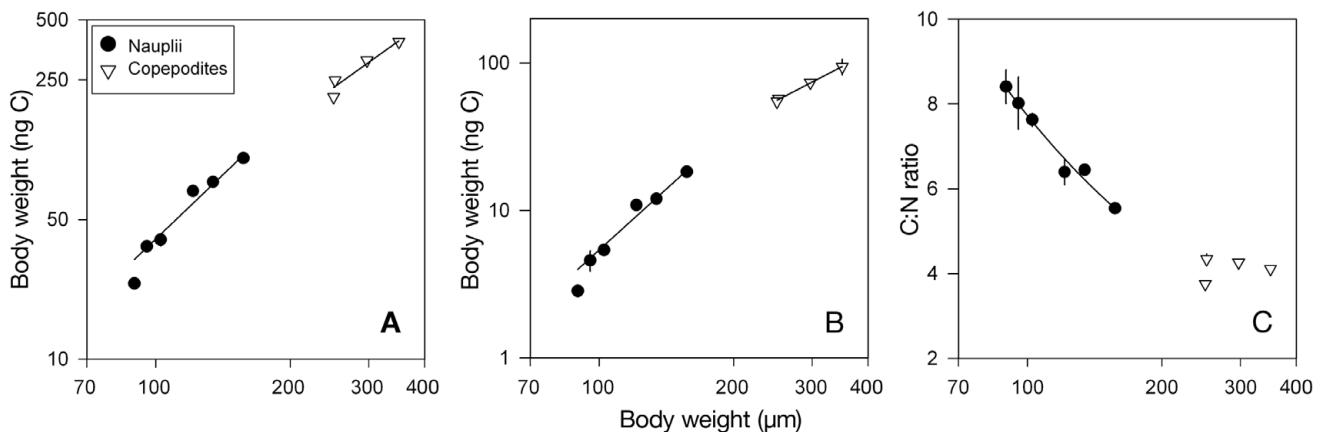


Fig. 1. *Oithona davisae*. Relationships between body length (total length for nauplii and prosome for copepodites) and (A) body carbon weight, (B) nitrogen weight and (C) the ratio of carbon to nitrogen (C:N) of the developmental stages. Error bars represent \pm SE

Survival

Naupliar survival was high (>91%) at all food levels, except at the lowest food concentration ($11 \mu\text{g l}^{-1}$), where survivorship declined to 58% by the end of the incubation (Fig. 2A). Regarding the temperature-effects experiment, naupliar survival was also high (85 to 93%) at all temperatures and decreased only slightly with rising temperature (Fig. 2B). In both experiments, differences between treatments started to be evident after the fifth incubation day (Fig. 2). We observed a slight increase in mortality in treatments where nauplii underwent metamorphosis to the CI developmental stage (Fig. 2).

Development rates

The cumulative abundance percentage of each naupliar stage over time at the different temperatures and food conditions is presented in Fig. 3. In all cases, these data fitted the Hill functions well ($p < 0.05$).

Effects of food concentration. The cumulative percentage fits among the low-food treatments covered a wider range than the higher food concentrations (Fig. 3, right panels) because of the slower development at these food levels. Cohorts reached CI within the 7 d incubation time at all food concentrations except in the lowest. MDT for each naupliar stage decreased with increasing food concentrations, leading to a decrease in the developmental stage duration (Table 2). Naupliar development was not isochronal, because the duration of the late naupliar stage, particularly NVI, was longer than other developmental stages. Naupliar development was nearly equiproportional at high food levels ($\geq 88 \mu\text{g C l}^{-1}$). Development rates (D , d^{-1}) related to food concentration (C , $\mu\text{g C l}^{-1}$) were fitted to the

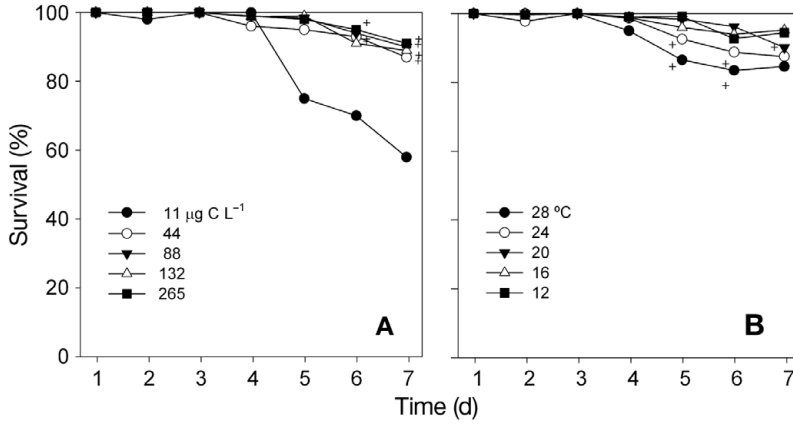


Fig. 2. *Oithona davisae*. Survival rates of early developmental stages reared for 7 d at (A) 5 food concentrations and (B) 5 temperatures. +: cohort was dominated by Naupliar Stage VI (NVI) and Copopodite Stage I (CI) (NVI–CI metamorphosis)

Table 2. *Oithona davisae*. Effect of food concentration on the median development time (MDT, d) and stage duration (SD, d) of early larval stages at 20°C. NII to NVI: Naupliar Stages II to VI; CI: Copepodite Stage I

	Food concentration (µg C l ⁻¹)									
	11		44		88		132		265	
	MDT	SD	MDT	SD	MDT	SD	MDT	SD	MDT	SD
NII	2.54	1.22	1.14	0.98	1.16	0.94	1.16	0.80	1.17	0.84
NIII	3.76	1.54	2.12	0.81	2.09	0.88	1.96	0.97	2.01	0.89
NIV	5.30		2.93	0.94	2.97	0.79	2.94	0.75	2.90	0.85
NV			3.87	1.33	3.76	1.12	3.68	1.08	3.75	0.98
NVI			5.20	1.83	4.89	1.72	4.76	1.62	4.74	1.56
CI			7.03		6.60		6.39		6.30	

Ivlev's equation (Fig. 4A):

$$D = D_{\max}(1 - e^{(-\beta C)}) \quad (9)$$

where D_{\max} is the maximum development rate (d^{-1}) and β is a constant (rate at which development approaches the maximum development rate). The parameters for the fitted Ivlev's function across different stages are presented in Table 3. Food concentrations required to achieve 95% of the maximum development rate (C_D , satiating food concentration) ranged from 40 to 56 $\mu\text{g C l}^{-1}$, depending on the naupliar stage (Table 3).

Effects of temperature. Temperature had a clear effect on development times; MDT and all stage durations decreased with rising temperatures (Fig. 3, Table 4). Cohorts only reached CI within the 7 d incubation time at high temperatures (20 to 28°C). Similar to the food concentration experiments, naupliar development of *Oithona davisae* was equiproportional, but not isochronal. The functional relationships between temperature (T , °C) and MDT (d^{-1}) were well described ($p < 0.05$) by Belehrádek's function (Fig. 4B):

$$\text{MDT} = a(T - \alpha)^{-2.05} \quad (10)$$

where a and α are constants (Corkett et al. 1986). The fitted Belehrádek's function for each naupliar stage and the applied temperature range are shown in Table 5. The equation parameter a increased gradually with the age of developmental stages (Table 5). Across all temperatures tested, Q_{10} values for development ranged from approximately 2.4 for NII and NIII stages (12 to 28°C) to 1.6 for CI stages (20 to 28°C). At temperatures $< 20^\circ\text{C}$, no individuals reached the CI developmental stage. Within stages, Q_{10} values were temperature dependent; for example, the NII produced Q_{10} values of 4.41 at from 12 to 20°C, but 1.19 at from 20 to 28°C. Using a common range of temperature (20 to 28°C) for all stages, Q_{10} values increased from 1.2 for Stages NII and NIII to 1.6 for Stages NIV to CI.

Body length and growth rates

Effects of food concentration. Naupliar body length decreased at the lowest food concentration (ANOVA, $p < 0.01$; Tukey's test, $p < 0.01$), with reductions ranging from 3% in Stage NII to 15% in Stage NV (Fig. 5A).

Growth rates were exponential and consistent across food levels, except at the lowest food concentration (Fig. 6A; ANCOVA, $F = 107.34$, $p < 0.01$). Naupliar specific growth rates (G , d^{-1}) relative to food concentrations (C , $\mu\text{g C l}^{-1}$) followed a saturation curve (Ivlev's equation) expressed by the function (Fig. 7A):

$$G = 0.296(1 - e^{(-0.034C)}), r^2 = 0.97 \quad (11)$$

where 0.296 is the maximum growth rate (d^{-1}) and 0.034 is a constant that indicates the rate at which growth approaches the maximum rate. The satiating food concentration (C_G) at which maximum naupliar growth became limited was 87 $\mu\text{g C l}^{-1}$.

Effects of temperature. Temperature had a significant effect and was inversely correlated to body length (Fig. 5B; ANOVA, $p < 0.05$). In early stages (NII to NIV), body size differences were only significant between the lowest and highest temperatures. For example, the body length for NIII individuals ranged from 114 μm at 12°C to 107 μm at 28°C (Tukey's test, $p < 0.05$), with differences becoming more evident at later stages (NV to NVI) (Fig. 5B).

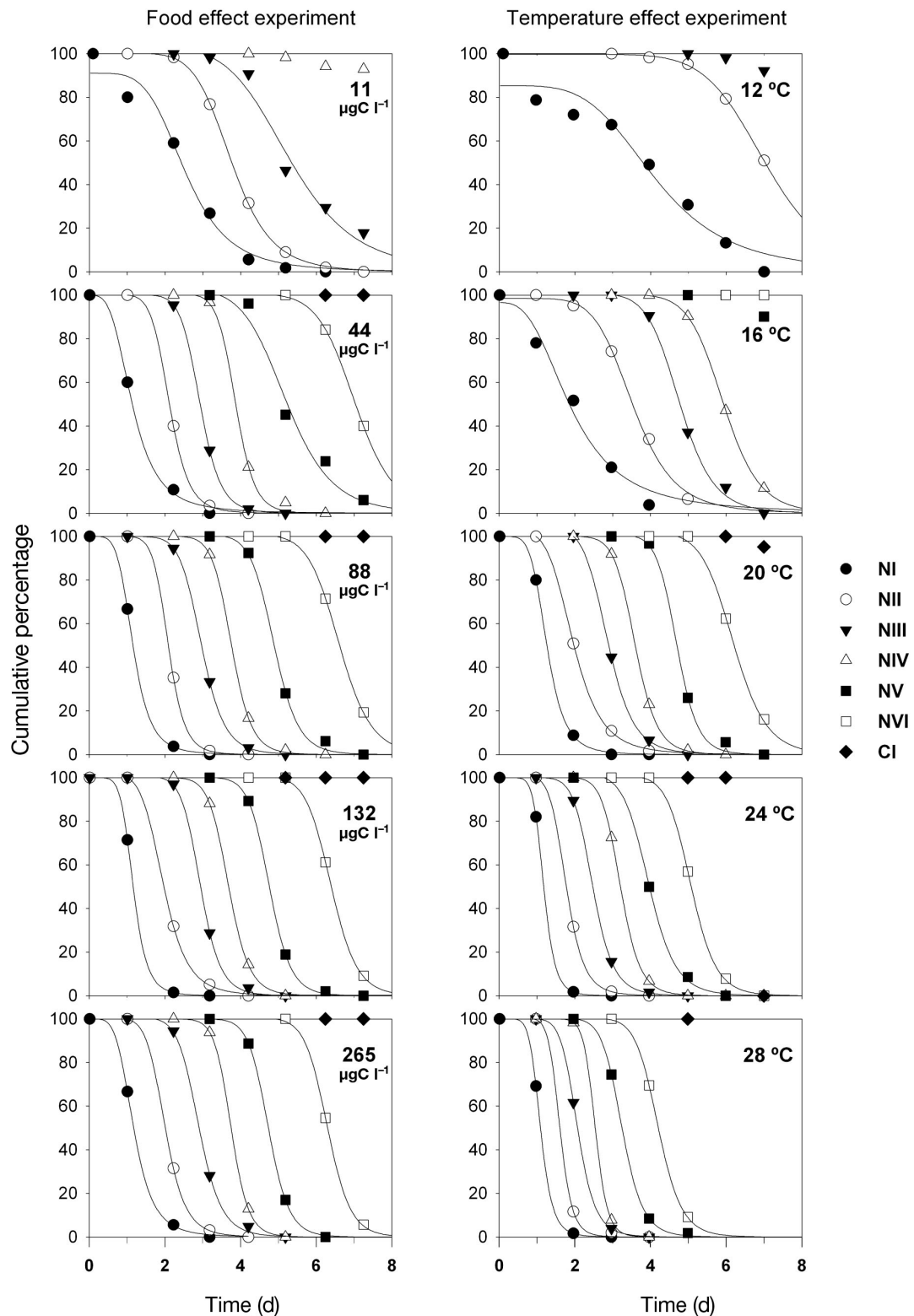


Fig. 3. *Oithona davisae*. Cumulative abundance percentages of all animals that have not yet passed a given stage, plotted against time. Left panels: for food concentration treatments; right panels: for temperature treatments. Successive stages from Naupliar Stage I (NI) to Copepodite Stage I (CI) are indicated by different symbols. Hill functions (Eq. 2) were fitted to the data, including all 100 and 0% values, which for clarity are not shown in the graphs except one, immediately before and after the occurrence of a stage, respectively. Stages older than CI are not shown

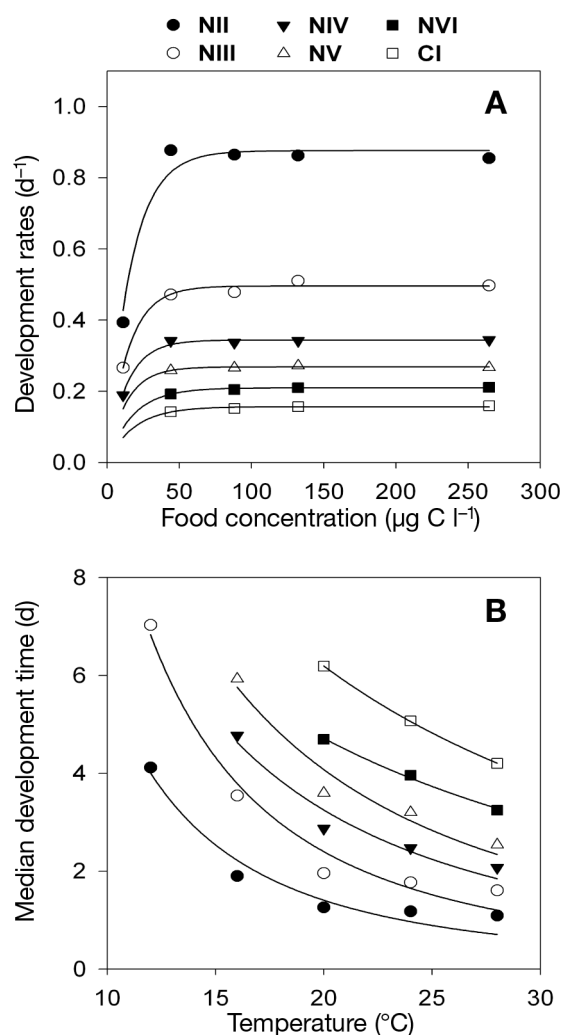


Fig. 4. *Oithona davisae*. (A) Relationships between food concentration and development rates for early larval stages. The fitted curves are described by Ivlev's functions. (B) Relationships between temperature and median development time for early larval stages under satiating food conditions. The fitted curves are described by Belehrádek functions

Growth rates were exponential and dependent on temperature (Fig. 6A; ANCOVA, $F = 13.81$, $p < 0.01$). Relationships between naupliar specific growth rates (G , d⁻¹) and temperatures (T , °C) were established by the model (Fig. 7B):

$$\log G = (0.053 \times T) - 1.721, r^2 = 0.87 \quad (12)$$

Q_{10} values for growth declined with rising temperatures (e.g. at 12 to 24°C $Q_{10} = 4.8$; at 16 to 24°C $Q_{10} = 2.8$; at 20 to 28°C $Q_{10} = 1.6$). The Q_{10} value was 3.6 across the range of temperatures tested in the experiments (12 to 28°C).

Table 3. *Oithona davisae*. Parameters of the Ivlev's equation (Eq. 9) used to describe the relationship between food concentration ($\mu\text{g C l}^{-1}$) and developmental rates (D_{max} and β , d⁻¹) for early developmental stages. S_D ($\mu\text{g C l}^{-1}$): the satiating food concentration for maximum development; r^2 : coefficient of determination; SE: standard error. NII to NVI: Naupliar Stages II to VI; CI: Copepodite Stage I

	D_{max} (\pm SE)	β (\pm SE)	r^2	S_D
NII	0.87 (\pm 0.02)	0.061 (\pm 0.008)	0.96	49
NIII	0.49 (\pm 0.05)	0.070 (\pm 0.005)	0.98	43
NIV	0.34 (\pm 0.04)	0.073 (\pm 0.005)	0.99	41
NV	0.27 (\pm 0.02)	0.074 (\pm 0.008)	0.80	40
NVI	0.21 (\pm 0.02)	0.056 (\pm 0.004)	0.93	53
CI	0.16 (\pm 0.02)	0.053 (\pm 0.005)	0.88	56

DISCUSSION

Elemental composition (C, N)

For ecophysiology studies, such as ours and especially for those examining growth, it is important to express data in biomass-specific units to facilitate comparison across studies. It is also crucial to have concurrent, accurate and reliable estimates of biomass, or at least robust body length–weight relationships, since using literature relationships may produce severe bias. Intra-specific differences, origin and condition of organisms, previous food intake and the method of sample preservation can result in different body length–weight relationships, especially when only longitudinal measurements are considered. For instance, the relationships we measured between body length and C weight for *Oithona davisae* copepodites differed from observations of the same species by Uye & Sano (1998).

The C:N ratios observed in *Oithona davisae* nauplii are consistent with those ratios commonly reported for

Table 4. *Oithona davisae*. Effect of temperature on median development time (MDT, days) and stage duration (SD, d) of early larval stages under satiating food conditions. NII to NVI: Naupliar Stages II to VI; CI: Copepodite Stage I

	Temperature (°C)									
	12		16		20		24		28	
	MDT	SD	MDT	SD	MDT	SD	MDT	SD	MDT	SD
NII	4.12	2.91	1.90	1.64	1.26	0.70	1.18	0.59	1.09	0.51
NIII	7.03		3.54	1.23	1.96	0.91	1.77	0.70	1.60	0.47
NIV			4.77	1.16	2.87	0.73	2.47	0.73	2.07	0.47
NV			5.93		3.60	1.10	3.20	0.76	2.54	0.71
NVI					4.69	1.50	3.96	1.11	3.25	0.96
CI					6.19		5.07		4.20	

Table 5. *Oithona davisae*. Parameters of the Belehrádek function (Eq. 10) used to describe the relationship between median development time (MDT, d) and temperature (T , °C) for early development stages. r^2 : coefficient of determination; SE: standard error; NII to NVI: Naupliar Stages II to VI; CI: Copepodite Stage I

	a (\pm SE)	α (\pm SE)	r^2	Temp. range (°C)
NII	650 (\pm 231)	0.04 (\pm 2.30)	0.94	12–28
NIII	1114 (\pm 230)	0.8 (\pm 1.4)	0.97	12–28
NIV	2423 (\pm 893)	-5.2 (\pm 4.2)	0.94	16–28
NV	3181 (\pm 1156)	-5.8 (\pm 4.3)	0.95	16–28
NVI	9721 (\pm 1446)	-21.4 (\pm 3.2)	0.99	20–28
CI	11049 (\pm 226)	-18.6 (\pm 0.4)	0.99	20–28

marine copepods (~3 to 14; Omori 1969, Postel et al. 2000). Since C:N ratios are related to lipid and protein ratios, the decrease in the C:N ratio observed with *O. davisae* development may be indicative of the gradual decrease in yolk lipids as development proceeds.

Survival

Mortality in early developmental stages strongly affects population dynamics among marine copepods (Peterson & Kimmerer 1994, Plourde et al. 2009). Stage-specific mortality depends on both intrinsic and external factors. Intrinsic factors that may affect early stage survival of copepods include shifts from yolk-related, endogenous foods to exogenous food sources. This food shift may explain the high, early mortality observed

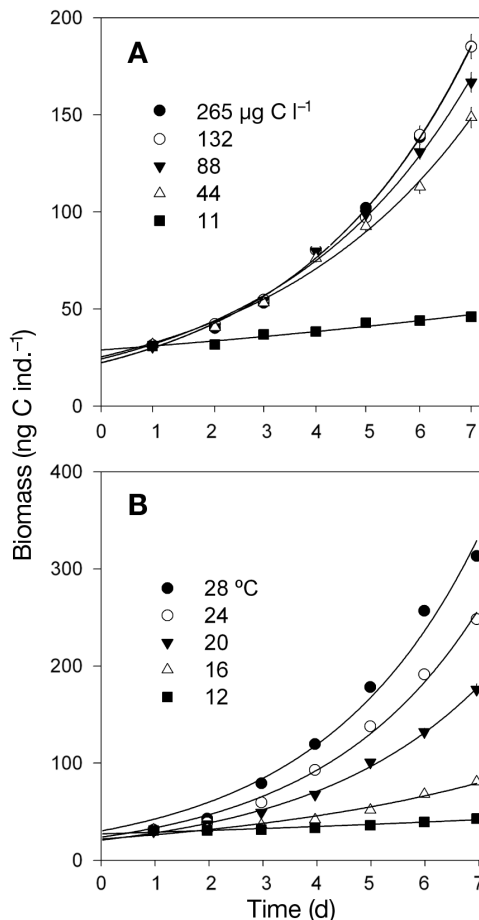


Fig. 6. *Oithona davisae*. Time course of carbon biomass of early larval stages in relation to (A) food concentration ($\mu\text{g C l}^{-1}$) and (B) temperature. Error bars represent \pm SE

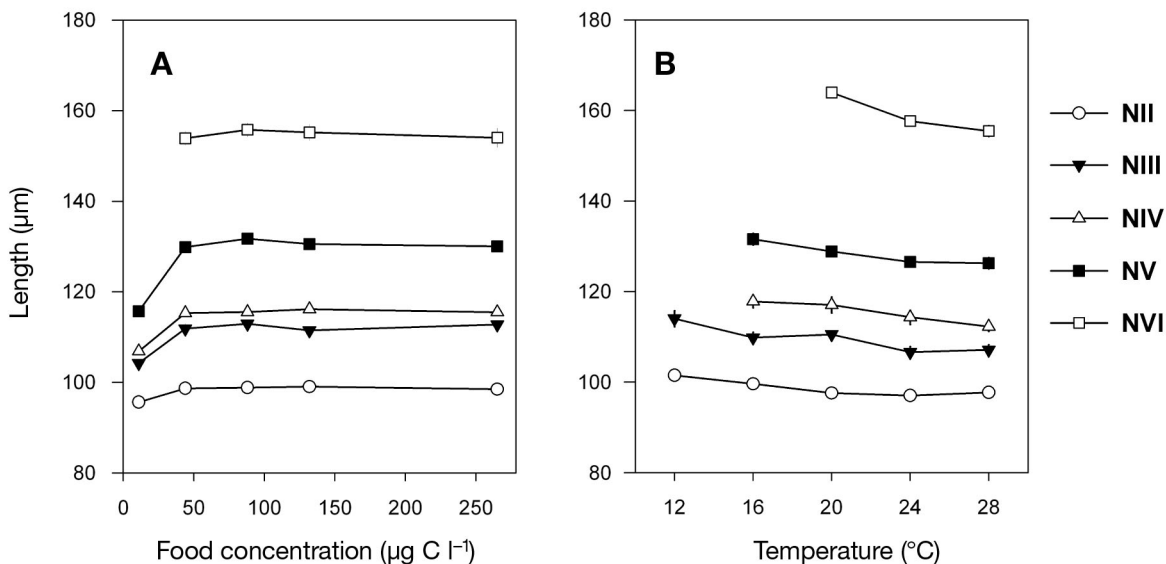


Fig. 5. *Oithona davisae*. (A) Effect of food concentration on length of naupliar stages at 20°C. (B) Effect of temperature on length of naupliar stages under satiating food conditions

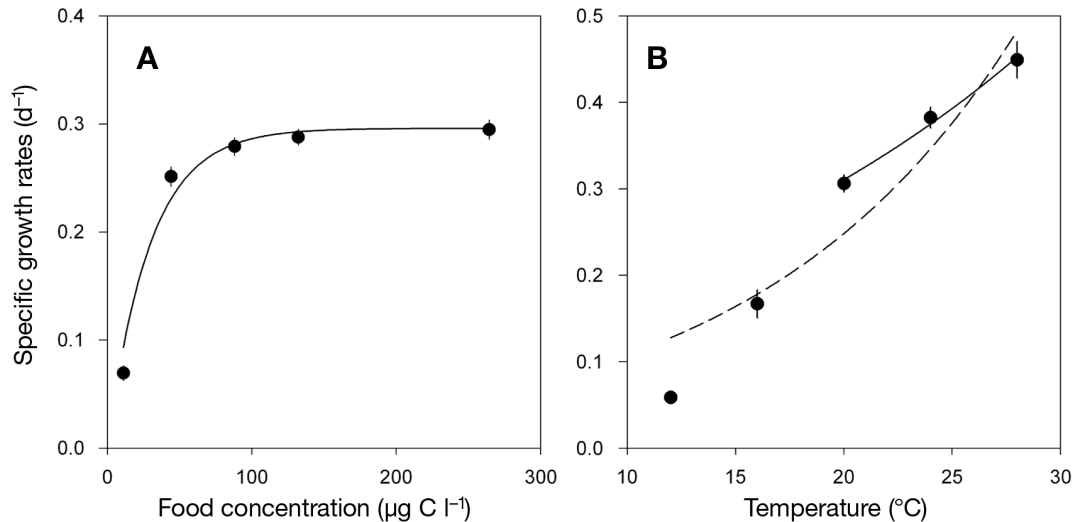


Fig. 7. *Oithona davisae*. (A) Specific growth rates (\pm SE) of naupliar stages as a function of food concentration ($\mu\text{g C l}^{-1}$). Fitted curves correspond to Ivlev's equation (see 'Results'). (B) Specific growth rates (\pm SE) of naupliar stages as a function of temperature. Fitted curves correspond to exponential models. The equations are: $\log G = (0.053 \times T) - 1.721$, $r^2 = 0.99$, for temperatures between 20 and 28°C (continuous line) and $\log G = (0.053 \times T) - 1.721$, $r^2 = 0.87$ (dashed line), for the total range of temperature (12 to 20°C), where G is the specific growth rate (d^{-1}), T is the temperature ($^{\circ}\text{C}$) and r^2 is the correlation coefficient

among some species (Trujillo-Ortiz & Arroyo-Ortega 1991). However, we did not observe this type of early mortality in *Oithona davisae*, which is consistent with observations that *Oithona* spp. nauplii start to feed after hatching (Uchima & Hirano 1986). Another intrinsic factor affecting early mortality relates to the large morphological and physiological changes associated with copepod development, particularly with the metamorphosis from nauplii to copepodite (Epp & Lewis 1980, Ferrari & Dahms 2007). This could be the cause of increased mortality observed in our experiments during *O. davisae* transitions from NVI to CI, as occurs in other copepods (Lonsdale 1981).

Regarding external factors, in addition to predation and disease (virus, bacteria, parasites, etc.), copepod mortality is mainly affected by starvation and temperature. The following conditions can influence these factors: famine duration, lipid reserves, food quality and developmental stage (Paffenhöfer 1971, Calbet & Alcaraz 1997, Ismar et al. 2008). Food concentrations that induce relevant mortality in *Oithona davisae* nauplii ($\sim 11 \mu\text{g C l}^{-1}$) were lower than those commonly reported for calanoid nauplii studied in laboratory settings (~ 36 to $100 \mu\text{g C l}^{-1}$; Paffenhöfer 1971, Berggreen et al. 1988, Cook et al. 2007, Ismar et al. 2008). Moreover, mortality of *O. davisae* nauplii was only significant after 5 d, suggesting that this species can withstand relatively long periods of poor food conditions.

As previously stated, food quality may influence naupliar mortality during development (Paffenhöfer 1971). The prey used in the present study (*Oxyrrhis marina*) are considered a high-quality food for *Oithona davisae*

nauplii due to its morphology (i.e. optimal size; Saiz et al. unpubl. data), biochemical composition (essential lipids; Klein Breteler et al. 1999), motility (Uchima & Hirano 1986) and digestibility (without a theca). Previously reported incidences of 100% mortality of *O. davisae* nauplii at high food concentrations (Uchima & Hirano 1986) are in complete disagreement with our results. The high mortality observed by Uchima & Hirano (1986) was probably a consequence of the poor nutritive quality of the prey used in their experiments (*Dunaliella* spp.; Klein Breteler et al. 1999, Dahl et al. 2009).

We did not observe any temperature-related effects, except for faster development at higher temperatures. This observation suggests an accelerated transition from NVI to CI stages, along with its associated mortality.

Development and growth rates

Post-embryonic development in copepods can follow different patterns. Isochronal development (i.e. constant stage duration across the entire lifespan) has been frequently reported in calanoid copepods (Miller et al. 1977, Klein Breteler et al. 1982) and in the cyclopoid *Oithona similis* (Sabatini & Kiørboe 1994). However, isochronal development was not observed in *O. davisae* nauplii. We noted 2 differences in the duration of naupliar stages relative to other copepods. First, in most calanoid copepods, pre-feeding stages are relatively short, but first-feeding stages (NII or NIII) are longer (Landry 1975, 1983). In contrast, early stages (NII) and late stages (NIV and NV) of *O. davisae* nau-

plii were of similar duration, which is probably because feeding starts just after hatching. Second, *O. davisae* undergo long NVI stages, unlike other copepods in which NVI passes rapidly (Uchima 1979, Peterson 2001). Our results support the rule of equiproportional development (Corkett 1984), as opposed to the isochronal rule, which seems to be a pattern generally found in copepod development (Miller et al. 1977, Hart 1990, Peterson 2001).

As typically occurs in copepods (McLaren 1978), the development time of *Oithona davisae* nauplii decreased with rising temperatures. The naupliar development time estimated by Uye & Sano (1998) based on theoretical assumptions (equiproportional rule) were 2 d longer than those stemming from our experimental results. At similar temperatures and under satiating food conditions, *O. davisae* development time (NI to CI) is comparable to that of other marine cyclopid and calanoid copepods, even at larger sizes (Hart 1990, Paffenhöfer 1993, Sabatini & Kiørboe 1994, Peterson 2001). This is consistent with previous studies (Hart 1990, Sabatini & Kiørboe 1994, Peterson 2001), which concluded that copepod development times in the presence of unlimited food resources were independent of adult body size. Therefore, despite the differences in size between cyclopid and calanoid copepods, generation times and the potential for recruitment might be similar (Peterson 2001). However, *O. davisae* development levels off at food concentrations ($\sim 50 \mu\text{g C l}^{-1}$ at 20°C) lower than those commonly reported for coastal calanoid nauplii ($> 200 \mu\text{g C l}^{-1}$ at 15°C ; Klein Breteler et al. 1982). While further confirmation is needed, this observation suggests a competitive advantage of *O. davisae* over other coastal copepods under low food conditions. Conversely, *O. davisae* showed higher satiating food concentrations for growth than for development, which was consistent with findings for other copepod species (Ban 1994, Campbell et al. 2001). Hence, nauplii could maintain maximum developmental rates at food concentrations that were limiting for somatic growth (i.e. development may be less sensitive than growth to food concentrations). This suggests that development and, consequently, recruitment may be prioritised over somatic growth for some copepod species.

It is difficult to compare our estimated naupliar growth rates with those from the literature, because available data are scarce and mostly examine calanoids (Calbet & Alcaraz 1997, Campbell et al. 2001, Lee et al. 2003, Leandro et al. 2006). In the case of oithonids, our understanding is that naupliar growth rates under saturating food conditions have only been reported for *Oithona similis* examined under laboratory conditions (Sabatini & Kiørboe 1994). These results were similar to our observations, albeit slightly

higher (0.20 d^{-1} at 15°C ; Sabatini & Kiørboe 1994). The smaller size of *Oithona* spp. would lead one to deduce higher weight-specific metabolic rates (Lynch 1977, Ikeda et al. 2001). However, the growth rates of *Oithona* spp. nauplii appear to be lower than those frequently reported for calanoids (0.27 to 0.50 d^{-1} ; Kiørboe & Sabatini 1995, Calbet & Alcaraz 1997, Leandro et al. 2006) and those predicted from global models (Huntley & Lopez 1992, Hirst & Lampitt 1998, Hirst & Bunker 2003).

The influence of temperature (Q_{10}) on growth rates was similar to the pattern mentioned above for naupliar development (NI to CI). Consistent with the Arrhenius equation, the Q_{10} is temperature dependent and decreases with rising temperatures. Therefore, the typical application of uniform values of Q_{10} calculated across different temperature ranges can result in errors in determining temperature effects on physiological rates. It is surprising that the relationship of growth rates to temperature did not follow the exponential model (i.e. Van't Hoff-Arrhenius law). As *Oithona davisae* is a thermophilic species experiencing its highest population densities during warm seasons (Uye & Sano 1995, Nakane et al. 2008), we think that the lower temperatures used in our experiments (12 and 16°C) might be sub-optimal, resulting in deviation from the exponential model. The exponential model seems to fit best when high experimental temperatures are considered (Fig. 7).

Ecological implications

Laboratory experiments under controlled conditions are a fundamental tool for understanding the effects of environmental variables on the distribution and activity of marine zooplankton. Nonetheless, caution is required when extrapolating laboratory results to the field (e.g. bottle effects, crowding and lack of turbulence).

In addition to factors such as predation and salinity, development and growth rates of wild copepods can be affected by both temperature and food availability. Development and growth of marine copepods are frequently food-limited in natural settings (Hirst & Bunker 2003, Saiz & Calbet 2007). The degree of food limitation can be highly variable among groups/species and across life-history stages (Hirst & Bunker 2003, Finlay & Roff 2006). Food concentrations producing satiation in *Oithona davisae* nauplii were lower than in calanoid nauplii studied in laboratories (Klein Breteler et al. 1982, Berggreen et al. 1988, Calbet & Alcaraz 1997, Leandro et al. 2006). Therefore, we expect that *O. davisae* would achieve maximum growth and development rates in nature with less food than calanoid

nauplii. The satiating food concentration for the growth and development of *O. davisae* nauplii is relatively low given the high food concentrations (~ 2 to $50 \mu\text{g}$ chlorophyll $a \text{ l}^{-1}$) of eutrophic coastal habitats (Uye & Sano 1995, Gifford et al. 2007, Nakane et al. 2008). This food concentration is equivalent to 94 to $1410 \mu\text{g C l}^{-1}$, using an average conversion factor of 47 (Riemann et al. 1989). In addition to food quantity, food quality (e.g. size, palatability, motility, nutritional value) should be considered when expressing food limitation in nature. *O. davisae* nauplii and adults only feed on relatively large and motile prey (Uchima & Hirano 1986, Tsuda & Nemoto 1988, Uchima 1988, Broglio et al. 2004, Atienza et al. 2006, Henriksen et al. 2007), which substantially reduces the amount of food available for ingestion. During warm seasons, the biomass of potential prey in some eutrophic waters inhabited by *O. davisae* is frequently close to their critical food concentration for development ($\sim 50 \mu\text{g C l}^{-1}$; Gifford et al. 2007 and $>500 \text{ cells ml}^{-1}$; Nakane et al. 2008). In addition, field naupliar growth rates reported for other *Oithona* species (Hopcroft & Roff 1998) are similar to those reported for *O. davisae* nauplii under satiating food conditions and at similar temperatures (0.49 d^{-1} at 28°C). The low satiating threshold exhibited by *Oithona* spp. nauplii would provide a competitive advantage over other copepods in these environments and under oligotrophic conditions.

Many hypotheses have been offered as to why oithonids are so abundant and ubiquitous relative to calanoids (Lampitt 1978, Lampitt & Gamble 1982, Paffenhöfer 1993, Castellani et al. 2005b). Copepod life strategies are adapted to food fluctuations. For example, when primary production declines, many calanoid species produce resting eggs that accumulate in sediments and hatch prior to the onset of the spring bloom. Oithonids do not produce resting eggs and must adapt to tolerate periods of low food availability and to maintain their populations throughout the year.

The success of oithonids over calanoids has been attributed to their wide array of prey preferences (Lampitt 1978, Uchima 1988, González & Smetacek 1994, Calbet et al. 2000) and low metabolic rates (Lampitt & Gamble 1982, Paffenhöfer 1993, Castellani et al. 2005). Differences in the motion/feeding behaviour may contribute to differences in metabolic requirements between calanoids and oithonids. Our study shows that development rates of *Oithona* spp. nauplii are similar to those of calanoid nauplii, but growth rates of *Oithona* spp. nauplii are lower than those of calanoid nauplii. In addition, naupliar development of *Oithona* spp. saturates at lower concentrations. Thus, *Oithona* spp. development is completed sooner and results in smaller sized individuals than that of calanoid copepods inhabiting oligotrophic regions. Moreover, in en-

vironments, such as oceans, with substantial predation (Verity & Smetacek 1996), reduced size and low motility may offer a competitive advantage that reduces predation risk. In summary, our study suggests that *Oithona* spp. in marine ecosystems may have an advantage over other copepods because of differences in food requirements that maximise survival and rates of development and growth.

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