Limnol. Oceanogr., 58(1), 2013, 376–387

doi:10.4319/lo.2013.58.1.0376

Effects of food concentration on egg production and feeding rates of the cyclopoid copepod *Oithona davisae*

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Abstract

Experiments to determine egg production and feeding rates of *Oithona davisae* were carried out under controlled laboratory conditions. From copepodite IV stage on, the animals were fed the heterotrophic dinoflagellate *Oxyrrhis marina* in a wide range of concentrations (from 10 μg C $L^{-1}$to 286 μg C L^{-1}), and adult females were daily monitored to study different aspects of their fecundity. Both clutch and egg-production rate increased with food concentration, with values from 8 to 20 eggs for the clutch size, and from 1.8 eggs to 6.3 eggs $female^{-1}$ d^{-1} for the egg production. In addition, to assess the efficiency of conversion of food intake into egg mass, two feeding experiments were conducted. Maximum weight-specific ingestion rates ($\approx$ 80% body C d^{-1}) and the egg-production efficiency (16%) were lower than those reported for free-spawning calanoid copepods. The fact that satiating food concentrations for feeding and egg production of adult females of *Oithona davisae* were rather low suggests an adaptation to exploit oligotrophic environments, and might explain the ecological success of the genus in situations when food becomes limiting for other groups of copepods.

It is widely accepted that small copepods ($<$ 1 mm) are important, but poorly studied components of marine pelagic communities (Turner 2004). They were often neglected from samplings in past years until several authors (Paffenhöfer 1993; Gallienne and Robins 2001) warned about the bias due to use of coarse mesh sizes ($>$ 200 μm) in plankton nets. This fact was actually not something new, because some studies from the early 20th century already pointed out the relevance of small copepods (Bigelow 1926; Fish 1936) and the need to use fine-mesh nets for correct estimates of zooplankton abundances (Evans 1973).

The marine cyclopoid copepods, and in particular the genus *Oithona,* have raised special interest in recent years due to its high abundance and ubiquitous presence (Uye and Sano 1998; Gallienne and Robins 2001) both in coastal and oceanic regions, and due to a range of distribution extending from polar to tropical latitudes (Nielsen and Sabatini 1996; McKinnon and Klumpp 1998). Besides their numerical dominance, *Oithona* also make up a significant fraction of the copepod biomass in some temperate areas (McLaren et al. 1989; Hay et al. 1991) and might be especially relevant at high latitudes in autumn and winter conditions when other copepods are not active in the upper layers (Kiørboe and Nielsen 1994; Nielsen and Sabatini 1996). Their described low metabolic rates (Lampitt and Gamble 1982; Nakamura and Turner 1997; Castellani et al. 2005*b*), coupled with an ambush feeding behavior and low motility, are considered the clue of their success (Paffenhöfer 1993) and of their capacity to maintain constant populations throughout the year (Lampitt and Gamble 1982; Sabatini and Kiørboe 1994).

Although new insights on the ecology of *Oithona* have been acquired in the past decade (Nielsen et al. 2002; Temperoni et al. 2011), knowledge on their vital rates is still very scarce. Some field studies report the feeding activity (Nakamura and Turner 1997; Castellani et al. 2005*a;* Atienza et al. 2006) and egg production (Ward and Hirst 2007; Dvoretsky and Dvoretsky 2009; Drif et al. 2010) of several *Oithona* species in different ecosystems. Moreover, very few laboratory studies have dealt with aspects related to their reproductive biology (Eaton 1971; Sabatini and Kiørboe 1994) and feeding responses (Drits and Semenova 1984; Saiz et al. 2003). This lack of studies on the ecophysiology of *Oithona* contrasts with the large amount of studies conducted on calanoid copepods on aspects related to feeding, growth, and egg production. In fact, to our knowledge, only Sabatini and Kiørboe (1994) have conducted laboratory experiments regarding the reproductive biology and growth of the congeneric species *Oithona similis.*

Here we present laboratory experiments done under controlled conditions to study the egg production and feeding rates of adult females of *Oithona davisae.* This species was originally distributed in coastal waters of the West Pacific Ocean, but presently it can also be found in coastal waters of the United States and Chile, the Black Sea, and in the Northwest Mediterranean as an invasive species (Razouls et al. 2005–2012). Our main goals were to study how food concentration affects the feeding and fecundity of *O. davisae;* to determine how clutch size and the fraction of ovigerous females vary with food availability; and finally, to assess their egg-production efficiency (gross growth efficiency, GGE). Such information on fecundity, growth rates, critical feeding thresholds, and maximum daily rations provides required information to better understand the life strategies within the genus and the species' capability to cope with environmental variability.

Methods

General procedure—Experiments were conducted on adult females of *Oithona davisae* coming from a continuous culture kept in our laboratory at the Institut de Ciències del

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Table 1. *Oxyrrhis marina*. Nominal initial food levels (in cells) and the corresponding actual average concentrations (in cells and biomass) of prey in the two feeding experiments conducted.

Experiment	Nominal concentration (cells mL^{-1})	Actual average concentration (cells mL^{-1})	Actual average concentration ($\mu g\ C\ L^{-1}$)
1	50	32±1.0	10±0.3
	100	63±1.0	20±0.4
	200	157±5.0	51±1.8
	400	318±4.0	104±1.5
	800	672±4.0	219±1.3
	1200	880±6.0	287±1.9
2	50	33±1.0	10±0.3
	100	72±1.0	21±0.3
	200	150±5.0	44±1.4
	400	288±9.0	85±2.6
	800	614±11.0	181±3.3
	1200	969±22.0	286±6.5

Mar (Barcelona, Spain) since October 2000 (Saiz et al. 2003). Individuals of *O. davisae* were kept in 15 liter transparent plexiglass cylinders (24 cm diameter) filled with 0.1 μm filtered seawater and grown under a 12 h light : 12 h dark cycle at 18°C in a temperature-controlled room. The copepods were routinely fed the heterotrophic dinoflagellate *Oxyrrhis marina* (equivalent spherical diameter, ESD = 16 μm), which were at the same time fed the cryptophyte *Rhodomonas salina* (ESD = 8 μm) grown in f/2 medium (Guillard 1975).

In order to examine the effect of food concentration on the egg production, a cohort of *Oithona davisae* was created and fed with different concentrations of *Oxyrrhis marina.* Figure 1 shows a schematic outline of the followed procedures. To begin the cohort, the stock culture of *O. davisae* was fed ad líbitum (i.e., > 1200 cells mL^{-1}) with *O. marina* during 24–48 h to maximize the egg production of the adult females. Females were carefully concentrated on a submerged 132 μm sieve, and then transferred into a new cylinder filled with filtered (0.1 μm) seawater for 24 h, to allow the hatching of the eggs. After that period, the females were removed from the cylinder using a 100 μm sieve submerged in seawater, and the recently hatched nauplii (NI) were fed ad líbitum until they reached the copepodite IV–V stage (CIV–CV). Then the culture was split into six aliquots and transferred into new cylinders filled with filtered seawater, in which copepods were kept under starvation for ~ 48 h in an attempt to homogenize the past well-fed conditions experienced in the stock cultures. After that time, food concentration in each cylinder was adjusted to the desired concentrations of *O. marina* (nominally 50, 100, 200, 400, 800, or 1200 cells mL^{-1}; Table 1). Food concentrations were daily checked using a Multisizer III particle counter (Beckman Coulter) and adjusted to keep them constant during the experimental time. The suspension in two-thirds of the cylinder was renewed every second day to ensure a fresh supply of food. The females were kept in acclimatization to the respective food levels and daily checked until the presence of the first egg sacs was observed (~ after 72 h). From that moment onward, egg production was monitored (Fig. 1, *see* below). All the incubations and experiments were conducted in a controlled-temperature room at 18° ± 1°C.

Monitoring of egg production in the cohort—During the experimental period, we determined the percentage of ovigerous females, the clutch size, and the size of both females and eggs in the six cylinders with the different concentrations of *Oxyrrhis marina.* A sample (~ 250 mL) was daily taken from each cylinder (except on day 6), and females were inspected under the stereomicroscope and dead animals removed (< 1%, mostly males). Afterward, the samples were preserved in 1% buffered-formaldehyde for later assessment of the percentage of ovigerous females and also to estimate clutch sizes by dissecting the egg sacs. The water volume in the cylinders was kept constant by adding either the corresponding fresh suspension of *O. marina* or filtered (0.1 μm) seawater.

Feeding and egg-production experiments—Two feeding and egg-production experiments were conducted during the experimental period at different reproductive phases. The first experiment was carried out on day 4, when females carrying eggs were not yet present at the lowest food condition (50 cells mL^{-1}); the second experiment was carried out on day 9, when in all food levels ovigerous females were most abundant.

Feeding rates were obtained by incubating adult females of *Oithona davisae* in bottles (treatment bottles) with the different suspensions of *Oxyrrhis marina* (Table 1) and measuring the change in prey concentration relative to the bottles with the same food suspensions but with no copepods (control bottles) after the incubation time. For each food level, three treatment, three control, and two start bottles (time 0) were prepared. The culture of *O. marina* used to prepare the prey suspensions was not fed for 48 h before the experiment started to ensure that only *O.*

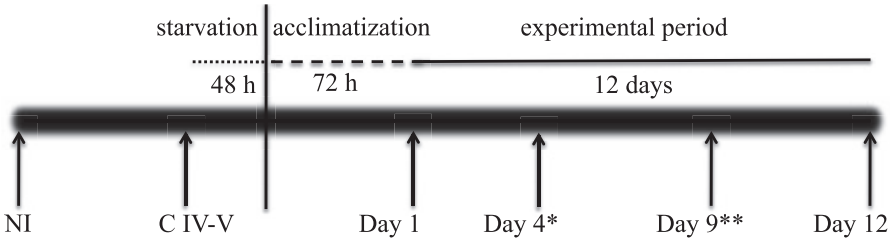

Fig. 1. Schematic representation of the experimental design. One asterisk (expt 1) and two asterisks (expt 2) indicate when the feeding experiments were carried out.

marina was offered as prey. Prey suspensions were prepared by filtering the stock culture using a 10 μm mesh (*O. marina* squeezes through the 10 μm mesh) to remove detrital material, and then by diluting the prey stock with filtered (0.1 μm) seawater to achieve the corresponding food concentrations (Table 1). A nutrient mixture (15 μmol L^{-1} NH_4Cl and 1 μmol L^{-1} Na_2HPO_4) was added to each food suspension to compensate for nutrient enrichment due to copepods' excretion.

Adult females were removed from the cylinders and carefully concentrated on a submerged sieve of 100 μm mesh, rinsed in filtered seawater, and then picked out and transferred to the corresponding food-level treatment bottles. Experiments with food levels of 50, 100, and 200 cells mL^{-1} were conducted in 310 mL Pyrex bottles with, respectively, 24, 33, and 40 adult females each; and experiments with higher food levels of 400, 800, and 1200 cells mL^{-1} were conducted in 130 mL Pyrex bottles with, respectively, 27, 31, and 34 adult females each. The bottles were completely filled, and plastic film was put over the mouth of the bottle to prevent the presence of air bubbles during the incubation. Food concentrations at time 0 of the experiment were checked by preserving 50 mL of each start bottle in 2% acid Lugol's solution, which were later counted under an inverted microscope. Bottles were placed on a plankton wheel (0.2 revolutions min^{-1}, end over end) at a fixed temperature (18° ± 1°C) in controlled light conditions (12 h light : 12 h dark) during the incubation. After the incubation time (~ 24 h) the females were checked under the stereomicroscope to ensure that they were alive and that they swam normally (97–100% of females were viable). Copepods were then transferred to small vials and fixed in 1% buffered-formaldehyde for later sizing and counting of both females and egg sacs. From each control and treatment bottle, a subsample of 75 mL was preserved in acid Lugol's solution (2% final concentration) and subsequently settled and counted under an inverted microscope for determination of *Oxyrrhis marina* concentration at the end of the experiments.

Clearance and ingestion rates were determined for each food level according to Frost's equations (Frost 1972), after verification that prey growth rates in treatment bottles were statistically different from those in the control bottles (*t*-test at the 0.05 significance level). Clearance rates were fitted to an exponential decay function as follows:

$$F = F_{\max} e^{-\lambda C} \tag{1}$$

where $F_{\max}$ is the maximum clearance, C is the concentration of food, and λ is the decay rate.

Ingestion rates were fitted to a Type II functional response model using the Ivlev (1961) equation as follows:

$$I = I_{\max}\left(1 - e^{-\alpha C}\right) \tag{2}$$

where $I_{\max}$ is the maximum ingestion rate, C is the food concentration, and α is the rate at which ingestion approaches the maximum rate. The critical or saturating food concentration (K_s; i.e., the threshold concentration below which feeding is food-limited), was calculated as the food concentration at which ingestion equals 95% of the maximum ingestion rate (Almeda et al. 2010).

For the females corresponding to the feeding experiments, the percentage of ovigerous females was determined, and their mean clutch size was quantified by dissecting all egg sacs present. The average population egg-production rates (EPR, eggs $female^{-1}$ d^{-1}), computed for the ensemble of ovigerous (i.e., carrying egg sacs) and non-ovigerous (i.e., not carrying egg sacs) females, was calculated using the egg-ratio method according to the following equation, modified from Uye and Sano (1995),

$$\mathrm{EPR} = \frac{\mathrm{CS} \times \mathrm{OF}}{\mathrm{TF} \times \mathrm{IT}} \tag{3}$$

where CS is clutch size (eggs $female^{-1}$), OF is the number of ovigerous females present in the sample, TF is the total number of females, and IT is the inter-clutch time (days). We have used the inter-clutch time determined by Uye and Sano (1995) instead of the hatching time (as can be found elsewhere in the literature [e.g., Sabatini and Kiørboe 1994; Castellani et al. 2005*a*]) because the inter-clutch time for *Oithona davisae* is longer than the embryonic time at the corresponding experimental temperature (respectively, 2.5 d and 1.8 d; Uye and Sano 1995).

Weight-specific rates were estimated from size measurements and carbon content–size relationships from the literature. In the case of *Oxyrrhis marina,* biovolume estimates from the Multisizer Counter were converted into carbon using the conversion factor 0.123 pg C μm^{-3} for this dinoflagellate provided by Pelegrí et al. (1999). The carbon weight of both eggs (C_{egg}, μg C) and females (C_{female}, μg C) of *Oithona davisae* were estimated by taking digital pictures with a camera attached to an inverted microscope, using a 40X magnification for the females and 100X for the eggs. For each experimental condition, ≥ 200 eggs and 20 females were measured from the digital pictures by using the image processing program ImageJ (W.S. Rasband, ImageJ, U.S. National Institutes of Health, Bethesda, Maryland; http://imagej.nih.gov/ij/, 1997–2011). The egg diameter (ED, μm) was estimated as equivalent circular diameter from the area measurements in ImageJ, and then the egg carbon content was calculated using the equation given by Uye and Sano (1995) for *Oithona davisae:*

$$C_{egg} = 5.32 \times 10^{-8} \times ED^{3.04} \tag{4}$$

where C_{egg} is the egg carbon content (μg C) and ED is the egg diameter (μm). For adult females, because we expected differences in individual biomass among the populations grown under different food concentrations (reflected as differences in length but also in width), we first estimated their individual biovolume (μm^3) at each food level by using the minor and major axis of the cephalothorax to build an ellipsoid. Then using only the major axis (homologous to the prosome length; PL, μm), we estimated carbon content of the females (C_{female}, μg C) for all conditions using the equation given by Uye (1982) for this copepod species:

$$C_{female} = 1.26 \times 10^{-4} \times PL^{1.31} \tag{5}$$

Finally, we computed an average carbon content : biovolume factor, $6.74 \cdot 10^{-8}$ μg C μm^{-3}, which was used in all

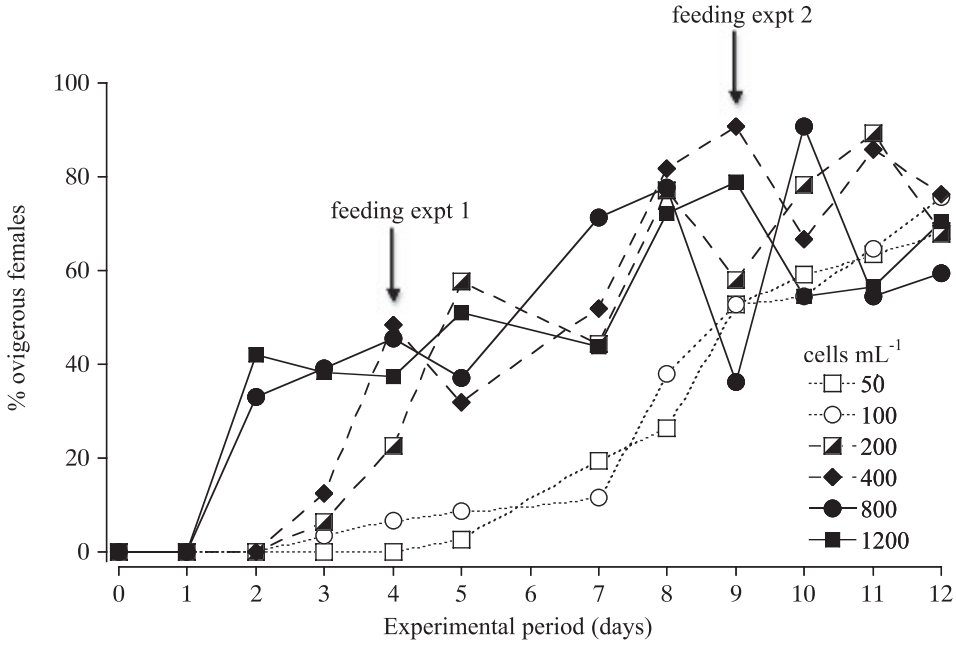

Fig. 2. Temporal development of ovigerous females (%) present in the population under different food levels (nominal concentrations, cells mL^{-1}). Days when the feeding experiments were carried out are indicated.

calculations to estimate the female biomass from the biovolume measurements.

The efficiency of conversion of ingested food into egg biomass (GGE) of adult females of *Oithona davisae* was calculated as the slope (in %) of a major axis (MA) fitting (i.e., Model II linear regression) between weight-specific ingestion (WSI) and egg-production (WSEPR) rates. We chose that model instead of ordinary least-squares regression fit (i.e., Model I) because both variables contain error (i.e., they were not controlled by the researcher). Nevertheless, because GGE is typically calculated as the slope of Model I linear fit (Castellani et al. 2005*a;* Almeda et al. 2010), we also applied this fitting method to obtain values comparable to other studies.

Results

Reproductive activity of the females—The time for the first appearance of ovigerous females in the population varied inversely with food concentration (Fig. 2). Females carrying egg sacs contributed ~ 40% of the population on day 2 in the highest food concentrations (800 and 1200 cells mL^{-1}); whereas, on the medium (200 and 400 cells mL^{-1}) and low (50 and 100 cells mL^{-1}) food concentrations that percentage was only achieved after, respectively, 5 and 8 d of the experimental period (Fig. 2). Close to the end of the experimental period, the proportion of ovigerous females in the population achieved similar values in all food treatments (≈ 75%; Fig. 2). The monitoring during the experimental period was discontinued after day 12 because the females population in the cylinders started to decline (data not shown), both because of the daily removal of individuals from the cylinders and the earlier mortality in the populations kept at the highest food levels.

Feeding and egg-production rates—Both feeding experiments provided similar rates (Fig. 3). Clearance rates found in this study declined as a function of food concentration (Fig. 3A), and the values (average ± SE) ranged from 7.3 mL ± 0.39 mL to 0.63 mL ± 0.06 mL $female^{-1}$ d^{-1} at the lowest and highest food concentration, respectively. Ingestion rates increased asymptotically with increasing food concentration, showing saturation food concentrations (K_s) of 249 cells mL^{-1} and maximum ingestion rates of 737 cells $female^{-1}$ d^{-1} (Fig. 3B).

In terms of weight-specific rates, daily ration (DR) varied from 30% of body C ingested d^{-1} at the lowest food concentration tested, to maximum values of 80% body C d^{-1} (Fig. 3C). The saturation food concentration of *Oxyrrhis marina* in terms of carbon was 56 μg C L^{-1}.

The effect of food concentration on the fecundity of *Oithona davisae* is shown in Fig. 4. Unlike the results obtained with ingestion rates, it was observed that although maximum values were similar between both experiments, the rate at which both clutch size and egg production reached those maximum values (the α parameter in the Ivlev's fits) were notably different. Females from expt 2 reached maximum EPRs at lower food levels than those from expt 1, and we interpreted that as being due to the young females from expt 1 lacking sufficient time to mature their gonads. For that reason we only refer to egg-production values from expt 2.

Both clutch size (eggs $female^{-1}$, both sacs together; Fig. 4A) and egg-production rate (eggs $female^{-1}$ d^{-1}; Fig. 4B) increased asymptotically with increasing food concentration. Clutch size varied on average from 8 eggs to maximum values of 20 eggs (Fig. 4A); and although the females produced eggs at the lowest food concentration (10–20 μg C L^{-1}), they never reached the clutch size of the

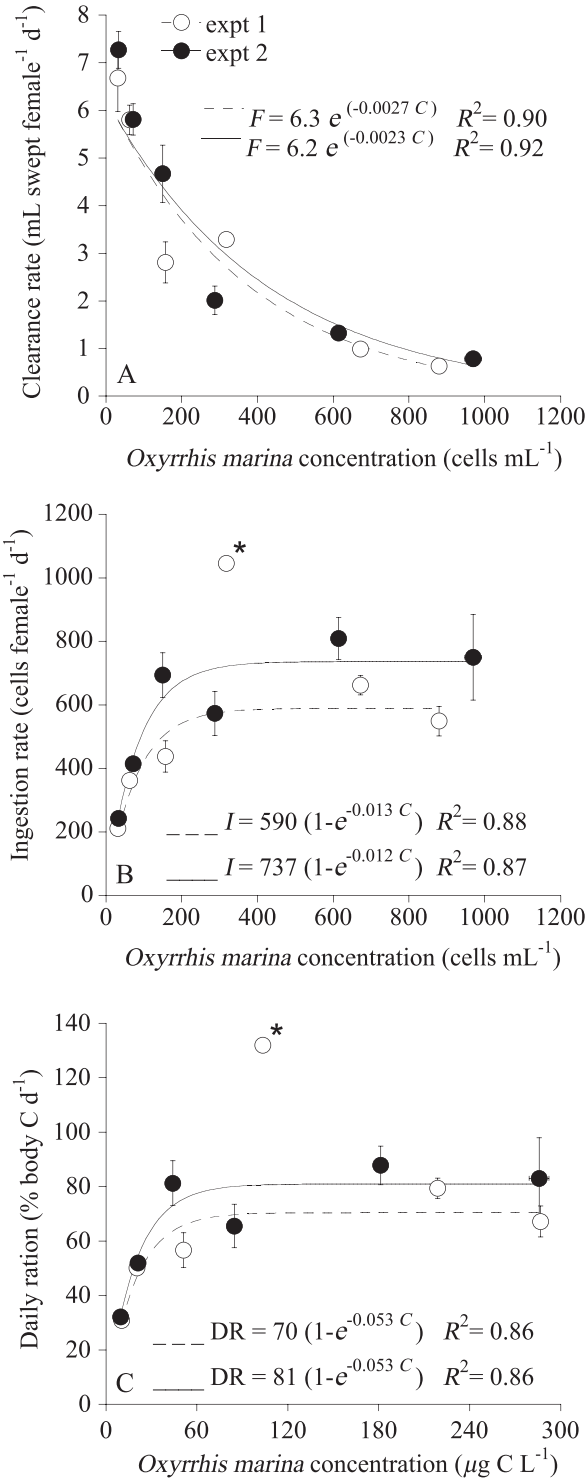

Fig. 3. *Oithona davisae* feeding rates as a function of food concentration (*C*). (A) Clearance rate (*F,* mL female^{-1} d^{-1}). (B) Ingestion rate (*I,* cells female^{-1} d^{-1}). (C) Weight-specific ingestion rate, as percentage of body carbon ingested per day (daily ration, DR, %). Mean values (n = 3) and standard errors (SE) are shown. Exponential decay and Ivlev's equations fits are also shown. Symbols marked with an asterisk correspond to extreme values not used in the equation fitting.

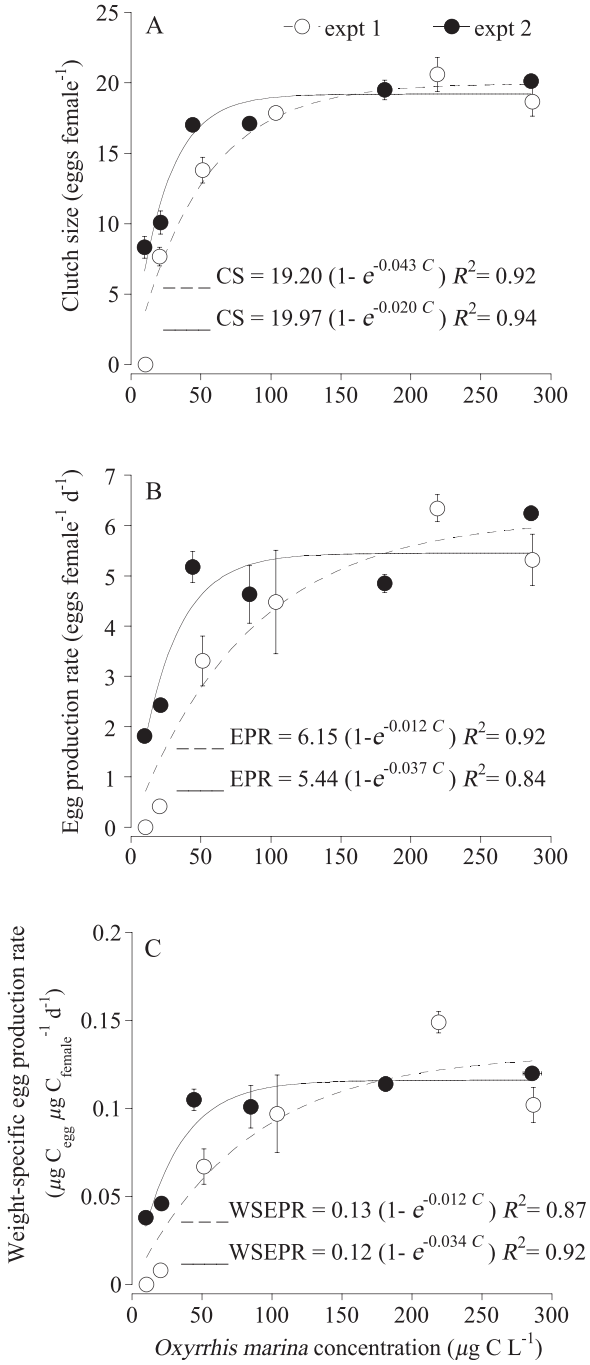

Fig. 4. Relationship between fecundity of *Oithona davisae* and food concentration (*C*) in terms of (A) mean clutch size (CS); (B) egg-production rate (EPR); and (C) weight-specific egg-production rate (WSEPR). Mean values and SE (n = 3) are shown. Ivlev's fits are displayed in the graphs.

highest food levels. The EPRs (eggs female^{-1} d^{-1}) found in this study varied from 1.8 ± 0.07 to 6.3 ± 0.14 (Fig. 4B). It is important to note that clutch size was only computed for ovigerous females; whereas, the egg-production rate was computed on a population basis (i.e., also includes non-ovigerous females). The critical concentration of food at which saturating values (K_s) for egg production (EPR)

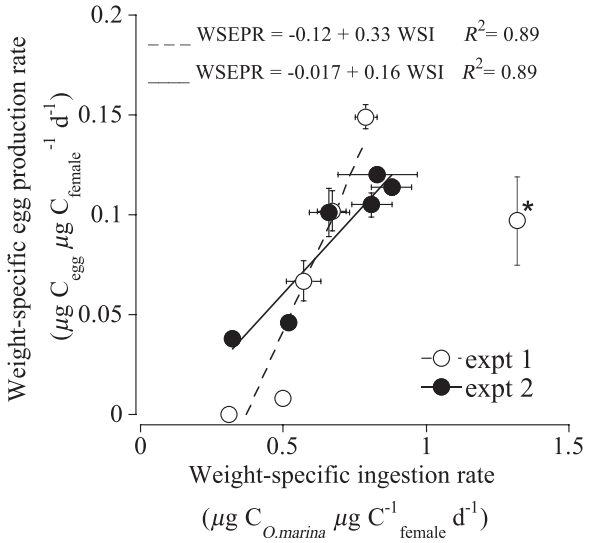

Fig. 5. Relationship between weight-specific egg production (WSEPR) and weight-specific ingestion (WSI). Mean values and SE (n = 3) are shown. Model II regression (major axis) fits to the data are also shown. Symbol marked with an asterisk corresponds to the outlier not taken into account for the fit.

were found was 81 μg C L^{-1}, with EPRs of ~ 5–6 eggs $female^{-1}$ d^{-1} above this threshold.

The weight-specific egg-production rates (WSEPR, μg C_{egg} μg C_{ind}^{-1} d^{-1}) are shown in Fig. 4C. Values (average ± SE) ranged from 0.04 ± 0.002 μg C_{egg} μg C_{ind}^{-1} d^{-1} to 0.12 ± 0.003 μg C_{egg} μg C_{ind}^{-1} d^{-1}. Maximum WSEPRs corresponded to those females carrying the largest clutch sizes (20 eggs, on average).

Consistent with what we mentioned above about a likely delay in the maturation of gonads in young females from expt 1, a fact that would lead to an overestimation of the egg-production efficiency (GGE; Fig. 5), we only used expt 2 for the assessment of GGE. After running the two different regression models for the estimation of the GGE, we found that both major axis (MA) and ordinary least-squares regression (OLS) fittings gave the same results (MA slope = 0.16, 95% CI = 0.081–0.232; and OLS slope = 0.16, 95% CI = 0.080–0.230). Therefore, we use that value of the slope (in percentage) obtained for further discussion (i.e., 16%; Fig. 5).

Egg and female size—Figure 6 shows the relationship between female size and female body weight with food level. Females grown at higher food concentrations were larger in prosome length and width (Fig. 6A), which resulted in an asymptotic increase in body weight from ~ 0.22 μg C $female^{-1}$ to 0.26 μg C $female^{-1}$ as food availability increased (Fig. 6B). On the other hand, the mean diameter of the eggs (ECD ± SE) varied from 41.8 μm ± 0.18 μm to 46.9 μm ± 0.24 μm, and was positively related to clutch size (R^2 = 0.67; Fig. 7A). There was also a positive relationship between clutch size and female body weight (Fig. 7B), but this relationship is spurious because it was mediated by the fact that the heaviest females corresponded to the populations grown under the highest food concentrations (Fig. 6B).

Discussion

Feeding rates—Clearance rates found for *Oithona davisae* decreased exponentially with food (Fig. 3A), with maximum rates (≈ 7 mL $female^{-1}$ d^{-1}) similar to the ones found in other studies for the same species (6 mL $female^{-1}$ d^{-1}, Saiz et al. 2003). In situ maximum clearance rates for other *Oithona* species have been reported to be higher than those found in the present study (36 mL $female^{-1}$ d^{-1}, Atienza et al. 2006; 23 mL $female^{-1}$ d^{-1}, Castellani et al. 2005*a*). But in most of the cases, the experiments were run with larger species and different temperatures, and natural seawater was used instead of a monospecific diet, which makes the comparison difficult. However, when only dinoflagellates were considered on in situ clearance rates of *Oithona,* those were lower than, or on the same range as, our values (1.7–3.1 mL $female^{-1}$ d^{-1}, Nakamura and Turner 1997; 0.6–10.1 mL $female^{-1}$ d^{-1}, Castellani et al. 2005*a;* 6–7 mL $female^{-1}$ d^{-1}, Atienza et al. 2006).

The ingestion rates of *Oithona davisae* followed a Holling Type II functional response (Holling 1959), with almost identical curves in both feeding experiments (Fig. 3B,C).

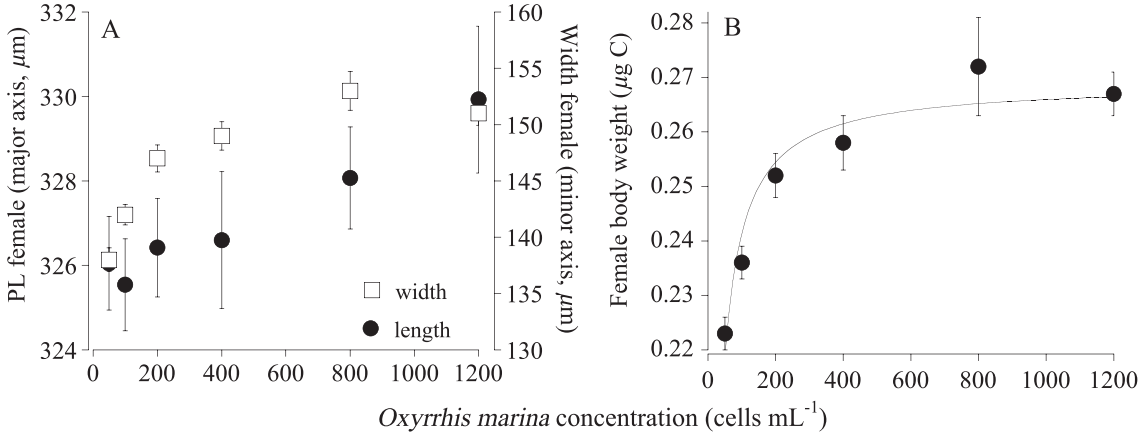

Fig. 6. (A) Relationship between food concentration (C) and female prosome length (PL, μm) and width (μm). (B) Michaelis–Menten relationship (R^2 = 0.94) between food concentration (cells mL^{-1}) and female body weight (μg C). Mean values and SE are shown.

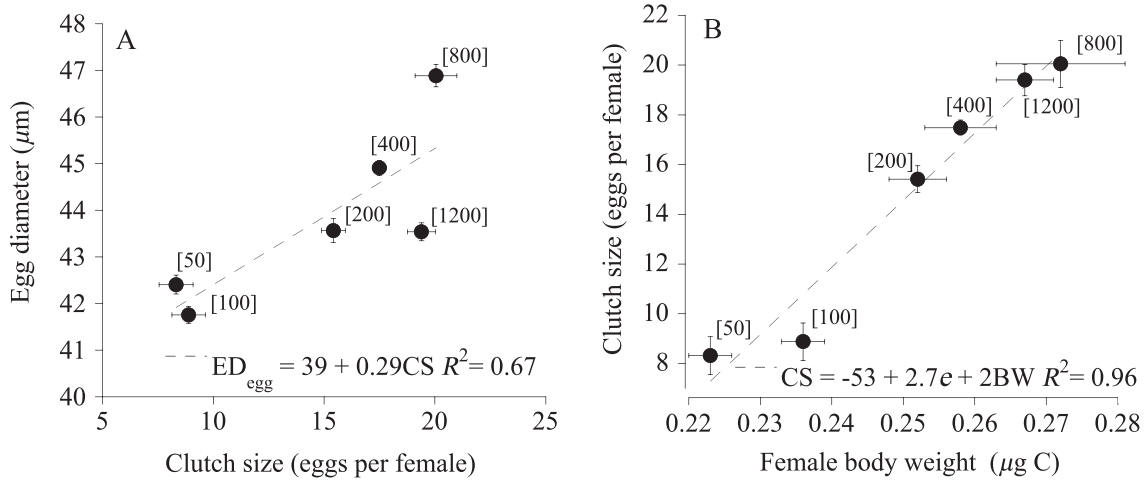

Fig. 7. Relationship between mean clutch size and (A) egg diameter (ED, μm), and (B) female body weight (BW, μg C). Mean values and SE are shown. The corresponding nominal concentrations (cells mL^{-1}) for each data point are also indicated.

The maximum feeding rates (ingestion and clearance) found in this study were similar to those reported for adult females and higher than those reported for males and early stages (Saiz et al. 2003; Kiørboe 2008; Almeda et al. 2010; *see* Table 2) of the same species. However, the functional pattern found here (Type II) for adult females is different from the one reported by Almeda et al. (2010) for early stages of *O. davisae,* which exhibited a Type III functional response with feeding threshold from 153 cells mL^{-1} to 235 cells mL^{-1} ($\approx$ 50–75 μg C L^{-1}). The lack of feeding threshold in adults of *O. davisae* could be explained as the result of differences in prey detection capabilities between adult and juveniles. Both juveniles and adults of *Oithona* are strict ambush predators that detect motile prey from hydromechanical signals (Paffenhöfer 1993; Svensen and Kiørboe 2000). It could be that different numbers and lengths of mechanoreceptors between developmental stages of copepods could explain differences in their feeding performances (Paffenhöfer 1998). In this regard, it has been described how copepod size is positively related to the sensitivity to fluid deformation in the detection of potential predators (Kiørboe et al. 1999: *Acartia tonsa*). Although those observations were focused on the stimuli that a potential predator may originate, we think it could also be applied to hydromechanical perception of prey. That would imply that later stages might have a better perceptive performance to detect prey than do earlier stages.

It is also important to note that the satiating food concentrations (K_s) reported in this study for adult females of *Oithona davisae* (249 cells $mL^{-1} \approx 56$ μg C L^{-1}) are much lower than those reported for the early stages of the same species by Almeda et al. (2010; from 700 cells $mL^{-1} \approx$ 200 μg C L^{-1} for NI–NII to 1130 cells $mL^{-1} \approx 320$ μg C L^{-1} for CII–III stages). This fact is unexpected, because it is typically considered that adult stages have higher satiating food concentrations than do earlier stages. However, low values of satiating food concentrations for adult females of *O. davisae* have been previously found in the same species (100 μg C L^{-1}, Saiz et al. 2003) and on *Oithona nana* (50–100 μg C L^{-1}, Lampitt and Gamble 1982). The lack of Type III Holling functional response (i.e., the lack of a feeding threshold concentration) of *O. davisae* adult females, and the comparatively low critical food concentration, seem to reflect a particular strategy in the adult stage to perform well at low food availability. In fact, it has been observed that *Oithona similis* can fed at very low concentrations (< 1 μg C L^{-1}, S. Zamora-Terol unpubl.), even below our lowest food level, which therefore indicates the possibility of a lack of feeding threshold for adults of *Oithona* spp.

Maximum specific ingestion rates found in this study ($\sim$ 80% body C d^{-1}) for adult females of *Oithona davisae* are very likely within the maximum possible rates for similar-sized *Oithona* species (80–125% d^{-1}, Saiz et al. 2003); and certainly much higher than most previously

Table 2. Comparison of literature data on maximum ingestion (I_{max}) and clearance rates (F_{max}) among different stages of *Oithona davisae* feeding on the same type of prey (*Oxyrrhis marina*) in the laboratory.

Stages	I_{max} ± SE (cells $female^{-1}d^{-1}$)	F_{max} ± SE (mL $female^{-1}d^{-1}$)	T (°C)	Reference
NI–NII	118±6	0.38±0.02	20.5	Almeda et al. 2010
NV–NVI	296±19	0.57±0.04	20.5	Almeda et al. 2010
C2–C3	517±25	1.11±0.05	20.5	Almeda et al. 2010
Males	640	2.6±0.30	22	Kiørboe 2008
Adult females	—	6	21	Saiz et al. 2003
Adult females	737	7.3	18	this study

reported maximum rates in the field for other *Oithona* species (e.g., 17% [Castellani et al. 2005*a*], 27% [Nakamura and Turner 1997] and 35% [Drits and Semenova 1984] found for *Oithona similis,* or 34% for *Oithona* spp. [Atkinson 1996]). Despite that, the maximum daily rations reported here are still lower than those typically reported for similar-sized free-spawning copepods (which can be up to two times higher; Paffenhöfer 1988) and egg-carrying calanoids (148% body weight, Paffenhöfer and Harris 1976: *Pseudocalanus elongatus*). Such difference on daily rations (DR, % body C ingested d^{-1}) between *Oithona* and calanoid copepods has been attributed to the ambush feeding behavior, low motility, and low respiration rates of *Oithona* (1.4–31.4% in a range of 4–30°C, Lampitt and Gamble 1982; Hiromi et al. 1988; Castellani et al. 2005*b*).

Egg production—Oithona davisae EPRs and clutch sizes found in this study are in good agreement with the in situ values reported for the same species by Uye and Sano (1995) in Fukuyama Harbour (i.e., 0.6 and 5.6 eggs $female^{-1}$ d^{-1} in winter and in summer, respectively). Overall the values reported here for *O. davisae* fall within the range of values reported in situ for other *Oithona* species, and in particular the maximum specific-egg-production rates we observed are very similar to the ones reported in the literature (Table 3). It is worth noting that, in our calculations of EPRs, we followed the approach by Uye and Sano (1995) of using the inter-clutch time instead of the embryonic time, which is more widely used in the literature. We assumed that the inter-clutch time was only dependent on the temperature, although we cannot discard the idea that, very likely, food availability may also affect it.

In our experiments, food concentration had an effect on egg production of *Oithona davisae* by influencing the clutch size and also the percentage of ovigerous females in the population (Fig. 2). Even at the lowest food concentrations, we observed the production of eggs, but with smaller clutch sizes (Fig. 4A). Larger clutch sizes corresponded to larger eggs, contrary to what is observed in other *Oithona* species (Castellani et al. 2007; Dvoretsky and Dvoretsky 2009). We also found a positive relationship between clutch size and female body weight, as has been found in other cyclopoid and calanoid copepods (Runge 1984; Castellani et al. 2007). In our particular case, however, food concentration determined the final size and carbon content of the females, thereby confusing the effects of any direct relationship between female body weight and clutch size. In the case of in situ studies, the largest clutches for certain *Oithona* species typically occur in the most favorable conditions within the year (i.e., when high availability of food is present in the water column [Uye and Sano 1995; Castellani et al. 2005*a;* but *see also* Temperoni et al. 2011 for the lack of seasonal variation]). In our study, however, the largest clutch sizes corresponded to the largest females (Fig. 7B), not necessarily due to a direct relationship but simply because those females were grown at the highest food levels, which makes it difficult to ascertain causal relationships.

Regarding the reproductive status of the population, the number of reproductive females in the population was affected by food availability and increased through time during the experimental period, reaching maximum values of 80% of females in ovigerous state (i.e., carrying egg sacs; Fig. 2). In agreement with our results, Sabatini and Kiørboe (1994) found similar percentages of ovigerous females (80%) on *Oithona similis* at the highest food levels tested (300 μg C L^{-1}). The females kept at low food concentrations lagged behind; they started to evidence the ovigerous state 5–8 d later than those at higher food levels. This trend suggests a limitation in the gonad development (Niehoff 2004).

We found that even at the lowest food concentrations (10 μg C L^{-1}) *Oithona davisae* showed relatively high WSI and EPRs ($\sim$ 30% and 4%, respectively). The capability of *O. davisae* to reach maximum EPRs at low food concentrations may explain the year-round egg production observed for this species and likely for other congeneric species. A similar strategy was described by Jonasdottir (1989) for the egg-carrying calanoid *Pseudocalanus newmani,* whose capability to achieve maximum EPRs at low food concentrations could explain the observed year-round production of eggs of *P. newmani* in Puget Sound. It is worth noting, however, that our results contrast with the observations for *Oithona similis* in the laboratory study carried out by Sabatini and Kiørboe (1994), in which no egg production was observed at flagellate concentrations below 20 μg C L^{-1}. Although differences in life strategies or body size between both *Oithona* species could explain that discrepancy in food threshold, an alternative explanation could be the use of a non-optimal diet, because the maximum clutch sizes reported for *O. similis* by those authors (13.7 ± 0.4 eggs $clutch^{-1}$) are lower than the values found in field studies for the same species (up to 20–30 eggs $clutch^{-1}$, Nielsen and Sabatini 1996; Castellani et al. 2007; Dvoretsky and Dvoretsky 2009; *see* Table 3).

The maximum WSEPR found in this study (0.12 d^{-1} at 18°C) for adult females of *Oithona davisae* was lower than the maximum specific growth rate reported for nauplii (0.33 d^{-1} at 20.5°C) but similar to copepodites (0.12 d^{-1} at 20.5°C) of the same species (Almeda et al. 2010). This is in agreement with the observations of Uye and Sano (1998) following the demography of the natural population of *O. davisae* in Fukuyama Harbour, in which the maximum weight-specific rates found for the adult females (0.14 d^{-1}) were lower than those for nauplii (0.35 d^{-1}), although they also reported high values for copepodites (0.44 d^{-1}). Sabatini and Kiørboe (1994) also found a similar pattern for *Oithona similis* (0.1 and 0.2 d^{-1} for, respectively, adult females and juveniles) in the laboratory. In the case of *O. davisae,* the discrepancy between growth rates found for adults (in the present study) and nauplii (Almeda et al. 2010), under presumably optimal and not limiting food conditions, could be explained by the negative relationship between specific growth rates and body weight under satiating food conditions described by Almeda et al. (2010). In any case, such differences between adult and juvenile weight-specific growth rates appear not to be only particular to *Oithona,* but also extended to calanoid egg-carrying

Table 3. Comparison of egg-production rates and clutch sizes among different species of *Oithona* from both field and lab studies.

Species	Location	Prosome length (μm)	Temperature (°C)	Type	Mean clutch size (eggs per female) ± SD	Range clutch size (eggs per female)	Egg production rate (eggs female^{-1} d^{-1})	Specific-egg production rate (d^{-1})	Reference
Oithona aruensis	Cape York rivers	280	22.2–30.6	Field	—	3–9	0.8–11.3	0.01–0.12	McKinnon and Klumpp 1998
Oithona attenuata	Exmouth Gulf	340	21.3–23.2	Field	11.4±0.2	7–18	3.2	0.023	McKinnon and Ayukai 1996
Oithona colcarva	Chesapeake Bay	650–770*	15	Field	15.0±2.4	—	2	0.045†	Lonsdale 1981*a,b*
	″	″	15	Lab	8.2±9.9‡	—	—	—	Lonsdale 1981*a,b*
	″	″	20	Field	20.0±4.2	—	3.6	—	Lonsdale 1981*a,b*
	″	″	20	Lab	6.1±4.2‡	—	—	—	Lonsdale 1981*a,b*
	″	″	25	Field	16.8±3.7	—	11.6	—	Lonsdale 1981*a,b*
	″	″	25	Lab	10.5±9.0‡	—	—	—	Lonsdale 1981*a,b*
Oithona davisae	Tokio Bay	—	20	Lab	9.9±4.6	3–20	3.7	0.14†	Uchima 1985
	Fukuyama Harbour	276–331	10–28	Field	—	10–30	0.6–5.6	0.08–0.39	Uye and Sano 1995
	Barcelona Harbour	326–330	18	Lab	15±3	8–21	1.8–6.3	0.04–0.12	This study
Oithona nana	Argentinian Sea	609±36*	10–21	Field	12±2§	9–15§	1–6	0.02–0.1	Temperoni et al. 2011
	Jamaican waters	325	28	Field	17.0±4.6	9–26	—	—	Hopcroft and Roff 1996
Oithona plumifera	South-east continental shelf	≈600	20	Field	11.6	7–16	3.8	0.08†	Paffenhöfer 1993
	Jamaican waters	540	28	Field	12.9±3.7	5–21	—	—	Hopcroft and Roff 1996
Oithona setigera	Indian Ocean	1140–1900*	25–28	Field	11	—	—	—	Sazhina 1985
Oithona similis	Halifax Harbour	—	10	Lab	9.3±4.7	4–19	1.6	0.03†	Eaton 1971
	Øresund	≈487	15	Lab (diet 1)‖	13.7±0.4	—	4.48	0.1†	Sabatini and Kiørboe 1994
	Øresund	450–487	15	Lab (diet 2)¶	≈8.2	6–9	1.5–1.9	0.04	Sabatini and Kiørboe 1994
	North Atlantic	498–510	≈3–11	Field	—	—	≈1.6–2.1	0.025–0.06	Castellani et al. 2005*a*
	Scotia Sea	—	−1.5–3.3	Field	15.8§	6–31	0.03–1.12	0–0.02	Ward and Hirst 2007
	Barents Sea	508–517	−1.6–10	Field	21.5±0.5	14–32	0.2–1.8	0.005–0.04	Dvorestsky and Dvoretsky 2009
	Northern North Sea	438–575	6.3–14.7	Field	14	5–22	0–4	0–0.12	Drif et al. 2010
	North Sea	493–585	7–12	Field	—	10–15§	1.01–5.21	0.014–0.10	Nielsen and Sabatini 1996

Table 3. Continued.

Species	Location	Prosome length (μm)	Temperature (°C)	Type	Mean clutch size (eggs per female) ± SD	Range clutch size (eggs per female)	Egg production rate (eggs female^{-1} d^{-1})	Specific-egg production rate (d^{-1})	Reference
Oithona simplex	Exmouth Gulf	270	21.3–23.2	Field	5.3±0.2	4–8	2.4	0.069	McKinnon and Ayukai 1996
	Jamaican waters	≈270	28	Field	7.5±1.6	4–10	—	—	Hopcroft and Roff 1996
Oithona spp.	North Atlantic	479–501	3–11.1	Field	10.5±1.5§	5–20§	1–6	0.017–0.13	Castellani et al. 2007
Oithona sp.	Cape York rivers	320	22.2–30.6	Field	—	3–9	2.3–15.3	0.02–0.13	McKinnon and Klumpp 1998

* Total length.
† Maximum specific-egg-production rate.
‡ Clutch size estimated from hatched nauplii.
§ Eggs per sac.
‖ Diet 1: *Rhodomonas baltica* + *Heterocapsa triquetra* + *Oxyrrhis marina*.
¶ Diet 2: *R. baltica* + *H. triquetra*.

species (Paffenhöfer and Harris 1976: *Pseudocalanus elongatus*). However, under optimal food conditions in the laboratory, small broadcasting calanoids exhibit maximum WSEPRs closer to the maximum specific juvenile growth rates (Berggren et al. 1988: *Acartia tonsa*). Our results, therefore, question the equivalence between weight-specific egg production and juvenile somatic growth for *Oithona,* the application of which in field studies could result in erroneous estimations of total copepod production.

Egg-production efficiency (GGE)—The estimated egg-production efficiency for *Oithona davisae* in the present study (16%) did not reach the typical 30% GGE assumed for egg production in calanoid copepods (Ikeda and Motoda 1978). It is indeed slightly lower than the value for juvenile stages of *O. davisae* (21%) reported by Almeda et al. (2010). The low growth efficiencies found during our study for *O. davisae* suggest, therefore, either higher metabolic costs or lower assimilation efficiencies than for calanoid copepods. It has been typically attributed to *Oithona* low metabolic rates (Paffenhöfer 1993; Sabatini and Kiørboe 1994; Nakamura and Turner 1997), so lower assimilation efficiency seems more likely. However, this contrasts with the study by Almeda et al. (2011) on early stages of *O. davisae,* who reported assimilation efficiencies no different from the range of values reported in the literature for calanoids.

We do not really know why assimilation efficiency would be so different between juveniles and adults. It could be argued that *Oxyrrhis marina* is not a suitable diet for egg production. However, *O. marina* has been shown to be a nutritionally good food item for calanoid copepods (Klein Breteler et al. 1982); furthermore, in our stock cultures, *Oithona davisae* has been easily maintained for years, which indicates that it is a suitable prey. An alternative and more likely explanation could be that maximum food intake of adult females of *O. davisae* (and probably also of late copepodites), constrained by the strict ambush feeding mode, is relatively low in comparison to metabolic requirements, which for this species at our experimental temperature would be on the order of 21% (Hiromi et al. 1988). We cannot dismiss either (when comparing them with free-spawning calanoids) that in cyclopoid species, spawning frequency is limited by the fact that a new clutch can only be released when the previous one has hatched; whereas, for nauplii, the somatic growth might not be too different. The lack of other studies with *Oithona,* however, does not allow for strong conclusions about our hypothesis. In this regard, it is also worth noting that Castellani et al. (2005*a*) found higher GGE for *Oithona similis* (47% on average), which was interpreted as a consequence of a preponderantly carnivorous diet (ciliates); differences in calculation methods could also help to explain the differences with our data.

From an ecological point of view, the comparatively low productive rates described for *Oithona* are probably counterbalanced by the expected lower encounter rate with predators, due to their low motility. In addition, the low critical food concentrations exhibited by adult females in

our study explain their capability to grow at maximum rates in very diluted environments. Therefore, we suggest that high abundances of *Oithona,* especially in situations of unfavorable trophic conditions for calanoid copepods, and their presence in a wide range of ecosystems, can be explained by their feeding and reproductive strategies.

Acknowledgments

This work was funded by the Spanish Ministry of Education and Science (current Ministry of Economy and Competitiveness) through a Ph.D. fellowship (BES-2008-004231) to S. Z. and the research project CTM2007-60052 and CTM2011-23480 to E.S. This is a contribution of the Marine Zooplankton Ecology Group (2009SGR-1283) at the Institut de Ciències del Mar.

We thank M. Antó and P. Jiménez for taking care of the stock cultures of algae and copepods. We also thank R. Almeda, A. Calbet, and M. Alcaraz for their advice. We finally thank M. R. Landry and two anonymous reviewers for their constructive comments on the manuscript.

References

Almeda, R., C. B. Augustin, M. Alcaraz, A. Calbet, and E. Saiz. 2010. Feeding rates and gross growth efficiencies of larval developmental stages of *Oithona davisae* (Copepoda, Cyclopoida). J. Exp. Mar. Biol. Ecol. **387:** 24–35, doi:10.1016/j.jembe.2010.03.002

———, M. Alcaraz, A. Calbet, and E. Saiz. 2011. Metabolic rates and carbon budget of early developmental stages of the marine cyclopoid copepod *Oithona davisae*. Limnol. Oceanogr. **56:** 403–414, doi:10.4319/lo.2011.56.1.0403

Atienza, D., A. Calbet, E. Saiz, M. Alcaraz, and I. Trepat. 2006. Trophic impact, metabolism, and biogeochemical role of the marine cladoceran *Penilia avirostris* and the co-dominant copepod *Oithona nana* in NW Mediterranean coastal waters. Mar. Biol. **150:** 221–235, doi:10.1007/s00227-006-0351-z

Atkinson, A. 1996. Subantarctic copepods in an oceanic, low chlorophyll environment: Ciliate predation, food selectivity and impact on prey populations. Mar. Ecol. Prog. Ser. **130:** 85–96, doi:10.3354/meps130085

Berggren, U., B. Hansen, and T. Kiørboe. 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. Mar. Biol. **99:** 341–352, doi:10.1007/BF02112126

Bigelow, H. B. 1926. Plankton of the offshore waters of the Gulf of Maine. P. Bull. U. S. Bur. Fish. **40:** 1–509.

Castellani, C., X. Irigoien, R. P. Harris, and N. P. Holliday. 2007. Regional and temporal variation of *Oithona* spp. biomass, stage structure and productivity in the Irminger Sea, North Atlantic. J. Plankton Res. **29:** 1051–1070, doi:10.1093/plankt/fbm079

———, ———, ———, and R. S. Lampitt. 2005*a*. Feeding and egg production of *Oithona similis* in the North Atlantic. Mar. Ecol. Prog. Ser. **288:** 173–182, doi:10.3354/meps288173

———, C. Robinson, T. Smith, and R. S. Lampitt. 2005*b*. Temperature affects respiration rate of *Oithona similis*. Mar. Ecol. Prog. Ser. **285:** 129–135, doi:10.3354/meps285129

Drif, K., A. G. Hirst, and S. Hay. 2010. Seasonal abundance and egg production rates of *Oithona similis* and *Pseudocalanus elongatus* in the northern North Sea: A first comparison of egg-ratio and incubation methods. Mar. Ecol. Prog. Ser. **415:** 159–175, doi:10.3354/meps08748

Drits, A. V., and T. N. Semenova. 1984. Experimental investigations on the feeding of *Oithona similis*, Claus. Oceanology (USSR) **24:** 755–759.

Dvoretsky, V. G., and A. G. Dvoretsky. 2009. Spatial variations in reproductive characteristics of the small copepod Oithona similis in the Barents Sea. Mar. Ecol. Prog. Ser. **386:** 133–146, doi:10.3354/meps08085

Eaton, J. M. 1971. Studies on the feeding and reproductive biology of the marine cyclopoid copepod, *Oithona similis*, Claus. Ph.D. thesis. Dalhousie Univ.

Evans, F. 1973. The permanent zooplankton of Northumberland coastal waters. Proc. Univ. Newc. Philos. Soc. **2:** 25–68.

Fish, C. J. 1936. The Biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. Biol. Bull. **71:** 168–187, doi:10.2307/1537414

Frost, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. **17:** 805–815, doi:10.4319/lo.1972.17.6.0805

Gallienne, C. P., and D. B. Robins. 2001. Is *Oithona* the most important copepod in the world's oceans? J. Plankton Res. **23:** 1421–1432, doi:10.1093/plankt/23.12.1421

Guillard, R. R. L. 1975. Culture of phytoplankton for feeding marine invertebrates, p. 26–60. *In* W. L. Smith and M. H. Chanley [eds.], Culture of marine invertebrate animals. Plenum Press.

Hay, S. J., T. Kiørboe, and A. Matthews. 1991. Zooplankton biomass and production in the North Sea during the Autumn Circulation experiment, October 1987–March 1988. Cont. Shelf Res. **11:** 1453–1476, doi:10.1016/0278-4343(91)90021-W

Hiromi, J., T. Nagata, and S. Kadota. 1988. Respiration of the small planktonic copepod *Oithona davisae* at different temperatures. Bull. Plankton Soc. Jpn. **35:** 143–148.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. **91:** 293–320, doi:10.4039/Ent91293-5

Hopcroft, R. R., and J. C. Roff. 1996. Zooplankton growth rates: Diel egg production in the copepods *Oithona*, *Euterpina* and *Corycaeus* from tropical waters. J. Plankton Res. **18:** 789–803, doi:10.1093/plankt/18.5.789

Ikeda, T., and S. Motoda. 1978. Estimated zooplankton production and their ammonia excretion in the Kuroshio and adjacent seas. Fish. Bull. **76:** 357–367.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press.

Jonasdottir, S. H. 1989. Effects of food concentration on egg-production rates of two species of *Pseudocalanus*: Laboratory observations. J. Exp. Mar. Biol. Ecol. **130:** 33–43, doi:10.1016/0022-0981(89)90016-6

Kiørboe, T. 2008. Optimal swimming strategies in mate-searching pelagic copepods. Oecologia **155:** 179–192, doi:10.1007/s00442-007-0893-x

———, and T. G. Nielsen. 1994. Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. I. Copepods. Limnol. Oceanogr. **39:** 493–507, doi:10.4319/lo.1994.39.3.0493

———, E. Saiz, and A. Visser. 1999. Hydrodynamic signal perception in the copepod *Acartia tonsa*. Mar. Ecol. Prog. Ser. **179:** 97–111, doi:10.3354/meps179097

Klein Breteler, W. C. M., H. G. Fransz, and S. R. Gonzalez. 1982. Growth and development of four calanoid copepod species under experimental and natural conditions. Neth. J. Sea Res. **16:** 195–207, doi:10.1016/0077-7579(82)90030-8

Lampitt, R. S., and J. C. Gamble. 1982. Diet and respiration of the small planktonic marine copepod *Oithona nana*. Mar. Biol. **66:** 185–190, doi:10.1007/BF00397192

Lonsdale, D. J. 1981*a*. Influence of age-specific mortality on the life history traits of two estuarine copepods. Mar. Ecol. Prog. Ser. **5:** 333–340, doi:10.3354/meps005333

———. 1981*b*. Regulatory role of physical factors and predation for two Chesapeake Bay copepod species. Mar. Ecol. Prog. Ser. **5:** 341–351, doi:10.3354/meps005341

Mckinnon, A., and T. Ayukai. 1996. Copepod egg production and food resources in Exmouth Gulf, Western Australia. Mar. Freshw. Res. **47:** 595–603, doi:10.1071/MF9960595

———, and D. Klumpp. 1998. Mangrove zooplankton of North Queensland, Australia. Hydrobiologia **362:** 145–160, doi:10.1023/A:1003138718716

Mclaren, I. A., M. J. Tremblay, C. J. Corkett, and J. C. Roff. 1989. Copepod production on the Scotian Shelf based on life-history analysis and laboratory rearings. Can. J. Fish. Aquat. Sci. **46:** 560–583, doi:10.1139/f89-074

Nakamura, Y., and J. T. Turner. 1997. Predation and respiration by the small cyclopoid copepod *Oithona similis*: How important is feeding on ciliates and heterotrophic flagellates? J. Plankton Res. **19:** 1275–1288, doi:10.1093/plankt/19.9.1275

Niehoff, B. 2004. The effect of food limitation on gonad development and egg production of the planktonic copepod *Calanus finmarchicus*. J. Exp. Mar. Biol. Ecol. **307:** 237–259, doi:10.1016/j.jembe.2004.02.006

Nielsen, T. G., E. F. Moller, S. Satapoomin, M. Ringuette, and R. R. Hopcroft. 2002. Egg hatching rate of the cyclopoid copepod *Oithona similis* in arctic and temperate waters. Mar. Ecol. Prog. Ser. **236:** 301–306, doi:10.3354/meps236301

———, and M. Sabatini. 1996. Role of cyclopoid copepods *Oithona* spp. in North Sea plankton communities. Mar. Ecol. Prog. Ser. **139:** 79–93, doi:10.3354/meps139079

Paffenhöfer, G. A. 1988. Feeding rates and behavior of zooplankton. Bull. Mar. Sci. **43:** 430–445.

———. 1993. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). J. Plankton Res. **15:** 37–55, doi:10.1093/plankt/15.1.37

———. 1998. On the relation of structure, perception and activity in marine planktonic copepods. J. Mar. Syst. **15:** 457–473, doi:10.1016/S0924-7963(97)00037-7

———, and R. P. Harris. 1976. Feeding, growth and reproduction of the marine planktonic copepod *Pseudocalanus elongatus* Boeck. J. Mar. Biol. Assoc. U. K. **56:** 327–344, doi:10.1017/S0025315400018956

Pelegrí, S. P., J. Dolan, and F. Rassoulzadegan. 1999. Use of high temperature catalytic oxidation (HTCO) to measure carbon content of microorganisms. Aquat. Microb. Ecol. **16:** 273–280, doi:10.3354/ame016273

Razouls, C., F. de Bovée, J. Kouwenberg, and N. Desreumaux. 2005–2012. Diversity and geographic distribution of marine planktonic copepods. [accessed 13 Sep 2012]. Available from http://copepodes.obs-banyuls.fr/en

Runge, J. A. 1984. Egg production of the marine, planktonic copepod, *Calanus pacificus* Brodsky: Laboratory observations. J. Exp. Mar. Biol. Ecol. **74:** 53–66, doi:10.1016/0022-0981(84)90037-6

Sabatini, M., and T. Kiørboe. 1994. Egg production, growth and development of the cyclopoid copepod *Oithona similis*. J. Plankton Res. **16:** 1329–1351, doi:10.1093/plankt/16.10.1329

Saiz, E., A. Calbet, and E. Broglio. 2003. Effects of small-scale turbulence on copepods: The case of *Oithona davisae*. Limnol. Oceanogr. **48:** 1304–1311, doi:10.4319/lo.2003.48.3.1304

Sazhina, L. I. 1985. Fecundity and growth rate of copepods in different dynamic zones of Equatorial Countercurrent of the Indian Ocean. Pol. Arch. Hydrobiol. **32:** 491–505.

Svensen, C., and T. Kiørboe. 2000. Remote prey detection in *Oithona similis*: hydromechanical versus chemical cues. J. Plankton Res. **22:** 1155–1166, doi:10.1093/plankt/22.6.1155

Temperoni, B., M. D. Viñas, N. Diovisalvi, and R. Negri. 2011. Seasonal production of *Oithona nana* Giesbrecht, 1893 (Copepoda: Cyclopoida) in temperate coastal waters off Argentina. J. Plankton Res. **33:** 729–740, doi:10.1093/plankt/fbq141

Turner, J. T. 2004. The importance of small planktonic copepods and their roles in the pelagic marine food webs. Zool. Stud. **43:** 255–266.

Uchima, M. 1985. Copulation in the marine copepod *Oithona davisae* Ferrari and Orsi. II: Relationship between copulation and egg-laying. Bull. Plankton Soc. Jpn. **32:** 31–36.

Uye, S. 1982. Length–weight relationships of important zooplankton from the Inland Sea of Japan. J. Oceanogr. Soc. Jpn. **38:** 149–158, doi:10.1007/BF02110286

———, and K. Sano. 1995. Seasonal reproductive biology of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. Mar. Ecol. Prog. Ser. **118:** 121–128, doi:10.3354/meps118121

———, and ———. 1998. Seasonal variations in biomass, growth rate and production rate of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. Mar. Ecol. Prog. Ser. **163:** 37–44, doi:10.3354/meps163037

Ward, P., and A. Hirst. 2007. *Oithona similis* in a high latitude ecosystem: Abundance, distribution and temperature limitation of fecundity rates in a sac spawning copepod. Mar. Biol. **151:** 1099–1110, doi:10.1007/s00227-006-0548-1

Associate editor: Michael R. Landry

Received: 07 June 2012
Accepted: 20 October 2012
Amended: 06 November 2012