

# Fecundity of marine planktonic copepods: global rates and patterns in relation to chlorophyll *a*, temperature and body weight

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**ABSTRACT:** Global rates and patterns of fecundity in marine epipelagic copepods were studied as a function of temperature, body weight of the female and concentration of chlorophyll *a*. We divided data into 3 groups: broadcast spawners, sac spawners (including calanoids, cyclopoids and harpacticoids) and poecilostomatoids; although the latter are sac spawners, they were treated separately, but data were too sparse to examine patterns. Fecundity was positively correlated with temperature and body weight in both broadcast and sac spawners. Michaelis-Menten relationships revealed that fecundity rates are significantly related to chlorophyll *a* (chl *a*) concentration for broadcasters, but not so for sac spawners. Broadcasting copepods have a maximum fecundity ( $f_{\max}$ ) of 47 eggs female<sup>-1</sup> d<sup>-1</sup>, with a half-saturation coefficient ( $K_m$ ) of 2.4 µg chl *a* l<sup>-1</sup>, for a body weight of 10 µg C individual<sup>-1</sup>, when all data are adjusted to 15°C. In contrast, fecundity rates in sac spawners are ca. 5 eggs female<sup>-1</sup> d<sup>-1</sup>. Of the broadcaster genera examined, *Centropages* spp. has the highest  $f_{\max}$  at 71 eggs female<sup>-1</sup> d<sup>-1</sup> (data corrected to 15°C), and *Paracalanus* spp. the lowest  $f_{\max}$  at 25 eggs female<sup>-1</sup> d<sup>-1</sup>. In the sac-spawning *Pseudocalanus* spp. we found a significant relationship between fecundity and chl *a*, with an  $f_{\max}$  of only 7.8 eggs female<sup>-1</sup> d<sup>-1</sup>, while for *Oithona* spp. no significant relationship was evident. By comparing *in situ* with laboratory food-saturated rates we were able to assess the degree to which fecundity is food-limited in the natural environment. The degree of food limitation increases with increasing temperature in sac spawners; at low temperatures (~5°C) *in situ* rates are similar to laboratory food-saturated rates, but at 25°C rates are 23% of laboratory food-saturation values. In nature, increasing food limitation with increasing temperature may be the result of greater food requirements to balance respiration demands, i.e. decreasing net growth efficiency in warmer situations. It may also be due to lower availability of suitable food in terms of quality or quantity with increasing temperature, possibly as a result of increased dominance of smaller phytoplankton size fractions (e.g. picoplankton) in warm waters. Food limitation in the environment may be more severe than these comparisons suggest, as laboratory food-saturated fecundity rates in broadcasters may be as low as 36% of the *in situ* maximum rates ( $f_{\max}$  rates).

**KEY WORDS:** Fecundity · Copepod · Chlorophyll *a* · Temperature · Body weight · Food · Food limitation

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## INTRODUCTION

Copepods are the most abundant metazooplankton throughout the world's oceans (Longhurst 1985), and make up the majority of its biomass in the epipelagic

zone. Their dominance, ubiquity, and importance in ocean food webs and biogeochemical cycles has probably led to them becoming one of the most studied metazoan groups in the plankton. Copepod egg production is a regularly measured demographic term; it

determines the potential rate of recruitment to a population, and has often been used to assess growth and secondary production in copepods (Runge & Roff 2000; although for problems see Hirst & McKinnon 2001). Recently Hirst & Bunker (2003) synthesised rates of weight-specific growth of juveniles and weight-specific fecundity of adult females. The latter do not relate to fecundity rates and patterns in a simple and straightforward way. This is because 2 species with the same weight-specific fecundity rates may express this equivalent growth in very different ways, while 1 may produce a small number of large eggs, the other may produce a large number of small eggs. It was therefore necessary to repeat the methods and analysis of Hirst & Bunker (2003) on a simple fecundity basis in order to understand these rates. Whilst growth is a physiological term, fecundity is not, but the latter is an important population demographic term. We are in clear need of a framework of fecundity rates, and how these may differ between copepods with different life-histories (Kjørboe & Sabatini 1995, Hirst & Kjørboe 2002, Hirst & Bunker 2003). Even after several decades of study on copepods, we estimate that much fewer than ~4% of marine planktonic calanoid species (~70 species) have had their fecundity measured. We may need to make predictions on the vast majority of species for which we currently have no measurements (and no realistic chance of making appropriate measurements soon).

The aims of the current paper were to examine the rates and patterns of fecundity in copepods (as eggs female<sup>-1</sup> d<sup>-1</sup>), and to explore aspects of what these rates may indicate with respect to demography and strategy. In this analysis we have chosen to examine patterns in 3 'functional' categories: broadcast spawners i.e. species that shed their eggs freely, sac spawners i.e. species that keep their eggs attached until the point of hatching (includes species from within the orders Calanoida, Cyclopoida and Harpacticoida), and poecilostomatoida (these are sac spawners, but have distinct characteristics that separate them from the sac-spawning group). The term 'sac spawner' as used by us is not an indication of the production of a true membraned sac, but simply the strategy of carrying the eggs attached to the female until hatching. This classification system was chosen for several reasons. Sac-spawning copepods have significantly longer egg-hatch times than broadcast spawners (Hirst & Bunker 2003), this difference may in part arise from the much lower vulnerability and mortality of sac-spawned eggs versus free eggs (Hirst & Kjørboe 2002). Many sac spawners produce fewer numbers of larger eggs than do broadcast spawners, but there appear to be important differences in the ratio of the fecundity rates of these 2 groups as a function of temperature and body weight (Kjørboe & Sabatini 1995, Hirst & Kjørboe

2002). Although poecilostomatoids are sac spawners, these were placed in another category. Virtually all poecilostomatoids are parasites or associates of other animals, and this is perhaps the most diverse order of copepods in terms of gross body morphology (Huys & Boxshall 1991). Within the poecilostomatoids, 4 families are planktonic and can be abundant in marine systems; of these the Corycaeidae and Sapphirinidae are visual predators, while the Oncaeidae are surface-feeders and tend to be found in association with mucoid aggregates, abandoned larvacean houses and other organisms (Huys & Boxshall 1991). The order Poecilostomatoida have radically different egg sizes from the other sac spawners (Fig. 1, Table 1). Although we include data for the poecilostomatoida for comparative purposes, these are too limited to describe patterns in this group.

In single species, fecundity has been related to body size (Landry 1978, Durbin et al. 1983, Runge 1984), age (Kimoto et al. 1986), temperature (Kimoto et al. 1986), salinity (Ambler 1985) and food (Durbin et al. 1983). Multi-species syntheses of fecundity have focused upon the relations to temperature and body size under both food-saturated (Kjørboe & Sabatini 1995) and *in situ* (Hirst & Kjørboe 2002) conditions; unfortunately neither of these studies examined relationships to food availability. We know that fecundity rates are typically food-limited in nature (Durbin et al. 1983, Frost 1985, Runge 1985, Beckman & Peterson 1986, Kjørboe & Nielsen 1994, Liang et al. 1994), but have little or no idea as to how this limitation varies. Although we know that copepods can switch prey, and feed selectively, strong significant relationships between fecundity and food proxies such as chl *a*, POC, PON and microplankton counts have been found (Table 2). Determining broad relationships between fecundity and food proxies, especially those that can be measured rapidly and easily, has clear advantages. We designed this study in order to examine how fecundity of marine copepods in the field relates to chl *a*, temperature and body weight, and to increase our ability to predict copepod *in situ* fecundity rates using the chl *a* term (where appropriate). Additionally we wanted to compare fecundity rates *in situ* to those under food saturation, and to explore food-limitation patterns for the different groups. Finally, we wished to see how fecundity differed between broadcast, sac spawners, and different genera.

## MATERIALS AND METHODS

***In situ* fecundity: data compilation.** We carefully screened data from the literature to obtain values likely to closely represent those *in situ*. A full descrip-

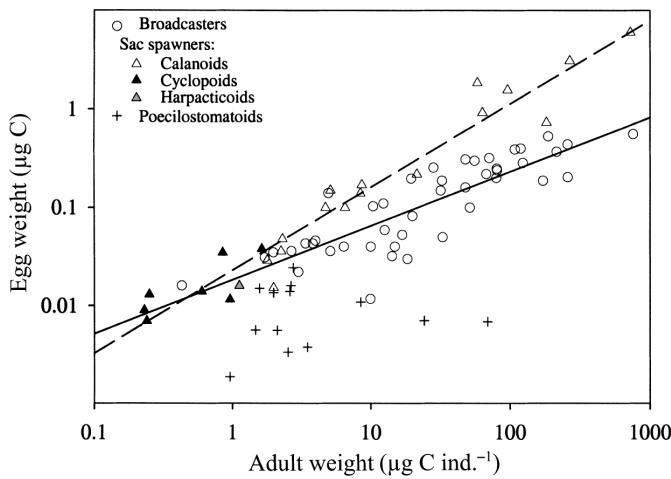


Fig. 1. Egg weights plotted against adult weights for marine epipelagic copepods. The 3 main groups for which we included data were broadcast spawners, sac spawners (calanoids, cyclopoids and harpacticoids) and poecilostomatoids. Data predominantly from Kiørboe & Sabatini (1995), includes the data of Sazhina (1985) with wet weights (WW) converted to carbon weight (CW) assuming  $CW = 6.4\%$  WW from (table on p 212 of Vinogradov & Sushkina 1987). We add data from Hopcroft & Roff (1998) converting ash-free dry weight to carbon, assuming  $AFDW = 89\%$  DW (Båmstedt 1986) and  $C = 40\%$  DW (Båmstedt 1986). Equations from this figure given in Table 1

tion of this screening process is given in Hirst & Bunker (2003). We used adult weights from the original source when these were given; when they were not we took these from Huntley & Lopez (1992), Kiørboe & Sabatini (1995) or from other individual sources of measurements (all data sets and details of conversions available upon request). When weights were given in terms of dry weight or ash-free dry weight they were converted to carbon, assuming this to be 40% of the dry weight (Båmstedt 1986); ash-free dry weight was assumed to be 89% of dry weight (Båmstedt 1986). In cases where authors gave fecundity rates for females in weight-specific terms, we converted back to fecundity as eggs  $\text{female}^{-1} \text{d}^{-1}$  using egg and adult weights. To be included in our analysis each fecundity rate required a 'food proxy' measurement in order to characterise the food environment in which the copepods were being incubated. Initially we included data where any food measure had been made, e.g. POC, PON, microplankton prey counts, size-fractioned and total chl *a* (see Table 3). This entire set was used to explore the role of temperature and

body size (see Tables 4 & 5, Figs. 2 & 3). However, when we then explored the role of food, we only considered a subset of data that included total chl *a* measurements. Unfortunately there were too few data to investigate patterns with the other proxies of food concentration.

The methods used to ascribe a chl *a* value to the fecundity rate measurement varied. From some studies we used chl *a* measurements made on the water used to fill the incubation vessel (e.g. Huntley & Escritor 1991, Uye & Shibuno 1992). However, the majority of values were taken from chl *a* profiles at the depth where incubation water was collected (e.g. Peterson & Kimmerer 1994, Jónasdóttir et al. 1995, Gómez-Gutiérrez & Peterson 1999). If no chl *a* measurement was available from the exact depth where the incubation water was collected, then values from within  $\sim 5$  m of this were accepted (e.g. Hay 1995). This analysis did not include food proxies that had been averaged over depth or integrated (e.g. Runge 1985, Shreeve et al. 2002), or where the fluorescence maximum value was cited but this was not close to the depth of water collection (e.g. Nielsen & Sabatini 1996). We chose volumetric values rather than depth-integrated measurements because the latter can be more poorly related to copepod rates (Calbet & Agustí 1999). We included GF/F, GF/C, 0.8  $\mu\text{m}$  Millipore and Millipore AA filtration as measures of 'total chl *a*', although GF/F overwhelmingly dominated the data set numerically. GF/C (pore size  $\sim 1.2 \mu\text{m}$ ), in addition to 0.8  $\mu\text{m}$  Millipore and Millipore AA pore sizes both  $\sim 0.8 \mu\text{m}$  should underestimate chl *a* in comparison to GF/F (pore size  $\sim 0.7 \mu\text{m}$ ). Under the vast majority of situations however this error will be relatively small, but it is variable and we have made no corrections here.

#### *In situ* fecundity: analyses and statistical treatment.

Species were divided on the basis of whether they represented sac-spawning species, broadcast-spawning species or poecilostomatoids. There were only 2 values of *in situ* fecundity for poecilostomatoids and these were presented graphically alongside the sac spawner

Table 1. Relationships between egg weight ( $\mu\text{g C egg}^{-1}$ ) and adult weight ( $\mu\text{g C ind.}^{-1}$ ) in broadcast- and sac-spawning (calanoids, cyclopoids and harpacticoids) and in poecilostomatoida copepods. n: number of data points; ns: not significant

Group	n	$\log_{10} \text{ egg weight} = a + b$		$r^2$	p
		Intercept (a)	Slope (b)		
Broadcasters	44	-1.736	0.550	0.717	<0.001
Sac spawners	24	-1.638	0.846	0.947	<0.0011
Poecilostomatoida	13	-2.130	0.046	0.005	>0.50 ns

Table 2. Published relationships describing fecundity ( $f$ , eggs female<sup>-1</sup> d<sup>-1</sup>) as a function of concentration of food proxies for marine planktonic copepods. In some instances temperature ( $T$ , °C) and/or body weight ( $\mu\text{g ind.}^{-1}$ ; DW: dry weight; CW: carbon weight; AFDW: ash-free dry weight) are included. Copepods were collected from the environment and immediately incubated in natural seawater, except those in bold face, which were fed natural seawater which had been stored or had its concentration altered by dilution, and those italicised, for which measurements are under artificial laboratory conditions. Letters in equations are resource descriptors (see resource descriptor annotations at end of legend); ln signifies log<sub>e</sub>, log signifies log<sub>10</sub>. In many cases authors did not give equations when relationships were not significant and hence these cannot be included here. A: chl  $a$  ( $\mu\text{g l}^{-1}$ ); B: chl  $a > 1 \mu\text{m}$  ( $\mu\text{g l}^{-1}$ ) averaged over water-column depth; C: chl  $a > 5 \mu\text{m}$  ( $\mu\text{g l}^{-1}$ ) averaged over water-column depth; D: chl  $a > 20 \mu\text{m}$  ( $\mu\text{g l}^{-1}$ ) averaged over water-column depth; E: chl  $a$  5–20  $\mu\text{m}$  ( $\mu\text{g l}^{-1}$ ) averaged over water-column depth; F: chl  $a$  1–5  $\mu\text{m}$  ( $\mu\text{g l}^{-1}$ ) averaged over water-column depth; G: chl  $a < 200 \mu\text{m}$  ( $\mu\text{g l}^{-1}$ ), environment concentration for water from 10 m depth but growth determined in 0.6  $\mu\text{m}$ -filtered seawater; H: Diatom carbon concentration ( $\mu\text{g l}^{-1}$ ), environment concentration for water

Species	Relationship fecundity (eggs female <sup>-1</sup> d <sup>-1</sup> )	Temp range ( $T$ , °C)	r <sup>2</sup>	p
<b><i>Acartia clausi</i> (<i>hudsonica</i>?)</b>	<b>-0.25m + 0.64A</b>	–	–	<b>0.10</b>
<b><i>Acartia omori</i></b>	<b>(0.000331[T + 12.0]<sup>3.25</sup> × A × CW)/(0.470 + A)</b>	<b>15</b>	–	–
<b><i>Acartia steueri</i></b>	<b>(0.0680[T-0.5]<sup>1.72</sup> × A × CW)/(0.912 + A)</b>	<b>20</b>	–	–
<i>Acartia tonsa</i>	3.9V-1.74	15–19	0.74	–
<i>Acartia tonsa</i>	39.16 (1-e <sup>-0.1461(X-1.58)</sup> )	20	–	–
<i>Acartia tonsa</i>	37.46 (1-e <sup>-0.0253(Y-44)</sup> )	20	–	–
<i>Acartia tonsa</i>	40.31 (1-e <sup>-0.00206(Z-377)</sup> )	20	–	–
<i>Acartia tonsa</i>	2.98Q + 19.71	15–19	0.21	–
<i>Acartia tonsa</i>	43.0 (1-e <sup>-0.757(Q-0.63)</sup> )	15–19	0.26	–
<i>Acartia tonsa</i>	47.4 (1-e <sup>-1.512(O-0.01)</sup> )	15–19	0.54	–
<i>Acartia tonsa</i>	47.2 (1-e <sup>-3.309(P-0.35)</sup> )	15–19	0.62	–
<i>Acartia tonsa</i>	54.01 (1-e <sup>-0.29(Q+0.17)</sup> )	12–21	0.78	<0.05
<i>Acartia tonsa</i>	52.94 (1-e <sup>-0.50(P+0.35)</sup> )	12–21	0.85	<0.05
<i>Acartia tonsa</i>	52.34 (1-e <sup>-0.64(O+0.33)</sup> )	12–21	0.80	<0.05
<i>Calanoides acutus</i>	43.2 (M + 14.7)/75.7 + (M + 14.7)	0.5	–	–
<i>Calanoides acutus</i>	16.3 (1-e <sup>-0.62 × b</sup> )	1.2–3.3	0.12	<0.05
<i>Calanoides carinatus</i>	73.698 (1-e <sup>-0.117A</sup> )	10.5–20	0.27	–
<i>Calanus agulhensis</i>	69.371 (1-e <sup>-0.135A</sup> )	9.5–22.5	0.38	–
<i>Calanus chilensis</i>	25.8 (1-e <sup>-0.216(O+0.10)</sup> )	14	0.61	–
<i>Calanus chilensis</i>	0.08Q + 0.87	14	0.46	–
<i>Calanus finmarchicus</i>	10 <sup>0.69 + 0.414(log a)</sup>	~ -1–9.8	0.26	<0.0001
<i>Calanus finmarchicus</i>	2.00S–6.00 (for S < 50), 49.4 (for S > 50)	5.5	0.93	–
<i>Calanus finmarchicus</i> & <i>Calanus glacialis</i>	27.8 (e <sup>-0.22/U</sup> )	0–2.0	0.31	<0.05
<i>Calanus glacialis</i>	3.3488 + 1.5459R	-0.5	0.779	<0.0001
<i>Calanus glacialis</i>	-5.7438 + 1.1467R	-0.5	0.882	–
<i>Calanus finmarchicus</i>	2.06A + 0.6T + 12.24	~4.5–14	–	–
<i>Calanus finmarchicus</i>	e <sup>(0.52 lnA + 0.26 lnT + 1.8)</sup>	~4.5–14	–	–
<i>Calanus helgolandicus</i>	2.83G + 13.8	8.5–17.6	0.144	0.05
<i>Calanus helgolandicus</i>	0.14H + 15.3	8.5–17.6	0.151	0.05
<i>Calanus helgolandicus</i>	0.21J + 13.5	8.5–17.6	0.235	0.01
<i>Calanus helgolandicus</i>	0.26K + 13.7	8.5–17.6	0.123	0.05
<i>Calanus helgolandicus</i>	2.86A - 0.66T + 17.8	~7–20.5	–	–
<i>Calanus helgolandicus</i>	e <sup>(0.85 lnA - 0.62 lnT + 3.3)</sup>	~7–20.5	–	–
<i>Calanus marshallae</i>	(14.94 + 0.0608c)/8 [for c < 3500]	10	0.774	–
<i>Calanus marshallae</i>	(198.5 - 0.0012c)/8 [for c > 3500]	10	0.0007	–
<i>Calanus pacificus</i>	0.154N + 1.47	–	–	–
<i>Calanus sinicus</i>	-1.85 + 5925 (1-e <sup>-0.0038B</sup> )	11.5–15.1	0.27	–
<i>Calanus sinicus</i>	3.03 + 66.4 (1-e <sup>-0.84C</sup> )	11.5–15.1	0.61	–
<i>Calanus sinicus</i>	4.17 + 42.5 (1-e <sup>-4.35D</sup> )	11.5–15.1	0.52	–
<i>Calanus sinicus</i>	-2.22 + 50.5 (1-e <sup>-4.38E</sup> )	11.5–15.1	0.23	–
<i>Calanus sinicus</i>	62.9–46.6F	11.5–15.1	0.52	–
<i>Calanus sinicus</i>	-0.87 + 24.4 (1-e <sup>-0.50B</sup> )	16.8–21.5	0.26	–
<i>Calanus sinicus</i>	-1.79 + 23.4 (1-e <sup>-1.63C</sup> )	16.8–21.5	0.40	–
<i>Calanus sinicus</i>	-3.45 + 22.7 (1-e <sup>-5.69D</sup> )	16.8–21.5	0.37	–
<i>Calanus sinicus</i>	0.83 + 21.1 (1-e <sup>-2.61E</sup> )	16.8–21.5	0.37	–
<i>Centropages abdominalis</i>	CW (0.330 lnT + 0.125 lnA - 0.678)/0.027	8.9–19.7	–	–
<i>Centropages brachiatus</i>	105.133 (1-e <sup>-0.401A</sup> )	11–21.3	0.10	–
<i>Nannocalanus minor</i>	42.335 (1-e <sup>-0.630A</sup> )	11–21.3	0.30	–
<i>Pseudocalanus</i> sp.	0.005N + 1.11	–	–	–
<i>Rhincalanus gigas</i>	18.9 (1-e <sup>-0.46 × b</sup> )	1.2–3.3	0.23	<0.005
<i>Temora longicornis</i>	1.49Q + 18.06	15–19	0.16	–
<i>Temora longicornis</i>	42.4 (1-e <sup>-0.566(O+0.28)</sup> )	15–19	0.38	–
<i>Temora longicornis</i>	53.5 (1-e <sup>-0.341(P+0.07)</sup> )	15–19	0.57	–
<i>Temora longicornis</i>	37.8 (e <sup>-2.9/W</sup> )	9–13	0.83	<0.0005
<i>Undinula vulgaris</i>	13.9 (1-e <sup>-0.0097(L-10)</sup> )	26.3	0.96	–

from 10 m depth; J: Colourless dinoflagellate carbon concentration ( $\mu\text{g l}^{-1}$ ), environment concentration for water from 10 m depth; K: Ciliate carbon concentration ( $\mu\text{g l}^{-1}$ ), environment concentration for water from 10 m depth; L: particulate carbon ( $\mu\text{g l}^{-1}$ ), environment concentration for water from ~1 m depth, copepods incubated not in this water, but in water from within 3 km; M: chl *a* ( $\text{mg m}^{-2}$ ) integrated over 0–150 m; N: chl *a* ( $\text{mg m}^{-2}$ ) integrated over 0–30 m; O: chl *a* ( $>20 \mu\text{m l}^{-1}$ ), values average of those collected at 1, 3 and 5 m depth; P: chl *a* ( $>10 \mu\text{m l}^{-1}$ ), values are average of samples from at 1, 3 and 5 m depth; Q: chl *a* ( $\mu\text{g l}^{-1}$ ), values average of those collected at 1, 3 and 5 m depth; R: chl *a* ( $\text{mg m}^{-2}$ ) integrated over 0–100 m; S: chl *a* ( $\text{mg m}^{-2}$ ) integrated over 0–20 m; U: chl *a* ( $>11 \mu\text{m l}^{-1}$ ) in surface water; V: total chl *a* ( $\mu\text{g l}^{-1}$ ) averaged over 0–10 m, regression only calculated over chl *a* range 1.0–6.0  $\mu\text{g l}^{-1}$ ; W: chl *a* ( $\mu\text{g l}^{-1}$ ), values integrated over 0–50 m; X: chl *a* ( $\mu\text{g l}^{-1}$ ), surface water; Y: nitrogen ( $\mu\text{g l}^{-1}$ ), surface water; Z: carbon ( $\mu\text{g l}^{-1}$ ), surface water; a: chl *a* ( $\text{mg m}^{-3}$ ), values integrated over 0–50 m; b: chl *a* ( $\text{mg m}^{-3}$ ), values integrated over 0–60 m; c: *Thalassiosira weissflogii* (cells  $\text{ml}^{-1}$ ), only this monospecific culture supplied as food

Location	Period	Source	
<b>Jackle's Lagoon, USA</b>	–	<b>Landry (1978)</b>	
<b>Onagawa Bay, Japan</b>	<b>Sep 1977</b>	<b>Uye (1981)<sup>1</sup></b>	
<b>Onagawa Bay, Japan</b>	<b>Sep 1977</b>	<b>Uye (1981)<sup>1</sup></b>	
Long Island Sound, USA	Sept–Oct 1984	Beckman & Peterson (1986)	
Narragansett Bay, USA	Jul–Sep 1979	Durbin et al. (1983)	
Narragansett Bay, USA	Jul–Sep 1979	Durbin et al. (1983)	
Narragansett Bay, USA	Jul–Sep 1979	Durbin et al. (1983)	
Long Island Sound, USA	Mar–Nov 1985	Peterson & Bellantoni (1987)	
Long Island Sound, USA	Mar–Nov 1985	Peterson & Bellantoni (1987)	
Long Island Sound, USA	Mar–Nov 1985	Peterson & Bellantoni (1987)	
Long Island Sound, USA	Mar–Nov 1985	Peterson & Bellantoni (1987)	
Long Island Sound, USA	Jul–Nov 1986	Dam et al. (1994)	
Long Island Sound, USA	Jul–Nov 1986	Dam et al. (1994)	
Long Island Sound, USA	Jul–Nov 1986	Dam et al. (1994)	
Gerlache Strait, Antarctica	Nov 1989	Lopez et al. (1993)	
South Georgia	Dec–Jan 1995/96 + 1998/99	Shreeve et al. (2002) <sup>7</sup>	
Benguela, South Africa	Sep–Mar 1993/94 + 1994/95	Richardson & Verheye (1998)	
Benguela, South Africa	Sep–Mar 1993/94 + 1994/95	Richardson & Verheye (1998)	
off Central Chile	Jan 1986	Peterson & Bellantoni (1987)	
off Central Chile	Jan 1986	Peterson & Bellantoni (1987)	
western North Atlantic	Jun + Nov 1996, Apr 1997	Campbell & Head 2000 <sup>6</sup>	<sup>1</sup> Only reproductively active females used
St. Lawrence, Canada	Jun 1991	Plourde & Runge (1993)	
West coast of Greenland	Jun–Jul 1992	Nielsen & Hansen (1995)	<sup>2</sup> Adult females taken from environment and incubated for 24 h in 0.6 $\mu\text{m}$ -filtered seawater
NE Greenland	early Jun 1991	Hirche & Kwasniewski (1997) <sup>5</sup>	
NE Greenland	early Jun 1991	Hirche et al. (1994)	
compilation of data	–	Harris et al. (2000)	<sup>3</sup> Egg production rates standardised to the average annual female body size
compilation of data	–	Harris et al. (2000)	
Coastal waters, Plymouth	Jan–Sep 94	Pond et al. (1996) <sup>2</sup>	<sup>4</sup> Adult females with dark oocytes in ovary and oviducts used
Coastal waters, Plymouth	Jan–Sep 94	Pond et al. (1996) <sup>2</sup>	
Coastal waters, Plymouth	Jan–Sep 1994	Pond et al. (1996) <sup>2</sup>	
Coastal waters, Plymouth	Jan–Sep 1994	Pond et al. (1996) <sup>2</sup>	
compilation of data	–	Harris et al. (2000)	
compilation of data	–	Harris et al. (2000)	
laboratory data	–	Peterson (1988) <sup>8</sup>	<sup>5</sup> Date from Hirche et al. (1994), but with only the last stations visited (201 to 263) used in equation derivation
laboratory data	–	Peterson (1988) <sup>8</sup>	
Dabob Bay, USA	Jan–Dec 1979 + 1982	Frost (1985) <sup>3</sup>	
Inland Sea of Japan	April 1994	Uye & Murase (1997)	<sup>6</sup> Adult females taken from environment and incubated for 24 h in 0.2 $\mu\text{m}$ -filtered seawater
Inland Sea of Japan	April 1994	Uye & Murase (1997)	
Inland Sea of Japan	April 1994	Uye & Murase (1997)	
Inland Sea of Japan	April 1994	Uye & Murase (1997)	
Inland Sea of Japan	April 1994	Uye & Murase (1997)	
Inland Sea of Japan	Jun 1994 + 1995	Uye & Murase (1997)	
Inland Sea of Japan	Jun 1994 + 1995	Uye & Murase (1997)	
Inland Sea of Japan	Jun 1994 + 1995	Uye & Murase (1997)	
Inland Sea of Japan	Jun 1994 + 1995	Uye & Murase (1997)	
Inland Sea of Japan	Jun 1994 + 1995	Uye & Murase (1997)	
Fukuyama Harbor, Japan	Nov 86–Nov 87	Liang et al. (1994) <sup>4</sup>	<sup>7</sup> Adult females taken from environment and incubated for 24 h in 0.2 $\mu\text{m}$ -filtered seawater; adjusted $r^2$ values; equations in original paper were in error-correct versions presented here (R. Shreeve, pers. comm.)
Benguela, South Africa	Sep–Mar 1993/94 + 1994/95	Richardson & Verheye (1998)	
Benguela, South Africa	Sep–Mar 1993/94 + 1994/95	Richardson & Verheye (1998)	
Dabob Bay, USA	Jan–Dec 1979 + 1982	Frost (1985) <sup>3</sup>	
South Georgia	Dec–Jan 1995/96 to 1998/99	Shreeve et al. (2002) <sup>7</sup>	
Long Island Sound, USA	Mar–Nov 1985	Peterson & Bellantoni (1987)	
Long Island Sound, USA	Mar–Nov 1985	Peterson & Bellantoni (1987)	
Long Island Sound, USA	Mar–Nov 1985	Peterson & Bellantoni (1987)	
Northern North Sea	Sep 1984	Kjørboe & Johansen (1986)	
near Kaneohe Bay, Hawaii	Jun–Dec 1991	Park & Landry (1993)	<sup>8</sup> Equations derived for eggs produced over an 8 d period; we therefore divide result by 8 to convert to eggs $\text{d}^{-1}$

data (see Figs. 2, 3 & 4), but not treated statistically. Regressions between  $\log_e$  fecundity and temperature were used to derive  $Q_{10}$  values (see Fig. 2 & Table 4). To standardise and remove the influence of temperature, rates of fecundity were then corrected to 15°C using each group-specific  $Q_{10}$  value; 1.12 and 1.54 for broadcast and sac spawners respectively. To examine the role of body mass these temperature-corrected rates were  $\log_{10}$ -transformed and regressed against  $\log_{10}$  body weight (see Fig. 3 and Table 5). When correction was necessary for the poecilostomatoida data we always used the sac spawner-specific scaling (temperature and body weight) factors to make these corrections.

Michaelis-Menten relationships were determined between fecundity and chl *a* concentration for broadcast and sac spawners. All rates were first corrected to a temperature of 15°C and a body weight of 10  $\mu\text{g C ind.}^{-1}$  using the appropriate group-specific slopes. Zero values were included in this analysis, and there was no log-transformation (although Fig. 4 shows the results on a log scale). As the genera *Calanus* and *Oithona* dominated the broadcast and sac spawner data sets respectively, these were removed and the relationships derived once again. We did this to test whether results were heavily biased by these 2 genera (results are presented in Table 6).

Although individual species within a single genera may saturate their egg production at different concentrations of food, (e.g. the differences between *Pseudocalanus newmani* and *P. moultoni* as observed by Jónasdóttir 1989), examining broad, single-genera-specific patterns are valuable. We may for example be able to describe the distribution, abundance and biomass of a genera with much less effort than those of a species—and in some cases issues of species distinctions are still being resolved. Data corrected to 15°C but with no correction for body weight were used to derive Michaelis-Menten relationships for individual genera. A relationship was only derived when there was greater than 95 measurements, this was the case for the genera *Acartia*, *Calanus*, *Centropages*, *Paracalanus*, *Pseudocalanus* and *Oithona* (see Fig. 5 & Table 6).

To examine any effect that temperature may have upon the Michaelis-Menten parameters we divided data that had been first corrected to a body weight of 10  $\mu\text{g C ind.}^{-1}$  into smaller temperature ranges ( $-2.3-5$ ,  $>5-15$ ,  $>15-25$  and  $>25-35^\circ\text{C}$ ) and examined relationships within each of these. Similarly, to examine the effect of body weight, the data were first corrected to 15°C, using their group-specific  $Q_{10}$  values, and divided into body weight ranges; 0.1–1, 1–10, 10–100 and 100–1000  $\mu\text{g C ind.}^{-1}$  (results of both analyses are presented in Table 7).

We used backwards stepwise regression to further examine the relationships, where the dependent variable was  $\log_{10}$  fecundity ( $f$ , eggs female $^{-1}$  d $^{-1}$ ) and the independent variables were temperature ( $T$ , °C),  $\log_{10}$  body weight (BW,  $\mu\text{g C individual}^{-1}$ ), and  $\log_{10}$  chl *a* concentration ( $C_a$ ,  $\mu\text{g chl a l}^{-1}$ ).  $F$ -to-enter was set at 4.0, and  $F$ -to-remove at 3.9. Where no independent variables were removed, a multiple linear regression relating  $\log_{10}$  fecundity to all the independent variables was completed (SigmaStat Package, SPSS) with the form  $\log_{10} f = a[T] + b[\log_{10} \text{BW}] + c[\log_{10} C_a] + d$ . If an independent variable did not add significantly to the prediction it was excluded, and the regression completed using the remaining variables. We chose to  $\log_{10}$  transform the  $C_a$  term as this approximately linearises the data. It is a mathematical impossibility to perfectly linearise a Michaelis-Menten function when the dependent term (fecundity) is logged, as is necessary when relating this term to both body weight and temperature (results are given in Table 8 together with  $R^2$  values and significance levels). A single regression was not derived combining sac- and broadcast-spawning fecundity rates; the 2 are so clearly different.

**Food-saturated fecundity: data compilation.** As a comparison for the *in situ* data we also compiled fecundity rates under laboratory conditions where food was supplied in what was believed to be excess. The food-saturated laboratory data were used to examine the degree to which *in situ* rates were food-limited at different temperatures and body sizes (see Figs. 6 & 7, and Tables 4 & 5). We began by re-examining the original data sources compiled by Kiørboe & Sabatini (1995) over the range 10 to 20°C; we however included a greater number of measurements across a wider range of temperatures. Additional data from other published sources were also added. We compiled mean maxima rates rather than absolute individual maximum. We have not included data for wild copepods that were collected, given excess food, and whose fecundity rates were measured shortly afterwards (e.g. Park & Landry 1993, Saiz et al. 1999), because copepods can take time to acclimate to changes in food and using these estimates may underestimate the food-saturated rates. ANCOVA analysis (SPSS package) was used to compare food-saturated with *in situ* fecundity rates by comparing  $\log_e$  fecundity rates versus temperature, and  $\log_{10}$  fecundity versus  $\log_{10}$  body weight (see Figs. 6 & 7). Slopes were first examined for parallelism and, if they were, intercepts were then tested for significant difference (see Table 9).

**Egg weight as proportion of adult weight: data compilation.** The present study describes fecundity rates as a function of temperature and body weight of

adults. In the paper of Hirst & Bunker (2003), relationships are presented between weight-specific fecundity and temperature and body weight, using the same set of data. It is possible to predict from the difference between these 2 relationships (fecundity and weight-specific fecundity) egg weight as a proportion of adult weight in respect to temperature and adult body mass in broadcast and sac spawners. Because such predictions are based upon experimental work that has been screened for suitability for describing fecundity rates, rather than body and egg weight, we chose to derive an independent set of data on these measurements in order to compare with our predictions. We compiled data on egg and adult size and temperature at which these animals were collected, including values given in Sazhina (1985), Huntley & Lopez (1992) and Hopcroft & Roff (1998). (For comparisons between predicted and measured values see Fig. 8 & Table 10).

## RESULTS

### *In situ* fecundity

The entire data set contains 3864 fecundity measurements from ~80 copepod species, with body sizes ranging from 0.199 to 3260  $\mu\text{g C ind.}^{-1}$ . The data set includes measurements made in environments from the tropics to the poles, with temperature ranging from  $-2.3$  to  $30.1^\circ\text{C}$ . Estuarine, coastal upwelling through to oligotrophic open-ocean data were included, and total chl *a* concentrations varied by more than 4 orders of

Table 3. Summary of copepod fecundity ( $f$ , eggs female $^{-1}$  d $^{-1}$ ) under *in situ* and food saturated laboratory conditions. All data (i.e. all food descriptors) used in the analyses presented in Figs. 2 & 3 and Tables 4 & 5 (for which food is not investigated). For subsequent analysis of chl *a* the total chlorophyll *a* data set is used. n (zero): number of non-zero data points used, and (number of zero values); N: number of species

Data type	Adult group	n (zero)	N
<b><i>In situ</i> fecundity</b>			
All food descriptors			
	Broadcasters	3081 (298)	59
	Sac spawners	450 (33)	17
	Poecilostomatoida	2 (0)	2
Total chlorophyll <i>a</i>			
	Broadcasters	1639 (212)	50
	Sac spawners	318 (33)	17
	Poecilostomatoida	2 (0)	2
<b>Food-saturated fecundity</b>			
	Broadcasters	121 (2)	28
	Sac spawners	23 (0)	12

magnitude from 0.016 to 321.6  $\mu\text{g chl } a \text{ l}^{-1}$ . Table 3 summarises the data set and food proxy types with 'total chl *a*' dominating the data entire data set, representing 2204 of the total 3864 measurements.

*In situ* fecundity increases significantly with temperature for both broadcast- and sac-spawning copepods ( $p < 0.001$ ) (see Fig. 2 & Table 4), although the  $r^2$  values are just 0.002 and 0.120 respectively, and hence in broadcasters the variability explained by temperature alone is very small indeed. The relationships between fecundity and temperature demonstrate sac spawners to have a higher slope and  $Q_{10}$  value than broadcasters, with  $Q_{10}$  of 1.54 compared to only 1.12. The results in Fig. 3 & Table 5 show that the fecundity of broadcast and sac spawners scales positively and significantly with body weight ( $p < 0.001$ ); again  $r^2$  values are low at just 0.004 and 0.112 respectively. Scaling appears to be much weaker in broadcasters than sac spawners (both in terms of the slope and the variability that can be explained by body weight). While broadcasters have a fecundity rate that is on average 3.4 times that of sac

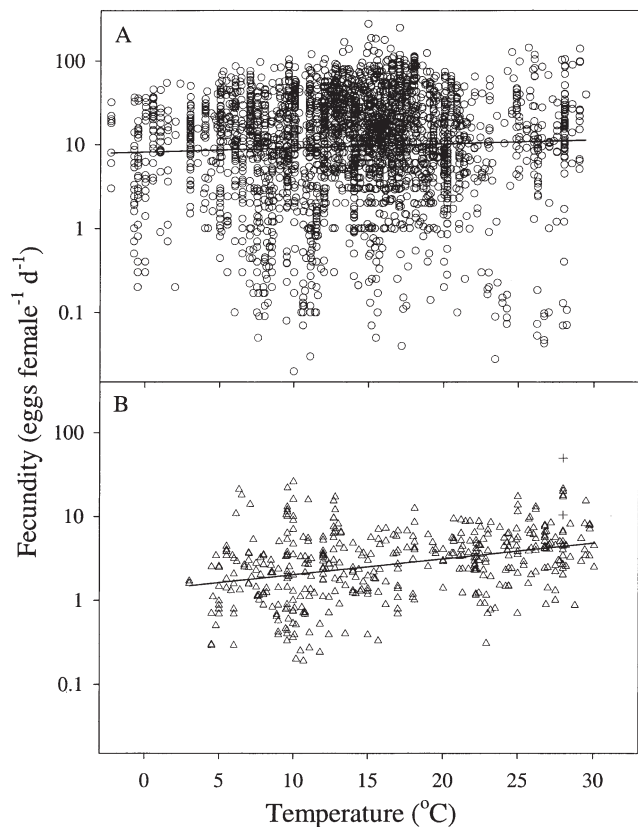


Fig. 2. Fecundity of copepods as a function of temperature. (A) Adult broadcasters; (B) adult sac spawners. Poecilostomatoida values included (+) for comparative purposes, but not included in regression analysis. Lines describe significant regression. Analysis results in Table 4, using  $\log_e$  in calculations

Table 4. Relationships between  $\log_e$  fecundity ( $f$ , eggs female $^{-1}$  d $^{-1}$ ) versus temperature ( $T$ , °C) (see Figs. 2 & 6).  $Q_{10}$  correction factor derived from slope as  $Q_{10} = e^{(10 \times \text{Slope})}$ . n (zero): number of data points on which regressions were performed (number of zero values excluded prior to regression analysis)

Adult group	n (zero)	Temp. range ( $T$ , °C)	$\log_e f = a + b[T]$		$r^2$	p	$Q_{10}$
			Intercept ( $a$ )	Slope ( $b$ )			
<i>In situ</i> fecundity							
Broadcasters	3081 (298)	−2.3–29.4	2.099	0.0111	0.002	<0.001	1.12
Sac spawners	450 (33)	3.0–30.1	0.271	0.0431	0.120	<0.001	1.54
Food-saturated fecundity							
Broadcasters	121 (2)	−1.5–30.0	2.532	0.0467	0.152	<0.001	1.60
Sac spawners	23 (0)	1.3–29.0	−0.056	0.1149	0.461	<0.001	3.15

spawners for individuals with a body weight of  $\sim 1 \mu\text{g C ind.}^{-1}$ , this falls to 1.8 times as body weight approaches  $100 \mu\text{g C ind.}^{-1}$  (as predicted from regressions through data sets). This has implications to demographic differences between the 2 groups (we will return to this point in the 'Discussion').

The results of the Michaelis-Menten plots for the copepod data corrected to  $15^\circ\text{C}$  and  $10 \mu\text{g C ind.}^{-1}$  are

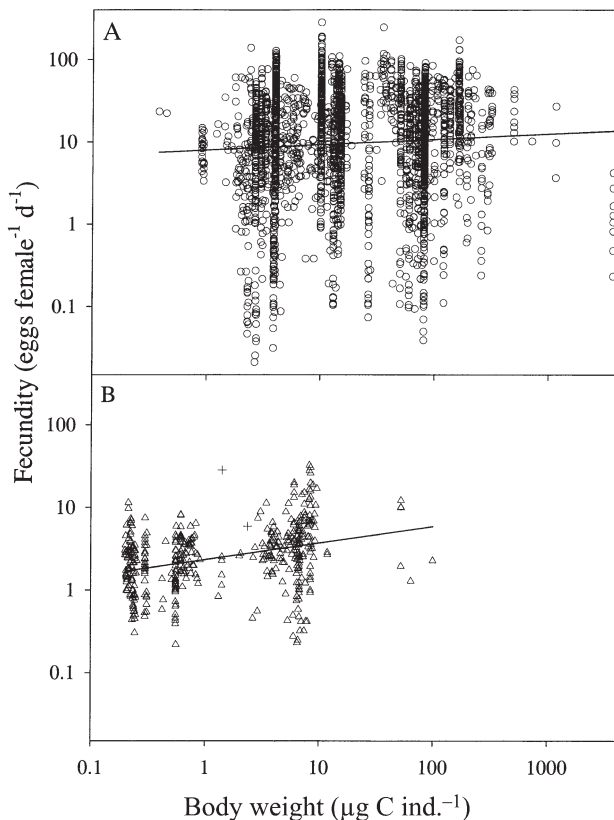


Fig. 3. Fecundity of copepods as a function of body weight. (A) adult broadcasters; (B) adult sac spawners. Poecilostomatoida values included (+) for comparative purposes, but not included in regression analysis. All fecundity rates corrected to  $15^\circ\text{C}$  using group-specific  $Q_{10}$  values in Table 4. Lines describe significant regression. Analysis results in Table 5

shown in Fig. 4 & Table 6. The fecundity of broadcast-spawning copepods is significantly related to chl  $a$  concentration ( $p < 0.0001$ ), achieving an  $f_{\text{max}}$  value of  $47.0$  eggs female $^{-1}$  d $^{-1}$  with a chl  $a$  concentration for half-saturation coefficient ( $K_m$ ) of  $2.4 \mu\text{g chl } a \text{ l}^{-1}$ . The

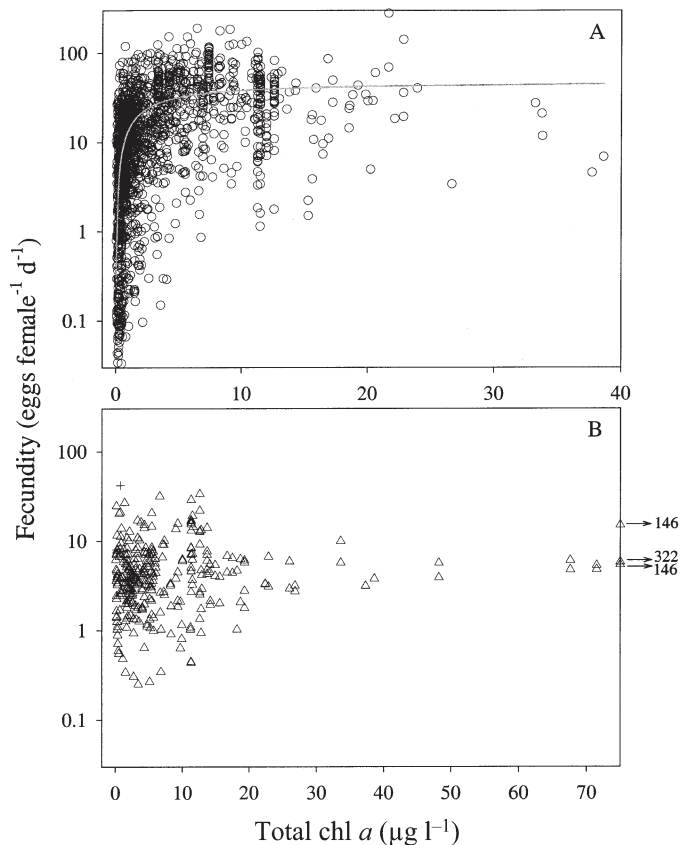


Fig. 4. Michaelis-Menten relationships between *in situ* fecundity ( $f$ , eggs female $^{-1}$  d $^{-1}$ ) and chlorophyll  $a$  concentration ( $C_a$ ,  $\mu\text{g chl } a \text{ l}^{-1}$ ). (A) Adult broadcasters; (B) adult sac spawners. Poecilostomatoida values included (+) for comparative purposes, but not included in regression analysis. All fecundity rates first corrected to  $15^\circ\text{C}$  and then to body weight of  $10 \mu\text{g C ind.}^{-1}$  using group-specific values. Analysis results in Table 6

Table 5. Relationships between  $\log_{10}$  fecundity ( $f$ , eggs female<sup>-1</sup> d<sup>-1</sup>) under both *in situ* and food-saturated laboratory conditions to  $\log_{10}$  body weight (BW,  $\mu\text{g C ind.}^{-1}$ ). All data corrected to 15°C using  $Q_{10}$  values given in Table 4 prior to analysis. n (zero): number of data points on which regressions were performed (number of zero values excluded prior to regression analysis)

Adult group	n (zero)	BW ( $\mu\text{g C ind.}^{-1}$ )	$\log_{10} f = a + b[\log_{10} \text{BW}]$ Intercept (a) Slope (b)		r <sup>2</sup>	p
<i>In situ</i> fecundity						
Broadcasters	3081 (298)	0.380–3620	0.900	0.065	0.004	<0.001
Sac spawners	450 (33)	0.199–119.2	0.369	0.198	0.112	<0.001
Food-saturated fecundity						
Broadcasters	121 (2)	1.5–356.0	1.207	0.201	0.192	<0.001
Sac spawners	22 (0)	0.924–722.0	0.974	–0.296	0.271	<0.02

relationship remains highly significant ( $p < 0.0001$ ) after removing *Calanus* spp., which made up almost 50% of the data, and the resulting values are remarkably similar ( $f_{\text{max}} = 50.8$  eggs female<sup>-1</sup> d<sup>-1</sup>,  $K_m = 2.2 \mu\text{g chl } a \text{ l}^{-1}$ ). It is noteworthy that while body weight and temperature singly each explain <0.5% of the variability in the fecundity of broadcasters (but significantly more in the sac spawners), for chl *a* the variability explained in broadcasters is almost 2 orders of magnitude greater at 26%. For sac spawners the relationship to chl *a* is not significant ( $p = 0.288$ ), and after removing the genus *Oithona* it remains non-significant, but only marginally so ( $p = 0.076$ ).

The Michaelis-Menten relationships for egg production are highly significant for each of the broadcaster genera ( $p < 0.0001$ ) and for the sac spawners *Pseudocalanus* spp. ( $p = 0.028$ ) (Fig. 5 & Table 6). The values of  $f_{\text{max}}$  for significant relationships vary from 24.8 to 71.5 eggs female<sup>-1</sup> d<sup>-1</sup> for the broadcasters *Paracalanus*

and *Centropages* respectively, with only 7.8 eggs female<sup>-1</sup> d<sup>-1</sup> for the sac spawners *Pseudocalanus* spp. Although *Centropages* spp. is not the heaviest genus analysed (mean body weight 20  $\mu\text{g C ind.}^{-1}$ ), its  $f_{\text{max}}$  is the greatest. The  $K_m$  values for broadcasting copepods are all very similar, ranging from 1.4 to 2.2  $\mu\text{g chl } a \text{ l}^{-1}$ ; however, the  $K_m$  for *Pseudocalanus* spp. is lower and outside this range at just 0.86  $\mu\text{g chl } a \text{ l}^{-1}$ .

Michaelis-Menten relationships were examined as a function of temperature and body weight over restricted data ranges (Table 7). Sac spawners revealed no significant relationships within all ranges studied ( $p > 0.05$ ); in contrast the broadcasters have significant relationships in all temperature and body weight ranges (Figs. 6 & 7). These results are consistent with the findings for the entire set of data. In broadcasters,  $f_{\text{max}}$  increases with increasing temperature from 17.5 eggs female<sup>-1</sup> d<sup>-1</sup> at –2.3 to 5°C to 101.4 eggs female<sup>-1</sup> d<sup>-1</sup> at 25 to 35°C. Across this range,  $K_m$  also

Table 6. Michaelis-Menten relationships between fecundity ( $f$ , eggs female<sup>-1</sup> d<sup>-1</sup>) and chlorophyll *a* concentration ( $C_a$ ,  $\mu\text{g chl } a \text{ l}^{-1}$ ) for all groups, and genera-specific relationships where  $n > 95$ . Fecundity rates corrected to 15°C using appropriate  $Q_{10}$  values in Table 4, and \* values corrected to body weight (BW) of 10  $\mu\text{g C ind.}^{-1}$  using slopes in Table 5. Zero values were included in all these derivations. n: number of data points; N: number of species

Group	n	N	Mean BW ( $\mu\text{g C ind.}^{-1}$ )	Temp. range ( $T$ , °C)	Chl <i>a</i> range ( $C_a$ , $\mu\text{g l}^{-1}$ )	$f = C_a [f_{\text{max}}]/(C_a + K_m)$ $f_{\text{max}}$ (SE) $K_m$ (SE)		r <sup>2</sup>	p
Broadcasters	1851	50	10*	0.0–29.0	0.016–38.62	46.99 (2.05)	2.40 (0.27)	0.259	<0.0001
Sac spawners	351	17	10*	3.0–30.1	0.069–321.6	5.13 (0.32)	0.07 (0.06)	0.003	0.2877ns
Broadcasters (without <i>Calanus</i> )	944	42	10*	0.0–29.0	0.061–38.62	50.78 (3.09)	2.21 (0.38)	0.201	<0.0001
Sac spawners (without <i>Oithona</i> )	211	10	10*	3.0–28.2	0.128–146.0	5.36 (0.55)	0.22 (0.18)	0.015	0.0758ns
<b>Broadcaster genera</b>									
<i>Acartia</i> spp.	366	12	4.99	3.0–29.0	0.140–33.75	46.17 (4.96)	2.18 (0.71)	0.190	<0.0001
<i>Calanus</i> spp.	907	9	121.43	0.0–25.0	0.016–33.79	39.90 (2.03)	2.02 (0.25)	0.333	<0.0001
<i>Centropages</i> spp.	192	5	20.19	3.0–28.0	0.140–33.24	71.48 (7.55)	1.82 (0.67)	0.206	<0.0001
<i>Paracalanus</i> spp.	101	3	2.80	8.0–28.2	0.161–38.62	24.77 (4.73)	1.36 (0.85)	0.190	<0.0001
<b>Sac spawner genera</b>									
<i>Pseudocalanus</i> spp.	98	3	7.99	3.0–18.1	0.140–12.60	7.837 (1.35)	0.864 (0.78)	0.050	0.0277
<i>Oithona</i> spp.	140	7	0.32	8.9–30.1	0.069–321.6	2.508 (0.17)	–0.030 (0.02)	0.011	0.2179ns

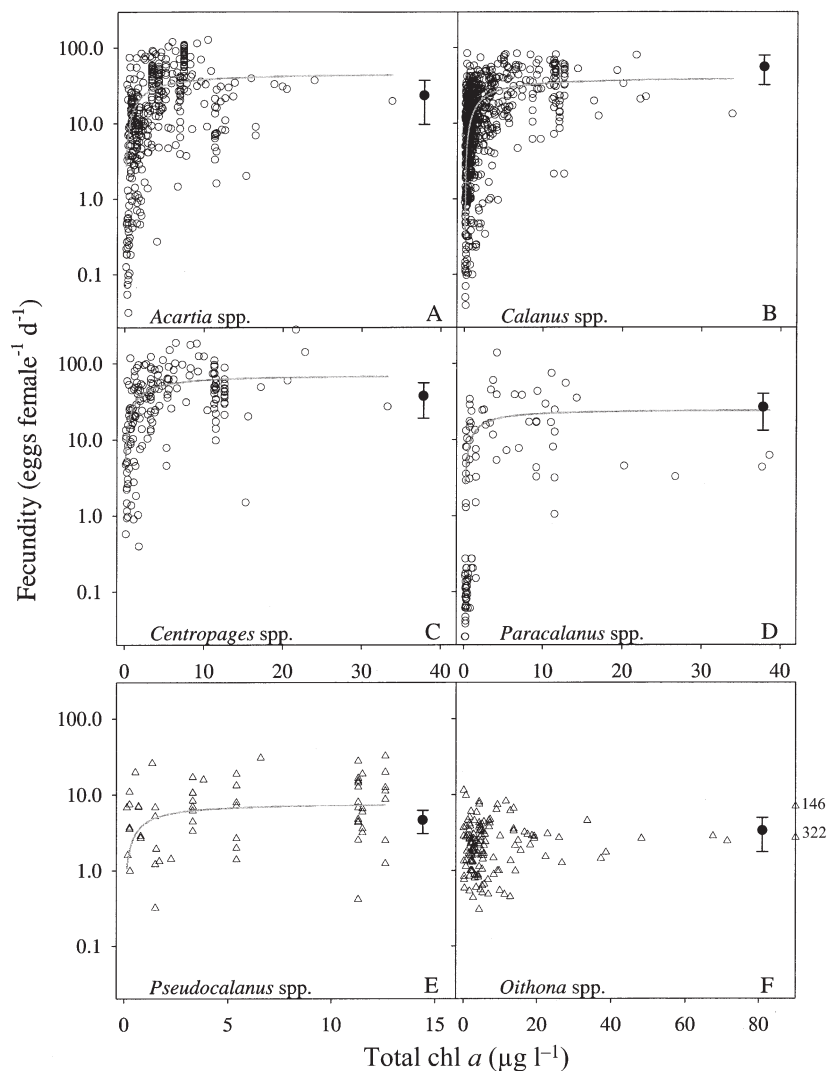


Fig. 5. Michaelis-Menten relationships between *in situ* fecundity ( $f$ , eggs female<sup>-1</sup> d<sup>-1</sup>) and chlorophyll  $a$  concentration ( $C_a$ ,  $\mu\text{g chl } a \text{ l}^{-1}$ ) for 6 copepod genera. (A) *Acartia* spp.; (B) *Calanus* spp.; (C) *Centropages* spp.; (D) *Paracalanus* spp.; (E) *Pseudocalanus* spp.; (F) *Oithona* spp. All individual fecundity rates corrected to 15°C using group-specific  $Q_{10}$  values, no body weight corrections made. Mean laboratory food-saturated rates (corrected to 15°C) given for comparison; (●) mean rate; error bars:  $\pm$ SD.

Analysis results in Table 6

tends to increase, from 0.54  $\mu\text{g chl } a \text{ l}^{-1}$  at  $-2.3$  to  $5^\circ\text{C}$  to 5.66  $\mu\text{g chl } a \text{ l}^{-1}$  at 15 to  $25^\circ\text{C}$ . Therefore in warmer waters their maximum potential egg production rates are higher; however the chl  $a$  levels to reach half-saturation also tend to be higher. Broadcasters in the weight range  $>10$  to  $\leq 100 \mu\text{g C ind.}^{-1}$  have the highest  $f_{\text{max}}$  and  $K_m$  values of 56.2 eggs female<sup>-1</sup> d<sup>-1</sup> and 3.02  $\mu\text{g chl } a \text{ l}^{-1}$ . Although generally large broadcasting copepods are able to produce more eggs when saturated than smaller copepods (Fig. 7), they do not have higher weight-specific fecundity rates, which actually

are on average lower (Hirst & Bunker 2003). They achieve their additional fecundity by producing eggs that are a smaller proportion of their adult size than those of the smaller broadcasters (as evident from the results in Figs. 1 & 8 and in Table 2).

The fecundity of broadcasters was found to be dependent upon all 3 variables, temperature, body weight and chl  $a$ , and hence a multiple linear regression was completed including all of these (Table 8). For sac spawners chl  $a$  was not found to add to the prediction, and was therefore removed prior to the regression analysis; this is consistent with the Michaelis-Menten relationships for this group not being significant.

#### Food-saturated fecundity

We included 146 measurements from 40 species, ranging in temperature from  $-1.5$  to  $30.0^\circ\text{C}$  (Tables 3 & 4) for laboratory food-saturated fecundity rates (Table 9). These are significantly related to temperature in both broadcast and sac spawners ( $p < 0.001$ ), with  $Q_{10}$  values of 1.60 and 3.15 respectively (Table 4). Food-saturated rates scaled significantly and positively with body size in broadcast adults ( $p < 0.001$ ), but negatively in sac spawners ( $p < 0.02$ ). The laboratory food-saturated rates were compared with *in situ* rates as a function of temperature (Fig. 6), and as a function of body weight (Fig. 7). Differences between food-saturated laboratory data and *in situ* data should give us an indication as to the degree of food limitation in the natural environment and also allow us to determine if the degree of food limitation alters with temperature or body weight.

ANCOVA analyses revealed that the slopes for laboratory food-saturated and *in situ* rates of fecundity against temperature are significantly different for sac spawners ( $p = 0.021$ ), with the degree of food limitation changing as a function of temperature. The slopes for laboratory food-saturated and *in situ* rates of fecundity against temperature were not significantly different for the broadcasters ( $p = 0.076$ ), while the intercepts were significantly different ( $p < 0.0001$ ), indicating that *in situ* rates are food-limited but that the degree of food limitation does not change with

Table 7. Michaelis-Menten relationships between fecundity ( $f$ , eggs female<sup>-1</sup> d<sup>-1</sup>) and chlorophyll *a* concentration ( $C_a$ ,  $\mu\text{g chl } a \text{ l}^{-1}$ ) for temperature and body weight groupings. †Fecundity rates corrected to 15°C using appropriate  $Q_{10}$  values in Table 4, \*values corrected to body weight (BW) of 10  $\mu\text{g C ind.}^{-1}$  using group-specific slopes in Table 5. Zero values were included in all these derivations. n: number of data points; N: number of species; ns: not significant

Adult group	Temp. range ( $T$ , °C)	n	N	BW ( $\mu\text{g C ind.}^{-1}$ )	Chl <i>a</i> range ( $C_a$ , $\mu\text{g l}^{-1}$ )	$f = C_a [f_{\text{max}}]/(C_a + K_m)$		$r^2$	p
						$f_{\text{max}}$ (SE)	$K_m$ (SE)		
Broadcasters	-2.3–5	145	10	10*	0.030–20.40	17.54 (1.54)	0.54 (0.23)	0.147	<0.0001
	5–15	863	26	10*	0.030–37.70	38.89 (2.37)	2.17 (0.37)	0.237	<0.0001
	15–25	759	30	10*	0.016–23.91	88.51 (8.91)	5.66 (1.07)	0.387	<0.0001
	25–35	84	15	10*	0.061–38.62	101.35 (17.45)	2.30 (0.88)	0.428	<0.0001
Sac spawners	-2.3–5	2	1	10*	0.800–0.80	–	–	–	–
	5–15	150	6	10*	0.140–12.80	4.82 (0.75)	0.60 (0.62)	0.013	0.165ns
	15–25	121	8	10*	0.230–321.6	6.80 (0.59)	0.16 (0.13)	0.020	0.120ns
	25–35	78	14	10*	0.069–71.50	9.18 (0.93)	-0.002 (0.03)	0.0001	0.977ns
Broadcasters15 <sup>†</sup>		463	25	>1–≤10	0.138–38.62	47.57 (4.31)	2.19 (0.59)	0.268	<0.0001
	15 <sup>†</sup>	1220	25	>10–≤100	0.016–33.79	56.23 (3.25)	3.02 (0.42)	0.286	<0.0001
	15 <sup>†</sup>	159	8	>100–≤1000	0.090–18.50	27.55 (2.16)	0.46 (0.19)	0.155	<0.0001
Sac spawners15 <sup>†</sup>		138	7	>0.1–≤1	0.069–321.6	2.545 (0.17)	-0.031 (0.02)	0.013	0.180ns
	15 <sup>†</sup>	202	7	>1–≤10	0.128–146.0	5.088 (0.56)	0.290 (0.24)	0.017	0.062ns
	15 <sup>†</sup>	10	5	>10–≤100	0.128–12.6	2.452 (1.68)	-0.065 (0.07)	0.054	0.519ns

temperature. Comparing laboratory food-saturated and *in situ* rate data against body weight revealed that the slopes are parallel in broadcasters ( $p = 0.133$ ), and the intercepts are significantly different ( $p < 0.0001$ ). Again broadcasters are food-limited *in situ*, but the degree of limitation does not alter with body weight. In comparison, slopes for sac spawners are not parallel ( $p < 0.0001$ ) (we will return to this issue in the 'Discussion').

Genera specific food-saturated rates were derived from the laboratory data for comparison against the Michaelis-Menten relationships from the *in situ* data. The laboratory saturated rates corrected to 15°C were: *Acartia* spp., 23.2 eggs female<sup>-1</sup> d<sup>-1</sup> ( $\pm 13.6$  SD); *Centropages* spp., 37.4 ( $\pm 18.4$  SD); *Calanus* spp., 55.0 ( $\pm 23.3$  SD); *Paracalanus* spp., 26.5 ( $\pm 13.4$  SD); *Pseudocalanus* spp., 4.6 ( $\pm 1.57$  SD) and *Oithona* spp. 3.4 ( $\pm 1.60$  SD).

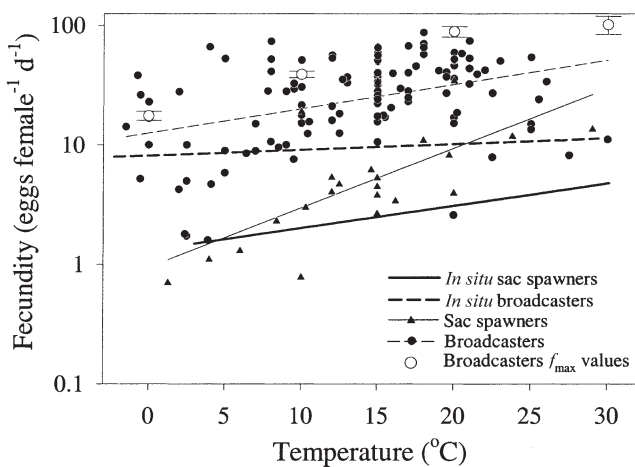


Fig. 6. Food-saturated fecundity ( $f$ , eggs female<sup>-1</sup> d<sup>-1</sup>) of broadcast and sac spawners versus temperature ( $T$ , °C). *In situ* relationships given for comparison;  $f_{\text{max}}$  and SE values plotted from Michaelis-Menten relationships of *in situ* data separated into temperature categories (see Table 7)

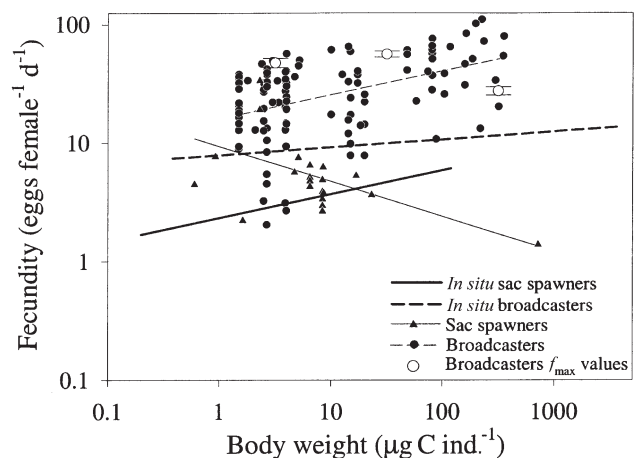


Fig. 7. Food saturated fecundity ( $f$ , eggs female<sup>-1</sup> d<sup>-1</sup>) of broadcast and sac spawners versus body weight (BW,  $\mu\text{g C ind.}^{-1}$ ). All fecundity rates corrected to 15°C using appropriate  $Q_{10}$ s in Table 4. *In situ* relationships given for comparison.  $f_{\text{max}}$  and SE values plotted from Michaelis-Menten relationships of *in situ* data separated into body weight categories (see Table 7)

Table 8. Results from regressions relating dependent variable  $\log_{10}$  fecundity ( $f$ , eggs female<sup>-1</sup> d<sup>-1</sup>) to independent variables temperature ( $T$ , °C),  $\log_{10}$  body weight (BW,  $\mu\text{g C ind.}^{-1}$ ) and  $\log_{10}$  total chlorophyll  $a$  concentration ( $C_a$ ,  $\mu\text{g chl a l}^{-1}$ ). Those independent variables not significantly adding to predictions were removed prior to completion of multiple linear regression analysis

Adult group	Ind. variables included	$\log_{10}f = a[T] + b[\log_{10}\text{BW}] + c[\log_{10}C_a] + d$					R <sup>2</sup>		p	(n)
		a	b	c	d	(T; $\log_{10}\text{BW}$ ; $\log_{10}C_a$ )				
Broadcasters	All included	0.017	0.191	0.706	0.323	0.311	<0.001; <0.001; <0.001		1639	

Adult group	Ind. variables included	$\log_{10} f = a[T] + b[\log_{10}\text{BW}] + c$				R <sup>2</sup>	p	(n)
		a	b	c	(T; $\log_{10}\text{BW}$ )			
Sac spawners	$C_a$ removed	0.026	0.208	-0.038	0.203	<0.001; <0.001		(318)

Table 9. Results of ANCOVA analysis comparing laboratory food-saturated of fecundity rates ( $f$ , eggs female<sup>-1</sup> d<sup>-1</sup>) against *in situ* rates. B: Broadcast spawners; S: sac spawners; BW: body weight

1	ANCOVA groups	Relationship	Fig. ref.	Significance (p)	Conclusion	
				Parallelism of lines	ANCOVA	
B <i>in situ</i>	B laboratory food-saturated	$\log_e f$ vs T	6	0.076	<0.0001	Slopes parallel, intercepts significantly different
S <i>in situ</i>	S laboratory food-saturated	$\log_e f$ vs T	6	0.021	-	Slopes not parallel
B <i>in situ</i>	B laboratory food-saturated	$\log_{10} f$ vs $\log_{10}$ BW	7	0.133	<0.0001	Slopes parallel, intercepts significantly different
S <i>in situ</i>	S laboratory food-saturated	$\log_{10} f$ vs $\log_{10}$ BW	7	0.001	-	Slopes not parallel

Table 10. Comparison of predicted relationships between egg weight/adult weight (EW/AW) versus adult body weight and temperature and values measured using compilations of data from literature. Predictions derived from the difference between equations for weight-specific fecundity given by Hirst & Bunker (2003) and those for fecundity given here. n: number of data points; ns: not significant

Measured	n	Intercept (a)	Slope (b)	r <sup>2</sup>	p
Predicted					
<b><math>\log_{10} \text{EW/AW} = a + b[\log_{10} \text{adult weight}]</math></b>					
Broadcasters					
Measured	44	-1.736	-0.450	0.629	<0.001
Predicted	-	-1.903	-0.316	-	-
Sac spawners					
Measured	24	-1.638	-0.154	0.370	<0.002
Predicted	-	-1.623	-0.030	-	-
<b><math>\log_e \text{EW/AW} = a + b[\text{temperature}]</math></b>					
Broadcasters					
Measured	174	-6.043	0.0495	0.155	<0.001
Predicted	-	-5.850	0.0352	-	-
Sac spawners					
Measured	74	-3.958	-0.0114	0.0197	>0.20ns
Predicted	-	-3.638	-0.0072	-	-

**Egg weight as a proportion of adult weight: data compilation**

A simple comparison of the relationships for fecundity against temperature and body weight with the relationships found for weight-specific growth (Hirst & Bunker 2003) allowed us to solve for egg weight as a proportion of adult weight against temperature and body weight (Fig. 8, Table 10). Broadcast and sac-spawned eggs both comprise a progressively smaller proportion of the adult weight as adult weight increases. At an adult weight of 1  $\mu\text{g C ind.}^{-1}$ , both groups have eggs that are ~2% of adult body weight on average; but the negative slope is much steeper for broadcasters, and at 100  $\mu\text{g C ind.}^{-1}$  sac spawners have eggs ~1.1% of adult weight, while for broadcasters this averages only 0.2%. Broadcasters show an increase in the proportional size of eggs with increasing temperature, while sac

spawners show no evidence of change with temperature. As the predictions are close to measurements taken from independent sources of egg and adult weight data, this confirms that the differences in the relationships between fecundity and weight-specific fecundity (Hirst & Bunker 2003) are not only a consequence of changes in the size of eggs in relation to adult weight as a function of temperature and body weight in the data set, but these differences are reflected in relative egg to adult size in nature too.

## DISCUSSION

*In situ* rates of fecundity in epipelagic copepods are significantly and positively correlated with temperature, and have  $Q_{10}$ s of 1.12 and 1.54 for broadcast and sac spawners respectively, which are much lower than the food-saturated rates of 1.60 and 3.15. Using the same data set, the  $Q_{10}$ s for *in situ* weight-specific fecundity are 1.59 and 1.43. We were able to demonstrate herein that differences in these values (slopes) between fecundity and weight-specific fecundity are driven by the changes in egg to adult weight that occur with changes in temperature (see last subsection of 'Results', Fig. 8 & Table 10). The  $Q_{10}$  values of *in situ* rates of fecundity and weight-specific fecundity are well below the food-saturated and food-unlimited rates of weight-specific fecundity; this is an indication of increasing food limitation with increasing temperature, and is discussed in more detail later.

Kjørboe & Sabatini (1995) found no body mass scaling in the fecundity rates of either broadcast or sac-spawning copepods under laboratory food-saturated conditions. However, in contrast, using a larger set of laboratory data, we found significant positive scaling in broadcasters. This group also demonstrated positive scaling for the *in situ* data. We found significant positive scaling in sac-spawner fecundity *in situ*, but significant negative scaling under food-saturated laboratory conditions (Fig. 7). Clearly there is contradiction between these 2 observations, as in some instances the *in situ* data exceeds the food-saturated data. This may be because our *in situ* data for sac spawners comprised few measurements with body weights  $>10 \mu\text{g C ind.}^{-1}$ , while the food-saturated data was very limited for body weights  $<2.3 \mu\text{g C ind.}^{-1}$ .

Oithonidae do not produce feeding currents, and in general have much lower daily rations (Price 1988), this may in part explain their generally lower weight-specific fecundity and fecundity rates. The genus *Oithona* has relatively low fecundity rates compared with suspension-feeding calanoid sac spawners of

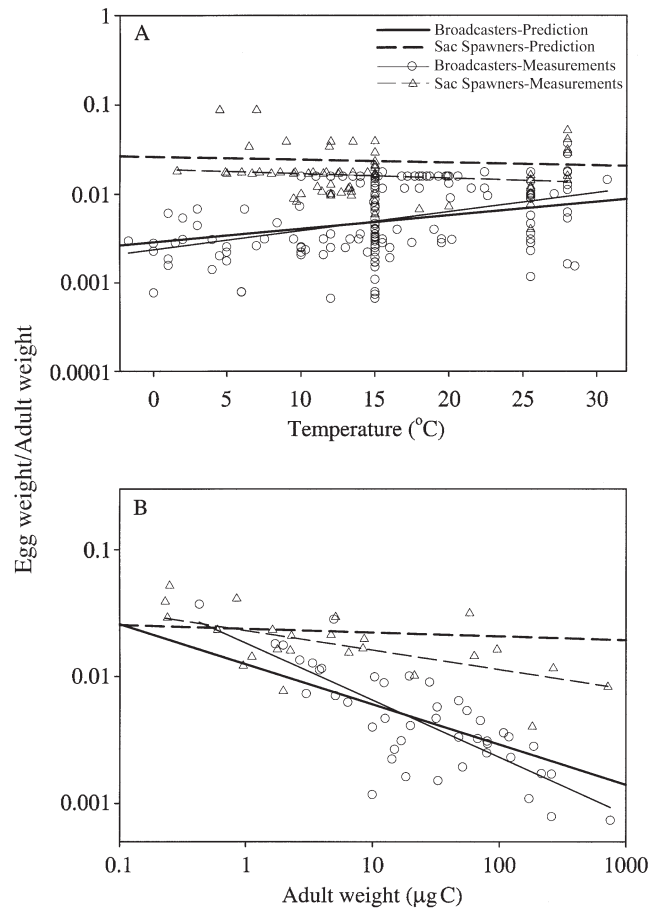


Fig. 8. Egg weight as a proportion of adult weight versus (A) temperature and (B) adult body weight in broadcast and sac spawners

medium body weight such as *Pseudocalanus*, *Clausocalanus* and *Eurytemora*, while the fecundity of very large carnivorous taxa such as *Euchaeta* can be very low. We therefore propose that sac-spawner fecundity may not scale with body weight in a simple linear form, but a dome-shaped relationship may be appropriate. This is the form for the relationship suggested for weight-specific fecundity also (Hirst & Bunker 2003). Unlike broadcasters, egg size for sac spawners is a relatively constant proportion of adult weight, and hence the pattern of weight-specific fecundity versus body weight is similar to that for fecundity. Because of insufficient data on food-saturated fecundity in sac spawners, we were unable to examine the degree of food limitation in this group.

Most broadcast spawners examined herein were calanoids, and these are omnivorous but often strongly herbivorous, especially when phytoplankton concentrations are high (Kleppel 1993, Halvorsen et al. 2001). Many sac spawners examined were cyclopoids, and for

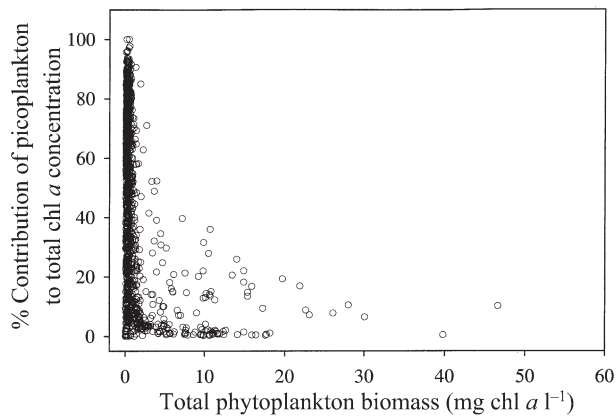


Fig. 9. Percentage contribution of picoplankton (<2  $\mu\text{m}$ ) to total chl *a* concentration in natural waters as a function of total chl *a* concentration. Data compiled by Agawin et al. (2000) and supplemented by additional sources, i.e. E. Mara $\acute{o}$ n pers. comm. (data from central Atlantic) and A. Clarke (data from Signy coastal waters, Antarctica)

many cyclopoids such as *Oithona* spp. omnivory can be heavily skewed towards predation on microzooplankton such as ciliates and heterotrophic flagellates (e.g. Nakamura & Turner 1997, Lonsdale et al. 2000). These factors could explain why the Michaelis-Menten relationship between fecundity and chl *a* was strongly significant for broadcasters ( $p < 0.0001$ ), but not for sac spawners ( $p = 0.288$ ), and why chl *a* was removed prior to backwards step-wise regression for this latter group. When *Oithona* spp. were removed from the sac spawner data set, the Michaelis-Menten relationship was marginally insignificant ( $p = 0.076$ ), while the relationship for *Oithona* spp. alone continued to be very poor ( $p = 0.218$ ). The feeding preferences and switching strategies of *Oithona* may explain why they can continue to have relatively high rates of fecundity and growth even in lower chl *a* environments, and why these rates are less variable in space and time than those of broadcasters. It is interesting that we found equally (and strongly) significant relationships between chl *a* levels and fecundity rates for large lipid-storing broadcasting genera as for smaller genera that are not renowned for high lipid content (Table 6). This was not expected, because many large copepods such as *Calanus* spp. can produce eggs when food is scarce (for example, during the pre-spring bloom period), and hence egg production can be more decoupled from food supply in such genera.

Although total chl *a* is not an ideal proxy of potential food, it dominates the global data set that we have at present, and hence our reliance upon it herein. Particle abundance, size fractionated and biochemical mea-

surements of the food environment may prove better descriptors of food available, especially for sac spawners. However, these measurements are scant, provide little global coverage (Table 3), and have often been made in ways that would not allow direct comparison between studies because of differences in protocols (Table 1). Copepods are generally regarded as being unable to prey upon the smallest phytoplankton, and yet picoplankton (<2  $\mu\text{m}$  in size) make up a very variable, and at times very high proportion of the total chl *a* in waters with less than  $\sim 5 \mu\text{g chl a l}^{-1}$  (Fig. 9). Size-fractionated chl *a* that excludes such small fractions may therefore be a better proxy of available food, and hence be better related to fecundity and growth. Indeed, many individual studies have demonstrated better relationships between fecundity and size-fractionated chl *a* than with total chl *a* (Table 1). Increased variability in fecundity and weight-specific growth of broadcasters at low chl *a* concentrations may also be due to a steep slope in the relationship over a small range, but also to possible prey-switching and the use of non-chl *a* bearing particles (Hirst & Bunker 2003). Also, as already mentioned, at high chl *a* levels ( $\geq 5 \mu\text{g chl a l}^{-1}$ ), the proportion of larger cells is relatively constant, while in low chl *a* environments the contribution that larger cells make towards total chl *a* is much more variable (Fig. 9).

Maximum fecundity rate ( $f_{\text{max}}$ ) of broadcasting copepods (standardised to  $10 \mu\text{g C ind.}^{-1}$ ) increased with increasing temperature from  $17.5 \text{ eggs female}^{-1} \text{ d}^{-1}$  in the  $-2.3$  to  $5^\circ\text{C}$  temperature range to  $101.4 \text{ eggs female}^{-1} \text{ d}^{-1}$  at  $25$  to  $35^\circ\text{C}$  (Table 8). In fact the  $f_{\text{max}}$  values derived from the *in situ* data were higher than the regression line through the laboratory 'food-saturated' data, but increased as a function of temperature and body weight similar to rates measured under food-saturated laboratory conditions (see comparison in Figs. 6 & 7). We may therefore conclude that fecundity rates under food-saturated laboratory conditions underestimate the true maximum rates in nature; thus, for example, the fecundity of broadcasters at  $20^\circ\text{C}$  under laboratory food-saturated conditions is predicted from the regression as  $32.0 \text{ eggs female}^{-1} \text{ d}^{-1}$ , whereas the comparable  $f_{\text{max}}$  value is  $88.5 \text{ eggs female}^{-1} \text{ d}^{-1}$ . This is the greatest divergence of these 2 measures; at  $0^\circ\text{C}$ , laboratory food-saturated fecundity is  $12.6 \text{ eggs female}^{-1} \text{ d}^{-1}$ , and  $f_{\text{max}}$  is  $17.5 \text{ eggs female}^{-1} \text{ d}^{-1}$ . Comparison between fecundity rates under laboratory food-saturated conditions and *in situ*  $f_{\text{max}}$  rates on a genera-specific basis (Fig. 5), reveals that the laboratory rates substantially underestimate maximum fecundity rates in *Acartia* spp. *Centropages* spp. and *Pseudocalanus* spp. The 2 estimates are very similar for *Paracalanus* spp. while for *Calanus* spp., the laboratory rates are actually higher than the *in situ*

$f_{\max}$ . It is not surprising that maximum fecundity (and also growth) rates are often underestimated in laboratory studies, as very limited numbers of prey species (often just 1) are typically used to feed the experimental animals. Monoculture and restricted diets may not provide all the components necessary to allow maximum rates of growth and fecundity. Reassuringly, however, the general similarity in the  $f_{\max}$  and maximum fecundity rates in the laboratory (although the latter are somewhat lower) do confirm the approximate pattern of food limitation in the natural environment with respect to temperature and body size, if not the absolute magnitude.

When Michaelis-Menten relationships were derived over the 10°C temperature ranges, half-saturation constants ( $K_m$ ) for broadcasters increased with increasing temperature up to 20°C. Thus, copepods generally need greater concentrations of chl *a* to half saturate their fecundity in warmer waters compared to cold. In order to assess potential food limitation of fecundity in nature we compared our  $K_m$  values with a compiled database of chl *a* values (Fig. 10). Provisionally, it appears that fecundity of broadcasters will often be food-limited in natural waters with high temperatures, as the chl *a* levels needed to half-saturate fecundity ( $K_m$  values) are typically higher than the chl *a* levels found in both oceanic and coastal areas. In contrast, at temperatures below ~10°C the chl *a* levels appear high enough for fecundity rates to be often half saturated in

coastal areas, but still typically higher than those found in oceanic areas. This also supports the finding that rates of fecundity *in situ* are increasingly below the maximum achievable rate as temperature increases (as in Fig. 6). For comparative purposes we also include in Fig. 10 rates for weight-specific growth of juvenile copepods, and weight-specific fecundity of adults from Hirst & Bunker (2003) corrected to 15°C and 10 µg C ind.<sup>-1</sup>. The  $K_m$  value for weight-specific fecundity is close to that of fecundity, as might be expected, while the values for weight-specific growth of juvenile broadcasters are much lower (i.e. more commonly and easily half-saturated), and those for juvenile sac spawners lower still (half-saturation of their weight-specific growth achieved in waters with chl *a* levels of just 0.02 µg l<sup>-1</sup>).

The increasing divergence between the slopes for fecundity of *in situ* and laboratory food-saturated sac spawners with increasing temperature demonstrates greater food limitation of *in situ* rates at higher temperatures (Fig. 6, see Table 9 for ANCOVA analysis). Thus while *in situ* rates are similar to laboratory food-saturated rates at low temperatures of ~5°C, they are on average only 23% of those under laboratory food saturation at 25°C. For broadcasters the slopes also appear to diverge with increasing temperature; however ANCOVA analysis did not reveal a significant difference between fecundity slopes for *in situ* and laboratory food-saturated individuals, although the intercepts were significantly different. Making predictions from the regressions for broadcasters we find that, at 0°C, *in situ* fecundity rates are 64.9% of laboratory food-saturated rates, while at 25°C they are just 26.6%. Hirst & Bunker (2003) found these slopes to be significantly different and to diverge when these adult broadcaster rates were expressed in weight-specific terms. The slope of weight-specific fecundity versus temperature is 0.0994 for broadcasters under food-saturated laboratory conditions (Hirst & Bunker 2003), but much shallower (only 0.047) for food-saturated fecundity (eggs female<sup>-1</sup> d<sup>-1</sup>). While the slopes for weight-specific fecundity versus temperature are 0.046 for broadcasters under *in situ* conditions (from Hirst & Bunker 2003), they are only 0.011 for their fecundity rates *in situ*, again much shallower. The differences between slopes for weight-specific fecundity and fecundity are driven by changes in the relative size of egg to adult weight that occur in the natural environment as a function of temperature (Fig. 8 & Table 10). In sac spawners, while eggs comprise a similar proportion of adult size in cold and warm waters, broadcasters eggs comprise a smaller proportion of the adult size in cold waters than in warm waters. Large sac spawners have eggs which on average comprise a

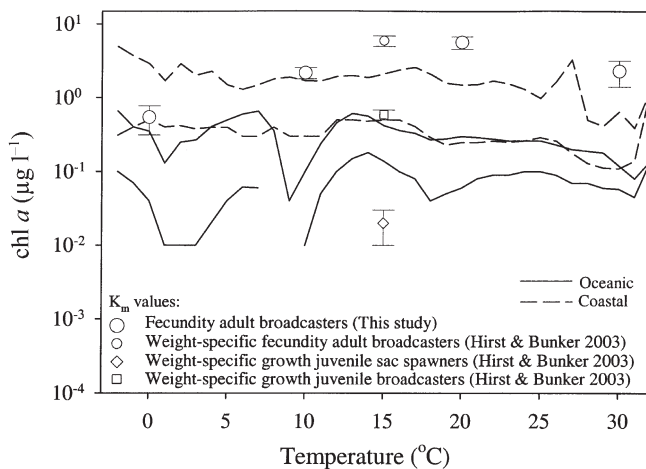


Fig. 10. Chl *a* levels needed to achieve  $K_m$  (half-saturation) of fecundity (this study) and weight-specific growth and weight-specific fecundity (from Hirst & Bunker 2003) for copepods as a function of temperature. For comparative purposes, global compilation of chl *a* measurements is included, taken from oceanic (>300 m bottom depth) and coastal surface waters (<300 m bottom depth) (data from US National Oceanographic Data Center, Silver Spring, Maryland, USA). Data were binned into 2°C intervals, and first and third quartile within each were used as ranges for values shown (data supplied by Á. López-Urrutia)

slightly smaller proportion of adult size than eggs of small species, but for broadcasters these differences are much more dramatic. Broadcasters with a body weight of  $\sim 0.1$  to  $1 \mu\text{g C ind.}^{-1}$  have eggs of a size similar to those of sac spawners of the same adult weight, whereas broadcasters with an adult weight of between  $\sim 100$  and  $1000 \mu\text{g C ind.}^{-1}$  have eggs that are almost 1 order of magnitude smaller than those of sac-spawned copepods of the same size.

It is generally considered that broadcasters produce a greater number of smaller eggs than sac spawners because their freely broadcast eggs are very much more vulnerable and have much greater mortality rates (Hirst & Kiørboe 2002). Broadcasters produce much smaller eggs as a proportion of adult weight than sac spawners in colder waters, while in warm waters the differences between the 2 are much less (Fig. 8). Sac spawners produce eggs that comprise a relatively constant proportion of the adult female size, regardless of temperature or adult weight. We are therefore led to ask the question 'why'? We can determine how many more eggs broadcasters will have to produce in comparison to sac spawners if we assume these two have broadly similar post-hatch mortality rates (see Fig. 6 of Hirst & Kiørboe 2002) and total egg to adult development times and sex ratios (Hirst & Kiørboe 2002). The net reproductive rate,  $R_0$ , (i.e. the number of offspring per female that survive until the next generation), is given by the rate of mortality ( $\beta$ ,  $\text{d}^{-1}$ ), the development time ( $D$ , d), [= time from being laid as an egg to moulting into adulthood], and the egg production rate of sac spawners ( $m_s$ , eggs female $^{-1}$  d $^{-1}$ ). For sac spawners there is no need to separate eggs and post-hatch individuals, and the equation is:

$$R_0 = (m_s/\beta)e^{-\beta D} \quad (1)$$

where  $m_s$  is the fecundity rate of sac spawners. The assumption that the mortality rate is age-independent is unrealistic for broadcast-spawning copepods because free eggs suffer much higher mortality rates than post-hatch stages. Instead, by using the ratio egg-hatching time ( $\tau$ , d) to development time ( $D$ , d) in broadcast spawners as compiled by Kiørboe & Sabatini (1994, 1995) of  $\tau/D = 0.05$ , and further assuming that free eggs have a mortality rate that is 10 times higher than the mortality of post-hatch stages (Kiørboe 1998), i.e.  $\beta_e = 10 \beta_h$ , then for broadcasters the equation becomes:

$$R_0 = (m_b/\beta_h)e^{-1.45\beta_h D} \quad (2)$$

where  $m_b$  is the fecundity rate of broadcast spawners.

Next if we assume that development times and post-hatch mortality rates are equal in the 2 groups, then

$$(m_s/\beta_h)e^{-\beta D} = (m_b/\beta_h)e^{-1.45\beta_h D} \quad (3)$$

which, simplified, allows us to derive the ratio of fecundity in broadcasters to fecundity in sac spawners ( $m_b/m_s$ ):

$$(m_b/m_s) = e^{0.45\beta_h D} \quad (4)$$

Using this equation we find that the ratio ( $m_b/m_s$ ) is 5.0 when temperature is  $3^\circ\text{C}$  (i.e.  $D = 67.4$  d and  $\beta_h \sim 0.053\text{d}^{-1}$  [derived from Hirst & Kiørboe 2002]), while at  $29^\circ\text{C}$  the ratio falls to 1.4 ( $D = 9.06$  d and  $\beta_h \sim 0.34\text{d}^{-1}$ ). Thus, in cold water, broadcasters must produce a dramatically greater number of eggs than sac spawners. By comparison regressions through the empirical data set presented herein (Fig. 2, Table 4) give ratios of 5.7 and 2.5 at  $3$  and  $29^\circ\text{C}$  respectively. The prediction and empirical data are therefore in relatively good agreement. More simply, although mortality of broadcast eggs (in units  $\text{d}^{-1}$ ) is lower in cold waters, the product of total mortality integrated over the whole hatch period is greater than in warmer waters. Broadcasters have very similar rates of weight-specific fecundity to those of sac spawners across the same temperature range (Hirst & Bunker 2003); hence broadcasters achieve the additional fecundity not by producing more egg mass, but by using this mass to produce smaller eggs. Our arguments are relatively simplistic, and closer examination of these assumptions and other consequences of making eggs that comprise a relatively smaller proportion of the adult weight need investigation. We lack a comprehensive understanding of the vulnerability of free eggs in the natural environment. How does egg mortality/vulnerability of free eggs alter with egg size? Does the critical assumption that the mortality rate of broadcast eggs is 10 times that of post-hatch individuals hold across a wide range of environments? Clearly much more work is needed before we can fully appreciate factors in the global ocean driving the observed patterns.

On a global scale, the percentage contribution of smaller phytoplankton (e.g. picoplankton) decreases dramatically as total phytoplankton biomass increases (Agawin et al. 2000 and our Fig. 9 which contains new additional data), and it has been observed that large phytoplankton cells dominate when total chl *a* levels are high (Richardson & Verheye 1998). Smaller phytoplankton are generally considered more accessible to smaller copepods (Hansen et al. 1994), and larger genera such as *Calanus* are considered to prefer large phytoplankton cells (Peterson & Bellantoni 1987). Therefore it might be expected that when total chl *a* levels are low (and hence a greater dominance of smaller sizes of phytoplankton), more food on average will be available to smaller herbivorous copepods than to large ones. However, in contrast to

these expectations there were no strong trends in  $K_m$  values for broadcasting genera differing greatly in their size. Thus, for example, *Calanus* spp. has a very similar  $K_m$  to the much smaller *Acartia* spp. (Table 6). Furthermore,  $K_m$  values do not show a consistent increase with increasing body weight when the data are divided into ranges (Table 7). Fig. 7 compares the fecundity rates of food-saturated broadcasters with *in situ* data with respect to body size. Although the slopes of these lines appear to visually diverge, the slopes are not significantly different (ANCOVA results: Table 9), suggesting on average no apparent increase in food limitation with increasing body weight. Hirst & Bunker (2003) found the slopes for weight-specific fecundity rates of *in situ* and laboratory food-saturated copepods to be parallel (i.e. the degree of food limitation did not on average increase with increasing size); in addition they found no clear pattern for changes in  $K_m$  values with increasing body weight, which is consistent again with the situation found herein for fecundity. Although there are individual examples of larger species/genera that need higher chl *a* levels to half-saturate their weight-specific growth and fecundity, no such pattern is clear when the data are divided into body weight groups and examined irrespective of taxa. Clearly this very important topic, which we have been unable to resolve (possibly due to our limited data), needs more attention in the future.

The Michaelis-Menten relationships partially explain the observation of increasing food limitation with increasing temperature.  $K_m$  values have a general tendency to increase in warmer waters (Table 7 & Fig. 10); i.e. greater levels of chl *a* have to be reached for saturation of fecundity to be achieved, whilst levels of total chl *a* in the natural environment are generally not any greater in warmer waters than in cold waters. Increasing  $K_m$  with increasing temperature may be a consequence of the copepods needing more food to sustain fecundity, i.e. a greater amount and also proportion of the assimilated matter is needed to meet respiration demands (Ikeda et al. 2001). There are other reasons, not necessarily mutually exclusive, that may also explain this pattern. The quantity of total phytoplankton chl *a* attributable to the small, presumably largely inaccessible picoplankton, also tends to increase in warmer waters, although this relationship is not strong and only applicable at very high temperatures, i.e.  $\geq 26^\circ\text{C}$  (Agawin et al. 2000).

For sac-spawning copepods, the Michaelis-Menten relationships were not significant for the entire data set (Table 6), or for the Michaelis-Menten relationships divided into body weight or temperature groups (Table 7). The average fecundity rates of sac spawn-

ers in low ( $< 1 \mu\text{g chl a l}^{-1}$ ) and in high ( $> 5 \mu\text{g chl a l}^{-1}$ ) food environments, are still very similar, at  $8.1 (\pm 9.6 \text{ SD})$  and  $8.6 (\pm 9.6 \text{ SD})$  eggs female $^{-1} \text{ d}^{-1}$  respectively. In contrast, broadcasting copepods produce an average of  $7.2$  eggs female $^{-1} \text{ d}^{-1}$  at low chl *a* concentrations and  $37.7$  eggs female $^{-1} \text{ d}^{-1}$  at high chl *a* concentrations. The ability of some sac spawners to continue to produce eggs in low chl *a* environments needs more thorough investigation, especially as the importance of small cyclopoids in low chl *a* environments can be great, and vast areas of the world's oceans have low chl *a* levels. Many poecilostomatoids have eggs that are much smaller than those of broadcasters and other sac spawners of similar adult body weight (Fig. 1), *Sapphirina* spp. for example can have eggs that are  $< 0.03\%$  of adult weight. However, *Corycaeus amazonicus* has egg weights that are around  $1\%$  of the adult weight (Hopcroft & Roff 1998), a value very similar to that of broadcast and sac spawners of the same adult size. We have insufficient data to accurately reflect the poecilostomatoids, yet these are a very ubiquitous and important group; small *Oncaea* species are amongst the most numerous copepod taxa in oceanic regions. It is long overdue that these species be systematically examined with respect to life-history (egg-hatch times, rates of fecundity and development, growth and mortality) and physiological rate processes. This was pointed out by Böttger-Schnack et al. in 1989, and is still relevant today.

On a global scale, adult fecundity is much more food-limited than juvenile weight-specific growth (see Hirst & Bunker 2003). Fecundity of broadcasters is more dependent upon food than temperature, except possibly at low temperatures. Spatio-temporal variability in the fecundity of adults should be increasingly driven by food as temperature increases. In temperate systems, greater variability has been observed in the fecundity of broadcasters than in that of sac spawners both temporally (e.g. Frost 1985, Kiørboe & Nielsen 1994, Sabatini & Kiørboe 1994), and spatially (e.g. Nielsen & Sabatini 1996), and small sac-spawning calanoids and cyclopoids have been found to maintain high fecundity rates in low chl *a* conditions (Frost 1985, Ohman 1985, Nielsen & Sabatini 1996). Herein we have confirmed these observations with a larger set of standardised and inter-comparable data. Given the more ready saturation of fecundity and growth in sac spawners (Hirst & Bunker 2003), and also their less variable egg mortality rates (Hirst & Kiørboe 2002), we suggest that the abundance and biomass of sac spawners will be more spatio-temporally uniform than those of broadcasters (Paffenhöfer 1993). Interestingly, *Pseudocalanus* spp. was the only sac-spawning genus for which

there was a significant Michaelis-Menten relationship, and its  $K_m$  of  $0.86 \mu\text{g chl a l}^{-1}$  was lower than any of the broadcaster genera (whose  $K_m$  values ranged from 1.36 to  $2.18 \mu\text{g chl a l}^{-1}$ ), while its mean body weight was not the lowest (Table 6). Frost (1985) also found egg production by the broadcaster *Calanus pacificus* to saturate at higher food concentrations than that of the sac spawner *Pseudocalanus* sp. In our extensive compilation we found the genus *Calanus* to have a 2.3-fold greater half-saturation constant ( $K_m$ ) for fecundity than the genus *Pseudocalanus*. Although broadcasters may need higher chl *a* levels to approach saturated rates of fecundity than sac spawners, the maximum fecundity rates they can achieve are greater too (Fig. 5). Where chl *a* is very low for long periods (e.g. polar waters), and/or when it is continually low (e.g. oligotrophic waters) we therefore predict from our observations of fecundity that the importance of sac spawners such as *Oithona* spp. would increase, and that they would continue to produce eggs in reasonable numbers when other species cannot.

Our study would not be complete without a discussion on the vertical structure of biota in the water column. Copepods and their prey can be distributed in discrete layers that vary temporally. There are certainly strong diel signatures in the gut fullness of many copepod species collected from the environment (Head et al. 1999), that may reflect an inherent diel pattern for the species, or be the result of migration associated with a changing food supply. This heterogeneity will not be represented correctly in a container in which a copepod is kept with a near-constant food supply for 24 h. This also makes the application of the equations derived herein more difficult. Strictly, the vertical distribution of both copepods and chl *a* need to be known. This is not an issue confined to our study, but it is currently largely overlooked in the application of almost all experimental rates of this form to field data. Typically, copepods are net collected at the surface or in a depth-integrated sample, and then 'picked' prior to incubation in natural seawater collected from a single or mixed depths (often from the fluorescence maximum). Other methods include incubating copepods with water that has been collected from various depths and then mixed to form the food medium. However, neither approach considers that copepods may experience heterogeneous food concentrations over short time intervals, or vertically migrate across large temperature and food concentration gradients. We continue to largely ignore these issues, presumably because they are hard to deal with when making such measurements. These issues need now to be tackled more comprehensively.

Huntley & Lopez (1992) synthesised development rates in copepods and converted these to juvenile growth rates. Using development times to predict juvenile growth rates does not accurately represent the natural variability in and the degree of food limitation affecting juvenile copepod growth rates (Hirst & Bunker 2003). Predictions of *in situ* juvenile growth rates are also very different from predictions of adult fecundity with respect to the degree of food limitation (adult fecundity is much more food-limited) and natural variability (adult fecundity rates are much more variable). The global temperature-dependency of juvenile weight-specific growth is not representative of the patterns of weight-specific fecundity (Hirst & Bunker 2003) or absolute fecundity (present study), because adult fecundity is much more food-limited than juvenile growth, and this food limitation increases in progressively warmer waters. As a consequence we cannot measure copepod fecundity alone and assume that this (as weight-specific fecundity) will represent juvenile growth rate, as has been assumed previously.

The relationships presented here are the first devised for copepod fecundity at this scale, and the first synthesis of copepod fecundity rates to include a proxy of food. We also give Michaelis-Menten relationships for several key genera. If we compare each measured value in the database with the predictions using the multiple linear regressions, then predictions fall within the measured values by a factor of 2 (i.e. between 0.5 and 2 times the measured values) on 42 and 63% occasions for broadcast and sac spawners respectively. Thus our framework appears to allow prediction of fecundity rates within broad but reasonable limits. Our ability to predict fecundity using this approach is similar to that for weight-specific fecundity, but much weaker than that for juvenile weight-specific growth. This synthesis highlights the fact that we lack measurements for many ubiquitous genera and species of sac spawners and broadcasters (e.g. *Temora*, *Clausocalanus*, *Euchaeta*, *Undinula*, *Metridia*, *Microsetella*, *Microcalanus*, *Ctenocalanus*) and the poecilostomatoids in general. The latter are often massively undersampled with traditional plankton nets, yet they occur worldwide and are very numerous (Hopkins 1985, Böttger-Schnack et al. 2001). In order to quantify their magnitude and contribution to the biogeochemistry of the ocean we will need concerted effort. Their incubation to derive natural rates may be difficult, given their feeding preferences, and approaches such as the egg-ratio method may be more suitable for studying their fecundity. Although chl *a* may not be the most appropriate proxy for food availability, this study demonstrates it is of more use for broadcasting copepods than for sac spawners, as

shown by the significance of the various Michaelis-Menten plots of fecundity versus total chl *a* concentration, and the multiple linear regression analysis. It is a common practice to use chl *a* as a food proxy for copepods, and this study highlights the limits (both explanatory and predictable) to such approaches, especially for sac spawners. It may be very illuminating to examine or measure other food proxies and specific compounds (such as fatty acids) together with adult fecundity/weight-specific fecundity on a global basis to see if these may better explain the increasing degree of food limitation in adults with increasingly warmer water.

In the present paper we studied patterns of egg production rates in relation to size, temperature and chl *a*. Clearly within these patterns there are important (sometimes subtle, sometimes not) differences between genera and between the species. These differences underpin important life-history differences between species. Comparisons of life-history and behaviour of individual species may eventually enable us to understand the attributes that different species have evolved, and why some species are so much more numerous than others. Our study is broad (global)-scale, grouping diverse forms and expressing degree of similarity in rates; there is still much to learn from the differences in the details.

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