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RESEARCH ARTICLE

Oithona similis in a high latitude ecosystem: abundance, distribution and temperature limitation of fecundity rates in a sac spawning copepod

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Abstract In this study we report the abundance, fecundity and an index of the relative survival of *Oithona similis* (nauplii to copepodites) across a large latitudinal and temperature range within the Southern Ocean. The abundance of *O. similis* was strongly related to temperature and to depth-integrated (0–100 m) chlorophyll *a*, abundance increasing with increasing temperature (and therefore decreasing latitude) and Chl *a*. In situ egg production rates and fecundity per female were also significantly and positively related to temperature and Chl *a*. Egg hatch times rapidly lengthen as temperature decreases and in sac spawning species the next batch of eggs cannot be produced until the previous clutch hatch. Consequently, we predict that in *O. similis*, fecundity must decline rapidly at low temperatures, especially below 5°C. A model comparing maximum rates of fecundity with in situ data suggested production rates were strongly food limited across our study region. However, the relationship of in situ and maximum rates to temperature were similar, confirming the importance of temperature. Further, as time taken to develop from egg to adult also rapidly extends with declining temperature, it is increasingly unlikely that *O. similis* will be able to maintain its population against mortality. Our findings have broad implications for the cold temperature (and hence geographic) limits of *O. similis*, but also for the distribution of other sac spawning copepods and planktonic species generally.

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Introduction

Plankton species that are truly cosmopolitan are the exception rather than the rule in the world's ocean. Most species appear to have centres of distribution within ranges that are variable in extent and which may often, but not always, be linked to particular physical features such as water masses. In the Southern Ocean the zonal distribution of copepod assemblages has been recently investigated by Atkinson and Sinclair (2000) who demonstrate the overwhelming numerical dominance of small species throughout the region. Although many species were distributed widely from the Antarctic zone proper to the sub-Antarctic and in some cases beyond, there was a tendency for most to be more abundant in certain parts of their ranges than in others. The underlying mechanisms that influence population demography and determine the distributional limits of species are however generally not well understood. In order to address this problem we focus here on *Oithona similis*, a member of a ubiquitous genus of sac spawning cyclopoid copepods found throughout much of the world's ocean.

O. similis is the most widely distributed member of the genus occurring through sub-tropical, temperate and polar waters. Knowledge of its true abundance, biomass and ecological role has advanced in recent decades (e.g. Paffenhöfer 1993; Kiørboe and Sabatini

1995; Nielsen and Sabatini 1996; Atkinson 1998; Gallienne and Robins 2001; Castellani et al. 2005.), and its importance within the metazoan zooplankton is increasingly recognised. Atkinson (1998) has reviewed aspects of its abundance, distribution and life-cycle in the Southern Ocean and concluded that *Oithona* spp. (mainly *O. similis*) frequently accounts for half of all copepod numbers, has an omnivorous diet, which may account for the apparent de-coupling of its life-cycle from primary production cycles, and may reproduce year round. It is also noticeably more abundant in the region of the Polar Front than near the Antarctic continent where it is comparatively rare. Detailed investigations of the population biology of this genus (e.g. fecundity, cohort structure, mortality) have been largely restricted to temperate (Sabatini and Kiørboe 1994; Uye and Sano 1995, 1998; Nielsen and Sabatini 1996; Eiane and Ohman 2004) and tropical waters (Hopcroft and Roff 1996, 1998; McKinnon and Klumpp 1998), we aim to redress this balance somewhat in this study.

The purposes of this investigation were to examine *O. similis* across a broad range of latitude in Antarctic waters, to determine its abundance and fecundity, and attempt to understand controls on its demography and distribution in this cold-water ecosystem.

Materials and methods

Sampling took place at a range of stations across the Scotia Sea and around South Georgia during two cruises onboard RRS James Clark Ross (Fig. 1). Cruise JR70 (59 stations) was located around South Georgia and took place in January 2002 and cruise JR82 (61 stations), spanning the Scotia Sea, took place in January–February 2003.

Environment

At each station chlorophyll *a* (Chl *a*) was measured with an Aqua Tracka fluorometer (Chelsea Instruments) attached to a Seabird 911 + CTD and carousel sampler equipped with twelve 10 l Niskin bottles (see Korb and Whitehouse 2004 for details). Fluorescence was binned every 2 m and calibrated against discrete samples of Chl *a* taken by water bottles at standard depths; (approximately 7, 20, 40, 60, 80 and 100 m) at each of the 120 stations sampled. Integrated Chl *a* (m^{-2}, 0–100 m) was determined by summation of values over depths. Mean temperature within the top 200 m was similarly determined by averaging CTD data collected at 2 m resolution.

Net sampling

During both cruises, zooplankton was collected using a motion compensated Bongo Net of mouth opening 61 cm diameter equipped with a 100 μm mesh net. The net was deployed from the surface to 200 m (cruise JR70) or to 400 m (cruise JR82) and hauled vertically back onboard the stationary vessel at a speed of ~0.22 m s^{-1}. Samples were preserved immediately in 10% Borax buffered formaldehyde for return to the laboratory. The locations of all stations where net samples were collected are presented in Fig. 1.

In the laboratory, samples were sub-divided using a Folsom plankton splitter and the aliquots examined for *O. similis* using a binocular microscope at 60× magnification. Copepodite stages of *O. similis* were separated from the larger co-occurring *O. frigida* and counts were made of adult males and females, copepodite stages (C1–C5 combined), and egg sacs. Egg sacs of *O. frigida* were easily distinguished from those of *O. similis* by virtue of their smaller size and flask shaped appearance containing low numbers of eggs. Naupliar stages of the two species were difficult to separate and so were combined. We are however confident that the vast majority were attributable to *O. similis* because: (1) across both cruises *O. similis* were on average 80 times more abundant than *O. frigida*, and (2) *O. frigida* eggsacs were much rarer than those of *O. similis*. We chose not to inflate our observed abundances to allow for net inefficiencies in capture, and values were standardised to ind m^{-2}. Using a 100 μm mesh net inevitably meant that the smaller nauplii stages would not be quantitatively sampled, although all stages were at least found to be present within the catch. Intact egg sacs were always longer than they were wide [average 333 μm (±50.6 μm SD) in length and 105 μm (±9.6 μm) in width], sufficiently large for us to have confidence that they would be quantitatively retained by the net. As a simple provisional test of this we separated out 50 egg sacs at random, suspended them in 500 ml of water and poured them onto a 100 μm filter and checked to see whether any passed through. This process was repeated five times with the mesh retaining all egg sacs on each occasion.

To investigate whether egg numbers per sac varied with latitude and temperature, 30 egg sacs were randomly taken at each of a total of 25 stations, individually dissected, and the total numbers of eggs per sac counted.

Fecundity

At the 25 stations where direct counts of eggs per egg sac were made, the number of egg sacs was multiplied

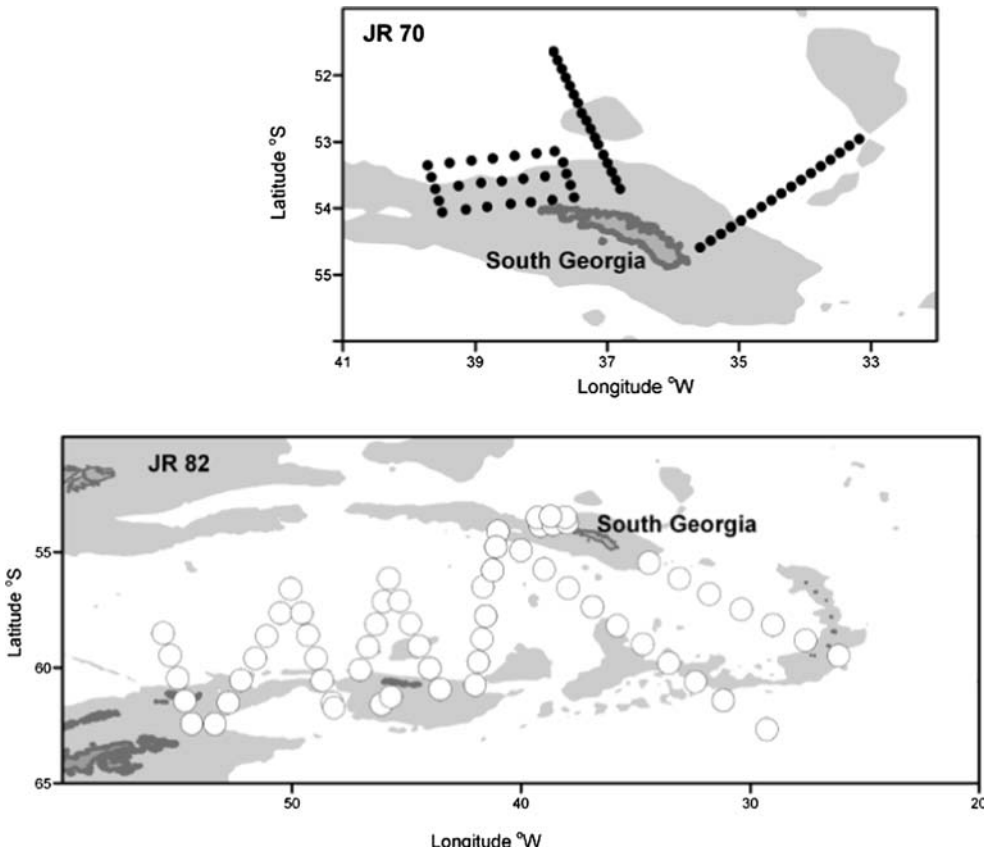

Fig. 1 Location of the sampling stations. Cruise JR70 *top panel*, cruise JR82 *lower panel*

by the mean number of eggs per sac to derive total egg numbers. At the stations where no direct counts of eggs per sac were made, the overall mean value of 15.8 eggs per sac was applied to derive the total numbers of eggs per m^2. Although the number of eggs held in a sac varies, as we discuss in detail later the average at any single location is relatively invariant, and hence any likely error introduced as a result of this approach will be small. The abundance of eggs sacs and adult females are important parameters that do vary between sites, and these were directly determined at all sites. Fecundity rates of *O. similis* (EPR, eggs female^{-1} day^{-1}) were determined using the egg-ratio method (Edmondson et al. 1962; Checkley 1980) as:

$$\mathrm{EPR} = \frac{E}{(A \times \mathrm{HT})}. \quad (1)$$

where E is the abundance (no. m^{-2}) of eggs in the sample (the product of numbers of sacs and mean numbers of eggs per sac), A the abundance of adult females (no. m^{-2}), and HT the predicted egg hatch time (days). Egg hatch times (HT, days) were predicted from temperature (T, °C) using the equation of Nielsen et al. (2002) as:

$$\mathrm{HT} = 1504.5(T + 7.6998)^{-2.05}. \quad (2)$$

In formulating this equation Nielsen et al. (2002) included measurements down to a temperature of –1°C, we have extrapolated beyond these limits but only down to –1.6°C.

A Michaelis–Menten relationship was not ideal for describing the relationship between fecundity and Chl *a* in *O. similis*, as this assumes the rate of egg production converges on zero as Chl *a* levels drop to zero. *Oithona* is widely known to be able to prey upon a diverse range of items that do not contain Chl *a* (see Atkinson 1998; Castellani et al. 2005), indeed we find that fecundity rates can still be reasonably high even for the very lowest of Chl *a* levels. Here we use a more appropriate relationship of the form:

$$\mathrm{EPR} = y_0 + \frac{ax}{b + x}. \quad (3)$$

This equation allows for a non-zero y-axis intercept, whilst still capturing the saturation of fecundity at high food concentrations. Here x is the food concentration (mg Chl *a* m^{-2}).

Eggs stripped from the sac were found to be approximately prolate spheroid in shape, with a long

axis averaging 75 μm and the shorter axis generally between 40 and 50 μm, giving a range of volumes of 12,566–15,708 μm^3. Assuming a carbon density of 0.14×10^{-6} μg C μm^{-3} this equates to 0.009–0.014 μg C egg^{-1}, the upper value coinciding with that of 0.014 μg C egg^{-1} given by Sabatini and Kiørboe (1994). To convert rates of egg production into mass-specific fecundity and to determine secondary production we assumed an egg carbon mass of 0.014 μg C and an adult female mass of 0.6 μg C (Sabatini and Kiørboe 1994; Kiørboe and Sabatini 1995).

Statistics

In order to examine the relationships between the dependent variables total egg production, abundance of eggs, nauplii, copepodites (C1–C5), adult females and males with the independent variables temperature and Chl *a*, we performed linear regression analyses with each independent variable separately. In addition, to allow for the interaction of these two, the effect of temperature and Chl *a*, and the effect of the interaction between these two variables on each of the dependent variables were tested using general linear models (GLMs). We constructed minimum adequate models (MAMs) using a backwards elimination selection procedure, retaining only significant terms ($P < 0.05$).

Results

Significant positive relationships were found between the total rate of egg production (eggs m^{-2} day^{-1}) and both temperature and Chl *a* across the study area, both when analysed as single linear regressions (see Table 1, Fig. 2), but also with a GLM including both terms (Table 2). Likewise the densities of copepodite (C1–C5) and adult females were also significantly related to temperature and Chl *a* when performing both linear regressions and when performing GLMs. However, the GLM method demonstrated that only the relationship with Chl *a* was significant in the case of nauplii and adult males (and not temperature). At –1°C the abundance of naupliar stages, and adult females and males was typically half of that observed at 2°C, whereas that of copepodite stages CI–CV was almost one quarter. On average across all sites the adult females outnumbered the males by ~10:1.

We have used the ratio of the abundance of nauplii (N1–N6) to that of copepodites (C1–C5) as an index of the survival rate across these stages. Although nauplii will be captured less efficiently than copepodites, we assume that the relative capture efficiency of the two groups does not vary systematically across the surveys. We also assume that the populations do not have a seasonal recruitment pulse that varied with temperature or Chl *a* (see Discussion), and that the stages have the same relative developmental times (equiproportional sensu; Corkett 1984) across the environmental gradient. This index of survivability is highly significantly related to temperature ($P < 0.001$, $r^2 = 0.255$) (Fig. 3b, Table 1), with a slope of –0.178. The slope is just –0.001 when the ratio is plotted against Chl *a*, but it is significant ($P < 0.002$, $r^2 = 0.080$) when performing a linear regression between the ratio and Chl *a* (Fig. 3a, Table 1). However, when considering both temperature and Chl *a* together, only temperature is found to be significant (Table 2). The lower the ratio the greater the survival across the naupliar to copepodite stages, hence the negative relationship indicates that survivability across these stages increased with increasing temperature and Chl *a* in our study. At the extremes of

Table 1 Descriptions of the linear regressions in Figs. 2 and 3

Variables (*y* vs. *x*)	Figure number	$y = a + bx$		*n*	r^2	*F* value	*P*
		a	*b*				
Total egg production vs. *T*	2a	7,696	4,166	120	0.225	34.25	<0.001
Nauplii abundance vs. *T*	2b	36,438	6,022	120	0.039	4.76	<0.05
Copepodite (C1–C5) abundance vs. *T*	2c	61,589	29,603	120	0.143	19.73	<0.001
Adult female abundance vs. *T*	2d	16,457	4,308	120	0.149	20.72	<0.001
Adult male abundance vs. *T*	2d	2,858	726	120	0.054	6.72	<0.01
Total egg production vs. Chl *a*	2e	8,111	38.8	120	0.205	30.35	<0.001
Nauplii abundance vs. Chl *a*	2f	31,298	114	120	0.145	19.99	<0.001
Copepodite (C1–C5) abundance vs. Chl *a*	2g	54,354	378	120	0.245	38.21	<0.001
Adult female abundance vs. Chl *a*	2h	16,660	42.4	120	0.152	21.09	<0.001
Adult male abundance vs. Chl *a*	2h	2,170	14.4	120	0.222	33.62	<0.001
Ratio of Nauplii to Copepodite (C1–C5) abundance vs. *T*	3a	0.775	-0.178	120	0.255	40.47	<0.001
Ratio of Nauplii to Copepodite (C1–C5) abundance vs. Chl *a*	3b	0.689	-0.001	120	0.080	10.22	<0.002

T is temperature (°C), Chl *a* is chlorophyll *a* (mg m^{-2}, integrated 0–100 m)

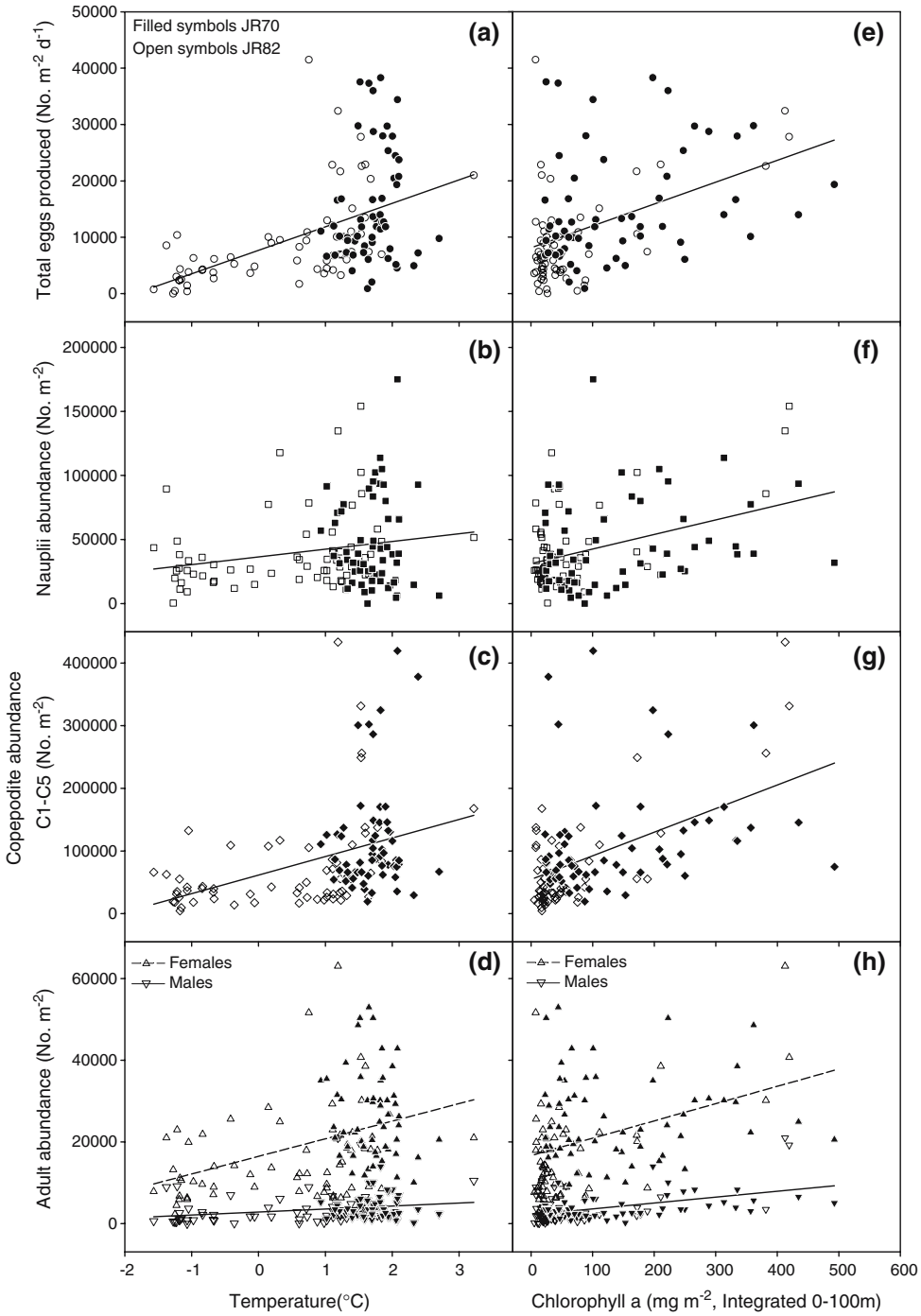

Fig. 2 Egg production rate and the abundance of various life stages of *Oithona similis* as a function of the surface water temperature (**a**–**d**) and chlorophyll *a* concentration (mg m^{-2}, integrated 0–100 m). *Filled symbols* represent data from JR70, *open symbols* from JR82. Note change in scale. All regressions (see Table 1) are significant ($P < 0.05$)

temperature the ratio differed from 1.054 to 0.202 (given by regression line), suggesting approximately a five fold greater proportion of animals survived across these stages at the warmer temperatures.

We examined a total of 747 intact individual egg sacs across the study area and found that the number of eggs per sac varied from 6 to 31. Although the number of eggs per sac varied five-fold the mean number of eggs per sac at any single station was relatively invariant, ranging from 12.0 to 17.3, with an overall mean across the whole study of 15.8 eggs sac^{-1} (and an SD across the site averages of just ±1.48). We used a relationship of the form described in Eq. 3 to examine how eggs per sac averaged at each site compared with

Table 2 Descriptions of the general linear models

Variables (y)	$y = a + b[T] + c[\text{Chl } a] + d[T \times \text{Chl } a]$				n	r^2
	a	b (P)	c (P)	d (P)		
Total egg production	6,056	3,109 (<0.001)	27.33 (<0.001)	–	120	0.312
Nauplii abundance	31,298	–	114 (<0.001)	–	120	0.145
Copepodite (C1–C5) abundance	19,873	34,067 (<0.001)	933 (<0.001)	–381 (0.009)	120	0.328
Adult female abundance	14,603	3,113 (0.002)	30.9 (0.002)	–	120	0.219
Adult male abundance	2,170	–	14.4 (<0.001)	–	120	0.222
Ratio of nauplii to copepodite (C1–C5) abundance	0.775	–0.178 (<0.001)	–	–	120	0.255

T is temperature (°C), Chl a is chlorophyll a (mg m^{-2}, integrated 0–100 m), – not significant

integrated Chl a (Fig. 4a) and found no significant relationship ($P = 0.073$). Neither was there a significant (linear regression) relationship between numbers of eggs per sac and temperature ($P > 0.50$) (Fig. 4b). The proportion of adult females with egg sacs varied from 0 to 0.67 but did not vary systematically with temperature (see Fig. 4d), while for Chl a we observed the phenomenon that the proportion of females carrying eggs was generally more scattered (and included many more lower values) at low Chl a levels. This is a pattern that is common to many rates of egg production in genera (see Hirst and Bunker 2003).

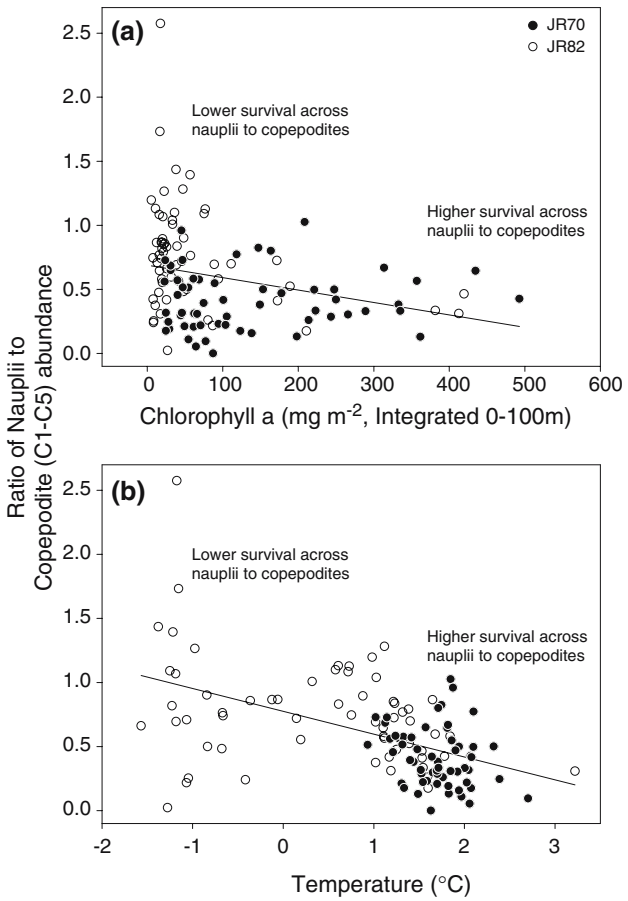

Fig. 3 Ratio of nauplii (N1–N6) to copepodite (C1–C5) abundance versus **a** chlorophyll a, and **b** temperature. High ratios indicate lower survival across these two stages, and lower ratios indicate higher survival across the two

The estimated fecundity of *O. similis* (eggs female^{-1} day^{-1}) versus Chl a concentration (mg m^{-2}, integrated over 0–100 m) is shown in Fig. 5. The line is described by:

$$\text{EPR} = 0.463 + \frac{0.516 \times C}{(375.5 + C)} \quad (4)$$

and is significant ($P = 0.0033$ and $r^2 = 0.093$).

Estimates of the secondary production of *O. similis* adult females across the entire geographic region averaged 0.168 mgC m^{-2} day^{-1}. There was a clear trend of increasing production with increasing Chl a concentration and temperature (see Fig. 2a and e, respectively), which is driven by both the general increase in abundance and the increase in growth rates (increasing fecundity rates) against these parameters.

Discussion and conclusions

In this study we investigated *O. similis* over a considerable latitudinal range (~51° S to 63° S). There was a strong gradient in both rates of egg production, and the abundance of nauplii, copepodites and adults. The cline in abundance in passing from low to higher latitudes has been observed previously, with the species being relatively rare near the Antarctic continental shelf but increasing by an order of magnitude in the northern part of the Southern Ocean (Atkinson 1998). Survival from nauplii to copepodites (C1–C5), as measured by the ratio of nauplii to copepodites increased with increasing temperature and Chl a (Fig. 3, Table 1) when examining each separately with linear regressions, however when we considered both these terms using a GLM approach (Table 2), it was evident that only temperature explained the ratio of nauplii to

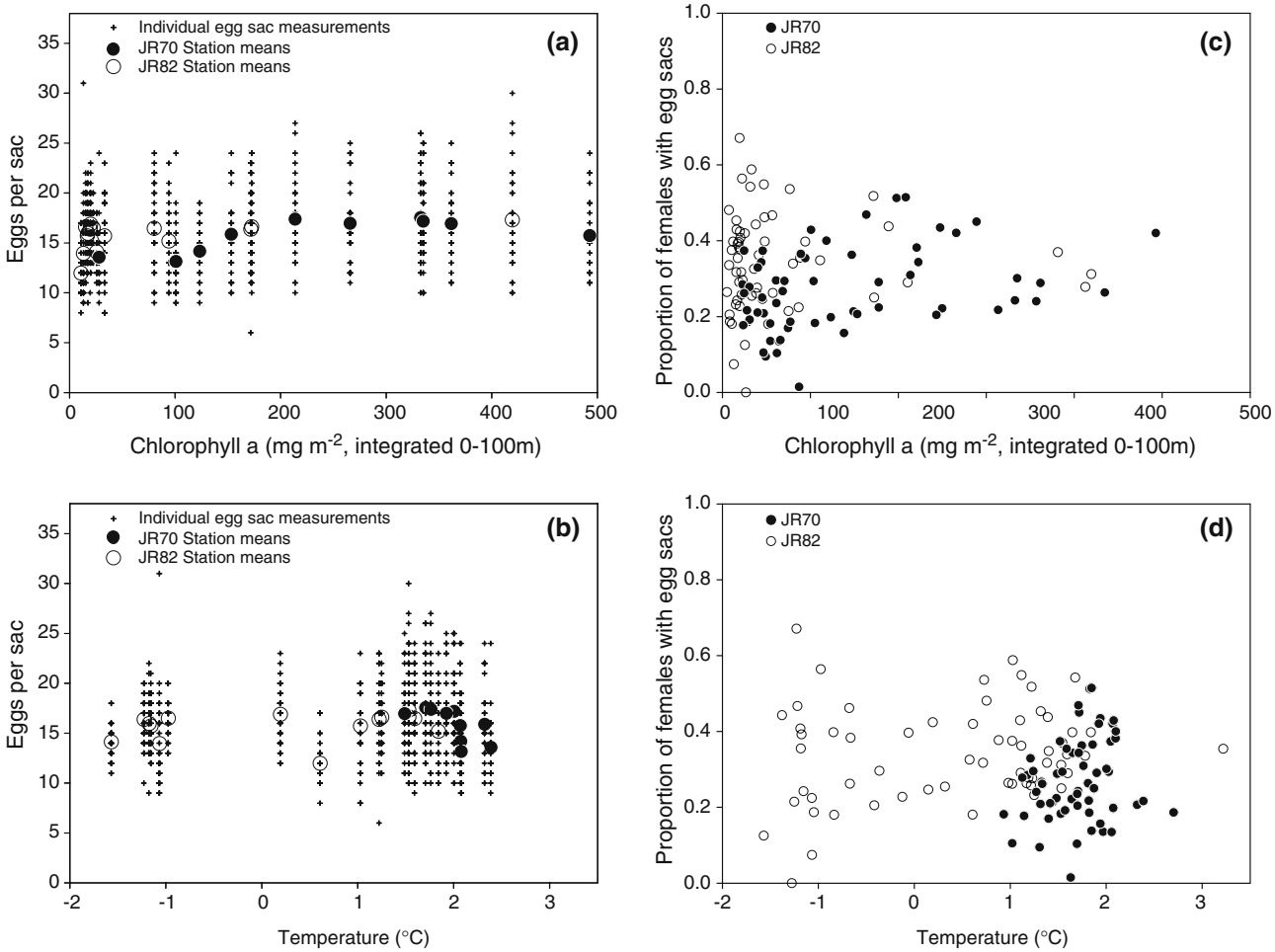

Fig. 4 Number of eggs per egg sac plotted against **a** chlorophyll *a* (mg m^{-2}, 0–100 m integrated), and **b** temperature. Proportion of females carrying eggs against **c** chlorophyll *a* (mg m^{-2}, 0–100 m integrated), and **d** temperature

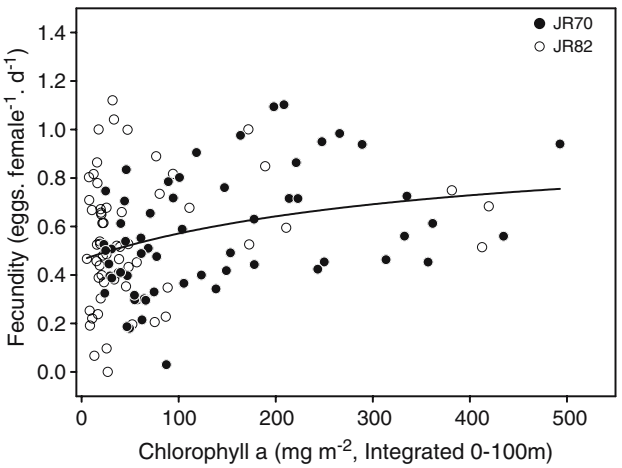

Fig. 5 Fecundity of *Oithona similis* (eggs $female^{-1}$ day^{-1}) versus chlorophyll *a* concentration (*C*, mg m^{-2}, 0–100 m integrated). The line is described by: $EPR = 0.463 + \frac{0.516 \times C}{(375.5+C)}$, where $P = 0.0033$ and $r^2 = 0.093$

copepodite abundance. It is unlikely that the trend in this ratio is due to a latitudinal difference in the progression of a cohort of recruits across the survey area as previous studies at several sites in the Southern Ocean have found that *O. similis* nauplii and copepodite stages occur throughout the year with no evidence of distinct cohorts in any season (Fransz and Gonzalez 1995; Metz 1996), although with an increase prior to the main productive season (see Atkinson 1998). The presence of females with egg sacs throughout the year also suggests more or less continuous reproduction (Fransz 1988; Fransz and Gonzalez 1995; Metz 1996). Interestingly our data clearly indicated that neither the proportion of females with egg sacs or the numbers of eggs per sac varied systematically with either temperature or Chl *a* (Fig. 4), further suggesting that cohort development was unlikely to be varying systematically with latitude.

Estimates of the seasonal variations in abundance of *O. similis* in the Southern Ocean are scarce. A low (relative to other species) fourfold variation in summer–winter abundance has been reported from the Weddell Sea (Fransz and Gonzalez 1995) which falls within the range of regional variation reported in Atkinson (1998). In contrast Atkinson and Ward (1988) found an average summer–winter abundance ratio of only 1.06 from the top 1,000 m in the oceanic regions of South Georgia.

O. similis is also a numerically dominant species in the Arctic Ocean and surrounding seas although its contribution to biomass is generally low (Ashjian et al. 2003). However, Møller et al. (2006) found that small species, including *O. similis*, dominated total copepod biomass in the Greenland Sea during summer when *Calanus* spp. descended for hibernation (see also Hopcroft et al. 2005). Reproduction of *O.similis* also continues year round in the Arctic with little evidence of clear cohort development, although Ashjian et al. (2003) observed greatest abundances of eggs and nauplii during spring and summer (June–August) compared to adults and copepodites which were more abundant in March. Data from Kongsfjorden also suggest a summer peak in abundance, although here the species undergoes a marked winter descent with the majority of the population occurring below 100 m at this time (Lischka and Hagen 2005). In contrast *Oithona* spp. in the Southern Ocean is a doubtful or weak seasonal migrant, living in the top 200 m layer for most of the year (Atkinson and Sinclair 2000; Metz 1995, 1996). Consequently the latitudinal differences in abundance and rates of egg production observed in this study are unlikely to be the result of seasonal vertical migration, since the bulk of the population is unlikely to be below the level of the nets, even at the southernmost stations.

Fecundity and secondary production

Bunker and Hirst (2004) found no relationship between fecundity and Chl *a* levels (measured slightly differently than here as they did not use depth integrated food concentrations) in their global synthesis of *Oithona* spp. using a Michaelis–Menten relationship. Here we used a model that allowed for a non zero–zero intercept. This demonstrated a highly significant relationship between fecundity and Chl *a* ($P = 0.0033$), albeit with a low predictive power ($r^2 = 0.093$). The equation gave an F_{max} (maximum fecundity) of 0.979 eggs female^{-1} day^{-1} and a K_m (half-saturation coefficient) of 20.3 mg Chl *a* m^{-2} (0–100 m integrated). This relationship was not driven by an increase in either numbers of eggs per sac or in the proportions of females carrying egg sacs as neither of these were significantly related to Chl *a*.

In order to estimate the rate of secondary production by adult female *O. similis* we multiplied the weight-specific fecundity rates by adult female biomass. Our values will have underestimated total production as we do not consider growth by pre-adults or adult males. The secondary production of *O. similis* adult females across the entire geographic region averaged 0.17 mgC m^{-2} day^{-1}, with a maximum of 0.58 mgC m^{-2} day^{-1}. Production was almost always less than 0.2 mgCm^{-2} day^{-1} in waters colder than 2°C, but often greater than this in the warmer waters in the north, resulting in a strong temperature, Chl *a* and latitudinally related gradient in secondary production (see Fig. 2a, e).

Maximum fecundity model

Data presented here and elsewhere suggest strong relationships exist between both fecundity rates and mass-specific fecundity of *Oithona* spp. and temperature (Fig. 6). Fecundity data from the Scotia Sea compares well with those from other investigations. However, in the cold waters of this study a more rapid decline than the general fecundity–temperature relationship is suggested (see Fig. 7). As temperatures fell below 5°C, fecundity (and weight-specific fecundity) declined very rapidly. This leads us to examine why. Sac spawning copepods can only produce the next batch of eggs once the previous batch has hatched. Egg hatch times increased in this species as water temperature decreased (see Nielsen et al. 2002), thus at 5°C the egg hatch time is 8.2 days, but at 0°C it is 22.9 days. In order to understand how this may set limits on the realised fecundity rates observed across our study area we produced a maximum fecundity model for *O. similis*. The number of eggs in a single egg sac rarely exceeded 24 (see Fig. 4b), taking this as a maximum value, then a female carries a maximum of 48 eggs at any one time. For our model we assumed that the period between eggs hatching and the production of a new clutch was 0.5 days (Sabatini and Kiørboe 1994), and was independent of temperature, as has been observed for *O. davisae* by Uye and Sano (1995). Maximum fecundity rates (MaxEPR, eggs female^{-1} day^{-1}) were therefore predicted from temperature (T, °C) by:

$$\mathrm{MaxEPR} = \frac{48}{\left(1504.5(T+7.7)^{-2.05}+0.5\right)}. \quad (5)$$

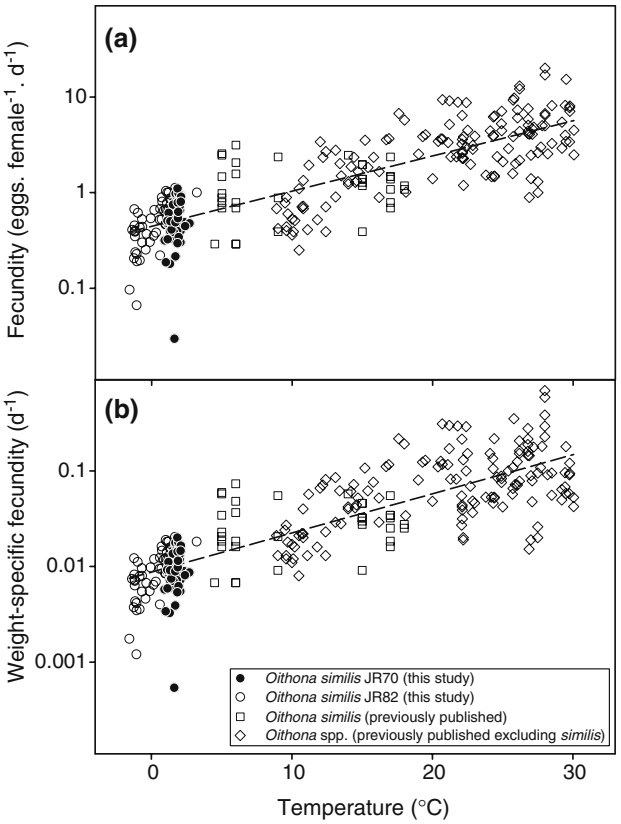

Fig. 6 **a** Fecundity and **b** weight-specific fecundity of *Oithona* versus temperature. Results from regressions through the entire sets of data give: $\log_{10}$ Fecundity = –0.353 + 0.037T ($P < 0.001$, $r^2 = 0.684$), and $\log_{10}$ Weight-specific fecundity = –2.059 + 0.041T ($P < 0.001$, $r^2 = 0.688$). Data for *Oithona* other than that derived here were obtained from the compiled sets of Hirst and Kiørboe (2002), Bunker and Hirst (2004) and Hirst and Bunker (2003)

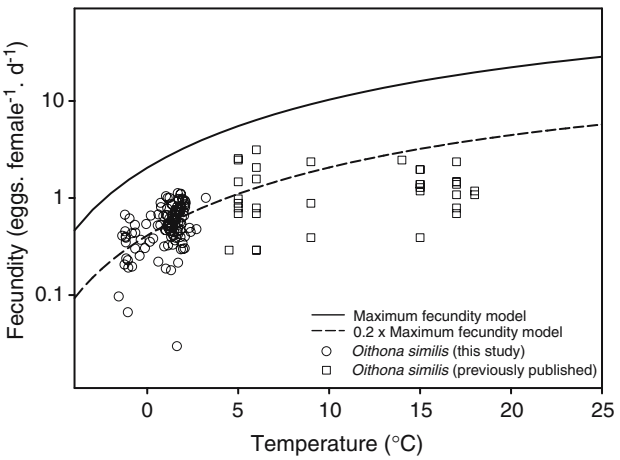

Fig. 7 Fecundity of *Oithona similis* in this study compared with values for the field from other publications. Values from the maximum fecundity model for this species are shown for comparative purposes, and also 0.2 times the maximum fecundity model

Results from the maximum fecundity model were compared against measured rates (Fig. 7). On average in situ fecundity rates were around one fifth of the values from the maximum egg production rate model, indicating that they are strongly food limited, although the degree of food limitation appears relatively constant (i.e. in situ rates appear to be ~1/5th of the maximum, regardless of temperature). Although there is scatter in the measured rates, and they are food limited, their general pattern strongly follows that of the maximum fecundity model (albeit at around 0.2 times the maximum rate, see Fig. 7). Rates rapidly decline as temperature falls below ~5°C. Maximum egg production rates in sac spawners are principally dictated by egg hatch times, which in turn are dictated by temperature, but furthermore in situ rates in this study also appear to be strongly controlled by temperature too. Within a species, development versus temperature generally follows a Bělehrádek relationship better than logarithmic (hence Q_{10}) relationship. This highlights that Q_{10} values (which are simply exponential functions) may not fit well a development time versus temperature relationships for single species.

Distribution restrictions by low temperatures

At low temperatures *O. similis* has rates of egg production that decline very rapidly with declining temperature (largely as a consequence of the extended egg hatch time) and in addition egg to adult times are also rapidly increasing. These two factors combined mean that to maintain its population the mortality rates that the population can afford to suffer falls rapidly with declining temperature, although the extending development time rather than the reducing fecundity is the main driver. We can describe the mortality rates that would result in steady-state population using the approach described in Kiørboe and Sabatini (1994) and Hirst and Kiørboe (2002). Here R_0 is the net reproductive rate (i.e. the numbers of offspring per female that survive to the next generation), EPR is the fecundity rate, D is the egg to adult development time (days), and β is the mortality rate (day^{-1}):

$$R_0 = (\mathrm{EPR}/\beta)\mathrm{e}^{-\beta D}. \quad (6)$$

We use a value of 1.1 for R_0 (from the average sex ratio found here of 10 females to each male), and the maximum fecundity model values to describe the egg production rate (MaxEPR, eggs female^{-1} day^{-1}) as a function of temperature. Egg to adult time (D) was predicted as a function of temperature using the Bělehrádek equation: D=11863(T + 7.6998)$^{-2.05}$, which

was derived using the α and b parameters for eggs, and using the development time at 15°C of 19.7 days obtained by Sabatini and Kiørboe (1994) in order to solve the parameter for a (11866) as the missing value. The mortality rates which result in a steady-state abundance are plotted as a function of temperature in Fig. 8. Below ~3°C these sustaining mortalities drop radically with declining temperature. Note that if realised mortality rates in the field are on average below this line the population would increase with time, whereas if they were above this line the population would decrease through time. In Fig. 8 the steady-state mortality is also indicated when fecundity is 0.2 times the maximum fecundity model (0.2MaxEPR), as appears on average to be the case in the field, and when development time from egg to adulthood is 1.5 times that under the laboratory situation (i.e. 1.5D). We chose this development time value as a mid-point, development extends from being equal to that at food saturation to about twice this (Campbell et al. 2001). The chosen value has commonly been found in field situations. Hirst and Kiørboe (2002) compiled field estimates of epi-pelagic copepod mortality, those for broadcasting (post-hatch) and sac spawning (egg and post-hatch) copepods are included in Fig. 8, although these data are predominantly from temperate sites. By comparing field mortality with sustaining mortality we observe that the two increasingly diverge as temperature falls, and therefore it will become increasingly unlikely that *O. similis* will be able to maintain itself as temperatures fall, especially below 1°C. To an extent this is borne out by the fact that the survivability index across the nauplii to copepodite (C1–C5) stages declines with falling temperature, and indeed *O. similis* was observed to be much less abundant below 1°C than at warmer temperatures (Fig. 2). Over the temperature range 5 to –1°C, the mortality rates against which the species could maintain its population in steady-state falls from 0.067 to 0.018 day^{-1}(assuming MaxEPR and D).

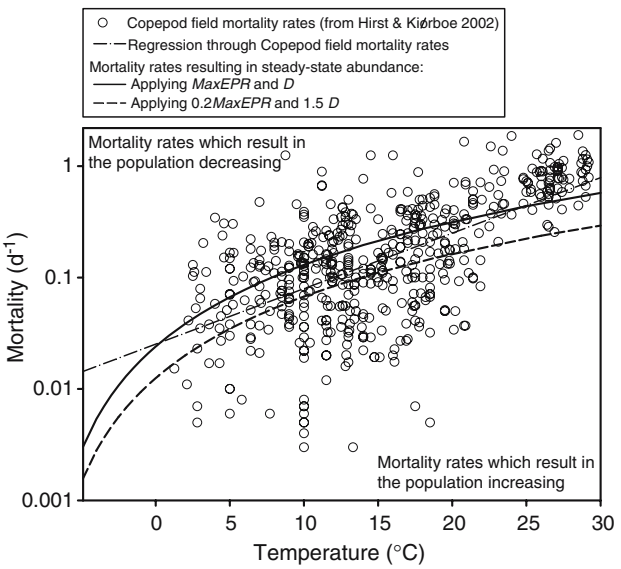

Fig. 8 *Solid line* indicates the mortality rates (day^{-1}) that would allow for a population of *Oithona similis* to be sustained at steady-state (Eq. 6) as a function of temperature applying the maximum fecundity model (*MaxEPR*) and development predicted from laboratory situation (*D*). The *short-dashed line* indicates steady-state situation when fecundity is 0.2 times the maximum fecundity (0.2*MaxEPR*), and development is 1.5 times longer than the laboratory. Epi-pelagic field mortality rates of sac spawning copepods (egg and post-hatch) and broadcasters (post-hatch) from Hirst and Kiørboe (2002) are given by individual data points for comparison, and a regression through these points is also indicated (*dash-dot line*)

Seasonal warming of near-surface layers in Antarctic waters during the summer means that although the north–south temperature gradient is maintained, overall temperatures will rise over the course of summer. This can be as much as 3–4°C in the near surface at South Georgia, although further south, in areas of seasonal ice-cover, the increase is less (~1°C). Warmer temperatures reduce egg hatch and egg to adult development times and hence increase the amount of mortality the population can tolerate, nonetheless, there will still be a major gradient in affordable mortality rates across the study region in summer. It is possible that in cold waters the species may have to be maintained by advection from warmer areas, deeper populations with lower mortality, or from warmer periods in the year when it is more successful. Additionally lower predation pressure in the colder parts of its range, particularly during the austral winter, would assist in population maintenance. However, we have used a maximum fecundity rate, which we know the population does not achieve, and an egg to adult time from well fed laboratory populations. As we demonstrate here, realised fecundity rates are lower in the environment than the maximum rate, and development times longer, both these factors result in the mortality at which the population will be able to sustain itself being lower than the predicted value (seeFig. 8).

Conclusion

This study highlights the impact of temperature on a sac spawning species' ability to maintain its population as temperature declines. The mechanisms involved may also be relevant to the control of populations in warmer water systems. For example many copepod species have development times which also fit well with Bělehrádek functions, but with the biological zeros

(when development is predicted to cease in the Bělehrádek function) occurring at higher temperatures. Hence similar effects of temperature on the population dynamics of sac spawning species inhabiting warmer waters may also be anticipated. Advection or seasonality may make the boundaries less distinct, or other physiological tolerance may come into play before the limits set by the interplay between rapidly increasing development and egg hatch times (and hence rapidly declining potential fecundity) and natural mortality rates are reached. The match between biological zero of development and the average temperature within a species range, was described in copepods by McLaren et al. (1969). We have gone a step further in putting forward demographic reasons that may explain the cold-water (and geographic) range of O. similis. Temperature impacts development rate and egg production, and in turn the mortality rates that the population can afford, these factors result in a population being increasingly unsustainable as temperature declines.

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