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

P Ward & AG Hirst

British Antarctic Survey, (Natural Environment Research Council), High Cross, Madingley Road, Cambridge, CB3 0ET, United Kingdom

E-mail: pwar@bas.ac.uk

Abstract

In this study we report the abundance, fecundity and an index of mortality of *Oithona similis* 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 (0-100m) chorophyll *a* (Chl *a*), abundance increasing with increasing temperature (and therefore increasing latitude) and Chl *a*. *In situ* total egg production rates and fecundity per female were significantly and positively related to temperature and Chl *a*. Egg hatch times lengthen as temperature decreases and in sac spawning species the next batch of eggs cannot be produced until the previous clutch hatch. Consequently, *O. similis* fecundity rates must rapidly decline at low temperatures, especially below 5^{o}C. *In situ* fecundity rates were compared with a model of maximum fecundity, and were generally much lower, thus suggesting strong food limitation across the region studied. However the relationships 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 typical field mortality. Our findings have broad implications for the lower temperature range and hence geographic limits of *O. similis*, but also for the distribution of other sac spawning copepods and planktonic species generally.

Introduction

Plankton species that are truly cosmopolitan are the exception rather than the rule in the world's ocean. Many species appear to have centres of distribution which have been linked to water masses, regions or temperature (McLaren et al. 1969). In the Southern Ocean the zonal distribution of copepod assemblages has been recently investigated by Atkinson & 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. The underlying mechanisms that influence population demography and determine the distributional limits of species are 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.

Oithona similis occurs widely throughout sub-tropical, temperate and polar waters. Knowledge of its true abundance, biomass and ecological role have all been progressed in recent decades (e.g. Paffenhöffer 1993; Nielsen & Sabatini 1996; Atkinson 1998, Gallienne & Robins 2001, Kiorboe & Sabatini 1995), 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. However detailed investigations of the genera's population biology (e.g. fecundity, development and mortality) have been largely restricted to temperate (Sabatini & Kiørboe 1994; Uye & Sano 1995, 1998; Nielsen & Sabatini 1996; Eiane & Ohman 2004) and tropical waters (Hopcroft & Roff 1996, 1998; McKinnon & Klumpp 1998). Our aims were to examine *O. similis* across a broad range of latitudes in Antarctic waters, to determine its abundance and fecundity, and attempt to understand controls on its demography and distribution in this cold-water ecosystem.

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 & 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 and100 m) at each of the 120 stations sampled. Integrated Chl *a* (m^{-2}, 0-100 m) was determined by summation of values over depths. Near surface sea temperature was recorded at each station from the ship's non-toxic sea-water supply located at 7 m depth.

Net sampling

During both cruises zooplankton were 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 ~0.22m sec^{-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 Figure 1.

In the laboratory samples were sub-divided using a folsom plankton splitter and the aliquots examined for *Oithona similis* using a binocular microscope at 60X magnification. Counts were made of adult males and females, copepodite stages (C1 to C5 combined), nauplii and egg sacs. We assumed that the net efficiency was 100% and abundances were accordingly 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 found to be present within the catch. Intact egg sacs were always longer than they were wide (average 333 μm (SD = 50.6) in length, and 105 μm (SD = 9.6) in width), sufficiently large for us to have confidence that they would be quantitatively retained by the net provided the sac stayed intact. To double check we separated out 50 egg sacs, 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 5 times with the mesh retaining all egg sacs on each occasion.

To investigate whether egg numbers per sac varied with temperature or Chl *a* 30 egg sacs were randomly taken at each of a total of 14 stations, dissected, and the total numbers of eggs per sac counted.

Fecundity

At the 14 stations where direct counts of eggs per egg sac were made, the number of egg sacs was multiplied by the mean number of eggs per sac to derive total egg numbers. At remaining stations, where we have no direct counts of eggs per sac, the overall mean value of 15.96 eggs per sac was used to estimate the total. Fecundity rates of *O. similis* (EPR, eggs female^{-1} d^{-1}) were determined using the egg-ratio method (Edmondson et al. 1962; Checkley 1980) as:

$$EPR = \frac{E}{(A \times HT)} \qquad 1$$

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, ^{o}C) using the equation of Nielsen et al. (2002) as:

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

In formulating this equation Nielsen et al. (2002) include measurements down to a temperature of -1°C, in only one instance have we extrapolated beyond these limits when we make a single prediction from the equation at -1.2°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), indeed we find that fecundity rates can still be reasonably high even for the very lowest of chlorophyll levels. Here we use a more appropriate relationship of the form:

$$EPR = y_0 + \frac{ax}{b + x} \qquad 3$$

This equation allows for a non-zero y-axis intercept, whilst still capturing the saturation of fecundity at high food concentrations.

Eggs stripped from the sac were found to be approximately prolate spheroid in shape, with a long axis averaging 75µm and the shorter axis generally between 40-50µm, giving a range of volumes of 12566-15708µm^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 & Kiørboe (1994). In order to convert rates of egg production into weight-specific fecundity and to determine secondary production we assumed an egg carbon mass of 0.014µg C (Sabatini & Kiørboe 1994). Measurements of female carbon mass of *O. similis* from the Southern Ocean are few and somewhat contradictory (see Fransz & Gonzalez (1995) and Swadling et al. (1997)). Adult female cephalothorax length did not vary significantly

over the study area and carbon mass was therefore determined by using the average length in the equation in figure 1 of Sabatini and Kiørboe (1994). This gave a value of 0.77μgC for adult females, based on an average cephalothorax measurement of 546μm (SD = 36 μm). This is somewhat larger than the average value of 0.6μg C reported by Sabatini & Kiørboe (1994), but this is expected as the females in our study had greater cephalothorax lengths.

Secondary Production

In order to gain a first approximation of the rate of secondary production by *Oithona similis* across the study region, we multiplied weight-specific fecundity rates by adult female and copepodite (C1-C5) biomass at each site. We use our estimate that females contain 0.77μgC ind^{-1}, and assumed a mean weight for copepodites in our samples of 0.2μgC ind^{-1} (the approximate weight of a copepodite stage 3 (Sabatini & Kiørboe 1994)). Although juvenile and adult female growth rates can be very different, these differences are generally least in cold waters (Hirst & Bunker 2003). We do not include nauplii as these will be greatly under-sampled, but in any case the contribution of nauplii to production is generally minor, i.e. typically <<25% of the total (Landry 1978; Mullin 1988; Mullin & Brooks 1970; Fransz & Diel 1985; Liang et al. 1996; Liang & Uye 1996). One station where no egg sacs were found was excluded from these calculations.

Results

Significant positive relationships were found between the total rate of egg production (eggs m^{-2} d^{-1}) and both temperature and Chl *a* across the study area (see Table 1 and Figure 2). Likewise the densities of nauplii, copepodite and adult stages were also

significantly related to temperature and Chl *a*. At 0°C the abundance of naupliar stages, females and males was around half that observed at 5°C, whereas that of copepodite stages CI-CV was around one quarter. Females outnumbered males by around 10:1 across the temperature range.

We have used the ratio of the abundance of nauplii (N1-N6) to that of copepodites (C1-C5) as an index of the total mortality 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. The relationship between the ratio of nauplii to copepodite abundance versus temperature has a slope of -0.137 and is highly significant ($P<0.001$, $r^2 = 0.301$), the slope is much flatter when the ratio is plotted against Chl *a* (-0.001), but it was still significant ($P<0.002$, $r^2= 0.080$) (Figure 3). The lower the ratio the lower the total mortality across the naupliar to copepodite stages, hence the negative relationship indicates that total mortality across these stages increased with temperature and Chl *a* in our study. At the extremes of temperature the ratio differs from 1.14 to 0.13 (given by regression line), suggesting approximately an order of magnitude greater proportion of animals survived across these stages at the warmer temperatures.

We examined a total of 420 intact individual egg sacs across the study area and found that the number of eggs per sac varied from 6 to 31. Although the individual values

were therefore quite variable, the mean number of eggs per sac at any single site varied between only 13.9 and 17.3, with an overall mean across the whole study of 15.96. A relationship of the form described in equation 3 between eggs per sac and integrated Chl *a* (Figure 4a) was significant ($P<0.05$), although the r^2 was very low at 0.099. There were no trends between numbers of eggs per sac and temperature (Figure 4b). The proportion of adult females with egg sacs varied from 0 to 0.67 but did not vary systematically with temperature (Figure 4d), while for Chl *a* we observed that the proportion of females carrying eggs was generally more scattered (and included many more lower values) at low Chl *a* levels (Figure 4c). Such a pattern is common to egg production in many genera of copepods (see synthesis of Bunker & Hirst 2004).

Fecundity rates of *Oithona similis* averaged 0.83 eggs female^{-1} day^{-1} across the entire study area. Fecundity rates (eggs female^{-1} day^{-1}) versus Chl *a* concentration (mg m^{-2}, integrated over 0-100m) are shown in Figure 5. The line is described by:

$$EPR = 0.620 + \frac{0.854 \times C}{(230.651 + C)} \qquad 4$$

and was significant ($P<0.0001$ and $r^2=0.15$).

Estimates of the secondary production of *O. similis* across the entire geographic region averaged 0.58 mgC m^{-2} d^{-1}, with a range of 0.02 to 3.8 mgC m^{-2} d^{-1}. There was a clear trend of increasing production with increasing temperature (Figure 6). This is driven by both the increase in abundance and the increase in growth rates (increasing fecundity rates) with increasing temperature.

Discussion

In this study we investigated *Oithiona similis* over a considerable latitudinal range (~ 51.5 ^{o}S - 63 ^{o}S). There was a strong gradient in both rates of egg production, and the abundance of nauplii, copepodites and adults. Across nauplii to copepodites (C1-C5) there is a decrease in our mortality index (ratio of naupii to copepodite abundance) with increasing temperature and Chl *a*. Although we cannot discount that this result might in part be due to a latitudinal progression in life cycle timing across the survey area, as found for large calanoids during cruise JR82 (see Ward et al. in press), this seems unlikely. Past studies have indicated that *Oithona* spp. is a doubtful or weak seasonal migrant living in the top 200 m layer for most of the year (Atkinson & Sinclair 2000; Metz 1995; Metz 1996). Consequently the bulk of the population is likely to be within the depth range sampled by the nets, even at the southern-most stations, where in any case the net sampled from 400 m to the surface. A cline in abundance in passing from low to higher latitudes has also been previously observed, 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). Several authors have also noted the lack of population cohorts and the fact that naupliar and copepodite stages occur throughout the year. The presence of females with egg sacs throughout the year also suggests more or less continuous reproduction (Fransz 1988; Fransz & Gonzalez 1995; Metz 1996).

Fecundity

Bunker & Hirst (2004) found no relationship between fecundity and Chl *a* levels in their global synthesis of *Oithona* spp. using a Michaelis-Menten relationship. By contrast we did find a significant relationship, but the model we prefer, which allows

for a non zero-zero intercept, demonstrates a highly significant relationship ($P<0.0001$), albeit with a low predictive power ($r^2=0.149$). The equation gives an F_{max} (maximum fecundity) of 1.47 eggs female^{-1} d^{-1} and a K_m (half-saturation coefficient) of 36.6 mg Chl *a* m^{-2} (0-100m integrated). The fact that the relationship exists is a combination of two factors, the relationship between eggs per sac and Chl *a*, and also the proportion of females with egg sacs and Chl *a*.

There were strong relationships between both fecundity rates and weight-specific fecundity of *Oithona* spp. and temperature (Figure 7); the data from the Scotia Sea fitting well with those from other investigations. At the temperatures of this study (-1.2 to 6.2^{o}C) fecundity averages 0.83 eggs female^{-1} d^{-1}. The relationship between $\log_{10}$ fecundity of *Oithona* spp. and temperature (^{o}C) is highly significant ($P<0.001$) with an r^2 of 0.595, the regression gives a prediction of fecundity for *Oithona* spp. of 0.55 eggs female^{-1} d^{-1} at 0^{o}C, rising to 5.3 eggs female^{-1} d^{-1} at 30^{o}C. However, closer inspection of our estimates of the fecundity of *Oithona similis* in the cold waters of this study suggest a much more rapid species-specific decline than the general temperature relationship (see Figure 8). As temperatures fall below 5^{o}C fecundity (and weight-specific fecundity) drops dramatically. 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 dramatically elongate in this species as water temperature cools (see Nielsen et al. 2002), thus at 5^{o}C the egg hatch time is 8.2 days, but at 0^{o}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 *Oithona similis*. The number of eggs in a single egg sac rarely exceed 24 (see Figure 4b), taking this as a maximum value, then a female carries a

maximum of 48 eggs at any one time. For our model we assume that the period between eggs hatching and the production of a new clutch is ~0.5 days (Sabatini & Kiørboe 1994), with no temperature dependence in this period as has been observed for *Oithona davisae* by Uye & Sano (1995). Maximum fecundity rates (*MaxEPR*, eggs female^{-1} day^{-1}) were therefore predicted from temperature (T, ^{o}C) by:

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

Results from the maximum fecundity model are compared against measured rates in Figure 8. On average, fecundity rates *in situ* are around one fifth of the values from the maximum egg production rate model, thus indicating they are strongly food limited but that the degree of food limitation does not appear to vary with 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 a lower absolute rate). Rates rapidly decline as temperature falls below ~5^{o}C. Maximum egg production rates in sac spawners are primarily dictated by egg hatch times, which in turn are dictated by temperature, but furthermore *in situ* rates in our 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.

Secondary Production

Our provisional estimates of the secondary production of *O. similis* across the entire geographic region averages 0.58 mgC m^{-2} d^{-1}, with a range that extends over 2 orders

of magnitude, from 0.02 to 3.8 mgC m^{-2} d^{-1} (see Methods for assumptions in deriving these estimates). These estimates are likely to be conservative because of the undersampling of copepodites by the nets, and the exclusion of nauplii in these calculations. Production was almost always less than 0.4 mgCm^{-2} d^{-1} in waters colder than 2^{o}C, but commonly greater than this at warmer temperatures, resulting in a very strong temperature (and latitudinal) gradient in secondary production by this species (Figure 6). By comparison Nielsen & Sabatini (1996) found maximum production rates for *Oithona* spp. in the North Sea of ~13 mgC m^{-2} d^{-1}, and rates commonly fell between 1 and 10 mgC m^{-2} d^{-1}. Our values are much lower because both biomass and growth/fecundity rates are much lower across our study region than in the North Sea. Comparable estimates of Southern Ocean copepod production are few. Fransz & Gonzalez (1995) estimated the annual production of *O. similis* south of 60^{o}S, to be ~500 mgC m^{-2} yr^{-1}, although noting that this is likely to be a conservative estimate as its abundance increased markedly further north. It is difficult to directly compare this annual estimate with our data but it is worth pointing out that the regression of C mass on prosome length used by Fransz & Gonzalez (1995) produces an estimate of female C mass more than double our own. At South Georgia, Shreeve *et al*. (2005) estimated that the production of *Calanoides acutus* copepodite stages 4 and 5 (around 25% of copepod biomass) averaged 26 mgC m^{-2} d^{-1}, based on 5 years of summer data. This was slightly higher than production estimates for Antarctic krill (22 mgC m^{-2} $d^{-1)}$, and although both copepod and krill biomass can be higher at South Georgia compared to elsewhere in the region (see Shreeve *et al*. 2005), production by *O. similis* during cruise JR70, which focussed on the island, was still much lower by comparison (Figure 6).

Mortality

In the low temperatures of this region, *O. similis* has rates of egg production that decrease as temperature declines (largely as a consequence of the extended egg hatch time), in addition egg to adult times are also rapidly increasing. These two factors combined result in populations of *Oithona similis* only being able to maintain themselves against increasingly lower mortality rates with declining temperature. We can describe the mortality rates that would result in a steady-state population using the approach described in Kiørboe & Sabatini (1994) and Hirst & 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 (d^{-1}):

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

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 (*EPR*, eggs $female^{-1}$ d^{-1}) as a function of temperature. *D* was predicted as a function of temperature using the Bělehrádek equation: $D = 14095(T + 7.6998)^{-2.05}$, which was derived using the α and *b* parameters for eggs (see equation 1), and using the development time at 15°C obtained by Sabatini & Kiørboe (1994) in order to derive the parameter for *a* (14095) (therefore assuming equiproproprotional development, as has commonly been observed in copepods (Hart 1990)). Predicted mortality rates which produce a steady-state abundance are plotted as a function of temperature in Figure 9. Below 5°C the mortality rate at which *O. similis* can maintain its population in steady-state drops radically with declining temperature. Note that if field mortality rates were on average below this line the population would

increase with time, whereas if field mortalities were above this line the population would decrease through time. Hirst & Kiørboe (2002) compiled field estimates of epi-pelagic copepod mortality rates, those for broadcasting (post-hatch) and sac spawning (egg and post-hatch) copepods are included in Figure 9, although these data are predominantly from temperate sites. Although we know little about mortality rates in the pelagic environment of polar waters, we suggest it becomes increasingly unlikely that this species is able to maintain itself as temperatures fall, especially below 1^{o}C. This is to an extent borne out by the evidence that across the nauplii to copepodite (C1-C5) stages the mortality index increases with declining temperature, and that abundances are consistently lower below 1^{o}C than at warmer temperatures (Figure 2). Over the temperature range 5 to 1^{o}C, mortality rates which allows a population to maintain steady-state falls from 0.012 to 0.0006d^{-1}, mortality rate above these being unsustainable for *Oithona similis* when achieving maximum fecundity rates. This almost 2 order of magnitude fall across a range of just 4^{o}C is much greater than the relative fall across the wider temperature range of 30 to 5^{o}C (at around just 1 order of magnitude). Seasonal warming of 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 by as much as 3-4^{o}C at South Georgia, although further south, in areas of seasonal ice-cover, the increase is less (~1^{o}C), this will act to reduce development times and hence increase the rate of mortality the population could withstand, but nonetheless there will still be a major gradient in the sustainable mortality rates. It is possible that in cold waters the species may have to be maintained by advection from warmer areas, deeper populations with lower mortality rates, or from warmer periods in the year when it is more successful.

This study highlights the impact of temperature on a sac spawning species' ability to maintain its population as temperature declines. This may not seem relevant to warmer water systems, but it is. Other sac spawning copepods have development times which also fit well with Bělehrádek functions, but often with biological zeros (the temperature at which development ceases) at higher temperatures. In such species higher temperatures would cause rapidly declining fecundity rates and rapidly elongating egg to adult times, and once again impacting their potential distribution. Advection or seasonality may make the temperature boundaries of copepods less distinct, or other physiological tolerance may come into play before the demographic limits we have detailed. The match between the biological zero of development and the temperature at which the distributional centre of a species is found was described by McLaren et al. (1969), specifically with respect to copepods. We have put forward demographic explanations, specifically how, through impacts of temperature upon development rates and egg production and in turn the mortality rates that can be sustained, that show maintenance of a population may become increasingly untenable as temperature declines.

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Table 1 Descriptions of the linear regressions in Figures 2 and 3. T is temperature (^{o}C), Chl *a* (mg m^{-2}, Integrated 0-100m).

Variables (y vs. x)	**Figure Number**	**y = a + b x**		**n**	**r^2**	**P**
		a	**b**			
Total egg production vs. T	2a	1784	5846	120	0.327	<0.001
Nauplii abundance vs. T	2b	21794	7367	120	0.116	<0.001
Copepodite abundance vs. T	2c	11000	28651	120	0.269	<0.001
Adult Female abundance vs. T	2d	10558	3652	120	0.215	<0.001
Adult Male abundance vs. T	2d	1559	724	120	0.107	<0.001
Total egg production vs. Chl *a*	2e	11713	66.2	120	0.220	<0.001
Nauplii abundance vs. Chl *a*	2g	31298	113.6	120	0.145	<0.001
Copepodite abundance vs. Chl *a*	2g	54354	377.8	120	0.245	<0.001
Adult Female abundance vs. Chl *a*	2h	16660	42.4	120	0.152	<0.001
Adult Male abundance vs. Chl *a*	2h	2170	14.4	120	0.222	<0.001
Ratio of Nauplii to Copepodite (C1-C5) Abundance vs. T	3a	0.978	-0.137	120	0.301	<0.001
Ratio of Nauplii to Copepodite (C1-C5) Abundance vs. Chl *a*	3b	0.689	-0.001	120	0.080	<0.002

Figure legends:

Figure 1 Location of the sampling stations. Cruise JR70 top panel, cruise JR82 lower panel. Grey tones represent the 2500 m isobath.

Figure 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 chl *a* concentration (mg m^{-2}, Integrated 0-100m) (e-h). Filled symbols represent data from JR70, open symbols from JR82. Note change in scale. All regressions (see Table 1) are highly significant ($P<0.001$).

Figure 3 Ratio of nauplii (N1-N6) to copepodite (C1-C5) abundance versus **a.** Chl *a*, and **b.** Surface temperature. High ratios indicate higher total mortality across these two stages, and lower ratios indicate lower mortality across the two.

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

Figure 5 Fecundity of *Oithona similis* (eggs $female^{-1}$ day^{-1}) versus Chl *a* concentration (C, mg m^{-2}, 0-100m integrated). The line is described by: $EPR = 0.620 + \frac{0.854 \times C}{(230.651 + C)}$, where $P<0.0001$ and $r^2=0.149$.

Figure 6 Estimated secondary production by *Oithona similis* versus Surface temperature across the study region. See text for details of calculation.

Figure 7 a. Fecundity and **b.** Weight-specific fecundity of *Oithona* versus Surface temperature. Results from regressions through the entire sets of data give: $\log_{10}$ Fecundity $= -0.263+0.033T$ ($P<0.001$, $r^2=0.595$), and $\log_{10}$ Weight-specific fecundity $= -1.971+0.037T$ ($P<0.001$, $r^2=0.616$). Data for *Oithona* other than that derived here were

obtained from the compiled sets of Hirst & Kiørboe (2002), Bunker & Hirst (2002) and Hirst & Bunker (2003).

Figure 8 Fecundity of *Oithona similis* in this study compared with values found for this species in published studies. Values for *Oithona* spp. (excluding *O. similis*) are also indicated.

Figure 9 Mortality rates (d^{-1}) that give a steady-state solution for population abundance of *Oithona similis* (equation 5) as a function of surface temperature given predicted rates of development and using the maximum fecundity model denoted by line. Epi-pelagic field mortality rates of sac spawning copepods (egg and post-hatch) and broadcasters (post-hatch) from Hirst & Kiørboe (2002) are given by individual data points for comparison.

Figure 1

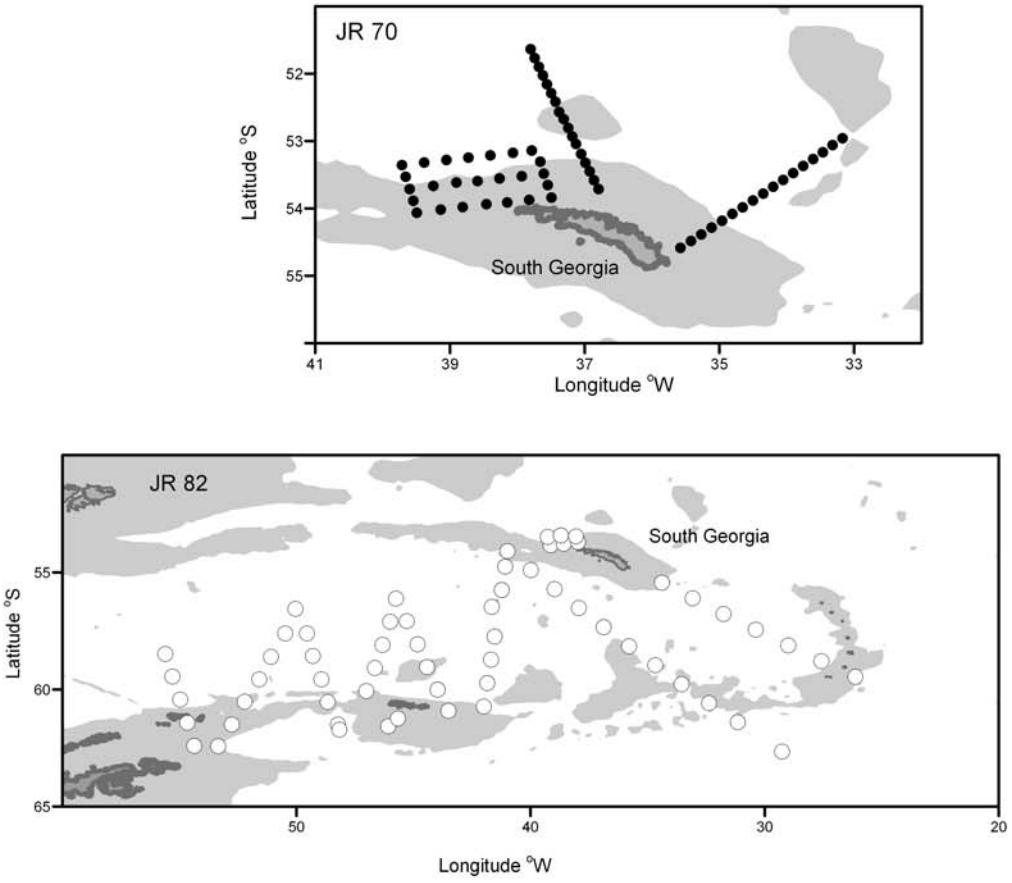

JR 70
South Georgia
Latitude °S
52
53
54
55
41
39
37
35
33
Longitude °W
JR 82
South Georgia
Latitude °S
55
60
65
50
40
30
20
Longitude °W

Figure 2.

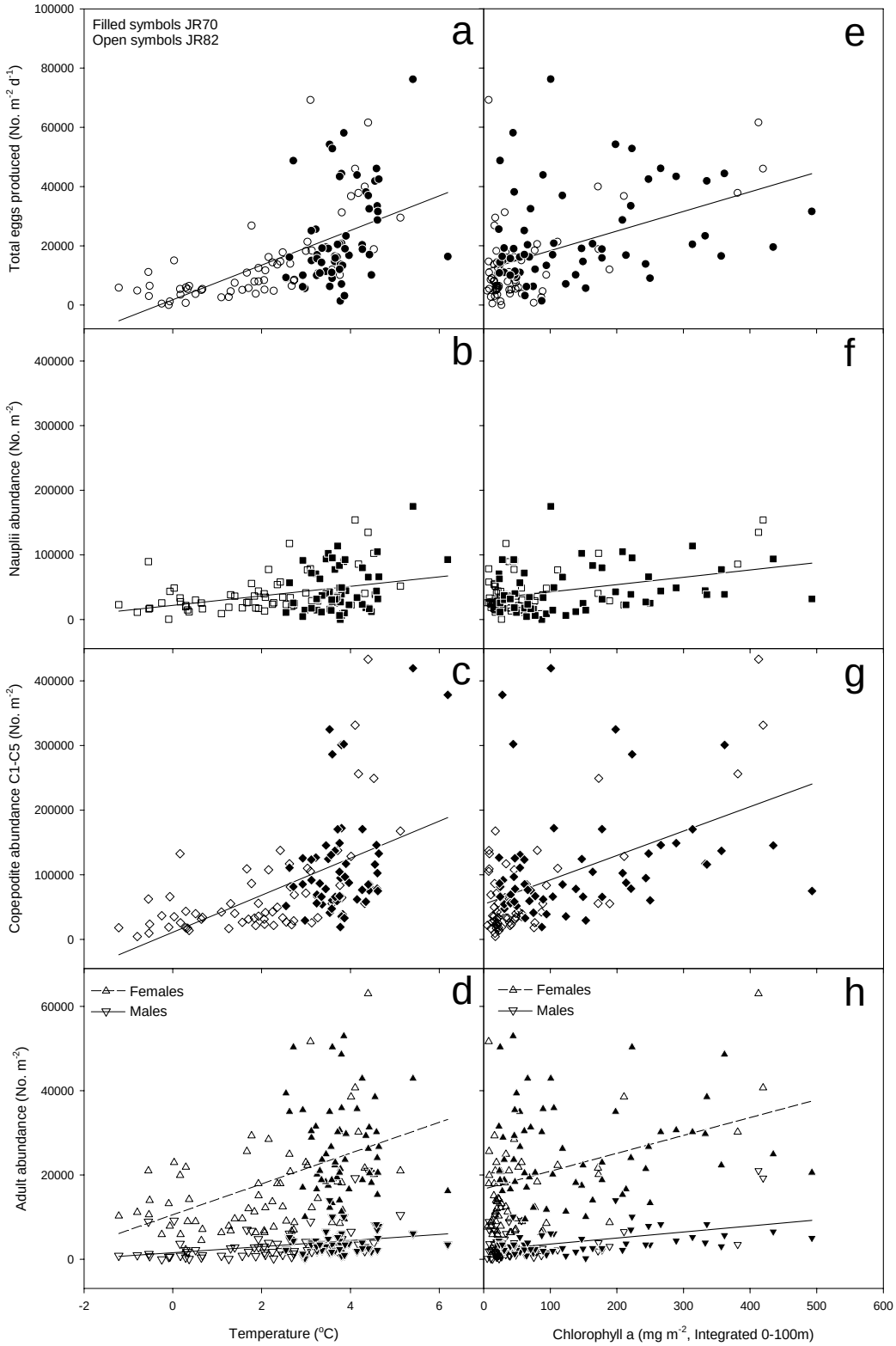

Filled symbols JR70
Open symbols JR82
a
b
c
d
e
f
g
h
Total eggs produced (No. m-2 d-1)
Naupliii abundance (No. m-2)
Copepodite abundance C1-C5 (No. m-2)
Adult abundance (No. m-2)
Females
Males
Temperature (oC)
Chlorophyll a (mg m-2, Integrated 0-100m)

Figure 3.

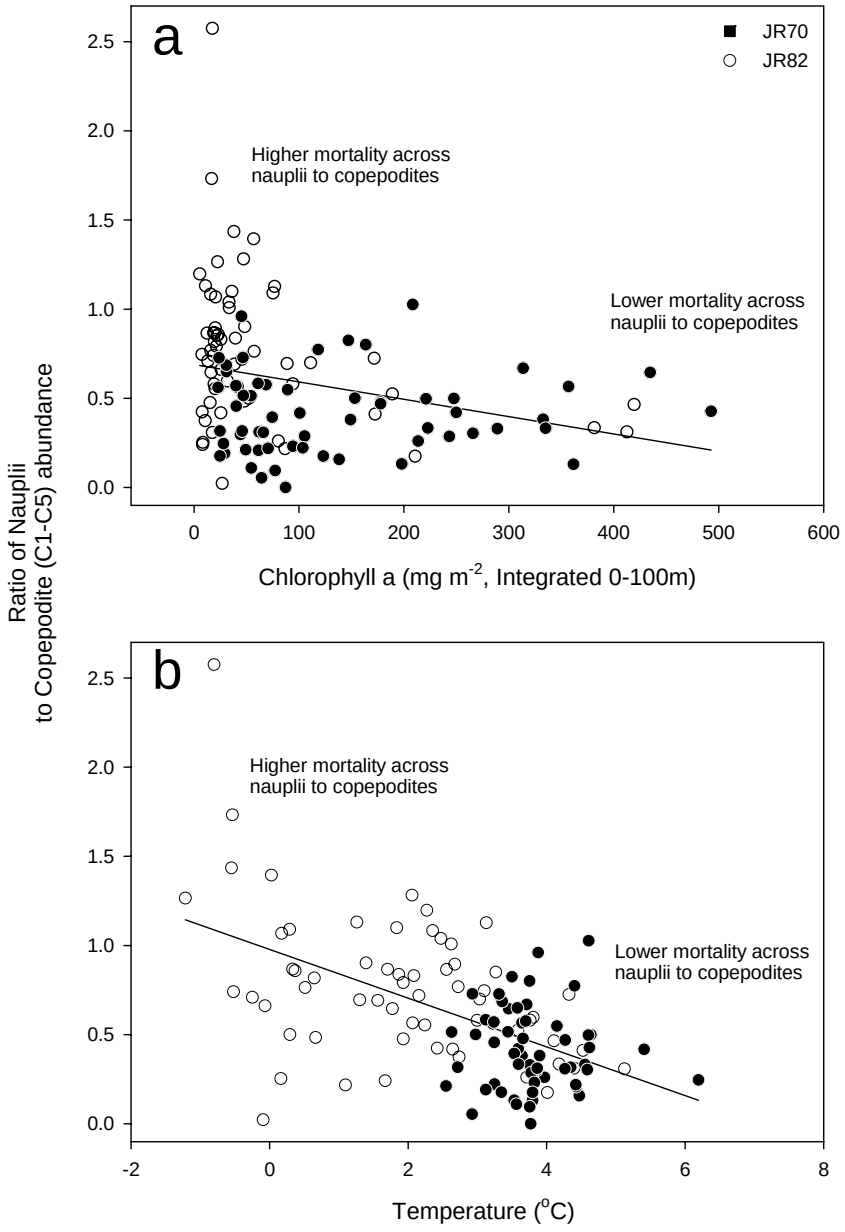

a
JR70
JR82
Higher mortality across nauplii to copepodites
Lower mortality across nauplii to copepodites
Ratio of Nauplii to Copepodite (C1-C5) abundance
Chlorophyll a (mg m-2, Integrated 0-100m)
b
Higher mortality across nauplii to copepodites
Lower mortality across nauplii to copepodites
Temperature (°C)

Figure 4.

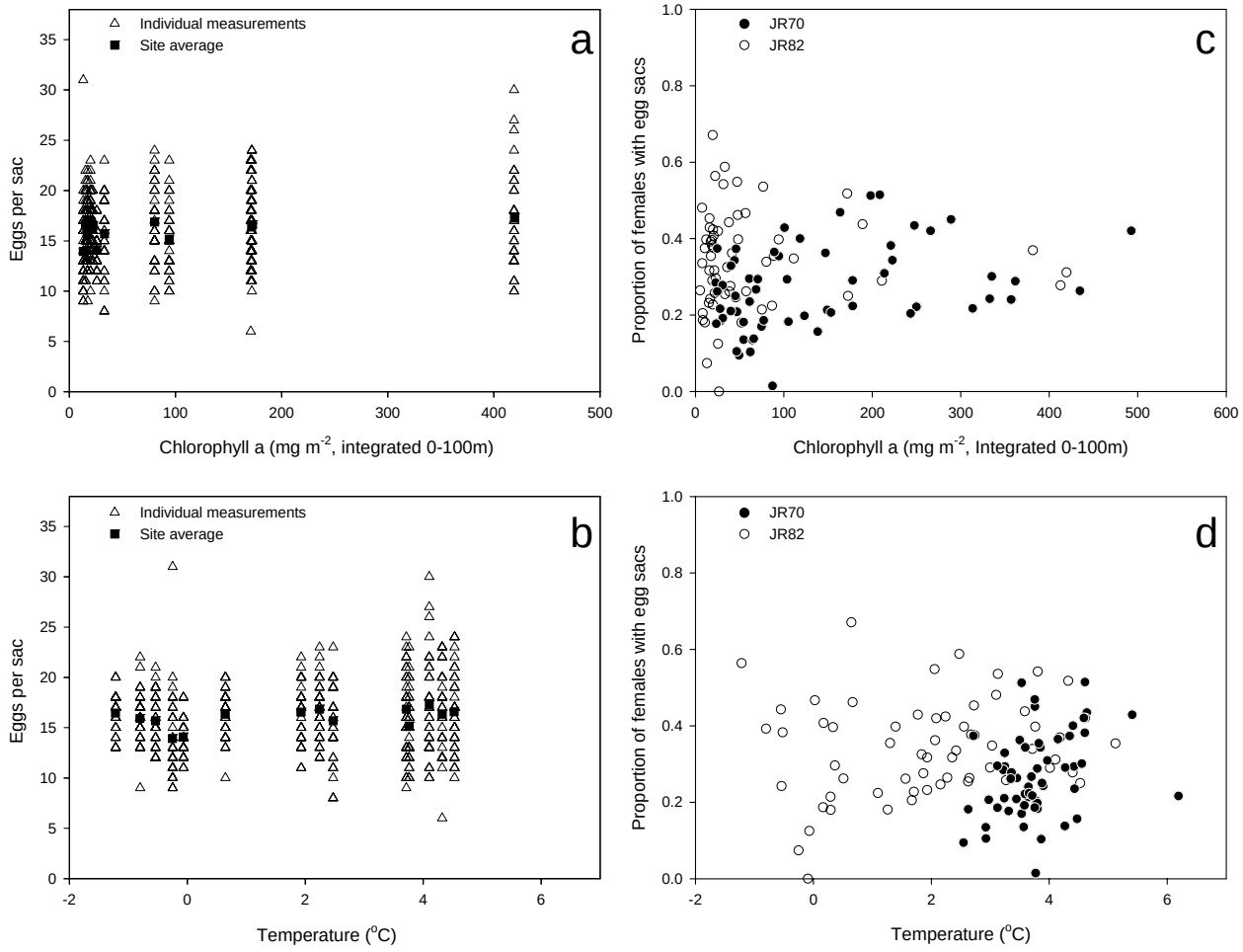

a
Individual measurements
Site average
Eggs per sac
Chlorophyll a (mg m-2, integrated 0-100m)
b
Individual measurements
Site average
Eggs per sac
Temperature (°C)
c
JR70
JR82
Proportion of females with egg sacs
Chlorophyll a (mg m-2, Integrated 0-100m)
d
JR70
JR82
Proportion of females with egg sacs
Temperature (°C)

Figure 5.

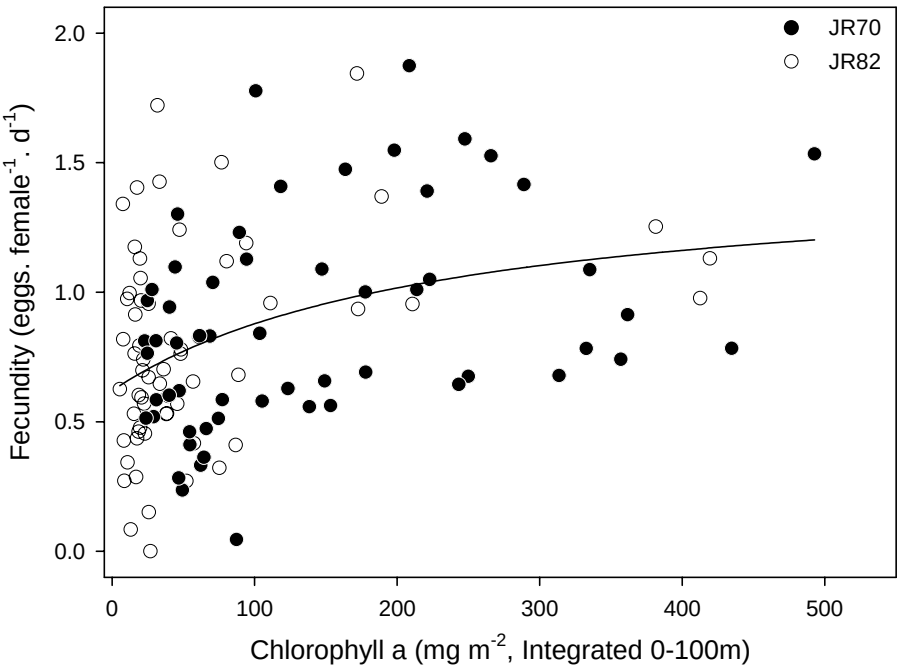

JR70
JR82
Fecundity (eggs. female-1 . d-1)
2.0
1.5
1.0
0.5
0.0
0
100
200
300
400
500
Chlorophyll a (mg m-2, Integrated 0-100m)

Figure 6.

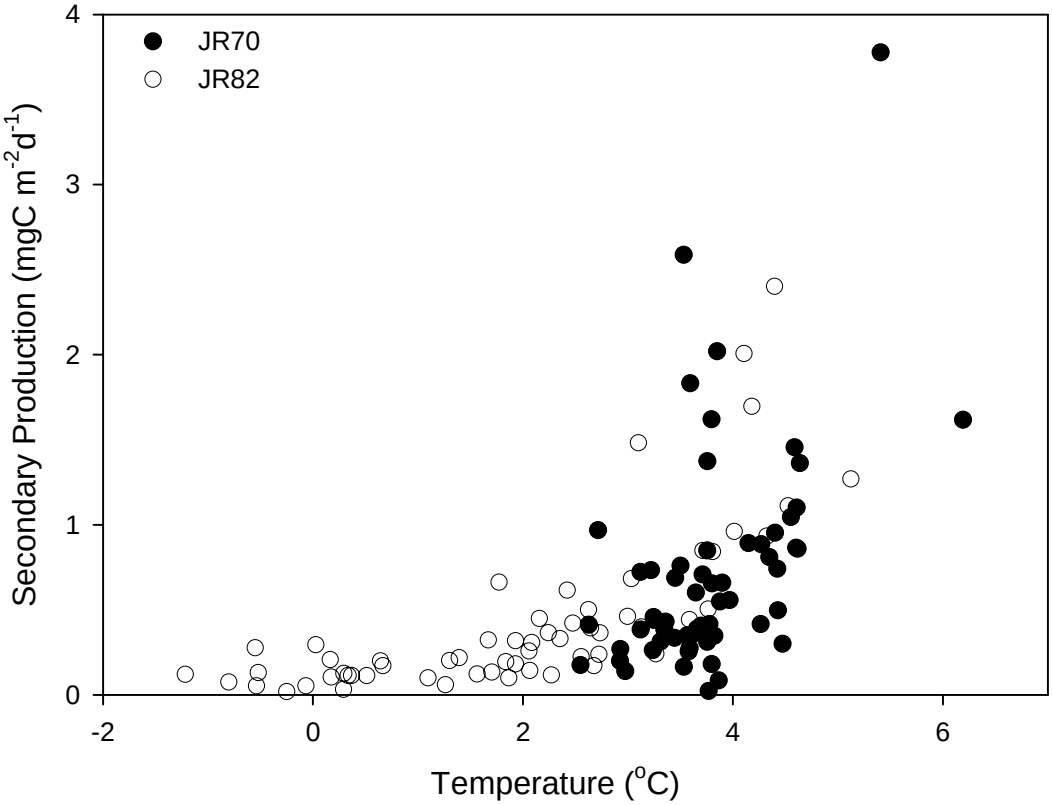

JR70
JR82
Secondary Production (mgC m-2d-1)
Temperature (oC)
4
3
2
1
0
-2
0
2
4
6

Figure 7.

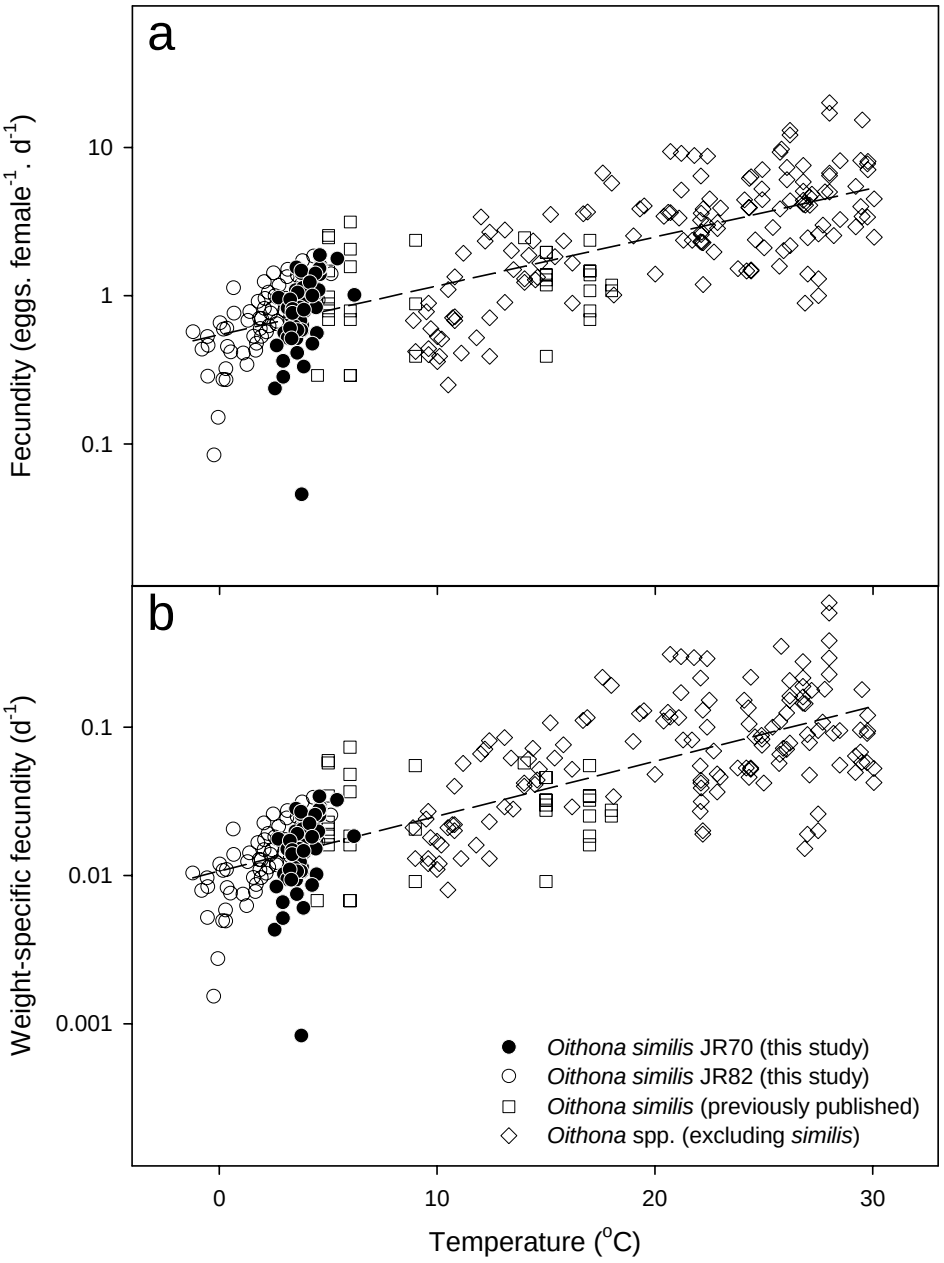

a
b
Fecundity (eggs. female-1. d-1)
Weight-specific fecundity (d-1)
10
1
0.1
0.01
0.001
0
10
20
30
Temperature (°C)
Oithona similis JR70 (this study)
Oithona similis JR82 (this study)
Oithona similis (previously published)
Oithona spp. (excluding similis)

Figure 8.

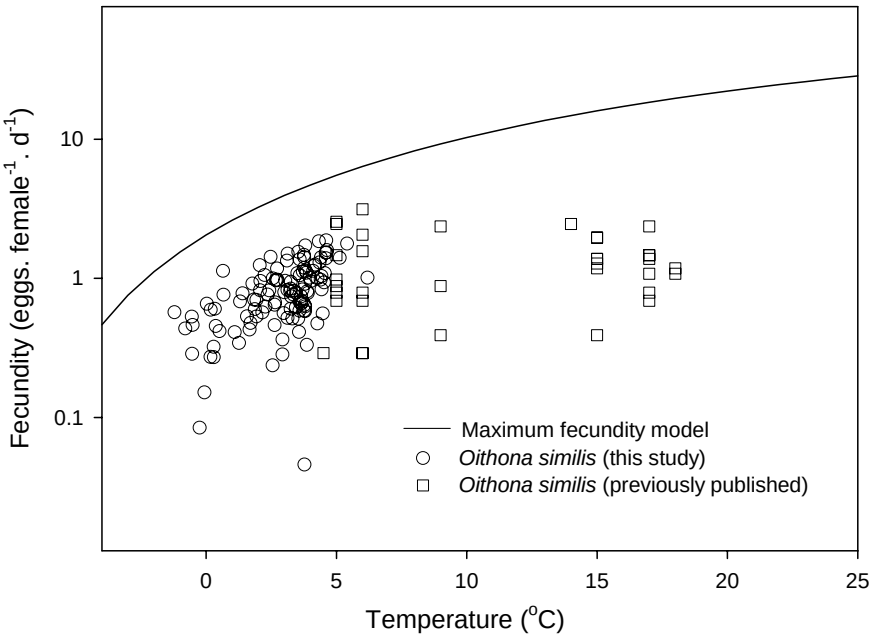
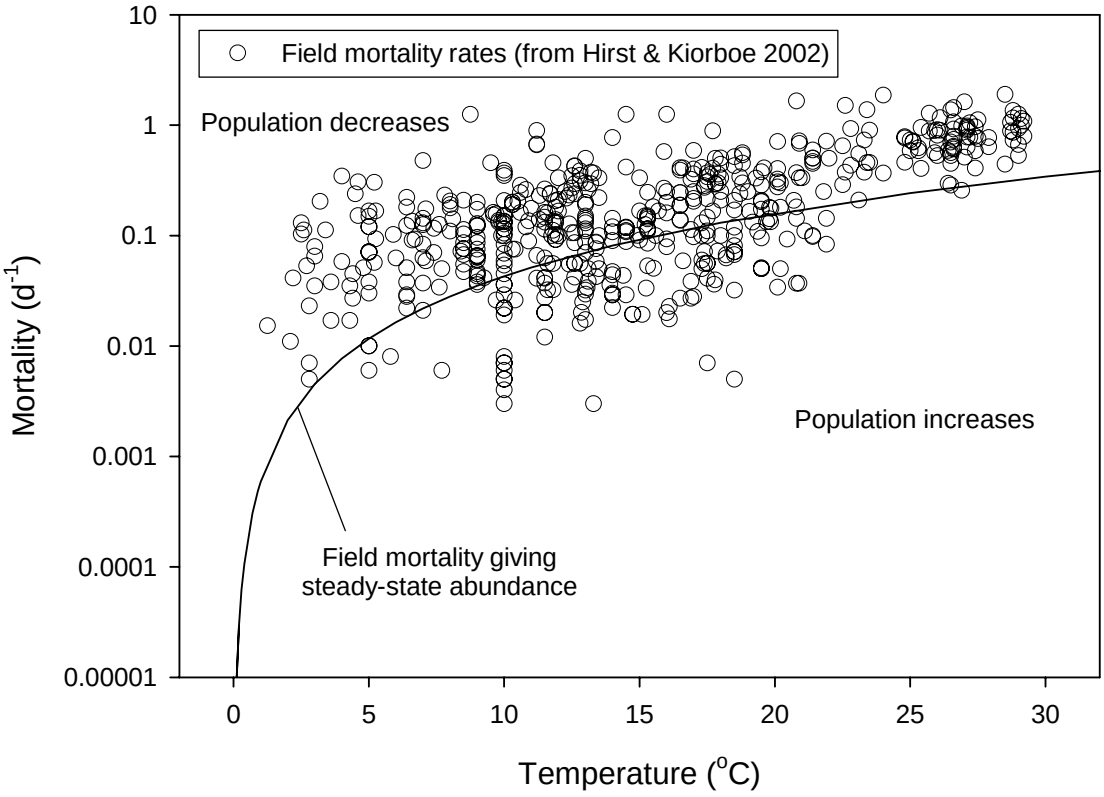

Fecundity (eggs. female-1. d-1)
10
1
0.1
0
5
10
15
20
25
Temperature (°C)
Maximum fecundity model
Oithona similis (this study)
Oithona similis (previously published)

Figure 9.


Field mortality rates (from Hirst & Kiorboe 2002)
Population decreases
Population increases
Field mortality giving
steady-state abundance
Mortality (d-1)
Temperature (oC)
10
1
0.1
0.01
0.001
0.0001
0.00001
0
5
10
15
20
25
30