

NOTE

Egg hatching rate of the cyclopoid copepod *Oithona similis* in arctic and temperate waters

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ABSTRACT: An equation is presented to facilitate estimation of the production of the cosmopolitan cyclopoid copepod *Oithona similis*. The egg hatching rate was studied from Arctic, subarctic and temperate waters covering a temperature interval from –1 to 20.5°C. Within this temperature range the hatching rate (HR) increased from 0.03 to 0.42 d⁻¹. Results from all experiments were fitted to a function $HR (\% d^{-1}) = 4.2176 + 1.7545T$ ($r^2 = 0.98$; $p < 0.0001$), where T = temperature. When combined with site-specific information on temperature, egg:female ratios and the carbon content of females and eggs, secondary production of this ubiquitous species can be readily estimated.

KEY WORDS: *Oithona similis* · Egg hatching rate · Egg production · Arctic

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Egg production of free-spawning copepod species has routinely been used to estimate copepod production, assuming that adult female copepods do not grow, but rather allocate the ingested carbon into the production of eggs. The weight-specific egg production rate (SEP) of the females is often assumed to equal the growth rate of the younger stages and the production can therefore be easily estimated from the SEP and the standing stock (but see Sabatini & Kiørboe 1994, Hopcroft & Roff 1998). While the SEP of free-spawning copepods is generally estimated over a single 24 h interval, this method cannot be directly applied to egg-carrying species that typically produce clutches of eggs less constantly and then carry the same clutch for several days. These include all cyclopoids, poecilo-

stomatoids and harpacticoids plus the important calanoid genera *Pseudocalanus*, *Euchaeta* and *Clausocalanus*, which combined constitute a significant fraction of marine copepods.

Of the egg-carrying marine copepods, the small cyclopoid *Oithona similis* is a cosmopolitan species with a wide geographical distribution, from the poles to the equator (Nishida 1985, Mazzocchi et al. 1995). Where investigated, *Oithona* has been shown to be one of the most abundant marine copepod genera (Turner 1982, Paffenhöffer 1993, Calbet & Agustí 1999). Unfortunately, the recommended use of nets with a mesh size of 200 µm for sampling of copepods (UNESCO 1968) still biases our knowledge about the quantitative importance of many small copepod species such as *Oithona* spp. Recent investigations using nets with smaller mesh size (e.g. 45 to 64 µm) or water bottles have documented that *Oithona* spp. contribute significantly to the standing stock of copepods in many marine ecosystems (Paffenhöffer 1993, Gonzales & Smetacek 1994, Nielsen & Sabatini 1996, Hopcroft et al. 1998). Knowledge about their production and potential grazing impact is therefore of key importance to the understanding of the productivity and dynamics of the world ocean.

The population-specific egg production rate (SEP, d⁻¹) of egg-carrying copepods can be accurately estimated by the egg-ratio method (Edmondson 1971). This method requires knowledge of the egg:female ratio of the population (i.e. including females not carrying eggs), the egg hatching rate (HR, d⁻¹) at *in situ* temperature, and the carbon content of the egg and female:

$$SEP = (\text{egg}/\phi) HR (\text{eggC}/\phi\text{C})$$

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Sabatini & Kiørboe (1994) have previously estimated the relationship between carbon content and the size of both eggs and females for *Oithona similis*. The aim of this paper is to establish the quantitative relationship between temperature and HR for *O. similis* to provide a simple method of estimating the production of this abundant copepod without routine experiments.

Materials and methods. The experiments were carried out during cruises in arctic (North Water polynya, Smith Sound, Canada; Disko Bay, western Greenland; the Greenland Sea), subarctic (Gulf of Alaska) and temperate (the North Sea) waters (Fig. 1). Temperature and salinity were recorded using a Seabird CTD, samples for chlorophyll *a* were filtered onto GF/F filters, extracted in ethanol or acetone and measured on a Turner fluorometer calibrated against a chlorophyll *a* standard.

Temperature, salinity, chlorophyll concentration, length of females and egg diameters at the study sites are summarised in Table 1. Copepods were collected from the surface water by slow vertical net hauls from the pycnocline to the surface using a net with 45 or 64 μm mesh size equipped with a large non-filtering cod-end. Immediately after sampling the con-

tent of the cod end was diluted in surface water in a large insulated container. Although females often lose their eggs sacs during collection, especially when seas are rough, generally some females are found with egg sacs intact. Female *Oithona similis* carrying egg sacs were placed individually in tissue culture trays (NUNC™ Multi wells) of 12 or 24 wells containing 3 or 5 ml of 45 μm filtered surface water and incubated at constant temperature. In general the experiments

Table 1. Range in surface salinity, temperature, chlorophyll *a*, cephalothorax length of female *Oithona similis* (mean \pm SE) and egg diameter (mean \pm SE) in the areas considered. Numbers in parentheses: number of measurements

Parameter	Smith Sound	Disko Bay	Greenland Sea	Gulf of Alaska	North Sea
Temperature, <i>in situ</i> ^a	-1.55 to -1.51	5-7	7.3-0.4	5-15	14
experimental	-0.4	2	-1.2	5-8	7
	-1, 1.4	0.2, 4.5, 7.5	-0.8, 2.3, 4.2	5, 10, 15, 18.5, 20.5	12
Salinity (psu)	30.3-30.4	32.6-33.6	32.7-35.0	29.0-32.4	34-35
Chlorophyll <i>a</i> ($\mu\text{g chl a l}^{-1}$)	4.1-5.0	1-3	0.3-1.0	0.7-2.0	0.1-0.5
Female length (μm)	477 \pm 5 (83)	441 \pm 9 (229)	473 \pm 3 (106)	454 \pm 6 (28)	532 \pm 26 (440)
Egg diameter (μm)	67.2 \pm 1.5 (35)	58.3 \pm 0.4 (165)	63.1 \pm 0.4 (439)	64.5 \pm 1.1 (36)	56.9 \pm 0.9 (600)

^aSecond line indicates temperature below thermocline, when thermocline was present within the water column

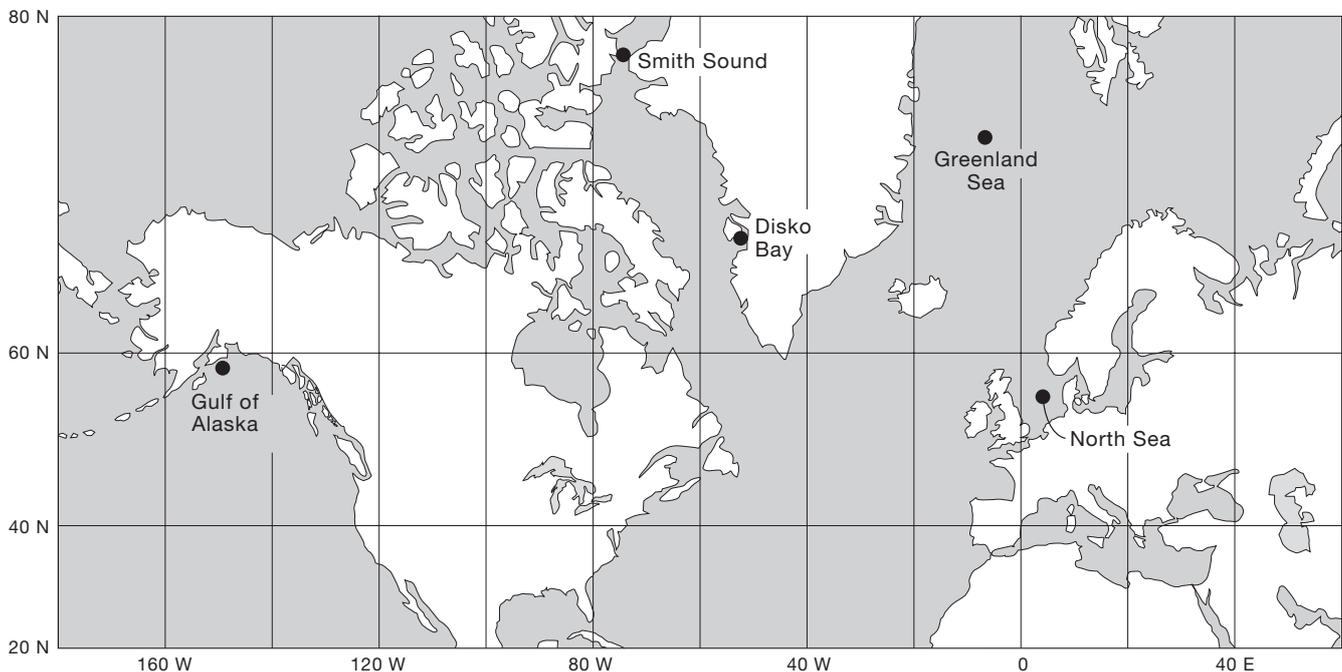


Fig. 1. Location of the study sites

were conducted at temperatures not different from those that the copepod would experience at the study site (Table 1), although females were exposed to several degrees beyond this at the warmest 2 experiments. Every 4 to 12 h, dependent on the incubation temperature, the wells were inspected under an inverted microscope, the temperature recorded and the number of females from the eggs had hatched was noted.

Hatching percentage was calculated from the number of clutches hatched divided by the number of females incubated. Incubation time was considered as the time at which observations were made. The hatching rate was calculated from the slope of a linear regression between the incubation time and the cumulative hatching percentage. The egg hatching time (HT) is defined as the time required to reach 100% hatching as predicted from these regressions.

Additional published data were available from experiments conducted at 12°C by Nielsen & Sabatini (1996), who found a hatching time of 4.48 d; and from experiments at 9 and 14°C by Eaton (1971), who found hatching times of 6.02 and 3.39 d, respectively. Eaton also presented an estimate for 14 d at 4.5°C, but noted that there were methodological problems at that temperature; these data were not included in the present analysis. These estimates were employed to establish a 'universal' equation between temperature, HR and HT.

Results. The various sites spanned a broad range of environmental conditions (Table 1). The salinity was similar (29 to 35 psu) at all sites, while temperature increased from the arctic to the temperate regions. Chlorophyll varied by an order of magnitude between locations, but in no systematic relationship to water temperature. Egg size was comparable at all locations.

The eggs in the sacs developed relatively synchronously until hatching. On several occasions we observed that nauplii escaped from the egg sacs within minutes of the onset of hatching. In other cases, hatching appeared to take several hours. During hatching, the nauplii often remained attached to the female for some time by remnants of the opened egg sac. In general, hatching success was high (>95%). During the experiments, no female mortality was observed, although some of the females were lost from the wells due to rough seas during the Disko Bay and Gulf of Alaska cruises.

HT time was inversely related to the water temperature, decreasing from 25.7 to 2.8 d⁻¹ across the temperature range tested (-1.0 to 20.5°C) (Fig. 2). Several equations were fit to the data, many of which provided a good overall statistical fit (Table 2). However, for those models with 3 fitted parameters, at least 1 parameter was not significant. The linear models (Fig. 3) gave a consistently better fit than the exponential models; however, the Bělehrádek model with the exponent fixed at 2.05 (McLaren et al. 1969) proved as satisfactory as the linear model and gave a comparable fit. We advocate the linear models between HR (% d⁻¹) or HT (in days) and temperature (T , °C), since these are mathematically simpler:

$$\text{HR} = 4.2176 + 1.7545T \quad (r^2 = 0.98, p < 0.0001, n = 16)$$

$$\text{HT} = (0.0464 + 0.0145T)^{-1} \quad (r^2 = 0.97, p < 0.0001, n = 16)$$

Although the fit of both equations is excellent, they are not perfect algebraic equivalents due to their independent statistical derivation. We are inclined to have greater faith in the HR equation, and note that the HT equation tends to slightly overestimate hatching time (determined as the reciprocal of HR prediction) at warmer temperatures and underestimate hatching time at colder temperatures.

Table 2. *Oithona similis*. Statistical summary of different models examined for hatching rate (HR) and hatching time (HT) vs temperature (T). For the Bělehrádek models, exponent was fitted, or set at 2.05 (McLaren et al. 1969)

	a	(±SE)	b	(±SE)	c	(±SE)	n	r ²	p<
HR vs T									
$a + b \cdot T$	4.2176	(0.6721)	1.75451	(0.0665)			16	0.98	0.0001
$a \cdot e^{(b \cdot T)}$	7.968	(0.7663)	0.0845	(0.0060)			16	0.94	0.0001
$c + a \cdot e^{(b \cdot T)}$	67.229	(43.211)	0.0214	(0.0114)	-62.351	(46.6143)	16	0.98	0.0001
$a \cdot (T + c)^b$	0.7027	(0.4981)	1.2655	(0.1954)	4.6412	(1.9087)	16	0.98	0.0001
$a \cdot (T + c)^{2.05}$	0.0327	(0.0029)			12.793	(1.1072)	16	0.98	0.0001
HT vs T									
$(a + b \cdot T)^{-1}$	0.0464	(0.0014)	0.0145	(0.0012)			16	0.97	0.0001
$a \cdot e^{(-b \cdot T)}$	23.610	(0.9293)	0.2088	(0.0194)			16	0.95	0.0001
$c + a \cdot e^{(-b \cdot T)}$	19.942	(0.5414)	0.3107	(0.0277)	3.2955	(0.5414)	16	0.98	0.0001
$a \cdot (T + c)^{-b}$	344.12	(444.29)	1.5759	(0.4258)	5.6103	(1.9311)	16	0.98	0.0001
$a \cdot (T + c)^{-2.05}$	1504.5	(202.13)			7.6998	(0.4970)	16	0.98	0.0001

Discussion. Of the egg-carrying marine copepods, the cyclopoid *Oithona similis* exists over a wider range of temperatures and salinity than most other marine copepods from temperate brackish coastal waters to subtropical oligotrophic oceans (Nishida 1985, Maz-

zocchi et al. 1995). In cold areas like the arctic and temperate regions, *Oithona* is often the most important winter copepod genus present, and reproduces year-round in surface waters (Kiørboe & Nielsen 1994, Uye & Sano 1995).

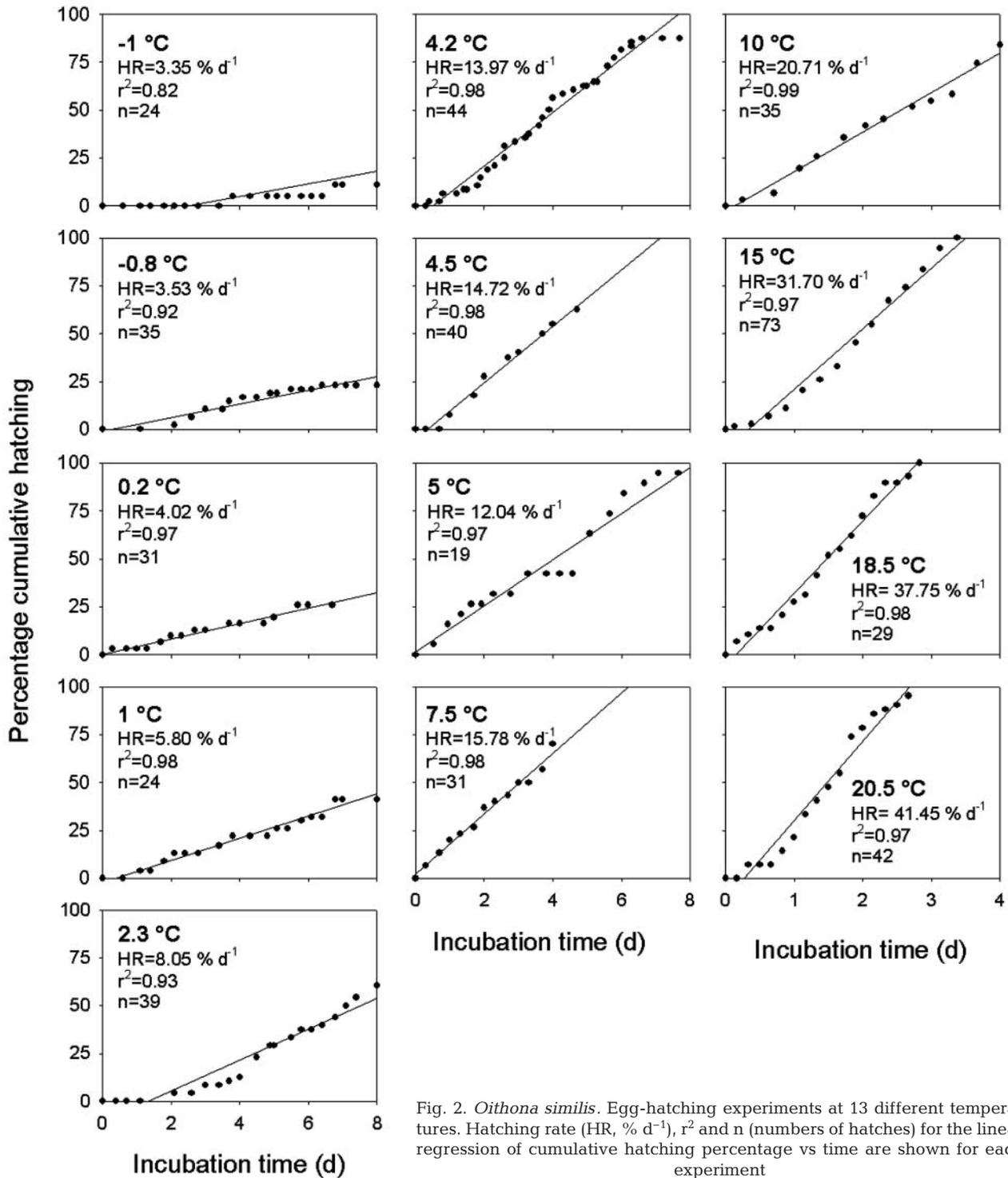


Fig. 2. *Oithona similis*. Egg-hatching experiments at 13 different temperatures. Hatching rate (HR, % d⁻¹), r² and n (numbers of hatches) for the linear regression of cumulative hatching percentage vs time are shown for each experiment

The copepod egg-hatching rate has been shown to be influenced by egg size, salinity and temperature. If equations such as those presented here have any applicability, influence from parameters other than temperature needs to be negligible. McLaren et al. (1968) demonstrated that the effect of salinity is minor compared with that of temperature. Additionally, the variation in salinity between locations is generally less than the variation observed within each area, further eliminating salinity as a potential source of bias. Kiørboe & Sabatini (1995) concluded that egg developmental time was independent of egg size within a size range larger than that observed during this investigation (57 to 67 μm : Table 1). Although chlorophyll varied by an order of magnitude between locations, this would affect clutch size and frequency, not hatching time (Hopcroft & Roff 1996). Thus, the measured differences in HR can safely be attributed to differences in temperature.

One potential shortcoming of this method is that it presumes that the copepods incubated are randomly

distributed throughout their egg-carrying cycle. In the tropics, where hatching time is short, diel patterns may preclude confident prediction of hatching time by our method. In such warm waters, it would appear necessary (and be logistically feasible) to observe both the production and hatching of clutches to directly determine the hatching time (e.g. Hopcroft & Roff 1996, Ambler et al. 1999). At cold temperatures, when hatching time is prolonged, this causes relatively little error in the final estimation of hatching rate.

Previous investigations of *Oithona* species hatching or development time cover a higher or smaller temperature range than in this study; e.g. *O. davis*: 10 to 30°C (Uye & Sano 1995, 1998); *O. similis*: 4.5 to 14°C (Eaton 1971). Eaton noted that her value at 4.5°C might be suspect, as we have confirmed, limiting her reliable data to only 9 and 14°C. Thus, our hatching rate measurements at colder temperatures, and over an extended temperature range make our equations applicable to a much larger geographical range.

To our knowledge, this note is the first attempt to establish a general equation for estimation of hatching rates of this very important copepod covering the full range of temperatures from arctic to temperate waters. The applied multi-well technique is a low-cost, space-efficient method and allows rapid handling of many replicates, yielding an easy establishment of temperature-dependent hatching rate relationships for sac-spawners. This facilitates routine estimation of productivity. More importantly, for preserved finer-mesh samples that contain both females and their detached egg sacs, our equations provide a critical step that allows prediction of secondary production of this abundant but often ignored component of the copepod community.

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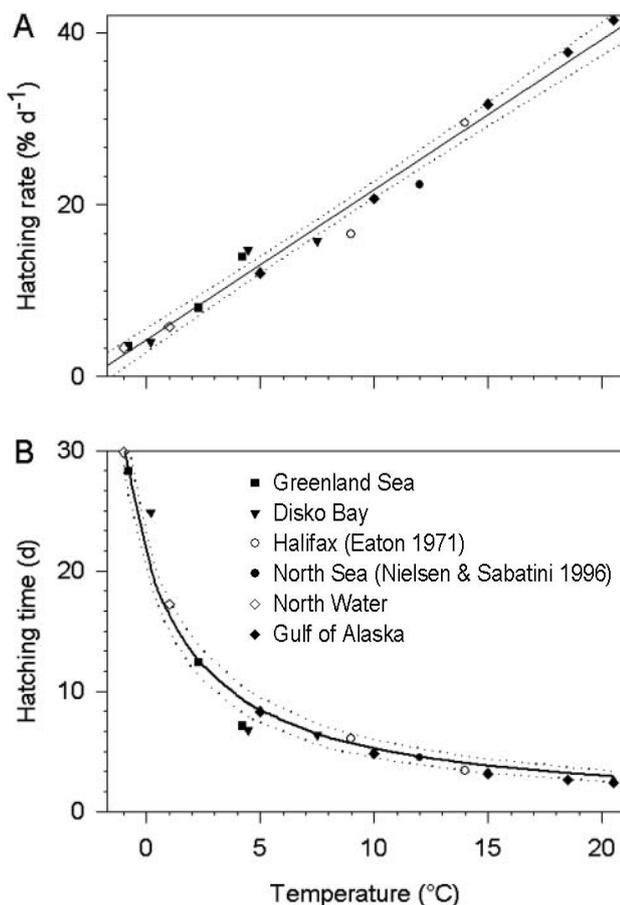


Fig. 3. *Oithona similis*. (A) Egg hatching rate and (B) hatching time as function of temperature. Dotted lines indicate the 95% confidence intervals for the filled lines

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