



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 $HR (\% d^{-1}) = 4.2176 + 1.7545 \cdot T$ ($r^2=0.98$; $P < 0.0001$). 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.

Introduction

Egg production of free spawning copepod species have 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 Hopcroft & Roff, 1998, Sabatini & Kjørboe 1994). While the SEP of free spawning copepods is generally estimated over a single 24 hour interval, this method can not 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, poecilostomatoids and harpacticoids plus the important calanoid genera *Pseudocalanus*, *Euchaeta*, *Clausocalanus* that combined constitute a significant fraction of marine copepods.

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

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) *in situ* temperature, and the carbon content of the egg and female:

$$SEP = (\text{Egg/female}) \cdot HR \cdot (\text{egg C/female C})$$

Sabatini & Kjørboe (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 egg hatching rate for *Oithona similis* to provide a simple method of estimating the production of this abundant copepod without routine experiments.

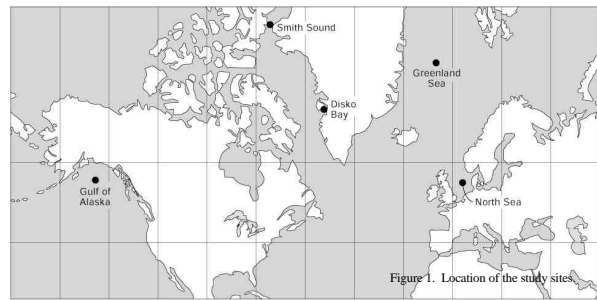


Figure 1. Location of the study sites.

Table 1 Range in surface salinity, temperature, chlorophyll *a*, female cephalothorax length ± SE and egg diameter ± SE the areas considered. Numbers in parenthesis is the number of measurements.

	Northwater	Disko Bay	Greenland Sea	Gulf of Alaska	North Sea
Temperature, <i>in situ</i> ^a	-1.55 - -1.51	5-7	7.3-10.4	-5.15	14
	-0.4	2	-1.2	5.8	7
Experimental temperature	-1, -1.4	0.2, 4.5, 7.5	-0.8, 2.3, 4.2	5.10, 16, 18.5,	20.5
Salinity (PSU)	30.3-30.4	32.6-33.6	32.7-35.0	29.0-32.4	34-35
Chlorophyll <i>a</i> (µg chl <i>a</i> l ⁻¹)	4.1-5.0	1-3	0.3-1.0	0.73-2.0	0.1-0.5
Female length (µm)	477±5 (83)	441±9 (229)	473±3 (106)	454±6 (28)	532±26 (440)
Egg diameter (µm)	67.2±1.5 (35)	58.3±0.4 (165)	63.1±0.4 (439)	64.5±1.1 (36)	56.9±0.9 (600)

^a If a thermocline was present, second line indicates the temperature below the thermocline.

Results

Across the different systems, the environment spanned a broad range (Table 1). The salinity at the different sites was the same (29.0-35 psu), while the temperature obviously increased from the arctic to the temperate regions. Chlorophyll varied an order of magnitude between locations, but in no systematic pattern with respect 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 having hatched. In other cases hatching appeared to occur over several hours, with nauplii frequently remaining attached to the female for some time by remnants of the opened egg sac. In general the hatching success was high (> 95%). During the experiments no female mortality was observed, although during the Disko Bay and Gulf of Alaska cruises where some of the females were lost from the wells due to rough seas.

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

$$HR = 4.2176 + 1.7545 \cdot T, r^2 = 0.98, P < 0.0001, n=16$$

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

Table 2. Statistical summary of different models examined for HR and HT vs. temperature. For the Belehrádek models, exponent was fixed, or set at 2.05 (McLaren et al. 1969), n=16, P<0.0001 in all cases

	a	(S.E.)	b	(S.E.)	c	(S.E.)	r ²
Hatching rate vs. temperature (T)	a+b ^a T	4.2176 (0.6721)	1.75451 (0.0665)				0.98
	a ^b e ^{cT}	7.968 (0.7663)	0.0845 (0.0060)				0.94
	c+a ^b e ^{cT}	67.229 (43.211)	0.0214 (0.0114)	-62.351 (46.6143)			0.98
	a ^b (T+c) ^b	0.7027 (0.4981)	1.2655 (0.1954)	4.6412 (1.9087)			0.98
	a ^b (T+c) ^{2.05}	0.0327 (0.0029)		12.793 (1.1072)			0.98
Hatching time vs. temperature (T)	(a+bT ^b) ⁻¹	0.0464 (0.0014)	0.0145 (0.0012)				0.97
	a ^b e ^{cT}	23.610 (0.9253)	0.2088 (0.0194)				0.95
	c+a ^b e ^{cT}	19.942 (0.5414)	0.3107 (0.0277)	3.2955 (0.5414)			0.98
	a ^b (T+c) ^b	344.12 (444.29)	1.5759 (0.4258)	5.6103 (1.9311)			0.98
	a ^b (T+c) ^{2.05}	1504.5 (202.13)		7.6998 (0.4970)			0.98

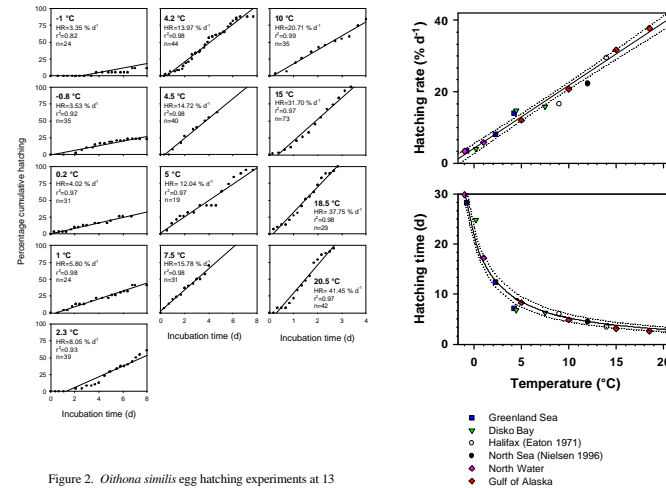


Figure 2. *Oithona similis* egg hatching experiments at 13 different temperatures. Hatching rate (HR, % d⁻¹), r² and n (numbers of hatches) for the linear regression of cumulative hatching percentage vs. time are shown for each experiment.

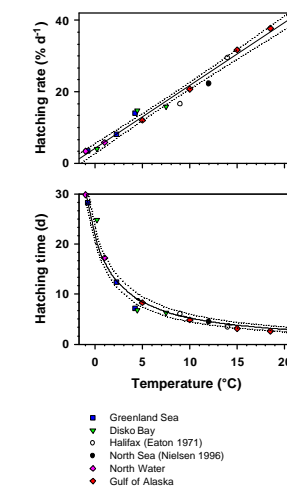


Figure 3. *Oithona similis* egg hatching rate a) and hatching time b) as function of temperature.

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 water to subtropical oligotrophic oceans (Nistida 1985, Mazzocchi 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 (Kjørboe & Nielsen 1994, Uye & Sano 1995).

One potential shortcoming of this method is that it presumes the animals incubated are randomly distributed throughout their egg-carrying cycle. If egg-laying (and hatching) follow a strongly diel cycle (Hopcroft & Roff 1996, Ambler et al., 1999), then there will be a bias introduced, creating a step-like pattern in the percentage hatching. At cold temperatures, when hatching time is long, this causes relatively little error in the final estimation of hatching rate. If the method is applied in the tropics, it would appear necessary (and be logistically feasible) to observe both the production and hatching of clutches to estimate the hatching time (e.g. Hopcroft & Roff 1996).

Previous investigations of *Oithona* species hatching or development time cover a higher or smaller temperature range than this study e.g. *Oithona davisae* - 10 to 30 °C (Uye & Sano 1995, 1998) and *Oithona similis* - 4.5 to 14 °C (Eaton 1971). Eaton noted that that her value at 4.5°C might be suspect, as we have confirmed, limiting her reliable data to only 9 & 14 °C. Thus, our hatching rate measurements at colder and extended temperatures, make the equations applicable for 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 low cost, space efficient, 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 for prediction of secondary production of this abundant but often ignored component of the copepod community.

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