SHORT NOTE

Peter Ward · Rachael Shreeve Egg hatching times of Antarctic copepods

Received: 27 March 1997 / Accepted: 17 August 1997

Abstract Egg hatching times were determined at a range of temperatures for four species of commonly occurring Antarctic copepods. At a given temperature the eggs of *Rhincalanus gigas* took longest to hatch, up to 9 days at 0°C, followed by those of *Calanoides acutus, Calanus propinquus* and *Calanus simillimus*. A Bělehrádeks temperature function with the parameter *b* fixed at -2.05 accounted for >95% of the variance for each species. There was an approximate doubling in hatching times between 5°C and 0°C for *R. gigas* and for the other species the increase in embryonic duration was 40–50% at the lower temperature.

Introduction

Relatively little is known about the reproductive biology of Southern Ocean copepods although some direct measurements of gonad maturation, clutch size and the spatial variability of egg production in relation to food supply have been made (see studies by Huntley and Lopez 1990; Kurbjeweit 1993; Roberts et al. 1994; Ward and Shreeve 1995). For copepods generally it has been concluded that mortality is greatest in the egg and naupliar stages (Kiørboe and Sabatini 1994; Peterson and Kimmerer 1994; Poulet et al. 1995) and therefore the determination of embryonic duration in relation to temperature is an important step towards a better understanding of the population dynamics of Antarctic species.

Corkett et al. (1986), McLaren et al. (1969, 1989), Uye (1988) and others have shown in a series of papers that embryonic development times for species of *Calanus*

P. Ward (⊠) · R. Shreeve British Antarctic Survey (NERC), High Cross Site, Madingley Road, Cambridge CB3 0ET, UK e-mail: PWAR@pcmail.nerc-bas.ac.uk; Fax: 01223 302093 and *Pseudocalanus*, over a range of temperatures, can be described by a Bělehrádek's temperature function $[D = a(T - \alpha)^b$, where D = stage duration in days, *a*, *b* and α are constants and T = temperature (°C)]. The constant alpha has been shown to be related to the temperature regime of the species and *a* proportional to egg diameter. In this paper we report work carried out during December 1996/January 1997 onboard RRS *James Clark Ross* in the region of South Georgia (53.5°S 37°W). Egg hatching times were determined at a range of temperatures for four of the large copepod species commonly occurring in the Southern Ocean, *Rhincalanus gigas, Calanus simillimus, Calanoides acutus* and *Calanus propinquus*.

Materials and methods

Hatching times were determined on eggs recovered from female R. gigas, Calanus simillimus, Calanoides acutus and Calanus propinquus, which were individually maintained in filtered sea water (FSW) in small perspex petri dishes (25 ml capacity) at ambient sea surface temperature (2.5°C). Dishes were examined every 2–3 h and any eggs laid were gently pipetted out into another petri dish containing FSW that was pre-chilled to experimental temperatures of 0°C, 2.5°C or 5°C. Dishes were then set to incubate in modified chest freezers. Clutches of between 30-50 eggs were transferred to each dish and the temperatures at which they were incubated chosen to reflect the range over which these species are known to occur. Replication was carried out for each species at each temperature. Experiments carried out at these temperatures on a previous cruise had established to within 12 h when the first eggs should hatch. From this point onwards the present experiments were inspected every 2 h until hatching was complete. A nauplius was judged to be fully hatched when it was clear of the egg membranes.

Calculation of embryonic duration

Embryonic duration was taken as the point at which 50% of the final number of hatchlings was observed (Peterson and Painting 1990). This was generally within 12 h of the first nauplii being observed, although in the case of *Calanoides acutus* and *Calanus*

simillimus hatching continued for up to 2.5 days after the first appearance of nauplii. *R. gigas* eggs generally all hatched within a 6-h period at all temperatures.

Results and discussion

Time to 50% hatching versus temperature for the three species is shown in Fig. 1. A Bělehrádek function $[D = a(T - \alpha)^{b}]$ relating embryonic duration (D = days) to temperature (T°C) was fitted to the data for each of the three species. Of the three parameters, α (temperature scale position of the response) and a (slope of the response) were determined (**Ta**ble 1), whereas b (curvature) was fixed as -2.05 (see McLaren et al. 1969). For each species the fitted response with b fixed accounted for >95% of the variance in the data. Values of α reflect differences in temperature adaptation between species (Corkett and McLaren 1970), with the lowest value being seen for Calanus propinquus and Calanoides acutus, followed by Calanus simillimus and R.gigas. This essentially reflects the geographic distribution of the species; i.e. Calanoides acutus and especially Calanus propinguus are particularly abundant in the colder parts of the Southern Ocean such as the Weddell Sea (Schnack-Schiel and Hagen 1994; Atkinson et al. in press) whereas the latter two species are more commonly found in the polar frontal regions and sub-Antarctic (Atkinson 1991; Ward et al 1996).

There were clear differences in embryonic duration between species with the fastest at a given temperature being Calanus simillimus followed by Calanoides acutus, Calanus propinguus and finally R. gigas. For R. gigas there was an approximate doubling in development time between 5°C and 0°C whereas for the other species the curvature of the temperature response was flatter and the increase in embryonic duration only some 40-50%greater at 0°C. Parameter a has been found to be related to egg diameter in related species of the genus Calanus (Corkett 1972). For the two species of Calanus in this study this relationship is consistent in that Calanus propinguus, the largest species, produces bigger eggs (**Table 1**) and has a larger value of a than Calanus simillimus. However, for both species a is considerably larger than would be predicted from Fig. 2 of McLaren

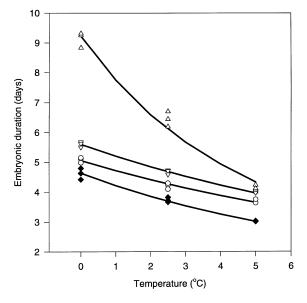


Fig. 1 Embryonic duration versus temperature for four species of Antarctic calanoid copepod. \triangle *Rhincalanus gigas*, \blacklozenge *Calanus simillimus*, ∇ *Calanoides acutus*, \bigcirc *Calanus propinquus*

et al. (1988), in which for a number of temperate and boreal members of the genus *Calanus*, *a* is plotted against egg diameter. The temperature ranges over which embryonic durations were determined by McLaren et al. (1988) exceeded the 5°C span of our experiments and, as a consequence, the values of *a* for their species may reflect an increased slope by virtue of values at the extremes of the range. In areas such as the Weddell Sea, the average temperatures that copepods may encounter during spawning can be below 0°C and, as Ross et al. (1988) have shown, development times for *Euphausia superba* eggs and early larvae increase dramatically below this temperature. Our experiments could therefore be usefully repeated and the temperature range extended in both directions.

Acknowledgements We thank the officers and crew of RRS *James Clark Ross* and our colleagues on cruise JR11 for their patient assistance in the field. A.W.A. Murray fitted the temperature functions and A. Hirst and Drs. A. Atkinson and J. Priddle read and commented on earlier drafts of this manuscript.

Table 1 Female prosome length, egg diameter and parameters *a* and α of the Bělehrádek equation $D = a(T - \alpha)^b$ fitted to egg hatching times for four species of Antarctic calanoid copepod. Measurements are means (±SD) for 20 females and 30 eggs respectively

Species	Prosome length (mm)	Egg diameter (μm)		a	α
		Inner membrane	Outer membrane		
Rhincalanus gigas Calanus simillimus Calanoides acutus Calanus propinquus	$\begin{array}{c} 7.02 \ (\pm 0.42) \\ 2.82 \ (\pm 0.14) \\ 4.10 \ (\pm 0.18) \\ 4.23 \ (\pm 0.15) \end{array}$	$-150 (\pm 5)$ -155 (±7)	$200 (\pm 5) 225 (\pm 10) 190 (\pm 8) 260 (\pm 15)$	1305 2475 4883 5077	-11.20 -21.42 -27.19 -29.14

References

- Atkinson A (1991) Life cycles of *Calanoides acutus, Calanus simillimus* and *Rhincalanus gigas* (Copepoda: Calanoida) within the Scotia Sea. Mar Biol 109:79–91
- Atkinson A, Schnack-Schiel SB, Ward P, Marin V (in press) Regional differences in the life cycle of *Calanoides acutus* (Copepoda: Calanoida) within the Atlantic sector of the Southern Ocean. Mar Ecol Prog Ser 150:99–111
- Corkett CJ (1972) Development rate of copepod eggs of the genus *Calanus*. J Exp Mar Biol Ecol 10:171–175
- Corkett CJ, McLaren IA (1970) Relationships between development rates of eggs and older stages of copepods. J Mar Biol Assoc UK 50:161–168
- Corkett CJ, McLaren IA, Sevigny J-M (1986) The rearing of the marine calanoid copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus* Kroyer with comment on the equiproportional rule. In: Schriever G, Schminke HK Shih C-t (eds) Proceedings of the 2nd International Conference on Copepoda, Ottawa 1984. Syllogeus 58:539–546
- Huntley ME, Lopez MDG (1990) Reproduction of Calanoides acutus during the spring bloom 1989. Antarct J US XXV:159–161
- Kiørboe T, Sabatini M (1994) Reproductive and life cycle strategies in egg-carrying cyclopoid and free spawning calanoid copepods. J Plankton Res 16:1353–1366
- Kurbjeweit F (1993) Reproduction and life cycle of dominant copepod species from the Weddell Sea, Antarctica. Ber Polarforsch 129:1–243
- McLaren IA, Corkett CJ, Zillioux EJ (1969) Temperature adaptations of copepod eggs from the arctic to the tropics. Biol Bull Woods Hole Mass 137:486–493
- McLaren IA, Sevigny J-M, Corkett CJ (1988) Body sizes, development rates, and genome sizes among *Calanus* species. In: Boxshall GA, Schminke HK (eds) The biology of copepods. Hydrobiologia 167/168:275–284

- McLaren IA, Sevigny J-M, Corkett CJ (1989) Temperature-dependent development in *Pseudocalanus* species. Can J Zool 67:559–564
- Peterson WT, Kimmerer WJ (1994) Processes controlling recruitment of the marine calanoid copepod *Temora longicornis* in Long Island Sound: egg production, egg mortality and cohort survival rates. Limnol Oceanogr 39:1594–1605
- Peterson WT, Painting SJ (1990) Developmental rates of the copepods *Calanus australis* and *Calanoides carinatus* in the laboratory, with discussion of methods used to calculate development time. J Plankton Res 12:283–293
- Poulet ŠA, Ianora A, Laabir M, Klein Breteler WCM (1995) Towards the measurement of secondary production and recruitment in copepods. ICES J Mar Sci 52:359–368
- Roberts KA, Kleppel GS, Burkart CA, Carter K (1994) Egg production of the copepod *Calanoides acutus* (Giesbrecht) in the Weddell Sea during spring. Antarct J US XXIX:155–157
- Ross RM, Quetin LB, Kirsch E (1988) Effect of temperature on developmental times and survival of early larval stages of *Euphausia superba* Dana. J Exp Mar Biol Ecol 121:55–71
- Schnack-Schiel SB, Hagen W (1994) Life cycle strategies and seasonal variations in distribution and population structure of four dominant copepod species in the eastern Weddell Sea, Antarctica. J Plankton Res 16:1543–1566
- Uye S-I (1988) Temperature-dependent development and growth of Calanus sinicus (Copepoda: Calanoida) in the laboratory. In: Boxshall GA, Schminke HK (eds) The biology of copepods. Hydrobiologia 167/168:285–293
- Ward P, Shreeve RS (1995) Egg production in three species of Antarctic calanoid copepods during an austral summer. Deep Sea Res 42:721–735
- Ward P, Shreeve RS, Cripps GC, Trathan PN (1996) Mesoscale distribution and population dynamics of *Rhincalanus gigas* and *Calanus simillimus* in the Antarctic polar open ocean and Polar Frontal Zone during summer. Mar Ecol Prog Ser 140:21–32