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Temperature Effects on the Egg Development Time and Hatching Success of Three *Acartia* Species (Copepoda: Calanoida) from the Strait of Malacca

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Teruaki Yoshida, Ching-Fong Liong, Abdul Mohamed Majid, Tatsuki Toda, and Bin Haji Ross Othman (2012) Temperature effects on the egg development time and hatching success of three *Acartia* species (Copepoda: Calanoida) from the Strait of Malacca. *Zoological Studies* **51**(5): 644-654. Development times and hatching success rates at 6 temperatures (10, 14, 18, 22, 27, and 31°C) are presented for eggs of 3 congeneric Acartiid copepods, *Acartia spinicauda*, *A. erythraea*, and *A. pacifica*, from the Strait of Malacca, Malaysia. Egg development times of the 3 species were significantly related to the incubation temperature and each fit Bělehrádek's function. Hatching success at 10°C was the lowest (13%) and significantly differed from those at other temperatures (by an ANOVA). Average hatching success rates at 14-31°C were 61% ± 26%, 78% ± 8%, and 87% ± 8% for *A. erythraea*, *A. pacifica*, and *A. spinicauda*, respectively. The temperature functions for egg development times of *A. erythraea*, *A. pacifica*, and *A. spinicauda* were $D = 294(T - 4.47)^{-2.05}$, $D = 545(T - 1.94)^{-2.05}$, and $D = 352(T - 4.30)^{-2.05}$, respectively. Values of the 'biological zero' for Acartia were significantly correlated with environmental temperatures, suggesting that differences in temperature adaptation of development rates of eggs can be described from a single parameter of the temperature response. The results observed in this study were compared to findings from previous studies performed on other Acartiid species and from other copepod genera. http://zoolstud.sinica.edu.tw/Journals/51.5/644.pdf

Key words: *Acartia*, Egg, Biological zero, Tropical coastal waters.

Researchers in many fields of biology often mathematically express the temperature dependence of rates of metabolic processes. When calculating secondary production of copepods in marine ecosystems, it is important to be able to predict rates or times of development at different temperatures, as rates of development are largely temperature dependent (Huntley and Lopez 1992, Ban 1994). Temperature affects the development time within a species and is commonly described by Bělehrádek's (1935) empirical equation relating physiological rates and temperature: $D = a(T - \alpha)^b$, where D is the development time (d), T is the temperature (°C) and a, α, and b are fitted constants. These parameters separately express the 3 properties of any monotonic temperature response: b approximates the 'shape' or 'curvature' of the

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response, α positions the curve on the arbitrary Celsius scale (often referred to as the 'biological zero'), and *a* determines the proportional response on the time or rate scale (McLaren 1995).

Copepods are one of the most important components of zooplankton in coastal waters and play major roles in the trophodynamics of marine ecosystems. Many species show marked seasonal changes in abundance, particularly in regions with strong climatic and upwelling influences (Smith 1995, Bonnet et al. 2005). Therefore, understanding the processes that control the abundance and production of copepods is an important objective in biological oceanography. Analysis of their population dynamics requires knowledge of life-history traits, such as development times, survival, and clutch size (Uye 1991). Differences in development times, individual variability, and other life-history traits can assist in understanding the coexistence of similar species in the same habitats and might provide clues about factors which shape their life cycles. This could be the case for *Acartia erythraea*, *A. pacifica*, and *A. spinicauda*, 3 similar congeneric species which co-occur in the Strait of Malacca (Rezai et al. 2004, Yoshida et al. 2006).

Temperature effects on egg development times are well studied in copepods, particularly in the genera *Acartia* (McLaren et al. 1969, McLaren 1978, Uye 1980, Geurrero et al. 1994, Norrbin 1996) and *Calanus* (Corkette et al. 1986, McLaren et al. 1988, Uye 1988). Other copepod species which were previously studied include *Paracalanus* (Checkley 1980, Uye 1991), *Pseudocalanus* (Corkette and McLaren 1970, McLaren 1978, McLaren et al. 1989a), and *Centropages* (McLaren et al. 1969 1989b, Liang et al. 1996). In those papers, authors showed that the constant, α, is commonly related to the temperature regime of the species, and the value of *a* is proportional to the egg diameter. Observations were made in the laboratory on the embryological development of *Acartia* eggs, and evidence suggested that findings are representative of those that occur in marine environments. However, development times of eggs can differ between closely related genera, within a genus, and even within the same species (Corkette and McLaren 1970). This is unexpected because of the general relationship between temperature and metabolic activity. Reported equations of egg development times (EDTs) of *A. clausi* differed between populations from different geographical locations; 'biological zero' values were -5.8 (Onagawa Bay, Japan; Uye 1980), -8.2 (Nova Scotia, Canada; McLaren et al. 1969), and -10.49°C (L. Striven, Scotland; McLaren 1978). Biological zero is the empirical temperature threshold at which growth stops. Eggs do not develop synchronously, and consequently there is a range of embryonic duration for each species.

Relatively little is known about the reproductive biology of tropical copepods although some direct measurements of gonad maturation, clutch size, and the spatial variability of egg production in relation to food supply were made (Huntley and Lopez 1992, Chen and Marcus 1997, Hopcroft and Roff 1998, Ara 2001). For copepods, it was generally concluded that mortality is greatest in the egg and naupliar stages (Kiorboe and Sabatini 1994, Peterson and Kimmerer 1994, Poulet et al. 1995), and therefore, determining the embryonic duration in relation to temperature is an important step towards a better understanding of the population dynamics of tropical species. Until recently, studies on *Acartia* egg development time focused on cold-water to temperate species (Uye 1980, Norrbin 1996). In the present study, we examined embryological development times of the congeners *A. erythraea*, *A. pacifica*, and *A. spinicauda* that make up an important component of the plankton in tropical coastal waters of the Strait of Malacca (Rezai et al. 2005, Yoshida et al. 2006).

MATERIALS AND METHODS

Zooplankton samples were collected at night at a shallow station at 2°24'N, 101°54'E (at a mean depth of 6 m) in coastal waters of the Strait of Malacca, on several occasions over a period from Sept. to Dec. 2008. Water temperature ranges 26.0-31.0°C throughout the year (Yoshida et al. 2006). Samples were obtained by multiple oblique tows from the bottom to the surface of a plankton net (with a mesh size of 300 μm and a mouth diameter of 0.5 m) fitted with a 500-mL cod-end. Live samples were brought back to the laboratory (Marine Research Station, Universiti Putra Malaysia research facility, Port Dickson, Malaysia) within 30 min. Gravid *A. pacifica*, *A. erythraea*, and *A. spinicauda* females were sorted under a dissecting microscope using a wide-mouth pipette. About 30 females were individually placed in 50-mL glass beakers with a false bottom (with a mesh sieve of 140 μm to avoid egg cannibalism) and were incubated at 26°C in the laboratory to obtain fresh eggs, with natural assemblage food

particles in a 10-50-μm size range as prey items. The beakers were checked every hour from the beginning of incubation under a dissecting microscope, and spawned eggs were transferred to 12-hole multi-well dishes (with 1 egg to each well) with 5 mL of 0.22-μm Millipore-filtered seawater (Millipore, Billerica, MA, USA) in each well, and incubation for the egg development experiment immediately ensued at different temperatures. Eggs that spawned within 1 h were used for the experiments.

Experiments were conducted as a series of incubations at temperatures of 10, 14, 18, 22, 27, and 31°C, and incubation periods continued until the eggs had hatched. A nauplius was judged to be fully hatched when it was clear of the egg membranes. Egg hatching was periodically checked according to experimental temperature conditions; hourly for 22, 27, and 31°C and a combination of hourly and daily observations for lower temperatures, taking into account estimated hatching times at each temperature. The seawater in some wells was replaced with freshly filtered seawater when it appeared dirty to avoid a bacterial or protozoan infestation which could have affected hatching. EDTs were observed and defined by Bělehrádek's (1935) temperature function ($D = a(T - \alpha)^b$). This equation was chosen over several alternatives for expressing the relationship of development to temperature such as the Parabolic, Tauti, and Arrhenius equations (Windberg 1971, Guerrero et al. 1994), due to its practicality in comparing the 'biological characteristics' of the observations among different species within the same taxon (McLaren 1995). Previous studies of embryonic duration of copepods beginning with McLaren et al. (1969) settled upon $b = 2.05$ on the basis of freely fitted values of various species within the same taxa (McLaren 1995). Eggs which had not hatched long after the predicted embryonic development time relative to the incubation temperature were considered non-viable. Hatching success was also calculated from the number of hatched and unhatched eggs at each temperature. Plot fitting of equations was conducted using the statistical program SigmaPlot 11.0® by Systat Software (Chicago, IL, USA). Tests for differences in hatching success and EDTs between species and experimental temperatures, and the interaction between the 2 factors were carried out using an analysis of variance (ANOVA) coupled with Tukey's multiple-range test.

RESULTS

Hatching occurred at all experimental temperatures (Table 1). However, egg hatching success rates were noticeably lower at 10°C for all 3 species. Average hatching success rates at 14-

Table 1. Egg development times and hatching success rates of 3 congeneric Acartiid species at various temperatures

Species	Temperature (°C)	No. of eggs	EDT (d)	S.D.	Hatching success (%)
Acartia erythraea	10	35	8.9	2.4	11
	14	14	2.1	0.1	43
	18	19	1.9	0.5	32
	22	11	1.9	0.6	64
	27	10	0.6	0.1	100
	31	9	0.4	0.1	67
A. pacifica	10	21	5.4	3.7	10
	14	14	3.4	0.6	86
	18	21	1.9	0.5	81
	22	25	1.5	0.5	80
	27	15	0.5	0.2	80
	31	11	0.4	0.1	64
A. spinicauda	10	33	10	0.6	18
	14	27	2.9	0.8	89
	18	35	2.1	0.5	80
	22	30	1.4	0.2	83
	27	21	0.5	0.1	81
	31	29	0.4	0.1	100

31°C were 61% ± 26%, 78% ± 8%, and 87% ± 8% for *A. erythraea*, *A. pacifica*, and *A. spinicauda*, respectively. The ANOVA for hatching success of the 3 *Acartia* species at 6 different temperatures (Table 2) showed no significant differences ($p > 0.05$) among species for this trait. The least-squares means for species and temperature (Table 3) showed that hatching success at 10°C was the lowest (13%) and significantly differed from those at other temperatures based on Tukey's multiple-range test. Hatching success at other temperatures did not significantly differ from each other, and the highest hatching success was 87% at 27°C.

For EDTs, the effects of species, temperature, and their interaction were all significant ($p < 0.001$, Table 4). The least-squares means for these effects and their interaction (Table 5) indicate that *A. pacifica* on average had the shortest EDT of 2.2 d, followed by *A. erythraea* at 2.6 d and *A. spinicauda* at 2.9 d. Using Tukey's simultaneous multiple comparison method, the mean EDT for *A. erythraea* significantly differed from that of *A. pacifica* ($p < 0.01$) but not from that ($p > 0.05$) of *A. spinicauda*, while a significant difference was found between *A. pacifica* and *A. spinicauda* ($p < 0.001$). Tukey's tests between temperatures indicated that EDTs at 10°C significantly differed from those at

Table 2. Analysis of variance (ANOVA) of hatching success rates (%) of 3 *Acartia* species at 6 different temperatures

Source of variation	*d.f.*	Sum of squares	Mean squares	*F*
Species	2	1528.4	764.2	2.87
Temperature	5	10514.9	2103	7.90**
Error	10	2663.6	226.4	

** $p < 0.001$, $R^2 = 81.9\%$.

Table 3. Least-squares means and their standard errors for hatching success (%) by species and temperature

Main effects	Subclass	Least squares means ± standard error
Species	*Acartia erythraea*	52.8 ± 6.6a[1]
	A. pacifica	66.8 ± 6.6a
	A. spinicauda	75.1 ± 6.6a
Temperature (°C)	10	13.0 ± 9.4a
	14	72.7 ± 9.4b
	18	64.3 ± 9.4b
	22	75.7 ± 9.4b
	27	87.0 ± 9.4b
	31	77.0 ± 9.4b

[1]Letters are used to signify differences at the 95% level by Tukey's multiple-comparison method. Within each main effect, the same letter for the least squares indicates no significant difference. Different letters indicate a significant difference.

Table 4. Analysis of variance (ANOVA) for egg development times (EDTs in days) for 3 *Acartia* species at 6 different temperatures

Source of variation	*d.f.*	Sum of squares	Mean squares	*F*
Species	2	12.7	6.3	17.02**
Temperature	5	550.3	110	293.90**
Species × temperature	10	40.2	4	10.74**
Error	220	82.3	0.3	

** $p < 0.001$, $R^2 = 91.5\%$.

other temperatures. EDTs at 14°C significantly differed from those at 18, 22, 27, and 31°C; EDTs at 18-22°C and at 27-31°C did not significantly differ. However, EDTs at 18 and 22°C significantly differed from those at 27 and 31°C.

Values of EDTs were fit to Bělehrádek's temperature function and were $D = 294(T - 4.47)^{-2.05}$ (r = 0.980) for *A. erythraea*, $D = 545(T - 1.94)^{-2.05}$ (r = 0.988) for *A. pacifica*, and $D = 352(T - 4.30)^{-2.05}$ (r = 0.996) for *A. spinicauda*. The results are expressed together with those of previously reported copepod species (Table 6, Fig. 1).

DISCUSSION

It was reported that the hatching success of eggs of the coastal copepod *Paracalanus* sp. was > 60% at 7.5-21.3°C but < 30% at higher temperatures (Uye 1991). The *Acartia* spp. studied here also exhibit similar hatching success (Table 1). However, the hatching success values at high temperatures (27-31°C) were still > 60%, unlike *Paracalanus* sp. (Uye 1991), probably due to population acclimation to tropical temperatures. Other reported hatching success rates of *Acartia* include those of *A. clausi* (Uye and Fleminger 1976), *A. steueri* (Uye 1980), and *A. tonsa* (Holste and Peck 2006) which were > 80% at respective temperature ranges of 18-25, 10-25, and 12.4-22.4°C. Hatching success rates at temperatures of 14-31°C for the 3 species in this study were similarly high, and it was considered that *Acartia* generally possesses eurythermic hatching success. This may be characteristic of coastal species which experience repeated temperature fluctuations due to sporadic terrestrial runoff, tidal influences, and the shallow nature of the coast.

Table 5. Least-squares means and their standard errors for egg development times (EDTs in days) by species, temperature, and their interaction

Main effects and interaction		Least squares means ± standard error
Species	*Acartia erythraea*	2.64 ± 0.10a[1]
	A. pacifica	2.18 ± 0.10b
	A. spinicauda	2.86 ± 0.06a
Temperature (°C)	10	8.10 ± 0.19a
	14	2.78 ± 0.11b
	18	1.93 ± 0.10c
	22	1.59 ± 0.10c
	27	0.55 ± 0.10d
	31	0.40 ± 0.12d
Species × temperature (°C)	*A. erythraea* × 10	8.94 ± 0.27
	A. erythraea × 14	2.05 ± 0.25
	A. erythraea × 18	1.87 ± 0.25
	A. erythraea × 22	1.89 ± 0.23
	A. erythraea × 27	0.67 ± 0.20
	A. erythraea × 31	0.43 ± 0.25
	A. pacifica × 10	5.40 ± 0.43
	A. pacifica × 14	3.40 ± 0.18
	A. pacifica × 18	1.89 ± 0.15
	A. pacifica × 22	1.50 ± 0.14
	A. pacifica × 27	0.48 ± 0.18
	A. pacifica × 31	0.40 ± 0.23
	A. spinicauda × 10	9.97 ± 0.25
	A. spinicauda × 14	2.88 ± 0.12
	A. spinicauda × 18	2.03 ± 0.12
	A. spinicauda × 22	1.39 ± 0.12
	A. spinicauda × 27	0.50 ± 0.15
	A. spinicauda × 31	0.37 ± 0.11

[1]Letters are used to signify differences at the 95% level by Tukey's multiple-comparison method. Within each main effect, the same letter for the least squares indicates no significant difference. Different letters indicate a significant difference.

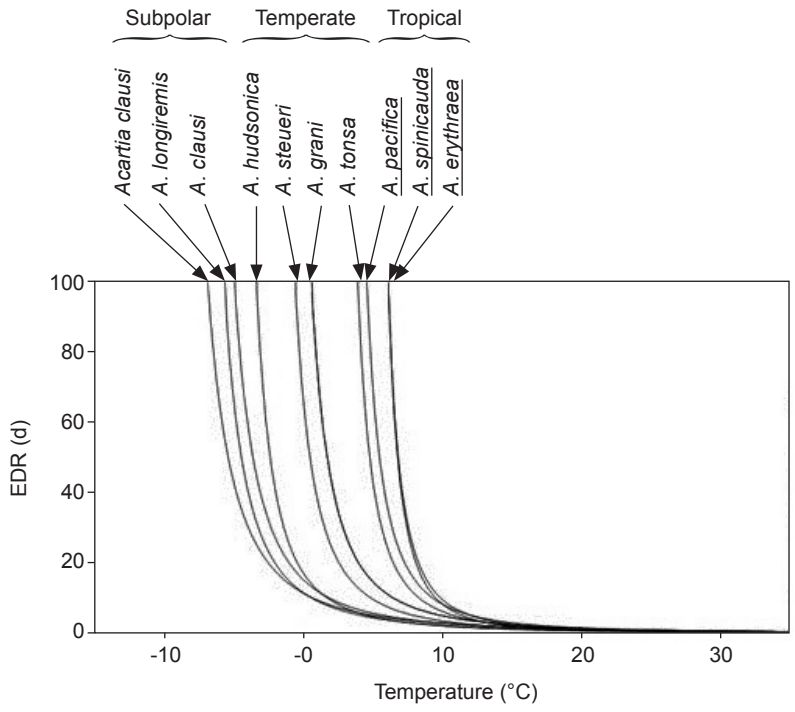

Fig. 1. Relationship between egg development times and temperature of Acartiid copepods. The constant, *b*, was adjusted to -2.05 for *Acartia grani* for comparison. Underlined species indicate results from this study. Temperature functions of the other species were obtained from references listed in table 6.

Table 6. Reported egg development times of various calanoid copepod species relative to temperature

No.	Species	Location	Equation	Authority
1	*Acartia grani*	S.E. Spain	$D = 28902(T + 2.99)^{-2.14}$	Guerrero et al. 1994
2	*Acartia spinicauda*	Malacca Straits	$D = 352(T - 4.30)^{-2.05}$	This study
	Acartia erythraea	Malacca Straits	$D = 294(T - 4.47)^{-2.05}$	This study
3	*Acartia tonsa*	Narragansette Bay	$D = 489(T - 1.8)^{-2.05}$	McLaren et al. 1969
4	*Acartia pacifica*	Malacca Straits	$D = 894(T - 1.94)^{-2.05}$	This study
5	*Acartia steueri*	Onagawa Bay, Japan	$D = 747(T + 3.2)^{-2.05}$	Uye 1980
6	*Acartia clausi*	Onagawa Bay, Japan	$D = 650(T + 5.8)^{-2.05}$	Uye 1980
7	*Acartia clausi*	Nova Scotia	$D = 1163(T + 8.2)^{-2.05}$	McLaren et al. 1969
8	*Acartia longiremis*	Tromso, Norway	$D = 1008(T + 8.7)^{-2.05}$	Norrbin 1996
9	*Acartia hudsonica*	L. Striven, Scotland	$D = 1442(T + 10.49)^{-2.05}$	McLaren 1978
10	*Paracalanus* sp.	Inland Sea of Japan	$D = 140(T + 2.2)^{-2.05}$	Uye 1991
	Paracalanus parvus	California	$D = 432(T + 2.97)^{-2.05}$	Checkley 1980
11	*Calanus finmarchicus*	Nova Scotia	$D = 691(T + 10.6)^{-2.05}$	Corkette et al. 1986
	Calanus helgolandicus	S North Sea	$D = 1014(T + 10.94)^{-2.05}$	Corkette et al. 1986
	Calanus marshallae	Seattle	$D = 831(T + 11.01)^{-2.05}$	McLaren et al. 1988
12	*Calanus glacialis*	Nova Scotia	$D = 1067(T + 12.97)^{-2.05}$	McLaren et al. 1988
	Calanus glacialis	Nova Scotia	$D = 975(T + 13.04)^{-2.05}$	Corkette et al. 1986
	Calanus finmarchicus	Tromso, Norway	$D = 1122(T + 14.1)^{-2.05}$	Corkette et al. 1986
	Calanus hyperboreus	Nova Scotia	$D = 1575(T + 14.4)^{-2.05}$	Corkette et al. 1986
13	*Calanus glacialis*	Frobisher	$D = 1491(T + 14.5)^{-2.05}$	Corkette et al. 1986
14	*Calanus pacificus*	Seattle	$D = 608(T + 7.39)^{-2.05}$	McLaren et al. 1988
15	*Calanus sinicus*	Inland Sea of Japan	$D = 545(T + 5.7)^{-2.05}$	Uye 1988

Each species has a range of temperature within which successful embryological development occurs. There were differences in embryonic durations among species with the fastest at a given temperature being *A. pacifica* followed by *A. spinicauda* and finally *A. erythraea*. However, *A. erythraea* and *A. spinicauda* showed similar functions, while *A. pacifica* exhibited a lower biological zero value (Table 6). Values of α reflect differences in temperature adaptations between species (Corkett and McLaren 1970). Similar Bělehrádek's function values (Fig. 1) reflect the habitat distribution of *A. erythraea* and *A. spinicauda*, which primarily inhabit tropical and subtropical waters, while a lower biological zero may be reflective of *A. pacifica*'s distribution which can extend to temperate regions as far as the Sea of Japan, the Inland Sea of Japan, and Jiaozhou Bay, China (Fig. 2, Brodskii 1981, Checkley et al. 1992, Zhong and Xiao 1992).

Parameter *a* was reported to be related to the egg diameter in *Pseudocalanus minutus* (McLaren 1966) and in related species of the genus *Calanus* (Corkett 1972). However, as McLaren (1966) pointed out, the parameter *a* is not proportional to the egg diameter. It was discussed how differences in egg size and their effects on *a* were not comparable to those occurring among more widely separated populations of a particular species. Nevertheless, development times within species or among closely related forms can partly be predicted from the egg size. The DNA content of eggs may also be related to inherent differences in the size and development rate (Commoner 1964), as eggs with a greater DNA content take longer to develop.

The relationship between copepod egg size and egg development time resembles predictions from mass transfer theory observed in the uptake of oxygen by fish eggs (Daykin 1965), and supports the idea that the egg development rate is superimposed on surface-volume restrictions on CO_2 exchange by the entire embryo (Berrill 1935). Egg sizes of *Calanus* are larger than those of *Acartia*, and this may be the reason the 2 genera possess relatively disjunctive EDTs (Table 6), with species of *Calanus* having longer developmental periods than species of *Acartia* for any given temperature.

The eggs of the 3 species have higher biological zero values than reported for temperate (40°N/S-60°N/S) and sub-arctic (60°N/S-80°N/S) *Acartia* species such as *A. clausi*, *A. tonsa* (McLaren et al. 1969), and *A. longiremis* (Norrbin 1996), suggesting the influence of geographically specific adaptations of each species. Copepods in those reports were collected from different geographical locations (Fig. 2). Biological zero values of the copepods decreased with an increase in the latitudinal distribution. Experimental results in previous studies indicated that both egg incubation temperature and parental acclimation

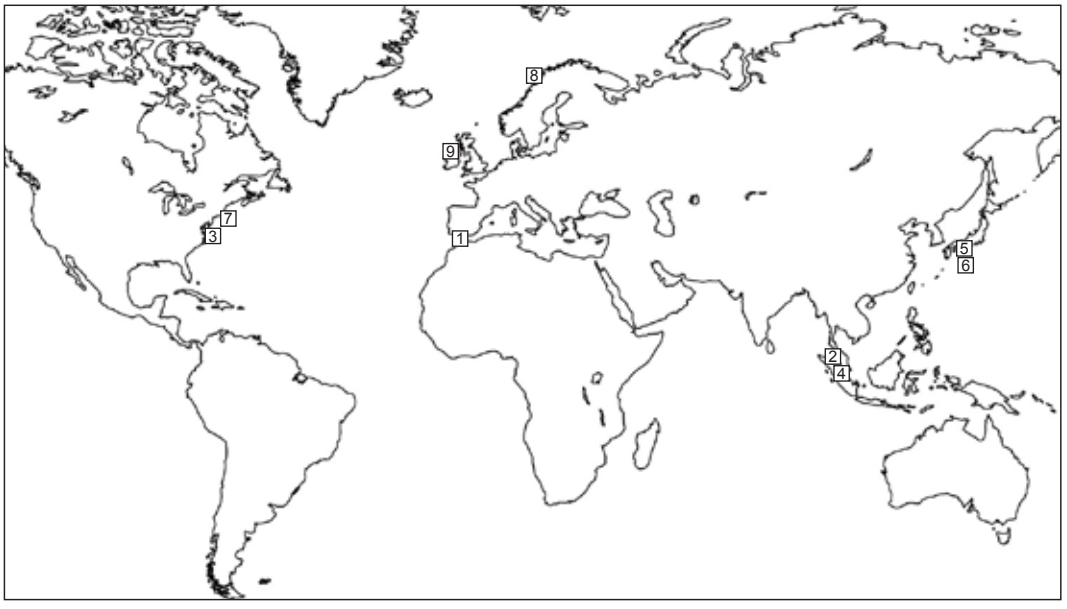

Fig. 2. Geographical records of egg development time studies of *Acartia* spp. Numbers refer to references listed in table 6.

temperature may have significant effects on egg hatching times. Landry (1975) found that eggs from *A. clausi* collected during winter (8-10°C) had significantly faster development rates under summer conditions (15-20°C) than those collected during summer (18-20°C). However, Uye and Fleminger (1976) and Uye (1980) failed to confirm Landry's (1975) results and concluded that eggs produced throughout the year by *A. clausi* have similar physiological properties. Central to this controversy is the question of whether the response of egg-hatching time to temperature is genetically determined or environmentally induced. Tester (1985) found for *A. tonsa* that the effects of parental acclimation temperature and egg-incubation temperature were additive if the long-term parental acclimation temperature was constant. A temperature change in the parent culture for time periods of 86 h to 8 d was sufficient to change egg-hatching times. The time required for a temperature change to affect egg-hatching times depend on the magnitude and direction of the temperature change.

Reported geographical records of the 3 *Acartia* species indicate that *A. pacifica* is more widely distributed than *A. erythraea* and *A. spinicauda* (Fig. 3). Its latitudinal distribution extends to sub-arctic regions of the Amur and Posyet Gulfs (Sea of Japan; Brodskii 1981), whereas the other species occur in the temperate-tropical periphery (Fig. 3). In the Strait of Malacca, a population increase of *A. pacifica* in the southern sector of the Straits was thought to have been due to the southern net current flow of water from the Andaman Sea in the north brought about by the SW monsoon trade winds

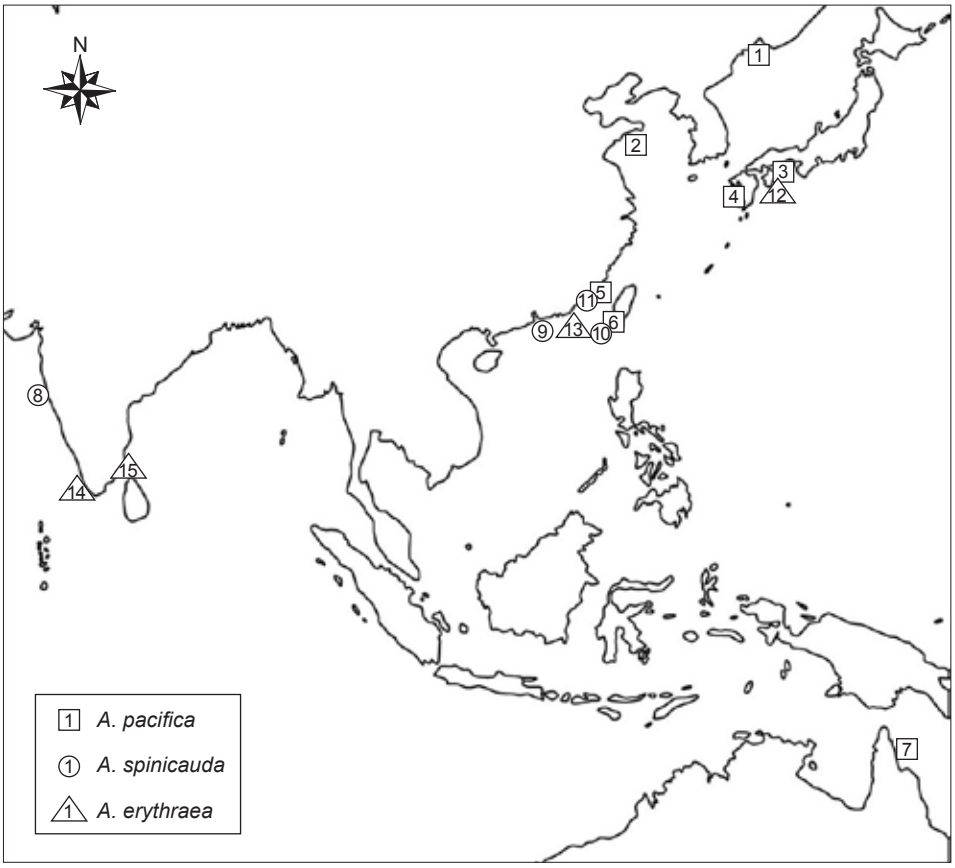

Fig. 3. Geographical records of *Acartia pacifica*, *A. spinicauda*, and *A. erythraea* occurrences throughout the East Asian region. Reference **1.** Posyet and Amur Gulfs, Sea of Japan (Brodskii 1981), **2.** Jiaozhou Bay, China (Zhong and Xiao 1992), **3.** Inland Sea of Japan (Checkley et al. 1992), **4.** Isahaya Bay, Japan (Ueda et al. 2003), **5.** Xiamen Bay, China (Jiang et al. 2004), **6.** Kaohsiung Harbor, Taiwan (Chang and Fang 2004), **7.** Moreton Bay, Brisbane (Preston et al. 2003), **8.** Bombay, India (Gajbhiye et al. 1991), **9.** Pearl River Estuary, China (Tan et al. 2004), **10.** Kaohsiung Harbor, Taiwan (Chang and Fang 2004), **11.** Xiamen Bay, China (Marcus 1996), **12.** Seto Inland Sea, Japan (Ueda 1991), **13.** Tolo Harbour, Hong Kong (Tang et al. 1994), **14.** Cochin estuary, India (Menon et al. 2000), **15.** Porto Novo, India (Krishnamurthy 1967).

(Yoshida et al. 2006). This means populations of *A. pacifica* were acclimated to the cooler (by 1-3°C) Andaman Sea waters compared to *A. erythraea* and *A. spinicauda*, both of which are found in warmer waters. This difference in acclimation temperatures could have been one of the reasons for the different biological zero values among the 3 species. The possible effect of higher salinities on the embryo development time may also have to be considered since the 2 water bodies also vary in salinity.

Values of α or biological zero seem to show a logical relationship with the environment (Fig. 4). Northern forms have lower values and warmer-water species have higher values of α. Significant differences were found in biological zero values for *Acartia* reported from sub-polar, temperate, and tropical regions (Table 7). The relationship between the α of Bělehrádek's temperature function for eggs of the 3 species of *Calanus* and 9 species of *Acartia* (including results from this study) against estimates of average temperature in their environmental ranges suggests that a single parameter of temperature response (α) can be used to describe differences in temperature adaptation of development rate of eggs of calanoid copepods. The correlation between α and approximate environmental temperatures makes it possible to predict development rates at any temperature of eggs of copepods of known geographical range from experiments at a single temperature.

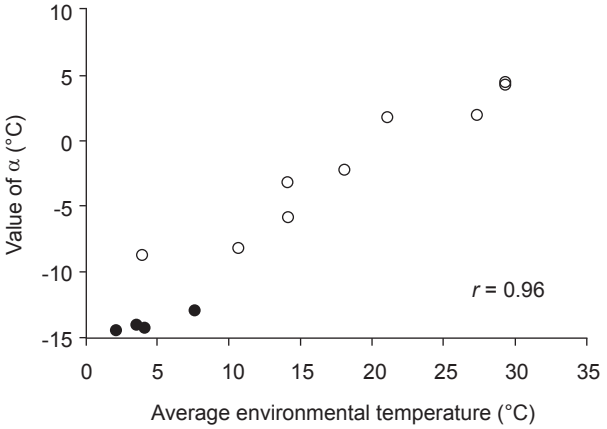

Fig. 4. Relationship between the 'biological zero' (α) and average environmental temperature for eggs of 3 species of *Calanus* (filled circles) and 9 species of *Acartia* including results from this study (blank circles). Values for the other species are from table 6.

Table 7. Analysis of variance (ANOVA) of the biological zero (α) for reported *Acartia* species from subpolar, temperate, and tropical regions

Source of variation	*d.f.*	Sum of squares	Mean squares	*F*
Regions	2	242.9	121.4	23.2**
Residual	7	36.6	5.2	
Total	9	279.5		

** $p < 0.001$.

It is important to know how EDTs may be affected by temperature changes, as many methods used to calculate secondary production by zooplankton require estimates of EDTs at various temperatures (Snell 1978, Keen and Nassar 1981, Hairston and Muns 1984). *Acartia* is a highly dominant genus, and we conjectured that its contribution to secondary production would be significant in zooplankton studies. Estimates of EDTs and egg hatching in the field from *in situ* temperatures are important steps to empirically determining the generation duration and population dynamics of plankton in coastal waters of the Strait of Malacca.

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