Upper temperature tolerance of ten bivalve species off Peru and Chile related to El Niño *

H.-Jörg Urban

Alfred-Wegener-Institut für Polar- und Meeresforschung, Columbusstraße, D-27568 Bremerhaven, Germany

ABSTRACT· The upper temperature tolerance of 10 commercially important South American bivalve species (*Gari solida, Semele solida, Semele corrugata, Protothaca thaca, Venus antiqua, Tagelus dombeii, Ensis macha, Aulacomya ater, Choromytilus chorus* and *Argopecten purpuratus*) off Peru and Chile was determined and compared in order to study some of the effects of El Niño. Due to higher habitat temperatures in Peru, LT_{50} (lethal temperatures for 50% of an experimental population) are higher than in Chile. In Chile LT_{50} for 6 of 8 species studied varied only by 1.2 °C. This might be explained by the similar temperatures and living conditions in the habitats of these species. Especially for Peru, observed differences in LT_{50} could be related to different geographical distributions. For all species temperature increases recorded during the strongest El Niño of this century (1982–83) did not exceed the temperature tolerance interval, TTI (difference between LT_{50} after 24 h and mean annual water temperature). It is noted that all species studied here are tolerant of temperature conditions occurring during moderate El Niño events.

KEY WORDS: Upper temperature tolerance · Bivalves · El Niño Peruvian-Chilean upwelling system

INTRODUCTION

Temperature is one of the most important environmental factors controlling the latitudinal distribution of marine benthic organisms. According to Vasil'eva (1978) the temperature tolerance of molluscs complies with their distribution. But, within one distribution area, temperature tolerance can also play a role in the zonation of species. Johnson (1965), Jansson (1967) and Ansell et al. (1980a) stated that upper temperature tolerance decreases with increasing distance from shore and with depth. Furthermore, Wilson (1981) found the upper depth limit of infaunal organisms buried in the substratum to be set by the upper temperature tolerance.

Mortality is a sigmoid function of temperature (Wolcott 1973, Hines et al. 1980), i.e. within a small temperature interval mortality increases from a low proportion to almost 100%. One way to deal with the temperature tolerance of different species or populations is the estimation of a temperature value lying within this interval (e.g. the temperature causing 50% mortality, LT_{50}). Adult individuals are able to acclimate to a certain range of environmental temperatures (Theede 1972), therefore, such estimated LT_{50} values are only valid for a fixed acclimation temperature. Wilson (1978) and Ansell et al. (1980b) stated that due to acclimation lethal habitat temperatures seldom occur. When considering the ecological importance of temperature tolerance, so-called sublethal factors have to be taken into account: Read & Cumming (1967) for example found upper temperature tolerance in *Mytilus edulis* to be about 28 °C. But during times of poor feeding conditions they observed high mortalities at 20 °C. Among various factors this can be explained by a higher demand of metabolic energy during higher but still sublethal temperatures. So, the scope of growth decreases and might even become negative (Widdows 1976).

Water temperatures in the upwelling system of Peru and Chile show little seasonal variability, while in the North Sea, annual water temperature variations of up

---

to 20 °C are not unusual (Arntz & Arancibia 1988). During a 2 yr investigation period in Peru and Chile annual water temperatures varied only by about 5 °C (pers. obs.). Furthermore, a characteristic of this upwelling system is similar water conditions over a broad range of latitudes along the South American Pacific coast, which implies a broad distribution range of many marine species in this area. Marine species in this ecosystem therefore seem to be adapted to fairly constant water temperatures, and it can be assumed that the annual water temperature cycle plays only a minor role in the distribution pattern and ecological success of sublittoral organisms in this area. However, this ecosystem is affected at irregular time intervals by a climate phenomenon called El Niño (EN) which leads to a sudden temperature increase (Arntz & Fahrbach 1991). During the strongest EN of this century, in 1982–83, temperatures of up to 10 °C above normal were recorded. High mortality rates in many marine species demonstrate the importance of EN (Arntz & Valdivia 1985, Arntz et al. 1988). Due to high primary production (Ryther 1969) suspension-feeding bivalves in the Peruvian and Chilean marine ecosystem can establish high biomasses and therefore several bivalve species are exploited commercially by Peruvian and Chilean small-scale (artisanal) fisheries. During EN 1982–83 catches of some bivalve species declined due to high mortality rates while other species, especially *Argopecten purpuratus*, increased their biomass, leading to a biomass boom (Arntz & Fahrbach 1991).

The objective of this paper was to determine and compare the upper temperature tolerance of the most important commercially exploited bivalves of Peru and Chile to study the possible effects of the sudden temperature increases which occur during EN.

MATERIAL AND METHODS

Bivalves were collected by SCUBA divers in the Bay of Independencia, Peru (14° 15' S, 76° 10' W) and the Bay of Dichato, Chile (36° 32' S, 73° 57' W) (Fig. 1). Species were sampled in the sublittoral at between 2 and 16 m depth at different sites. Water temperature and salinity were recorded at the sampling sites at monthly intervals. Annual water temperatures in both areas showed little variation (Peru: between 16 and 21 °C; Chile: between 12 and 16 °C), salinity in Peru varied between 35.0 and 35.5‰ and in Chile between 30 and 34‰. In Peru the species studied were *Gari solida*, *Semele solida*, *Semele corrugata* and *Argopecten purpuratus* and in Chile *G. solida*, *S. solida*, *Protothaca thaca*, *Venus antiqua*, *Tagelus dombeii*, *Ensis macha*, *Choromytilus chorus* and *Aulacomya ater*. All species are exploited commercially in Peru and Chile. Individ-

Fig. 1. Location of the 2 investigation areas

uals were kept in aquaria with flowing unfiltered seawater for 1 wk at water temperatures of 16 °C (Peru) and 13 °C (Chile) (except for *A. purpuratus* from Peru, for which experiments were carried out in late summer at a temperature of 19 °C). During the acclimation period animals fed on natural seston. Living conditions did not differ substantially from natural conditions. The experiments were performed with adult individuals of equal size.

Upper temperature tolerance was studied in the following way. For each species experimental populations of 20 individuals were placed in aquaria with different experimental temperatures. Temperatures were maintained constant (± 0.3 °C) by electric heaters and a high oxygen concentration was obtained by aeration. To prevent evaporation from affecting the salinity the aquaria were covered with transparent lids. To distinguish between living and dead specimens, inactive individuals were stimulated mechanically. If no reaction was observed those individuals were removed to cool water for at least 24 h to see if recovery took place, which however occurred very seldom.

For technical reasons, 2 different methods were used in both study areas. In Peru dead individuals were removed at certain time intervals until 50 % of a population was dead. Thus, during this time-mortality approach (Bliss 1937) for different temperatures the times leading to a 50 % response (i.e. mortality) were estimated. In Chile after 24 h at different temperatures the number of dead animals was determined and mortality (expressed as percentage of the original number present in each experimental aquarium) was calcu-

Table 1. Experimental temperatures and time intervals for the determination of the upper temperature tolerance of bivalve species from Peru and Chile

Area	Date	Temp. (°C)	Time interval (h)
Peru	Aug–Sep 1990, Feb 1991	23, 25, 27, 29, 32, 34, 36	0.5, 1, 3, 6, 12, 18, 24, 36, 48, 60, 72, 84, 96
Chile	Jul–Aug 1991	20, 22, 24, 25, 26, 28	Always 24 h

Fig. 2. Plot of temperature and time to 50% mortality for 4 Peruvian bivalve species

lated (dosage-mortality approach). Hence, different responses for given temperatures associated with a fixed time were calculated. To compare the different lethal temperatures of the 2 locations all values were related to 24 h and temperatures causing a 50% lethal response (LT_{50} after 24 h) were estimated. Table 1 gives experimental temperatures, time intervals and dates of experiments.

The nonlinear relationships between time and lethal temperatures (Peru) and between temperature dosage and mortality (Chile) were plotted (Figs. 2 & 3, respectively). From these plots the LT_{50} after 24 h were determined graphically. Confidence intervals for LT_{50} (from Peru) were estimated by linear regression analysis: a logarithmic transformation of the time gave a linear relationship (Wallis 1977) and the LT_{50} after 24 h were calculated applying the equation:

$$LT_{50} = a + b\log(t) \qquad (1)$$

where t = time (h), and a, b are constants of the regression equations.

By means of a linear regression analysis the 95% confidence intervals of LT_{50} were calculated applying standard statistical methods [Eqs. (2) & (3), from Snedecor & Cochran 1980]:

$$S(\mu_{yx}) = S_{yx}\sqrt{(1/n + x^2/\Sigma x^2)} \qquad (2)$$

$$CI_{95} = \mu_{yx} \pm t_{0.05}\, S(\mu_{yx}) \qquad (3)$$

where S_{yx} = the square root of mean square error from regression analysis, and CI_{95} is the 95% confidence interval.

Confidence intervals of LT_{50} (from Chile) were estimated by probit analysis (Fisher & Yates 1963, Cavalli-Sforza 1972).
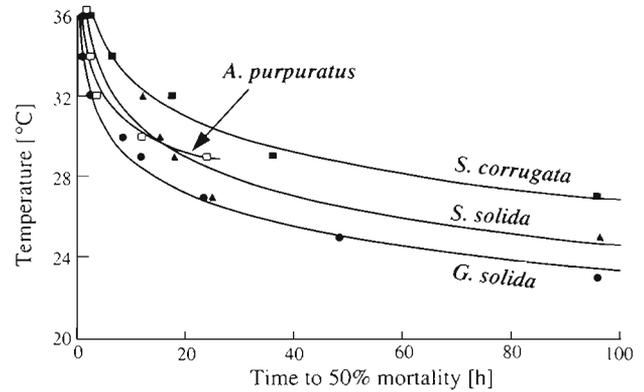
The investigation areas are separated by 22° latitude and therefore are chararacterized by different water temperatures. In order to compare the effect of a sudden temperature increase in 2 areas with different
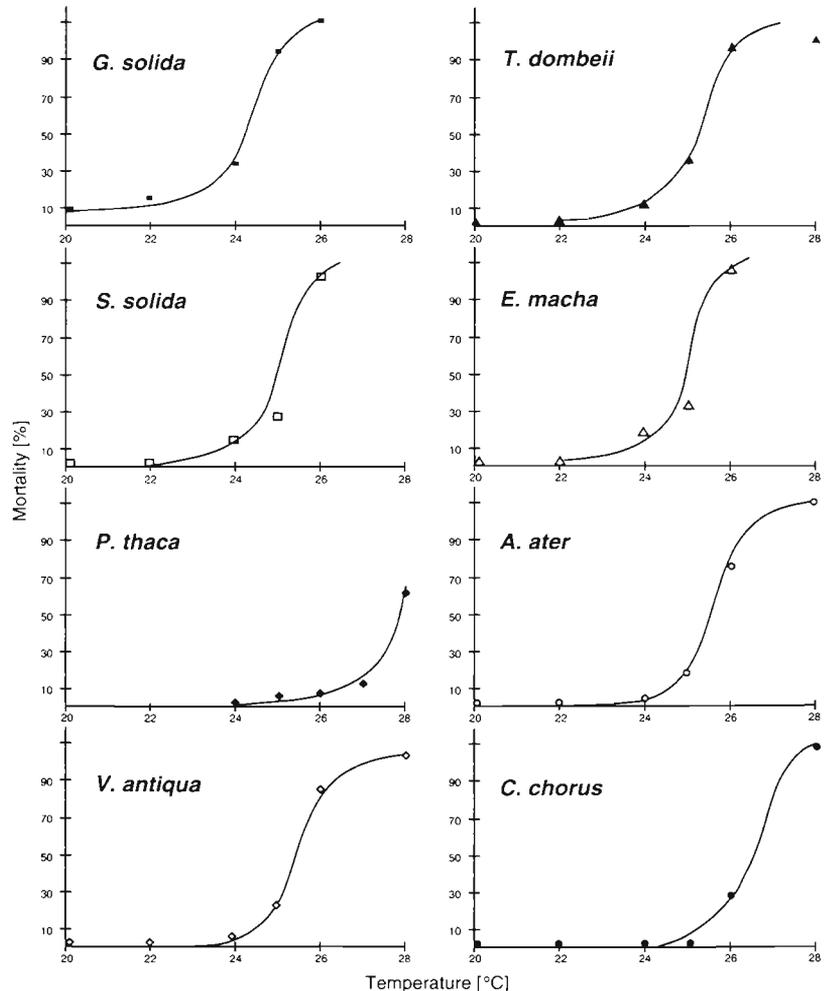

Fig. 3. Plot of mortality and temperature for 8 Chilean bivalve species

Table 2. Parameters a and b of the linear regression analysis (Eq. 1) to calculate the LT_{50} of Peruvian species after 24 h. r^2 = correlation coefficient

Species	a	b	r^2
Gari solida	34.506	−5.522	0.99
Semele solida	37.344	−6.403	0.91
S. corrugata	38.896	−6.029	0.99
Argopectan purpuratus	34.861	−4.274	0.94

water temperatures the 'temperature tolerance interval' (TTI, in °C) was developed. TTI is defined as the interval by which temperatures may suddenly increase above the mean annual water temperature without killing more than 50 % of the population:

$$TTI = LT_{50} - T_m \tag{4}$$

where T_m = mean annual water temperature, calculated from monthly recordings.

RESULTS

Temperatures associated with 50 % mortality are plotted for each time interval in Fig. 2 (Peru), while in Fig. 3 (Chile) mortality is plotted against temperature. In Fig. 3 there is a typical sigmoid relationship between mortality and temperature. Table 2 gives a summary of the linear regression analysis performed using Eq. (1) to calculate the LT_{50} after 24 h. The LT_{50} together with their 95 % confidence intervals for all species from 2 areas are shown in Table 3. Individuals from Peru acclimated to higher water temperatures have higher lethal temperatures than those from Chile. In Chile, the LT_{50} of Semele solida, Venus antiqua,

Tagelus dombeii, Ensis macha, Choromytilus chorus and Aulacomya ater only vary by 1.2 °C. Table 3 also gives the lethal temperatures determined graphically. Regression and graphical methods led to very similar results. In Fig. 4 the TTI for all species are given, and show a rather homogeneous distribution.

DISCUSSION

The LT_{50} of the 2 species studied in both areas (Gari solida and Semele solida), are about 3 °C higher in Peru than in Chile. This can be explained by associated differences in acclimation temperature: mean water temperatures at the sampling sites in Peru are about 2 to 5 °C higher than in Chile. All individuals from Chile were sampled in the sublittoral zone of a rather small area (12 km²) with very similar temperature conditions. This might explain why 6 of 8 Chilean species (S. solida, Venus antiqua, Tagelus dombeii, Ensis macha, Choromytilus chorus and Aulacomya ater) have very similar LT_{50}, between 25.1 and 26.3 °C. Similar temperature tolerance may therefore be explained as an adaptation to the similar temperature conditions in the Peruvian and Chilean upwelling system.

However, this statement does not seem to account fully for all species studied here. In Chile, Gari solida seems to have a rather low LT_{50} and Protothaca thaca a rather high LT_{50}. In Peru the LT_{50} of Semele corrugata and Argopecten purpuratus were higher than that of the other 2 species (G. solida and S. solida). These differences can be explained partly by their distribution areas, given together with the prevailing water temperatures in Table 4 (Bernard 1983). According to Bernard (1983), S. corrugata and A. purpuratus have northern distribution limits of 2° S and 6° S respec-

Table 3. Lethal temperatures for 50 % of an experimental population after 24 h (LT_{50}) for 10 bivalve species of Peru and Chile determined graphically, and statistically by regression (Peru) or probit (Chile) analysis. Upper and lower 95 % confidence intervals are given as well as the acclimation temperature (AT)

Area	Species	LT_{50} (°C)		95% confidence intervals		AT
		Graphically	Statistically	Upper	Lower	(°C)
Peru	Gari solida	27.0	26.9	28.1	25.7	16
	Semele solida	27.0	28.5	31.4	25.6	16
	S. corrugata	31.0	30.6	31.7	29.5	16
	Artopecten purpuratus	29.0	29.0	32.0	26.0	19
Chile	G. solida	24.8	23.7	24.2	23.2	13
	S. solida	25.2	25.1	26.4	24.7	13
	Protothaca thaca	27.9	28.1	29.0	27.3	13
	Venus antiqua	25.7	25.6	25.9	25.2	13
	Tagelus dombeii	25.5	25.1	25.4	24.7	13
	Ensis macha	25.2	25.0	25.4	24.7	13
	Choromytilus chorus	26.5	26.3	26.9	25.7	13
	Aulacomya ater	26.0	25.6	26.0	25.3	13
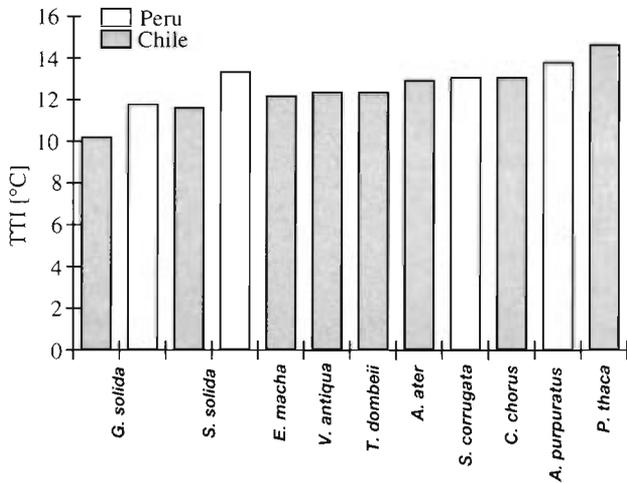
Fig. 4. TTI (temperature tolerance interval) of 10 bivalve species of Peru and Chile
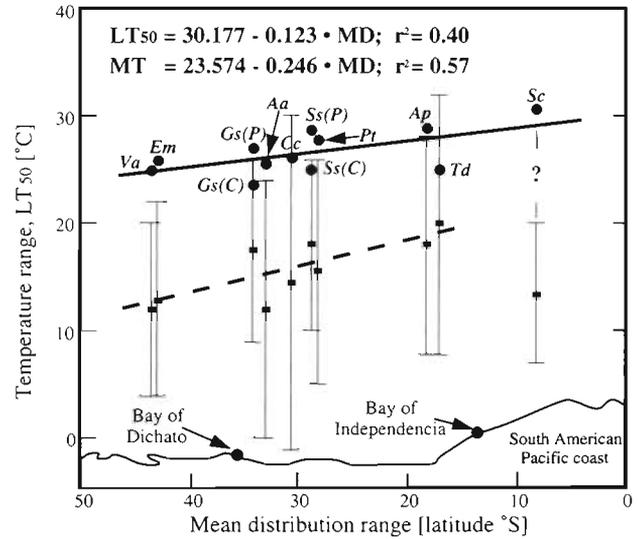

Fig. 5. Overlay plot of LT_{50} after 24 h (●) and temperature range (■ and vertical bars) against mean distribution of 10 South American bivalve species. Regression equations and regression lines of the relationship LT_{50} and mean distribution (MD) as well as mean temperature (MT) and mean distribution are given. *Semele corrugata* is not included in the regression of mean temperature and mean distribution because these values probably are not correct; see text. Data see Tables 3 & 4. Aa: *Aulacomya ater*; Ap: *Argopecten purpuratus*; Cc: *Choromytilus chorus*; Em: *Ensis macha*; Gs: *Gari solida*; Pt: *Protothaca thaca*; Sc: *S. corrugata*; Ss: *S. solida*; Td: *Tagelus dombeii*; Va: *Venus antiqua*. (C): Chile; (P): Peru

tively while *G. solida* and *S. solida* are found up to 14° S and 12° S only (the value for *G. solida* was corrected according to own observations). On the other hand, the geographical distribution does not explain all findings regarding different LT_{50}. This is particularly true for *P. thaca*, which has a comparatively high LT_{50} but a similar distribution area to the other Chilean species. Other factors affecting the estimated temperature tolerance could be the burrowing depths of the infaunal species (except *Aulacomya ater* and *Choromytilus chorus* all species studied here are infaunal). In Peru as well as in Chile *G. solida* had the lowest LT_{50} and from all infaunal species studied, *G. solida* belongs to the group with the deepest vertical distribution (Urban 1992).

In several cases the results from Bernard (1983) are incomplete: *Gari solida* is found up to 14° S, which is

11° further north than stated by Bernard (1983). (It is exploited commercially at 14° S, Bay of Independencia, Peru; pers. obs.) Also, to the author's knowledge, no *Semele corrugata* are found up to 45° S (Chile). It is difficult to distinguish *S. solida* and *S. corrugata*; therefore, most likely recordings of *S. corrugata* so far south are the result of misidentification. Thus, *S. corrugata* has a more northerly distribution than *S. solida* and the distribution areas of both species overlap at ca 14° S. Assuming that the given latitude range for *S. corrugata* is correct, its corresponding upper temperature range value (21 °C) seems to be too low. Very likely, temperatures at 2° S are higher than 21 °C. This assumption is supported in Fig. 5, showing the overlay plot of the temperature range and LT_{50} against the mean distribution. In this plot most of the LT_{50} values lie on or near the upper end of the corresponding temperature range, presented as vertical bars. An exception is *S. corrugata*. Following the pattern of the other species, for *S. corrugata* an upper temperature range value from 8 up to 29 °C could be possible. The regression line fit-

Table 4. LT_{50} after 24 h for 10 South American bivalve species compared with their distribution areas (in latitudes along the west coast of the South American continent) and temperature range (from Bernard 1983). *Corrected according to own observations; see text. Genera as in Table 3

Species	LT_{50} (°C)	Distribution area	Temperature range (°C)
G. solida	24.4, 26.9	(*14° S) 25° S – 54° S	9 – 26
E. macha	25.3	33° S – 54° S	4 – 22
S. solida	25.4, 28.5	12° S – 45° S	10 – 26
A. ater	25.8	12° S – 54° S	0 – 24
T. dombeii	25.9	9° N – 43° S	8 – 32
V. antiqua	26.3	33° S – 54° S	4 – 20
C. chorus	26.5	6° S – 55° S	–1 – 30
P. thaca	27.9	12° S – 45° S	5 – 26
A. purpuratus	29.0	6° S – 30° S	8 – 28
S. corrugata	30.6	2° S – 45° S (* ≈ 14° S ?)	8 – 21

ted to the LT_{50} values in Fig. 5 indicates that, progressing from southern latitudes towards the equator, the means of the distribution range have higher associated LT_{50} values. This can be explained by increasing habitat temperatures towards the equator as shown by the regression line fitted to the mean temperatures.

During EN 1982–83 *Argopecten purpuratus* was favoured by the high temperatures while *Semele corrugata* suffered a high mortality rate. Wolff (1985), following Waller (1969), considered that *A. purpuratus* is the relict of a miocene tropical fauna and therefore is well adapted to high temperatures. It seems contradictory that *S. corrugata* has a higher LT_{50} (30.6 °C) than *A. purpuratus* (29 °C). This may however be explained by the fact that the sampling site of the *S. corrugata* population is located at 5 m depth, while that of *A. purpuratus* was at 10 m. EN events therefore affect water temperatures of this latter sampling site more than that of *A. purpuratus*. Of all stations, the highest annual variability of water temperature was observed at the station where *S. corrugata* was sampled (Urban 1992). According to Johnson (1965), Jansson (1967) and Ansell et al. (1980a) this is probably the reason for a higher LT_{50} of *S. corrugata* in this region.

This investigation was performed to study some of the effects of EN on bivalves. Bivalves cannot escape EN by moving to other areas as has been reported for many pelagic species (Arntz & Fahrbach 1991). To study the temperature effects of EN the temperature tolerance interval is a helpful measure. In Fig. 4 the rather homogeneous distribution of the TTI indicates that the higher LT_{50} of the Peruvian species (which are distributed nearer the equator and therefore are affected more strongly by EN than the Chilean species) are probably a result of different acclimation temperatures, rather than genetic differences. Fig. 4 also shows that even a temperature increase of 10 °C, which probably occurs only once or twice every century (e.g. 1982–83) lies within the TTI. Therefore, it seems that generally the studied populations are not strongly affected by EN. However, it has to be taken into account that:

(1) The LT_{50} values were calculated for 24 h. EN on the other hand lasts several months. Ansell et al. (1980a, b) stated for 6 bivalve species that most mortality occurs during the first 24 h. Fig. 2 shows that there are still individuals dying during the following days.

(2) EN is not only linked to increasing temperatures but also to a decrease of primary production (Barber & Chávez 1986, Carrasco & Santander 1987). Therefore, sublethal temperatures as well — during weaker EN for example — could lead to mortality, as was reported by Read & Cumming (1967) for mussels.

(3) In this study only adult individuals were considered. Loosanoff et al. (1951) and Kinne (1970) reported

that larvae are much more sensitive to increasing temperature than adults. Therefore, EN probably affects recruitment.

(4) Temperature tolerance depends on acclimation temperature. Therefore, the full tolerance potential is not recorded if lethal temperatures are calculated on the basis of 1 acclimation temperature only. However, this error can be assumed to be small because the variability of annual water temperature in both studying areas is also small (< 5 °C). Fry et al. (1942, 1946; in Brett 1956) reported for 2 fish species a 1 °C increase of the upper lethal temperature for every 3 to 7 °C increase in acclimation temperature. During EN the temperature changes are so rapid that acclimation is not likely to occur.

EN occurs every 4 to 7 yr, in most cases leading only to temperature increases of about 5 °C. It is probable that these EN do not cause high mortality rates and that the populations are not in danger of extinction. Taking into account that (1) under higher temperatures more metabolic energy is necessary, (2) that poor feeding conditions could increase the negative effect of high temperatures and (3) that larvae are more sensitive towards high temperatures, significant negative effects on growth, recruitment and production may follow for some of the species studied here, depending on their living and reproductive strategies (Urban 1992).

The situation is different however during a 'Super El Niño', like the event of 1982–83, which can lead to a temperature increase of 10 °C above normal. Although the TTI permits a short-term temperature increase of 10 °C for 24 h, this 1982–83 EN that lasted several months caused high mortality rates and it has been reported that some of the species studied here became locally extinct (see review by Arntz & Fahrbach 1991). After such an EN it might take years until those populations affected have recovered.

LITERATURE CITED

Ansell, A. D., Barnett, P. R., Bodoy, A., Massé, H. (1980a). Upper temperature tolerance of some European molluscs. I. *Tellina fabula* and *T. tenuis*. Mar. Biol. 58: 33–39

Ansell, A. D., Barnett, P. R., Bodoy, A., Massé, H. (1980b). Upper temperature tolerance of some European molluscs. II. *Donax vittatus*, *D. semistriatus* and *D. trunculus*. Mar. Biol. 58: 41–46

Arntz, W. E., Arancibia, H. (1988). Fluctuaciones en el écosistema bentodemersal del Pacífico sur-oriental y el del norte de Europa: una comparación. Memorias del Simposio Internacional de los Recursos Vivos y las Pesquerías en el Pacífico Sudeste, Rev. Pacífico Sur (Número Especial): 35–47

Arntz, W. E., Fahrbach, E. (1991). El Niño — Klimaexperiment der Natur. Birkhäuser Verlag, Berlin

Arntz, W. E., Valdivia, E., Zeballos, J. (1988). Impact of El Niño 1982–83 on the commercially exploited invertebrates (mariscos) of the Peruvian shore. Meeresforsch. 32: 3–22

Arntz, W. E., Valdivia, J. (1985). Incidencia del fenómeno El Niño sobre los mariscos en el litoral peruano. In: Arntz, W. E., Landa, A., Tarazona, J. (eds.) El Niño — su impacto en la fauna marina. Bol. Inst. Mar Perú-Callao, Vol. Extraord., p. 91–101

Barber, R. T., Chávez, F. P. (1986). Ocean variability in relation to living resources during the 1982–83 El Niño. Nature 319: 279–285

Bernard, F. R. (1983). Catalogue of the living bivalvia of the Eastern Pacific Ocean: Bering Strait to Cape Horn. Spec. Publ. Can. Fish. Aquat. Sci. 61: p. 102

Bliss, C. I. (1937). Calculation of the time-mortality curve. Ann. appl. Biol. 24: 815–852

Brett, J. R. (1956). Some principles in the thermal requirements of fishes. Q. Rev. Biol. 31 (2): 75–87

Carrasco, S., Santander, H. (1987). The El Niño event and its influence on the zooplankton off Peru. J. geophys. Res. 92 (C13): 14405–14410

Cavalli-Sforza, L. (1972). Biometrie — Grundzüge biologisch-medizinischer Statistik. Gustav Fischer Verlag, Stuttgart

Fisher, R. A., Yates, F. (1963). Statistical tables for biological, agricultural and medical research. Oliver & Boyd, Edinburgh

Fry, F. E. J., Brett, J. R., Clawson, G. H. (1942). Lethal limits of temperature for young goldfish. Rev. can. Biol. 1: 50–56

Fry, F. E. J., Hart, J. S., Walker, K. F. (1946). Lethal temperature relations for a sample of young speckled trout (*Salvelinus fontinalis*). Publ. Ont. Fish. Res. Lab. 55: 1–35

Hines, A., Anderson, S., Brisbin, M. (1980). Heat tolerance in the black abalone *Haliotis cracherodii* Leach, 1814: effects of temperature fluctuation and acclimation. Veliger 23 (2): 113–118

Jansson, B. O. (1967). Diurnal and annual variation of temperature and salinity of interstitial water in sandy beaches. Ophelia 4: 173–201

Johnson, R. G. (1965). Temperature variation in the infaunal environment of a sand flat. Limnol. Oceanogr. 10: 114–120

Kinne, O. (1970). Temperature: animals — invertebrates. In: Kinne, O. (ed.) Marine ecology, Vol. 1, Environmental factors. Wiley Interscience, London, p. 407–514

Loosanoff, V. L., Miller, W. S., Smith, P. B. (1951). Growth and setting of larvae of *Venus mercenaria* in relation to temperature. J. mar. Res. 10: 59–81

Read, K. R. H., Cumming, K. B. (1967). Thermal tolerance of the bivalve molluscs *Modiolus modiolus* (L.), *Mytilus edulis* (L.) and *Brachidontes demissus* Dillwyn. J. comp. Biochem. Physiol. 22: 149–155

Ryther, J. H. (1969). Photosynthesis and fish production in the sea. Science 166: 72–76

Snedecor, G. W., Cochran, W. G. (1980). Statistical methods. The Iowa State University Press, Ames

Theede, H. (1972). Zur zellulären Hitzeresistenz mariner Evertebraten. Oecologia 11: 17–31

Urban, H.-J. (1992). Ökologie ökonomisch wichtiger Muschelarten im Auftriebssystem der Pazifikküste Lateinamerikas. Dissertation, University of Bremen

Vasil'eva, V. S. (1978). Heat resistance of cells of upper sublittoral bivalve molluscs of sandy infauna in Peter the Great Bay (Sea of Japan). Sov. J. mar. Biol. 4(1): 523–526

Waller, T. R. (1969). The evolution of the *Argopecten gibbus* stock (Mollusca: Bivalvia), with emphasis on the tertiary and quartenary species of eastern North America. J. Paleontol. 43: 1–125

Wallis, R. L. (1977). Some apects of the thermal tolerance of *Trichomya hirsuta* (Mollusca: Bivalvia) of Eastern Australia. Mar. Biol. 43: 217–223

Widdows, J. (1976). Physiological adaptation of *Mytilus edulis* to cyclic temperatures. J. comp. Physiol. 105: 115–128

Wilson, J. G. (1978). Upper temperature tolerance of *Tellina tenuis* and *T. fabula*. Mar. Biol. 45: 123–128

Wilson, J. G. (1981). Temperature tolerance of circatidal bivalves in relation to their distribution. J. therm. Biol. 6: 279–286

Wolcott, T. G. (1973). Physiological ecology and intertidal zonation in limpets (Acmaea): a critical look at 'limiting factors'. Biol. Bull. 145: 389–422

Wolff, M. (1985). Fischerei, Ökologie und Populationsdynamik der Pilgermuschel *Argopecten purpuratus* (L.) im Fischereigebiet von Pisco (Peru) unter dem Einfluß des El Niño 1982–83. Dissertation, Christian Albrecht University, Kiel