

Potential impact of temperature change on epibenthic predator–bivalve prey interactions in temperate estuaries

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Abstract

Temperate estuaries are indispensable as refuelling areas for long-distance shorebirds, where they depend on intertidal benthic fauna, such as bivalves, as food source. Bivalve recruitment is thought to be, at least partly, top-down regulated by epibenthic predators (the shrimp *Crangon crangon* and the crab *Carcinus maenas*) but this interaction is part of a complex predator–prey system since various fish species prey upon the crustaceans.

The impact of climate change in temperate estuarine food web will be determined by how the various size-selective interactions are affected by temperature. This will depend on the temperature sensitivity of each species' growth and on how food conditions allow them to fill in this growth potential. In this paper, the focus is on the first aspect: temperature sensitivity of the epibenthic predators compared with that of the bivalve prey and among the various predator species. Our results show that crustaceans have higher temperature sensitivity and tolerance range compared with their potential predators and with their bivalve prey. It is hypothesized that a temperature increase can potentially lead to an overall higher predation pressure in these systems with negative impacts in bivalve recruitment and hence, in the functioning of temperate estuaries as fuelling stations. However, prevailing food conditions for bivalves and predators will determine to what extent the potential impacts of an increase in temperature will be realized.

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1. Introduction

Temperate estuaries are an indispensable chain of essential resting and so-called fuelling stations for millions of wading birds on their migratory pathways (e.g. Piersma, 1994; Van de Kam et al., 2004). In these shallow estuarine areas, the main food source for birds consists of intertidal benthic fauna, whereby a main component is formed by bivalves (e.g. Piersma, 1994; Zwarts, 1997). Wading birds encounter large seasonal and annual variation in their food supply, both in terms of abundance and composition, due

to year-to-year fluctuations in the recruitment success of their bivalve prey (e.g. Zwarts and Wanink, 1993; Larsen and Guillemette, 2000).

Bivalve recruitment results from a combination of both abiotic conditions and biological interactions of which abundance of predators is one of the most important (Beukema et al., 1998; Van der Veer et al., 1998; Philippart et al., 2003) indicating, at least partly, top-down control of bivalve recruitment by predation. Among the epibenthic predators of newly settled bivalve spat, one of the most important are juvenile crustaceans, especially the brown shrimp *Crangon crangon* (Pihl and Rosenberg, 1984; Keus, 1986; Van der Veer et al., 1998) and the shore crab *Carcinus maenas* (Jensen and Jensen, 1985; Sanchez-Salazar and Seed, 1987; Van der Veer et al., 1998). This picture is even more complex because, instead of a single

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predator (shrimp)–prey (bivalve spat) interaction, mortality of bivalve spat and ultimate bivalve recruitment will be the result of multispecies interactions (Pihl, 1985a, b). Not only shrimps, but also shore crabs *C. maenas* and flatfish species, plaice *Pleuronectes platessa*, and flounder *Platichthys flesus* prey upon bivalve spat (De Vlas, 1979; Afman, 1980). These interactions are further complicated by the occurrence of cannibalism of adult shrimps on juveniles (Pihl and Rosenberg, 1984) and predation by *Pomatoschistus* species (Van Beek, 1976; Del Norte-Campos and Temming, 1994), shore crabs and flatfish upon adult shrimps (De Vlas, 1979; Afman, 1980). Finally, top predators in the system should also be considered. These include young cod (*Gadus morhua*) and sea bass (*Dicentrarchus labrax*), who prey upon both the predatory crustaceans and the various fish species (*Pomatoschistus* spp. and flatfishes) (Pihl, 1982; Van der Veer, 1986). Experimental studies (Jensen and Jensen, 1985; Keus, 1986) and field observations (Pihl and Rosenberg, 1982; Möller and Rosenberg, 1983; Günther, 1992; Van der Veer et al., 1998) have shown that predation by these species is size selective.

Since we are dealing with poikilothermic animals, both bivalve growth and shrimp predation are temperature related. Variability and trends in climate are expected to cause shifts in species distributional ranges (Kennedy et al., 2002; Walther et al., 2002) and, besides the immediate effects on interspecies competition, these changes can also have secondary impacts in predator–prey interactions (Scavia et al., 2002). In case of bivalve spat–shrimp relationship, a temperature increase could influence the recruitment success of bivalve prey. Supportive evidence is based on the observation that after severe winters, reduced and a delayed epibenthic predation occurred (Strasser and Gunther, 2001) which allowed bivalves to outgrow their predators (Hiddink et al., 2002) or at least overtake their prey size spectrum (Jensen and Jensen, 1985).

A recent analysis of various long-term data sets in the western Dutch Wadden Sea suggested that an increase in seawater temperature will result in a spring advancement of bivalve spawning, and in an overall decrease in reproductive output (Philippart et al., 2003). In addition, a narrowing of the time gap between bivalve spawning and post-settlement predation by shrimps was suggested and hence an overall decrease in recruitment at increasing seawater temperature (Philippart et al., 2003). However, these studies were based on correlations instead of causal relationships, whereby only a single predator–prey interaction and a similar reaction of both predators and prey to temperature were assumed.

The reaction of the various predators and prey to temperature depends on a combination of their temperature tolerance and sensitivity together with prevailing food conditions. For instance, on the one hand, growth in bivalves in the Wadden Sea appears to be food limited (Hummel, 1985; Kamermans et al., 1992; Kamermans, 1993; Beukema et al., 2002; Cardoso et al., 2006), while for

some predators (flatfishes) food conditions seemed to be optimal and only determined by prevailing temperature (Zijlstra et al., 1982; Van der Veer et al., 1991). For most other potential predators it is unknown whether they are food limited at present or not. This means that even when the temperature dependence of the various species would be similar, their ultimate reaction to changes in temperature might be different due to differences in prevailing food conditions.

In this paper, we analyse part of the problem by focusing on the indirect effect of temperature on bivalve recruitment via predator–prey interactions. Subsequent papers will deal with the prevailing food conditions of both bivalves and various predator species. The temperature dependence is a reflection of the species type (cold water versus intermediate or warm water species), which can be illustrated and quantified by the optimal temperature of the various species, their temperature tolerance range and their sensitivity to temperature within their tolerance range. So far, such an analysis has only been made for the various bivalve prey species (Van der Veer et al., 2006) and the flatfishes as predator (Van der Veer et al., 2001). The data on flatfish suggests that their temperature tolerance and sensitivity differs from that of the bivalves, which might have large implications for the overall impact of the epibenthic predator complex on bivalve spat. However, data for the other predatory species is missing. The aim of this paper is: (1) to determine and estimate the temperature tolerance range, optimal temperature and temperature sensitivity of the various epibenthic predators, (2) to determine whether differences exist between epibenthic predators and prey and amongst the various predator species and finally, (3) to conclude whether from this point of view climate change can potentially affect bivalve spat recruitment—via changes in the epibenthic predators–prey interactions.

2. Material and methods

2.1. Methods

2.1.1. Temperature range

Each species can only perform within a specific temperature range, i.e. its temperature tolerance range. This range is a reflection of both metabolism, showing a steady increase with temperature and also ingestion, increasing only until an abrupt decline occurs at high temperatures. As a result, growth is characterized by a steady increase with increasing temperature until a maximum followed by a sharply defined upper boundary (for plaice and flounder see for instance Fonds et al., 1992). Information on the temperature tolerance of a species is based on data on food intake or growth in relation to temperature. For the temperature tolerance range, the temperature interval is determined where the reaction rate is positive, i.e. zone of above-zero performance (Huey and Kingsolver, 1989).

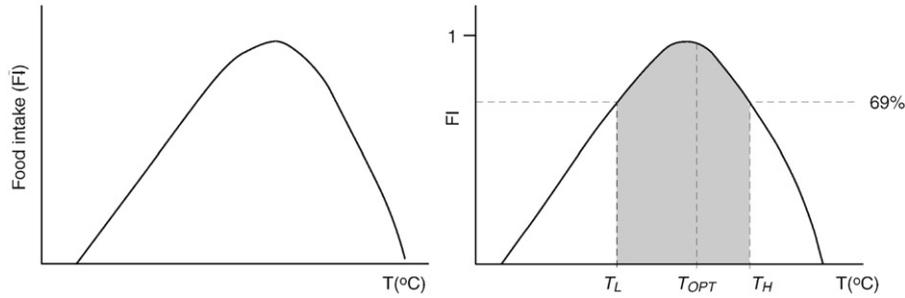


Fig. 1. Estimation procedure of optimal temperature T_{OPT} , temperature tolerance range and temperature performance breadth. Left panel: relationship of temperature (T ; °C) with food intake FI. Right panel: same relationship after scaling of the maximum food intake to 1. Optimal temperature T_{OPT} is the temperature at which the scaled FI is 1; and temperature performance breadth is the temperature range where activity is more than 69% of the maximum observed activity (grey area between T_L and T_H); temperature tolerance range is the range with positive FI values.

Within the temperature tolerance range, the temperature performance breadth is defined as the range of body temperatures over which performance is greater than or equal to an arbitrary level of performance (Angilletta et al., 2002). Estimation of the thermal performance breadth is based on the quantitative formulation by Sharpe and De Michele (1977) (see Kooijman, 2000). In short, this formulation is based on the idea that the rate is controlled by an enzyme that has an inactive configuration at high and low temperatures, respectively, above and below the optimum temperature. This means that the reaction rate has to be multiplied by the enzyme fraction that is in its active state in relation to prevailing temperature:

$$\left(1 + \exp\left[\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right] + \exp\left[\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right]\right)^{-1} \quad (1)$$

In this way, four extra parameters are needed: T_L and T_H , which relate to the lower and upper boundary of the tolerance range where 69% ($= \ln 2$) of the enzymes are active and T_{AL} and T_{AH} , which are the Arrhenius temperatures for the rate of decrease at both boundaries. In this study, the thermal performance breadth is the range between T_L and T_H , where the reaction rate is above 69% ($= \ln 2$) of the maximum rate.

The optimum temperature is defined as the temperature at which the reaction rate (growth or food intake) is maximal. The various definitions are based on Willmer et al. (2000) and the procedure for estimation is illustrated in Fig. 1.

2.1.2. Temperature sensitivity

Temperature sensitivity refers to rate at which the reaction increases with temperature. Therefore, estimates of temperature sensitivity are based on the part of the temperature tolerance range where rates, preferably oxygen consumption, increase exponentially with increasing temperature. Traditionally, Q_{10} quotient has been used to provide an indication of temperature sensitivity. It quantifies the effect of temperature on reaction rates by comparing a rate at two temperatures differing by 10 °C. Despite its wide utilization, some have questioned the

accuracy and the variance of this factor within a temperature range (see for instance Willmer et al., 2000). As an alternative, the Arrhenius relationship, based on the Van't Hoff equation has been applied, usually providing a good explanation for the variation in the temperature dependence of metabolic rate across species (Gillooly et al., 2006). The Arrhenius temperature T_A can be estimated as

$$\dot{k}(T) = \dot{k}(T_1) \times \exp\left[\frac{T_A}{T_1} - \frac{T_A}{T}\right], \quad (2)$$

where $\dot{k}(T)$ is a physiological rate at the ambient temperature T (K), $\dot{k}(T_1)$ is the physiological rate at the reference temperature T_1 (normally set at 293 K) and T_A is the species-specific Arrhenius temperature (K). T_A results from the slope of plots of $\ln(\dot{k})$ against $1/T$. The procedure is illustrated in Fig. 2.

2.2. Materials

Estimation of the various temperature dependence parameters was performed for the various epibenthic species while for the bivalve species, data published in Van der Veer et al. (2006) was used. The estimation of the temperature parameters for the epibenthic species was based on information published in various literature references in combination with experimental data.

Laboratory experiments were carried out at the NIOZ aquarium facilities over the years using standard experimental conditions as described in De Blok (1975) and Fonds et al. (1992). In brief, crustaceans and fish were caught in the neighbourhood of the institute and held in tanks of $2.5 \times 0.5 \times 0.5$ m with running seawater at constant temperatures. Small individuals were kept in perforated plastic crates of $50 \times 35 \times 25$ cm, suspended in the larger constant-temperature tanks. Tanks and crates were aerated and for flatfish a small layer of sand was put at the bottom. Crustaceans and fish were acclimatized before the start of the experiments. For more information see Fonds et al. (1992). Some information has been presented in NIOZ student reports (Van Beek, 1976; Van der Gaag, 1977; Van Lissa, 1977) and these references are

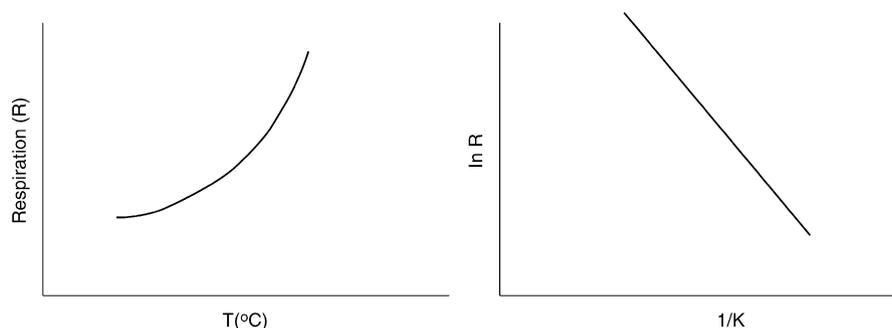


Fig. 2. Estimation procedure of temperature sensitivity T_A (K) on respiration R . Left panel: relationship of temperature (T ; °C) with respiration R . Right panel: after log transformation of Y -axes. Slope reflects the temperature sensitivity T_A (K).

available through request in the NIOZ library (E-mail address: bib@nioz.nl).

With respect to published information several references were used: temperature sensitivity was estimated mainly on experiments on oxygen consumption after Van Donk and De Wilde (1981) for the shrimp *C. crangon*; Klein Breteler (1975) and Young et al. (2006) for the shore crab *C. maenas*; Fonds et al. (1992) for plaice *P. platessa*, and flounder *P. flesus*; Fonds and Veldhuis (1973) and Petersen and Petersen (1990) for sand goby *Pomatoschistus minutus* and common goby *Pomatoschistus microps*; Jobling (1988) and Pedersen and Jobling (1989) for cod *G. morhua* and Claireaux and Lagardère (1999) for sea bass *D. labrax*. Optimal temperature and temperature tolerance was estimated based on information on growth or food intake in relation to temperature, after Van Lissa (1977) for *C. crangon*; Fonds et al. (1992) for *P. platessa* and *P. flesus*; Fonds (1973) and Van der Gaag (1977) for *Pomatoschistus* spp.; and Jobling (1988) and Pedersen and Jobling (1989) for cod *G. morhua*; for *C. maenas* information on peripheral neuronal function in relation to temperature from Young et al. (2006) was used while, for *D. labrax* information on metabolism in relation to temperature (Claireaux and Lagardère, 1999) was utilized.

In relation to bivalve species, the published literature list used to determine the temperature dependence parameters can be consulted in Van der Veer et al. (2006).

3. Results

3.1. Temperature range

For many species, information at both the extreme low and high ends of the temperature range was lacking and, therefore, the temperature tolerance range and thermal performance breadth had to be interpreted.

For the various bivalve species, the temperature tolerance range and thermal performance breadth differed (Fig. 3). *Macoma balthica* had the smallest tolerance range and performance breadth, 17 and 8 degrees, respectively. The tolerance range and performance breadth for the other species was larger and shifted from *Mytilus edulis*, *Mya*

arenaria to *Cerastoderma edule* towards higher temperatures. Also the optimal temperature differed between species. *M. balthica* and *M. edulis* had the lowest optimal temperatures 283 K (10 °C) and 290 K (16 °C), respectively, followed by *M. arenaria* (293 K; 20 °C) and *C. edule* (298 K; 25 °C). Results for *M. arenaria* and *C. edule* indicate that these species are able to tolerate high temperatures in the upper 20 s °C (Fig. 3).

For the epibenthic predators, all species could tolerate temperatures as low as 273 K (0 °C), except *D. labrax* (Fig. 4). The high temperature tolerance limit showed larger differences between species. *C. crangon* could tolerate 303 K (30 °C), *D. labrax* 305 K (32 °C) and *P. microps* even 307 K (34 °C). The other fish species could only tolerate lower temperatures: the flatfish species up to 299 K (26 °C) and *G. morhua* only up to 297 K (24 °C). The temperature performance breadth was almost similar between species, between 10° and 13°. The optimal temperature for most species was also very similar (Fig. 4) around 293 K (20 °C). Only *C. crangon* and *D. labrax* had slightly higher values of 296 K (23 °C) and 295 K (22 °C), respectively. *G. morhua* has a much lower value (287 K; 14 °C). A comparative overview of the different parameters can be observed in Fig. 5. No information was available for *P. minutus*.

The various parameters are combined for all species in Table 1 and illustrate the differences in temperature tolerance, performance breadth, optimal temperature and temperature sensitivity between the various prey and predator species.

3.2. Temperature sensitivity

The estimates of the temperature sensitivity (\pm SE) for the various bivalve species differed between 5290 ± 1108 and 7051 ± 453 K, however, with relatively large standard deviations (Fig. 6). The analysis for all species combined resulted in a statistically significant estimate of 5826 ± 195 K ($n = 281$; $R^2 = 0.99$), and, since similarity in temperature sensitivity in related species is expected (Kooijman, 2000), a value of 5800 K was adopted for all species.

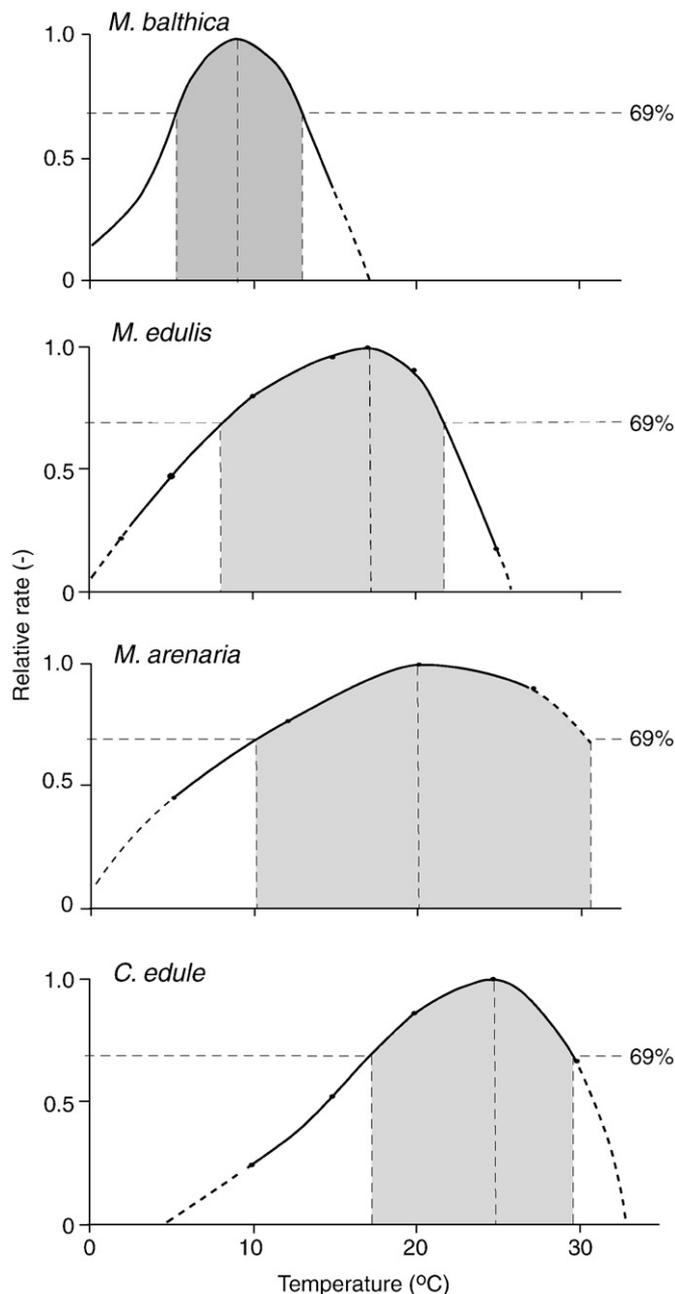


Fig. 3. Optimal temperature (vertical line) ($^{\circ}\text{C}$), temperature performance breadth (grey range) and tolerance range (total range of positive rate) for the bivalve species *Macoma balthica*, *Mytilus edulis*, *Mya arenaria* and *Cerastoderma edule* based on data of food intake and/or growth in relation to temperature. Rates are scaled to the maximum rate, which has been set to 1.0. For more information and references see text and Van der Veer et al. (2006).

For the various epibenthic predators, the temperature sensitivity differed (Fig. 7). For crustaceans, the estimate of the Arrhenius temperature (\pm SE) for *C. crangon* was in the order of 7351 ± 266 K, while for *C. maenas* a value of 6498 ± 920 K was found. Low values were found in the gobies, 2963 ± 165 K in *P. minutus* and 3418 ± 184 K in *P. microps*. Combining the data sets for both species resulted in an average value of 3191 ± 125 K for these two

related gobies. For both flatfish species, the estimate ranged from 6519 ± 163 K for *P. platessa* to 8974 ± 178 K in *P. flesus*. Since these two species are closely related, data were combined resulting in an estimate of 7747 ± 183 K for both species. The data for *G. morhua* resulted in an estimate of 5345 ± 220 K and for *D. labrax* an estimate of 5651 ± 298 K.

The Arrhenius temperature T_A can be compared with Q_{10} quotient using

$$\frac{1}{10} \ln Q_{10} = \frac{T_A}{T_1(T_1 - 10)},$$

where T_1 is the reference temperature (normally set at 293 K). An Arrhenius temperature of 3000 K roughly corresponds with a Q_{10} of 1.5, and an Arrhenius temperature of 6000 K with a Q_{10} of 2.

4. Discussion

4.1. General impact of temperature

Fluctuations in water temperature in shallow coastal systems usually follow the air temperature, which in term is determined by local weather conditions. Although water temperature is buffered by the higher heat capacity of water compared to air, large changes and fluctuations in water temperature can occur not only at an annual scale but also on a daily and tidal basis (Pihl and Rosenberg, 1982; Van der Veer and Bergman, 1986). For instance, along the Swedish coast the seasonal fluctuations in water temperature are between 0 and 20°C , however, in summer, values up to 30°C can occur (Pihl and Rosenberg, 1982). Sessile bivalves will experience more fluctuations in temperature conditions than their mobile potential epibenthic predators that are able to carry out migration movements.

The basic action of temperature on reaction rates is via its link with the molecular motion in a material. With increasing temperature, the average motion increases and a larger portion of the molecules moves fast enough to collide and react with other molecules. In biological systems a similar process is assumed; however, instead of molecules, biochemical reactions are catalysed by enzymes, whereby, the reaction rate rises steadily with temperature due to thermal effects on the reaction of substrates with enzymes and the consequent faster release of products. Above an upper thermal limit, reactions are drastically reduced or cease altogether as the biochemical structures involved are damaged (Willmer et al., 2000). In line with the above, the temperature tolerance is quantified in this study by a formulation that is based on the idea that the rate is controlled by an enzyme that has an inactive configuration at high and low temperatures, respectively, above and below the optimum temperature (Sharpe and De Michele, 1977). Although this quantitative formulation by Sharpe and De Michele (1977) works out well, it cannot

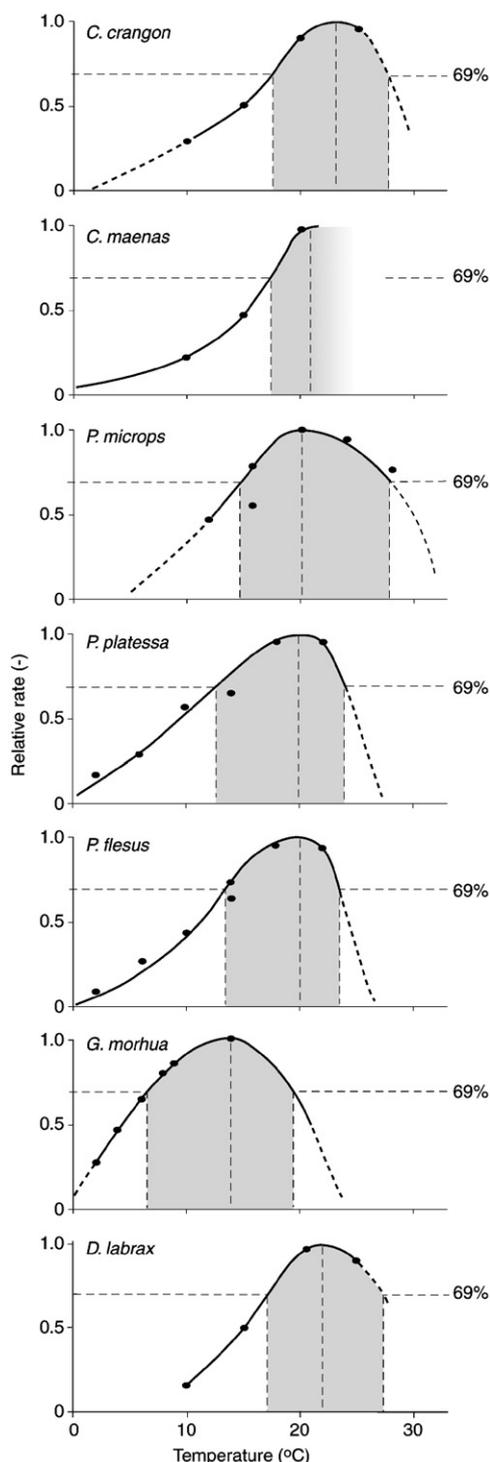


Fig. 4. Optimal temperature (vertical line) ($^{\circ}\text{C}$), temperature performance breadth (grey range) and tolerance range (total range of positive rate) for the crustacean species *Crangon crangon* and *Carcinus maenas*; the common goby *Pomatoschistus microps*; the flatfishes *Pleuronectes platessa* and *Platichthys flesus*; the gadoid species *Gadus morhua* and the sea bass *D. labrax*. Based on data of food intake and/or growth in relation to temperature. Rates are scaled to the maximum rate, which has been set to 1.0. For more information and references see text and Van der Veer et al. (2006).

hide our lack of detailed knowledge on the mechanistic functioning of temperature on ectotherms.

Any analysis of the impact of temperature is complicated by a number of factors. First of all, there is variability in temperature tolerance between the different life stages. For plaice, temperature tolerance is highest during the larval stages. Both during the egg stage and from the juvenile stage onwards, temperature tolerance decreases (Ryland et al., 1975; Talbot, 1976; Kuipers and Fonds, 1978; Fonds et al., 1992). This might be a general phenomenon at least in fish species and be responsible for the often observed positive relationship between fish size and water depth, the so-called Heincke's law (Heincke, 1913). Secondly, variability might occur between individuals and, also over the range of most bivalve and epibenthic species genetic subpopulation structure can be distinguished (Gysels et al., 2004a,b; Hoarau et al., 2004; Roman and Palumbi, 2004; Luttikhuisen et al., 2007). Whether genetic subpopulations also differ in their temperature tolerance and sensitivity is unclear at present. Furthermore, temperature sensitivity and tolerance range of an individual and a population can be affected by adaptation and acclimation to local conditions (Willmer et al., 2000), whereby also local temperature conditions may show spatial and temporal variability. A pronounced example of adaptation to local condition is the irreversible non-genetic adaptation (Kinne, 1962), whereby changes in the environment during the egg stage induce functional non-genetic adaptation, which was not reversible during the subsequent life of the individual. Counter-gradient growth compensation (Conover and Present, 1990), where populations from different latitude show compensation for length of the growing season might be a reflection of non-genetic adaptation at the population level. In the present analysis, these various factors are not taken into account and discussed and the focus is restricted to general patterns in optimum temperature, temperature performance breadth and temperature tolerance range.

4.2. Temperature effect on prey and predator species

From the optimal temperature, temperature performance breadth and tolerance range of the various bivalve prey species, it is clear that *M. balthica* with an optimal temperature at 283 K (10°C) and a tolerance range to about 290 K (17°C), can be considered as a cold water species. Its temperature performance breadth and tolerance range indicate that under the present conditions *M. balthica* might already suffer from suboptimal to too high temperatures in temperate areas in summer (Fig. 8), a suggestion recently confirmed for the western Wadden Sea (Cardoso et al., 2006). A slight increase in temperature might therefore have a negative effect on *M. balthica* causing a lower growth and hence longer period of predation. For the other bivalve species, an increase in temperature will remain in their tolerance range and even

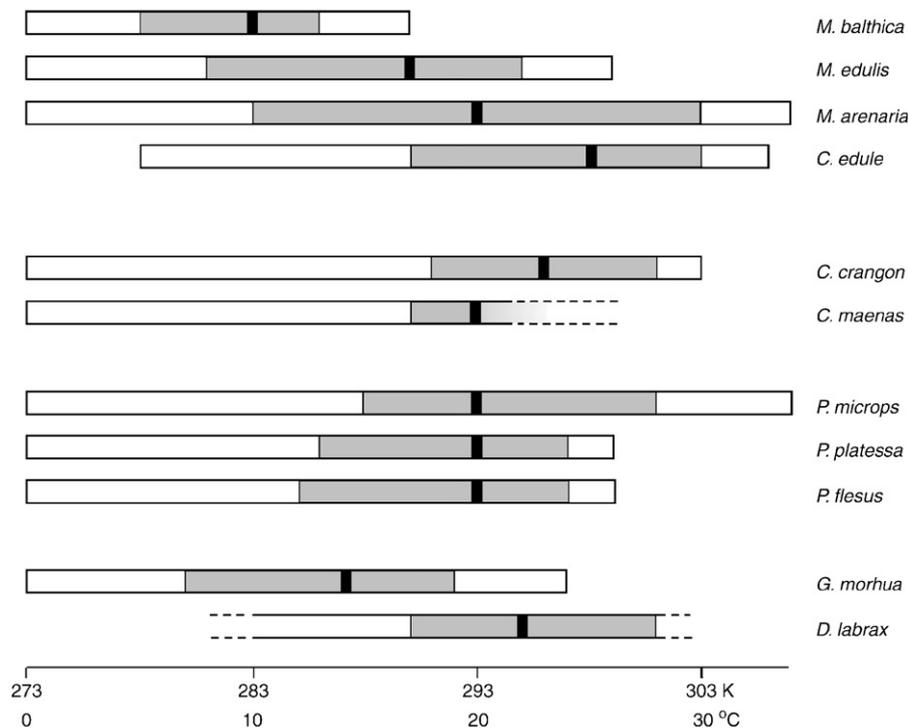


Fig. 5. Overview of optimal temperature (bold vertical bar), temperature performance breadth (grey horizontal bar) and temperature tolerance range (total horizontal bar) of the various bivalve and epibenthic predator species.

Table 1
Temperature sensitivity (T_A ; K), optimal temperature (T_{OPT} ; °C, K), temperature performance breadth and temperature tolerance range for various bivalve and epibenthic predatory species

| Symbol | T_A (K) | T_{OPT} (°C (K)) | Temperature performance breadth (K) (range between T_L and T_H) | Temperature tolerance range (K) (range with positive reaction rate) |
|-------------------------------|------------|--------------------|--|---|
| Bivalve species | | | | |
| <i>Macoma balthica</i> | 5800 | 10 (283) | 8 (278–286) | 17 (273–290) |
| <i>Mytilus edulis</i> | 5800 | 17 (290) | 14 (281–295) | 26 (273–299) |
| <i>Mya arenaria</i> | 5800 | 20 (293) | 20 (283–303) | 34 (273–307) |
| <i>Cerastoderma edule</i> | 5800 | 25 (298) | 13 (290–303) | 28 (278–306) |
| Epibenthic predators | | | | |
| <i>Crangon crangon</i> | 7351 ± 266 | 23 (296) | 10 (291–301) | 30 (273–303) |
| <i>Carcinus maenas</i> | 6498 ± 920 | 20 (293) | 11 (290–301) | 30 (273–303) |
| <i>Pomatoschistus minutus</i> | 3191 ± 125 | | | |
| <i>Pomatoschistus microps</i> | 3191 ± 125 | 20 (293) | 13 (288–301) | 34 (273–307) |
| <i>Pleuronectes platessa</i> | 7749 ± 183 | 20 (293) | 11 (286–297) | 26 (273–299) |
| <i>Platichthys flesus</i> | 7749 ± 183 | 20 (293) | 12 (285–297) | 26 (273–299) |
| <i>Gadus morhua</i> | 5345 ± 345 | 14 (287) | 12 (280–292) | 24 (273–297) |
| <i>Dicentrarchus labrax</i> | 5651 ± 298 | 23 (296) | 11 (290–301) | 26 (280–306) |

For more information see text and Van der Veer et al. (2006). Interpolated values in italic.

in their temperature performance breadth in the neighbourhood of their optimal temperature.

With respect to the predator species, the present environmental conditions in most temperate areas along the European coast (Fig. 8) are near the optimal temperatures for most species, except for the cod

G. morhua. Therefore, any increase in temperature will release the other epibenthic species from predation by cod; however, its role in the food web will probably be replaced by sea bass *D. labrax*, a species with a higher temperature tolerance and a similar function in the trophic web. For the other species, an increase in temperature will fall within

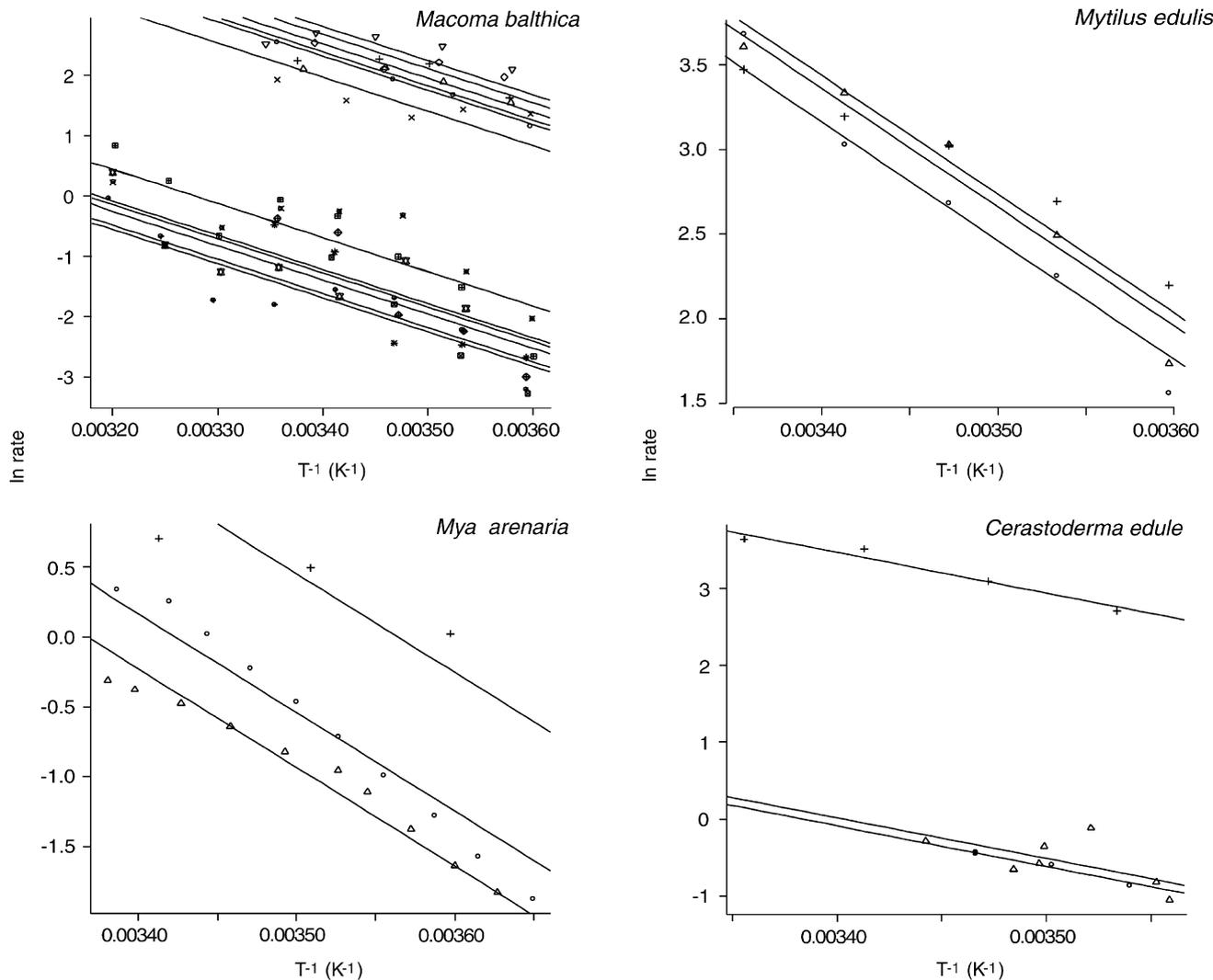


Fig. 6. Arrhenius plot (ln rate versus $1/T$) for the oxygen consumption data for various bivalve species. Each line represents a different data set. Arrhenius temperature (\pm SE)—*Macoma balthica*: 5672 ± 522 K ($n = 57$; $R^2 = 0.94$); *Mya arenaria*: 7051 ± 453 K ($n = 30$; $R^2 = 0.95$); *Cerastoderma edule*: 5290 ± 1107 K ($n = 11$; $R^2 = 0.98$); *Mytilus edulis*: 7022 ± 552 K ($n = 11$; $R^2 = 0.94$). All species together (including estimates for *Crassostrea gigas*): 5826 ± 195 K ($n = 281$; $R^2 = 0.99$). For references see text.

their temperature performance breadth, which means that this will not result in a change in species composition. The present distribution pattern of the various crustaceans, flatfish and gobies species at their southern edge all along the Portuguese coast confirms this analysis (Campos and Freitas, unpublished). The various epibenthic predatory species show differences in their Arrhenius temperature. Since predator–prey relationships are often size-based (Pihl and Rosenberg, 1984; Van der Veer et al., 1997; Van der Veer et al., 1998), differences in Arrhenius temperature will potentially be able to change interactions between the epibenthic species because it implies a difference in reaction and hence in growth between them. In this respect, cod, sea bass and both goby species show much lower values than the crustaceans and the flatfishes. This means that an increase in temperature will relatively release the crustaceans from predation by cod and sea bass and especially by

gobies. As a consequence, crustaceans may become a more dominant component of the epibenthic predator complex.

4.3. Temperature effect on predator–prey interactions

The fact that in the present situation, *M. balthica* already suffers from suboptimal temperature conditions means that any further increase in temperature will have a negative impact on the *M. balthica* population. This implies that the relative contribution of the other bivalve species will increase, becoming more vulnerable to predation. In addition, an increase in temperature will automatically imply a higher predation pressure by the epibenthic predators through an increase in their food intake. The lower Arrhenius temperature of bivalves (5800 K) compared with that of its main predators, the crustacean species (6500–7350 K), and especially the shrimp *C. crangon*,

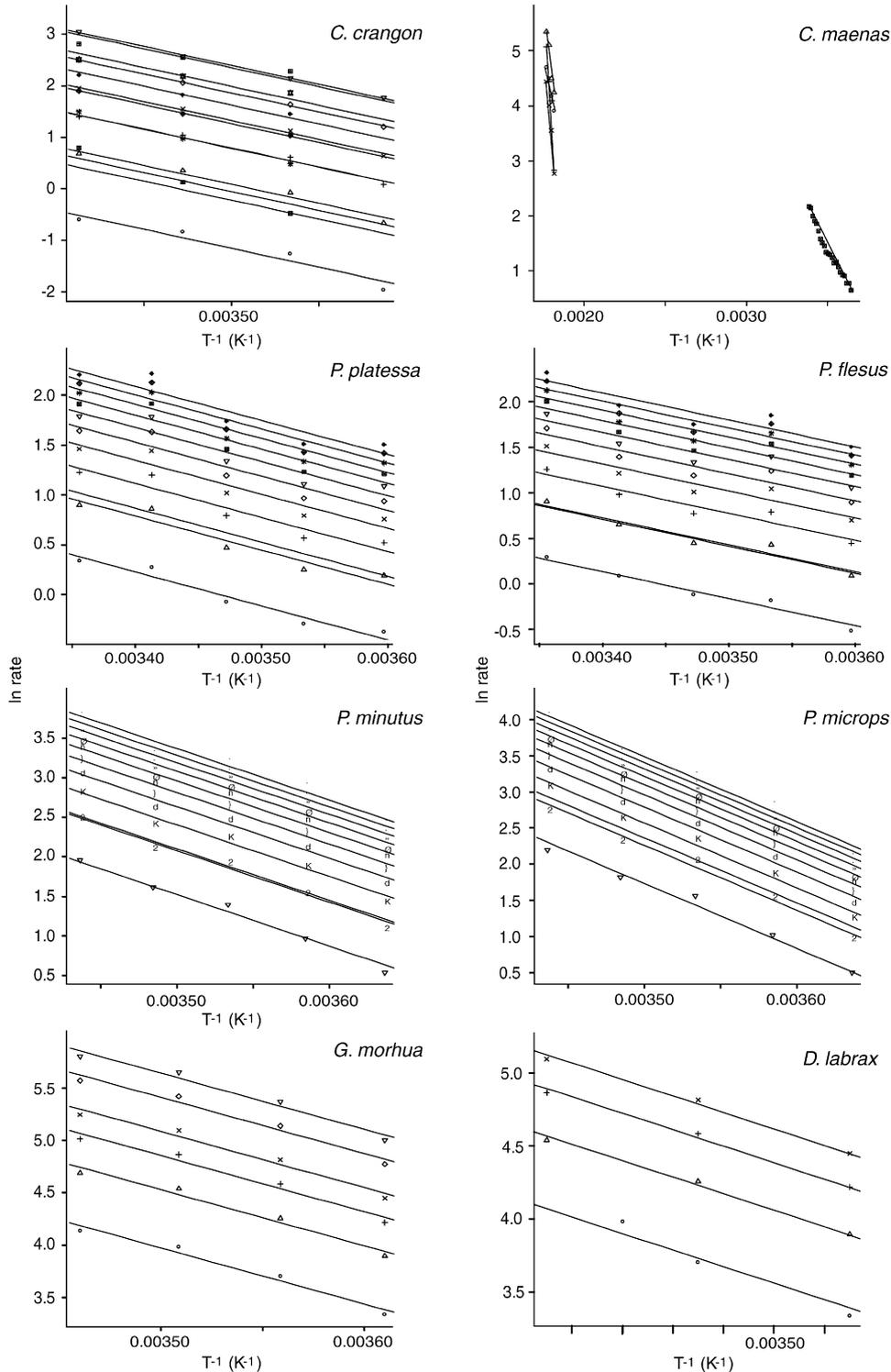


Fig. 7. Arrhenius plot (ln rate versus $1/T$) for the oxygen consumption data for various bivalve species. Each line represents an individual data set. Arrhenius temperature (\pm SE)—*Crangon crangon*: 7351 ± 266 K ($n = 42$; $R^2 = 0.99$); *Carcinus maenas*: 6498 ± 920 K ($n = 38$; $R^2 = 0.95$); *Pleuronectes platessa*: 6519 ± 163 K ($n = 100$; $R^2 = 0.97$); *Platichthys flesus*: 8974 ± 178 K ($n = 100$; $R^2 = 0.97$); *Pomatoschistus minutus*: 2963 ± 165 K ($n = 50$; $R^2 = 0.97$); *P. microps*: 3418 ± 184 K ($n = 50$; $R^2 = 0.97$); *Gadus morhua*: 5345 ± 220 K ($n = 24$; $R^2 = 0.98$); *Dicentrarchus labrax*: 5651 ± 298 K ($n = 12$; $R^2 = 0.99$). See text.

implies that the growth potential of the predators increases more than that of their prey.

Within the epibenthic predator complex also a shift will occur in favour of the crustaceans and especially the

shrimp *C. crangon* because of the exclusion of cod, an important predator. The implications for the food web structure and the various predator–prey interactions might be insignificant in case other predator species fill in the gap,

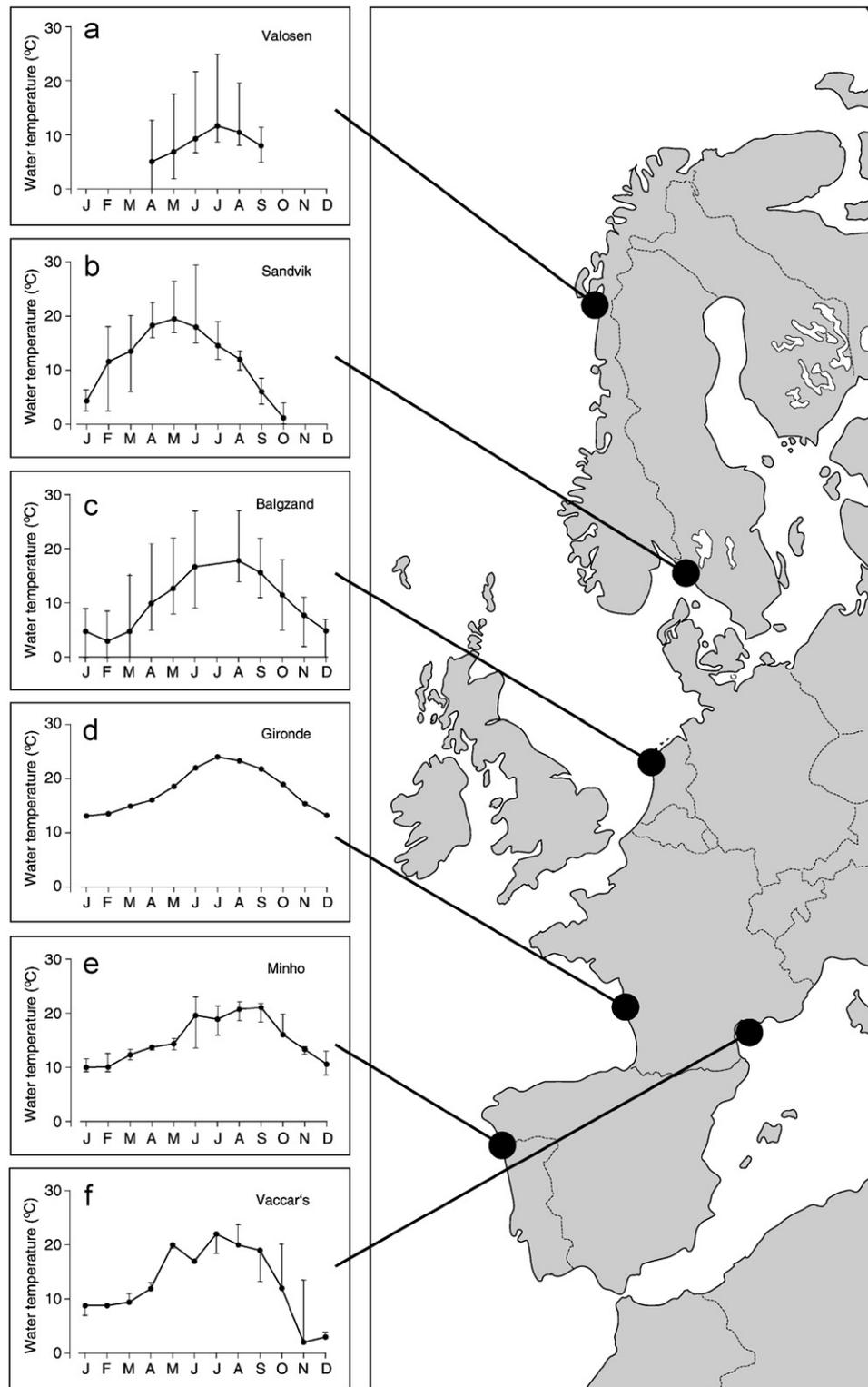


Fig. 8. Seasonal pattern in water temperature along the European Atlantic coast. Data source: Valosen Norway (Campos and Freitas, unpublished), Sandvik Sweden (Pihl and Rosenberg, 1982), Balgzand The Netherlands (Van der Veer and Witte, unpublished), Gironde France (Bachelet, 1986), Minho Portugal (Campos and Freitas, unpublished) and Vaccarès (Gellin et al., 2000). Mean values are presented together with observed range (if present).

for instance, in case sea bass replaces cod as predator. However, if the disappearance of an important predator is not filled in, it might imply a change in predator–prey interactions and result in shifts in the food web structure. Such regime shifts related to changes in environmental

conditions have already been observed for the Wadden Sea (Weijerman et al., 2005). This study corroborates with the suggestion of other studies, that climate induced changes in different trophic levels of the ecosystem can have important consequences in food web structure and

functioning (Frank et al., 2005) and, in this specific situation, a potential change in species composition in favour of some key species, such as *C. crangon* may have cascade effects in all the food web.

These three main impacts of temperature on the predator–prey interaction ((1) a general increase in absolute predation pressure; (2) release of main predators of bivalve spat, the shrimps, from predation by fish species and (3) increase in relative growth potential of predators), all work out in a similar way towards a higher potential predation pressure by *C. crangon* upon the bivalve spat. A next step will be detailed studies on the food conditions for the predator and prey species in the field. Ultimately, the processes determining recruitment of the predatory species should also be taken into account. In this respect, regulating mechanisms might even vary between areas as it has been suggested for *C. crangon* by the work of Siegel et al. (2005) and Henderson et al. (2006).

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