The effect of temperature on the filtration rate of *Solen cylindraceus* (Hanley) (Mollusca: Bivalvia)

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Filtration rates of the infaunal estuarine bivalve *Solen cylindraceus* were determined. The filtration rate of animals collected in summer (26°C) and winter (16,5°C), although significantly different, exhibit only slight variation in absolute rate, and may be expressed as a function of shell length, by the equations $y = 0{,}247x^{1{,}066}$ (winter) and $y = 0{,}758x^{0{,}826}$ (summer). *Solen cylindraceus* acclimates to both high and low temperatures under laboratory conditions. Filtration rates show a thermal optimum in the range 15–35°C, declining at higher and lower temperatures. Q_{10} values of filtration decrease rapidly from greater than 4 to less than 2 when the thermal optimum is reached. Maximum rates generally occur approximately 5°C above the temperature to which the animal has been acclimated.

Die filtrasietempo van die modderbewonende tweeklep *Solen cylindraceus* van riviermondings is vasgestel. Alhoewel die filtreertempo's van diere wat in die somer (26°C) en winter (16,5°C) versamel is, betekinsvol verskillend was, was daar slegs effense verskille in die absolute tempi. Die absolute tempi kan uitgedruk word as funksies van skulplengte deur die vergelykings $y = 0{,}247x^{1{,}066}$ (winter) en $y = 0{,}758x^{0{,}826}$ (somer). *Solen cylindraceus* pas by beide hoë en lae temperature aan onder laboratoriumtoestande. Optimale filtreertempi word ondervind in die temperatuurreeks 15–35°C, en verminder teen hoër en laer temperature. Q_{10}-waardes van filtrasie verminder spoedig van groter as 4 tot minder as twee, waneer die termale optimum bereik word. Hoogste tempi word gewoonlik gevind ongeveer 5°C bo die temperatuur waarvoor die dier aangepas was.

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Solen cylindraceus (Hanley, 1843) is an infaunal bivalve mollusc found inhabiting intertidal mudbanks of many southern African estuaries (Day 1981). It is particularly abundant in the Kariega, an east Cape estuary (33°41′S / 26°41′E), where densities of 400 m^{-2} have been recorded (Hodgson 1987). The Kariega, owing to its small and highly regulated catchment (Allanson & Read 1987), is a marine dominated estuary in which marine influences penetrate virtually its entire length, and salinities approximate that of sea water (35–38‰). Temperature, however, has been shown to fluctuate throughout the year, with a range of *ca* 7–22°C in winter and 14–33°C in summer, and on a short-term basis by as much as 10–12°C (within a single tidal cycle) dependent on upwelling conditions (Taylor 1988). Temperature rather than salinity is thus considered to be one of the environmental variables more likely to play a major role in determining the filtration activity of *Solen cylindraceus* in the estuary. The filtration rate of an animal is of great ecological importance (for reviews see Jorgensen 1975; Winter 1978; Newell 1979; Newell & Branch 1980) and the effect of temperature on filtration rate of bivalves is a well known and recurrent feature in the literature (e.g. Winter 1969; Ali 1970; Widdows & Bayne 1971; Schulte 1975; Newell, Johnson & Kofoed 1977). However, despite this wealth of information, and besides some recent work (Griffiths & King 1979; Griffiths 1980; Buxton, Newell & Field 1981; Stenton-Dozey 1986), very little information is available on southern African species, particularly local, infaunal estuarine bivalves.

Newell & Branch (1980) distinguish three time phases in the response of an animal to a change in temperature:

(i) An immediate (acute or short-term) response.
(ii) An acclimation (longer or seasonal) response by the animal, which follows on a longer period of exposure to the changed temperature condition.
(iii) Very long term responses to changes in environmental temperatures over many generations, which may favour the appearance of genetic variants adapted to the new thermal regime.

The general concept of thermal adaption therefore, includes both genetic and non-genetic aspects (Bayne, Thompson & Widdows 1976). The genetic aspects, which influence factors such as the upper and lower tolerance limits of the species have been examined in *Solen corneus (= cylindraceus)* by McLachlan & Erasmus (1974). Their work comprises virtually the only published knowledge on thermal responses in this species to date. This investigation aims to examine the 'nongenetic' adaptations by considering the rate of filtration of *Solen cylindraceus* in response to temperature. Both immediate and acclimation responses of the animal to a variety of temperature conditions, which the animal may normally or episodically encounter, are examined.

Materials and Methods

Comparison of summer and winter collected animals

Filtration rates were initially compared on animals collected during summer (water temperature 26°C), and winter (water temperature 16,5°C). Animals within the size range 38–80 mm were collected and transferred to plastic pots (220 mm diameter, 270 mm depth) filled with mud at the site of collection. To allow the animals to establish themselves under conditions as normal as possible, pots were left in the estuary and collected the next day. The pots were transferred into tanks containing estuarine water (salinity, 35°/∞) held in constant environment (C.E.) rooms, at a temperature set to match that measured in the field during collection. Animals were allowed a 3-week period to adjust to laboratory conditions of a 6 h tidal cycle and a 14 : 10 h light : dark regime for summer collected animals, and a 12 : 12 h light : dark period for winter collected animals. Animals were fed a suspension of the green algae *Tetraselmis seucica* every three days. Aquaria water was changed every 7–10 days.

After this period, animals were removed from the pots, thoroughly rinsed in filtered estuarine water and tied onto a glass platform (50 mm × 10 mm × 20 mm high), with a thin cotton thread. They were then transferred to glass jars containing 1 l of 0,45 μm filtered estuarine water at the same temperature and allowed one hour to recover from handling. All debris produced during this time was removed by siphoning, resulting in *ca* half the volume of water being lost. The remaining volume was made up to 2 l with freshly filtered estuarine water (35°/∞) containing a suspension of *Tetraselmis seucica* to give a final concentration of 20×10^6 cells l^{-1}. Algal cells were maintained in suspension by a magnetic stirrer. A 10-ml aliquot was removed every 30 min for three consecutive half-hour-periods and the cell count determined immediately using a Coulter Counter model Z_b fitted with a 50 μm aperture, and using counting volumes of 0,05 ml. After measurement, the volume of each aliquot was made up back to 10 ml (generally only 1–2 ml required), using a stock solution of *Tetraselmis seucica* (concentration: 20×10^6 cells l^{-1}), and returned to the test chamber. This prevented any significant changes in volume or cell concentration as a result of counting. A control chamber was set up under identical conditions containing plasticine-filled *Solen* valves of the same dimensions as the experimental animal. The filtration rate is expressed as a mean value of three determinations per animal and calculated according to Coughlan (1969). Only particles in the size range 6–9 μm were counted, as this was the modal size range of the *Tetraselmis* culture used. This particle size has been shown to be retained with 100% efficiency (de Villiers & Allanson 1988). Previous work using a flow-through, rather than a closed system (de Villiers & Allanson 1988), with filtration rate calculated according to Hildreth & Crisp (1976) gave comparable results. However, as available equipment allowed for a greater number of determinations to be run simultaneously using the closed system, this method was used.

Filtration rate — Temperature response

The modal size for *Solen cylindraceus* in the Kariega estuary is 50–60 mm shell length, and all animals used in these experiments fell within that size range. Three experiments were performed:

(i) Filtration rate – temperature responses of thermally acclimated animals.
(ii) Acute filtration rate – temperature responses of thermally acclimated animals, subjected to sudden temperature changes.
(iii) Re-acclimation rate of filtration following exposure to acute temperature change.

The first two are dealt with together:
(i and ii) Six temperature regimes were considered (10, 15, 20, 25, 30, 35°C), and the experiments were performed in two parts. The first involved animals collected in winter (water temperature 18°C), and acclimated to temperatures of 10 to 25°C. In the second, animals were collected in summer (water temperature 27°C) and acclimation temperatures of 30 and 35°C were examined. Collection was as previously described, and animals were transferred to C.E. rooms, where temperature and salinity had been set to match those recorded in the field.

Animals were acclimated for 3 days to a 6 h tidal cycle, and a photoperiod of 12 : 12 or 14 : 10 light : dark for experiments at 20°C or less and 25°C or above, respectively. After this initial three-day period, temperature was changed by 1°C per day, until the desired temperature had been reached. Animals were then allowed a 30-day acclimation period at that temperature. Temperatures were held constant at ± 1°C and salinity at 35°/∞ ± 2°/∞. After this period, 10 animals were removed from each of the different experimental temperatures and their filtration rates determined as previously described. The final filtration rates are given as mean values obtained from three measurements on each animal for all 10 animals from each acclimation group. A further 10 animals from each of the different acclimation temperatures were then removed from the pots and transferred to the experimental containers for filtration rate determinations at each of the exposure temperatures i.e. 10, 15, 20, 25, 30, 35 and 40°C. Each acclimated group was thus subjected to six exposure temperatures. Results are again given as a mean of three determinations per animal for a total of 10 animals.

(iii) Filtration rate adjustments, following exposure to sudden changes in temperature were determined over a 14-day period, for both summer and winter acclimated animals (25 and 15°C respectively). Animals for the winter experiment were collected during winter and early spring (water temperature 16–16,5°C), following the procedure previously described. They were acclimated (following direct transfer) to laboratory conditions of 15°C, a 12 : 12 light : dark regime and a 6 h tidal cycle for a period of three weeks. Animals for the summer experiment were collected during late spring and early summer (water temperature 20–23°C) and subject to a 14 : 10 h light : dark regime and a 6 h tidal cycle. Temperature was increased by 1°C per day to 25°C, at which the animals were acclimated for three weeks.

After this three-week acclimation, the water temperature in the different aquaria was altered rapidly and maintained within 1°C of the desired exposure temperature for the duration of the experiment. Each group of animals, acclimated to either summer or winter conditions, was thus subject to six different exposure temperatures. The control in each case consisted of one group of 10 animals maintained at the original acclimation temperature of 15 or 25°C. Three animals were removed from each of the different temperature regimes every 12 h for the first 216 h (9 days), and then every 24 h up to 336 h (14 days) for filtration rate determination as previously described. Filtration rates are given as a mean of three determinations per animal for a total of three animals per time interval.

Results

Comparison of filtration rates for summer- and winter-collected animals

Filtration rates for summer- and winter-collected animals are shown in Figure 1 which demonstrates almost linear and proportional increases in filtration rate with size. Although fitted regressions for summer and winter animals are significantly different ($p = 0{,}000$; F statistic = 31,23), the absolute 'seasonal' rates do not differ markedly. The regression values fitted to the data are given in Figure 1.

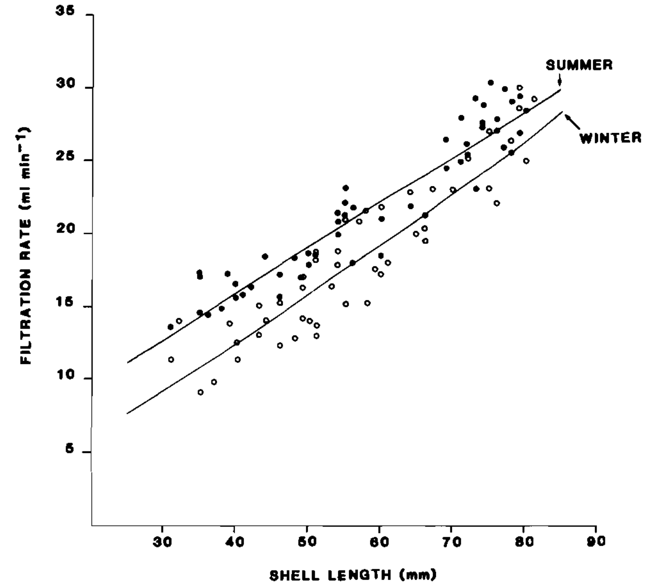

Figure 1 Filtration rates of *Solen cylindraceus* as a function of shell length. (●) Animals collected during the summer (26°C) ($n = 50$) $y = 0{,}758x^{0{,}826}$ ($R^2 = 0{,}889$). (○) Animals collected during the winter (16,5°C) ($n = 49$) $y = 0{,}247x^{1{,}066}$ ($R^2 = 0{,}823$).

Filtration rate – Temperature response

The filtration rate of animals acclimated to particular temperatures and exposed to different temperatures are shown in Figures 2A & B, and Table 1. The acclimated filtration rate – temperature curve (Figure 2A) indicates a thermal optimum for filtration rate over the range 15–35°C with a maximum rate (22,86 ± 4,36 ml min^{-1}) recorded at 25°C. The 15°C and 25°C results compare favourably with the filtration rates measured for summer- and winter-collected animals of the same size (Figure 1). The filtration rate values for 40°C shown in Figure 2A, were obtained by taking the mean value of the last five days data points of the 40°C exposure curve from Figure 3B. Maximum filtration rates in most cases were highest at the test temperature above that to which the animals were acclimated (Figure 2B). This holds for all animals acclimated to temperatures of 10–30°C. However, animals acclimated to 35°C, when exposed to 40°C exhibit a slight decrease in filtration rate. The rate-temperature curve of animals acclimated to 10°C

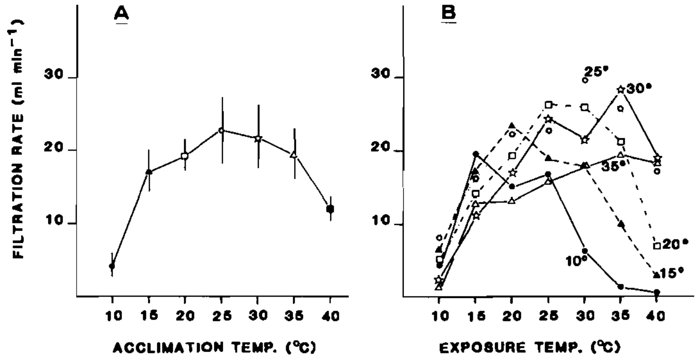

Figure 2 (A) Acclimated filtration rate of *Solen* (50–60 mm shell length). (B) The acute filtration rate response of animals acclimated to specific temperatures (indicated on graph) and exposed to different temperatures. Standard deviations from the mean are not shown in the figure (see Table 1).

Table 1 Filtration rates (ml min^{-1}) for groups of *Solen* (50–60 mm shell length) acclimated to temperatures of 10–35°C and exposed to temperatures of 10–40°C. Control values for each group are shown in bold. Values for each group are a mean ± Sx from 10 animals, three determinations per animal

Acclimated	Exposure temperature						
temperature	10°C	15°C	20°C	25°C	30°C	35°C	40°C
10°C	**4,20 ± 1,43**	19,54 ± 3,10	14,95 ± 5,60	16,85 ± 4,74	6,10 ± 2,92	1,33 ± 1,35	0,46 ± 0,63
15°C	6,30 ± 2,15	**17,14 ± 2,57**	23,58 ± 3,93	18,88 ± 4,89	17,78 ± 5,01	9,93 ± 3,29	2,69 ± 2,16
20°C	4,99 ± 2,50	13,94 ± 3,17	**19,10 ± 2,06**	26,32 ± 4,50	26,31 ± 3,13	21,02 ± 3,87	6,73 ± 3,10
25°C	8,03 ±2,56	16,32 ± 3,84	22,48 ± 5,10	**22,86 ±4,36**	29,88 ± 3,68	25,85 ± 3,64	17,15 ± 4,72
30°C	1,88 ± 1,70	11,04 ± 4,09	16,98 ± 4,45	24,35 ± 5,03	**21,81 ± 4,13**	28,47 ± 3,74	18,25 ± 5,28
35°C	1,28 ± 1,27	12,76 ± 4,00	13,37 ± 2,92	15,85 ± 3,57	17,66 ± 1,64	**19,58 ± 3,61**	18,23 ± 2,17

shows a substantial increase in filtration on exposure to temperatures of 15, 20 and 25°C, followed by a rapid decrease as temperature increases further, with virtually no filtering activity recorded at 40°C (Figure 2B). A similarly shaped curve is described for animals acclimated to 15 and 20°C, but with slightly elevated filtration rates recorded. Animals acclimated to 25, 30 and 35°C all show high filtration rates at elevated exposure temperatures. There appears to be a lateral shift of the rate-temperature curve to the right, following acclimation to warmer temperatures (20–35°C). In all instances temperature has a very pronounced effect below 15°C and in most cases above 30–35°C.

Results for the adjustment of filtration rate by *Solen cylindraceus* acclimated to winter (15°C) and summer (25°C) conditions, and exposed to different temperatures are shown in Figures 3A & B respectively. In both cases the controls (results from animals which were maintained at their original acclimation temperature) are indicated as a single mean ± Sx value (17,45 ± 1,68 ml min^{-1} for winter and 22,22 ± 1,91 ml min^{-1} for summer acclimated animals). Filtration rates of animals acclimated at 15°C, and exposed to 20, 25 and 30°C (Figure 3A) all increased initially, but decreased and levelled off after *ca* 144 h at somewhat more than the control rate. Those animals exposed to 35 and 40°C, showed a marked initial decrease in filtration rate which gradually increased and, in the case of the 35°C curve, levelled off slightly above the control value after *ca* 180 h. However, filtration rates of animals exposed to 40°C,

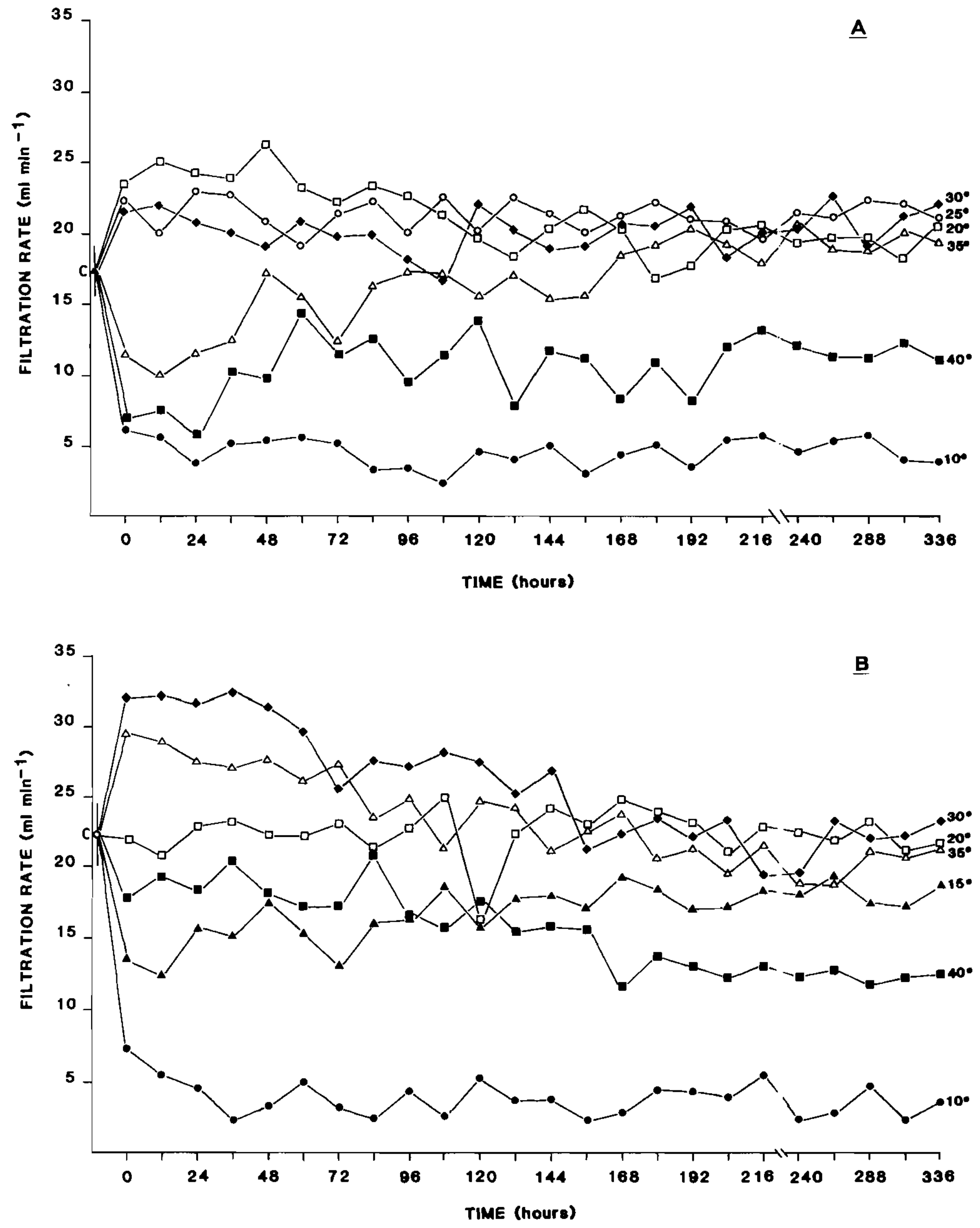

Figure 3 Filtration re-acclimation rate for animals acclimated to: (A) Winter (15°C) and (B) Summer (25°C), and exposed to different temperatures. C = Control: animals maintained at the acclimated temperature. Error bars excluded to avoid cluttering. At no point is the Sx greater than ± 2,96.

stabilized substantially lower than those recorded for any of the 15–35°C temperatures. On exposure to 10°C, filtration rate decreased markedly and remained depressed for the duration of the experiment (Figure 3A).

Animals acclimated to 25°C (Figure 3B), showed an initial increase in filtration rate on exposure to temperatures of 30 and 35°C, which gradually decreased after *ca* 156–168 h to approximately the same value as the control (*ca* 22 ml min^{-1}). Exposure to 20°C exhibited no substantial variation from the control value, whereas animals exposed to 15°C showed an initial decreased filtration rate which persisted for *ca* 24 h, and then gradually increased and levelled off at just below the 25°C control value, but at approximately the same level as the 15°C control value (*ca* 17 ml min^{-1}) shown in Figure 3A. Exposure to 40°C is characterized by only a slight initial decrease in filtration rate which gradually declined further, stabilizing after *ca* 192 h at a value markedly lower (*ca* 12 ml min^{-1}) than that for the 15–30°C temperatures, but not dissimilar from the 40°C value recorded in Figure 3A. A decrease in temperature to 10°C, resulted in a substantially lowered filtration rate (*ca* 5 ml min^{-1}) which remained as such for the duration of the experiment.

Discussion

Jorgensen (1960) comments on the often conflicting filtration rate results obtained for bivalves by different workers even on the same species. He attributes this principally to different experimental techniques and animal sensitivity, in which changes in the environment may cause them to react by altering water transport rates. Further, Jorgensen (1975) suggests that many of the data obtained are often of restricted value because of the uncertainty as to the extent that laboratory results represent unimpeded activity in nature. Often the values measured for infaunal bivalves tend to be low since, in most cases measurements have been made on animals outside their natural sediment substrata. In the experiments presented here, the reaction of *Solen cylindraceus* to changes in a single environmental variable — temperature — is described. While every attempt was made to maintain conditions as natural as possible during the experiments, animals were nevertheless subjected to the stress of being removed from their burrows in order to determine filtration rate. Animal disturbance is thus a valid criticism. We nevertheless feel that the results presented are a reasonable reflection of the animals' natural filtration rate responses to changes in temperature.

Filtration rate has been shown to vary with season in a number of bivalve species. Walne (1972) records a definite maximum for *Venerupis decussata* and *Crassostrea gigas* during the summer months, whereas *Mytilus edulis* and *Ostrea edulis*, although exhibiting an increased rate in summer, do not show as marked a maximum. Worral, Widdows & Lowe, (1983) note a distinct seasonal variation in filtration rate for *Scrobicularia plana* and, further, that filtration rate varied in different *Scrobicularia* populations. Rao (1953) has reported a variation of filtration rate in *Mytilus californianus* populations collected at different latitudes, and indicates that these animals are capable of a temperature-compensating response. In populations of *Chlamys opercularis*, a measure of the filtration rate of summer- and winter-collected animals give virtually the same values (Vahl 1972; Mclusky 1973). Similarly, *Solen cylindraceus* shows only a minimal difference in filtration rate between summer- and winter-collected animals.

According to van't Hoff's law, filtration rate should double for every 10°C rise in temperature (Shulte 1975). The temperature coefficients (Q_{10}) for *Solen cylindraceus* are compared with a variety of other species in Table 2. An increase in temperature from 10–20°C results in a rise of *ca* 350% (Q_{10} of 4,54) in the filtration rate, while a further increase, 15–25°C, shows only an increase of *ca* 33% (Q_{10} of 1,33). A nett decrease in the filtration rate of *ca* 14% (Q_{10} of 0,85) is recorded when temperature is increased from 25–35°C. Based upon the average filtration rate results of the last five days for animals held at 40°C (Figure 3B) a Q_{10} value of 0,56 is obtained between 30 and 40°C, corresponding to a 43% decrease in the filtration rate. Widdows & Bayne (1971) suggest that Q_{10} values reflect the degree of acclimation, and regard values approaching unity as indicative of full

Table 2 Temperature coefficients (Q_{10}) of acclimated filtration rates for *Solen cylindraceus* compared to values obtained for other Lamellibranchs

Species	Temperature (°C)	Filtration rate (l h^{-1})	Q_{10}	Author
Arctica islandica	10	3,56	1,23	Winter 1969
	20	4,30		
Hiatella arctica	10	0,0165	0,75	Ali 1970
	20	0,0121		
Mytilus edulis	10	1,100	1,13	Theede 1963
	20	1,240		
	10	1,468	1,22	Schulte 1975
	20	1,796		
	15	1,751	1,001	
	25	1,798		
	20	1,796	0,059	
	30	0,106		
Solen cylindraceus	10	0,252	4,54	Present study
	20	1,146		
	15	1,028	1,33	
	25	1,371		
	20	1,146	1,14	
	30	1,308		
	25	1,371	0,85	
	35	1,175		
	30	1,308	0,56	
	40*	0,740		

*Determined from the values of the last five days in Figure 3B.

acclimation. Q_{10} values calculated from acclimated filtration rates (Figure 2A) for *Solen cylindraceus* in this study (Table 2), appear to reinforce such a hypothesis. A drop in temperature from 15–10°C, results in a *ca* 75% drop in the filtration rate, whereas an increase in temperature from 35– 40°C shows a decrease of *ca* 37%. The optimal temperature range for filtration is thus fairly clearly defined as 15–35°C. This wide temperature range is indicative of a eurythermal subtropical species. The reduced filtration rate at 40°C is interpreted as a response to thermal stress. McLachlan & Erasmus (1974) have indicated an upper lethal temperature under *in vitro* conditions of 44,5°C for *Solen corneus (= cylindraceus)*. The thermal tolerance determined for a species may vary, depending on the techniques used, the acclimated state of the animal and the period of exposure (Kinne 1963; Newell & Branch 1980). Generally, lethal temperatures are determined from short-term exposure experiments, and are of limited ecological significance (Read & Cumming 1967). Nevertheless, lethal temperatures are a function of habitat and reflect adaptation to different latitudinal and microgeographical temperature regimes (Kennedy & Mihursky 1971; Read 1967). The lethal temperature of 44,5°C and the maximum temperature of 40°C used in these experiments, are both higher than any temperature to which *Solen cylindraceus* is likely to be exposed to in the natural environment. The rate at which the animal filters at these extremes varies however, and is related to its past acclimatory history (Figure 2B). *Solen* appear to exhibit a lateral shift of the rate-temperature curves to the right following acclimation to higher temperatures. Similar responses have been reported for other filter feeding bivalves, *Mytilus edulis*(Schulte 1975), *Ostrea edulis* (Newell *et al.* 1977 and Buxton *et al.* 1981) as well as for the filter-feeding gastropod *Crepidula fornicata* (Newell & Kofoed 1977). The initial response of animals, and the time taken to acclimate to different exposure temperatures (Figure 3A & B), will vary depending upon the conditions to which the animals have been acclimated, but generally follow the three phases for non-genetic adaptation as described by Kinne (1963), i.e. immediate response to environmental change, the stabilization of this response, and a new steady state. In the experiment presented here, animals previously acclimated to 15°C and 25°C, subsequently acclimated to exposure temperatures in the range 15–35°C, within 120–168 h (5–7 days). However, animals exposed to extreme temperatures of 10°C exhibited no acclimatory response, and those at 40°C displayed a gradual, limited acclimation. As an intertidal animal, it is unlikely that *Solen cylindraceus* will be exposed to only one single temperature, but will respond rather to short-term fluctuations within the tidal period, reflecting the difference between estuarine and sea water temperatures. To this end the acute response will probably reflect more accurately the filtering activity of the population.

It is suggested that for *Solen cylindraceus* there is a temperature range within which complete acclimation (Precht Type 2) occurs, and beyond which only a partial (Precht Type 3 for 40°C) or no (Precht Type 4 for 10°C) acclimatory response is recorded (see Newell & Branch 1980). *Solen cylindraceus* exhibits an effective seasonal compensation in filtration rate, and appears to acclimate fairly rapidly over its thermal optimal range (15–35°C), provided exposure conditions persist for several days. Such plasticity would allow for optimal filtration throughout the year. However, *Solen cylindraceus* appears incapable of adjusting its filtration rate sufficiently rapidly so as to fully accommodate short-term temperature fluctuations (within a single tidal cycle) which, under conditions of severe upwelling may vary by as much as 10–12°C (Taylor 1988).

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