

## BEHAVIORAL THERMOREGULATION IN THE AMERICAN LOBSTER *HOMARUS AMERICANUS*

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### Summary

It is generally accepted that water temperature has a strong influence on the behavior of the American lobster *Homarus americanus*. However, there is surprisingly little behavioral evidence to support this view. To characterize the behavioral responses of lobsters to thermal gradients, three different experiments were conducted. In the first, 40 lobsters acclimated to summer water temperatures (summer-acclimated,  $15.5 \pm 0.2$  °C, mean  $\pm$  S.E.M.) were placed individually in an experimental shelter, and the temperature in the shelter was gradually raised until the lobster moved out. Lobsters avoided water warmer than  $23.5 \pm 0.4$  °C, which was an increase of  $8.0 \pm 0.4$  °C from ambient summer temperatures. When this experiment was repeated with lobsters acclimated to winter temperatures (winter-acclimated,  $4.3 \pm 0.1$  °C), the lobsters ( $N=30$ ) did not find temperature increases of the same magnitude ( $\Delta T=8.0 \pm 0.4$  °C) aversive.

The second experiment was designed to allow individual summer-acclimated lobsters ( $N=22$ ) to select one of five shelters, ranging in temperature from 8.5 to 25.5 °C. After 24 h, 68% of the lobsters occupied the 12.5 °C shelter, which was slightly above the ambient temperature

(approximately 11 °C). In a similar experiment, winter-acclimated lobsters ( $N=30$ ) were given a choice between two shelters, one at ambient temperature ( $4.6 \pm 0.2$  °C) and one at a higher temperature ( $9.7 \pm 0.3$  °C). Winter-acclimated lobsters showed a strong preference (90%) for the heated shelter.

In the final experiment, summer-acclimated lobsters ( $N=9$ ) were allowed to move freely in a tank having a thermal gradient of approximately 10 °C from one end to the other. Lobsters preferred a thermal niche of  $16.5 \pm 0.4$  °C and avoided water that was warmer than 19 °C or colder than 13 °C. When standardized for acclimation temperature, lobsters preferred water  $1.2 \pm 0.4$  °C above their previous ambient temperature. Collectively, the results of these studies indicate that lobsters are capable of sensing water temperature and use this information to thermoregulate behaviorally. The implications of these findings for lobster behavior and distribution in their natural habitat are discussed.

Key words: lobster, temperature, thermoregulation, *Homarus americanus*, behavior.

### Introduction

It is generally accepted that temperature has a pervasive influence on the behavior and movements of lobsters (Herrnkind, 1980; Factor, 1995). For example, pelagic lobster larvae actively avoid passing through a thermocline, choosing to remain in water warmer than 17 °C (Boudreau *et al.* 1992), adult lobsters appear to follow isotherms to stay in warmer water (Ennis, 1984) and autumn migrations of spiny lobsters *Panulirus argus* seem to be triggered by large decreases in temperature, coincident with autumn storms (Kanciruk and Herrnkind, 1978). Furthermore, it has been proposed that inshore-offshore migrations of *Homarus americanus* are strongly influenced by broad-scale thermal gradients (Saila and Flowers, 1968; Cooper and Uzmann, 1971). It is possible that these large-scale movements, like the seasonal offshore migrations of hermit crabs *Pagurus longicarpus* (Rebach, 1974) and blue crabs *Callinectes sapidus* (Warner, 1976), have evolved to maximize

residence in warm water and thus enhance growth and/or reproduction (Aiken, 1980; Aiken and Waddy, 1986).

In lobsters, there is a complex relationship between temperature, growth and reproduction. Molting is inhibited below 5 °C, and growth rate is proportional to temperature between approximately 8 and 25 °C (Aiken, 1977). In addition, 'temperature is the major factor controlling size at maturity, oocyte maturation, incidence, timing and synchronization of spawning, success of egg attachment and incubation, and time of hatching' (Waddy *et al.* 1995). Higher water temperatures have also frequently been related to increased catches and landings (Flowers and Saila, 1972; Campbell *et al.* 1991; Hudon, 1994). Yet, despite the broad impact of water temperature on many aspects of lobster biology, it remains unclear whether lobsters actively seek and utilize particular temperature regimes.

Several studies have provided experimental evidence for behavioral thermoregulation in aquatic crustaceans, primarily crayfish. *Astacus astacus* avoid warm temperatures ( $>20^{\circ}\text{C}$ ) in a  $10\text{--}25^{\circ}\text{C}$  gradient and water colder than  $10^{\circ}\text{C}$  in a cooler gradient ( $4\text{--}18^{\circ}\text{C}$ ) (Kivivuori, 1994). *Procambarus clarkii* also exhibits both temperature preference and avoidance reactions when exposed to a broad thermal gradient (Espina *et al.* 1993). To our knowledge, only one similar study has been performed with lobsters: Reynolds and Casterlin (1979a) reported that adult lobsters in a shuttlebox apparatus appeared to have a thermal preference of approximately  $16^{\circ}\text{C}$  (range  $15\text{--}20^{\circ}\text{C}$ ). Given the pervasive effects of temperature on many aspects of lobster reproduction, development and physiology, the present investigation expands upon the work of Reynolds and Casterlin (1979a) and more thoroughly quantifies the behavioral thermoregulatory capabilities of this important commercial species.

Three different experiments were carried out to determine the range of water temperatures that lobsters find preferable and aversive. In all experiments, lobsters generally preferred water between  $12$  and  $18^{\circ}\text{C}$ , or temperatures slightly warmer than the ambient temperatures at the time of testing, and avoided water warmer than  $20\text{--}23^{\circ}\text{C}$  and colder than  $10^{\circ}\text{C}$ . These findings are consistent with earlier crustacean studies and support the hypothesis that lobsters thermoregulate behaviorally. This behavior may serve to maximize their potential for growth, development and/or reproduction (Waddy *et al.* 1995).

## Materials and methods

### Lobsters

Adult lobsters *Homarus americanus* (Milne-Edwards),  $82\text{--}92$  mm carapace length, were purchased from commercial fishermen or captured using University of New Hampshire (UNH) research traps in either the Great Bay Estuary or New Hampshire coastal waters. Animals were held in running seawater tanks at the UNH Coastal Marine Laboratory (CML) in New Castle, NH, USA. All lobsters were in intermolt stage C4 (Drach and Tchernigovtzeff, 1967; Waddy *et al.* 1995), were fed frozen herring weekly, and were held for at least 2 weeks prior to experimentation. In all experiments, approximately equal numbers of both sexes were used. Experiments were carried out at the CML throughout the year; ambient temperatures in the natural habitat and in the flow-through seawater tanks inside the laboratory ranged from  $1^{\circ}\text{C}$  in winter to  $18^{\circ}\text{C}$  in summer. All values are presented  $\pm$  the standard error of the mean (S.E.M.). In the description given below, lobsters acclimated to summer temperatures of  $11\text{--}18^{\circ}\text{C}$  are referred to as summer-acclimated; winter-acclimated lobsters are those acclimated to winter temperatures of  $1.5\text{--}5^{\circ}\text{C}$ .

### Temperature avoidance/aversion assay

Individual lobsters ( $N=40$  in summer,  $N=30$  in winter) were placed in a  $2.5\text{ m}\times 0.5\text{ m}$  tank, filled to a depth of  $13\text{ cm}$  with

running sea water. A shelter constructed from a  $25\text{ cm}$  wide polyvinyl chloride pipe, bisected lengthwise, was sited at one end of the tank, and a stand-pipe drain at the other (similar to the salinity avoidance tank shown in Fig. 2 of Jury *et al.* 1994). The shelter was mounted on a temperature-regulated stainless-steel plate. The temperature in the shelter was controlled by circulating either cold or warm antifreeze (ethylene glycol) from a temperature-regulated water bath through channels in the stainless-steel plate. For warm shelters, additional heating was achieved by using submersible heaters placed inside the shelter. A thermistor was used to monitor the temperature inside the shelter. Vertical stratification of the water was minimized using aeration. The combination of the heated shelter and flowing sea water yielded a thermal gradient from inside the shelter to the far end of the tank. The entire apparatus was surrounded by a black plastic screen to prevent visual disturbance during the experiment. As lobsters are negatively phototactic (Factor, 1995), some light was allowed to enter from above the tank, giving the lobsters an incentive to occupy the shelter. The lobsters were observed using a video camera mounted above the far end of the tank.

Prior to an experiment, the lobsters were allowed to acclimate to the chamber for  $60\text{ min}$ . During the final  $30\text{ min}$  of this acclimation period, the lobsters were observed and, if they remained in the shelter during this period, the experiment continued. If a lobster rejected the shelter during this period, it was not used in the experiment. After the acceptance criteria had been reached, the temperature-controlled shelter was activated and the lobster was observed. On average, the temperature in the shelter increased at a rate of  $0.5^{\circ}\text{C min}^{-1}$ , increasing from ambient ( $15.5^{\circ}\text{C}$ ) to approximately  $25^{\circ}\text{C}$  in the summer ( $4.3\text{--}12.3^{\circ}\text{C}$  in the winter) during the first  $30\text{ min}$  of the experiment and then staying at that level for the next  $30\text{ min}$ . This protocol heated the shelters in both the summer and the winter to at least  $8^{\circ}\text{C}$  warmer than ambient. As soon as the lobster left the shelter (defined as more than one body length away, or approximately  $30\text{ cm}$ ), the temperature inside the shelter was recorded as the warm-avoidance threshold for that animal. If no response occurred within  $1\text{ h}$ , the experiment was terminated. Different lobsters were used in control runs (summer  $N=20$ , winter  $N=14$ ), during which the experimental design was identical except that the temperature-controlled plates attached to the shelters were perfused with ambient (summer  $15.5\pm 0.2^{\circ}\text{C}$ ; winter  $4.3\pm 0.1^{\circ}\text{C}$ ) sea water rather than warm antifreeze.

### Temperature preference assays

Individual summer-acclimated (ambient temperature approximately  $11^{\circ}\text{C}$ ) lobsters ( $N=22$ ) were allowed to choose between five shelters, held at five different temperatures (approximately  $8.5$ ,  $12.5$ ,  $15.5$ ,  $20.5$  and  $25.5^{\circ}\text{C}$ ), using the temperature-controlling units described above. The shelters were arranged in a circular tank ( $2.5\text{ m}$  diameter) as shown in Fig. 1. Each experiment lasted for  $24\text{ h}$ , with the position of the lobster noted three times during this period, at  $07:00$ ,  $13:00$  and  $20:00\text{ h}$ . During the experiment, lobsters typically explored

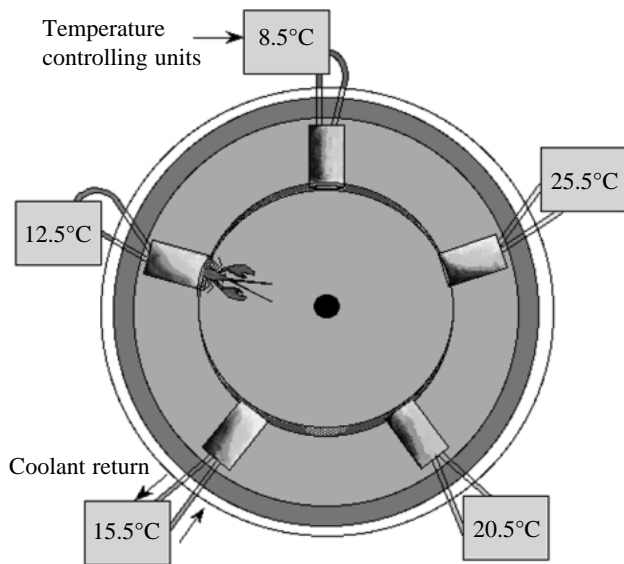


Fig. 1. Temperature preference tank. Each shelter was held at a different temperature by circulating antifreeze from temperature-controlled baths through stainless-steel plates attached to the bottom of the shelter. Ambient sea water flowed continuously through the large circular tank. Individual lobsters were placed into the tank and allowed 24 h to take up residence in one of the shelters. Arrows indicate the direction of coolant flow.

each shelter, then selected a particular shelter and remained there throughout the experiment. Only the shelter choices after 24 h were used in further analyses. As in the avoidance assay, the experimental apparatus was surrounded by black plastic to avoid visual interference. Control experiments ( $N=23$ ) were identical, except that all shelters were held at the same temperature by perfusing the stainless-steel plates with ambient sea water.

In a simplified version of this experiment, only two shelters were offered to winter-acclimated lobsters ( $N=30$ ), one held at ambient ( $4.6 \pm 0.2^\circ\text{C}$ ) and one at a higher temperature ( $9.7 \pm 0.3^\circ\text{C}$ ,  $\Delta T = 5.1 \pm 0.2^\circ\text{C}$ ) in a 1 m diameter circular tank. Individual lobsters were placed between the two shelters and were monitored for 1 h using an overhead video camera. A 15 min acclimation period preceded the experiment to determine whether lobsters were actually making a choice. Only lobsters which came into contact with both shelters before taking up residence were used in the final data analyses (30 of 33). Once this criterion was met, the experiment proceeded and the ultimate shelter and temperature chosen were recorded. Each time the experiment was carried out, a different shelter was used as the heated shelter, to eliminate the possibility that animals were selecting a particular shelter using some factor other than temperature.

#### Temperature gradient experiment

A thermal gradient tank, similar to that used by Haro (1991) to measure the thermal preference of eels, was modified for use with lobsters (Fig. 2). The range of the temperature gradient

within the tank was recorded every 12 min by two HOBO temperature dataloggers (Onset Computer Co., Falmouth, MA, USA) submerged at either end of the tank. Gradients ranged from a minimum of  $6.9\text{--}19.2^\circ\text{C}$  in one experiment to a maximum of  $15.2\text{--}26.2^\circ\text{C}$  in another. On average, the temperature ranged from  $12.0 \pm 1.0^\circ\text{C}$  to  $22.0 \pm 0.8^\circ\text{C}$ .

All animals used in this experiment were summer-acclimated (held for 1–2 weeks in recirculating ambient water ranging from  $12.0$  to  $18.0^\circ\text{C}$ ). Just prior to the experiment, a HOBO temperature logger in a waterproof case ( $6.25\text{ cm} \times 8.75\text{ cm} \times 2.5\text{ cm}$ ) was attached to the lobster's dorsal carapace using a neoprene backpack. Individual lobsters ( $N=9$ ) were placed for 30 min in the center of the thermal gradient tank in a 20 cm diameter polyvinyl chloride pipe and then released. The dataloggers on each lobster, together with those at either end of the tank, made it possible to monitor continuously the temperature chosen by the lobster and the range of temperatures available throughout the 2 day experiment. However, because these dataloggers had a response time of 20 min (for a  $5^\circ\text{C}$  change) and data were recorded at 12 min intervals, occasional rapid excursions by lobsters into water of a different temperature would not have been recorded, even though long-term patterns were accurately represented. Temperatures cooler and warmer than ambient were always available for selection. Animals that preferred temperatures within  $1^\circ\text{C}$  of the coldest or warmest available temperatures in the gradient tank were not used in the final data analyses ( $N=2$ ) because these individuals may have been striving to achieve a temperature outside the range available. The entire experimental chamber was covered with blue translucent plastic to minimize visual disturbance but to allow ambient light to enter. At least 50% of the tank water was changed between experiments. Acute preferenda (Reynolds and Casterlin, 1979b) are not presented. Rather, the final temperature preferendum (Haro, 1991), which was considered to be the mean of the temperatures selected during the second complete day of the experiment, was determined.

Controls ( $N=5$ ) were carried out in the same tank with no temperature gradient present to determine whether animals were affected by the tank design. The positions of the animals in control experiments were monitored using a time-lapse video recorder and a low-light-sensitive video camera mounted over one end of the tank. The positions of animals in some of the experiments with the temperature gradient functioning were also recorded in order to confirm the accuracy of the datalogger technique. Twelve of the 48 h of datalogger data were compared with video tapes recorded during that same time interval. Video recordings were analyzed to obtain (1) the number of times an animal entered a given area of the tank during a 12 h time interval, and (2) the total time spent in each area during the same time period.

## Results

### Temperature avoidance/aversion

Forty-four lobsters were observed in the temperature

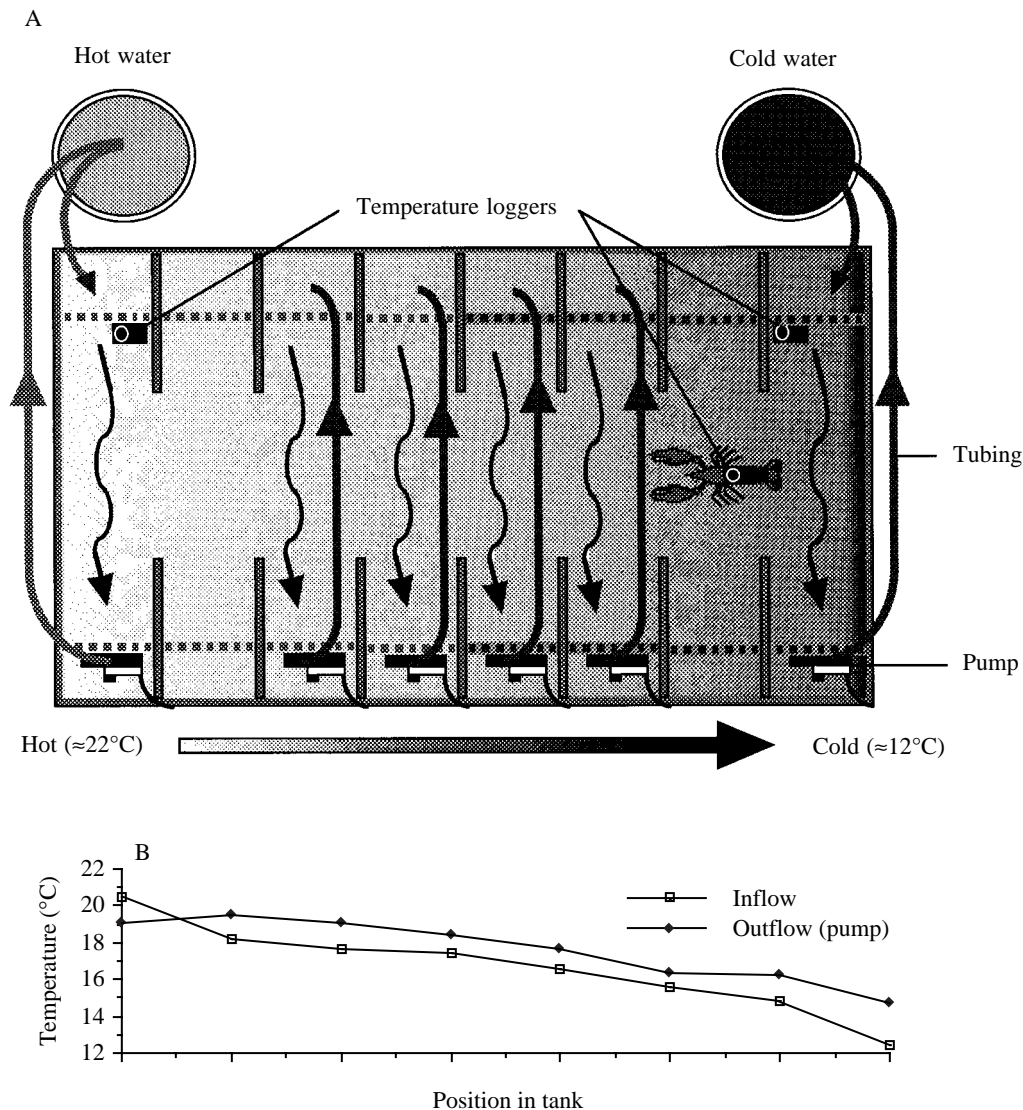


Fig. 2. (A) Thermal gradient tank viewed from above, modified from Haro (1991). The  $1\text{ m}\times 1.8\text{ m}$  (width  $\times$  length) tank was separated into sixteen  $20\text{ cm}\times 25\text{ cm}$  chambers, and the depth of the water was maintained at  $10\text{ cm}$ . A thermal gradient was achieved by circulating warm sea water, from a heated reservoir, through the chamber at one end and cold sea water, from a cooled reservoir, through the chamber at the opposite end. Mixing of warm and cold water was minimized by creating a flow of water between chambers on opposite sides of the tank, perpendicular to the temperature gradient, using small aquarium pumps. The range of the temperature gradient within the tank was recorded every 12 min by two HOBO temperature dataloggers submerged at either end of the tank. Individual lobsters were equipped with similar dataloggers and then released into the tank. During the subsequent 2 day period, the dataloggers continuously recorded the temperature range in the tank, as well as the temperature of the water in the immediate vicinity of the lobster. (B) The temperatures in each chamber during a typical experiment. The chambers at the top of the illustration in A are designated the inflow chambers, and those on the bottom are the outflow chambers.

avoidance tank during the summer when the ambient temperature was  $15.5\pm 0.2^{\circ}\text{C}$  (range  $13\text{--}17^{\circ}\text{C}$ ). Of the lobsters tested, three would not enter the shelter and one did not stay in the shelter for the full 30 min acclimation period. As they failed to meet experimental criteria, they were dropped from subsequent data analyses, yielding a total of 40 lobsters, 20 male and 20 female.

When the temperature in the experimental shelter was gradually increased towards  $25^{\circ}\text{C}$ , an increase of  $8.0\pm 0.4^{\circ}\text{C}$  from ambient, most (62.5%) lobsters left the shelter for the cooler surrounding waters (Fig. 3A,  $\chi^2$ -test for independence,

$P<0.01$ ). The mean thermal-avoidance temperature for lobsters that left the shelter was  $23.5\pm 0.4^{\circ}\text{C}$ . The smallest change in temperature that elicited a response was an increase of  $3.1^{\circ}\text{C}$  from  $15.9^{\circ}\text{C}$  to  $19^{\circ}\text{C}$ ; several lobsters did not respond even when the temperature reached  $25^{\circ}\text{C}$ . In contrast, 100% of the control lobsters ( $N=20$ ) failed to leave the shelter (Fig. 3A).

To determine whether lobsters found an increase of approximately  $8^{\circ}\text{C}$  (as opposed to an absolute maximum temperature of greater than  $23.5^{\circ}\text{C}$ ) aversive, 15 winter-acclimated lobsters of each sex ( $N=30$ ) were also tested. Starting from an ambient temperature of  $4.3\pm 0.1^{\circ}\text{C}$  (range

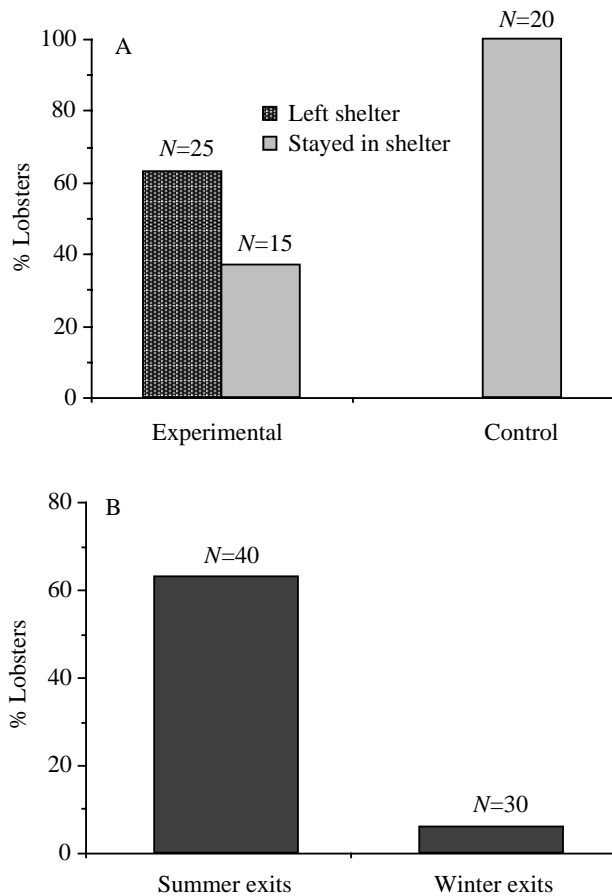


Fig. 3. Responses of summer and winter lobsters to temperature increases in temperature-avoidance assays. (A) When the temperature in the shelter was increased, most lobsters moved out to cooler water. The threshold temperature eliciting this avoidance response was  $23.5 \pm 0.4^\circ\text{C}$ . There was a significant difference ( $P < 0.01$ ) between the experimental and control groups, which did not have their shelters heated and therefore did not leave. (B) Responses of winter- and summer-acclimated lobsters. When the water temperature was raised by approximately  $8^\circ\text{C}$  (from  $15.5$  to  $23.5^\circ\text{C}$ ),  $62.5\%$  of the summer-acclimated lobsters found the heated shelter aversive. Winter-acclimated lobsters experiencing a similar increase of  $8^\circ\text{C}$ , from  $4.3$  to  $12.3^\circ\text{C}$ , tended to stay in the heated shelter.

$3\text{--}5.5^\circ\text{C}$ ), shelters were gradually heated to  $12.3 \pm 0.3^\circ\text{C}$  (range  $10.5\text{--}16.5^\circ\text{C}$ ), representing an average temperature change of  $8.0 \pm 0.4^\circ\text{C}$ . Only two out of 30 (6%) of the winter lobsters left the heated shelter (Fig. 3B). This was not significantly different from the behavior of control winter lobsters (one of 15 left the shelter;  $\chi^2$ -test for independence,  $P > 0.05$ ), but was different from the response of summer lobsters (Fig. 3B,  $\chi^2$ -test for independence,  $P < 0.05$ ). These data suggest that lobsters find water warmer than  $23.5^\circ\text{C}$  aversive and were not responding simply to temperature increases of a particular magnitude.

#### Temperature preference

Results from the avoidance experiment described above

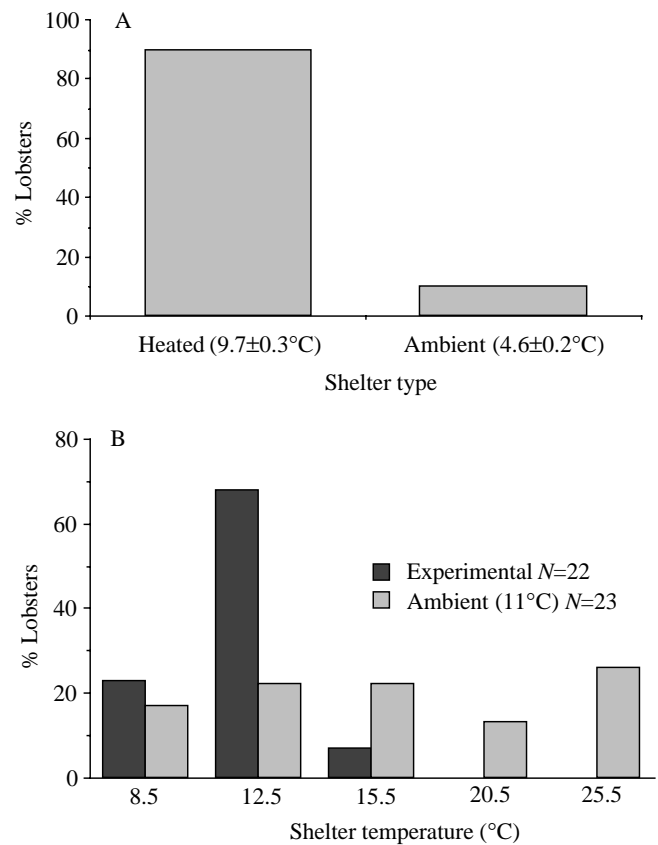
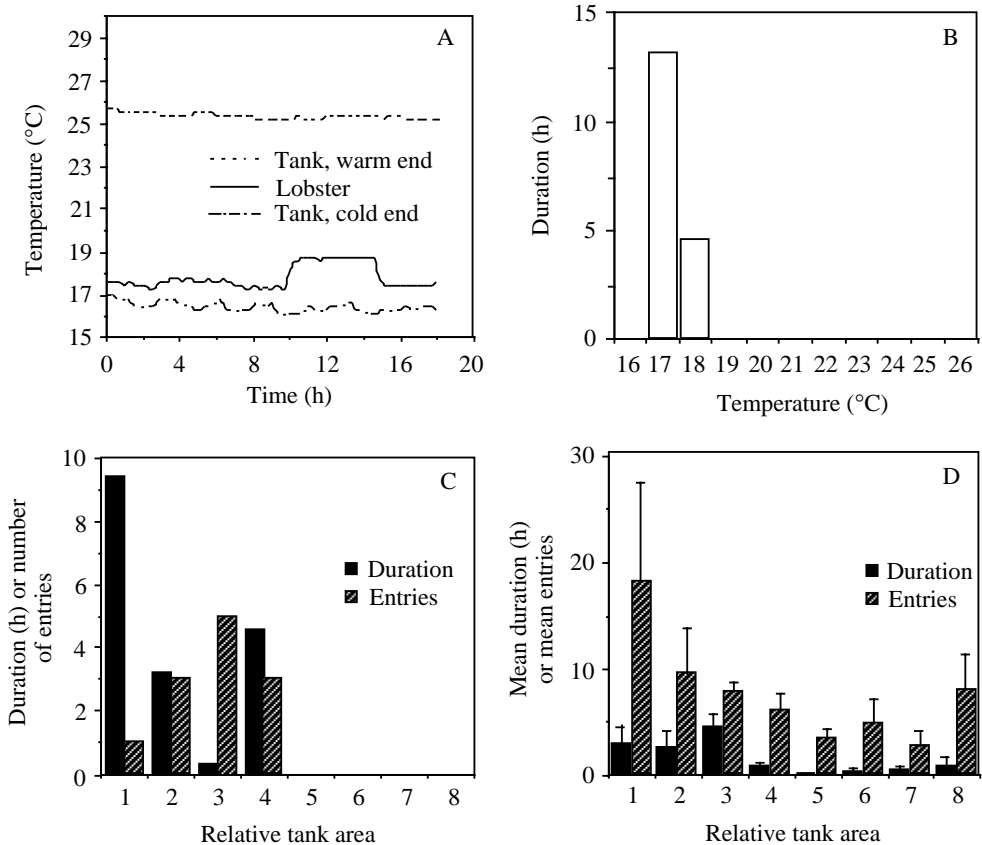


Fig. 4. (A) Temperature preference of winter-acclimated lobsters in a two-shelter-choice tank. Winter-acclimated lobsters were placed in a tank of sea water held at ambient temperature ( $1.5\text{--}6.5^\circ\text{C}$ , mean  $4.6 \pm 0.2^\circ\text{C}$ ), which contained two shelters: one at ambient temperature and one heated to  $6.5\text{--}12.5^\circ\text{C}$  (mean  $9.7 \pm 0.3^\circ\text{C}$ ). There was a significant preference for the heated shelter ( $P < 0.05$ ), with  $90\%$  of the lobsters choosing it over the shelter held at ambient temperature. (B) Temperature preference of lobsters given a choice of shelters held at five different temperatures. Animals were tested individually, and the data illustrated represents the shelter choice of animals after 24 h. Control animals were tested with all shelters at the same ambient temperature. Experiments were carried out with summer-acclimated animals (ambient water temperature approximately  $11^\circ\text{C}$ ). The lobsters preferred water slightly warmer than ambient ( $P < 0.05$ ). Control animals displayed no shelter preference ( $P > 0.05$ ).

indicate that winter-acclimated lobsters find warmer water more attractive than water at ambient temperatures. To address this question more fully, 30 winter-acclimated lobsters, 17 female and 13 male, were given a choice between two shelters; one held at ambient temperature ( $1.5\text{--}6.5^\circ\text{C}$ , mean  $4.6 \pm 0.2^\circ\text{C}$ ) and another at a warmer temperature ( $6.5\text{--}12.5^\circ\text{C}$ , mean  $9.7 \pm 0.3^\circ\text{C}$ ). The majority of lobsters chose the heated shelter ( $\chi^2$  goodness of fit,  $P < 0.05$ ) (Fig. 4A). As suggested above, this further indicates that lobsters prefer to occupy water within a certain temperature range.

In another version of this experiment, we expanded the range of temperatures available (Fig. 4B). When given a choice of five shelters held at temperatures ranging from  $8.5$  to  $25.5^\circ\text{C}$ ,

Fig. 5. Comparison of temperature-preference data obtained using dataloggers with analyses of time-lapse videos for a 92 mm carapace length female lobster. (A) Data were obtained from three dataloggers; one attached to the carapace of the lobster (middle trace) and one at each end of the tank (upper and lower traces). (B) Data from the lobster datalogger converted to give the time spent in each section of the tank. (C) Data from the video analysis giving the time spent in a given area of the tank: areas 1–8 represent a temperature gradient of approximately 16.5–25.5 °C; the total number of times a lobster moved into each area (entries) is also shown. (D) Control experiments ( $N=5$ ) in the absence of a temperature gradient and with all data obtained using time-lapse video. No area of the tank was chosen significantly more often ( $P>0.60$ ) in terms of either time spent in an area or number of entries. Values are means  $\pm$  S.E.M.



summer-acclimated lobsters ( $N=22$ , 50% each sex) consistently occupied the 12.5 °C shelter, which was just above the ambient temperature (approximately 11 °C) (Kolmogorov–Smirnov test,  $P<0.05$ ). No lobsters chose the two warmest shelters, which were just below and just above the temperature-avoidance threshold (23.5 °C) determined in our previous experiments. Under control conditions ( $N=23$ ), with no temperature difference between the shelters, the choice of shelters was not different from random (Kolmogorov–Smirnov test,  $P>0.05$ ) (Fig. 4B).

#### Behavior in a thermal gradient tank

Two methods were used to assess the thermal preference of lobsters in a thermal gradient tank. The first involved monitoring the temperature on the dorsal carapace of the lobsters using a temperature datalogger, similar to the thermistor approach utilized by Crawshaw (1974) and Kivivuori (1994). An example of the data obtained using this method is shown in Fig. 5A. To confirm the accuracy of this approach, we simultaneously recorded the position of several lobsters using both the dataloggers and time-lapse video. Both methods yielded similar results (Fig. 5B,C).

Control experiments in which there was no thermal gradient demonstrated that animals ( $N=5$ ) did not show a preference for any single section of the thermal preference tank (Fig. 5D, Kruskal–Wallis test,  $P>0.60$ ), both in terms of number of times an animal entered a given section of the tank and the amount of time spent in each section. Examination of the video tapes

revealed that there was a tendency for individual animals to occupy one section of the tank, but they frequently moved throughout the tank and investigated all the other sections. When a thermal gradient was established, the range of areas sampled narrowed considerably, and less overall exploration of the tank occurred. These observations suggest that animals avoided areas of the tank that they perceived as being either too warm or too cold.

When lobsters ( $N=9$ , four males, five females) were placed in the thermal gradient tank with a choice of temperatures ranging from approximately 12.0 to 22.0 °C, they occupied an average temperature niche of  $16.5\pm 0.4$  °C (Fig. 6A). Within the population of animals tested, a wide range of temperatures were selected, although individual lobsters maintained a relatively small thermal range of  $3.9\pm 1.1$  °C. This narrow range may have been due to attraction to a given temperature or to general avoidance of water colder than 13 °C and warmer than 19 °C. Certainly, warm-water avoidance would be a behavior consistent with the results from the studies presented above. Although there were minor differences between male and female responses, these were not statistically significant. We are currently investigating this further.

The experiments in the thermal-preference chamber were carried out over several months, and the ambient temperature varied from 12.0 to 18.0 °C (mean  $15.4\pm 0.8$  °C). This may explain the wide range of temperature preferences in the animals tested. When temperature preference was normalized

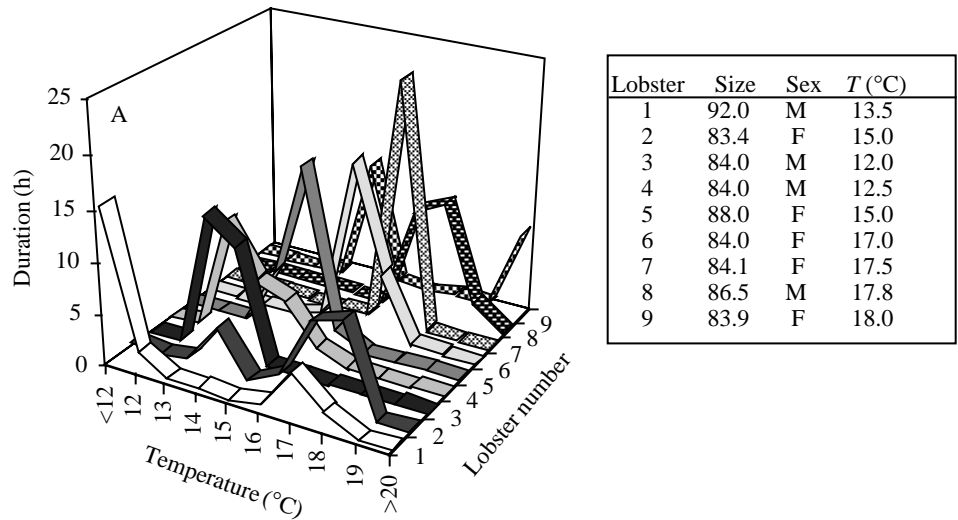
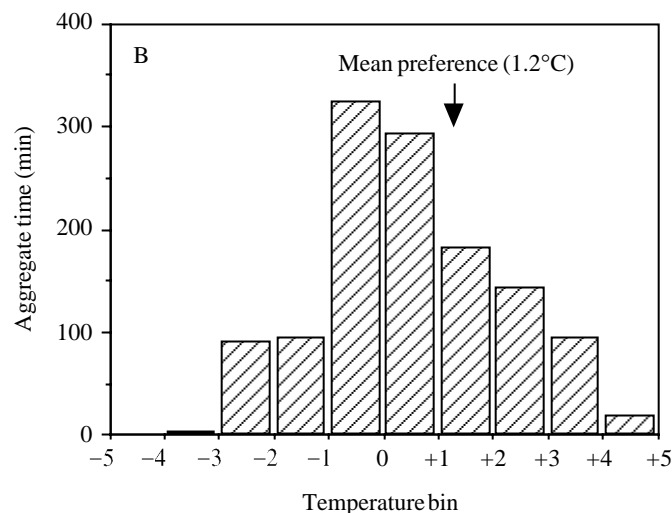


Fig. 6. (A) Preferred temperatures of lobsters in a thermal gradient. The mean preferred temperature of nine lobsters was  $16.5 \pm 0.4^\circ\text{C}$ , and they seemed to avoid water at less than  $13^\circ\text{C}$  and greater than  $19^\circ\text{C}$ . Each temperature shown on the  $x$ -axis represents a  $1^\circ\text{C}$  range of temperatures. The size (carapace lengths in mm), sex and acclimation temperature ( $T$ ) for each lobster are presented in the adjacent table. (B) Preferred temperatures standardized for acclimation temperature (preferred temperature minus acclimation temperature) of summer-acclimated lobsters. Lobsters spent most time at a temperature slightly warmer ( $1.2 \pm 0.4^\circ\text{C}$ ) than their acclimation temperature. Each bar represents the aggregate number of minutes in each preferred standardized temperature bin by the same nine lobsters shown in A. +, - indicate temperatures above and below their acclimation temperature respectively.



to ambient temperature (Fig. 6B), there was a tighter relationship and stronger evidence for behavioral thermoregulation. On average, animals spent the most time in water that was slightly ( $1.2 \pm 0.4^\circ\text{C}$ ) warmer than their acclimation temperature. In the null hypothesis of no temperature preference relative to acclimation temperature, one would predict a normal distribution of the data, i.e. approximately equal aggregate time spent above and below the acclimation temperature. To test this hypothesis, we used the  $g_1$  statistic (Sokal and Rohlf, 1969), which measures the departure from normality, or the skewness of the data. In this case,  $g_1$  was positive (0.45), indicating that the data were skewed to the right. Thus, lobsters tended to occupy temperatures higher than the temperatures to which they were acclimated. Avoidance of water more than  $4^\circ\text{C}$  warmer than ambient was also evident. Thus, in both of the experiments in which lobsters were presented with a range of temperatures, they preferred areas or shelters that were at, or slightly warmer than, the ambient water temperature and they avoided water that was significantly warmer.

## Discussion

The present study demonstrates that adult American lobsters (*Homarus americanus*) are capable of sensing differences in water temperature and using this information to thermoregulate behaviorally. In each experiment, lobsters avoided water that was warmer than approximately  $20^\circ\text{C}$  and generally preferred areas that were slightly warmer than ambient water and between  $12$  and  $18^\circ\text{C}$ . Other aquatic ectotherms are also known to occupy a thermal niche close to ambient water temperatures, and it is likely that this behavior keeps them at temperatures that are energetically favorable (Crawshaw, 1977; Magnuson *et al.* 1979; Beitinger and Fitzpatrick, 1979; Coutant, 1987; Foyle *et al.* 1989).

The influence of acclimation *versus* genetic predisposition in determining the thermal preference of ectotherms has been the subject of considerable debate. It has been proposed by Fry (1947) and others (reviewed by Reynolds and Casterlin, 1979b) that, during the first 2 h of a thermal choice experiment, animals exhibit an acute preference that is related to their acclimation temperature. They then begin gradually to

gravitate towards a final preferendum (where acclimation and preferred temperatures are equal), which is more species-specific and less influenced by acclimation temperature. Unfortunately, many of these concepts and terms, together with some of the methods employed, have been developed in conjunction with studies of fish, which may have behavioral and physiological requirements that are different from those of crustaceans.

In the present study and the only previous study of lobster behavioral thermoregulation (Reynolds and Casterlin, 1979a), data were collected for up to 2 days and, thus, the preferred temperatures exhibited should represent the final thermal preferenda of the American lobster. We obtained thermal preferendum of 16.5 °C in the thermal gradient experiment with animals acclimated to approximately 15 °C and of 12.5 °C in the heated-shelter-preference experiment using animals acclimated to approximately 11 °C. Reynolds and Casterlin (1979a) reported a final thermal preferendum of 16–17 °C, but they did not provide data concerning the acclimation temperature of their animals or the season during which the experiments were conducted. Given the range of final thermal preferenda that we found in lobsters, it is likely that acclimation temperature does play some role in their long-term behavioral thermoregulation. This conclusion is further supported by the observation of Reynolds and Casterlin (1979a) that lobsters lost their tendency to thermoregulate behaviorally after 6 days in their shuttlebox apparatus. This would be unlikely if the final preferendum were species-specific and thus not under the influence of acclimation temperature. Instead, it is possible that animals in a thermal gradient or shuttlebox apparatus experience such a range of temperatures that they re-acclimate within this broad range and no longer have a well-defined thermal preference. Studies are currently under way in our laboratory to examine more rigorously the role of acclimation in the thermoregulatory behavior of lobsters.

It has been proposed that lobster movements and migrations are strongly influenced by environmental temperature (Aiken and Waddy, 1986; Factor, 1995). It is often argued that lobsters and other crustaceans move into warmer water in order to enhance their rate of growth and reproduction (Aiken and Waddy, 1986; Factor, 1995). The data in the present study, and recent field studies with estuarine *H. americanus*, are also consistent with this view. For example, lobsters move into the Great Bay estuary in the spring/summer and towards the coast in the autumn (Vetrovs, 1990; W. H. Watson, W. H. Howell and A. Vetrovs, in preparation). Munro and Therriault (1983) noted that lobsters moved into shallow lagoon areas when the temperature increased seasonally to above 11 °C and moved out of these same areas in the autumn when temperatures decreased below 11 °C. They suggest that 'the migration of the lobster may be linked to seasonal isotherm displacements of 8–11 °C'. While estuarine habitats provide the most drastic temperature gradients in which to investigate the influence of temperature on lobster locomotion and physiology, it is likely that comparable thermally directed movements also occur in

nearshore coastal areas. In fact, Ugarte (1994) recently demonstrated that mature female lobsters moved rapidly into warmer water during the spring and, as predicted, that this accelerated the growth and development of both the ovaries and embryos.

It is unclear how lobsters integrate thermal information from their environment into a behavioral response. Despite the abundance of data indicating that crustaceans respond to differences in water temperature, little is known about how these animals sense temperature (Ache and Macmillan, 1980). It is unknown whether temperature is perceived through distinct thermoreceptors (Cook, 1984) or by modulation of a receptor for some other modality (Ache and Macmillan, 1980). Preliminary studies in our laboratory, using a bradycardia assay similar to that adapted by Offutt (1970) to investigate lobster sensitivity to sound, indicate that lobsters are capable of detecting changes in temperature of less than 2 °C (Crossin *et al.* 1995; S. H. Jury, unpublished data). Larimer (1964) also observed bradycardia responses to temperature shifts in the crayfish *Astacus astacus*. Although we have yet to identify the receptors responsible for mediating this behavior, our preliminary physiological data provide further evidence that lobsters are quite sensitive to the thermal properties of their environment.

There is a general consensus that the thermal preferences of ectothermic animals represent the temperatures at which their metabolism is most efficient (Beitinger and Fitzpatrick, 1979). In a sense, this may be the 'thermal neutral zone' of ectotherms, where small changes in temperature have little influence on metabolic rate. Evidence in support of this hypothesis comes primarily from studies in fish, which show that growth rate is optimal at their preferred temperature (Magnuson *et al.* 1979; Beitinger and Fitzpatrick, 1979) and that their metabolic rate increases when temperatures are shifted away from ambient (Claireaux *et al.* 1995). There is also evidence supporting this hypothesis in crustaceans. The crayfish *Astacus astacus* rights itself most quickly at temperatures between 15 and 20 °C (Kivivuori, 1980), and maximal survival of the crayfish *Orconectes rusticus* occurs at its preferred temperature of 22 °C (Mundahl and Benton, 1990). In the lobster *Homarus americanus*, it has been reported that maximum growth of juveniles and adults occurs between 15 and 20 °C (J. T. Hughes, personal communication, cited in Reynolds and Casterlin, 1979b), and little molting, growth, locomotion or feeding takes place below 10 °C (McLeese and Wilder, 1958; Aiken and Waddy, 1986; Factor, 1995). Furthermore, locomotion appears to be independent of temperature between 15 and 20 °C (McLeese and Wilder, 1958; Reynolds and Casterlin, 1979a). Thus, it is possible that behavioral thermoregulation in lobsters could serve to optimize their growth, time to maturation and/or reproductive potential. The further elucidation of these relationships remains an exciting area of future research owing to their strong influence on the behavior of these economically important animals.

There is a substantial body of literature demonstrating that fish species occupy thermal niches in nature that coincide with



the thermal preferenda they exhibit in the laboratory (e.g. Beitinger and Fitzpatrick, 1979). Thermal cues may also initiate certain behaviors in the field that are related only indirectly to preference. For example, in the American eel *Anguilla rostrata*, downstream migration appears to be initiated as temperature decreases below the thermal preferendum (Haro, 1991). If we extend these concepts and the data presented in the present study to lobsters in the field, they would be expected to move towards areas that are warmer but to stop when they reached extreme temperatures, which approach lethal limits (McLeese, 1956). This type of thermally directed activity could manifest itself as inshore migrations in the summer and offshore movements in the autumn, as coastal waters cool more rapidly than offshore water (Ennis, 1984; Cooper and Uzman, 1971). In addition, at the southern end of the geographic range of lobsters or within certain habitats (e.g. estuaries), acclimation to warmer temperatures may also shift an individual's thermal preferendum to a warmer temperature, and it may move into warmer waters than predicted. This type of behavior was exhibited by some of the lobsters (obtained commercially in New Jersey) in the experiments of Reynolds and Casterlin (1979a). At the end of the 12 day experimental period, some of the 10 lobsters had thermal preferences between 26 and 29 °C. While our laboratory data may help to explain some of the behavior patterns observed in the field, the influence of temperature relative to other abiotic stimuli, such as salinity, turbidity, shelter availability, etc., has yet to be adequately explored. Thus, while temperature has a profound influence on lobster behavior in the laboratory, under normal 'multivariate' circumstances, many other factors may override a natural tendency to inhabit areas that fall within their fundamental thermal niche and may ultimately determine their distribution.

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### References

- ACHE, B. W. AND MACMILLAN, D. L. (1980). Neurobiology. In *The Biology and Management of Lobsters*, vol. 1, *Physiology and*

- Behavior* (ed. J. S. Cobb and B. F. Phillips), pp. 165–213. New York: Academic Press.
- AIKEN, D. E. (1977). Molting and growth in decapod crustaceans with particular reference to the lobster *Homarus americanus*. *Div. Fish. Oceanogr. Circ. (Aust. CSIRO)* **7**, 41–73.
- AIKEN, D. E. (1980). Molting and growth. In *The Biology and Management of Lobsters*, vol. 1, *Physiology and Behavior* (ed. J. S. Cobb and B. F. Phillips), pp. 91–162. New York: Academic Press.
- AIKEN, D. E. AND WADDY, S. L. (1986). Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. *Can. J. Fish. aquat. Sci.* **43**, 2258–2270.
- BEITINGER, T. L. AND FITZPATRICK, L. C. (1979). Physiological and ecological correlates of preferred temperature in fish. *Am. Zool.* **19**, 319–329.
- BOUDREAU, B., SIMARD, Y. AND BOURGET, E. (1992). Influence of a thermocline on a vertical distribution and settlement of post-larvae of the American lobster *Homarus americanus* Milne-Edwards. *J. exp. mar. Biol. Ecol.* **162**, 35–49.
- CAMPBELL, A., NOAKES, D. J. AND ELNER, R. W. (1991). Temperature and lobster, *Homarus americanus*, yield relationships. *Can. J. Fish. aquat. Sci.* **48**, 2073–2082.
- CLAIREAUX, G., WEBBER, D. M., KERR, S. R. AND BOUTILIER, R. G. (1995). Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating temperature conditions. *J. exp. Biol.* **198**, 49–60.
- COOK, D. P. (1984). Chemoreception, thermoreception and osmoreception in three marine decapod crustaceans. PhD dissertation. University of CA – Santa Barbara. 140pp.
- COOPER, R. A. AND UZMANN, J. R. (1971). Migrations and growth of deep-sea lobsters, *Homarus americanus*. *Science* **171**, 288–290.
- COUTANT, C. C. (1987). Thermal preference: when does an asset become a liability? *Env. Biol. Fishes* **18**, 161–172.
- CRAWSHAW, L. I. (1974). Temperature selection and activity in the crayfish, *Orconectes immunis*. *J. comp. Physiol.* **95**, 315–322.
- CRAWSHAW, L. I. (1977). Physiological and behavioral reactions of fishes to temperature change. *J. Fish. Res. Bd Can.* **34**, 730–736.
- CROSSIN, G., WATSON III, W. H. AND HOWELL, W. H. (1995). The effects of temperature on lobster (*Homarus americanus*) behavior. *Abstracts of the 1995 Benthic Ecology Meetings*. Rutgers University, New Brunswick, NJ.
- DRACH, P. AND TCHERNIGOVITZEFF, C. (1967). Sur le methode de determination des stades d'intermue et son application generale aux Crustaces. *Vie Milieu (Ser. A. Biol. Mar.)* **18**, 595–610.
- ENNIS, G. P. (1984). Small-scale seasonal movements of the American lobster *Homarus americanus*. *Trans. Am. Fish. Soc.* **113**, 336–338.
- ESPINA, S., HERRERA, F. D. AND BUCKLE, L. F. (1993). Preferred and avoided temperatures in the crawfish, *Procambarus clarkii*. *J. therm. Biol.* **18**, 35–39.
- FACTOR, J. R. 1995. (ed.) *Biology of the Lobster Homarus americanus*. Boston: Academic Press.
- FLOWERS, J. M. AND SAILA, S. B. (1972). An analysis of temperature effects on the inshore lobster fishery. *J. Fish. Res. Bd Can.* **29**, 1221–1225.
- FOYLE, T. P., O'DOR, R. K. AND ELNER, R. W. (1989). Energetically defining the thermal limits of the snow crab. *J. exp. Biol.* **145**, 371–393.
- FRY, F. E. J. (1947). Effects of the environment on animal activity. *University of Toronto Studies Biology Series Publications* **55**, 1–62.
- HARO, A. J. (1991). Thermal preferenda and behavior of Atlantic eels (genus *Anguilla*) in relation to their spawning migration. *Env. Biol. Fish.* **31**, 171–184.

- HERRNKIND, W. F. (1980). Spiny lobsters: Patterns of movement. In *The Biology and Management of Lobsters*, vol. 1, *Physiology and Behavior* (ed. J. S. Cobb and B. F. Phillips), pp. 349–407. New York: Academic Press.
- HUDON, C. (1994). Large-scale analysis of Atlantic Nova Scotia American lobster (*Homarus americanus*) landings with respect to habitat, temperature and wind conditions. *Can. J. Fish. aquat. Sci.* **51**, 1308–1321.
- JURY, S., KINNISON, M. T., HOWELL, W. H. AND WATSON III, W. H. (1994). The behavior of lobsters in response to reduced salinity. *J. exp. mar. Biol. Ecol.* **180**, 23–37.
- KANCIRUK, P. AND HERRNKIND, W. F. (1978). Mass migrations of spiny lobsters, *Panulirus argus* (Crustacea: Palinuridae): Behavior and environmental correlates. *Bull. mar. Sci.* **28**, 601–623.
- KIVIVUORI, L. A. (1980). Effects of temperature and temperature acclimation of the motor and neural functions in the crayfish *Astacus astacus* L. *Comp. Biochem. Physiol.* **65A**, 297–304.
- KIVIVUORI, L. A. (1994). Temperature selection behaviour of cold- and warm-acclimated crayfish (*Astacus astacus*). *J. therm. Biol.* **19**, 291–297.
- LARIMER, J. L. (1964). Sensory-induced modifications of ventilation and heart rate in crayfish. *Comp. Biochem. Physiol.* **12**, 25–36.
- MAGNUSON, J. J., CROWDER, L. B. AND MEDVICK, P. A. (1979). Temperature as an ecological resource. *Am. Zool.* **19**, 331–343.
- MCLEESE, D. W. (1956). Effects of temperature, salinity and oxygen on the survival of the American lobster. *J. Fish. Res. Bd Can.* **13**, 247–272.
- MCLEESE, D. W. AND WILDER, D. G. (1958). The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. *J. Fish. Res. Bd Can.* **15**, 1345–1354.
- MUNDAHL, N. D. AND BENTON, M. J. (1990). Aspects of thermal ecology of the rusty crayfish *Orconectes rusticus* (Girard). *Oecologia* **82**, 210–216.
- MUNRO, J. AND THERRIAL, J. C. (1983). Migrations saisonnières du homard (*Homarus americanus*) entre la côte et les lagunes des Îles-de-la-Madeleine. *Can. J. Fish. aquat. Sci.* **40**, 905–918.
- OFFUTT, G. C. (1970). Acoustic stimulus perception by the American lobster, *Homarus americanus* (Decapoda). *Experientia* **26**, 1276–1278.
- REBACH, S. (1974). Burying behavior in relation to substrate and temperature in the hermit crab, *Paragus longicarpus*. *Ecology* **55**, 195–198.
- REYNOLDS, W. W. AND CASTERLIN, M. E. (1979a). Behavioral thermoregulation and activity in *Homarus americanus*. *Comp. Biochem. Physiol.* **64A**, 25–28.
- REYNOLDS, W. W. AND CASTERLIN, M. E. (1979b). Behavioral thermoregulation and the ‘final Preferendum’ paradigm. *Am. Zool.* **19**, 211–224.
- SAILA, S. B. AND FLOWERS, J. M. (1968). Movements and behavior of berried female lobsters displaced from shore areas to Narragansett Bay, Rhode Island. *J. Cons. Perm. int. Expl. Mer.* **31**, 342–351.
- SOKAL, R. R. AND ROHLF, F. J. (1969). *Biometry*. San Francisco: W. H. Freeman and Co., pp. 112–125.
- UGARTE, R. A. (1994). Temperature and distribution of mature female lobsters (*Homarus americanus*, Milne Edwards) off Casco, N.S. PhD thesis. Dalhousie University, Nova Scotia.
- VETROVS, A. (1990). The distribution of lobsters (*Homarus americanus*) in the Great Bay Estuary. MS thesis. University of New Hampshire, Durham, NH, USA.
- WADDY, S. L., AIKEN, D. E. AND DEKLEIJN, D. P. V. (1995). Control of growth and reproduction. In *Biology of the Lobster Homarus americanus* (ed. J. P. Factor), pp. 217–259. Boston: Academic Press.
- WARNER, W. (1976). Winter ‘drudging’ lifts crabs from their beds. *Smithsonian* **6**, 82–89.