Behavioral and physiological responses of the lobster, Homarus americanus, to temperature: A new synthesis

Steven Harold Jury

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BEHAVIORAL AND PHYSIOLOGICAL RESPONSES OF THE LOBSTER, HOMARUS AMERICANUS, TO TEMPERATURE: A NEW SYNTHESIS

BY

Steven H. Jury
BA University of New Hampshire, 1988
MS University of Massachusetts, 1992

DISSERTATION

Submitted to the University of New Hampshire in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy in

Zoology

May, 1999
This dissertation has been examined and approved.

Dissertation Director, Winsor Watson III
Professor

W. Hunting Howell, Professor

John Sasner, Professor

Joseph Ayers, Professor

Richard Wahle, Associate Professor

5/5/99
Date
DEDICATION

I grew up in Western Massachusetts and when I was about 10 years old my father came home with some lobsters for dinner. Being only ten, I asked him if we could let them go. He said, "O.K. but where should we release them". I asked him if we could let them go in the lake and he explained that we couldn't do that because these animals were from the ocean and that would kill them. I thought about it and thought about it...my parents ended up having the lobsters for dinner...and I thought about it some more. Finally I realized that I wanted to understand WHY I couldn't release the lobsters in the lake. Now it's 20 years later and I know why.

So, for introducing to me to marine biology (whether they knew it or not) and for always supporting me in whatever I wanted to do, I dedicate this dissertation to my parents Jack and Renee Jury.
ACKNOWLEDGEMENTS

My love and thanks go to my wife, Heather, for her support, encouragement and keeping me grounded in reality. Thanks also for staying married to me even after going through the graduate school process.

Many thanks to my committee who accepted my multidisciplinary approach and helped me to hone the many facets of this project into a successful product. In particular I'd like to thank Win Watson and Hunt Howell who have provided me with an unparalleled atmosphere in both of their labs in which to conduct research and explore my many interests. Thanks also to John Sasner for his astute grasp of physiology, Rick Wahle for imparting his insight on lobster biology, and Joe Ayers for being one of the finest techno-biologists I've ever known.

Thanks to Noel Carlson at the UNH Coastal Marine Lab and Deb Lamson and Rich Langan at the UNH Jackson Estuarine Lab for housing animals, diving, and logistic support. I would also like to thank Mark Monaco, Moe Nelson, John Field, Steve Brown, Steve Stone and Tony Lowery of NOAA's Strategic Environmental Assessment Division for guidance into the world of ecological modeling and large scale fishery management. Many thanks to Bob Champlain and the UNH machine shop for multiple construction projects and putting up with the engineering skills of a biologist. Finally I'd like to thank the many NH lobstermen who supported field data collection and supplied lobsters.

Special thanks also go to the many graduate and undergraduate students who made this research possible through their hard work, brainstorming, or logistic support. These people include: Chris Dufort, Dan O'Grady, Paul Barcell, Christina Rockel, Tara Nye, Stacey Brown, Sue Schreiber, Sue Krull and Torrey Tyrell. Thanks to Colin McGuire and Dan Reves who made many of the drawings. Also thanks to Steve Wakefield for constructing the final version of the thermal preference chamber and all the
members of the SOLE Ocean Projects group for working out some of the methods for running lobsters with HOBOs attached. Finally, the behavioral thermoregulation experiments would not have been possible without the collaboration of Glen Crossin and Saud Al-Ayoub.

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ABSTRACT

BEHAVIORAL AND PHYSIOLOGICAL RESPONSES OF THE LOBSTER, *HOMARUS AMERICANUS*, TO TEMPERATURE: A NEW SYNTHESIS

by

Steven H. Jury

University of New Hampshire, May, 1999

Temperature has a pervasive influence on lobster behavior, physiology and ecology and affects their subsequent distribution in thermally variable habitats such as estuaries and coastal areas. A multidisciplinary approach, including field and laboratory studies, was used to show: 1) that lobsters sense temperature with warm and cool thresholds as small as 0.1-0.2 °C; 2) the relationship between temperature and activity is not linear, but instead switches between a high activity level in warmer months (10-20°C) and a lower level in colder months (<10°C), with transition periods in the spring and fall; 3) Parallel studies in the lab and field show that daily levels of activity are not greatly influenced by small temperature variations (i.e. tidally induced changes of 1-4°C), but activity levels are significantly higher in the field (249±55.1 m/d) than in the laboratory (88±12.0 m/d); 4) lobsters prefer a narrow range of temperatures over others available in a thermal gradient and avoid temperatures >23.5±0.4°C, suggesting that they behaviorally thermoregulate. While this preferred temperature shifts seasonally,
the final preferred temperature (FPT) remains at 15.9°C. Finally, at certain
temperatures, males prefer warmer temperatures than females.

The degree of thermosensitivity and responsiveness observed in these studies
appears sufficient to guide thermally directed movements in the field. These thermally-
influenced movements may ultimately contribute to patterns of distribution and
abundance, and affect local catch rates, in thermally variable areas (e.g., male biased
sex ratios in estuaries). A spatially explicit model incorporating the behaviorally
determined responses to temperature described above, along with known behavioral
responses to salinity, shows a significant correlation with estimates of field-derived
population distributions from coastal NH and the Great Bay Estuary. Thus while
temperature is not the only factor influencing seasonal movements in this system, it
appears to be one of the most important factors controlling the spatial and temporal
patterns of lobster distribution in estuaries, and perhaps other habitats as well.
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INTRODUCTION

Temperature may be one of the most studied, and pervasive, influences on the behavior, physiology and ecology of *Homarus americanus* (Cobb and Phillips 1980, Factor 1995). However, our understanding of how lobsters sense and respond to temperature is limited (MacKenzie and Moring 1985, Aiken and Waddy 1986, Factor 1995). This study used an integrated, multidisciplinary approach (Cobb 1995) to determine the response of lobsters to temperature and relate these to the effect of temperature on estuarine and coastal populations. Due to the high variability of temperature, salinity, etc. in estuaries, such as the Great Bay estuary of NH (Fig. 1.2), these habitats have proven to be useful model systems for studying the effects of environmental variability on lobster behavior and ecology (Vetrovs 1990, Howell et al. submitted, Watson et al. in press).

Based upon previous research, changes in temperature present various costs and benefits to lobsters and other decapods. Increased temperatures below thermal maxima may provide various benefits including: enhanced molting and growth; faster development; increased or more successful reproduction; or increased food availability or quality (Aiken and Waddy 1986, Hines et al. 1987, Waddy et al. 1995). Costs of high temperatures may include increased metabolic rate and correspondingly increased consumption rate; increased susceptibility to predation due to increased foraging; and potential harm to gametes, eggs, or larvae, etc. because their tolerance to temperature seems to differ from adults. For the purposes of hypotheses testing, we can assume that lobsters optimize their behavior to take advantage of various temperatures to increase their fitness. Thus if lobsters are sufficiently sensitive to temperature would prefer certain temperatures over others either spatially (e.g., along an estuarine gradient) or temporally (e.g., seasonally).
A literature review of the effects of temperature on lobster life history is presented below. In addition, because lobsters from Great Bay Estuary, NH are used in several subsequent chapters as a model for lobsters experiencing temporal and spatial thermal variability, the present state of knowledge on this system is also reviewed.

Review of the Effects of Temperature on Lobsters

Behavioral Effects

The spatial and temporal distribution of lobsters is strongly influenced by their sensitivity and/or responsiveness to temperature. "Water temperature appears to be the most important single determinant of migration, whereas food sources and bottom conditions control wandering behavior (Haakonsen and Anoruo 1994)". In a large scale analysis of Nova Scotian lobster landings it was found that abundance was not limited by habitat availability but instead was due to the thermal characteristics of the region (Hudon 1994, Koeller 1999). Seasonal movements of lobsters have been documented on many occasions. For example, lobsters may move to shallower, inshore waters to gain the benefits of warmer coastal temperatures in the spring and/or summer and move back offshore in the fall (Saila and Flowers 1968, Cooper and Uzmann 1971, Pezzack and Duggan 1986, Karnofsky 1989a, Haakonsen and Anoruo 1994). This movement may be initiated at certain temperatures which have been postulated to be from 8-14°C (Ennis 1984, Aiken and Waddy 1986) or 10-17°C (Cooper and Uzmann 1971, Ugarte 1994). Fall migrations of spiny lobsters (Panulirus argus) (Kanciruk and Herrnkind 1978) also appear to be triggered by large drops in temperature, coincident with fall storms. However, while it is generally accepted that locomotory activity is temperature dependent (McLeese and Wilder 1958, Herrnkind 1980, Reynolds and Casterlin 1979) detailed information about the influence of temperature on lobster locomotion and behavioral
thermoregulatory ability is scarce (Ache and MacMillan 1980, Factor 1995). Nonetheless, "...an organism that undertakes seasonal return migrations of greater than 50 km, and that exhibits localized homing behavior probably relies on well-developed sensory cues to govern movement patterns and seasonal habitat utilization (Lawton and Lavalli 1995)." It follows that if temperature is directly or indirectly related to seasonal movement it may be the sensory cue used to guide movements. In addition, movements that ultimately 'optimize' temperature exposure could involve horizontal (onshore offshore, estuaries) and/or vertical movements (deep to shallow) depending on location and timing of initiation (Haakonsen and Anoruo 1994).

A wide range of aquatic poikilotherms also occupy "thermal niches" and exhibit thermoregulatory behavior (see Magnuson et al. 1979, Prosser 1991). In these instances temperature may be both a proximate and an ultimate factor. Genetically determined thermal preferences and the associated sensory mechanisms may ultimately help to define a species niche in space and time, and thus may be adaptively selected traits (Reynolds 1977, Johnson and Kelsch 1998). In addition, some preferences may have a learned component as well, leading to behavioral plasticity which is manifest in an adaptive response. There is experimental evidence that adult lobsters in a shuttlebox apparatus have a thermal preference of ≈16°C (range of 15-20°C)(Reynolds and Casterlin 1979). These data and information from several ecological studies suggest that lobsters behaviorally thermoregulate but the mechanism and relationships remain unclear.

**Effects on Catch**

Because *H. americanus* is fished commercially, a great deal of attention has been placed on determining factors which may predict future catch. Temperature has been suggested to affect catch rates through: 1) fishery recruitment of adults via growth effects (i.e., molting into legal size class) (Fogarty 1988, Lawton and Lavalli 1995, Campbell et al. 1991); 2) larval recruitment via time lagged reproductive effects from increased
population or increased survivability of larvae; 3) increased catchability at higher temperatures due to increased activity and subsequently increased probability to enter traps (McLeese and Wilder 1958, Saila and Flowers 1972, Fogarty 1988, Pezzack 1992). Temperature may increase the tendency of lobsters to enter traps because their metabolic rate approximately doubles with every 10°C increase in temperature; causing them to be more active and require more food (McLeese and Wilder 1958, Richards et al. 1983, Auster 1985, Miller 1990).

Lobster catch has been correlated to temperature (Cooper and Uzmann 1971, Fogarty 1988, Campbell et al. 1991) in some studies but this relationship appears to depend on spatial and temporal scale, and may also be a function of changes in effort that may correlate with temperature changes (e.g. weather, currents, etc.) (Koeller 1999). Studies in the Great Bay estuary also suggest that temperature is correlated with catch (Figs. 1.4 & 1.5) but there is high variability in this relationship (Watson et al., in press).

There is also some inconsistency in the literature about the relationship between temperature and locomotory activity, and subsequent effects on catch, because while the inshore fishery is most productive at temperatures between 10-20°C in many areas of the U.S., McLeese and Wilder (1958) suggest that activity is temperature-independent within this range. Thus while temperature appears to influence catch at some temperatures, it may not be influencing catch at all temperatures. In addition, temperature induced movements may compound the effect of temperature on catch as distribution of lobsters are shifted via immigration and emigration to certain habitats. Thus, the relationship between temperature, activity, movement and catch, is presently unclear.

Effects on Reproduction and Growth

The ultimate causes for temperature preference in lobsters are most likely related to the effect of temperature on growth and reproduction. "Temperature is the most pervasive influence on lobster growth (Waddy et al. 1995)" and this is also true for several aspects
of lobster reproduction. Growth and metabolism increase between 8-25°C and lobsters grow faster, mature earlier, and mature at a smaller size in warmer areas of their range compared to colder areas (Waddy and Aiken 1995). However, maturing earlier can obscure patterns of growth from field data because maturation has a negative effect on growth as more energy is put into reproductive vs. somatic growth. This is particularly true of mature females, but males grow faster than females at all sizes. Summer temperature directly correlates with geographic variation in size at maturity which can vary from 55 mm CL in Long Island Sound to 110 in Bay of Fundy. This effect appears to be environmental and not genetic because juveniles raised at the same temperature mature at the same time even if they are from parental stocks with different sizes at maturity (Waddy and Aiken 1995).

Temperature similarly affects the growth of larvae in the lab with weight increase per molt, time to molt, and survival of larvae being greatest at 15-18°C (MacKenzie 1988) vs. higher or lower temps. It is unclear if this relationship is true in the field but survivorship of larvae is likely to depend on the thermal history of eggs because lipid conversion efficiency of embryos and thus remaining yolk is temperature dependent (Sasaki et al. 1986). The effect of thermal history may also be very important to the survival and growth of other life history stages.

Spawning generally occurs from June to October, but spawning is earlier in warmer temperatures and thus is dependent upon location and intra-/interannual variability in temperature. In the field hatching (based upon catches of stage I larvae) extends from 9-12.7°C in the southern gulf of Maine to 7.9-13.9°C farther north (Ennis 1995). Peak hatching occurs around 12.5°C, but there is a great amount of variability in the literature. This may be related to the initiation of hatching being determined by season or photoperiod length (and thus occurring at a higher temperature in the south vs. the north) while the duration and synchrony of the hatching period is determined by temperature (and thus warmer areas show a smaller range of temperatures for hatching than cooler
areas). In one lab study hatching occurred from 15-20°C, and was most intense at 20°C (Hughes and Mathesein 1962)

Reproductive cycles, and ultimate reproductive success, appear to be regulated primarily by temperature and season and secondarily by photoperiod (Waddy et al. 1995). However, the relationship between temperature and reproductive physiology and behavior is complex. For example, while there is no ovarian development at <5°C, an extended period below 6-8°C and a subsequent increase to >10°C is necessary to induce ovarian maturation, initiate spawning and synchronize molting and reproductive cycles. This can lead to situations where if it is too warm in the winter there is an increased percentage of molting the following summer, but little spawning. Alternately, if it is too cold in the summer then ovarian development may be aborted and molting delayed. Thus, the effect of temperature and season is very important to both reproduction and growth.

Temperature profoundly affects development and reproductive fitness as well. Embryogenesis lasts 9-12 months in the field but only 3-4 months in lab at 20-22°C. However, at temperatures >20°C there may be adverse effects on egg, sperm and larvae including decreased egg attachment, reduction in viable sperm, and subsequent decreased reproductive success (Waddy et al. 1995). Consistently low temperatures (<5°C) may also decrease reproductive success by decreasing ovarian maturation, growth and mating behavior.

There are distinct sexual differences in how temperature effects reproductive success. For example, onset of maturity is temperature dependent for males, but there are no seasonal differences in sperm production or mating capacity once maturity is reached. However, physiological maturity in males is very different than functional maturity and is also dependent upon the reproductive state of females. Functional maturity is probably related to temperature because of the importance of size in social behavior and the subsequent importance of dominance on reproductive success (Atema and Voigt 1995). Female size may also be proportional to reproductive success because larger abdomens
carry more eggs and there may be some competition for dominant males among females. However, focusing energy into egg production and viability (i.e. reproductive growth) is probably more important for females. In addition, ovigerous females move sooner, deeper, and farther in fall as temperatures decrease compared to immature females or males (Lawton and Lavalli 1995). This suggests a link with egg and larval production. Thus while temperature does not seem to be as important in regulating the reproductive cycle of males as it is for females, it does appear to influence the reproductive success of both sexes.

**Thermosensitivity**

Although several of the aforementioned studies (e.g., Reynolds and Casterlin 1979, Boudreau et al. 1992) infer that lobsters and other decapods can sense changes in temperature, thermoreception *per se* is virtually unstudied in any crustacean (Ache and McMillan 1980). There may be distinct thermoreceptors as in some invertebrates (Prosser and Nelson 1981) or thermal sensation may be transduced by a receptor for some other modality. Integration within the central nervous system may play an important role in ultimate behavioral response. Nonetheless, the location and mechanism of thermoreception remain unknown in lobsters.

Transduction in thermoreceptors in other species has been suggested to be due to temperature dependencies of: 1) ion pumps (Ehn and Tichy 1996); 2) conductance of channels (Ehn and Tichy 1996, Komatsu et al. 1996); and/or 3) membrane fluidity (MacIver and Roth 1982, Komatsu et al. 1996). However, the role of nonspecific neuronal effects of increasing temperature on thermoreception are unclear. These effects include resting membrane potential depolarization, increased membrane resistance, and increased action or synaptic potential amplitude (MacIver and Roth 1982, Prosser and Nelson 1984, Kuramoto and Tani 1994). In addition, neurons in some invertebrate have been shown to be warm-sensitive while others are cold-sensitive (Prosser and Nelson
1981, Miles 1985, Ehn and Tichy 1996). It is also unclear how, or if, information such as magnitude, rate of change, direction of change, etc. is important in signal integration. Finally, modulation of excitability or transducer gain to compensate for changing environmental temperatures may be an important mechanism evolved by poikilotherms to control behavioral responses to variable conditions (Paztor 1989).

The relationship between temperature and neural activity is complex and seems to vary by species. Several examples illustrate the intriguing but incomplete state of knowledge for decapods. Kerkut and Taylor (1956) documented that decreasing temperature (25-15°C) caused an initial increase in firing rate of the isolated thoracic and abdominal ganglia of the crayfish but a subsequent decrease below baseline. Upon warming (15-25°C) firing rate transiently decreased and subsequently increased above the baseline rate at 15°C. In another study on the spiny lobster, Panulirus japonicus, it was found that ligamental nerves increased their firing in response to cold stimulation (Kuramoto and Tani 1994). P. argus antennular chemoreceptors are sensitive to temperature increases of 1-2°C (Ache and McMillan 1980). A study of the thermal sensitivity of the dactyl receptors of Cancer antennarius, C. anthonyi, and P. interruptus strongly suggests that the animals possess a thermal receptor system capable of integrating temperature information for use in thermally-cued behavior (Cook 1984). Thus, depending on the species, thermoreception may occur internally, externally, or in highly localized areas (Prosser and Nelson 1981) and even though the relationship between temperature and neural activity is not clear, it is highly pervasive.

**Physiological effects of temperature**

The lethal levels of temperature, salinity, and oxygen tension for lobsters (acclimated to various combinations of these factors) have been determined in terms of LD50 values at 48 hrs (McLeese 1956). Acclimation to temperature was considered complete after 24 days and no differences were found in temperature tolerance between
lobsters of different size, fed vs. starved, or those from different locations. Under experimental acclimation conditions in the laboratory of 5°C, 20 ppt salinity, and 2.9 mg/l oxygen, lobsters may have an upper lethal temperature as low as 20.6°C, but the lethal temperature is, on average, greater than 27°C (McLeese 1956). McLeese (1956) also found that as the salinity decreased to less than 20 ppt, tolerance for high temperature was depressed below 20.6°C. Animals acclimated to 17 and 27.5°C had lower lethal temperature estimates of 1.8 and 5°C. Great Bay temperatures reach this low in the winter but it is unknown what percentage of the population overwinters there. In addition, these upper and lower lethal temperatures were determined at 48 hrs, and it is probable that length of exposure, magnitude of change and rate of change may affect their tolerance to temperature.

McLeese’s (1956) values defining the fundamental thermal niche are conservative because animals will probably show behavioral avoidance before temperatures reach these lethal levels and thus their realized thermal niche will be narrower. For example, in the upper Great Bay estuary in the summer the long term mean temperatures are approximately 20°C (Fig. I.3). These temperatures are not necessarily lethal but they are probably aversive, particularly if they are combined with low salinities or tidal shifts in temperatures that may reach lethal levels of >25°C. Indeed, preliminary data show that tagged animals do move out of the upper estuary late in the summer (Watson et al., in press). Similarly, adults lobsters do not enter the upper regions of Narragansett Bay due to high temperatures (Wahle 1993). Recruitment is also limited in the upper regions of estuaries but it is presently unclear how this relates to temperature (Wahle 1993).

Temperature is one of the most important factors influencing the metabolic rate of lobsters (McLeese 1964, Mercaldo-Allen and Thurberg 1987) and other decapods (Fig. I.1). *H. americanus* generally shows a Q_{10} of approximately 2 over their thermal range (0-25°C) (McLeese 1964, Mercaldo-Allen and Thurberg 1987). However, the maximum locomotory capability of *H. americanus* only increases between 2-10°C and 20-25°C,
while it is fairly constant between 10-20°C (McLeese and Wilder 1958, Fig. I.1). Why there is an uncoupling between the effect of temperature on metabolic rate vs locomotion is unknown. A study by Gutermuth and Armstrong (1989) found that although smaller Dungeness crabs increase their oxygen consumption from 6-14°C, the rate does not change from 14-18°C; and the rate for larger crabs is more stable at the lower temperatures (6-14°C). This finding may reflect an adaptation for small crabs which must tolerate higher temperatures in the estuarine intertidal flats; whereas, the larger crabs are emigrating to colder coastal waters as they mature. This may be similar to how lobsters respond to temperature. In another example, *Carcinus maenas* osmoregulates more effectively at 10°C, representative of winter temperatures, than at 18°C, representative of summer temperatures, but crabs acclimated to 10°C are more active in response to rapid decreases in salinity than those acclimated at 18°C. This suggests that while osmoregulation is more demanding at 18°C the animal does not avoid low salinity as readily as at 10°C. Complex relationships such as this suggest that differences in avoidance responses depending upon the season may reflect the seasonally different benefits of the same habitat (Taylor et al. 1977).
Figure 1.1. Relationship between temperature and $O_2$ consumption, ventilation, and locomotion. While the metabolic rate (left panel) of $H. americanus$ increases linearly from 0 to 25°C, locomotory activity (right panel) shows little change between 10-20°C even though the rate of change <10 or >20°C is similar to the change in metabolic rate. Data are from McLeese (1964, $O_2$ consumption.), Mercaldo-Allen & Thurberg (1987, ventilation), and McLeese & Wilder (1958, locomotion).
Models utilizing temperature

Temperature is often incorporated as the key abiotic variable into population dynamic, abundance, production and forecast models for decapod crustaceans (see Saila and Marchesseault 1980, Campbell et al. 1991, and Fogarty 1995 for reviews). Most of these models estimate fisheries parameters and utilize temperature data over very large spatial and temporal scales (e.g., regional yearly sea surface temperature). However, while spatially explicit models of movement and/or habitat selection on smaller spatial and temporal scales exist for several terrestrial vertebrates (Weins et al. 1993, Lima and Zollner 1996), few have been documented for any marine invertebrate (Reyes et al. 1994). This type of model is based on the information available to an animal as it moves through the environment and how this information is used to select a habitat (Weins et al. 1993, Dusenberry 1996). This type of modeling spans the different spatial scales typical of behavioral and ecological studies (Lima and Zollner 1996). There has also been interest in this type of model from resource managers to provide a mechanistic understanding of the interaction of individuals with their environmental "landscape" based upon available information (Brown et al. submitted). A goal of the present study is to use this approach to mechanistically relate behavioral and physiological data collected in the laboratory to distribution and abundances observed in the field.

Overview of Great Bay Estuarine Lobsters

Lobsters are found from Newfoundland to North Carolina, in habitats from the intertidal zone to the edge of the continental shelf. These habitats include nearshore rocky areas, offshore canyons, enclosed embayments, and estuaries (Factor 1995). All of these habitats differ in their biotic and abiotic variability, and heterogeneity, on many spatial and temporal scales. Most lobster research focuses on the nearshore population in the Gulf of
Maine due to its accessibility, historical data availability, and importance to the fishery. However, many insights into the biology of the species may be gained by studying other habitats; in particular those at the limits of the species biogeographic range. For example, estuarine habitats are at the edge of lobsters' physiological tolerance in terms of salinity and temperature (Jury et al. 1994a & b), nonetheless, they are regularly found in estuaries throughout New England and Canada (e.g., Great Bay Estuary-Vetrovs 1990, Watson et al. in press; Saco River-Reynolds and Casterlin 1985; Biddeford River-Thomas 1969; Iles de la Madeleine-Munro and Therrieault 1983; Narragansett Bay-Wahle 1993; Long Island Sound- Briggs and Mushacke 1979).

Lobsters and other decapods may utilize estuarine habitats for a variety of reasons including: 1) enhanced molting and growth, due to seasonally high temperatures and high productivity (Aiken and Waddy 1986, Hines et al. 1987, Vetrovs 1990); 2) protection from predation and/or cannibalism, due to increased shelter quality or availability and/or increased turbidity (Hines et al. 1987, Shirley et al. 1990); 3) facilitation of post-molt absorption of water for exoskeleton expansion (Hines et al. 1987); and/or 4) feeding or nursery areas for juveniles or postlarvae (Aiken and Waddy 1986). In the Great Bay estuary, predation on adult intermolt lobsters is probably limited (Lawton and Lavalli 1995) and the quality/quantity of food is roughly equal between the estuary and the coast (Becker 1996). Thus the predominant benefits of moving into estuaries seem to be directly, or indirectly, related to the relatively higher temperatures found there (Vetrovs 1990, Jury et al. 1994a), while the predominant cost appears to be the physiological stress imposed by low salinities (Jury et al. 1994b, Rockel 1996).

The Great Bay estuarine system of southeastern New Hampshire is a typical New England well-mixed estuary with extensive intertidal mud flats, eelgrass beds, rocky zones, and deep, narrow channels (Fefer and Schettig 1980, Short 1992). In contrast to coastal waters, estuarine habitats are characterized by widely fluctuating daily and seasonal changes in temperature and salinity (Fig. I.3). In Great Bay, the freshwater
contribution from seven rivers can be substantial, particularly in the spring and after storm events (Jury et al. 1995). For example, the salinity typically drops to levels approaching 10 ppt in the spring (vs. 30 ppt at the coast), and in the summer the temperature is about 10°C warmer than the Gulf of Maine (Loder et al. 1983, Vetrovs 1990, Short 1992, Fig. I.2). Periodically, large spring runoffs may even cause the salinities to fall to 1 ppt in some areas, e.g., in the fall of 1996 at the Jackson Estuarine Lab (Fig. I.3) (R. Langan, personal communication). Both coastal and estuarine waters approach 0°C in the winter, but deeper coastal waters are usually warmer than estuarine waters in the late fall and winter.

Temperature, and/or salinity-temperature interactions, have been implicated in the movements and distribution patterns of many estuarine decapods (Hines et al. 1987, Day et al. 1989, Gutermuth and Armstrong 1989). For example, the blue crab, *Callinectes sapidus* shows seasonal variations in abundance, size composition, and sex ratio in the Chesapeake Bay. Males use the warmer upper estuarine salt creeks as molting habitats and less than 10% of the animals found in these areas were females. Females apparently remain in the river basin of the subestuary, possibly due to decreased fluctuation in salinity and temperature and increased efficiency of larval dispersion (Hines et al. 1987, Shirley et al. 1990). Indeed, temperature is often implicated in the movements, distribution, abundance, and activity of many large vagile decapods of fishery interest.
Figure I.2. Map of Study Sites, Great Bay Estuary. Studies were conducted on or within the Great Bay Estuary. Arrows indicate locations of field sites where temperature and salinity data were logged (see Fig. I.3) Thermosensitivity studies (Chapter 1) were conducted at UNH, activity studies (Chapters 2 and 3) at the Jackson Estuarine Lab (JEL), and thermoregulation studies (Chapters 4 and 5) at the Coastal Marine Lab (CML).
Figure 1.3. Average monthly salinities (ppt) and temperatures (°C) at JEL and CML. Average monthly data from 1989-93 show long term, seasonal trends in temperature and salinity. The water in the upper estuary (JEL) is colder than the water in at the mouth of the estuary (CML) during the winter, but in the summer the estuary is considerably warmer than the mouth. The salinity at the mouth of the estuary (CML) is relatively constant throughout the year. In contrast, during the spring, and to a lesser extent in the fall, rains and/or melting snow lead to a large influx of water from several rivers and a subsequent drop in the salinity in the upper estuary (JEL) (see Fig. 1.2 for locations).
Tag and recapture studies of more than 3,000 lobsters and tracking of an additional 26 lobsters with sonar transmitters in Great Bay have demonstrated that seasonal migrations of lobsters (Watson et al., in press), as well as movements in response to storms (Jury et al. 1995), are also closely associated to changes in temperature and salinity. Larger animals moved farther than smaller animals, and females farther than males. While there was some movement up into the estuary in the spring, the predominant direction of migration was downstream toward the coast in the summer and fall (Figs. I.4 & I.5).

These studies indicate that lobsters undertake seasonal migrations; moving up the estuary in the spring and summer and toward the ocean in the late summer and fall (Vetrovs 1990, Watson et al., in press). These investigations also showed that the sex ratio was highly skewed in favor of males in the upper estuary (Vetrovs 1990, Howell et al. submitted, Fig. I.4). In addition, fewer animals were caught in the upper estuary during the winter and early spring, but their abundance increased in the summer and early fall (Fig. I.5). These data are consistent with previous studies of lobster movements in several Canadian bays and estuaries (Munro and Therriault 1983).

In addition to temperature variability, extreme reduction in salinity is a common seasonal occurrence in estuaries, due to factors such as spring run-off and heavy rains (Fig. I.4) (Loder et al. 1983, Jury et al. 1995). Heavy benthic invertebrate mortalities, including those among lobsters, have been reported in several estuaries after heavy spring runoffs (Thomas 1968, Thomas and White 1969) and after unusually severe storm events such as Hurricane Bob in 1991 (Jury et al. 1995) and the fall storm of 1996 (Jury unpublished data). Thus, the estuary may be a lethal environment at certain times of the year for some individuals due to osmoregulatory stress (McLeese 1956, Scarrat and Raine 1967, Aiken and Waddy 1986). Nonetheless, laboratory experiments show that many intermolt lobsters are able to tolerate the range of salinities normally found within
The 1989-93 catch data (Watson et al., in press) show that large males predominate far up into the estuary (Nannies) where the potential for low salinity is highest. The sex ratio (M:F) approaches 1:1 at the Coastal Marine Lab (CML) at the mouth of the estuary. Abundance of all lobsters is typically highest near the coast. (See Fig. I.2 for locations)
Figure I.5. Temporal components of the lobster population of the Great Bay Estuary. The 1989-93 catch data (adapted from Watson and Howell, unpublished) show that lobsters are first caught in the estuary in the late spring (April-May). Catch increases into the summer and then decreases again in the fall. The distance traveled by tagged animals also follows the same seasonal pattern. These movements correlate with seasonal changes in temperature and salinity (see Fig. 1.3).
the estuary (McLeese 1956, Charmantier et al. 1988) down to as low as 5 ppt (Rockel 1996). Rockel (1996) also showed that estuarine lobsters are better osmoregulators than coastal animals, and males were better than females.

Behavioral mechanisms appear to allow reproductively mature lobsters to minimize their exposure to low salinities (Jury et al. 1994a). Observations of bradycardia in response to dropping salinity indicate that lobsters are able to sense drops in salinity that are > 5 ppt, and occasionally lobsters respond to drops of < 2 ppt (Dufort 1997). This information is most likely used to avoid low salinity areas. For example, when the salinity is lowered in the vicinity of their shelters, most lobsters move to avoid the osmotic stress before it reaches potentially lethal levels (Jury et al. 1994a). Female lobsters tend to find low salinity more aversive in these experiments but the differences are not significant. In addition, osmoregulation is energetically more costly for females (Jury et al. 1994b) and they cannot survive as long in water below 10 ppt. (Rockel et al. 1996). It is unclear whether females avoid low salinity because they are poor osmoregulators per se or whether they are capable of osmoregulating but have additional reproductive or developmental costs associated with exposure to low salinities (i.e., effect of low salinity on egg retention, survival or viability) (Waddy et al. 1995). Nonetheless, avoidance of low salinity may account in part for the observed population distribution in the Great Bay estuary (Jury et al. 1994a).

While salinity is an important factor limiting lobster abundance and distribution in estuaries, temperature still has a strong influence due to its effect on growth and reproduction. Based upon previous studies (Vetrovs 1990, Jury et al. 1994a & b, Howell et al. submitted, Watson et al. in press), the present model to explain the distribution of Great Bay estuarine lobsters is: As temperatures seasonally shift and become warmer in the estuary vs. the coast, lobsters increase activity and follow a temperature gradient into the estuary in the spring and out in the fall. However, residence and location within the estuary is limited by low salinity which can be potentially lethal.
and metabolically costly. As a result, the population does not increase in the upper estuary until late May or June, when the salinity rises above 18 ppt (Fig. 1.3). In June/July animals remain in the estuary until they molt and then they leave the estuary. In the fall, a drop in water temperature, and the probability of lower salinity due to increasing storm activity, triggers a down-estuary migration into deeper, higher salinity, and warmer water. Both sexes avoid the estuary in the winter and early spring because, although the potential for low salinity still exists, the benefits of increased temperature, and possibly other factors, do not. Then, as temperatures rise again in the late spring/early summer, many animals enter and move into the estuary (Figs. 1.4 & 1.5).

Conclusions

Temperature plays a key role in much of the life history of lobsters. However, many of the effects of temperature on behavior and physiology remain unclear. Temperature appears to be most influential environmental in terms growth, reproduction, and the development of juveniles and adults (Aiken and Waddy 1986). Warmer temperatures may: 1) cause lobsters to molt more frequently and thus grow faster (Mackenzie and Moring 1985, Ennis 1986, Watson et al. in press); 2) influence the size at which lobsters reach maturity (Briggs and Mushacke 1979, Krouse 1981); 3) influence embryo incubation, maturation and time of release of larvae (Aiken and Waddy 1986, Fogarty 1995, Ugarte 1994); and 4) influence the efficiency of osmoregulation or other metabolic processes. An understanding of the responses of the Great Bay estuarine lobster subpopulation to temperature may serve as a useful model in our understanding of how temperature influences lobster behavior and subsequent location within thermally heterogenous habitats. By assessing the results of the laboratory experiments presented in the following chapters, concurrently with field data, it will be demonstrated how, and
why, estuaries are utilized by certain components of the subpopulation. These insights are pertinent to the Gulf of Maine lobster population by providing information on the effect of the environment on lobster behavior, ecology, and catchability. They are also extremely beneficial to management, and crustacean biology, by describing the thermal niche of various segments of lobster populations and explaining how and why individuals may be utilizing temperature as a habitat resource (Magnuson 1979).
CHAPTER 1

THERMOSENSITIVITY OF THE LOBSTER, HOMARUS AMERICANUS, AS DETERMINED BY CARDIAC ASSAY

Summary

It is generally accepted that crustaceans detect, and respond to, changes in water temperature, yet few studies have directly addressed their thermosensitivity. In this investigation a cardiac assay was used to demonstrate that American lobsters (Homarus americanus) can sense temperature changes as small as 0.1-0.2°C. The typical cardiac response to brief (1 min.) application of thermal stimuli, either warmer (n=19) or colder (n=17) than the holding temperature of 15°C, consisted of a short bradycardia (26.3 ± 5.4 sec) followed by a prolonged tachycardia (184.0 ± 16.9 sec). Lobsters (n=7) exposed to both fast (4°C/min.) and slow (0.5°C/min.) thermal shifts exhibited comparable cardiac responses and thermosensitivities. However, fewer of the animals exposed to slow rates of change exhibited cardiac responses (57% vs. 100% at the faster rate). A comparison of winter vs. summer lobsters acclimated for >4 weeks at 15°C, revealed that while their detection thresholds were similar, winter lobsters (n=18) had a significantly lower baseline heart rate (34.8 ± 4.4 bpm) and a shorter combined cardiac response (174 sec) than summer lobsters (n=18; 49.9 ± 5.0 bpm, and 320 sec respectively), when exposed to warm or cool seawater. This suggests that some temperature-independent seasonal modulation of cardiac activity may be occurring. The results from this study indicate that the thermosensitivity of lobsters is sufficient to guide their movements in thermal gradients and provide them with some of the critical sensory information necessary to behaviorally thermoregulate in their natural habitat.
Introduction

Temperature is one of the most important and pervasive environmental influences on the American lobster, *Homarus americanus* (Cobb and Phillips, 1980; Aiken and Waddy 1986, Factor 1995). It is generally accepted that their locomotory activity is temperature dependent (McLeese and Wilder 1958, Reynolds and Casterlin 1979, Haakonsen and Anoruo 1994) and that they carry out seasonal inshore/offshore migrations to gain the developmental benefits of warmer coastal temperatures in the spring and/or summer (Cooper and Uzmann 1971, Pezzack and Duggan 1986, Karnofsky et al. 1989, Haakonsen and Anoruo 1994, Factor 1995, Watson et al. in press). Laboratory studies have demonstrated that *H. americanus* has a thermal preference of =16°C (Reynolds and Casterlin 1979, Crossin et al. 1998) and it has been proposed that behavioral thermoregulation may allow them to occupy thermal niches which maximize their metabolic and/or behavioral efficiency. If lobsters are sufficiently sensitive to the levels of temperature change existing in the field, then temperature may be one of the primary sensory cues used to guide their movements along, or within, the thermal gradients they often encounter in their natural habitat.

Thermosensitivity may be mediated by distinct thermoreceptors, as in some invertebrates (Prosser and Nelson 1984), or detected by a receptor for some other modality. While behavioral studies (Reynolds and Casterlin 1979, Crossin et al. 1998) strongly suggest that *H. americanus* can sense temperature, only one study has addressed the response of neural elements to changes in temperature in this species. In this study, firing of cells associated with thoracic ganglia connectives changed from silent to bursting over the range of 10-17°C, which is within the normal thermal scope for this species (Konishi and Kravitz 1978). Thus, while it is clear that temperature has a strong influence on behavior, we still know little about the location of thermoreceptors in
lobsters or how these receptors function (Dorai Raj and Murray 1962, Ache 1982, Komatsu et al. 1996).

In situations where the precise receptors have not been identified, or are not readily accessible to electrophysiological investigation, cardiac assays have provided a valuable tool for preliminary investigations of sensory capabilities (Larimer 1964, Offut 1970, Florey 1974, Dufort 1997). For example, many crustacea exhibit a drop in heart rate in response to novel stimuli (Maynard 1960, Larimer 1963, McMahon and Wilkens 1972, DeWachter and McMahon 1996). This cardiac response has been used to measure the ability of *H. americanus* to detect sound (Offutt 1970) and salinity (Dufort 1997).

While a number of studies have addressed the effect of temperature on decapod heart rates at time scales ranging from hours to days (Ahsanullah and Newell 1971, Florey and Kreibel 1974, Defur and Magnum 1979, DeWachter and McMahon 1996, DeWachter and Wilkens 1996, Hokkanen and Demont 1997) few have characterized the initial response (i.e. <5 min.) to brief changes in water temperature. The present study utilized a cardiac assay technique to determine the ability of *H. americanus* to sense small (1-4°C) changes in water temperature. The responses of lobsters acclimated to the same temperature (15°C) in the summer and the winter show that lobsters are extremely sensitive to temperature shifts during both seasons. However, the characteristics of the cardiac response differ, suggesting some type of temperature independent modulation.

**Materials and Methods**

**Animals**

Adult (82-92 mm carapace length, CL), intermolt lobsters were acclimated to 15 ± 1°C (30 ± 1 ppt) for > 4 weeks prior to use and all experiments were initiated at this temperature. Experiments were carried out both in the summer and winter. In the summer the thermosensitivity of 18 lobsters was determined (cold stimuli, n=9; warm stimuli,
n=9) and in the winter, identical experiments were carried out using lobsters acclimated to 15°C (cold stimuli, n=8; warm stimuli, n=10).

**Recording temperature and heart activity**

Small wire electrodes were inserted through the dorsal carapace above the heart and used to record heart rate using a UFI impedance converter (model #2991). Because of the inherent sensitivity of the impedance recording technique to temperature in preliminary trials, the method was verified by simultaneously monitoring the electrical activity associated with lobster heart contractions using a Grass model 7D polygraph. Internal temperature was recorded using a small (3mm x 1mm) thermistor (MacLab, Inc., resolution of ± 0.15°C) inserted dorsally and laterally above the pericardial chamber. External temperature was monitored with an identical thermistor placed on the dorsal carapace.

**Experimental chamber**

After insertion of the electrodes, lobsters were placed in a recording chamber, which was continuously perfused with 15 ± 1°C, 30 ± 1 ppt seawater (Fig. 1.1). The recording chamber consisted of an 18 cm diameter PVC pipe covered on the top and bottom by perforated plates through which seawater continuously flowed. This arrangement kept lobsters relatively immobile and ensured that changes in temperature within the recording chamber were rapid and relatively homogeneous. To insulate the chamber, it was placed into a plexiglass insert (30x30x30 cm) which was then placed into a temperature controlled 120 L aquarium. Ambient seawater was continuously pumped (2 L/min.) through the recording chamber, into the insert, and back to the temperature controlled bath. Thermal stimuli were delivered by switching the source of seawater from the temperature controlled bath to the stimulus bath. The stimulus bath was filled from the ambient bath to minimize novel chemosensory cues (Fig. 1.1) and brought to the
appropriate temperature using aquarium heaters or cooling coils. The recording chamber was covered with black plastic to minimize visual disturbance and the lobster was left in the experimental apparatus. Preliminary studies indicated that lobsters were much more sensitive to stimuli if given sufficient time to recover from electrode placement and become accustomed to the recording chamber.

The following day, after measuring the basal heart rate for at least 30 min., each animal was exposed to a +1°C warm or a -1°C cold stimulus for approximately 1 min. These were followed by stimulus treatments of ±2°C and then ±4°C above, or below, the ambient acclimation temperature (15 ± 1°C) (Fig. 1.2). The actual warm stimuli were approximately 16, 17, and 19°C and the cold stimuli were 14, 13, and 11°C. These treatments are referred to as: +1, +2, and +4°C warm stimuli and -1, -2, and -4°C cold stimuli. Dilution within the recording chamber resulted in actual exposure temperatures that were somewhat different from the applied temperatures. For example, when a +4°C stimulus was delivered the actual temperature change measured by the thermistor located on the dorsal carapace was +2.5°C. All temperatures presented are those recorded by the thermistor located externally above the dorsal carapace, unless otherwise stated, and thus relative levels are consistent. Only warm (i.e., +1, +2 or +4°C) or cold (-1, -2, or -4°C) treatments were tested in a given day. Which stimuli were tested on the first day was assigned randomly and the other set of stimuli (warm or cold) were tested on the following day. To minimize adaptation, stimulus applications were at least 30 min apart. Controls were conducted prior to application of any thermal stimuli using the same protocol described above, but without changing the temperature in the stimulus bath.

The effect of rate of temperature change was tested by exposing 7 lobsters to the identical protocol described above for a +4°C stimulus, but with a +0.5°C/min flow rate through the recording chamber, instead of a rate of +4°C/min. Experiments conducted using the slower rate of change resulted in an actual rate of +0.25°C/min., as detected by

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Figure 1.1. Experimental apparatus used to record lobster cardiac responses to changes in temperature. Lobsters are placed in a chamber that is suspended in another container, which in turn, sits in a large temperature-controlled aquarium. Seawater (15°C) flows continuously from temperature controlled reservoirs through perforated plates above and below the lobster in the animal chamber (direction of flow indicated by clear arrows). Heart rate is recorded using dorsally implanted electrodes connected to an impedance converter. Switching the stopcock changes the source of water from the ambient seawater bath to seawater from the stimulus bath, which is held at a different temperature (direction of flow indicated by dark arrows). A thermistor placed externally over the dorsal carapace are used to monitor temperature during the experiment.
the thermistor in the chamber. In these trials, a lobster was first tested at the +4°C/min "fast" rate and then allowed >3 hours to recover with 15°C seawater flowing through the chamber at the slower rate. The same lobster was then tested with a +4°C stimulus at the "slow" rate.

A 25% change in heart rate, i.e., bradycardia (decrease) and/or tachycardia (increase), was used as an indicator that lobsters sensed a change in water temperature (Offutt 1970, Dufort 1997). Digitized records were analyzed to determine the following: 1) delay to a response; 2) duration of bradycardia and/or tachycardia; 3) minimum beats per min (bpm) during bradycardia and; 4) maximum bpm during tachycardia. In addition, thermosensitivity thresholds were measured by recording the water temperature at the time of the initial cardiac response.

Results

Typical response to a change in temperature

The typical cardiac response to both warm and cold stimuli consisted of a short bradycardia, lasting 26.3 ± 5.4 s, followed by a significantly longer tachycardia (184.0 ± 16.9 s) (paired t-test, p<0.0001) (Figs. 1.2 & 1.3). In general, changes in heart activity were similar in response to both warm and cold stimuli. However, even though not statistically significant (Fishers exact test p>0.4) 84% of animals tested (n=19) showed both bradycardia and tachycardia in response to a +4°C stimulus, whereas in response to a -4°C stimulus, 82% exhibited bradycardia, while only 47% showed tachycardia (n=17). Thus, there may be some inherent differences in the detection of, or response to, warm vs. cold stimuli.
Figure 1.2. **Typical cardiac response to a change in temperature.** A warm water stimulus was added to the experimental chamber for 60 sec (see dashed vertical lines), while simultaneously monitoring the lobster ECG (top trace shows raw data, second trace displays the computed heart rate), and both the external water temperature and the internal body temperature of the lobster. This lobster showed the typical response to an acute temperature change: a brief bradycardia followed by prolonged tachycardia. Note that the internal temperature changes more slowly and less extensively than external temperature. The response occurred suddenly and the estimated change in temperature necessary to trigger the response (threshold) was less than 0.2°C.
Sensitivity to warm and cold stimuli

Lobsters were found to be extremely sensitive to both warm and cold stimuli (Figs. 1.3 & 1.4). For example, when subjected to a +4°C stimulus lobsters responded after just 3.8 ± 0.5 seconds, when the temperature in the chamber had only changed by 0.09 ± 0.04°C. Lobsters exposed to the -4°C stimulus responded after a drop of only 0.13 ± 0.09°C, and the latency to respond (4.6 ± 1.8 s) was not significantly different than during a warm stimulus (Fig. 1.3). These values are considered to be conservative due to the inherent time constant and resolution of the thermistor (± 0.15°C) used to measure these thresholds.

For all treatments heart rates measured after exposure to control stimuli were not significantly different from initial heart rates measured at the beginning of each trial (paired, t-test p>0.1) (Fig. 1.5). There were also no significant differences between the sexes in thermal sensitivity thresholds (paired t-test, p>0.1) and lobsters exhibited comparable responses to ± 1, 2 and 4 °C stimulus treatments (see Fig. 1.4, Kruskal Wallis, p>0.3). There were also no significant differences in the number of animals responding to each treatment (Chi square test, p>0.3). However, though not statistically significant, fewer animals responded to smaller temperature changes. Therefore, the +4°C and -4°C stimulus treatments were used in the two studies described below.
Figure 1.3. **Time course of applied temperature stimuli and subsequent cardiac responses.** The upper two graphs show the rates of change of the internal and external temperatures in response to stimuli that were 1, 2, and 4°C warmer or colder than the ambient temperature (15°C). The response time is similar for both internal and external changes; however, the magnitude of temperature change is higher externally, while the return to the pre-stimulus temperature takes longer internally. The lower figure (B) shows the mean response latency, duration of bradycardia and duration of tachycardia in response to a +4°C or -4°C stimuli (highlighted in A.). While the latency to respond, and thus thresholds (see Fig. 1.4), are similar between seasons, the duration of both bradycardia and tachycardia tended to be longer in summer animals (unpaired t-tests, p<0.1)

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Figure 1.4. External temperature change required to initiate bradycardia. Applied stimuli (1, 2 or 4°C warmer or colder than 15°C; see Figure 1.3 for actual internal and external values) all elicited cardiac responses at similar temperature thresholds, ranging from 0.02 to 0.75 °C (Kruskal Wallis, p>0.03). These values are conservative due to the inherent response time of the thermistor used to measure external temperatures. Summer and winter animals were pooled for this analysis because no differences in thresholds were found between seasons.
Figure 1.5. Response to cold and warm stimuli by summer and winter animals. For all treatments, application of control 15°C stimuli to lobsters acclimated to 15°C did not cause a statistically significant change in heart rate (paired t-tests, p>0.5). Lobsters in both seasons responded to +4°C or -4°C stimuli with a short bradycardia followed by a longer tachycardia. In addition, animals in the winter showed significantly lower initial heart rates (paired t-tests, p<0.05). Thus, even though all animals were acclimated to 15°C there appears to be some temperature-independent seasonal modulation of heart rate.
Effect of rate of temperature change

Lobsters (n=7) were exposed to both a fast and a slow rate of temperature change (see methods) and six responded to both stimuli with bradycardia and/or tachycardia. The thermal detection thresholds were slightly higher for the slow rate (a change of 0.4 ± 0.22°C) than the fast rate (0.08 ± 0.06°C), but these differences were not significantly different (paired t-test p>0.4). The duration and magnitude of bradycardia and tachycardia were also similar. However, fewer lobsters responded with bradycardia (n=4) or tachycardia (n=6) after exposure to slow rates of temperature change, in comparison to the fast rate (100% displayed both bradycardia and tachycardia).

The influence of season

The characteristic cardiac response of lobsters to a change in temperature (a short bradycardia followed by a longer tachycardia) was similar for both lobsters tested in the winter and those tested during the summer. However, the following differences were apparent: 1) the mean baseline heart rate was significantly lower in winter (34.8 ± 4.4 bpm), compared to summer, lobsters (49.9 ± 5.0 bpm) (Fig. 1.5; unpaired t-test p<0.005); 2) the duration of bradycardia and tachycardia responses tended to be shorter in the winter (Fig. 1.3; unpaired t-tests p<0.1) and; 3) winter lobsters tended to respond to temperature changes with both tachycardia (83%) and bradycardia (72%), whereas in the summer only 50% of the lobsters responded with tachycardia, while 94% showed bradycardia (Fig. 1.6; Fishers exact test, p=0.18). Thus, even though all animals were acclimated to 15°C for at least a month, and tested with temperatures warmer or colder than this holding temperature (15°C), winter and summer lobsters appear to have different basal physiological states, and potentially behavioral states. As a result, they also have distinct responses to the same thermal stimuli.
Figure 1.6. Percent of animals responding with bradycardia or tachycardia in winter vs. summer lobsters. Cardiac responses to 4°C increases, or decreases, in water temperature were qualitatively similar in winter and summer lobsters (see Fig. 1.5). However, the percent of animals responding tended to differ by season. While not statistically significant, lobsters responded less with bradycardia in the winter and more with tachycardia; while the opposite situation existed in lobsters tested in the summer. This may be due to the lower baseline heart rates in the winter months (see Fig. 1.5).
Discussion

While several studies infer that lobsters can sense changes in temperature (e.g., Reynolds and Casterlin 1979, Crossin et al. 1998), to our knowledge the present study is the first to directly demonstrate thermoreception in *H. americanus*. Assuming that the initiation of a cardiac response indicates detection of environmental change, lobsters can conservatively sense both increases and decreases in water temperature of <0.1-0.2°C (Fig. 1.4). Similar thermal sensitivity has been documented in a number of terrestrial arthropods (Kerkut and Taylor 1957, Murphy and Heath 1983, Altner and Loftus 1985). For example, the spider *Cupiennus salei* has a warm receptor with a detection threshold between 0.08-0.6°C (Ehn and Tichy 1996). Although there have been fewer studies of thermoreception in aquatic species, the thresholds obtained are similar to those reported in the present study. For example, Forward (1990) found that crab larvae (*Rhithropanopeus harrisi* and *Neopanope sayi*) ascend or descend in a water column in response to absolute temperature changes of 0.29-0.49°C; as long as the rate of change is fast enough (0.06-0.24°C/min depending on larval stage and species). Thus, the American lobster is probably not unusual in its ability to detect small changes in temperature, although the extent to which this level of thermosensitivity exists in other crustaceans remains to be investigated.

Although several behavioral studies indicate that crustaceans are quite sensitive to changes in temperature little is known about thermoreceptors in this large group of aquatic invertebrates. A study of the thermal sensitivity of the dactyl receptors of *Cancer antennarius, C. anthonyi, and P. interruptus* strongly suggests that they possess a thermal receptor system capable of integrating temperature information for use in thermally-cued behavior (Cook 1984). However, identification of actual thermoreceptors has not been completed in these species. In lobsters, a number of neurons change their rate of firing in response to shifts in temperature, but it is not clear if these cells are
actually serving the function of thermoreceptors. For example, firing of *H. americanus* root cells off of thoracic ganglia connectives changes from silent to bursting over the range of 10-17°C (Konishi and Kravitz 1978) and in the spiny lobster, *Panulirus japonicus*, ligamental nerves increase their firing in response to cold stimulation (Kuramoto and Tani 1994). While these thermally-sensitive neurons are located internally, the short latency of the cardiac response to a change in temperature in our experiments (Fig. 1.3) strongly suggests externally located thermoreceptors. However, ablation studies indicate that lobsters missing antennae (n=4), antennules (n=4), and/or walking legs (n=3) respond to a +4°C stimulus just like intact animals (Jury, unpublished data), suggesting that while these appendages may contain thermoreceptors, they are not necessary for lobsters to exhibit a cardiac response to temperature. Mechanisms of thermoreception are beginning to be elucidated in some other invertebrates (Komatsu et al. 1996, McCleskey 1997) and studies are currently underway in our lab to localize thermoreceptors in lobsters and other crustaceans.

While gradual changes in temperature have a profound, well-documented, influence on the metabolism and cardiovascular function of lobsters (Mercaldo-Allen and Thurberg 1987, McMahon 1995, DeWachter and McMahon 1996), brief decreases in heart rate following acute temperature changes are also common in crustaceans (McMahon and Wilkens 1972, McMahon 1995, DeWachter and McMahon 1996). It is unlikely that these short latency responses are due to a direct impact of temperature on the heart for the following reasons: 1) While Q10 values for heart rates of intact lobsters generally range from 1.5-2.5 (Mercaldo-Allen and Thurberg 1987, Schreiber et al. 1998) excised lobster hearts are not very sensitive to changes in temperature over the range of 12-19°C, and they generally have lower Q10's than intact animals (Schreiber et al. 1998); 2) the initiation of a cardiac response is immediate and robust and the response extends well beyond the duration of the temperature stimulus (Figs. 1.2 & 1.3); 3) the response is similar (i.e., bradycardia followed by tachycardia) whether hot or cold stimuli are applied.
(Figs. 1.4 & 1.5); 4) the magnitude of the response is not proportional to the size of the stimulus, although the percent of animals responding is dose-dependent (Fig. 1.6); 5) excised hearts exposed to acute thermal shifts of + 4°C, at the same rate of change as used in the whole animal experiments, do not respond with any significant change in heart rate (paired t-test, p>0.1, n=3; Jury, unpublished data) and; 6) *C. magister* (Guirgis and Wilkens 1995) and *H. americanus* (Jury and O'Grady, unpublished data) with cut cardio regulatory nerves do not change their heart rate in response to acute environmental stimuli, including temperature changes. Therefore, although temperature can have a long-term, direct influence on heart rate and cause release of modulatory substances from the pericardial organs of lobsters (Kuramoto and Tani 1994), all current data strongly suggests that in lobsters, and probably in many other crustaceans as well, some type of thermoreceptor senses a change in temperature which then causes a change in heart rate through activation of inhibitory and excitatory cardio regulatory nerves.

Lobsters do not appear to have seasonal differences in their ability to detect temperature. However, winter-acclimated lobsters have lower basal heart rates, and respond somewhat differently than summer lobsters, to shifts in temperature. These differences suggest the presence of some type of seasonal modulation of the lobster cardiovascular system, similar to the actions of thyroid hormones in frogs (Miller and Mizell 1972). Biogenic amines, such as serotonin and octopamine, have been shown to increase cardiac output and seasonal changes in circulating levels of these, or similar, neuromodulators might increase basal heart rates in the summer and/or alter how the heart responds to input from cardio regulatory nerves (Fingerman et al. 1994, Weiger 1997, Wood et al. 1997). This type of seasonal modulation is likely to influence responses to a wide variety of stimuli, in addition to temperature. In a separate study on lobster cardiac responses to changes in salinity, we observed that animals with elevated basal heart rates were less likely to exhibit tachycardia (Dufort 1997). In the current study, summer animals had elevated heart rates, in comparison with winter animals, and while almost all
(94%) responded to temperature changes with bradycardia, only 50% expressed tachycardia. The precise mechanisms underlying these seasonal changes in the cardiovascular system of crustaceans remain to be resolved. A recent study of blue crabs, *Callinectes sapidus*, which documented seasonal differences in their behavioral responses to injected biogenic amines and proctolin (Wood et al. 1995), suggests that seasonal variability in the expression of receptors may be the cause.

The rate of temperature change may be an important variable in detection of thermal shifts in the environment. Florey and Kriebel (1974) found that in *Cancer* species the rate of change must be > 0.33°/min. to "avoid hysteresis effects". This is interpreted as meaning that acute bradycardias and/or tachycardias were seen at rates of change faster than this but only long-term changes in heart rate were observed at slower rates. This threshold rate is very close to the rate (0.5°C/min) used in our "slow rate" experiments, where fewer lobsters responded. Based on these data, it is likely that lobsters might show little cardiac response to rates of change which are an order of magnitude slower. Crab larvae (*R. harrissii*) descend in the water column when the temperature is elevated at rates ranging from 0.07-0.24°C/min, and they ascend when the temperature decreases at rates of 0.06-0.1°C/min. However, "the average absolute amounts of temperature change needed to evoke a response was independent of the rate of change at rates above threshold and ranged from 0.29 to 0.49°C (Forward 1990)". In New Hampshire coastal and estuarine waters, where water temperature ranges from 0-25°C, seasonal changes in temperature might occur too slowly to directly stimulate lobster thermoreceptors. However, tidal changes and/or thermoclines may change fast enough to be detected. Indeed lobsters have been found in some studies to aggregate at thermoclines (Ennis 1984, Estrella and Morrissey 1997). We have measured rates of temperature change as high as 0.33 °C/min in the Great Bay estuary, even though average rates are approximately 0.004°C/min (based upon hourly Licor CTD readings, R. Langan, unpublished data). Movement of lobsters within this thermally heterogeneous habitat may
increase the realized rate of change experienced and thus result in thermal shifts which are within their sensitivity range. The combination of lobster mobility and their sensitivity to small temperature changes probably provides them with sufficient information to behaviorally thermoregulate in their natural habitat in the same manner observed in small thermal gradient tanks (see Chapters 4 & 5).

In this study we used changes in the heart rate to determine the sensitivity of lobsters to thermal stimuli. While this assay is useful for determining their ability to sense small changes in temperature, it is unknown if similar changes in heart rate occur in lobsters when they encounter thermal shifts in their natural habitat. In our experiments the sensitivity of lobsters to environmental stimuli may have been enhanced because they were held for >12 hours in a state of "sensory deprivation". Crustaceans in this state have been reported to be much more responsive to a wide variety of stimuli (Offutt 1970, Florey and Kriebel 1974). In contrast, lobsters that are not given sufficient time to recover from handling have high basal heart rates and often do not exhibit typical responses to thermal stimuli. Thus, while lobsters in their natural habitat are probably capable of sensing very small changes in water temperature, these thermal stimuli may not always lead to the types of cardiac responses observed in quiescent laboratory animals. Studies are currently underway to test this hypothesis, by recording from freely moving lobsters as they are subjected to acute changes in temperature and while they spontaneously move through thermal gradients.
CHAPTER 2

A COMPARISON OF THE ACTIVITY RHYTHMS OF LOBSTERS, HOMARUS AMERICANUS, RECORDED IN THE LABORATORY AND FIELD USING A NEW TECHNIQUE

Summary

The locomotory activity of lobsters, *Homarus americanus*, was monitored to quantify, and determine the effect of environmental conditions on, the activity rhythms of lobsters in the lab and under natural field conditions. Locomotion was measured using magnetic reed switch assemblies to determine when a lobster fitted with a magnet passed through one of two shelters located on opposite sides of an enclosed 1 m diameter racetrack.

The results of this study demonstrate that: 1) light is the most important exogenous variable influencing daily lobster activity patterns in estuarine habitats, even though temperature, salinity, and tidal currents are highly variable; 2) lobsters in the field are significantly more active than those tested in the laboratory; and 3) the activity patterns of blindfolded lobsters suggest that they have endogenous rhythmicity which is strongly modified by exogenous cues. These studies also showed that lobsters have low, but consistent, levels of daytime activity in the field and that the average daily distance moved by lobsters in the field deployed activity apparatus (249 ± 55.1 m/d) was comparable to distances moved during tag-recapture and telemetry tracking studies.
Introduction

Locomotor activity in crustaceans is affected by many environmental factors including light, currents, and temperature, which can interact with, and even override, endogenous rhythms (Rebach 1987, Chatterton and Williams 1994, Archiega and Rodriguez-Soza 1997). Lobsters, *Homarus americanus*, like many crustaceans, are generally considered to be nocturnally active (Cobb 1969, Reynolds and Casterlin 1979, Cooper and Uzzmann 1980, Karnofsky et al. 1989, Waddy and Aiken 1991, Factor 1995) and it is widely accepted that inshore lobsters inhabit shelters during the day, forage at night, and then return to their "home" before dawn (Cooper and Uzzmann 1980, Ennis 1984, Lawton 1987). This pattern of behavior generally results in small local movements, although longer nomadic or migratory movements are not uncommon (see Watson et al. in press, Lawton and Lavalli 1995). In the field, lobsters have been observed becoming restless as sunset approaches and then emerging from their burrows within 1-3 hours after sunset (Cooper and Uzzmann 1980, Ennis 1984, Karnofsky 1989). Several lab studies suggest that activity is circadian with a periodicity of 24 hr and peak activity occurring nocturnally (Cobb 1969, Krekorian et al. 1974, Zeitlin-Hale 1978, Reynolds and Casterlin 1979, Lawton 1987). In these studies, activity generally showed a crepuscular peak within 2-5 hrs after dark which then waned throughout the night, dropping to a low before sunrise. There was little activity reported during daytime periods. Nonetheless, there was a large amount of variation in this daily rhythmicity, possibly due to environmental or intraspecific variables (Zeitlin-Hale and Sastry 1978, Lawton 1987). Thus, the degree to which the nocturnal pattern of locomotion by *H. americanus* is endogenously vs. exogenously mediated is unclear. It is also unknown if the timing and magnitude of lobster activity measured in the laboratory are comparable to activity expressed under more natural conditions.
There is a substantial body of literature concerning biological rhythms in decapod crustaceans (reviewed in Archiega et al. 1993). In several species, both lab and field studies indicate the presence of an endogenous circadian rhythm, which is strongly influenced by light (Atkinson and Naylor 1976, Herrnkind 1980). Previous studies suggest that *H. americanus* also has an endogenous component to its activity rhythm (Cobb 1969). However, the evidence is equivocal due to the overriding influence of exogenous stimuli and the paucity of published tests of truly circadian rhythmicity.

Light is usually considered to be the most important exogenous variable entraining and modifying activity in lobsters (Cobb 1969, Lawton and Lavalli 1995) and in some deep and/or turbid habitats where light levels are consistently low, lobsters may be active throughout the day (Stewart 1972, Lawton and Lavalli 1995). For example, studies on *Nephrops norvegicus* show that they emerge from their burrows at approximately the same light intensities regardless of depth (Page and Larimer 1972, Archiega and Atkinson 1975, Chapman 1975). As a result, deep water lobsters are active throughout the day, while shallow water lobsters are strictly nocturnal (Atkinson and Naylor 1976). While *H. americanus* are generally considered to have high nocturnal activity and minimal diurnal activity, in some habitats there is also evidence for increased activity in relation to tidally variable currents, temperatures or turbidity (Howard and Nunny 1983, Karnofsky et al. 1989, Lawton and Lavalli 1995). In general, the timing, and rhythmicity, of the activity of an organism in its natural environment is often a combination of direct responses to exogenous environmental stimuli superimposed on an endogenous pattern which is determined by an internal timer (Rebach 1987, Williams and Dean 1989).

Several techniques have been used to study patterns of locomotory activity in decapods, but none of these have compared lab and field data concurrently. The methods traditionally used are automated activity monitoring devices including mechanical displacement of objects in a tank (Cobb 1969), tripping light beams (Reynolds and Casterlin 1979), video monitoring (Lawton 1987), and even strain gauges to measure...
pressure changes as lobsters move in a suspended cage (Koike et al. 1997). In the field, acoustic or electromagnetic tracking, telemetered tilt switches, and SCUBA observations have been used to estimate daily activity (Ennis 1984, Jernakoff, 1987, Karnofsky et al. 1989, Smith et al. 1998, Watson et al. in press). The present study utilized magnetic reed switch assemblies to determine when a lobster fitted with a magnet passed through one of two shelters in a racetrack. By using this method in both the lab and the field to determine the daily activity patterns of *H. americanus*, we have expanded upon previous observations and experiments by showing 1) light is the most important exogenous variable influencing lobster activity even in estuarine habitats where temperature and salinity show considerable daily variation; 2) there are significant differences in activity between lobsters in the lab vs. those in the field; 3) the activity patterns of blindfolded lobsters suggest endogenous rhythmicity which is strongly modified by exogenous cues.

**Materials and Methods**

**Monitoring Locomotory Activity**

Lobsters with a 1x1 " magnet attached to their dorsal carapace were placed in a 1 m diameter x 25 cm wide racetrack made of plastic-coated wire mesh (Fig. 2.1). As they walked around the track they passed through two PVC conduits located on opposite sides of the racetrack. These conduits were fitted with five magnetic reed switches so that when a lobster passed through a conduit, it caused one of the switches to close and the resulting voltage was recorded by a datalogger (MacLab, Inc.). These magnetic proximity switches proved to be much more reliable than optoelectronic detectors due to transient but persistent turbidity in the estuary which varied the light levels and tended to give false trips of the detectors. The magnetic technique was verified on three occasions by videotaping lobsters moving in the racetrack while simultaneously recording from the reed switches and it was found to be 100% accurate (n=3 animals >12hr/animal). Recordings
were obtained for 2 days and data from the second 24 hrs, noon to noon were analyzed by counting the number of passes from one shelter to the other per hour. Distances moved were determined by multiplying the number of passes by 3 m (the circumference of the center of the racetrack).

A self contained racetrack of similar design was constructed to enable us to obtain the same type of data in the natural habitat. This racetrack was identical except that it was enclosed in wire mesh on all sides to prevent escape. The lobster was placed into the racetrack which was then lowered to the bottom off the dock at the UNH Jackson Estuarine Lab (JEL) to a depth of 3-5 m, depending upon tide. The racetrack was weighted with approximately 35 pounds of cement to keep it from moving on the bottom (tidal currents at this site have been recorded at 1.0 m/s or greater (Short 1992)). A waterproof cable connected the track to a waterproof case on the dock where data were logged to a Tattletale Lite computer (Onset Computer Co., Falmouth, MA). This allowed a comparison of locomotion in the lab to activity under field conditions.

For the laboratory experiments, individual adult lobsters (n=11 male and 7 female) 81-91 mm carapace length were captured in the Great Bay Estuary or nearby coastal New Hampshire. Animals were held at JEL for at least 4 weeks communally and fed approximately weekly prior to being placed in a racetrack. Only intermolt individuals were tested. Two animals were run simultaneously; each in one of two racetracks in a flow-through 2 m diameter circular tank located in a greenhouse at the JEL. The tank continuously received water from the Great Bay estuary and the depth was maintained at 40 cm. The racetracks were visually shielded from each other within the tank, as well as from movement outside the tank, by sheets of black plastic which were oriented such that ambient light still entered the tank. For the field experiments, male (n=4) and female (n=4) adult lobsters were captured in the Great Bay Estuary and were run within 1 week of capture. Prior to experimentation, they were held on the bottom in a wire cage near where the field experiments were conducted.
Figure 2.1. Activity track. Individual lobsters were placed in a 1 m diameter x 25 cm wide racetrack made of plastic-coated wire mesh. Five magnetic reed switches are attached to two PVC conduits located at opposite ends of the racetrack. When a lobster passes through a conduit, a magnet (1x1") attached to its dorsal carapace will cause one of the switches to close and a subsequent voltage will be sent to a MacLab datalogger. Temperature and light were continuously logged using HOBO dataloggers. In the lab, two of these tracks were visually shielded and placed in a 3 m diameter flow-through tank. In the field the entire track was enclosed in plastic-coated 1 inch wire mesh and placed off the dock in approximately 3-5 m of water in the Great Bay Estuary.
A. Example of an activity monitoring recording. By moving once around the racetrack, a lobster will trip magnetic reed switches in one shelter followed by a subsequent trip in the opposite shelter and then return to the initial shelter. One pass around the racetrack was a distance of 3 m. Sheltering behavior could be seen by sequential multiple trips in either shelter. B. The activity of an adult male lobster. An adult male monitored from 9/13/97 to 9/15/97 was primarily nocturnal with crepuscular peaks in activity. Temperature and light data were obtained from HOBO dataloggers in the track. The temperature data shows the variability experienced within the experimental tank, which is influenced by the temperature of the estuary as well as by solar warming. In the field the temperature varied directly with the tides. Light levels in the laboratory were also much higher than they were in the field (Fig. 2.3). Note that lobsters become active when the light begins to decrease.
Environmental variability

HOBO temperature and light dataloggers (Onset Computer, Co. Falmouth, MA) were placed within the center of the racetrack(s) during each trial and set to log data at 5 minute intervals. Temperature was measured in °C while light was measured in illumination intensity using units of lux. Because ambient seawater was used to acclimate animals, salinities (ppt) were somewhat variable (26.5±0.33, mean ±SEM). Only animals exposed to salinities >25 ppt are presented in this paper. All experiments were conducted from late June to early September in 1997 or 1998.

Simulating constant darkness

The effect of exogenous vs. endogenous rhythmicity was tested in both the lab (n=3) and the field (n=3) by running "blindfolded" animals for at least 2 days under a normal light-dark cycle, and then several additional days under simulated constant darkness. The term "blindfolded" is used because lobsters were fitted with a "hood" made of 3 layers of duct tape covering the lobsters eyes, attached with cyanoacrylate glue above and below the rostrum. In the lab the entire tank was also enclosed in several layers of black plastic after the initial control light-dark days. In the field it was only possible to blindfold the lobsters but light levels were already relatively low (see Fig. 2.3). When the light meter was covered in the same manner as the blindfold technique it reduced light levels to <0.012 lux, which is the lower limit of the range of the light logger used. Nonetheless, this technique would not eliminate light input via possible extraocular photoreceptors on the ventral surface of the tail (Wilkens and Larimer 1976, Simon and Edwards 1990).
Figure 2.3. Light data in the laboratory and field. Light levels (lux) recorded using HOBO dataloggers during activity experiments were consistently higher in the laboratory tank than in the estuary at a depth of 3-5 m. It is possible that the greatly reduced light levels in the field were responsible for the differences in activity between laboratory and field lobsters.
Results

**Daily activity rhythms in the lab and in the field**

The magnetic reed switch technique used was found to be very suitable for measuring the locomotory activity of lobsters and it was especially useful in the turbid and low light conditions of the estuary (Figure 2.2). Lobsters exhibited crepuscular, nocturnal activity patterns (Figs. 2.2 & 2.3) similar to those reported in several previous studies (Cobb 1969, Cooper and Uzmann 1980, Lawton and Lavalli 1995). There were no significant differences in activity between sexes (unpaired t-test, p>0.05).

Lobsters in both the lab and the field showed significantly higher activity at night than daytime (Unpaired t-tests, p<0.001). Lobsters in the field expressed significantly higher activity than those in the laboratory (Mann-Whitney U test, p<0.0001), including higher daytime activity (Table 2.1; Fig. 2.4).

Lobsters in the laboratory studies moved an average of 88 ±12.0 m/d. Under natural field conditions the daily distances moved (249± 55.1 m/d) (Table 2.1) were much higher and were very similar to estimates reported for free ranging animals in the Great Bay estuary based upon tag-recapture (278 m/d) or ultrasonic telemetry (268 m/d) data (Watson, et al., in press).

**Environmental variability**

Light levels differed substantially between the laboratory tank and the racetrack in the field (unpaired t-test, p<0.05; see Fig 2.3). Absolute illuminance was much higher in the lab than in the field with a mean maximum daily light level in the field of only 5.0 ± 1.2 lux compared to 60.3 ± 26.2 lux in the lab. The rate of change of illuminance peaked at dawn and dusk in both locations, but in the field light was generally more variable; probably due to diurnal changes in turbidity caused by tidal currents and/or runoff events.
Figure 2.4. Laboratory vs. field daily activity data. Lobsters in both the lab and the field showed significantly higher activity at night vs. daytime (Unpaired t-tests, p<0.001). The peak number of passes was at sunset suggesting a light as an important zeitgeber for their crepuscular activity. There was also significantly greater activity in the field (Mann-Whitney U test, p<0.0001). When the level of activity in the field is transformed to distance moved/day the values are similar to estimates reported for free ranging animals (see Table 2.1).
Table 2.1. Distances moved by day and night in LD and DD.
Distance moved was determined for day, night, and 24 hour periods for each treatment (LD=light:dark treatment; DD=dark:dark treatment when lobsters were blindfolded). Note that lobsters were generally more active at night but in the field in particular there was significant daytime activity.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Day</th>
<th>Night</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lab (LD)</td>
<td>18</td>
<td>24 ± 4.8</td>
<td>64 ± 8.7</td>
<td>88 ± 12.0</td>
</tr>
<tr>
<td>Field (LD)</td>
<td>8</td>
<td>95 ± 24.4</td>
<td>155 ± 36.0</td>
<td>249 ± 55.1</td>
</tr>
<tr>
<td>Lab (DD)</td>
<td>3</td>
<td>33 ± 10.5</td>
<td>52 ± 4.0</td>
<td>85 ± 14.5</td>
</tr>
<tr>
<td>Field (DD)</td>
<td>3</td>
<td>42 ± 19.3</td>
<td>72 ± 25.5</td>
<td>114 ± 42.0</td>
</tr>
</tbody>
</table>
The mean daily temperature in the lab (19.6±0.27°C) was similar to that in the field (19.6±0.46 °C). However, there was much greater variability in temperature in the field where temperatures showed daily fluctuations of 2.3-4.7°C over tidal cycles. Inside the laboratory these differences were dampened to 0.8-3.0°C.

Effect of blinding on activity

Lobsters appear to have a weak endogenous rhythm based on the phase shifting under D:D conditions; suggestive of a free running rhythm of <24 hr (Fig. 2.5). In addition, when the blindfolds were removed normal activity patterns were restored (Fig. 2.5). It is notable that blindfolded lobsters in the laboratory showed similar, albeit shifted, levels of activity compared to those experiencing normal L:D conditions, while blindfolded lobsters in field showed a level of activity that was reduced, albeit not significantly (unpaired t-test, p=0.19), to a level similar to that seen in the laboratory (Table 2.1).
Figure 2.5. Results from one lab and one field experiment before, during, and after blindfolding. A. Lab run from 8/98 B. Field run from 9/97. Activity is expressed as number of passes/hour and is given for each hour of the day. L:D denotes normal light-dark conditions. DD denotes lobsters fitted with a blindfold to eliminate light cues. 'Missing' data means data was not collected primarily due to power outages.
Discussion

This study utilized a novel method of measuring locomotory activity to demonstrate that lobsters have crepuscular and nocturnal increases in activity which appear to have a weak endogenous component that is strongly modified by the environment. Trials with blindfolded animals suggest that while an endogenous component exists in lobsters, it is strongly modified by variable light levels under natural light-dark conditions. In the field, where light levels were consistently dim in the daytime, activity often persisted. Thus, activity patterns under environmentally variable estuarine and coastal conditions are highly dependent upon local light conditions as has been reported in other habitats (Stewart 1972, Jemakoff 1987, Lawton and Lavalli 1995, Smith et al. 1998).

The technique used in the present study has several advantages over other options: 1) high turbidity and varying light levels do not affect recording; 2) additional light, which may effect behavior, is not necessary as in some techniques (i.e. video); 3) the system is readily adaptable to field use, and is relatively inexpensive; 4) availability of shelters may lead to a more natural expression of behavior (Zeidan-Hale and Sastry 1978); and 5) distance traveled and rate of movement can be estimated by knowing the distance between shelters and the time required to pass from one shelter to another. In general daily foraging and meandering movements of lobsters are considered to be <300m (Cooper and Uzmann 1980). This is very similar to the estimates of daily movement for lobsters in the Great Bay Estuary determined by tag-recapture methods and ultrasonic telemetry (Watson et al. in press). It is also very similar to the estimates determined in the present study, particularly in the field trials. Therefore, this new technique appears to be suitable for monitoring normal activity and movement patterns and may be useful in studies of home range, dispersion, or catchability.
There is some precedence for studying activity using magnetic techniques (Krum and Sheehan 1992) or electromagnetic tags (Jernakoff 1987, Smith et al. 1998). A system similar to ours was developed to identify moving fish while excluding stationary fish by means of a moving magnet attached to a fish which induced a voltage in a coil of wire when it passed through the coil (Krum and Sheehan 1992). The activity of the closely related, Homarus gammarus, was studied using electromagnetic tags with tilt switches incorporated to estimate locomotion (Smith et al. 1998). To our knowledge this is the first time a system such as the one employed in the present study has been used to study activity in any benthic species in the lab and the field concurrently.

There is the possibility that attaching magnets to animals will affect their activity in some way because some species use the earth's magnetic field as an orientation cue (Wiltschko and Wiltschko 1995). In addition, it has been suggested, but primarily discounted, that magnetic cues could serve as circadian zeitgebers (see Wiltschko and Wiltschko, 1995 for discussion). Magnetic orientation has been reported in the spiny lobster Panulirus argus, which appears to possess a magnetic compass sense based upon field polarity (Lohman et al. 1995). However, the transduction mechanisms responsible for magnetoreception are still unknown for any multicellular organism. It is possible that H. americanus has similar abilities but even if this is the case, it is unlikely that this affected our results for the following reasons: 1) experiments run with video controls did not show any differences in behavior between magnet vs. non-magnet trials (unpublished data); 2) because the magnetic stimulus was constant it is likely that adaptation occurred; 3) direction of movement was not measured, only distance and relative activity. Thus orientation, even if altered by the magnet, would not have affected our results.

Our data compare favorably to the timing and magnitude of activity seen in other published studies using "non-magnetic" methods (Cobb 1969, Lawton 1987, Karnofsky et al. 1989). In the lab the pattern generated was almost completely nocturnal whereas in the field there was significantly more daytime activity, even though peak activity still
occurred nocturnally. The difference in activity levels and timing between field and lab seen in this study may be explained by an increase in exogenous cues modifying behavior in the field compared to the lab. There was also some increased day and night-time activity during flooding tidal periods as was seen by Karnofsky et al. (1989) but these results were equivocal. In the field there was a large crepuscular peak that was greatly reduced when visual cues were removed. Interestingly, the level and pattern of activity were similar in both the lab and field when animals were blindfolded suggesting visually mediated differences in normal lobsters.

The evidence for a weak endogenous component to the activity rhythms of lobsters is equivocal but consistent with prior studies (Cobb 1969). Cobb (1969) showed that "an endogenous circadian rhythm of locomotory activity exists in DD, but its expression appears to be inhibited during the winter and spring months when the water temperature is low." We have also found that activity is greatly reduced in spring and winter at temperatures <10°C such that there is no evident pattern in daily activity (see Chapter 3). Interestingly Cobb (1969) also found that offshore lobsters, which were acclimated to lower light levels, expressed less rhythmicity than inshore lobsters. This is similar to the comparison of our field data (where light was lower) to our lab data where light was higher. Lastly, offshore lobsters also showed significantly lower activity levels in constant darkness compared to normal L:D and even lower levels in constant light. However, while inshore lobsters, which were acclimated to relatively high light levels, showed reduced activity in constant light conditions, levels of activity in constant dark conditions were similar to those in normal L:D. These data are strikingly similar to our findings where blindfolded animals in the field showed lower activity compared to L:D but those in lab did not. The mechanisms behind these findings are unclear but may be related to dynamic vs. static exogenous conditions.

Light seems to be the most important exogenous factor influencing daily activity of lobsters (Cobb 1969, Zeitlan Hale and Sastry 1978, Jernakoff, 1987, Lawton 1987, 

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Lawton and Lavalli 1995). Light levels do not only change with movement of the sun; they may also be affected by water depth or water clarity (Cooper and Uzmann 1980, Smith et al. 1998). For example, offshore lobsters which are acclimated to lower daytime light levels than inshore lobsters because of differences in light with depth show a less tightly coupled activity rhythm (Cobb 1969). This "may be an indication that animals which are not chronically exposed to relatively large diel variations in light intensity tend to exhibit imprecise and poorly expressed rhythms of locomotor activity (Cobb 1969)."

In deeper, or turbid, water where light levels are lower lobsters have often been seen out of shelter during the day (Stewart, 1972, Briggs and Muschacke 1979, Howard and Nunny 1983, Lawton and Lavalli, 1995; R. Cooper personal communication in Karnofsky et al., 1989). Lower light levels may influence behavior of lobsters by changing the timing of activity due to release from inhibition at different times or by allowing increased activity because of a reduced need for antipredator behavior (Abrahams and Kattenfeld 1997). Thus, even though lobsters are primarily active at night, some lobsters, particularly those in the field, showed bursts of diurnal activity which may be related to variable light intensity or rate of change. At least some lobsters in Great Bay and nearby coastal areas show diurnal activity because we have also had unexpectedly high catches of lobsters during day time soak periods of <6 hrs (Jury unpublished data). These were corroborated with underwater video observations where many lobsters were observed approaching and entering a trap, or approaching tethered juvenile lobsters, during the daylight in waters <10m (Jury unpublished data). In addition, light levels decrease as one moves up the Great Bay Estuary such that in July the depth for 1% light reaching the bottom is approximately 5m at JEL but >14m at Portsmouth Harbor (Daly, et al, 1979). These light levels also change seasonally such levels reaching the bottom are generally lower in the spring (1% light levels generally at <5m throughout the estuary) and increase through the summer and fall. This is primarily
due to runoff induced changes in turbidity Daly, et al, 1979). Thus the realized activity of lobster may depend upon local habitat conditions.

Evidence for low, but consistent, diurnal activity is widely available in other decapods as well (Kanciruk and Herrnkind 1973, Lipcus and Herrnkind 1985, Rebach 1987, Lawton 1987, Smith et al., 1998). Electromagnetic telemetry showed low but consistent movements of H. gammarus between reef units during diurnal periods even though nocturnal activity was much greater (Smith et al. 1998). Cancer novaezelandiae that were studied in the lab and in potting surveys in the field, also showed high nocturnal activity but some crabs were active and captured during the day, primarily during flood tide in late afternoons (Chatterton and Williams 1994). Nephrops norvegicus in laboratory studies showed an endogenous nocturnal rhythm regardless of depth of origin (Aregchiga and Atckinson 1975). However, in the field, the catch of lobsters (an indication of activity) was directly related to light level and light level was directly related to depth, such that N. norvegicus is active in day and night periods in deep water, but only at night in shallow water. Another example of the strong inhibitory effect of light on activity is that the full moon has been shown to decrease catch of spiny lobsters (Nagata and Koike 1997). Thus light appears to have a direct effect upon activity but it may also have an indirect effect by controlling availability of food, activity of predators and prey, and susceptibility to predators.

The illumination level at the beginning of the hour of peak activity for H. americanus in the laboratory lab was below 0.054 lux. H. americanus has also been suggested to initiate activity at light intensities below 2x10^{-2} W/cm² (Weiss 1970) (unfortunately these units cannot be directly converted to lux). Indeed it is likely that lobsters are even more sensitive to light levels than these values suggest because below this level activity is initiated but is not necessarily the threshold for detection. Nagata and Koike (1997) determined that in Panulirus japonicus light levels higher than 1.8x10^{-5} lux were sufficient to alter night-time activity patterns and thus this species is expected to be
sensitive to light of this low intensity. In *N. norvegicus*, there is an attraction to light at 0.1-1.0 lux but an avoidance of light at 10-10⁴ lux, while between these levels there is a mixed response of avoidance and attraction (Arechiga and Rodriguez-sosa 1997). The thresholds for attraction and avoidance are also 1-2.5 log units lower at night than during daylight, and the latencies for response are shorter. Thus, it is expected that the effect of light on activity will be influenced by behavioral state of *H. americanus* as well.

In general, this study indicates that small environmental variations due to tidal fluctuations (e.g., temperature, salinity, currents, etc.) do not influence daily activity as much as light. Jemakoff (1987) came to this same conclusion in a field study of the spiny lobster *P. cygnus*. While a tidal component was not obvious in the present study, there were occasional activity changes that were related to changing tides. This type of weak but evident response to tidal changes has been reported to affect the activity of lobsters in other studies as well (Howard and Nunny 1983, Karnofsky et al. 1989, Smith et al. 1998). For example, while not significant, Karnofsky et al 1989 showed a trend toward higher activity during high tide observations compared to low tide. High current speeds, due to the tidal stage, have also been reported to affect activity (Auster 1985, Howard and Nunny 1983, Karnofsky et al. 1989). Thus, while temperature is generally considered to be the trigger for seasonal changes in activity (see Chapter 3; Cobb 1969, Smith et al. 1998), there is little evidence that the daily changes in temperature over tidal cycles strongly effect activity. Finally, while not tested directly in this study it must be recognized that social interaction, size, and possibly hunger may affect the activity of free ranging lobsters in the field, depending upon the density of animals and the habitat (Lawton 1987, Zeitlan Hale and Sastry 1978). Thus, rhythmicity is coupled to environmental variation, primarily light, and the onset and offset of activity will vary dependent upon the environment (Cobb 1969).

In conclusion, while a weak endogenous component appears to exist in *H. americanus*, it is strongly modulated by light. This is true even in highly variable
estuarine environments with large tidal variations in temperature and salinity. This combination of exogenous and endogenous components has often been observed in other crustaceans. Indeed Rebach, (1987) in his work with *C. irroratus* suggested that "Locomotor activity may be only weakly coupled to endogenous circadian and/or circa-tidal oscillators, and in most species, simply under the exogenous control of the environment". As was found for crabs (*C. novaezelandiae*), "the present study illustrates the importance of exogenous factors in regulation of timing of activity of epifaunal decapod crustaceans, and shows the value of carrying out quantitative field and lab experiments to determine the relative contribution that endogenous and exogenous variables make to activity patterns observed in the field (Chattemon and Williams 1994)." The differences and similarities between the laboratory and the field further argue for complementing the control of lab studies with the "reality" of field studies to elucidate behavioral and ecological relationships.
CHAPTER 3

THE EFFECT OF TEMPERATURE ON THE LOCOMOTORY ACTIVITY OF LOBSTERS, *HOMARUS AMERICANUS*

**Summary**

It is widely accepted that seasonal increases in temperature cause increased locomotory activity in the American lobster, *Homarus americanus*. This view is based primarily upon the laboratory study of McLeese and Wilder (1958). Studies of activity over the range of temperatures typically encountered by lobsters in the Great Bay estuary, NH were conducted to examine this relationship in more detail. These studies, and a careful examination of the literature, shows that activity is not linearly related to temperature but instead appears to shift between various 'activity states'. Activity is low, and relatively temperature dependent <10°C; is generally higher and relatively temperature independent between 10-20°C; and is higher still but once again temperature dependent, as potentially lethal water temperatures are approached at >20°C. This relationship was also evident when environmental co-variables (salinity, light, etc.) were controlled by heating or cooling lobsters by approximately 5 °C in the spring, summer, or fall and recording short term alterations in activity after 48 hrs.

Catchability is also commonly considered to be temperature dependent largely based upon McLeese and Wilder's (1958) description of this relationship for temperatures between 3-12°C. However, a synthesis of the present findings, data from McLeese and Wilder (1958) and other previous studies shows that the relationship between temperature, activity and catchability, while present, should be interpreted cautiously due to temperature dependent factors that may affect catchability independent of activity.

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Introduction

It is commonly accepted that seasonal changes in *H. americanus* locomotor activity are directly related to temperature, with greatest activity at the warmest temperatures (McLeese and Wilder 1958, Cobb 1969, Ennis 1984, Karnofsky et al. 1989, Lawton and Lavalli 1995). McLeese and Wilder (1958) showed that induced walking rate in response to bright light was directly related to temperature between 2-10°C and 20-25°C. However, it was fairly temperature independent between 10-20°C (McLeese and Wilder 1958), which encompass the most common temperatures in New England waters during the fishing season. It is also generally accepted that in the field, as temperature rises, increased activity, nomadic movements, and/or directed migration generally results in the re-occupation of warmer shallow waters in the spring and summer (Ennis 1984, Karnofsky et al. 1989, Lawton and Lavalli 1995, Watson et al., in press). Tagging studies have also shown that lobster movements into inshore and estuarine areas often closely follow local changes in temperature (Cooper and Uzmann 1980, Munro and Theriault 1983, Lawton and Lavalli 1995, Smith et al. 1998, Watson et al. in press). However, it is unclear how naturally occurring seasonal temperature changes effect the activity of lobsters acclimatized to seasonally realistic conditions. It is also unknown if the thermal independence of activity between 10-20°C found by McLeese and Wilder (1958) is evident in freely behaving lobsters.

As activity increases, catchability of lobsters also increases as an individuals likelihood of entering a trap increases (McLeese and Wilder, 1958). McLeese and Wilder’s (1958) study is repeatedly cited as the key evidence for this relationship, and they show that catchability does increase with temperatures from 3-12 °C. However, in the same paper they suggest that activity is not temperature dependent between 10-20°C. Based upon these data alone, there is no reason to predict that catchability would be temperature dependent between 10-20°C; temperatures which are common at certain times.
Table 3.1. Relationship between temperature and activity in the literature.

Activity has been shown to be both temperature dependent and temperature independent in previous studies depending upon the range of temperatures tested and the particular experiment conducted. These studies are consistent with activity being temperature-independent between 10-20°C, but temperature dependent otherwise.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Type of Study</th>
<th>Temperature Dependence</th>
<th>Temperature Range (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>McLeese &amp; Wilder 1958</td>
<td>activity (lab)</td>
<td>yes</td>
<td>0-10 and 20-25</td>
</tr>
<tr>
<td>McLeese &amp; Wilder 1958</td>
<td>activity (lab)</td>
<td>no</td>
<td>10-20</td>
</tr>
<tr>
<td>Reynolds &amp; Casterlin 1979</td>
<td>activity (lab)</td>
<td>yes</td>
<td>10-15 and 22-28</td>
</tr>
<tr>
<td>Reynolds &amp; Casterlin 1979</td>
<td>activity (lab)</td>
<td>no</td>
<td>15-21</td>
</tr>
<tr>
<td>Ennis 1984</td>
<td>activity (field)</td>
<td>yes</td>
<td>-1-12</td>
</tr>
<tr>
<td>Karnofsky et al. 1989</td>
<td>activity (field)</td>
<td>no</td>
<td>10-24</td>
</tr>
<tr>
<td>McLeese &amp; Wilder 1958</td>
<td>catchability (field)</td>
<td>yes</td>
<td>3-12</td>
</tr>
<tr>
<td>Ennis 1973</td>
<td>feeding activity (field)</td>
<td>yes</td>
<td>-1-14</td>
</tr>
</tbody>
</table>
of the year in many habitats throughout the species biogeographic range. Several studies have also shown that activity, and potentially catchability, are not necessarily temperature dependent between 10-20°C (Table 3.1). Nonetheless, catch data may show temperature dependence even above 10°C, depending on location and spatial and temporal scale (Koeller 1999). For example, monthly catch data (n=44) from one location in Portsmouth Harbor shows a weak but consistent correlation with temperature from 3-17°C (Fig. 3.1; W. Watson, unpublished data).

Temperature may affect catch through mechanisms other than activity. Increased molt probability and growth into a catchable size may be greater at warmer temperatures (Flowers and Saila 1972, Fogarty 1988, Pezzack 1992). Longer term changes in catch may also be due to temperature effects on eggs, development, larval recruitment, and subsequent survival of early life history stages (Aiken and Waddy 1986, Waddy et al. 1995). In addition, behavioral preference for 15.9°C or avoidance of temperatures >23°C (Crossin et al. 1998) could lead to small local differences in catch if lobsters are selecting habitats based upon these temperatures and if there is sufficient thermal heterogeneity to perceive these 'choices' (see Chapter 5). Temperature may also affect survival or fitness indirectly through effects on general ocean productivity and subsequent food supplies, predator-prey relationships, and intra-/interspecific competition. Fogarty (1988) examined the interaction between some of these multiple effects using time series data from the coast of Maine. He found that there were significant temperature effects at 1 and 6 year time lags. The 6 year lag is expected to be due to long term temperature dependent effects on growth and recruitment, whereas the one year affects were due to increased catchability at increased temperatures presumably due to increased activity (Fogarty 1988, Pezzack 1992, Hudon 1994, Koeller 1999).

Temporal and spatial fluctuations in temperature are common in the Great Bay estuary and may play a critical role in the locomotor activity of estuarine lobsters (Howell et al. submitted, Watson et al. in press). The distances moved by tagged lobsters increase
seasonally as temperatures increase (Cooper and Uzmann 1971, Estrella and Morrissey 1997, Smith et al. 1998, Watson et al. in press). However, daily fluctuations in temperature do not seem to greatly affect the activity patterns of lobsters (see Chapter 2). In estuaries low salinity also appears to effect the timing of lobster movements because lobsters move up into the Great Bay estuary after spring runoff and also move out of estuary after extreme low salinity events (e.g., hurricanes) (Jury et al. 1994, Jury et al., 1995, Watson et al., in press). If lobsters are able to sense changes in environmental conditions, increased locomotor activity may be a mechanism to utilize optimal, or avoid damaging, temperatures. Activity experiments and field observations have historically been conducted in the warmer months of the year for logistical reasons, and thus less is known about how activity of naturally acclimated animals changes with seasonally realistic environmental changes. The present study was conducted to determine the activity of lobsters under naturally occurring environmental conditions in a thermally variable estuarine habitat so that the results could be interpreted in an ecologically realistic manner (Kanciruk and Herrmkind 1973).
Figure 3.1. Monthly temperature vs. Catch per unit effort (CPUE) at the mouth of the Great Bay Estuary. CPUE determined as the mean monthly catch per trap haul for 1988-96 at the UNH Coastal Marine Lab shows a positive trend but with high variation ($y = -0.773 + 0.270x$, $r^2 = 0.265$). This relationship between temperature and catch may indicate preference, or increased activity, at higher temperatures that are influencing catchability. However, other interacting behavioral factors may account for the high variation.
Materials and Methods

Measuring Locomotory Activity

The methods used in this study are described in Chapter 2 where diel activity patterns were presented for the summer lobsters shown in this chapter. Briefly, individual adult lobsters (81-92 mm carapace length; n=33 males and 22 females) were placed into a 1 m diameter x 25 cm wide racetrack located in a flow through tank in an outdoor greenhouse at the UNH Jackson Estuarine Lab (JEL). Three magnetic reed switches were attached to each of two PVC conduits located at opposite ends of the racetrack. When a lobster passed through a conduit, a magnet (1x1") attached to its dorsal carapace caused one of the switches to close and a subsequent voltage was sent to a datalogger. Activity was determined by counting the number of passes from one conduit to another in a 24 hr period. Distance moved/ day was approximated by multiplying the circumference of the center of the racetrack (3 m) times the number of passes. Daily activity was determined for each lobster tested as the total number of passes, or distance moved, per day. Data are presented as mean ± SEM unless otherwise stated.

After placement in the race track, lobsters were allowed to become accustomed to the tank overnight. Twenty four hours of locomotion data was then collected at the ambient environmental conditions in the flow through tank. These experiments were run in 1996-1998 in all seasons: Winter (December, January, February; n=8) Spring (March, April, May; n=11) Summer (June, July, August; n=19) and Fall (September, October, November; n=17). Daily temperature (°C) in the tank was recorded using a HOBO datalogger (Onset, Inc.) and salinity (ppt) was measured with an Endeco datalogger near the intake to the flow through tanks at JEL. Salinities were lowest in the spring and winter (14.4 ± 1.0 and 17.1 ± 1.3) respectively, and consistently higher in the summer and fall (25.7 ± 0.5 and 27.1 ± 0.2). Temperatures were as follows: winter 4.7 ± 0.7, spring 9.1 ± 0.7, summer 19.9 ± 0.2, and fall 14.4 ± 0.6. Daily variation in temperature was
highest in summer (standard deviations (SD) ranged from 0.28-0.91) and lowest in winter (SDs ranged from 0.04-0.54). Lobsters were exposed to ambient light levels which varied seasonally.

**Heating/Cooling Experiments**

To test the effects of acutely changing temperature, independent of other seasonal environmental changes, lobsters were tested under ambient conditions and then exposed to temperature changes of 5°C. Lobster activity was measured as described above for 24 hours and then the tank was heated approximately 5°C above ambient temperature over the course of the second day. The activity of these temperature-challenged animals was then recorded on the third day. These experiments were conducted using approximate 5°C increases from 10, 15, and 20°C. In the spring ambient temperatures of 9.8±0.61 °C were heated to 16.2±0.88 °C (n=9); in the summer ambient temperatures of 19.5±0.34°C were heated to 24.5±0.64 °C (n=9); and in the fall ambient temperatures of 14.2±0.45°C were heated to 18.5±0.21°C (n=9).

To determine if cooling also effected activity, a second set of trials (n=6) were conducted with lobsters in the fall which were acclimated to 15.8 ± 0.54 °C, and then exposed to cooler recirculating seawater of 9.3 ± 1.06 °C over the second day. Activity was recorded on the third day as described for the heating experiments. Control animals (n=13) were kept at ambient temperature (20.3 ± 0.21°C) for 3 days (the same amount of time as experimental trials) to determine if there was any change in activity within the racetrack over time independent of temperature changes.
Results

Seasonal Changes in Activity

In general lobsters were more active during the warmest months. In the summer the average daily number of passes was 30.6±4.0, followed by 24.1±4.3 in the fall, 12.2±5.3 in the spring and 3.5±1.4 in the winter. There were significant differences between seasons (ANOVA, p<0.001) with significantly higher activity in the summer vs. the winter, fall vs. winter, and summer vs. spring (Tukey's post hoc test, p<0.05). However there were no significant differences in activity between winter and spring, summer vs. fall, or spring vs. fall (Fig. 3.2). There were also no significant differences in activity between the sexes (paired t-test, p>0.40) (Fig. 3.3).

The relationship between activity and temperature is not linear. Instead, a temperature of approximately 10°C in the spring and fall appears to be a "thermal switch", triggering a change in activity to a new state (Figs. 3.2 & 3.3). This may be affected in the spring in estuarine areas by increasing salinity as well (see Fig. 3.2), but it is not possible to separate the effects of these two co-variables in naturally occurring conditions. Nonetheless, in the summer and fall, when salinities were high and temperatures were decreasing, there was no evidence of thermally dependent activity (Fig. 3.2).

Heating/Cooling Experiments

In control trials, where lobsters were run for 3 days at ambient temperatures there were no significant differences in their activity each day (Repeated measures ANOVA, p >0.10); day 1 =25.9±4.5, day 2 =28.5±5.2, day 3 =31.9±5.1 passes/day. Thus, activity did not change over time due to the experimental protocol alone.
Figure 3.2. Julian Day vs. ambient temperature and salinity and activity (distance moved/day). Seasonal changes in activity closely correlate with environmental changes. Temperature and salinity covary and both could be effecting changes in activity. Note that activity shows two distinct states in winter compared to summer. This transition occurs at approximately 10°C in the spring and fall and appears to be related to temperature and differences in physiological state between seasons.
Figure 3.3. The relationship between activity and temperature or salinity. Activity (in distance moved per day) vs. ambient temperature (A.) is not linear, but appears to increase to a new level when the temperature was >10°C. Activity vs. salinity (B.) seems to indicate that activity remains low at <18 ppt, the same salinity that lobsters avoid in laboratory assays (Jury et al., 1994a). Unfortunately, due to covariation it is not possible to definitively separate the effects of temperature and salinity at this time. There was no difference in male vs. female activity (unpaired t-test, p>0.10).
These experiments were designed to test the hypothesis that acute temperature changes of approximately ± 5°C in any season (i.e., acclimation temperature) do not affect activity. The findings show that when moving into the 10-20°C range in the spring from cooler temperatures (9.76±0.61 to 16.2±0.88°C), animals did not show an increase in activity within 48 hours (paired t-test p>0.10); mean passes 15 ± 6.2 to 13 ± 6.3) (Fig. 3.4). Thus heating in the spring does not immediately result in increased activity, even though activity eventually increases in the summer (Fig. 3.2). When fall acclimated animals were heated (14.2±0.45 to 18.5±0.21) there was also no significant change in activity (t-test p>0.10). However, summer animals heated from 19.5±0.34 to 24.5±0.64°C; and thus moving out of the 10-20°C range; showed a significant trend to increase their activity (t-test, p<0.10). Similarly when moving out of the 10-20°C range in the fall upon cooling (15.8±0.54 to 9.3±1.06°C) there was a trend to decrease their activity (paired t-test; p=0.11). Thus, these experiments suggest that locomotory activity between 10-20°C is thermally-independent, and when the temperature is shifted out of this range, locomotion either decreases (<10°C) or increases (>10°C) (Figs. 3.2 & 3.3).

Under ambient conditions, i.e. on the first day of recording prior to a temperature challenge, there was no significant difference in activity (ANOVA, p>0.10) between seasons. However there was a high amount of variability in activity between individuals in each season, with some lobsters which showed high activity and some which moved very little (spring: 0-51 passes/day; summer 2-50; fall 3-66). This is similar to the findings for all lobsters tested under ambient conditions (Fig. 3.2).
Figure 3.4. Short term effect of heating or cooling at various temperatures. When spring or fall animals were acclimated to approximately 10 or 15 °C and then heated to 5 °C warmer than ambient there was no significant change in activity (paired t-test p>0.10). However, when summer acclimated animals (19.5±0.34°C) were raised by 5°C there was a significant increase in activity. There was also a significant decrease in activity when fall acclimated animals (15.8±0.54°C) were cooled to 9.3±1.06°C. Thus, when leaving, but not upon entering, the temperature range from 10-20°C, there is a significant change in activity. Entering this zone from cooler temperatures must ultimately lead to an increase in activity (as seen in animals acclimated to 15°C) however the transition apparently occurs slowly.
Patterns of lobster activity may be broadly characterized as daily (e.g., diel or circadian rhythmicity) and seasonal. Chapter 2 describes the daily activity of lobsters using methods identical to those in this chapter. Lobsters are primarily nocturnal with weak endogenous rhythms. This pattern is strongly modified by environmental cues, primarily light, with lobsters exhibiting little response to tidal variations in temperature and salinity. The present study focused upon seasonal differences in activity and concludes that while temperature does have an influence on locomotory activity, the relationship is not linear. Instead lobsters appear to have two distinct "activity states". There is limited activity at <10°C, which is highly temperature dependent (Ennis 1984, Karnofsky et al. 1989, Smith et al. 1998); at >10°C a new state is achieved which is temperature-independent up to 20°C (McLeese et al. 1958, Reynolds and Casterlin 1979); and at >20°C activity tends to increase, possibly due to avoidance behavior (Crossin et al. 1998) as the upper lethal limit is approached (McLeese 1956). Thus, activity increases seasonally and peaks in the months that are warmer than 10°C. It is also possible that some temperature independent factors (e.g. photoperiod) may affect physiological state and subsequently general activity level. Seasonal temperature-independent effects were seen in Chapter 1, where heart rates were higher in summer than in winter in lobsters acclimated to 15°C. Thus, seasonal differences in physiological state and subsequent behavioral state or 'motivation' may be affecting activity in a manner that is presently unclear but worthy of further investigation.

A model incorporating information from this study and previous studies defines the relationship between lobster activity and seasonal differences in temperature (Fig. 3.5). The findings from the present study are consistent with those of McLeese and Wilder (1958) and Reynolds and Casterlin (1979) who found that induced walking
Figure 3.5. Overview of the effect of temperature on lobsters. Monthly temperatures are presented for the temperatures near the northern and southern end of lobsters geographical range (Memorial Univ. Lab, Newfoundland (J.A. Brown personal communication) and Cape Hatteras, NC, National Ocean Service buoy # DSLN7 from www.nodc.noaa.gov). Final preferred temperature (FPT) is shown as a dashed line within the preferred thermal zone of 10-20°C where activity is temperature independent but at a relatively high level (McLeese and Wilder 1958). Based upon other studies, this zone is expected to be optimal for growth, development and reproduction (Crossin et al. 1998, Reynolds and Casterlin, 1985). Lobsters also seem to require both temperatures below 5°C and above 10°C at some time in the year to synchronize their molting and reproduction (Waddy 1995) and this is reflected in the temperatures at the limits of their geographic ranges. Within the cold zone (i.e., <5°C) it is expected that there is temperature induced immobility and torpor as the lower critical thermal tolerance is approached (McLeese 1956, Karnofsky et al. 1989, Waddy 1995). As temperatures move into the transitional zone in the spring and fall, it is expected that metabolism and activity are higher and highly temperature dependent (McLeese and Wilder 1958, Waddy 1995). Lastly, temperatures above 20°C in the warm zone are avoided as the upper critical thermal tolerance is approached (see Chapter 4, Crossin et al. 1998, McLeese and Wilder 1958, McLeese 1956). It is expected that the realized temperature inhabited by a lobster will differ somewhat from the fundamental temperatures shown here because field habitat selection will depend upon a suite of factors.
increased rapidly between 0-10°C and above 20°C, but did not change between 10-20°C. At temperatures of less than 5°C there is little or no activity. It is possible that animals become effectively metabolically "trapped" in a given area when temperatures drop too low and thus overwintering habitat may need to be anticipated prior to this incapacitation. Lobsters increase their tendency to move and feed up to 10°C (Ennis 1973, Karnofsky et al. 1989). This seems to be a transitional period between activity states where activity is directly correlated with temperature (McLeese and Wilder 1958). In the region of 10-20°C there is an overall higher level of activity, with high variation between individuals, but within this range temperature does not seem to greatly effect activity (Reynolds and Casterlin 1979, McLeese and Wilder 1958). The final preferred temperature of lobsters (15.9°C) also falls in the middle of this range (Reynolds and Casterlin, 1979, see Chapter 4 and 5) and thus there may be some adaptive reason to remain within this thermal niche (see Chapter 4 and 5). While high levels of activity are probably possible at >20°C, they are approaching damaging or even lethal levels (McLeese 1956) and lobsters avoid them (see Ch. 4 and Crossin et al., 1998). Extremely warm temperatures are uncommon throughout most of the habitat range of this species, but do seasonally occur in estuarine areas or habitats at the southern end of lobster's geographic range. Thus, temperatures near 10°C appear to serve as a "thermal switch" that upregulates internal mechanisms resulting in the potential for higher activity. This "potential" is not necessarily realized depending upon competing factors that affect activity levels (e.g., molt stage, intraspecific competition, predation risk, etc.).

Several environmental variables also change seasonally and may affect activity. In the present study, salinity and daylength (i.e., photoperiod) are covariables with seasonal temperature changes and have been shown to affect the behavior of *H. americanus* (Aiken and Waddy 1986, Jury et al. 1994, Jury et al. 1995, Lawton and Lavalli 1995). For example, in the laboratory, lobsters become restless when salinities drop to <18.4 ppt and they actively avoid salinities of <12.6 ppt (Jury et al. 1994). In the present study, this
may have affected the activity levels recorded in the spring, and possibly winter, but probably did not affect summer or fall activities (Fig. 3.2). It is quite possible that under ambient environmental conditions these and possibly other internal variables affect activity in lobsters. For example, Karnofsky et al. (1989) found that there was a peak in activity of lobsters in a shallow cove just prior to the molt. While under natural conditions it is likely that temperature interacts with several variables, temperature does affect activity independent of other environmental changes as determined by the heating and cooling experiments. While many cues are available, and multiple cues may alter behaviors, temperature may be the most consistent seasonal cue to trigger changes in activity states. Multiple exogenous cues also influence P. argus such that photoperiod is probably most important in influencing daily rhythms but temperature fluctuations also have triggering effects (Kanciruk and Herrmkind 1973). For example, fall migrations of P. argus appear to be triggered by large drops in temperature coincident with fall storms and not by photoperiod. Many different stimuli may affect seasonal movements and migrations in vagile decapods and this versatility may allow behavioral modifications for different habitats within the range of a given species (Rebach 1987). Seasonal modulation of physiological states due to temperature, or some other environmental variable, may also modify behavioral outputs that result in adaptive habitat selection.

The model of lobster activity in response to temperature outlined above could explain some inconsistencies from the literature relating to the local thermal conditions in the area of these studies (see Table 1). For example, Ennis (1984) working in Newfoundland, studied the activity of lobsters in the field by conducting dive surveys and recording the number of times an individual was seen outside a shelter vs. the number of times it was seen anywhere. These relative estimates of activity were closely related to temperature, but the temperature range when observations were taken was -1 to 14°C. In contrast Karnofsky et al. (1989), using similar diving methods, found that activity increased seasonally, with highest levels in summer; but it did not closely follow
temperature. They concluded that temperatures above 10°C did not predict activity as closely as found by Ennis (1984). This study however, had observations at temperatures up to 24°C, with most of the observations within the range of 10-20°C. Also while catchability of American lobsters are often considered to be temperature dependent based upon the findings of McLeese and Wilder (1958), they only present catch data from 3-12°C. Thus models incorporating the relationship of temperature, activity, and catchability should consider the temperature range of the area under consideration in combination with the local ecological context.

Information on seasonal differences in activity due to environmental changes increases our understanding of lobster habitat utilization and may assist in estimating lobster catchability and management of the fishery (Smith et al. 1998). Our results show that there is diel (see Chapter 2) and temperature dependent seasonal variability in activity which may be affecting catchability. However, this relationship only seems to be valid from 0-10 or 20-25°C, while between approximately 10-20°C activity is relatively temperature independent (McLeese and Wilder 1958, Reynolds and Casterlin 1979). Interestingly, there may be some relationship between catch and temperature within 10-20°C at small scales as lobsters may prefer to be at 15.9°C (Crossin et al. 1998) and seek areas near this temperature. In the Great Bay Estuary, tag-recapture studies (Watson et al. in press) show that there is a relationship between month, distance moved, and direction moved that appears to be related as much to spatial differences in temperature as to kinetically induced increased activity in the warmer months (see Chapter 5). The amount of lobsters available to the fishery, and subsequent catch, could also be affected by temperature through increased molt probability at warmer temperatures (Saila and Flowers 1972, Fogarty 1988, Pezzack 1992, Hudon 1994); effectively moving prerecruits into a catchable size at a time of year when temperatures are warmest. Changes in fishing effort that correlate with changing temperatures due to weather conditions may also result in misleading interpretations of catch vs. temperature (Koeller 1999). Thus the relationship
between temperature and catchability in the short term appears to consist of multiple mechanisms which may interact with, and even mask, each other depending upon time and location. Thus the relationship(s) between activity, temperature, and catch, while present and significant in terms of fishery management, should be "...interpreted cautiously" (Koeller 1999).
CHAPTER 4

BEHAVIORAL THERMOREGULATION IN THE AMERICAN LOBSTER, 
HOMARUS AMERICANUS

Summary

It is generally accepted that water temperature has a strong influence on the behavior of the American lobster Homarus americanus. To initially characterize the behavioral responses of lobsters to thermal gradients, two different experiments were conducted. In the first, 40 lobsters acclimated to summer water temperatures (summer-acclimated, 15.5 ± 0.2°C, mean ± SEM) 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 ± 0.4°C, which was an increase of 8.0 ± 0.4°C from ambient summer temperatures. When this experiment was repeated with lobsters acclimated to winter temperatures (winter-acclimated, 4.3 ± 0.1°C), the lobsters (n=30) did not find temperature (ΔT=8.0 ± 0.4°C) increases of the same magnitude aversive.

The second experiment was designed to allow summer-acclimated lobsters (n=9) 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 ± 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 ± 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.
Additional thermal gradient tank experiments testing the effects of sex and acclimation are discussed in Chapter 3. (Some of these data are presented in Crossin et al. 1998)

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 (Hines et al. 1987), have evolved to maximize residence in warm water and thus enhance growth and/or reproduction (Aiken 1980, Aiken and Waddy 1986, Waddy et al. 1995).

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 (Waddy et al. 1995). 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 catch and landings (Flowers and Saila 1972, Fogarty 1988, Campbell et al. 1991, Hudon 1994, Koeller 1999). 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°C) in a 10-25°C gradient, and water colder than 10°C in a cooler gradient (4-18°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°C (range 15-20°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.

Two experiments were carried out to determine the range of water temperatures that lobsters find preferable and aversive. In all trials, lobsters generally preferred water between 12 and 18°C, or temperatures slightly warmer than the ambient temperatures at the time of testing, and avoided water warmer than 20-23°C. These findings are consistent with earlier crustacean studies and confirm that lobsters behaviorally thermoregulate. 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), 82-92 mm carapace length (CL), 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 sea water tanks at the UNH Coastal Marine Laboratory (CML) in New Castle, NH, USA. All lobsters were in intermolt stage C4 (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 sea water tanks inside the laboratory ranged from 1°C in winter to 18°C in summer. All values are presented ± the standard error of the mean (SEM). In the description given below, lobsters acclimated to summer temperatures of 11-18°C are referred to as summer-acclimated; winter-acclimated lobsters are those acclimated to winter temperatures of 1.5-5°C.

**Temperature Avoidance Assay**

Individual lobsters (n=40 in summer, n=30 in winter) were placed in a 2.5 m x 0.5 m tank, filled to a depth of 13 cm with running sea water. A shelter constructed from a 25 cm wide polyvinyl chloride pipe, bisected lengthwise, was placed 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 min. During the final 30 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 were 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°C/min, increasing from ambient (15.5°C) to approximately 25°C in the summer (4.3 to 12.3°C in the winter) during the first 30 min of the experiment, and then staying at that level for the next 30 min. This protocol heated the shelters in both the summer and the winter to at least 8°C warmer than ambient. As soon as the lobster left the shelter (defined as more than one body length away, or approximately 30 cm), the temperature inside the shelter was recorded as the warm-avoidance threshold for that animal. If no response occurred within 1 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 ± 0.2°C; winter=4.3 ± 0.1°C) sea water rather than warm antifreeze.
Temperature Preference Assays

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. 4.1). 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 6.9-19.2°C in one experiment, to a maximum of 15.2-26.2°C in another. On average, the temperature ranged from 12.0 ± 1.0°C to 22.0 ± 0.8°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°C). Just prior to the experiment, a HOBO™ temperature logger in a waterproof case (6.25cm x 8.75cm x 2.5 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°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°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 trials. Acute preferenda (Reynolds and Casterlin 1979b) were not measured. 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 trials were monitored using a time-lapse video-tape recorder and a low-light-sensitive video camera mounted over one end of the tank. The positions of animals in some of the trials with the temperature gradient functioning were also recorded in order to confirm the accuracy of the datalogger technique. Twelve of the 48h of datalogger data were compared to videotapes 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 the 12h time interval and; 2) the total time spent in each area during the same time period.
Fig. 4.1. (A) Thermal gradient tank viewed from above. 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, at the opposite end. Mixing of warm and cold water was minimized by creating a flow of water between chambers 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.
**Results**

**Temperature Avoidance**

Forty-four lobsters were observed in the temperature avoidance tank during the summer when the ambient temperature was 15.5 ± 0.2°C (range = 13-17°C). Of the lobsters tested, 3 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 to 8.0 ± 0.4°C greater than ambient, most (62.5%) lobsters left the shelter for the cooler surrounding waters (Fig. 4.2A, Chi-squared test for independence, P<0.01). The mean thermal-avoidance temperature for lobsters that left the shelter was 23.5 ± 0.4°C. The smallest change in temperature that elicited a response was an increase of 3.1°C from 15.9°C to 19°C; several lobsters did not respond even when the temperature reached 25°C. In contrast, 100% of the control lobsters (n=20) remained in the shelter (Fig. 4.2A).

To determine whether lobsters found an increase of approximately 8°C, as opposed to an absolute maximum temperature of greater than 23.5°C, aversive, 15 winter-acclimated lobsters of each sex (n=30) were also tested. Starting from an ambient temperature of 4.3 ± 0.1°C (range: 3-5.5°C), shelters were gradually heated to 12.3 ± 0.3°C (range: 10.5-16.5°C), representing an average temperature change of 8.0 ± 0.4°C. Only two out of 30 (6%) of the winter lobsters left the heated shelter (Fig. 4.2B). This was not significantly different from the behavior of control winter lobsters (one of 15 left the shelter; Chi-squared test for independence, P>0.05), but was different from the response of summer lobsters (Fig. 4.3B, Chi-squared test for independence, P<0.05). These data suggest that lobsters find water warmer than 23.5°C aversive, and were not responding simply to temperature increases of a particular magnitude.
Figure 4.2. 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 $23.5 \pm 0.4^\circ C$. 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 approximately $8^\circ C$ (from $15.5-23.5^\circ C$), 62.5% of summer-acclimated lobsters found the heated shelter aversive. Winter-acclimated lobsters experiencing a similar increase of $8^\circ C$, from $4.3$ to $12.3^\circ C$, tended to stay in the heated shelter.
Temperature Preference

- The thermal preference of lobsters was measured by 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) while allowing the lobster to select temperatures in a thermal gradient tank. An example of the data obtained with this method is shown in Fig. 4.3A. 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 (Figs. 4.3B & 4.3C).

Control trials 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. 4.5D, Kruskal-Wallis test, P>0.60), both in terms of number of times an animal entered a given section of the tank and duration of time spent in each section. Examination of the videotapes 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 lobsters' sampled narrowed considerably, and less overall exploration of the tank occurred. These observations suggest that lobsters 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 12.0-22.0°C, they occupied an average temperature niche of 16.5 ± 0.4°C (Fig. 4.4A). 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 ± 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. These summer-acclimated animals did not show significant differences in preference between the sexes however differences do exist when acclimation is considered (see Chapter 5).

The trials 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 ± 0.8°C). This may explain the wide range of temperature preferences in the animals tested. When temperature preference was normalized to ambient temperature (Fig. 4.6B), there was a tighter relationship, and stronger evidence for behavioral thermoregulation. On average, animals in this study spent the most time in water that was slightly (1.2 ± 0.4°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 g1 statistic (Sokal and Rohlf 1969), which measures the departure from normality, or the skewness of the data. In this case, g1 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. The effect of acclimation and sex on temperature preference is extensively considered in Chapter 5.
Fig. 4.3. Comparison of temperature-preference data obtained using dataloggers with analysis of time-lapse video, for a 92 mm carapace length female lobster. (A) Data 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 duration spent in a given area of the tank: areas 1 to 8 represent a temperature gradient of approximately 16.5 to 25.5°C; the total number of times a lobster moved into each area (entries) is also shown. (D) Control trials (n=5) with no temperature gradient present and all data obtained using time-lapse video. No area of the tank was chosen significantly more often (p>0.60), in terms of either duration in an area or number of entries. Values are means ± SEM.
Fig. 4.4. (A) Preferred temperatures of lobsters in a thermal gradient. The mean preferred temperature of nine lobsters was 16.5 ± 0.4°C. Each temperature on the x-axis represents a 1°C range of temperatures. The carapace lengths in mm, sex, and acclimation temperature (°C) for each lobster is provided in the adjacent table. (B) Preferred temperatures standardized for acclimation temperature (preferred temperature minus acclimation temperature) of summer-acclimated lobsters. Most time was spent at a temperature slightly warmer (1.2 ± 0.4°C) than their acclimation temperature. Each bar represents the aggregate number of minutes in each preferred standardized temperature bin by the nine lobsters shown in (A). +,- indicate temperatures above and below their acclimation temperature respectively. 12,383 minutes of positional data are represented.

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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°C and generally preferred areas that were slightly warmer than ambient water and between 12 and 18°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, Beittinger 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 a 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. For lobsters acclimated to 11-18°C, we obtained a final preferred temperature of 16.5°C. Reynolds and Casterlin (1979a) reported a final thermal preferendum of 16-17°C for *H. americanus*, 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 prefer specific temperatures (i.e., behaviorally thermoregulate) after 6 days in their shuttlebox apparatus (see Chapter 5 for discussion of acclimation effects).

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 (Vetrov 1990, W.H. Watson et al. in press). 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" (Munro and Therriault 1983). 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, 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 $< 2^\circ$C (see Chapter 1). Larimer (1964) also observed bradycardia responses to temperature shifts in crayfish. Although we have yet to identify the receptors responsible for mediating this behavior, our preliminary data provide 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 optimum temperature is where growth rate is maximized (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 right themselves most quickly at temperatures between 15 and 20$^\circ$C (Kivivuori 1980), and maximal survival of the crayfish Orconectes rusticus occurs at their preferred temperature of 22$^\circ$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$^\circ$C (J.T. Hughes, personal communication, cited in Reynolds and Casterlin 1979b), and little molting, growth, locomotion or feeding takes place below 10$^\circ$C (McLeese and Wilder 1958, Aiken and Waddy 1986, Factor 1995). Furthermore, locomotion appears to be independent of temperature between 10 and 20$^\circ$C (McLeese and Wilder 1958, Reynolds and Casterlin 1979a; see Chapter 3). Thus, it is possible that behavioral thermoregulation in lobsters...
could serve to minimize time to maturation and maximize their growth and/or reproductive potential. The further elucidation of these relationships remains an exciting area of future research due to their 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 temperatures decreases below their 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 toward areas that are warmer, but stop when they reached extreme temperatures, which approach lethal limits (McCleese 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 (Cooper and Uzmann 1971, Ennis 1984). 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 they 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 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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CHAPTER 5

THE EFFECT OF SEX AND ACCLIMATION ON THE THERMAL PREFERENCE OF THE LOBSTER, *HOMARUS AMERICANUS*

Summary

Evidence for behavioral thermoregulation was presented in Chapter 4. This chapter expands upon that evidence by focusing upon the effects of sex and thermal history (i.e., acclimation) on behavioral thermoregulation. Thermal preferences of sexually mature lobsters, *Homarus americanus*, were determined in the laboratory using a thermal gradient tank. Males consistently preferred warmer temperatures than females, showing a final preferred temperature of 16.3 °C (i.e., the temperature where acclimation temperature equals selected temperature), whereas females had a final preferred temperature of 14.3°C. Lobsters preferred significantly warmer temperatures in colder months (2.8 ± 0.66 warmer than ambient temperatures of 8.2 ± 0.3°C) than in warmer months (0.2 ± 0.39 warmer than ambient temperatures of 15.5 ± 0.4 °C). These data were then compared to catch data from five sites in the Great Bay estuary of N.H. from 1989-1993. Catch per unit effort (CPUE) of lobsters significantly correlated with temperature and the highest CPUE values were at temperatures similar to the preferred temperatures determined in the laboratory. In addition, above 14°C male CPUE was significantly higher than female CPUE, further suggesting that males prefer warmer temperatures than females. A mechanistic model of the behavioral response to temperature is presented and related to the distribution of lobsters in the field. These results indicate that laboratory and field derived estimates of thermal preference of lobsters yield similar results and that models including temperature as a parameter to predict
lobster distribution and abundance may benefit by incorporating both sex and acclimation effects.

Introduction

Behavioral mechanisms allow many ectotherms to minimize or maximize their exposure to various temperatures (Magnuson et al. 1979, Taylor 1984, Stephens 1985, Kelsch and Neill 1990, Kivivouri 1994). As long ago as 1909, the optimum temperature of the lobster, *Homarus americanus*, was estimated to fall between 10.0-15.6°C based upon observations of seasonal movements (Herrick 1909). Since this time, thermal preferences have been inferred from many studies in the field where lobsters seem to be concentrated at temperatures in the range of 8-14°C (Ennis 1984, Aiken and Waddy 1986) or 10-17°C (Cooper and Uzmann 1971, Munro and Therriault 1983, Ugarte 1994). Higher water temperatures have also frequently been related to increased catch and landings (Flowers and Saila 1972, Fogarty et al. 1988, Campbell et al. 1991, Hudon 1994) and it has been suggested that the cause is the temperature dependence of locomotory activity (McLeese and Wilder 1958, Reynolds and Casterlin 1979).

The thermal preferences of lobsters may play a significant role in the directionality and distance of their movements during different seasons and life history stages. For example, many adult lobsters move inshore in the summer and off-shore in the fall, as coastal waters cool more rapidly than off-shore waters (Saila and Flowers 1968, Cooper and Uzmann 1971, Ennis 1984, Pezzack and Duggan 1986, Karnofsky et al. 1989). Lobsters have shown similar movements into and out of estuaries (Munro and Therriault 1983, Watson et al. in press, Howell et al. submitted). Movements seem to be initiated in the spring when temperatures rise above 8-11°C, whereas in the fall, movements appear to be triggered when temperatures drop due to seasonal and/or storm-induced decreases in water temperature. Tag-recapture and sonar tracking studies of the seasonal migrations of estuarine lobsters in the Great Bay estuary, N.H. have demonstrated that larger animals
moved farther than smaller animals, and that the sex ratio was consistently skewed in favor of males in the upper estuary (Vetrov 1990, Watson et al. in press, Howell et al. submitted). Thermal cues have also been shown to initiate movements by American eels (*Anguilla rostrata*) (Haro 1991) and spiny lobsters (*Panulirus argus*) (Kanciruk and Herrnkind 1978). In general, the distribution and abundance of lobsters in the field appears to be greatly influenced by their behavioral response to temperature.

Laboratory evidence for thermal preference by the lobster, *Homarus americanus* was presented in Chapter 4. This study showed that, in the summer individuals left a shelter in response to temperatures above 18°C, which was an increase of 5°C from ambient. However, in the winter, when lobsters were at 5°C, raising the temperature by as much as 8°C did not cause them to leave. This suggests that lobsters find very warm water (>18°C) aversive, and not simply increases in temperature. It also suggests that there are seasonal differences in the response to temperature. Reynolds and Casterlin (1979a) provided additional experimental evidence that lobsters behaviorally thermoregulate by showing that adult lobsters in a shuttlebox apparatus had a thermal preference of ≈16°C (range of 15-20°C). These findings are consistent with earlier crustacean studies, and support the hypothesis that a wide range of aquatic ectotherms occupy "thermal niches" and exhibit thermoregulatory behavior (see Magnuson et al. 1979). This behavior may serve to maximize their potential for growth, development, reproduction, and/or performance by allowing maximal locomotory efficiency or freedom from thermal disturbance to behavioral processes (Taylor 1984, Huey and Kingsolver 1989, Waddy et al. 1995).

Behavioral thermoregulation in some ectotherms has been shown to vary depending on several factors, such as previous thermal history (i.e., acclimation), starvation, hypoxia, size and intraspecific interaction (Magnuson et al. 1979, Kivivouri 1994, Kelsch and Neill 1994, Swain 1997). However, few studies have addressed the effect of sex on temperature preference (Swain 1997). Data presented in Chapter 4.
showed that summer acclimated lobsters presented with a temperature gradient (n=9) selected temperatures slightly above their ambient acclimation temperature (1.2°C) and showed a final thermal preference of 16.5°C. These experiments were conducted in the summer months and the effect of sex and acclimation temperature upon behavioral thermoregulation were not presented. Acclimation has been shown to play a significant role in the temperature selection behavior and motor functions of other aquatic ectotherms such as crayfish (Kivivuouri 1980, Kivivuouri 1994). Our studies in the highly thermally variable Great Bay Estuary, led us to question the possibility that sex and/or seasonal acclimation may affect the temperatures selected by lobsters. The present study shows that males and females tested using the thermal gradient tank technique during warm (summer) and cold (spring and fall) seasons select different temperatures. These lab-derived preferences correspond to catch rates and movements in the field and may help to explain the skewed sex ratios observed in nearshore habitats, including estuaries.

Materials and Methods

Laboratory Thermal Gradient Tank

Lobsters, 82-92 mm carapace length (CL), were purchased from commercial fishermen, or captured with University of New Hampshire (UNH) research traps, from New Hampshire coastal waters. Experiments were carried out from 6/96 to 8/97 when ambient temperatures in the natural habitat, and in the flow-through seawater tables where the animals were held, ranged from 6.8°C to 18.0°C. Methods for the determination of selected temperature were the same as presented in Chapter 4. Briefly, a thermal gradient tank, similar to the one used by Haro (1991) to measure the thermal preference of eels, was modified for use with lobsters. Depending on the ambient temperature, gradients used ranged from an average temperature of 12.1±0.48°C to 21.9±0.44°C in the warm months and 8.4±0.55°C to 18.6±0.76°C in the cold months. Just prior to an experiment a
HOBO™ temperature logger in a waterproof case (6.25 x 8.75 x 2.5 cm) was attached to the lobster's dorsal carapace using a neoprene backpack. Individual lobsters (n=38) were placed for 30 min. in the center of the thermal gradient tank in a 20 cm diameter PVC pipe, and then released. Temperatures cooler and warmer than the ambient temperature to which the animal was acclimated were always available for selection. Animals that preferred temperatures <1°C warmer than the coldest available (or <1°C colder than the warmest available) were not used in the final data analyses (n=7, i.e., 18% of all animals tested) because they 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. Acute preferences (Magnuson et al. 1979, Reynolds and Casterlin 1979b) were not measured. Rather, the final temperature preference (Haro 1991), which was considered to be the mean of the temperatures selected during the second complete day of the experiment, were determined for males (n=15) and females (n=16).

Acclimation temperatures were considered be to the ambient temperature of the holding tank on the day the animal was removed for experimentation. While there is some variation introduced using this method it approximates what the animal encounters for acclimation conditions in the natural environment. Warm-acclimated (WA) animals were those tested from June-September (mean ± SEM=15.5±0.4 °C) while cold-acclimated (CA) animals were those tested from November or May (8.2±0.3°C). Animals were not run from Dec-April due to the reduced mobility of animals collected and held at these low temperatures (i.e., <5°C).

**Catch Data**

Complete methods and site locations are described in Howell, et al., (submitted). Briefly, monthly catch per unit effort (CPUE) at five sites along an estuarine gradient in the Great Bay Estuary were compiled from 1989-1993 to obtain catch estimates for 5
sites, for each month fished, for both males and females. This resulted in a sample size of 91 'site-months'. Mean monthly temperatures were determined using daily recordings from the UNH Jackson Estuarine Lab (JEL) (Endeco CTD datalogger) and the UNH Coastal Marine Lab (CML) (mercury thermometer) on Portsmouth Harbor. Temperatures for the 3 sites along the estuarine gradient between these two labs were determined by linear extrapolation. Because lobsters also avoid salinities <18 ppt (Jury et al. 1994b), only CPUE data from site-months when the salinity was >25 ppt were used in this analysis.

Behavioral Model

A simplistic mechanistic model was developed to illustrate how temperature may affect the movements of lobsters in the field. Mean monthly temperatures available to lobsters in the Great Bay Estuary from 1989-1991 were estimated as described above for catch data. The thermal gradient potentially driving detection, orientation, avoidance, or preference was determined by subtracting CML from JEL temperatures. This also assigned a directionality to the gradient such that it was warmer in the estuary than at the coast in the summer months but the opposite situation existed in the winter. Relative preference for males and females were determined using monthly acclimation temperatures in the regression equations (see results section) determined from the laboratory thermal gradient tank studies (assuming that the available temperature in that month was the acclimation temperature for the lobster) (see Fig. 5.1). Relative Incentive was determined by subtracting the preferred temperature at any time and place from the temperature available (i.e., JEL temperature in Fig 5.1A in this example). This will determine the incentive of estuarine lobsters to move to a given temperature. Thus any points >0 would indicate an incentive to move to warmer temperatures and any <0 would indicate an incentive for cooler temperatures. Directionality from the estuary to the coast, or inshore to offshore, was estimated using the direction of the available thermal gradient.
Relative movement was determined by multiplying relative incentive times the available thermal gradient. Thus any points >0 indicate movement up the estuary and any <0 indicate movement down estuary.

The model results were then compared to tag-recapture data for >70 mm CL male (301) and female (183) lobsters tagged in Great Bay estuary from 1989-1991 and subsequently recaptured within one month (Watson et al., in press). These data were only collected between April and September. Straight line rate of movement was estimated as distance (nautical miles) per unit time (standardized to month) between tag and recapture. Note that the sample sizes are much smaller in the first and last month of data collection and this should be included in the biological interpretation of the results. Methods for the tag-recapture data collection and analysis of all pooled data are presented in Watson, et al. (submitted).

Results

Laboratory Thermal Gradient Tank

When lobsters (n=31) were placed in a thermal gradient tank with a choice of temperatures above and below their acclimation temperature, WA lobsters occupied areas with an average temperature of 15.7±0.36 °C and CA lobsters preferred areas with 11.0±0.63 °C (Fig. 5.1). Lobsters tended to spend the most time in areas that were slightly warmer than the temperatures to which they were acclimated. When these values were corrected for acclimation temperature WA lobsters selected water 0.2±0.39°C above ambient whereas CA animals selected water significantly warmer than ambient (2.8±0.66°C) (unpaired t-test p<0.005). The mean difference between the maximum and minimum temperature selected by individual lobsters during the 24 hours of testing was 2.7±0.40 °C. Interestingly the mean range selected by WA animals was 3.3±0.56 °C which tended to be larger than that selected by CA animals (1.79±0.42 °C) (unpaired t-test
p<0.10). This may be due to increased movement in warmer water or decreased specificity of their thermal preference as ambient temperatures approached the final preferred temperature.

The final preferred temperature (FPT) is defined as the point where acclimation temperature equals selected temperature (Magnuson et al. 1979, Reynolds and Casterlin 1979b). Pooling lobsters in this study, the FPT was 15.9°C based upon the regression line: y=6.17+0.61x (Fig 5.1A). This line is significantly different from the isothermal line (ANCOVA p<0.05) suggesting that behavioral thermoregulation is occurring throughout the range of temperatures tested. In addition there is a significant difference between the preferred temperatures of males (FPT=16.3°C, based upon regression of y=9.52+0.42x) and females (FPT=14.3°C, based upon regression of y=3.23+0.77x) (ANCOVA p<0.05) (Fig. 5.1B). This is primarily because males preferred much warmer temperatures than females in the colder months of the year. It is not expected that these curves are valid at less than 5°C or greater than 20°C (Fig. 5.2) due to immobility at, and/or avoidance of, these temperatures (Karnofsky et al. 1989, Factor 1995; Chapter 4).
Figure 5.1. Preferred temperatures of lobsters vs. acclimation temperature. A. Lobsters preferred temperatures warmer than their acclimation temperature (shown by isothermal line) at all temperatures below their final preferred temperature (FPT) (ANCOVA, p<0.05). The gray areas show the upper and lower lethal temperatures (LD50 values) for *H. americanus* depending on acclimation temperature (adapted from McLeese, 1956). B. The same data presented in A. are presented separately for males and females. Males preferred warmer temperatures than females at all temperatures approaching the FPTs. Both regression lines are significantly different from each other (ANCOVA p<0.05). Shaded areas show the lower temperature at which animals are expected to be immobile and higher temperatures which they avoid if possible. Note that removal of the one male "outlier" results in a correlation coefficient of $r^2=0.743$ for the male regression.
Catch Data

Both male and female CPUE are significantly correlated with temperature (Spearman rank correlation; male p=0.011, female p<0.001) (Fig. 5.2A). Catch of males and females also show higher values near their preferred temperatures (arrows) (Kruskal Wallis tests; male p=0.039, female p<0.001) (Figure 5.2B). Interestingly, at temperatures greater than 14 °C, males show significantly higher catches than females (paired t-tests, p<0.05). This suggests that there may be more males at the warmer sites in the estuary, and/or that catchability of males is higher at the higher temperatures.

Behavioral Model

The model (Fig. 5.3A), based solely on laboratory derived behavioral data and field temperature measurements, illustrates the directionality of monthly lobster movements in the Great Bay estuary. While this univariate model does not presume to indicate all of the competing factors influencing lobster movements (e.g., intraspecific competition for shelters, predation, salinity, etc.), it shows the role that temperature preference may play in influencing movements toward various temperatures dependent upon sex and acclimation history. The movements predicted by the model also match the observed movements of males (n=301) and females (n=183) based upon tag-recapture data (Fig. 5.4). These data suggest a possible mechanism explaining the skewed sex ratios of lobsters in estuaries (Howell et al. submitted). Both males and females move up estuary in the spring but males may move further up, in greater numbers, or for longer periods. In addition both sexes move down estuary in the summer and movements tend to decrease as fall and winter approach.
Figure 5.2. Male and female catch per unit effort (CPUE) vs. temperature. A. Monthly catch data from 1989-1993 at five sites in the Great Bay Estuary, NH show that catch of both males and females is significantly correlated with temperature (Spearman rank correlation, $p<0.05$). Catch of males and females also shows maximum values near the preferred temperatures determined behaviorally in the lab (shown by arrows). B. CPUE of both males and females is higher near their preferred temperatures (Kruskal Wallis tests $p<0.05$). However, at temperatures greater than 14 °C, males show significantly higher catch rates than females (paired t-tests, $p<0.05$). This suggests that there may be more males at the warmer sites in the estuary, and/or that catchability of males is higher at the higher temperatures (*=$p<0.05$, **=$p<0.001$)
Figure 5.3. Spatial and temporal relationships of available to preferred temperatures and their comparison to sex ratios in the Great Bay Estuary, NH.

A. Monthly available temperatures are presented in the top panel based upon data from the UNH Jackson Estuarine Lab (estuary) and UNH Coastal Marine Lab (coast) for the years 1989-1991. B. The gradient between these temperatures was determined by subtracting CML temperatures from JEL temperatures in a given month. C.) Preferred temperatures for males and females were determined by making the available temperature in a given month (i.e., the acclimation temperature) the x value in the male and female regression equations from Fig. 5.1. Note that these values will differ spatially and temporally depending upon where and when a lobster is located in a particular habitat. D.) Relative Incentive by sex indicates the willingness to move based upon the difference between preferred (panel C) and available temperatures in a given month (JEL temperatures in this example from panel A). Thus any points >0 would indicate an incentive to move to warmer temperatures and any <0 would indicate an incentive for cooler temperatures. E.) Relative movement was determined by multiplying relative incentive (panel D) times the direction of the thermal gradient (panel B). This shows directionality by sex, from the estuary to the coast, (or inshore to offshore) such that any points >0 indicate movement up the estuary and any <0 indicate movement down estuary.
Figure 5.4. Expected (A.) vs. Observed (B.) movement by month.
Movement data based on tag recapture data (B.) from 1989-1991 (adapted from Watson, et al., in press) for lobsters >70 mm carapace length tagged within the Great Bay Estuary and recaptured within the following month were compared to relative movements (A.) estimated from the model presented in Figure 5.3 for April-September (the only months that tag-recapture data were available). These data show that variability in temperature preference observed in the lab may account for the observed differences in movement and sex ratio observed in the field.
Discussion

This study expands upon the findings presented in Chapter 4 and confirms that adult American lobsters (*Homarus americanus*) are capable of behaviorally thermoregulating. The results show that both sex and acclimation play a role in the thermal preference of lobsters. Similar to many ectotherms, lobsters select warmer temperatures following acclimation (i.e., chronic exposure) to warmer temperatures up to their final preferred temperature (Kelsch and Neill 1990, Kivivouuri 1994). At higher temperatures avoidance behavior plays a role and very low temperatures may also be avoided until metabolic torpor reduces mobility. In doing this, lobsters shift their selected temperature closer to that of their final preferred temperature at any given acclimation temperature. This pattern of temperature preference, being a positive function of acclimation temperature, appears to be a common adaptation for ectotherms living in highly variable thermal environments (e.g., temperate areas, estuaries, etc.) and may serve to maximize their scope for activity and/or metabolism (Kelsch and Neill 1990, Johnson and Kelsch 1998). Acclimation occurs in response to seasonally changing temperatures (i.e., temporal acclimation) but it can also occur if temperatures are spatially heterogeneous (i.e., inshore vs. offshore in summer). Thus, by moving to more preferable temperatures mobile animals can effectively adjust their acclimation temperature in the process of behaviorally thermoregulating.

It has been proposed that acute thermal preferences of ectotherms, measured in the first few hours in a thermal gradient, are influenced by their acclimation temperature but that FPT is not acclimation influenced (Magnuson et al. 1979, Reynolds and Casterlin 1979a & b). Because of the close agreement between Reynolds and Casterlin's (1979a) estimate of 16°C as an FPT (based upon animals purchased in New Jersey) and our estimate of 15.9°C it appears that the FPT is fairly species specific and probably has a genetic component. Nonetheless, our measurements were taken from the second day in
the gradient and the temperature selected was still dependent upon acclimation temperature, particularly in the winter. Reynolds and Casterlin (1979a) found that the final preferred temperature was attained during the first few hours in their shuttlebox and remained stable over a 6 day period. Whether or not a winter acclimated lobster in our gradient tank would eventually reach the final preferred temperature of 15.9°C in our gradient tank, and how long this would take, is unclear. Reynolds and Casterlin (1979a) did show however, that lobsters lost their tendency to thermoregulate after 6 days in a shuttlebox apparatus. It is also unclear why this occurred, but it may be related to the fact that as the animal becomes acclimated to the final preferred temperature the actual range of selected temperatures increases, centering around the final preferred temperature. Warm acclimated animals showed a wider range of selected temperatures vs. cold acclimated animals in our study as well. Interestingly, this finding may be related to the temperature independence of activity between 10-20°C (McLeese and Wilder 1958; see Chapter 3).

It has been suggested that complete acclimation to temperature takes 24 days (McLeese 1956) and thus selection of the final preferred temperature may take weeks even if the temperature is available. This study shows the importance of the time of year selected to study thermal preference, and the time allowed for the animal to make selection, on the ultimate interpretation of findings. The methods used to determine temperature preference may also influence the results. For example, the shuttlebox apparatus similar to the one used by Reynolds and Casterlin (1979a) may cause animals to maintain a disturbed state for long periods without rest (Kivivouri 1994). Although thermal preference behavior is complex, our study exposed lobsters to temperatures approximating existing field conditions and showed that temperature selection over a controlled period of time results in gravitation toward a FPT.

The tolerable temperature range of lobsters was determined by McLeese (1956) as LD50 values after 48 hours exposure (see Fig. 5.1A). These lethal levels of temperature, salinity, and oxygen tension for lobsters (acclimated to various combinations of these
factors) were not found to differ between size, fed vs. starved, or lobsters from different locations. Under these experimental acclimation conditions in the laboratory (5°C, 20 ppt salinity, 2.9 mg/l oxygen), lobsters may have an upper lethal temperature as low as 20.6°C, but the lethal temperature is, on average, greater than 27°C (McLeese 1956). Lobsters acclimated to 17 and 27.5°C had lower lethal temperature estimates of 1.8 and 5°C. Behavioral compensation to temperature change may be limited at the lower end of the range because locomotion decreases substantially at < 10°C (McLeese and Wilder 1958, Reynolds and Casterlin 1979a) and lobsters generally move very little at <5°C (Karnofsky et al. 1989) (Fig. 5.2).

This study shows that male lobsters prefer warmer temperatures than females, particularly when the ambient temperature (i.e., acclimation temperature) is relatively low. This difference decreases as both sexes approach their FPT. Therefore, even though movements of lobsters may be affected by many variables including food availability, reproductive status, salinity, light levels, shelter availability, and size (Magnuson et al. 1979, Jury et al. 1994, Factor 1995), preference for certain temperatures may also influence the movements and subsequent distribution of males and females in space and time (Figs. 5.2 and 5.3). While equal sex ratios (1:1) have been reported for many lobster populations, (Krouse, 1973, Campbell, 1992, Howell, et al., submitted) skewed sex ratios are also common (Munro and Therriault 1983, Robichaud and Campbell 1991, Karnofsky et al. 1989, Estrella and Morrissey 1997, Howell et al. submitted). Several explanations for this have been suggested including differential catchability (Miller 1990), intraspecific competition (Karnofsky et al. 1989), and fishery regulations against one sex over the other (Estrella and Morrissey 1997). However, Howell et al. (submitted) and Vetrovs (1990) show that in at least one well studied system, the Great Bay estuary in NH, the skewed sex ratio of lobsters appears to be due to differential movements of the sexes where males move earlier and/or farther into warmer waters than females (Fig. 5.4). Munro and Therriault (1983) also conclude that males move more than females into
lagoon systems of Iles-de-la-Madeleine on the Canadian coast. Males in the lagoons and in estuaries tend to be larger than males in nearby coastal areas (Howell et al. submitted). Movements of rock lobsters, *Panulirus ornatus*, have also been suggested to bias sex ratios toward males (Skewes et al. 1994) as a greater number of females left a given area earlier in the season than males. The mechanistic model presented in Fig. 5.4 which predicts differential movements by sex based solely upon sexual differences in thermal preference closely matches the movements of lobsters observed in the Great Bay estuary. Thus, the differential movements of males, females, or both in response to temperature are likely to influence the ultimate distribution and potentially catch of lobsters.

Lobster catch has been correlated to temperature in several studies (Cooper and Uzmann 1971, Fogarty 1988, Campbell et al. 1991, Cobb 1995, Lawton and Lavalli 1995; see Chapter 3). Catch in the Great Bay estuary support these findings (Fig. 5.2) however the correlation is not necessarily linear. Peak catch seems to occur near the preferred temperatures, when these temperatures are available. However, the high variation inherent in catch data (primarily due to many sites and months with low catches) make it difficult to fit a polynomial or other regression. Temperature may be increasing lobsters tendency to enter traps because their metabolic rate approximately doubles with every 10°C increase in temperature; causing them to be more active and require more food (McLeese and Wilder 1958, Miller 1990). Temperature may also affect catch by increasing fishery recruitment through accelerated growth or increased molt probability. On a small scale temperature may effect catch rates and/or composition via differential movements by various segments of the population. For example, as described above, in the Great Bay Estuary, males move farther up into the estuary and stay longer, or females move farther out of the estuary or stay for shorter periods, and thus the sex ratio becomes skewed (Howell et al. submitted, Watson et al. in press). It is interesting that the difference between male and female CPUE increases at warmer temperatures (>14°C) but not at cooler temperatures. It is possible that catchability is lower for both sexes at cooler
temperatures but once some threshold is reached and activity is no longer temperature limited (McLeese and Wilder 1958; see Chapter 3) then movement mediated differences in local population composition become apparent and this is evident in the catch.

There are distinct sexual differences in how temperature effects the reproductive success of male and female lobsters. 'Realized' maturity in male decapods is very different than functional maturity because it is dependent upon successful competition with other males and the reproductive state of females. In blue crabs, *Callinectes sapidus*, large males mate with larger females and are more successful in competing for females in general (Jivoff 1997). In addition, large males pass a larger volume of ejaculate to each mate and thus are more successful in sperm competition (Jivoff 1997). In lobsters, time to maturity is temperature dependent for males, but it is unclear if there are seasonal differences in sperm production or mating capacity once maturity is reached (Waddy et al. 1995). Dominance may be more important to reproductive success of males than females. For example male dominance has been correlated with mating success in mesocosm experiments, and subordinate "...large and small males were often seen moving rapidly around the tank in repetitious blind circles which may have been attempts to migrate (Kamofsky and Price 1989)". Thus realized maturity for males may be temperature dependent through the importance of temperature on growth and the subsequent importance of size in reproductive behavior (Kamofsky and Price 1989). In other words, a predominant male forcing function may be "get big quick" (i.e., somatic growth). Female size may also be proportional to reproductive success because larger abdomens carry more eggs and there may be some competition for dominant males among females. However, temperatures that are too warm are detrimental to developing eggs (Waddy and Aiken 1995). Thus, focusing energy into egg production and viability (i.e. reproductive growth) may be more important for females. Ovigerous females have been reported to move sooner, deeper, and farther in fall as temperatures decrease compared to immature females or males (Aiken and Waddy 1986, Lawton and Lavalli 1995). This suggests a
link between temperature and egg or larval production. Thus, while temperature may not be as important in regulating the reproductive cycle of males vs. females per se, it may be integral to the ultimate reproductive success of both sexes (Waddy and Aiken 1995) and differentially drive movements of the two sexes.

Temperature is often incorporated into population and forecast models of invertebrate fisheries as one of the key abiotic variables (see Saila and Marchesseault 1980, Campbell et al. 1991, and Fogarty 1995 for reviews). However, most of these models estimate fisheries parameters whereas spatially explicit models of movement and/or habitat selection may give further insight into the mechanisms determining abundance and distribution of marine invertebrates (Reyes et al. 1994). This type of model is based on the information available to an animal as it moves through the environment and how this information is used to select a habitat (Lima and Zollner 1996). This type of modeling spans the different spatial scales typical of behavioral and ecological studies (Lima and Zollner 1996). The present study has shown that differences in thermal preferences exist depending on sex and acclimation history and these could contribute to skewed distributions in the field depending upon the scale of spatial and temporal temperature regimes (Howell et al. submitted, Watson et al. in press). Modeling these behaviors using field estimates of available temperatures illustrates how temperature may influence movements, and subsequent distribution of lobsters. It is expected that this type of model would be valid for any areas that are thermally variable and within the scale of movement, and perceptual range, of lobsters in a given period of time (monthly in this example). It is unlikely, that temperature is the only factor involved in determining lobster distribution, for example salinity avoidance may differ by sex (Jury et al. 1994), but if the behavioral data were available, this type of mechanistic model could be developed for other combinations of variables to explore the relationship between multiple biotic and abiotic factors.
In conclusion, temperature has been implicated as strongly influencing the seasonal movements of male and female lobsters (Cooper and Uzmann 1971, Pezzack and Duggan 1986, Karnofsky et al. 1989, Vetrovs 1990, Howell et al. submitted, Watson et al. in press). In particular, the seasonal sex ratio of lobsters in the Great Bay estuary appears to be related to differences in temperature preference between the sexes. The mechanistic model presented, based on the thermal preferences of individual lobsters, accurately predicts the movements of male and female lobsters in this estuary. These findings help to explain differential movements and distributions of males and females dependent upon their location and season. It is likely that behavioral thermoregulation in lobsters may serve to facilitate movements that result in optimization of growth, time to maturation, behavioral performance, and/or reproductive potential. The effect of temperature induced movements on the distribution patterns of adults and juveniles decapods appears to be fairly widespread and it would be fruitful to explore the relationships found here in other species. For example, behavioral effects of temperature have been suggested to be key determinates of distribution and movements of Dungeness crab, *Cancer magister* (Gutermuth and Armstrong 1989), spiny lobster, *Panulirus argus* (Kanciruk and Herrnkind 1978) and the blue crab, *Callinectes sapidus* (Hines et al. 1987, Shirley et al. 1990) yet little is known about the thermal preferences of these species. The further elucidation of these relationship between temperature and behavioral response remain an exciting area of future research due to their importance to fisheries and their relevance to reproductive success.
CHAPTER 6

MODELING THE EFFECT OF TEMPERATURE AND SALINITY ON LOBSTER DISTRIBUTION AND ABUNDANCE IN THE GREAT BAY ESTUARY

Summary

A discrete spatially explicit model was developed to simulate the movements of lobsters in the Great Bay Estuary of N.H. and the impact of these movements on their distribution and abundance. The model, created using STELLA software, was based upon mechanistic cause and effect movement relationships between laboratory derived behavioral responses to temperature and salinity and monthly temperature and salinity values measured in the estuary.

The model resulted in outputs predicting the spatial and temporal distribution of lobsters which closely resembled the field distributions and sex ratios determined from actual catch data. Thus, incorporating lab derived behavioral responses into spatially explicit models appear to be a useful approach to generate predictions and test hypotheses of distributions of decapods in the field. While models of the sort described here are oversimplifications of complex biological phenomena, construction and manipulation of a mathematical model is a practical approach to achieve a better understanding of the mechanisms involved in the distribution and abundance of aquatic organisms. Results from this study suggest that lobsters behavioral responses to temperature and salinity play an important role in determining their distribution in estuaries and may also explain field distributions in other areas. Testable hypotheses derived from the model are discussed as well as the potential for developing predictive capabilities.
Introduction

Several approaches have been taken to model the distribution of mobile marine organisms including: dynamic spatial models, which allow conditions in each cell to vary over time as both predators and prey move among cells (Sklar and Costanza 1990); individual based models, which track the spatial and temporal trajectories of individuals; habitat suitability models, which statically apply an index of suitability to habitat units and relate this to carrying capacity (Terrel 1982, Soniat and Brody 1988, Brown et al. submitted); and discrete spatially explicit models, which simplify complex “landscapes” while maintaining the biologically and physically relevant environmental heterogeneity that determines animal movement (Wiens et al. 1993, Reyes et al. 1994, Grunbaum 1998). Many of these models assume animals choose patches at random, that patches are equally accessible and that patches are equally detectable from all others (Lima and Zollner 1996). Modeling approaches such as these are frequently used in ecological studies to predict the distribution and abundance of organisms based upon known variables. Such models can also be useful to test hypotheses to determine if they are mechanistically realistic. In other words, while the mechanism used in the model may or may not be the actual one used in natural conditions, the model inputs are sufficient to result in realistic outputs. Thus, “mechanistic models provide a way to display and integrate a wide variety of assumed cause and effect relationships between variables when determining habitat suitability and they may be sufficiently useful as a planning tool, a generator of hypotheses, and ultimately useful for predictions (Terrel et al. 1982).”

Spatially and temporally variable environmental conditions are characteristic traits of many aquatic environments, including estuaries (Gibson 1994). Behavioral responses to patchy environments are key determinants influencing the distribution of vagile organisms. However, behavioral responses are usually studied in the laboratory while ecologically we would like to know the effect of these behaviors on distribution and
abundance of animals in the field. Within estuaries, habitat suitability for lobsters, as well as other species, is likely to vary temporarily due to short and long-term environmental changes (e.g., seasonal temperatures, light levels, etc., as well as spatially due to factors such as depth, proximity to freshwater source, shelter availability, etc.). Behavioral preference or avoidance in response to the suite of abiotic (i.e., water temperature, salinity, and substrate type) and biotic variables (i.e., competition, food availability, predation, recruitment, etc.) available will determine, in part, which habitats can be called “suitable” (McCall 1990, Gibson 1994). In addition, from an individual’s perspective, local, rather than large scale conditions will determine suitable habitat (Brandt and Hartman, 1993). Because habitat is defined by many variables in the field, but most of our information on behavior is based upon lab studies, simulation models may allow insight into how behavioral preference or avoidance may affect the distribution and abundance of a given species in explicitly defined habitats (Dusenberry 1996).

Reyes et al. (1994) used a discrete spatially explicit modeling approach to investigate the mechanistic rules that determine movements of migratory fish in the field and how these movements effect distribution and abundance of this species in a tropical lagoonal system. This model predicted spatial and temporal movements throughout a grid of cells based upon their tolerance to various environmental and biological parameters: temperature, salinity, chlorophyll (as a surrogate of food availability), birth and mortality. Even though the model was simplistic it did demonstrate that fish have deterministic physiological and behavioral cues that drive migratory movements. (Reyes et al. 1994). They concluded that “the simulation of large, density-dependent, spatial processes such as migration can be understood with a grid-based mechanistic...model because its rule-based design for movement allowed organisms to respond to ecological processes and adjust to changing environmental conditions (Reyes et al. 1994).”

The present study describes a similar model which simulates the dynamic distribution of a closed population of lobsters in the Great Bay estuary, N.H. The lobster...
population has been extensively sampled in this system (Watson et al. in press, Howell et al. submitted) and these data show that lobsters move up into the estuary in the spring and down the estuary later in the summer and fall. In addition, the sex ratio is also highly skewed toward males in the upper estuary (>4:1 males:females) vs. the lower estuary (1:1). Characterization of the behavioral responses to temperature and salinity; the environmental conditions in the estuary; and the patterns of distribution, abundance and sex ratio have been described in earlier chapters. (see Introduction and Chapters 2-5).

In the model the estuary was divided into grid cells, relative indices of habitat quality were assigned to these discrete areas based upon laboratory-derived preference or avoidance responses to temperature and salinity. Movements of the population between grid cells were then dynamically modeled in response to spatially and temporally variable conditions. Habitat was quantified using only field derived water temperature and salinity data. The two primary hypotheses tested in the present analysis were: 1) Models based on laboratory derived estimates of behavioral response to temperature and salinity can result in realistic simulations of the spatial and temporal distribution of lobsters in the field; and 2) Small sexual differences in temperature preference measured in the lab are sufficient to result in skewed sex ratios similar to those observed in the field.

Materials and Methods

The Study Area

The Great Bay estuarine system was divided into 7 cells (Fig. 6.1) in a manner similar to the model described by Reyes et al. (1994). Spatial scale was determined by lobster activity data assuming average activity of approximately 249 m/d or approximately 7500 m/month in the field (see Chapter 2). In addition, tagging studies in Great Bay show that lobsters travel in spurts remaining in one location for long periods and then moving rapidly at rates of approximately 0.26 km/d which is equivalent to 7.7 km/month (Watson
et al., in press). The maximum rates of movement in these tagging studies were estimated at 1.6-3.4 km/d. Thus a cell size of 2.5 km² in a time step of one month was chosen as a conservative level of resolution. Spatial and temporal scale chosen for any model is a compromise between small cell size for resolution and computing power and data availability (Brandt and Hartman 1993, Reyes et al. 1994).

**Model Parameters**

Each cell was assigned an average monthly temperature and salinity based upon a linear extrapolation of existing data from the UNH Jackson Estuarine Lab and the UNH Coastal Marine Lab time series data from 1989-1991 (Figs. 6.2 & 6.3).

Based solely upon laboratory determined behavioral preference and avoidance data, suitability indices (SI) were developed to express the relative intensity of association of lobsters to all levels of temperature (0-25°C) and salinity (0-35 ppt) (see chapter 3; Jury et al, 1994a)(Fig. 6.3A). These indices extend from 0.0 (unsuitable) to 1.0 (highest quality habitat) with the assumption that there is a relationship between the SI and lobster density (Brown et al., submitted) or some other measure of habitat suitability (e.g., catch per unit effort). Salinities of <18.6 ppt were determined to be unsuitable (SI=0.0) while salinities ≥18.6 were considered to suitable (SI=1.0) (Jury et al. 1994). Temperature SI curves were determined for males and females, and averaged for both. For all these curves, temperatures >23°C were considered unsuitable (SI=0.0) based upon avoidance responses (see Chapter 4) and LD50 data (McLeese 1956). Female and male suitabilities were maximum (SI=1.0) at their preferred temperatures (15-16°C and 16-17°C respectively) and decreased as temperatures approached the upper or lower avoidance levels of 23°C and 0 °C respectively. Suitabilities were higher for females than males at all cooler temperatures because males prefer warmer temperatures in this region (see Chapter 5). In addition, based upon activity data (Chapter 3) and several field observations (Ennis 1984, Karnofsky et al.)

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Figure 6.1. Map of Great Bay Estuary used in the model. A map of the estuary is shown with overlain cells showing grid size, trapping sites (dark circles), and locations of the temperature/salinity monitoring sites (open squares). Temperature and salinity determine the aggregate habitat suitability of individual areas of the Great Bay Estuary. Where lobsters move to, or from, in time and space is determined by their suitability index (SI) which is a mechanistic description of how lobsters respond to temperature and salinity. These SIs were determined from laboratory preference and avoidance assays.
Figure 6.2. Temperature and salinity at Jackson Estuarine Lab (JEL) and Coastal Marine Lab (CML) for 1989-1991. While the annual cycles of temperature and salinity remain constant, there is a fair amount of inter-annual variability. This variability is generally higher at JEL. For example, note that 1991 was a relatively warm and wet (i.e., lower salinity due to runoff) year than either 1989 or 1990.
Figure 6.3. Model parameters. A. Temperature and salinity suitability indices (SI) based upon behavioral preference and avoidance experiments in the laboratory. B. Temperature (°C) and salinity (ppt) values were determined in the field at Jackson Estuarine Lab (JEL) and Coastal Marine Lab (CML) and extrapolated to other sites within the estuary. These values were then input into the model described in Fig. 6.4.
1989) no movement was allowed between cells if temperature was <5°C because of reduced locomotion at lower temperatures. This does not necessarily assume avoidance of these lower temperatures, but instead just reduced potential to move from cell to cell.

**Model Description**

Using STELLA software (Costanza, et al., 1998) the model parameters outlined above were incorporated by assigning a temperature and salinity value to each cell at each monthly time step. SIs for each cell at each time step were determined by the temperature and salinity in a given cell. SIs for temperature \( T_x \) and salinity \( S_x \) at time \( x \) were then weighted equally and combined into an aggregate habitat suitability index (HSI) value by using the following geometric mean equation:

\[
HSI = (S_x \cdot T_x)^{1/2}
\]

Because all SI terms are between zero and one, model outputs also ranged between zero and one and if any individual term was zero (indicating unsuitable habitat based upon that parameter) then the entire HSI was also zero (Brown et al. submitted). For example, if temperature was unsuitable in a given area at a given time but salinity was at a preferred level, then the habitat would still be unsuitable overall.

Because the actual total abundance of lobsters in Great Bay is not known, a closed population of 10,000 was assigned and the population of animals in a cell at a given time step was assumed to be the relative population abundance or density in each cell. These estimates are by necessity relative to other cells because the actual initial density of animals is not known. The population was initially started in cell 1 (coastal site) and the model was allowed to run for 12 years (144 time steps) to reach equilibrium. However, consecutive simulations with different initiation cells showed that the model would equilibrate to similar end points no matter where the population was started. Model outputs were derived from the final 3 years of these simulations.
Table 6.1. Rules and assumptions of the model.

Several simplifying assumptions were made to delineate the mechanistic model. These assumptions were intended to be as biologically realistic as possible while maintaining model tractability within the limits of the available data and computing power.

- the percent of the population leaving a cell at a given time step is determined by the suitability of the cell at that time such that 1-HSI is the proportion available to move. For example, if a cell is already optimal (i.e., HSI=1) then none will leave but if it is only half optimal (i.e., HSI=0.5) then half will leave that cell and half will stay in that cell at that time step.

- direction of movement (up or down estuary) was determined by the suitability of adjacent habitats, whether >, <, or = in suitability. For example, if a downstream cell had a higher HSI then all animals available to move will move to this cell. However, if a cell has the same or a lesser HSI then none will move from a given cell into that cell at a given time step. If there are two adjacent cells with equal HSIs that are higher than a cell located between them, then the individuals available to move were divided between them equally.

- movements are only based on behavioral responses to temperature and salinity

- no mortality, births, immigration, or emigration occur in the closed population

- animals can sense differences in temperature and salinity between cells (i.e., the perceptual range of lobsters allows them to select between habitat options on the spatial and temporal scale of the model)

- environmental gradients are linear within any one month along the estuary; environmental conditions are also homogenous within a given cell

- temperature and salinity are equally important in determining habitat suitability

- behavioral preference for temperature or salinity is density independent

- suitability index curves do not change between seasons or life stage
Figure 6.4. Model overview and organization. A. The Great Bay Estuary was divided into 7 cells as shown in Fig. 6.1. B. The population in each cell was driven at each time step by the suitability of that cell in terms of temperature and salinity. Animals would move into a cell if temperature and/or salinity were more preferable and out of a given cell if temperature and/or salinity were more preferable in an adjacent cell(s). Movements were also proportional to the difference in suitability between cells.
Because "we know remarkably little about the sorts of information available to animals at the scale of ecological landscapes, and we know even less about how such information is used in decisions regarding movement and patch/habitat selection (Lima and Zollner 1996)" several reasonable, albeit arbitrary assumptions and rules were made that determined how animals moved between cells (Table 6.1).

**Verification of Model**

Catch data from 1989-1991 (the same years as the salinity and temperature data) were used to test the model. Data from one site within each cell was used as verification data (Fig. 6.1). These data were collected weekly using methods described in Watson et al. (in press). Two models were run to test each of the primary questions posed. To assess model outputs vs. CPUE, an average temperature preference SI curve was used. To assess model outputs vs. sex ratio male and female temperature preference SI curves were run separately and the outputs by site and month for each of 3 years were used to determine relative sex ratios (M:F). In order to compare the large range of model output values (0-3683) to the relatively smaller range of CPUE values (0-8.6), assuming that model outputs equal x, these data were square root transformed according to Zar (1974) using the equation:

\[ x' = \sqrt{x + 0.5} \]
Results

Model Outputs

By simulating environmental changes between available habitats and incorporating rules for preference and avoidance of temperature and salinity (Fig. 6.2), movement between cells resulted in relative distributions for each site at each monthly time step. Relative seasonal movements inferred from model outputs (Fig. 6.5) closely mirrored migratory movements seen using tag recapture and sonar telemetry (see Watson et al. in press and Great Bay Estuarine Lobster Overview in Introduction section). Note that abundance is higher at more coastal areas (CML, Simplex) and lower within the estuary (Fox, JEL). Nonetheless, seasonal changes in abundance occur such that animals move into the estuary in the late spring and early summer. For example, 10-20% of the closed population of 10,000 moves into Fox in the early summer, but increase at that site specifically is almost 100%. Also note that in the upper estuary (e.g., JEL) there are relatively few animals and this is very dependent upon the annual environmental conditions. For example, in 1991 there was a relatively mild winter and a cold water upwelling at the coast in the early summer (Fig. 6.2). This may have been responsible for the increased movement into the estuary in the summer of 1991 (Fig. 6.5). Lastly, note that a pulse of animals is seen at the coast as lobsters move out of the estuary.

Overwintering is predominantly at the coast (and probably outside of the estuary) but based upon the present model there is a fair amount of overwintering within the lower estuary as well (e.g. Simplex). Thus this model demonstrates that behavioral response to temperature and salinity alone can result in movements that closely match distributions seen in the field.
Figure 6.5. Sample of model output for four locations in the estuary. Model outputs closely mirrored movements and subsequent distributions of lobsters in the Great Bay estuary compared to tag recapture and CPUE data (Vetrovs, 1990). Abundance was higher at more coastal areas (CML, Simplex) and lower within the estuary (Fox, JEL). Nonetheless, seasonal changes in abundance occurred such that animals moved into the estuary in the late spring and early summer, and out again later in the fall. (W=Winter, Sp=Spring, Su=Summer, F=Fall)
Model Outputs vs. Catch

Model outputs positively correlate with catch per unit effort data (n=95; 19 months at 5 locations for 3 years 1989-1991) (linear regression slope is significantly greater than zero, p<0.0001) (Fig. 6.6). The variance in this relationship is high ($r^2=0.30$). This is not unexpected because catch data also tends to be highly variable and is considered to be a poor index of abundance due to the issues of catchability and trap saturation (Fogarty and Addison, 1997). Thus it is particularly interesting that there is a significant relationship. Also because the curve is asymptotic (i.e. showing a plateau at high levels of abundance) this may suggest that high catches are limited by trap saturation and not necessarily the amount of animals on the bottom. A rank comparison of CPUE in the field vs square root abundance in the model is also highly significant (Spearman rank p<0.0001) and further supports the fact that the model realistically simulates CPUE data even though the predictive power is relatively poor.
Figure 6.6. Square root transformation of model output vs. catch per unit effort data. Model outputs positively correlate with catch per unit effort data (n=95; 19 months at 5 locations for 3 years 1989-1991) (linear regression slope is greater than zero, p<0.0001). The variance in this relationship is high (r²=0.30) but this is not unexpected because catch data is considered to be a poor index of abundance due to the potential for trap saturation. Thus it is particularly interesting that there is a significant relationship (Spearman rank correlation, p<0.0001).
**Model Outputs vs. Sex Ratio**

The relationship between sex ratios at various sites for each of the three years vs. model output at the same spatial and temporal scale shows a positive linear regression slope with relatively good predictive power ($n=18$; 6 locations for 3 years from 1989-1991, $r^2=0.71$) (Fig. 6.7). In addition, these data are significantly correlated (Spearman rank correlation, $p<0.0001$). Because salinity preferences were the same for both sexes in this model, this suggests that behavioral response to temperature alone is sufficient to create unequal distributions of the sexes that can manifest themselves in unequal sex ratios in the field.

Sex ratio may be a more accurate test of this model because as an index of abundance it is less dependent upon the variability introduced by catch data. In other words, if catch is dependent upon variables other than temperature and salinity (e.g., trap saturation, bait quality, soak time, etc.) then the model in its present form could not reliably predict catch. However assuming that catchability is equal between the sexes (Howell et al. submitted) then the ratio of males to females should consistently represent a proportion of the true population of males and females.
Figure 6.7. Sex ratios determined by model vs. observed sex ratios. The relationship between sex ratios at various sites for each of 3 years to model output at the same spatial and temporal scale shows a positive correlation with relatively good predictive power (n=18 at 6 locations for 3 yrs from 1989-1991, $r^2=0.71$). These data are significantly correlated (Spearman rank correlation, $p<0.0001$) suggesting that the model reliably predicts sex ratio. Thus differences in temperature preference between the sexes is sufficient to simulate sex ratios similar to those observed in natural populations.
Discussion

While models of the sort described here are necessarily oversimplifications of complex biological phenomena, constructing and manipulating a mathematical model is a useful approach to achieve a better understanding of the mechanisms which give rise to the distribution and abundance of any organism in space and time (Reyes et al. 1994). This model has shown that laboratory derived behavioral data can be incorporated into models that realistically simulate distribution and abundance in the field. It has also shown that small differences in preference for temperature between sexes is sufficient to result in the large variation in sex ratios observed in Great Bay Estuary. Finally, a model of this sort may ultimately be predictive of catch. While catch data significantly correlate with the outputs of the model in its present form, additions to the model and an increased understanding between catchability and density would decrease the variance in this relationship and thereby increase the predictive capabilities of the model.

This model has also provided several novel, testable insights into the ecology of Great Bay lobsters. For example, overwintering based upon presently accepted lobster literature would be expected in coastal and offshore areas (Thomas 1968, Lawton and Lavalli 1995). Overwintering based on the model occurred primarily in the coastal areas. However it also occurred in the lower reaches of the estuary. The model assumes that lobsters do not move much at cold temperatures (i.e., <5°C) and thus if a lobster is going to “choose” where to overwinter it must anticipate when to leave and where to go or else where a lobster overwinters may be a function of getting “stuck” in a certain place as their metabolism decreases below some threshold at decreasing temperatures.

Another insight derived from this model is that if we assume that animals behave adaptively by moving in the direction of greatest detectable resource abundance or the best detectable living-site then they must have the sensory abilities to discriminate among alternatives (Lima and Zollner 1996). Thus the concept of perceptual range, defined as
“the distance from which a particular landscape element can be perceived as such (or detected) by a given animal (Lima and Zollner 1996)”, is very important to how an animal behaves within its environment. The threshold or rate of detection that an animal’s senses can perceive will determine what information is available to the animal in order to make a decision or habitat selection choice. In the present model perceptual range is assumed to be a function of their sensitivity to temperature and salinity. Lobsters can sense both salinity (Dufort 1997) and temperature (Chapter 1) but the actual rates of change experienced by an individual in the field will be a function of the rate of change of the environment, spatial heterogeneity in the variable of interest, and movement of an animal through a heterogeneous environment. Sensitivity may also be modified depending on synergy or antagonism between different variables or seasonal modification in physiological and/or behavioral state (Paztor 1989, Wood et al. 1997). Thus, while lobsters can sense both salinity and temperature in the laboratory, their perceptual range in the field, and how they use temperature and salinity information (and other environmental cues) to orient, is unknown and is a fruitful area for future studies.

The ultimate goal of many ecological models is to reliably predict future animal distributions based upon some set of known present variables such as environmental variability, physiological responses, time series of catch data, etc. While many different types of models have been developed and even used to manage certain species, the key limitation is often how to verify the outputs. When there is variance between model outputs and some measure of reality, the options are to modify the model or assume that the verification data is not a suitable estimate of “reality”. For example, “the major limitation of mechanistic HSI models, based on suitability index graphs, is that the accuracy of their output cannot be directly verified (Terrel et al. 1982)”. Thus while one can always modify a model, and this is regularly done in sensitivity analysis, care must be taken in selecting appropriate verification data.
The high variance in some of the results must be interpreted with the possibility that the model may be the cause, and/or that the verification data (i.e., CPUE) may be the cause. Model verification is often difficult because of problems with the data requirements necessary to accurately test the model outputs. In this case, we are testing relative lobster density from the model outputs vs. catch data from the field. Lobster catch data is derived from traps which may not adequately sample all components of a population due to differences in catchability between sizes and habitats. More importantly, the effect of trap saturation, soak time and intra- and interspecific behavioral interactions may all effect catch independent of actual density (Fogarty and Addision 1997). Thus, while catch data is our best indicator of lobster abundance at the present time, until the problems inherent in catch data can be remedied, modifications to this model to increase its predictive capabilities of density are somewhat speculative. Nonetheless, the model may be modified to predict catch if appropriate indices of catchability were known and subsequently incorporated.

Thus, verification of the present model is problematic due to the quantity and quality of data available for real population abundance and distribution (Brown et al. submitted). It is possible that extensive bottom surveys through diver or visual methods would yield more suitable density information however, these methods are not without their problems; the most glaring being expense at the scale necessary to model migratory processes. It may also be possible to enhance our knowledge of the relationship of CPUE to density through studies of catchability, trap saturation, etc. and this is an approach that we are presently undertaking. Whatever the approach, research into better estimates of lobster abundance and density is clearly warranted (Fogarty and Addison 1997).

Habitat suitability is a function of behavioral preference and physiological tolerance for a given set of conditions, but actual distribution will also be a function of competing parameters such as predation pressure, food availability, recruitment etc. As mentioned above, it is possible that given more information, certain modifiers could
increase the predictive capability of the present model. For example, to increase the
resolution of the model or to incorporate more realistic complexity one could: 1) use
additional environmental parameters; 2) use cell specific biological parameters (i.e. food
availability, birth, mortality, recruitment, etc.); 3) incorporate ontogenetic or size-specific
changes in behavior (i.e. molting, growth rate, sexual maturity); or 4) incorporate
interactions with other species (competition, predation, feeding, etc.) (Reyes et al. 1994).
Nonetheless, even if additional variables were added, these additions may not necessarily
increase the predictive power of the model because many interactions in the field may not
be readily predictable. To interpret field data and model data correctly, the value (to the
animal) of the environment here depends on the value of the environment there. This
implies that the animal has the sensory capability to make this discrimination and the
motor ability to act upon the alternatives. In addition, there may be obstacles restricting
an animal from getting from 'here' to 'there', and even when it can, there may not be
enough time for it to do so before the environment changes again (Neill and Gallaway
1989). Thus, the scale of spatial and temporal patchiness in habitat quality and/or
quantity will determine where and when animals will be able to “select” certain habitats
(Gibson 1994). While it is likely that many variables and behaviors are involved in
determining ultimate distribution and abundance, it is unlikely that sufficient information
on all of these variables will be available or desirable to include when model complexity
becomes a limitation. Thus, focusing on only those behavioral traits that are likely to be
important to the question under study is necessary in order to keep models reasonably
tractable (Lima and Zollner 1996).

Regardless of the speculative model enhancements and inherent biological
relationships, simple mechanistic models are sufficient to answer (and ask) many
questions. The fact that mechanistic models can be readily modified to incorporate new
information on habitat requirements and site specific considerations, provides the user
with a high degree of flexibility to meet research goals (Terrel et al. 1982). Indeed, even
the relatively simplistic behavioral relationships determined in laboratory studies were sufficient to realistically model lobster movements in this study, and may be sufficient for many marine species. Modeling the active migration of mobile organisms as a function of behavioral relationships to measurable environmental variables may give ethologists, ecologists, and managers a tool to evaluate the effects of natural and anthropogenic impacts over several spatial and temporal scales.
CONCLUSIONS

This study has used a multidisciplinary approach to show that lobsters can sense warm or cold temperature changes of \(<0.1-0.2^\circ\text{C}\) and use this ability to behaviorally thermoregulate by positioning themselves in preferred thermal niches (see Chapters 1 & 4). The relationship between activity and temperature found in naturally acclimated lobsters was consistent with those published by McLeese and Wilder (1958) and Reynolds and Casterlin (1979) (see Chapters 2 & 3). The relationship between activity and temperature is non-linear, increasing between 0-10°C and above 20°C, but remaining relatively temperature independent between 10-20°C. In the region of 10-20°C there is an overall higher level of activity compared to lower temperatures, with high variation between individual levels of activity. At temperatures of less than 5°C there was little or no activity. The final preferred temperature (15.9°C) also falls within the middle of this range and thus there may be some adaptive reason to remain within these temperatures (see Chapter 4 & 5). Lobsters avoid temperatures of \(>23.5^\circ\text{C}\) (see Chapter 4) and while high levels of activity are possible at these temperatures, they are approaching damaging or even lethal levels (McLeese 1956). Thus, temperatures near 10°C appear to serve as a "thermal switch" that upregulates internal mechanisms resulting in the potential for higher activity. This "potential" is not necessarily realized depending upon competing factors that effect behavioral responses to the environment. In addition, there also appears to be some type of seasonal modulation occurring such that summer lobsters are physiologically, and possibly behaviorally, different than winter lobsters even when they are held at the same temperatures (see Chapter 1).

Great Bay has proven to be a useful "model habitat" to study the sensory biology of of \(H.\ amercianus\). Empirical data and modeling have shown that lobster distribution and abundance, and thus potentially catch, are affected by behavioral preference for certain thermal habitats. Thus, depending upon catchability, increasing activity and
movement to preferred temperature may affect catch on local scales. The difference in preferred temperatures of males (16.3 °C) and females (14.3°) was also incorporated into a spatially explicit model which showed that behavioral differences may result in movements or migrations that affect the distribution, abundance, and sex ratios of lobsters on relatively small scales (see Chapters 5 & 6). In particular, the model presented here shows that temperature alone may be causing the skewed sex ratios observed in the Great Bay estuary. Thus, mechanistic models are useful to describe and ask questions about the relationship of behavioral response to environmental variables and distribution in the field. All studies conducted indicate that temperature has a very strong influence on lobster distribution but the relationships are more complex than previously considered.
LITERATURE CITED


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