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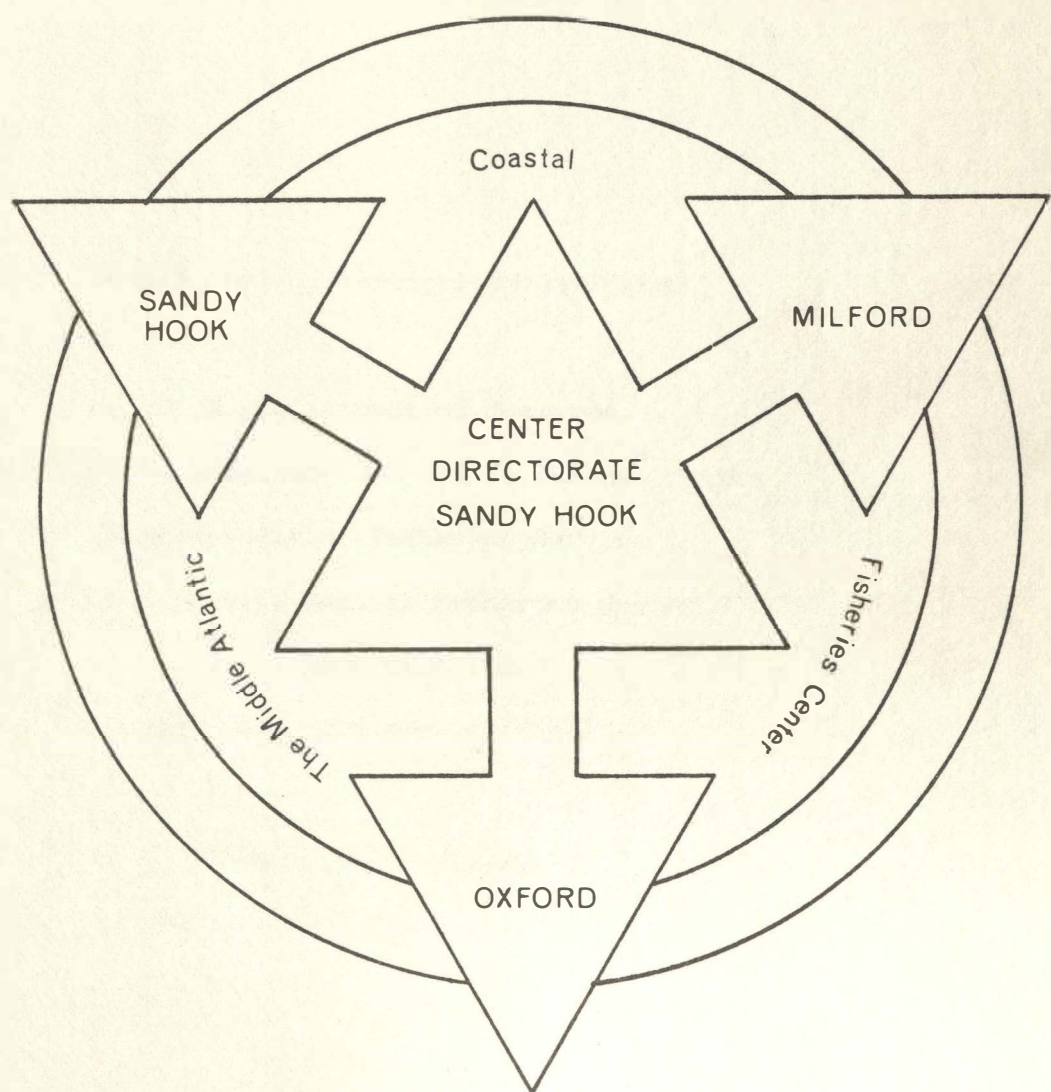
BEHAVIORAL MEASURES OF ENVIRONMENTAL STRESS: MARINE FISHES AND
INVERTEBRATES. ENERGY RESEARCH AND DEVELOPMENT ADMINISTRATION
FINAL REPORT
CONTRACT NO. AT(49-7)3045, July 1, 1975 - June 30, 1976

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Region



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MIDDLE ATLANTIC COASTAL FISHERIES CENTER



Informal Report No. 112

June 1976

ENERGY RESEARCH AND DEVELOPMENT ADMINISTRATION REPORT

No. AT (49-7)3045 (1976)

- A. Environmental Stress and Behavior: Response Capabilities of Marine Fishes. In press. Proceedings of the Symposium on the Comprehensive Analysis of the Environment. UN/FAO Joint Program for Cooperation in the Field of Environmental Protection, Honolulu, Hawaii, October 22-26, 1974.
- B. The Effect of Temperature on Activity, Feeding and Social Behavior of Adult Turtles. Turtles units.
- C. Growth and Survival of Adult Turtles. Turtles units.
- D. The Effect of Temperature on the Behavior of Marine Invertebrates.

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- B. The Effect of Temperature on Activity, Feeding and Social Behavior of Adult Tautog, Tautoga onitis.
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INTRODUCTION

The Progress Report consists of five sections, the format of each depending upon the degree to which each research effort has been completed.

The sections are as follows:

A. Environmental Stress and Behavior: Response Capabilities of Marine Fishes.

This completed paper, currently in press, was presented in Honolulu, in October 1975 at a conference entitled: "U.S./U.S.S.R. Joint Program for Cooperation in the Field of Environmental Protection." It synthesizes and discusses our findings on comparative aspects of thermal perturbations on marine fish species and the significance of the results as they may be applied to the habitat within which each species resides.

B. The effects of temperature on activity, feeding and social behavior of adult tautog, Tautoga onitis.

Results which are presented are from two long-term studies performed on separate groups of adult tautog. The findings are not in final form but, nevertheless, represent the bulk of what will be included in a paper currently being prepared for publication.

C. Courtship and spawning behavior of adult tautog, Tautoga onitis.

The findings presented here also represent the major portion of a manuscript currently in preparation for publication. Photographs and drawings as well as a discussion integrating and comparing the behavior of other species have not been included since they were not completed by the time this report was prepared. This paper should be ready for publication within the next two months.

- D. The effect of temperature on the behavior of marine invertebrates. The work presented on the behavior of the blue crab, Callinectes sapidus, represents approximately six months of actual observations, with the preceding months spent in setting up the research laboratory facilities including various observation aquaria and temperature control systems.
- E. A short synopsis of field study results on shelter-dependence in young tautog, and home range and shelter orientation in juvenile cunner, Tautoglabrus adspersus, is included, although the research is still at least one year from completion.

A.

**Environmental Stress and Behavior:
Response Capabilities of Marine Fishes 1/**

Bori L. Olla and Anne L. Studholme

The search for sensitive and ecologically pertinent measures of pollutant effects on aquatic organisms has stimulated research in a variety of disciplines including animal behavior. Recent work has shown that knowledge of the life habits and requirements of an organism may be used in a variety of ways to measure and predict the effects of contaminants in marine and estuarine ecosystems (for example, see Olla, 1974). Prior to any contaminant experiments in the laboratory, understanding of the organism's normal behavioral repertoire, including its scope of response to natural stresses, may form a sound basis for speculation on its survival potential in man-induced stress. While the organism itself may be able to survive or remain unaffected by a specific pollutant, disruption of components within the ecosystem of which it is dependent (e.g., shelter, food resources) may indirectly reduce its survival capability.

For laboratory studies, localities may be established using selected behaviors which play an identifiable role in the life habits of the animal. However, the efficacy of the experimental design will depend on the degree to which these behaviors transcend field and laboratory, and are separate and distinct from those induced by the laboratory environment. Departures from these norms will indicate contaminant effects which the results of these studies often directly relate to.

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For laboratory studies, baselines may be established using selected behaviors which play an identifiable role in the life habits of the animal. However, the efficacy of the experimental design will depend on the degree to which these behaviors transcend field and laboratory, and are separate and distinct from those induced by the laboratory environment. Departures from these norms will indicate contaminant effects with the results of these studies often directly related to the survival capabilities of the individual or population in the natural environment. However, the confidence with which such extrapolations can be made, will depend on the knowledge of normal and the careful integration of laboratory and field results.

Studies to define normal behavior in situ may be carried out either by direct observations with the use of mask and snorkel, SCUBA, viewing boxes and submersibles (mobile and fixed units) or indirectly with remote sensing devices such as underwater television, sonar and acoustic tags (Olla, 1974). Habits can also be inferred indirectly from commercial and sport catches, stomach contents and various sampling techniques, primarily used for scientific assessment of populations. All of these procedures contribute information on spatial distributions, activity patterns, daily and seasonal shifts in abundance, feeding and food habits, reproduction, territoriality and other habits and requirements which can be used in the formulation and design of laboratory experiments that are ecologically relevant.

Our philosophy and method of approach of using changes in behavior to measure stress on aquatic organisms can best be illustrated by examples taken from our previously published work. The studies were aimed at furthering our understanding of the comparative aspects of the behavioral response to temperature in selected marine fishes. In this paper, we will limit our discussion to two pelagic species, bluefish, Pomatomus saltatrix, and Atlantic mackerel, Scomber scombrus, and one demersal species, tautog, Tautoga onitis.

We chose temperature as the stress stimulus for our initial studies for two main reasons: 1) it represented a current as well as a future problem for a small but significant number of marine ecosystems being subjected to heated effluents from electrical generating plants, and 2) the design of almost any study on contaminant effects requires

consideration of temperature as a primary experimental variable because of the obvious short and long term fluctuations of this parameter in estuarine and inshore marine zones.

Although both pelagic species are quite different taxonomically as well as in the specifics of their life habits, there are, nevertheless, similarities in the way in which they are related to the environment. Both species occupy the upper pelagic zone, travel in schools, and are seasonal migrants. Seasonal movements of these fish appear to be related to changing photoperiod, while their location at a particular time is closely correlated with temperature.

We conducted laboratory studies on each species separately, using small groups of adult fish held under controlled conditions in a 121-liter aquarium (Olla, Marchioni & Katz, 1967). Water quality was maintained primarily by recirculating the water through a filtrant of sand, gravel and crushed oyster shell. Water temperature was controlled indirectly by room temperature and by the addition of water from a well-point located in Sandy Hook Bay. A specialized lighting system simulated diurnal changes in light intensity and duplicated natural seasonal changes in photoperiod.

Both the bluefish and Atlantic mackerel possessed a clearly defined diurnal rhythm of activity although they swam continuously day and night (Olla & Studholme, 1972; Olla, Studholme, Bejda, Samet & Martin, 1975). Continuous swimming in Atlantic mackerel was not so surprising since they lack any hydrostatic organ, making swimming obligatory to maintain

their position in the water column. The bluefish, although possessing such an organ, also swam continuously, but at much lower speeds and with a higher degree of variability, especially at night. Both species generally swam around the tank in a school, although the bluefish were more variable in this activity especially at night.

The introduction of live food (small bait fish of various species for bluefish; grass shrimp for Atlantic mackerel) caused an almost immediate breakdown of schooling with the fish feeding more or less as individuals (for bluefish, see Olla, Katz & Studholme, 1970; for Atlantic mackerel, Olla, pers. obs.). As would be expected for schooling animals inhabiting the upper pelagic zone where light levels are relatively high, the fish were highly visually oriented, using vision as a primary modality for feeding.

While the introduction of food would cause a breakdown in the integrity of the school, the introduction of a "fright" stimulus had the opposite effect. Stimuli such as a sudden flash of light, especially at night, a splash at the surface, or the sudden appearance of an observer above the aquarium would cause an increase in cohesion and speed. At times, the initial response to a startle stimulus would be for the animals to separate, followed within several seconds by regrouping, with the fish significantly closer than before the introduction of the startle stimulus. The fish were highly responsive to any altering stimulus both day and night with avoidance being manifested by increased speed and reduced interfish distance.

Initial acclimation levels for both species (adult bluefish, 19.9°C, juvenile bluefish, 20.0°C and Atlantic mackerel, 13.3°C) were based on

correlations between temperature and distribution. For bluefish, peak abundance off the eastern coast of North America appears to be about 18-20°C (Walford, unpublished) with inshore appearances in the spring along the Middle Atlantic and New England regions occurring as temperatures reached 12-15°C and departures in the fall at 13-15°C (Lund & Maltezos, 1970). Limits for distribution of Atlantic mackerel along this coast are from about 7-8°C (Sette, 1950) up to approximately 18-20°C (Recksiek & McCleave, 1973) with 12-14°C cited by Dannevig (1955) as the optimal range for Scomber scombrus in the eastern North Atlantic.

The response of both species to gradual increases in temperature (0.02°C/h) from these acclimation levels was an increase in speed (Figs. 1a, b, 2) and a decrease in fish-to-fish distance (Olla & Studholme, 1971; Olla, Studholme, Bejda, Samet & Martin, 1975). As temperatures reached stress levels, the daily rhythmic pattern was no longer evident as the fish schooled at high speed both day and night. Juvenile bluefish, in separate experiments, responded similarly (Figs. 2, 3; Olla, Studholme, Bejda, Samet & Martin, 1975) even though the rate of rise was more rapid (mean rate 1.38°C/h). Maximum cruising speeds were reached by juvenile bluefish at 32-33°C and by Atlantic mackerel at 20-22°C, several degrees below lethal levels.

The response of these two species to increasing temperature, based on even the most rudimentary physiological interpretation, was not surprising. However, the responses of the adult fish to decreases in temperature from similar acclimation levels, 19.5°C for bluefish, 7.9°C for Atlantic mackerel, (Olla & Studholme, 1971; Olla, Studholme, Bejda, Samet & Martin, 1975), were most interesting, if not surprising.

A decrease in temperature (mean rate 0.013-0.03°C/h) resulted in an increase in speed similar to that observed in response to a temperature increase (Figs. 1a, b, 2). As they had at high stressful temperatures, adult Atlantic mackerel reached maximal cruising speeds before temperature reached lower lethal levels (Fig. 1b).

Although the response to low temperature might be opposite to what would normally be expected, the distribution of these animals in nature is so obviously correlated with temperature that our laboratory findings simply confirmed that temperature is an important parameter influencing their distribution. These pelagic species (it remains to be investigated in other marine pelagics) have the capability of actively avoiding or selecting certain thermal regimes. The data indicate that the temperatures avoided or "preferred" were not specific, but rather fell within a range dependent on the specific environmental requirements of each species.

The similarity in response to both increasing and decreasing temperatures by species with similar normal patterns of behavior reflects what has been termed behavioral thermoregulation (see Fry, 1971; Stevens, 1973, for examples and discussion of directed movements in response to temperature). It has been shown in situ in fresh water (Neill & Magnuson, 1974) and demonstrated under controlled laboratory conditions (Rozin & Mayer, 1961; Neill, Magnuson & Chipman, 1972; Neill & Magnuson, 1974) that certain fishes have the ability to regulate body temperature behaviorally by selecting water temperatures.

Bluefish and Atlantic mackerel, which are not associated with a specific place but rather to specific thermal ranges (as well as with other environmental parameters), have the capability to move in response to changing temperature, thereby avoiding potentially stressful conditions and maximizing their presence in zones which are selectively

advantageous.

We suggest that animals such as these possess the capability of generally avoiding stresses including other contaminants. Whether avoidance actually occurs will depend on a host of variables including their motivation to be in a particular area, the characteristics of the contaminant, the ability of the animal to detect it and whether or not it represents, within the context of the animal's scope of responsiveness, a noxious or "danger" stimulus.

In contrast to these pelagic fishes are species which are more restricted both in activity and movements. The tautog, one of two members of the Labrid family found in inshore temperate waters of the western Atlantic, is found on or near the bottom, in association with objects which provide shelter, such as rocks, pilings, jetties, and various forms of vegetation. Our knowledge of the natural habits and requirements of this demersal fish was gained from field studies on populations located in Great South Bay, New York, specifically within the Fire Island Inlet (Olla, Bejda & Martin, 1974; 1975). In our studies, we employed various techniques including direct observation with SCUBA, remote sensing with ultrasonic tracking, as well as examination of digestive tracts of captured specimens.

From our direct underwater observations we found distinct differences in the behavior of the tautog from day to night (Olla, Bejda & Martin, 1974). During the day they were active and highly responsive, swimming in the water column and feeding along the pilings and rubble in the basin. During evening twilight, the number of fish in proximity to the basin increased. By nighttime, the fish were

settled in or on almost any object that afforded cover, lying quiescent and unresponsive throughout the night to the extent that they could be touched or captured with a net. The tautog resumed activity during morning twilight.

Thus, as is the case with the pelagic species, these fish have a diurnal rhythm of activity, but with the important difference that at night they are completely quiescent with significantly reduced ability to respond to altering stimuli.

Results from sonically tracking adult fish (39-50 cm) from July to October showed that these large tautog would move away from the homesite each morning (some travelling as far as 500 meters) and return each night. In contrast with these adults, young tautog (< 25 cm) remained in proximity to the basin throughout the day, close to objects affording shelter.

Underwater observations of the areas where the adults spent significant amounts of time showed large quantities of blue mussels, Mytilus edulis. It seemed probable that the daily dispersal of these large fish was related to feeding.

Analysis of the digestive tract contents supported this view, indicating that blue mussels, averaging about 12 mm in length, comprised the major food item. The size of mussels ingested, by even the largest tautog, was limited by the pharyngeal mill at the opening of the esophagus. Since tautog of all sizes are restricted in the size of mussels they can ingest, mussels less than three years old would be the largest

potential food resource for which this population would compete. The daily dispersal of the adults from the homesite was probably related to more effective utilization of available resources, reserving mussels at the homesite as a food for the young fish.

These patterns of activity and feeding were typical for this tautog population from July through October. However, as temperatures dropped from the 16-24°C range of summer and early fall to about 10°C in November, we no longer saw tautog larger than 30 cm. This corresponds to the results of Cooper (1966) who found that fish of similar size moved out of Narragansett Bay, Rhode Island, to winter offshore in a relatively dormant state. In contrast, our results showed that young fish remained in proximity to the homesite, wintering over in a torpid, non-feeding state. It was apparent that for the first 3-4 and possibly 5 years, young fish are highly restricted in their movements, associating closely with the shelter throughout the year regardless of temperature.

There are a number of possible reasons for shelter dependence, but one of the most obvious and important for young and adult tautog is protection from predation, especially critical during the periods of lowered responsiveness. It seemed probable that this high degree of dependence on shelter might well limit or preclude any ability to avoid or escape potentially lethal environmental stress, and we hypothesized that tautog, particularly the young fish, might have different behavioral capabilities for response than we had observed with pelagic fishes.

Based on this premise, we tested the response capabilities of young tautog in the laboratory to high, stressful temperature. Two experimental aquaria (1,400 and 1,500 l) isolated in temperature-controlled rooms and equipped with lighting systems which simulated day-night cycles, were used for testing (Olla & Studholme, 1975). One to two clay drainage tiles were placed on the sand bottom of each tank to provide shelter. Temperature was regulated by thermostatically controlled units. In each of four tests, two fish of nearly similar size were acclimated at 19.8-21.1°C while observations of behavior patterns were recorded.

After an initial period of adjustment to the laboratory, the fish would be active during the light period, swimming about, searching for food and engaging in aggressive behavior. The larger of the two fish was always dominant, occupying the shelter, and aggressively defending it against the subordinate. The subordinate would dig a depression in the sand adjacent to the aquarium wall, which would serve as a shelter site. When small clumps of mussels were placed on the sand, the dominant fish, if not satiated, would defend this area, chasing and nipping at the subordinate if it tried to feed. At night, both fish would remain generally inactive and quiescent.

The agreement between behaviors observed in both field and laboratory again indicated that these patterns transcended both situations and could be used as baselines in evaluating thermal stress.

As temperature increased from acclimation levels of 19.8-21.1°C (mean rate 1.26°C/h), at about 28°C (absolute levels varying among fish)

activity decreased as association with shelter increased. As the temperature was held at about 30°C (the level varying within a 2°C range between tests), the activity of the fish diminished still further (Figs. 2, 4) and they became generally unresponsive, showing little or no motivation to feed (Table I). Aggression decreased to the extent that the subordinate fish, now highly motivated to enter and share the shelter tile, could do so without being attacked by the dominant (Table I). Preliminary findings on the effects of high but sublethal temperatures on adults, indicated that activity as well as aggression was significantly reduced (Fig. 2).

The decrease in activity and responsiveness and the accompanying increase in association with shelter at high temperature resembled typical nighttime behavior of tautog. Since we had observed tautog in the natural environment seeking shelter when pursued by predators or when startled by divers, it seemed clear that closer association with shelter would serve as protection during periods of lowered responsiveness, whether the stimulus was the onset of nighttime or a stress such as temperature.

When exposure to sublethal temperatures was of short duration, and the temperature returned to 20°C, several of the fish were able to survive, resuming feeding and normal activity within a few days. In the natural environment, they could apparently withstand thermal increases of a transient nature, but if exposure were to be prolonged (dependent also on the rate of increase and temperature attained), survival would be impaired since it does not appear that these fish

have the behavioral capability to regulate body temperature by moving to more optimal thermal regions.

Other species, with similar dependence on shelter (e.g., many of the coral reef species) may also be restricted in the capacity to move from a given locale under stressful conditions (Sale, 1971; Stevenson, pers. comm.)

Reduced capability for response may also depend on when the stress is imposed. It is apparent that the capability of tautog to respond to or escape altering stimuli at night, when responsiveness is low, would be significantly less than during the day. This is in direct contrast with the pelagic fishes which were highly responsive both day and night.

The contrasting responses of the pelagic species and tautog to thermal stress support our contention that it is important to define, species by species, the normal behavioral capabilities of each as related to their specific environmental requirements before attempting to predict the effects of potentially lethal stresses. While certain physiological and biochemical responses to temperature (and even other contaminants) may be common to a number of species, how an animal may act when subjected to stress is based on its normal scope of behavior. Generalizations cannot be postulated until more is known about species for which only the most meagre information now exists.

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TABLE I. Behavior of young tautog (Tautoga onitis) at acclimation and elevated temperature derived from four experiments, including aggressive encounters (mean frequency), shelter occupancy (mean % time) and feeding (mean weight in grams or number of ingestions of Mytilus edulis). Modified from Olla & Studholme, 1975.

	Temperature Range °C	No. of Agressive Encounters	Wt. Ingested (g)*	Feeding No. of Ingestions**	Shelter Occupancy % Time		
					Dominant	Subordinate	Shared
Acclimation	19.8-21.1	16.48	5.50	23.4	37.40	4.88	0.05
Test	26.9-32.0	5.04	1.35	1.3	51.14	24.3	13.72

* Based on three tests in which clam was used for food.

** Based on one test in which clumps of Mytilus were used for food.

Fig. 1. Activity recorded during low and high temperature experiments for: A) adult bluefish, and B) adult Atlantic mackerel.

Points represent the high and low mean swimming speeds for 4 or 5-day periods at the mean temperature for each period.

Relation between activity and temperature is indicated by a median curve (after Olla, Studholme, Bejda, Samet & Martin, 1975).

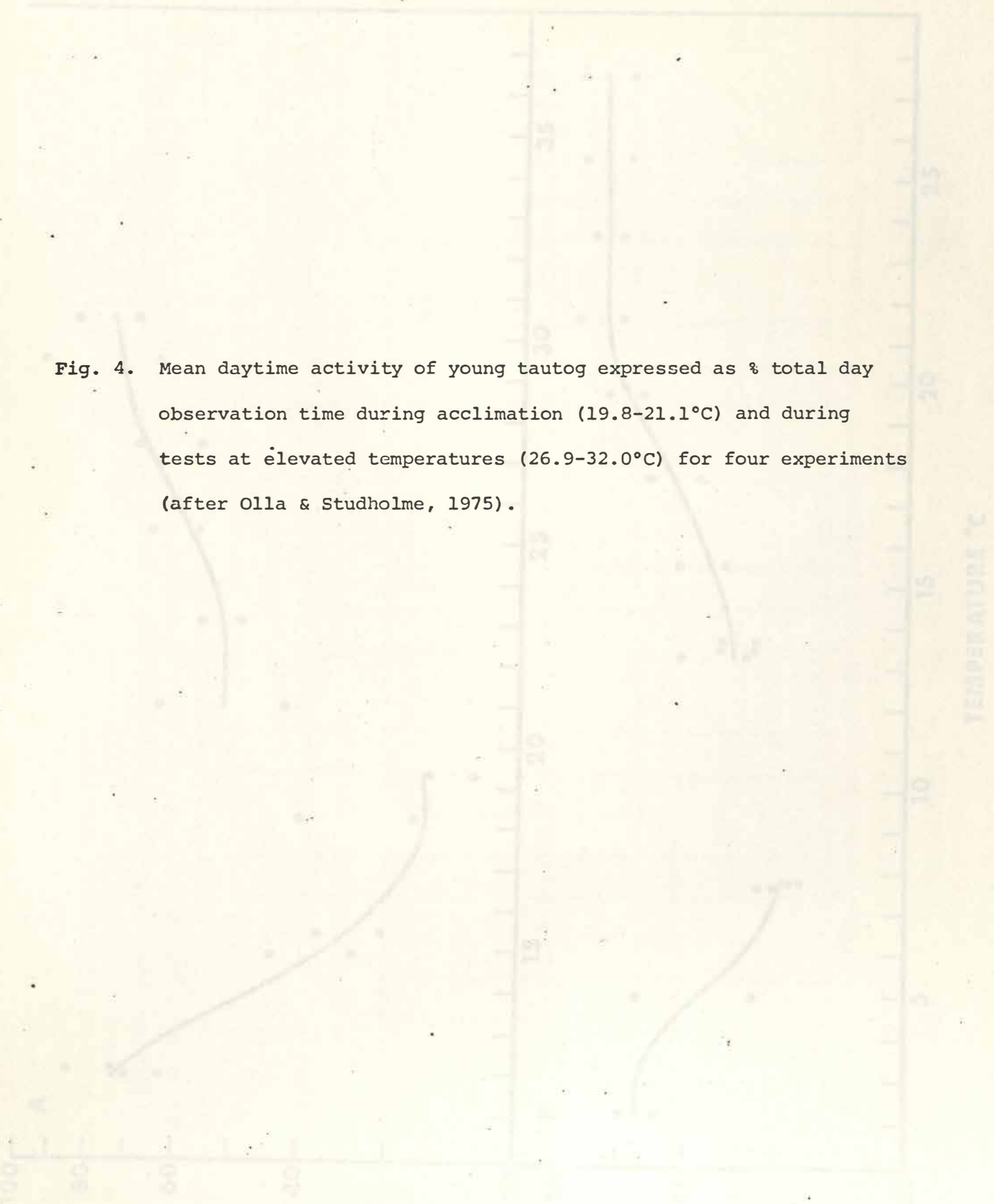
Fig. 2. Comparison of activity at normal and stress temperatures for adult Atlantic mackerel; adult and juvenile bluefish; adult and young tautog (after Olla, Studholme, Bejda, Samet & Martin, 1975).

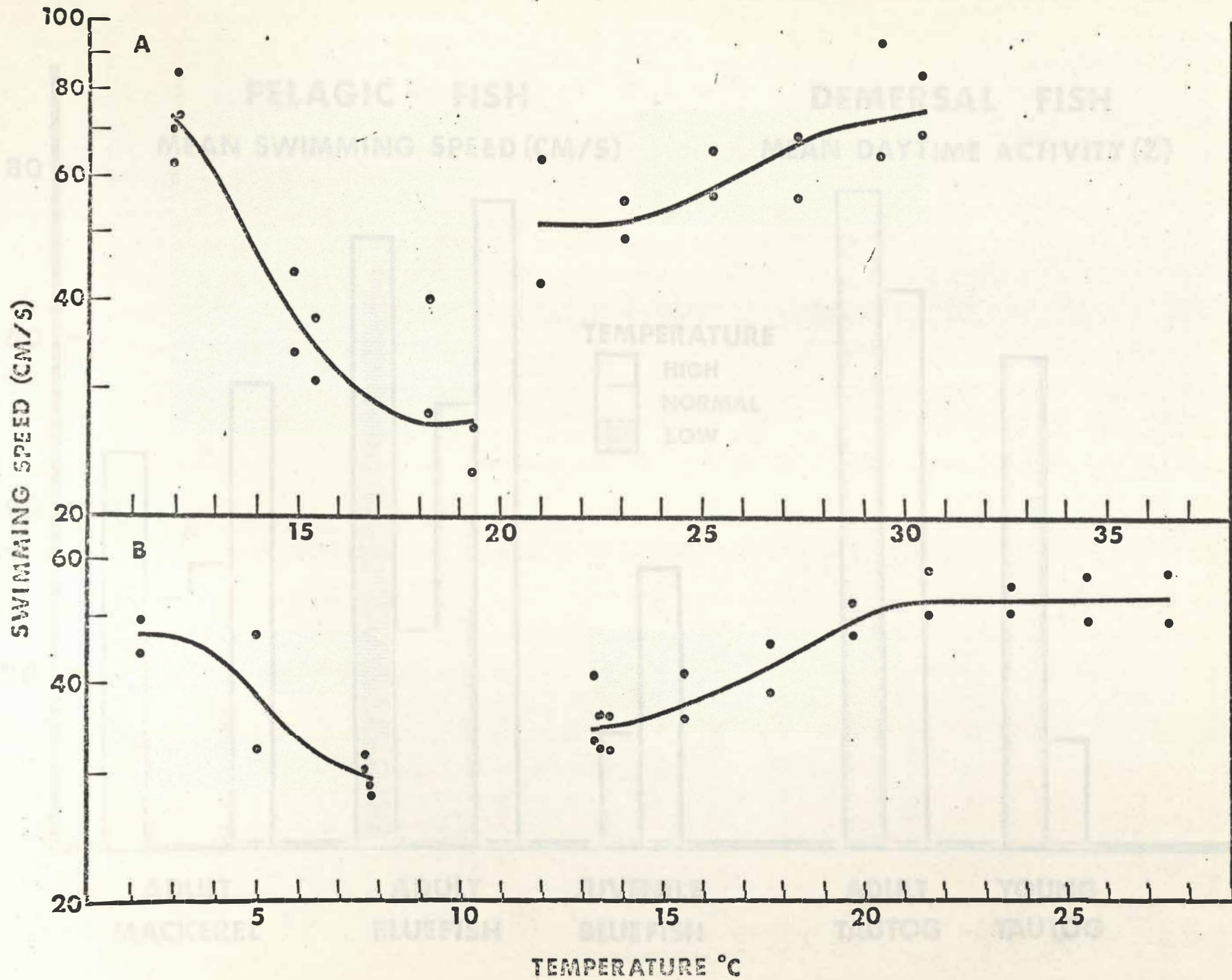
Fig. 2. Mean daytime activity of young water expressed as a total day

alteration time during acclimation (19.5-21.1°C) and during

Fig. 3. Mean swimming speeds of four groups of juvenile bluefish during tests at elevated temperature (24.9-25.0°C) for four experiments temperature rise (after Olla, Studholme, Bejda, Samet & Martin, 1975).

Fig. 4. Mean daytime activity of young tautog expressed as % total day observation time during acclimation (19.8-21.1°C) and during tests at elevated temperatures (26.9-32.0°C) for four experiments (after Olla & Studholme, 1975).



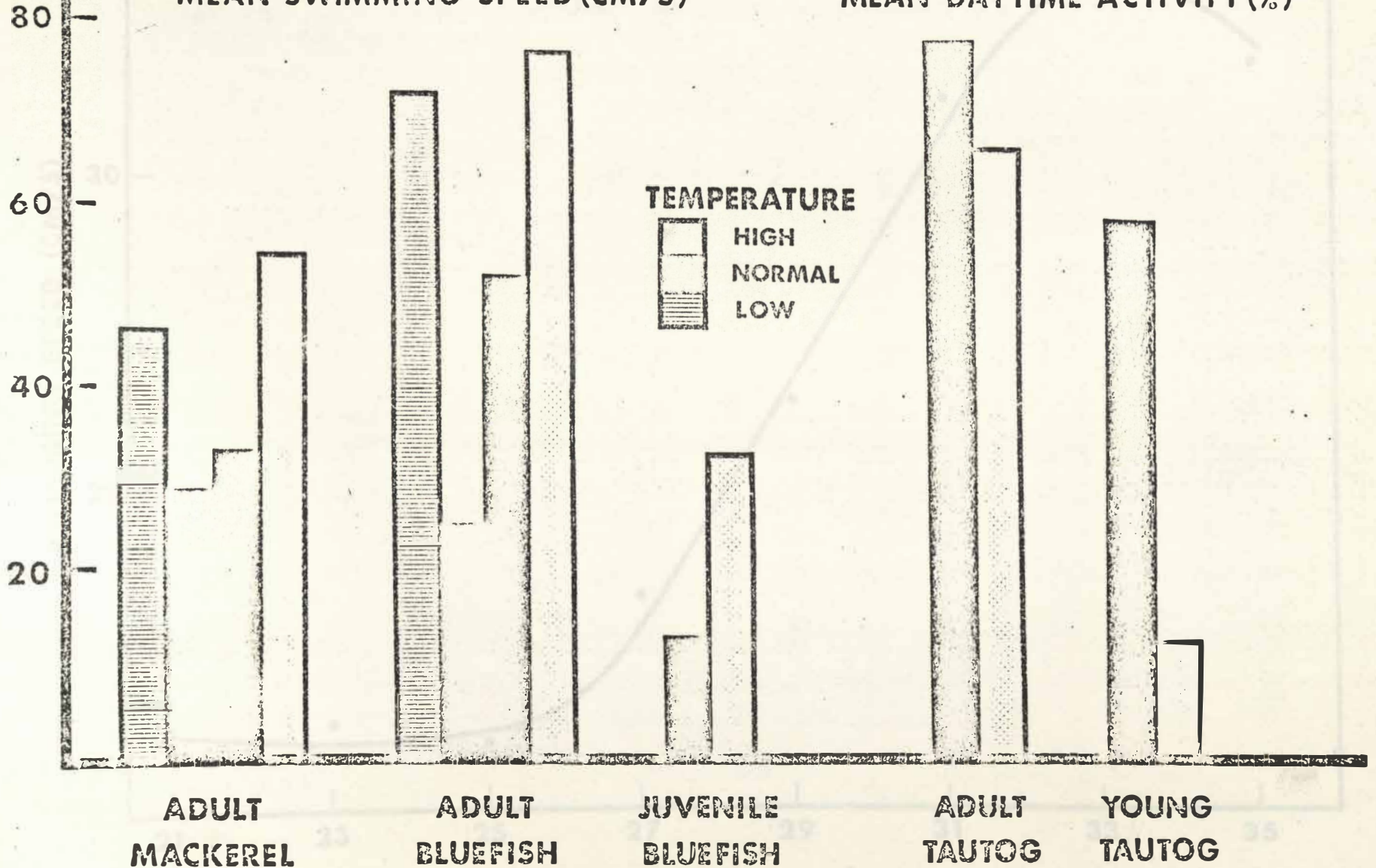


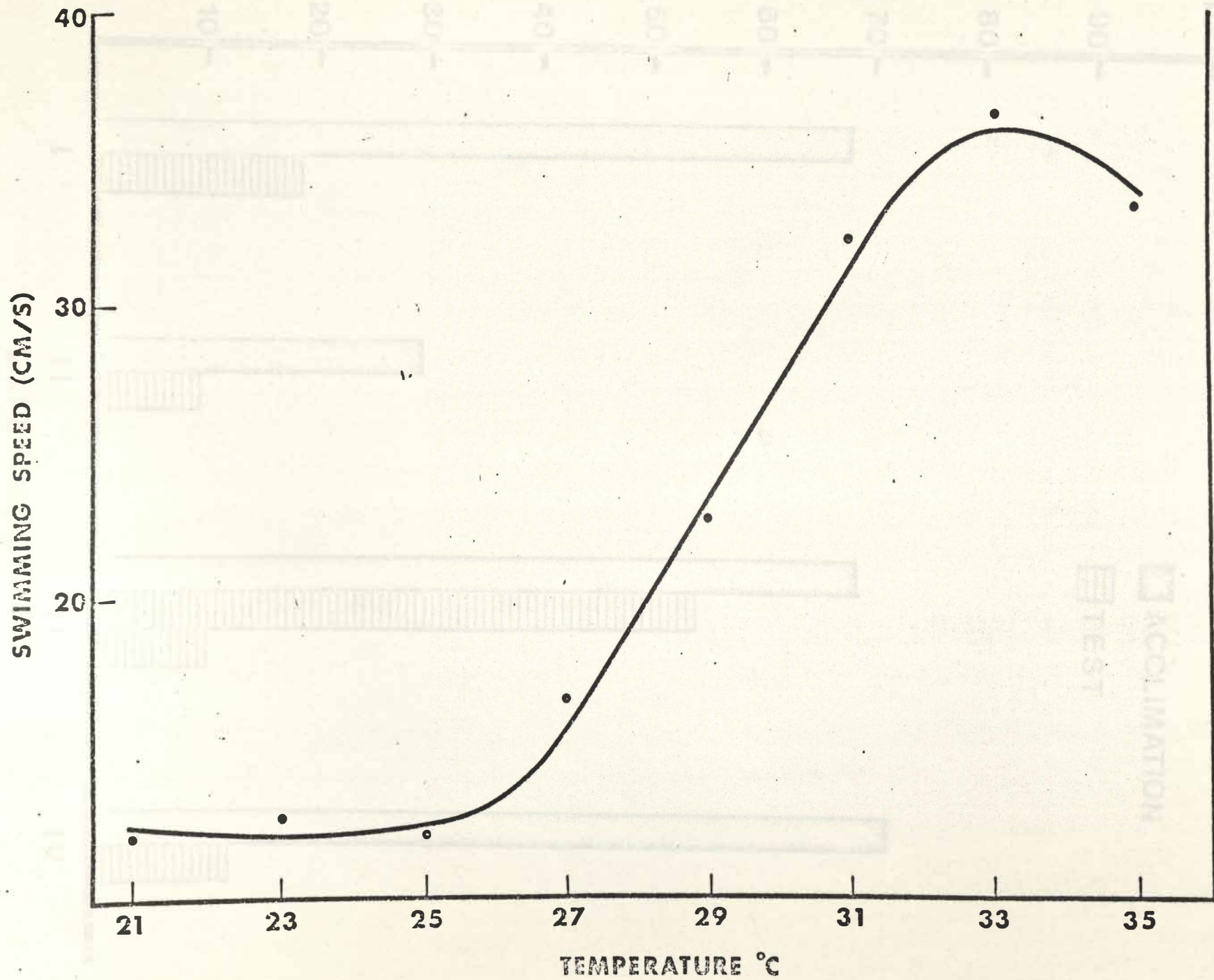
PELAGIC FISH

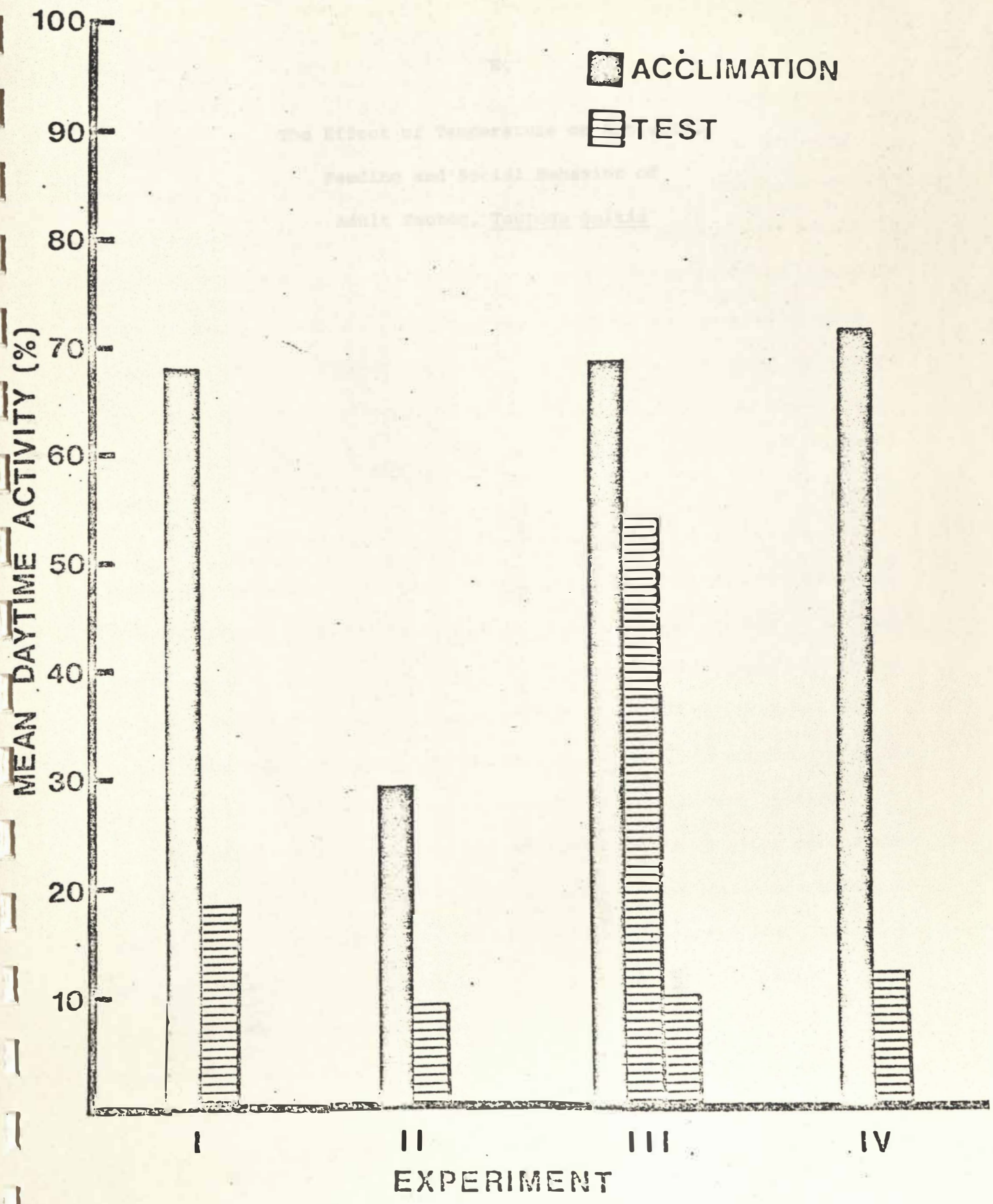
MEAN SWIMMING SPEED (CM/S)

DEMERSAL FISH

MEAN DAYTIME ACTIVITY (%)







ACCLIMATION

TEST

MEAN DAYTIME ACTIVITY (%)

EXPERIMENT

I

II

III

IV

B.

The Effect of Temperature on Activity,
Feeding and Social Behavior of
Adult Tautog, Tautoga onitis

A study on the effects of elevated temperatures on young tautog, Tautoga onitis, showed that at high, but sublethal levels, activity increased while shelter occupancy increased (Jolie and Stubbins, 1973). Accompanying these changes, approximately 50% of the young died with the result that the fish tended to occupy the same area. The effects of temperature on young tautog were compared with those on two pelagic species, Atlantic mackerel, Scomber pomorus, and bluefish, Pomatomus saltatrix, and the responses related to the life habits and selective advantages for each species, (Jolie et al., 1975; Jolie and Stubbins, 1976; see Report).

Since it was shown under natural conditions that adult tautog possessed different life habits than young fish (Jolie et al., 1974) a natural extension of the research was to examine the effects of elevated temperature on adults. Our large 201-l experimental aquaria provided an ideal facility in which to measure and qualify the movements and social interactions among these adult fish which had not been possible in the small experimental systems in which the young were studied.

The study on adult tautog was performed over a 2-year period with two different groups of fish studied each year. Ten males and a female were acclimated to captivity over a several month period while baseline measures were made of their feeding, activity and social interactions, including aggression and dominance. Following the establishment of stable patterns of these activities, temperatures were raised and the effects measured.

INTRODUCTION

A study on the effects of elevated temperatures on young tautog, Tautoga onitis, showed that at high, but sublethal levels, activity decreased while shelter occupancy increased (Olla and Studholme, 1975). Accompanying these changes, aggression was inhibited with the result that the fish tended to occupy the same area. The effects of temperature on young tautog were compared with those on two pelagic species, Atlantic mackerel, Scomber scombrus, and bluefish, Pomatomus saltatrix, and the responses related to the life habits and selective advantage for each species, (Olla et al., 1975b Olla and Studholme, 1976; see Report).

Since it was shown under natural conditions that adult tautog possessed different life habits than young fish (Olla et al., 1974) a natural extension of the research was to examine the effects of elevated temperature on adults. Our large 121-k1 experimental aquarium provided an ideal facility in which to measure and quantify the movements and social interactions among these adult fish which had not been possible in the small experimental systems in which the young were studied.

The study on adult tautog was performed over a 2 -year period with two different groups of fish studied each year. Two males and a female were acclimated to captivity over a several month period while baseline measures were made of their feeding, activity and social interactions, including aggression and dominance. Following the establishment of stable patterns of these activities, temperature was raised and the effects measured.

MATERIALS AND METHODS

Two experiments were conducted over a 2-year period on two separate groups of adult tautog, Tautoga onitis, with two males and one female comprising each group. These fish were trapped during the late summer and early fall off the coast of Fire Island, New York, at temperatures ranging from 19° to 24°C and at photoperiods ranging from 13.0 to 14.17 h.

The fish were held in an elliptical 121-k1 seawater aquarium (10.6 x 4.5 x 3.0 m) located in a temperature-controlled room (Olla et al., 1967). To simulate a natural bottom substrate, the floor of the aquarium was covered with layers of gravel and an upper layer of 0.6 to 0.8 mm sand. A network of pipes under the gravel transported the seawater to a series of sand and gravel filters, providing continual circulation and filtration. Normally operated as a semi-closed system, the addition of new seawater also contributed to maintaining water quality. For both experiments, salinity ranged from 24.0 to 25.2 o/oo, oxygen from 5.6 to 8.0 ppm and pH from 7.0 to 7.5.

Water temperature was controlled primarily by room temperature and by the addition of incoming water. However, in Experiment 2, a thermal exchanger and associated heating unit were used during the temperature increase. Water temperature was remotely monitored at bottom, mid-water and surface in the aquarium with the mean used as the experimental temperature. During each experiment, the mean of the hourly temperature from 0100 to 2400 was considered the mean daily temperature.

Diurnal changes in light intensity from morning to evening civil twilight were simulated by banks of fluorescent bulbs mounted on the walls above the aquarium and controlled by a series of timers (Olla et al., 1967). Incandescent bulbs, programmed to come on before the last row of fluorescents was extinguished, maintained a low level night illumination of 0.07 ft-c. At the beginning of each experiment, the photoperiod was set to match the natural day-length under which the fish were captured. As it decreased to approximately 12 h, day-length was held constant and remained fixed throughout each test.

Clumps of blue mussels, Mytilus edulis, 5-15 kg were placed on the bottom of the tank to allow ad libitum feeding on a natural food source (Olla et al., 1974). New clumps were added periodically as needed.

Based on field observations of the normal requirements of these fish (Olla et al., 1974) a shelter was constructed and placed on the bottom, approximately 3 m from one end of the aquarium. It consisted of three clay drainage tiles (30.5 x 60.9 cm), cemented in a triangular shape, and was positioned to allow the observer to see within.

To facilitate measurements such as interfish distance, relation to food and shelter, and access to all regions of the aquarium, the floor of the tank was mapped into 15 zones, with the shelter comprising the 16th. Based on preliminary observations of the fish's behavior, zones were mapped according to "use" patterns and consequently were of unequal size with the mean area averaging 2.84 m². Visual demarcation of zone boundaries was accomplished by using features already present in the

tank; i.e., window edges, drains, etc. so that no additional indicators were necessary. All distances used in subsequent data analysis were estimated from midpoint to midpoint of each zone.

During the light period, observations were made for 15 min each hour for 12 h (0700-1800) recording for each fish in sequence for 50 counts: 1) activity (min swimming in the water column or moving about on the sand); 2) number of feeding ingestions; 3) aggressive interactions between fish including number of attacks and identity of fish; 4) zone locations. Periodically, motion pictures were taken to supplement these observations.

From these data we computed specific indicators which were used for subsequent statistical analysis of both tests. These included:

- 1) Activity. The mean activity for each hourly observation of the three fish was used to compute a daily mean which was converted into percent of time active.
- 2) Feeding. The total number of ingestions by all three fish was used as the daily measure of feeding.
- 3) Aggression. The total number of interactions among the three fish was used as the daily measure of aggression.
- 4) Interfish distance. Every fifth count of our 50-count observations, we computed a straight-line distance from midpoint to midpoint of zones occupied by each of the fish and used the mean as the hourly measure of interfish distance. If two fish were in the same zone, the distance was considered 0. The daily mean interfish distance was then used for analysis.

- 5) Shared Zones. When more than one fish occupied a zone during a count, this was termed a shared zone. The total number of shared zones per day was used as the daily measure and converted to percent of total daily observations.
- 6) Mobility Index. An ordered frequency count was computed daily of occupancy of each fish in each of the 16 zones. A mobility index, $M = \frac{\text{median zone occupancy}}{\text{maximum zone occupancy}} \times 10^3$, was derived to indicate access of each fish to all areas of the aquarium. The daily mean index was computed for the three fish and used as the daily indicator of mobility.

Observations were made in 4-day periods with intervals up to 3 days between periods during which no measurements were made.

Experiment 1

One male (51 cm) and one female (50 cm) were introduced into the aquarium on 9/20/74, with a second male (56 cm) added 7 days later. The three fish were held at a mean temperature of 19.1°C for 50 days during which the photoperiod was reduced to 12.25 h and held constant. Observations to establish normal baselines were begun on Day 25 with mean temperature for the observation period averaging 18.8°C. Beginning at light onset on Day 51, the water temperature was gradually increased over a 9-day period (mean rate 0.04°C/h) and held at a mean temperature of 28.7°C for 11 days. Then the temperature was gradually decreased over an 8-day period (mean rate 0.05°C/h) and held at a mean level of 18.6°C for 33 days.

Experiment 2

Two males (50 and 53 cm) and one female (44 cm) were introduced into the aquarium on 8/28/75. The fish were held at a mean temperature of 21.3°C for 80 days while photoperiod was reduced and held at 12.32 h. Observations to

establish normal baselines began 54 days after the fish were introduced (mean temperature for observation period was 20.8°C). Beginning at light onset on Day 81, the water temperature was gradually increased over a 9-day period (mean rate 0.03°C/h) and held at a mean temperature of 28.7°C for 11 days. The temperature was gradually decreased over an 8-day period (mean rate 0.04°C/h) and held at a mean temperature of 20.6°C for 33 days.

was based primarily on size with the largest fish dominant over the other fish. In turn, the next largest was dominant over the smallest. A fish occupying a dominant position was identified as such by being the prime initiator of an aggressive act which would result in a submissive response by another animal.

There was, however, one notable exception to the size-dominance hierarchy. In Experiment I, the largest fish in each tank was introduced into the aquarium 7 days after another male (the dominant animal) and a smaller female had been established. This newly introduced animal was subordinate to the other two fish, with the hierarchy evidently determined by prior dominance rather than by size. After 34 days of the largest fish being subordinate, it asserted dominance over the female. Then 28 days after its introduction, under elevated temperature (see below), the largest fish asserted dominance over the smaller male. This hierarchy persisted until temperature returned to baseline 285 days later.

Aggressive behavior, while occurring primarily within the context of some company conflicts, still could not be considered territorial in the classical sense. The territory of each tank was defined by

RESULTS

AGGRESSION

Once the fish had acclimated to captivity, it was apparent that a dominance hierarchy was present. Dominance, as had been previously described for young fish in the laboratory (Olla and Studholme, 1975) was based primarily on size with the largest fish dominant over the other fish. In turn, the next larger was dominant over the smallest. A fish occupying a dominant position was identified as such by being the prime initiator of an aggressive act which would result in a submissive response by another animal.

There was, however, one notable exception to the size-dominance hierarchy. In Experiment 1, the largest fish (a male) was introduced into the aquarium 7 days after another male (the dominant animal) and a smaller female, had been established. This newly introduced animal was subordinate to the other two fish, with the hierarchy evidently determined by prior occupancy rather than by size. After 34 days of the largest fish being subordinate, it assumed dominance over the female. Then 59 days after its introduction, under elevated temperature (see below), the largest fish finally established dominance over the smaller male. This hierarchy remained unchanged until the dominant died (unknown causes) 185 days later.

Aggressive behavior, while occurring primarily within the context of space occupancy conflicts, still could not be considered territorial in the classical sense. The territory or space occupied by the dominant was,

in a general sense, the total area of the tank. Subordinates could be displaced from any location with the dominant animal moving about the aquarium completely unrestricted. The amount of area that the fish swam through or rested in each day was expressed as an index of mobility and was to a certain extent reflective of the dominance hierarchy, with the most subordinate fish always the least mobile.

While the entire tank was under the control of the dominant, there were two areas at which dominance was particularly focused, the feeding area and the shelter. The control of the feeding area, the location most occupied by the dominant, was clearly exemplified by the fact that the subordinate fish, particularly the most subordinate, rarely approached the area or attempted to feed when the dominant was present. In Experiment 2, although the percent of time spent by the subordinate male in the feeding area was high, this fish was continually chased and displaced by the dominant (see below). In addition, when subordinates did feed, they frequently did not ingest the food within the feeding area, but picked up a clump of mussels and carried them to another locale to complete ingestion.

The control of the shelter was such that even in the absence of the dominant, subordinates rarely entered. The dominant would rest in or on top of the shelter, or swim through one of the tiles, from time to time, during the day. Where observations were made during the hour preceding or following the light period, the dominant was found within the shelter, presumably spending the night quiescent period. The relation of a dominant animal to shelter agreed with the results of a previous laboratory study on

young tautog (Olla and Studholme, 1975) which showed the dominant fish defending and occupying shelter.

Aggressive acts were manifested at varying levels of intensity, the most intense involving actual physical contact in the form of nipping or biting by the dominant. In these cases, the dominant animal would swim rapidly towards a subordinate (75 to 100 cm/sec) and nip the flanks or tail. Flight of the subordinate would result as the dominant pursued and chased for as long as 30-45 sec, covering 1-2 circuits of the tank during the most intensive bouts.

At the other extreme, the most subtle action of the dominant animal might elicit a displacement and submissive posture by a subordinate. The subtlety of the dominant's behavior often made it difficult to determine what elicited a response from a subordinate. The dominant, lying on the sand, oriented towards a subordinate, might elicit a submissive response, while at other times, no response was discernible. Between overt, intense aggression and subtle aggressive intention movements, there was a continuum of levels of varying intensities.

Following an aggressive act by the dominant animal, if a subordinate were not displaced, the submissive posture of a subordinate consisted of tilting the dorsal surface towards the dominant at an angle ranging from a few degrees to a complete 90°, the animal completely on its side. A subordinate could also assume this posture as it swam in a wide circuit of the area in which the dominant was resting, an action we considered an avoidance response.

During acclimation, aggressive encounters among all fish occurred significantly more often in Experiment 1 ($\bar{x}/\text{day} = 191.5$) than in Experiment 2 ($\bar{x}/\text{day} = 108.8$; $P < 0.01$, t-Test; Table II, Fig. 1). While in Experiment 2, the largest number of aggressions was always between the dominant and subordinate males ($P < 0.01$, Sign Test), in Experiment 1 there was no significant difference in the number of attacks initiated by the dominant fish towards either of the two subordinates ($P > 0.05$, Sign Test). This may have been due to the instability in the dominance hierarchy in Experiment 1. Not only were the number of attacks more frequent in this experiment, but other differences in the interfish interactions between the two groups reflected the more stable hierarchy which existed initially in Experiment 2. For example, in Experiment 1, mobility was equated with rank, with the dominant male having the greatest access to all areas of the tank, followed by the other fish in order of rank ($P < 0.01$, Sign Test). During the period that the largest male was subordinate to the other fish, it was generally restricted about 86% of the time to one end of the aquarium. Following the shift in dominance between the two subordinate fish, 34 days after the three fish had been introduced, the female (now lowest ranking) was similarly restricted to the other end of the aquarium about 53% of the time.

In Experiment 2, day-to-day comparison showed there was no significant difference in mobility between the dominant and subordinate males ($P > 0.05$, Sign Test), although the female was significantly less mobile than either ($P < 0.01$, Sign Test). During acclimation in this test, the subordinate male had access to all areas of the tank except the shelter, and in fact,

spent more time in the feeding area (29.4%) than did the dominant (17.7%) although this was the preferred area for both. Similar to Experiment 1, the female spent about 53% of the time at the end of the aquarium.

The higher level of aggression in the first experiment resulted in generally greater distances maintained between these fish ($\bar{x} = 4.76$ m) than between the three fish in Experiment 2 ($\bar{x} = 3.69$ m, Table II, Fig. 2). Correspondingly, the occurrence of two or three fish in the same zone at the same time also differed between the two tests. Shared zones between any two fish in Experiment 1 occurred 4.4% of the time; in Experiment 2, 23%. Shared zones between all three fish occurred 0.05% in Experiment 1; 2% in Experiment 2.

ACTIVITY

Based on our field observations of adult tautog in their natural habitat (Olla et al., 1974), as well as on laboratory studies of young tautog (Olla and Studholme, 1975) we had determined that these fish were diurnally active remaining quiescent and generally unresponsive at night. In the field, activity would begin anywhere from 0.17 h before to 1.15 h after the onset of morning twilight (Olla et al., 1974), while in the aquarium, the fish would become active and begin feeding usually within 1-2 min of light onset. During this first hour of the light period, activity was generally high but towards mid-morning swimming activity tended to decrease as the fish, although alert and responsive, rested on

the bottom or, in the case of the dominant, within shelter. By afternoon swimming activity again increased, dropping once more about 0.5 h before light offset. Based on our observations in Experiment 1, the fish appeared to have settled in and become almost completely inactive about 5-10 min after light offset. In the field, cessation of activity was variable ranging from 3.7 h before to 1.15 h after civil twilight (Olla et al., 1974).

When active, a fish would swim in the water column at speeds normally averaging 20-30 cm/sec. Occasionally, a fish would be oriented perpendicular to the bottom, head up, with ventral surface parallel to the wall, maintaining this position by sculling with the pectoral fins. A fish could either swim or remain inactive for the entire 15-min observation period, but more typically would alternate between bouts of activity and rest. When inactive, the dominant fish could settle anywhere, resting in the shelter, lying next to the mussel clump or settling in one of the depressions in the sand bottom (made by the animals) adjacent to the aquarium wall. These depressions may have served as alternate shelter sites for the subordinate fish.

During acclimation in Experiment 1, overall activity levels were generally high for all three fish ($\bar{x}_{DM} = 74.6\%$; $\bar{x}_{SM} = 73.9\%$; $\bar{x}_{SF} = 70.5\%$), with no significant difference between them when compared on a day-to-day basis ($P > 0.05$, Sign Test). In Experiment 2, day-to-day comparison of mean daily activity among the three fish showed that the subordinate male was significantly more active ($\bar{x}_{SM} = 64.8\%$) than the dominant male ($\bar{x}_{DM} = 37.6\%$),

which in turn, was more active than the female ($\bar{x}_{SF} = 18.4\%$; $P < 0.01$, Sign Test).

FEEDING

From our field studies, we had determined that blue mussels Mytilus edulis, comprised the major component in the diet of adult tautog, at least in the region where these fish were studied (Olla et al., 1974). To supply a natural diet for the fish, a clump of mussels (up to 15 kg) was provided in one specific area of the tank, allowing ad libitum feeding.

Feeding began almost immediately after light onset and continued intermittently throughout the day. Although we have no data on nighttime feeding during the two experiments (except for the hour preceding light onset and following light offset in Experiment 1 in which no feeding was observed), based on digestive tract samples taken in the field (Olla et al., 1974), feeding begins around morning twilight and continues until evening, with little or no feeding at night.

Generally, if not prevented from approaching the feeding area by the dominant animal, a fish could feed at anytime. To feed, the fish would visually scan the mussel clump, select a particular item, and seize it with the canine teeth, pulling and tearing small clusters or single mussels free. If the mussels were too large to ingest and crush, the fish would repeatedly expel and re-ingest them, each time reducing the size of the clump until it could be crushed by the pharyngeal teeth. This was similar to feeding behavior of young tautog previously observed in the laboratory (Olla et al., 1974; Olla and Studholme, 1975).

Feeding patterns appeared to be associated with dominance, not only in terms of access to the feeding area, but also in amounts ingested by each fish. In each experiment during acclimation, the feeding area was the preferred region of the dominant fish. It would lie adjacent to or even on top of the mussels, frequently rubbing its flank and ventral surface across the shells. If a subordinate approached, the dominant would often displace or chase it from the feeding area. In Experiment 2, for example, the highest percentage of aggressions initiated during acclimation towards the subordinate male occurred when the dominant was in the feeding zone (22.9%). The motivation for the subordinate male to enter the feeding area was high as reflected in the amount of time spent there even though this elicited a heightened level of aggression by the dominant male. Thus, the highest percentage of aggressive attacks received by the subordinate male occurred when it was in the feeding zone (31.1%). If the dominant was in proximity to the mussels, subordinate animals would usually swim wide of the feeding area, picking up small clumps of mussels that lay on the perimeter, grasping them in its jaws, and swimming to another area of the tank to complete ingestion.

Dominance also appeared to affect amounts ingested. In Experiment 1, day-to-day comparison between fish indicated that the dominant male ingested the greatest amount, followed by the fish in order of rank ($P < 0.01$, Sign Test). This was true even after the shift in the dominance hierarchy (described above). In Experiment 2, although there was no significant difference between the dominant and subordinate males, the female ingested

significantly less ($P < 0.05$, Sign Test). In Experiment 1, ingestions per day for the three fish averaged 28; in Experiment 2, 15 (Table I).

As the temperature began to increase above acclimation levels, changes in established behaviors began to occur. While there were differences between the two tests as to when effects began to be manifested, in general, disruption of normal social patterns, decreases in activity and feeding, and changes in interfish distance occurred under elevated temperature, continuing for varying lengths of time even after the temperature returned to acclimation levels (Tables I and II).

EXPERIMENT 1.

Temperature Rise

During the gradual increase in temperature ($0.04^{\circ}\text{C}/\text{h}$), although activity levels did not increase significantly ($\bar{x}_3 \text{ fish} = 83.3\%$, Table I) there was a significant increase in the mobility of both subordinate fish to the extent that the dominant animal was not always the most mobile ($P < 0.05$, Sign Test).

The fish continued to feed normally until the last 2 days of the rise (27.6° to 28.4°C) when the number of ingestions began to decrease (Table I). Throughout the rise, the dominant fish still selected the feeding area as the preferred zone.

As the temperature continued to rise, spacing normally maintained between the animals began to change (Fig. 2). Beginning on the 5th day of the increase (25.1°C) distances between the subordinate male and the other fish began to decrease. As the temperature continued to rise during the

next 4 days (25.8-28.4°C), mean distance maintained between all three fish decreased to 3.78 m, a drop of 20.5% from normal (Table II). As the temperature reached 28.4°C, there was an increase in the frequency of shared zones to 22%, another indication of disruption of normal interfish spacing (Table II).

While levels of aggression remained substantially unchanged between the dominant male and the two subordinate fish for the first 8 days of the rise (20.9-27.6°C) there was an increase in the number of aggressions by the subordinate male toward the female ($P < 0.01$, End Count Test). However, about 0.5 h after light onset on the final day of the increase (28.4°C) there was a series of intense aggressive interactions between the dominant and subordinate males. At the outset, both fish swam in a small tight circle in the middle of the aquarium, with the dominant continually chasing and nipping the subordinate. Gradually the fish moved up in the water column and the encounter ended in a mouth-to-mouth attack lasting approximately 3 min and culminating in both fish breaking the water surface. As a result, the larger of the two, the former subordinate, became the dominant animal, while the smaller male was second in rank. This dominance hierarchy, now based on size, remained stable for the duration of the test.

The shift in dominance was also reflected in shelter occupancy. Until this point, the larger male had been excluded from the shelter. Now, assuming the dominant position, this animal had unrestricted access with the smaller male excluded.

Temperature Hold

As the temperature remained at 28.7°C, there was a further breakdown in the normal social interactions among the fish. Observations during 8 of the 11 days of exposure to high, sublethal temperature indicated that mean interfish distance now averaged only 3.35 m, 29.6% less than normally maintained (Fig. 2) with the fish residing in the same zone 28.8% of the time (Table II). As the same time, the level of aggression continually decreased (Table II, Fig. 1), until on the 10th day under 28.7°C, only 4 interactions were observed (this as compared with the daily total of 185 under acclimation) and on the 11th day, only 5. Not only were there no attacks by the dominant towards the subordinate male on this last day, but the two fish frequently rested together in the feeding zone. Shared zones for the two males in all areas of the aquarium reached 33%, higher than on any previous day.

As compared with levels recorded during the temperature increase, activity decreased significantly ($P < 0.01$, End Count Test) for the dominant male (57.1%) and female (67.3%) with mean levels for the three fish averaging 66.8% (Table I). Mobility continued to remain generally high (Table I), but with no correlation between rank and mobility as had existed during acclimation. Shelter access by the subordinates was still restricted, possibly because of conditioning under normal temperature conditions. The subordinate male now occupied the feeding zone 25.6% of the time, seldom attacked or chased by the dominant.

Although the subordinate male continued to feed, ingestion levels of the female and dominant male dropped significantly during the first 4 days of the temperature hold ($P < 0.05$, End Count Test). Amounts ingested during the 11-day exposure to 28.7°C decreased by 52.7% as compared with normal (Table I).

Temperature Decrease and Recovery

Continued disruption in normal behavior patterns indicated that the fish were still stressed during the 8-day decrease in temperature from 28.6°C to 18.8°C (mean rate $0.05^{\circ}\text{C}/\text{h}$).

Measures of feeding, activity, mobility, spacing and aggression made during the last four days of the drop (24.2°C to 21.6°C) indicated that not only were the fish not returning to normal levels, but in several instances were more affected than during exposure to high temperature (Tables I and II).

There were, however, differences among the three fish as to the extent to which each was affected, with the dominant male apparently the most severely stressed. While combined activity levels were depressed 61.4% below acclimation levels (Table I), the dominant male was active only 9.8% of the time, a decrease of almost 87% from normal. Correspondingly, mobility was also significantly reduced, particularly so for the dominant which spent 28% of the time resting in the shelter and 40% in a bottom depression adjacent to the aquarium wall, seldom feeding or showing aggression towards the subordinates. Distance between the three fish continued to decrease (Fig. 2) and by the time the temperature reached 22.2 to 21.6°C , interfish spacing

averaged only 2.79 m, 41.7% below normal (Table II). This was partly due to the continued high frequency of shared zones (Table II), with the largest percentage (17.5%) between the dominant male and female.

Another indication that the fish continued to be stressed was evident by the degree of shelter occupancy. Although the female was still restricted in access, the subordinate male was less so, spending an average of 9.2% of the time in one of the tiles, the highest occupancy observed for either subordinate fish during the test. This fish appeared to be the least affected, continuing to be active 44.9% of the time, with the highest mobility and ingestion rate of the three fish. The subordinate male also continued to be aggressive towards the female with interactions increasing slightly as compared with the last four days of exposure to high temperature.

Following the return to acclimation temperature, the fish gradually began to recover, showing increases in activity, aggressions (Fig. 1) and spacing (Fig. 2), with a corresponding decrease in shared zones as compared with levels observed under high temperature stress (Tables I and II).

However, just as there had been variation in the degree to which each fish had been affected by high temperature, it was also evident that recovery, as measured in terms of return of normal behavior patterns was also variable.

For the first 2 to 5 days after return to acclimation temperature, the two subordinate fish continued to be more active than the dominant ($\bar{x}_{SM} = 52.8\%$; $\bar{x}_{SF} = 41.4\%$; $\bar{x}_{DM} = 16.0\%$). Correspondingly, their mobility was also higher

as the dominant continued to rest (about 28% of the time) in the depression next to the wall of the aquarium, initiating few aggressions and frequently allowing the female to occupy the same zone. Feeding by the subordinates was also higher with these fish (particularly the male) able to approach and feed at will, without eliciting an aggressive response from the dominant.

Beginning about 12-15 days after the return to 18.6°C, there were shifts in these behaviors which indicated that, as the dominant fish began to recover, the normal social patterns, disrupted during stress, were becoming re-established.

As the dominant resumed feeding, it once again chose the feeding area as the preferred zone, spending an average of 41.5% of the time in proximity to the mussels. As a result, access to the food by both subordinates, particularly the female, was restricted, the male averaging 3.4% of the time in the feeding zone, the female only 1.2%. This shift in access to the food was evidenced by a decrease in ingestions by subordinates, especially by the female.

Another indication that the dominant fish was recovering was evidenced by the steadily rising number of aggressions initiated by it towards both subordinates (Table II, Fig. 1). This resulted in continually increasing distances maintained between them (Table II) and a corresponding shift in shared zones, with the highest frequency now occurring between the two subordinates.

By the 16th day of the return to 18.6°C as had been typical during acclimation, the most subordinate fish (the female) was once again restricted

to the end of the aquarium. For the remainder of the test, time in this area for this fish averaged 94.8% with the mobility index dropping to 0.

Although, with the exception of interfish distance, none of the combined quantitative measures indicated that the fish in this test had completely returned to those levels established during acclimation, the qualitative nature of the behaviors was such that it indicated that normal patterns of social interaction had been reestablished. Whether the establishment of a new norm could be attributed to the final stabilization in the dominance hierarchy or was an after-effect of exposure to sublethal thermal stress, we could not state unequivocally.

EXPERIMENT 2.

Temperature Rise

In this test, significant changes in activity and aggression began to occur at 24.4°C, only 3.6°C above mean acclimation temperature. Combined activity of the three fish at this temperature increased 44% above normal levels and was the highest average recorded for the entire test. The female showed the greatest increase, spending 51% of the time swimming about the aquarium, less restricted than usual. Coupled with increased activity was a high index of mobility (higher than previously observed for the two subordinates) reflecting the movement and activity of the fish throughout all areas of the aquarium. This is similar to the increased mobility of subordinates observed during Experiment 1 as

the temperature began to rise (Table I).

Aggression also increased at this temperature (Table II) primarily between the dominant and subordinate males. When the temperature had reached 25.2°C, even though activity and aggression remained substantially unchanged, shared zones reached 72.2%, with 32.2% occurring between the two males as the subordinate male attempted to occupy the same area as the dominant, only to be chased or displaced.

For the next 4 days of the temperature increase (25.8 to 28.2°C), similar to the response observed in Experiment 1, although aggressions remained high (Fig. 1) interfish distance steadily decreased (Table II, Fig. 2). At 28.2°C, mean distance between the three fish averaged 1.95 m, 47% below that maintained at 20.8°C, with all fish selecting the area at the end of the aquarium as their preferred zone. Correspondingly the frequency of shared zones continued to remain significantly higher than during acclimation ($P < 0.05$, End Count Test, Table II) ranging from 45.5 to 79.2% (this highest level reached at 28.2°C when the occurrence of three fish in the same zone rose to 31.5%, nearly 16 times higher than normal).

While the only fish showing a significant decrease in activity during the final 4 days of the rise was the female ($P < 0.05$, End Count Test), it should be pointed out that mobility for all three animals had begun to decrease as the temperature rose above 28°C.

Another indication that the fish were becoming stressed was evident in the decline in feeding. At 28.2°C, only 10 ingestions were re-

corded for all three animals, less than on any preceding day.

Temperature Hold

As the temperature was held at 28.7°C for the next 11 days, activity decreased significantly ($P < 0.05$, End Count Test) for each of the three fish, with the combined average 44.9% below acclimation levels (Table I).

However, as had been evident in Experiment 1, there was considerable variation in the degree to which each animal was affected. When measured by changes in activity, mobility, feeding and aggression, the most severely stressed in each test appeared to be the dominant male. In Experiment 2, it was the dominant male which showed the greatest decrease in swimming time from normal (66%) as well as the lowest average activity (12.6%) during exposure to high temperature. In addition, while mobility was also reduced for all fish, the dominant was affected to the extent that the female often had a higher daily mobility index, less restricted than during acclimation.

While there was also variation in feeding among the three fish, overall ingestions were reduced by 62.7% as compared with normal ($P < 0.01$, End Count Test, Table I). The dominant male was most severely affected with only 11 ingestions recorded for this fish during the 11-day period at 28.7°C.

Similar to the response observed in Experiment 1, as the tempera-

ture was held at 28.7°C, normal social interactions among the fish were disrupted. The level of aggression dropped significantly ($P < 0.01$, End Count Test, Table II, Fig. 1) while interfish distance continued to be lower than normal averaging only 2.82 m, 24% below mean distance at 20.8°C (Table II, Fig. 2). In contrast with the intense aggression observed during the temperature rise when the fish were in close proximity, they now frequently rested together in the same depression, with shared zones averaging 60.3% (Table II). When interactions did occur, they were seldom intense (i.e. chases) but consisted primarily of displacements in which a subordinate responded by moving usually less than 1 m.

The region at the end of the aquarium still served as the primary choice for all three fish, although the secondary area for the dominant was the shelter. During the last 3 days of exposure to high temperature, this animal spent 22.7% of the time resting within one of the tiles. Another indication of lowered aggression was reflected by the fact that at this time the subordinate male was allowed limited access to the shelter, spending 6.2% of the time within the structure.

Temperature Decrease and Recovery

During the 8-day decrease from 28.7°C to 20.5°C (mean rate 0.04°C/h) the levels of activity, feeding, aggression and interfish distance remained comparable to those measured during the exposure to 28.7°C (Tables I and II).

The fish continued to be generally inactive with combined levels

47.1% lower than normal (Table I). However, the subordinate male was significantly more active (36.9%) than either the subordinate female (12.6%) or the dominant male (14.3%) ($P < 0.01$; Sign Test), with the latter continuing to be the most severely affected. (Swimming time for this animal was 62% lower than during acclimation). In addition, the reduced distance between the animals (2.98 m) and the continued high incidence of shared zones (58.0%) combined with continued low levels of aggression (38/day) reflected the continued effect of exposure to high temperature (Table II).

Mobility was generally low (Table I) as each of the three fish remained in the area at the end of the aquarium more than 40% of the time, although the dominant male continued to select the shelter as a secondary area (17.5%).

As the temperature was held at 20.6°C, similar to the response of the fish in Experiment 1, there was considerable variation among the individual animals in both length of time and degree to which recovery was comparable with the behavioral norms established during acclimation.

One of the first indications that the fish were beginning to recover was evident in the increase in feeding. Combined levels for the three fish began to rise as the temperature reached 20.6°C (Table I) and remained comparable to normal levels for the remainder of the Experiment. Also the pattern of feeding was reestablished; i.e., day-to-day comparison indicated there was no significant difference between the

ability of the three fish also shifted during the recovery period. Dominant and subordinate males with the female ingesting significantly less ($P < 0.05$; Sign Test). It is interesting to note that throughout the decrease in temperature and for the first 5 days during the recovery, the dominant male occupied the area in which the food was maintained, restricting access by the subordinates. As recovery continued, the normal pattern observed during acclimation also became reestablished, i.e., the subordinate male spent more time in the feeding area (18.6%) than the dominant (10.9%). However, with only three exceptions, it was no longer the preferred zone for these fish. Instead, all three animals continued to spend more than 30% of the time swimming or resting in the area at the end of the aquarium which had been their primary choice during high-temperature stress.

Combined activity, measured 2 to 5 days after the temperature reached 20.6°C was still reduced (Table I) with the dominant male continuing to be the least active of the three (21.2%), and still apparently, the most affected. For the next 19 days, activity slowly increased but variability remained high with continued day-to-day stability evident only after about 24 days. By this time, not only had combined activity for the three animals reached near normal levels (38.3% as compared with 40.2% during acclimation) but the activity patterns of the individual fish were reestablished with the subordinate male significantly more active (60.7%) than the dominant male (31.2%), and the female once again, the least active (23.0%).

Mobility of the three fish also shifted during the recovery period. Initially (for the first 8 days at 20.6°C) the subordinate had the highest mobility index with no difference evident between the dominant male and female. However, as the dominant gradually resumed normal activity, the pattern of mobility that had existed during acclimation was reestablished, i.e., no significant difference between the two males ($P < 0.05$; Sign Test) with the female the most restricted.

Another indication of the recovery of the animals was the increase in interfish distance. Within 3 days after reaching 20.6°C, distance between the fish began to rise significantly ($P < 0.01$; End Count Test). Although there was some day-to-day variation, mean level for the recovery period averaged 3.35 m (Table II, Fig. 2), with no significant difference as compared with acclimation ($P < 0.05$; End Count Test).

Although distance had begun to increase almost immediately, the first indication of changes in aggression did not occur until 10 days after the temperature reached 20.6°C. This may have been due in large measure to the slow recovery of the dominant animal, which even allowed the subordinate male to have limited access to the shelter during this period. However, as the dominant once again became active, the frequency of chases and displacements was increased with the subordinate again completely restricted from the shelter. For

the remainder of the test, although the interactions were significantly higher than during exposure to 28.7°C ($P < 0.01$; End Count Test) they averaged 52.9% below acclimation (Table II).

Also decreasing significantly ($P < 0.01$; End Count Test) as the temperature was held at 20.8°C was the frequency of zones shared, although remaining significantly higher than during acclimation (Table II). There was, however, a shift in the pairing. For example, as compared with acclimation, shared zones between the dominant male and female increased by 96%; between the subordinate male and female by 104%; and by 275% for all three fish. The only decrease in shared zones occurred between the dominant and subordinate males (33%).

In this Experiment, with the exception of quantitative levels of aggression and zone sharing, activity, feeding and interfish distance eventually returned to levels established during acclimation and reflected the recovery of the fish. Perhaps more importantly, the re-establishment of the majority of the behavioral patterns characteristic of this group of animals, which had also been disrupted during exposure to sublethal temperature, was a significant indicator of return to normality.

DISCUSSION

Similar to the responses observed in young tautog (Olla and Studholme 1975) adult fish also decrease their level of activity when subjected to elevated temperature. This reduction is obviously an adaptive behavior, with the animals expending energy towards physiological acclimation rather than towards seeking more optimal temperatures. Although there are undoubtedly differences between the young and adult fish as to their capability for withstanding sublethal temperatures, apparently if the exposure is of short duration, both groups possess a high recovery potential. This is in contrast to what we had found with young bluefish, Pomatomus saltatrix, and Atlantic mackerel, Scomber scombrus (Olla et al. 1975b).

While young tautog sought shelter under thermal stress, the adults did not show the same degree of shelter-dependence, even though the temperature appeared to be equally debilitating. This is not surprising when the normal habits and behavioral repertoire of young and adults are considered. Results of our previous field studies (Olla et al. 1974) have indicated that the young fish remain in proximity to a specific homesite throughout the year, restricted in their movements and always found in close association with shelter. When pursued by predators, or during periods of lowered responsiveness (as during night or winter) these young fish seek cover. In contrast,

adults move from shelter by day to feed and, in addition, migrate offshore in the late fall, returning inshore in late spring, indicative of less dependence on shelter. The large fish are of a size where predation is not as critical as it is for young animals.

Although the natural habits of the adults seemed to imply a capability for moving away from stress, the behavior in the aquarium indicated that, while there was a short period of increased activity and mobility as the temperature began to rise (particularly evident in the second experiment), the response was not comparable to that observed in pelagic species studied previously (Olla and Studholme 1971, 1976; Olla et al. 1975b). Whereas with tautog the level of activity decreases as the temperature remains elevated, the pelagic species not only increase activity but maintain high swimming speed as the temperature departs from their optimal or "preferred" range. These pelagic species evidently have the capability to move in response to changing temperature, thereby avoiding unfavorable thermal regimes and maximizing their presence in areas where temperature is optimal.

Aggression was also significantly inhibited in both young and adult tautog with the fish showing an increased tendency for grouping and a corresponding reduction in normal spacing. In the young fish, the animals occupied the shelter together while the adults occupied the same zone. Indications from preliminary studies on an-

other labrid species, the cunner, Tautoglabrus adspersus, have shown that these fish also increase grouping under high temperature.

The reason for such a response is not readily apparent, but may suggest some similarity with pelagic species which also increase grouping tendency under stress, with the response transcending even widely separated taxonomic groups.

TABLE 1. Grouping tendency of fishes and other taxa under various temperatures. Data are presented as mean ± standard error.

Species	Temp. (°C)	MEASURE 1		MEASURE 2	
		Mean	SE	Mean	SE
MULLUS	20.0	30.3	66.7	379	100
	25.0	34.0	57.4	314	114
	30.0	28.7	71.0	333	108
	35.0	74.3	57.0	310	110
GOMPHUS	20.0	37.7	57.0	310	110
	25.0	39.5	58.4	314	114
	30.0	38.0	57.9	302	108
	35.0	70.6	47.7	310	110
SERRANUS	20.0	30.7	48.3	310	110
	25.0	30.7	48.3	310	110
	30.0	31.0	48.3	310	110
	35.0	31.0	48.3	310	110
LABRID	20.0	31.0	48.3	310	110
	25.0	31.0	48.3	310	110
	30.0	31.0	48.3	310	110
	35.0	31.0	48.3	310	110
OTHER	20.0	31.0	48.3	310	110
	25.0	31.0	48.3	310	110
	30.0	31.0	48.3	310	110
	35.0	31.0	48.3	310	110

TABLE 1. Grouping tendency of fishes and other taxa under various temperatures. Data are presented as mean ± standard error.

TABLE I. Mean activity (%), mean mobility index and total number of feeding ingestions for three adult tautog, Tautoga onitis in each Experiment. Data is presented as mean of 2 days.

Test Condition	Mean °C		ACTIVITY (%)		MOBILITY INDEX		INGESTIONS (No.)	
	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2
<u>ACCLIMATION</u>	18.8	20.8	52.3	44.7	109	99	46	31
			56.0	52.4	118	103	63	53
			68.7	33.0	128	59	83	43
			75.2	38.0	108	74	83	47
			87.7	39.0	110	60	99	54
			89.5	36.4	134	67	111	50
			74.0	35.9	90	71	119	41
			78.6	42.7	68	83	86	55
<u>RISE</u>	20.9	20.9	80.7	44.3	84	95	66	42
	to	to	86.7	53.5	146	101	78	36
	28.4	28.2	84.9	42.9	188	64	65	43
			81.0	43.3	268	40	44	17
<u>HOLD</u>	28.7	28.7	68.4	25.4	239	24	16	6
			69.7	24.7	108	26	27	10
				28.0		36		29
			67.1	20.0	146	50	60	30
			62.0	14.7	158	29	60	10
			20.6*		31*		20*	
<u>DROP</u>	27.1	27.7		20.9		67		19
	to	to	26.9	22.4	51	16	35	13
	18.8	20.9	29.5	20.2	33	16	57	24
			21.7		19		38	
<u>RETURN</u>	18.6	20.6	34.9	21.9	38	26	42	38
			38.8	32.0	50	59	36	60
			46.0	33.4	92	42	48	32
			59.9	36.7	92	64	40	48
			67.6	30.2	46	24	49	46
			71.6	41.5	62	72	68	52
			73.6	31.7	48	43	43	43
			64.5	37.9	34	54	52	38
			44.9	37.5	33	62	51	73
			49.0	39.5	59	36	87	42

*Data for one day only.

TABLE II. Mean interfish distance (m), total number of aggressive interactions, and frequency of zones shared (%) for three adult tautog, *Tautoga onitis* in each Experiment. Data is presented as mean of 2 days.

Test Condition	Mean °C		DISTANCE (m)		AGGRESSIONS (No.)		SHARED ZONES (%)	
	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2
<u>ACCLIMATION</u>	18.8	20.8	no data	4.10	105	122	no data	22.3
			4.19	4.02	204	162	15.2	25.7
			4.78	3.58	168	112	4.0	28.2
			5.03	3.30	241	115	2.2	30.8
			4.69	2.91	166	79	3.2	25.3
			4.88	4.22	217	79	1.0	32.5
			4.98	3.49	182	70	1.8	21.8
			161	132	1.0	31.8		
<u>RISE</u>	20.9	20.9	4.63	4.11	194	124	2.3	25.3
	to	to	4.29	3.38	191	234	2.0	55.5
	28.4	28.2	4.09	3.29	195	155	1.8	53.3
			3.46	2.34	213	139	13.0	71.7
<u>HOLD</u>	28.7	28.7	3.36	2.38	108	56	16.7	62.8
			3.55	2.46	34	68	26.2	54.8
				2.90		43		66.3
			3.43	3.15	41	21	25.3	57.8
			3.05	3.12	5	14	47.2	57.0
	2.91*		25*		61.7*			
<u>DROP</u>	27.1	27.7		3.30		22		39.3
	to	to	3.54	2.94	28	48	17.0	61.7
	18.8	20.9	2.80	2.86	28	33	26.8	63.0
			2.83		48		68.0	
<u>RETURN</u>	18.6	20.6	3.18	3.57	32	45	16.2	60.5
			2.89	3.35	38	44	27.7	36.5
			3.24	2.95	53	46	15.2	47.7
			3.23	3.64	58	66	12.7	40.7
			4.22	3.58	72	54	17.3	47.7
			4.37	3.53	83	66	17.8	39.3
			4.62	2.96	103	59	18.2	44.7
			4.65	3.34	89	60	12.5	45.0
			4.53	3.44	44	41	19.7	29.0
			4.72	3.10	44	34	12.2	34.2

*Data for one day only.

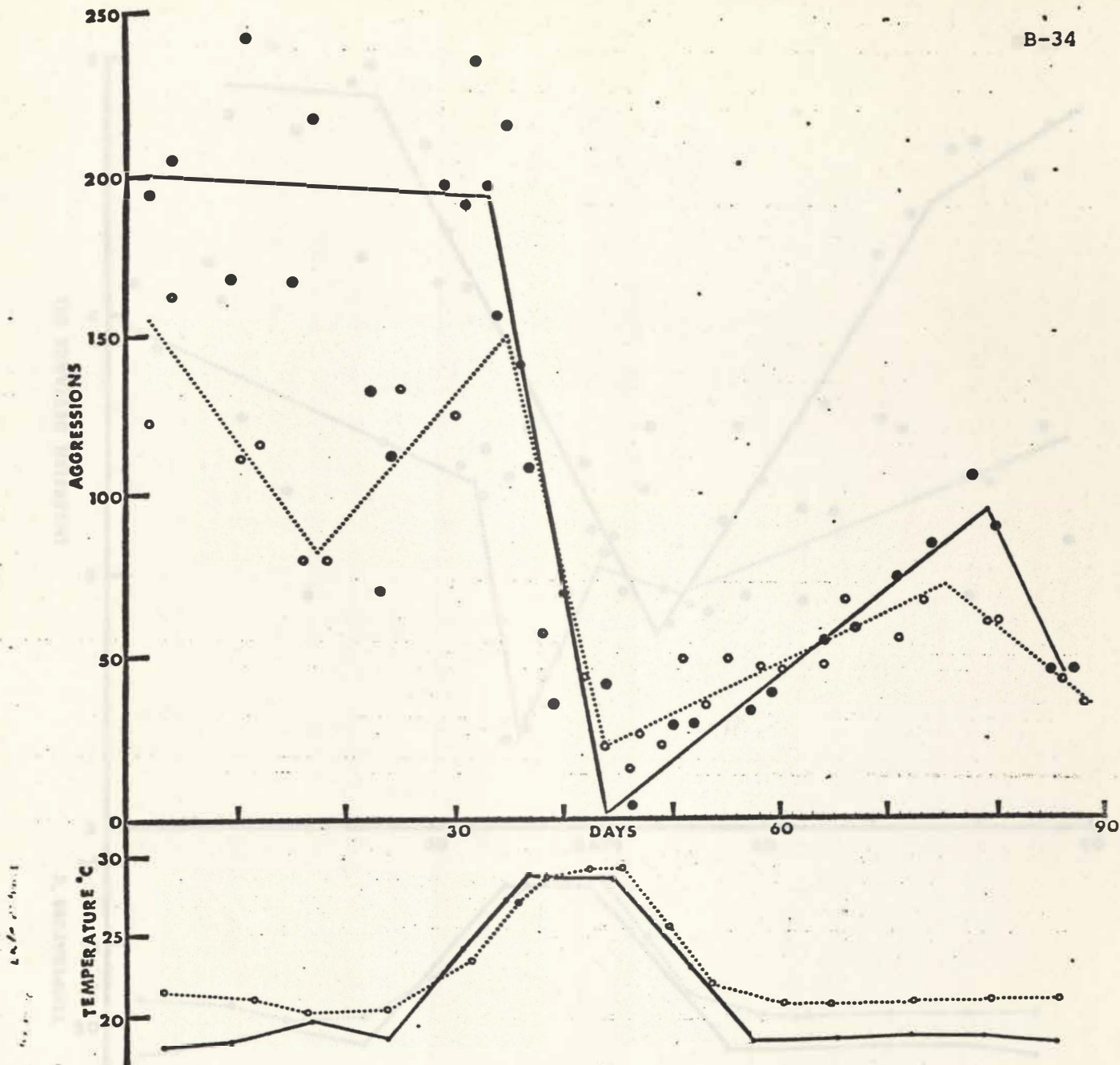


Figure 1. Aggressive interactions between dominant and subordinate adult tautog, *Tautoga onitis*, expressed as 2-day averages for Experiment 1 (●) and Experiment 2 (○). Correlation between changing aggression and temperature is indicated by solid (Experiment 1) and broken lines (Experiment 2).

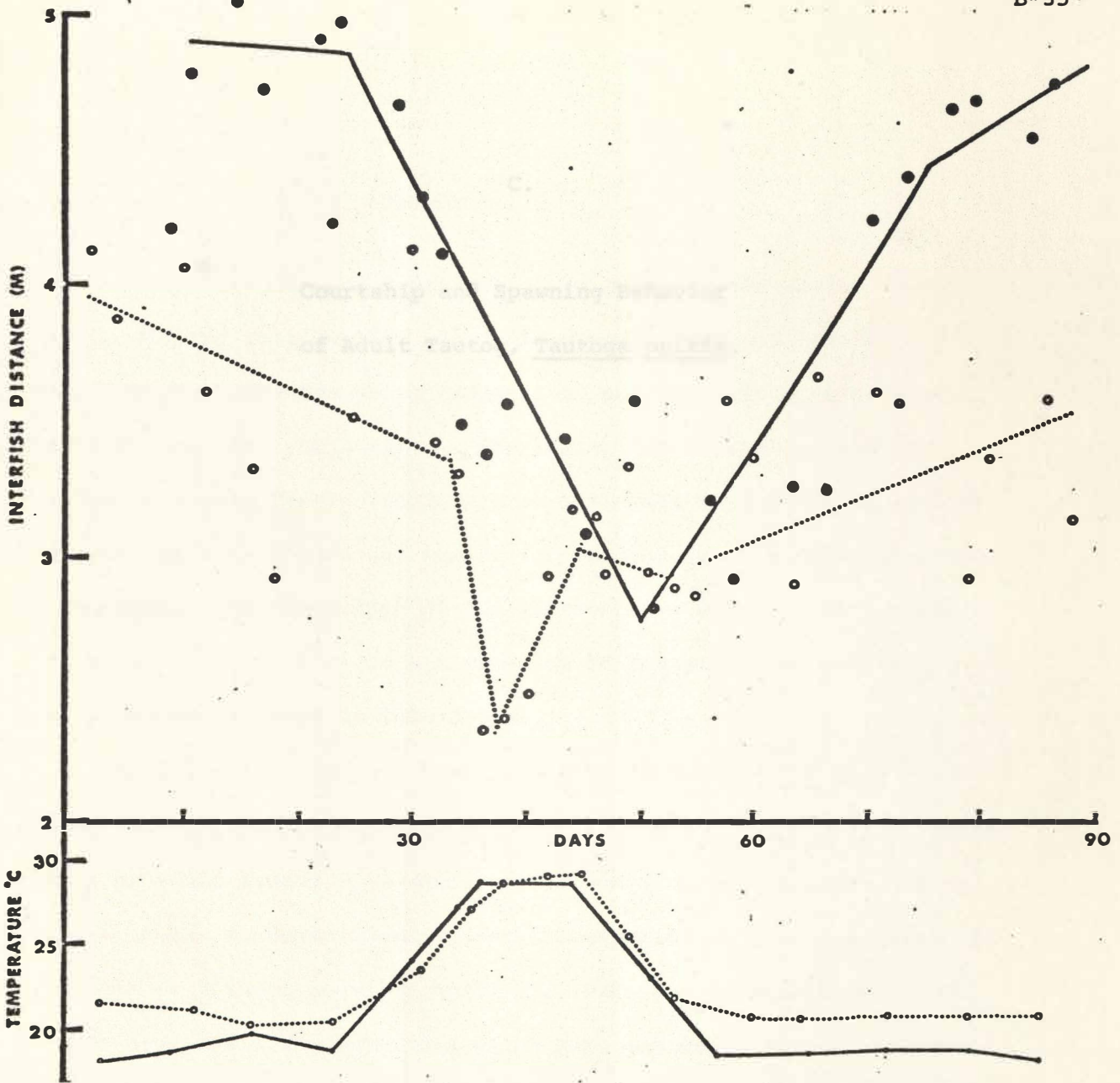


Figure 2. Interfish distance (m) expressed as 2-day averages of mean distance maintained between 3 adult tautog, *Tautoga onitis* in Experiment 1 (●) and Experiment 2 (○). Correlation between distance and temperature is indicated by solid (Experiment 1) and broken lines (Experiment 2).

C.

INTRODUCTION

The Courtship and Spawning Behavior of Adult Tautog, Tautoga onitis. The manuscript should be considered still preliminary. Some photographs are being prepared as are some paragraphs that will be used for publication. The reason for including this description in the Yearly Progress Report is that we are now engaged in evaluating the effects of temperature stress on this behavior. The integration and comparison of the reproductive behavior with other species, which will be in a discussion in the published manuscript, will not be included in this Report.

The general method of handling and observing the two sets of animals in each study is described in the report on the effect of temperature on adult tautog. In addition to 35-min hourly observations on the animals, we began 60-min observations prior to each spawning. In Experiment 1 these began on April 21, 1975, and in Experiment 2, on March 19, 1976. The behaviors which were measured during this 60-min period included aggression, interactions between the dominant male and the female, habitat utilization and the final courtship behaviors preceding and including spawning. Observations were then continued for at least another 35 min or less when it appeared a second spawning was being in error.

INTRODUCTION

The description of reproductive behavior in the tautog should be considered still within the draft stage. Drawings from cine and still photographs are being prepared as are some photographs that will be used for publication. The reason for including this description in the Yearly Progress Report is that we are now engaged in evaluating the effects of temperature stress on this behavior. The integration and comparison of the reproductive behavior with other species, which will be in a discussion in the published manuscript, will not be included in this Report.

The general method of holding and observing the two sets of animals in each study is described in the Report on the effect of temperature on adult tautog. In addition to 15-min hourly observations on the animals, we began 60-min observations prior to each spawning. In Experiment 1 these began on April 21, 1975, and in Experiment 2, on March 19, 1976. The behaviors which were measured during this 60-min period included aggressions, interactions between the dominant male and the female, habitat utilization and the final courtship behaviors preceding and including spawning. Observations were then continued for at least another 45 min or less when it appeared a second spawning was going to occur.

RESULTS

The most obvious manifestation of the approaching reproductive phase was the change in aggression between the dominant male and the female. Certain components of behaviors, which were formerly aggressive, were no longer so, and eventually became part of the courtship repertoire. Prior to this change, there was a clear dominance hierarchy based on size, with the largest fish of each group, a male, being dominant over a smaller male and still smaller female. In turn, the smaller male was dominant over the female.

Aggressive acts were manifested at varying levels of intensity with the most intense involving actual physical contact in the form of nipping or biting by a dominant. In these cases, a dominant animal would swim rapidly towards a subordinate (75 to 100 cm/sec) and nip the flanks or tail. Displacement would occur and at times continued as the dominant pursued a subordinate. The duration of the chase varied from bout to bout, as well as the swimming speeds and the distances covered. In the case of the dominant male, chases could last as long as 30-45 sec, with escape speeds reaching 100 to 200 cm/sec, and the fish swimming the length of the tank.

At the other extreme, subtle actions of a dominant animal could elicit displacement of a subordinate. The subtlety of this was such that the dominant, simply facing towards a subordinate, as much as a full tank length away (9.3 m), could elicit a displacement. Then there were instances in which an action similar to this did not elicit any response by

a subordinate. This variation in response by the subordinate was due to our not being able to assign an observable cause as regards to the actions of the dominant. It was only through the subordinate's behavior that we could, in fact, detect the generation of an aggressive intention signal by the dominant male.

Aggressions by the dominant, besides eliciting displacement, also caused a subordinate to assume what we interpreted to be a submissive posture. This involved the animal tilting its dorsal surface towards the dominant, at an angle ranging from about 5 to 90°, occurring either in the water column or in contact with the bottom. Frequently when a subordinate was swimming about the tank and approaching an area in which the dominant was present, it would show the submissive posture as it bypassed and clearly avoided the dominant. The distance at which this would occur varied, ranging from 1.0 to 3.0 m.

Beginning in early April, 1975 (Experiment 1) and in late January, 1976 (Experiment 2), we noted marked changes in the aggressive relationship between the dominant male and the female of each group. The major change and the one we first observed was that a rapid approach of the dominant, which in the past had represented the initiation of an aggressive act, neither caused the female to be displaced or show submission. She simply remained in place no matter how closely or swiftly the male approached. Typically, the male, beginning several meters away, would swim rapidly towards the female, but then veered off when approaching as close as 5-10 cm. At times, as the male veered off, the magnitude of the water

displacement from the force of the caudal thrusts was great enough to stir the adjacent sand and cause the female to be moved several cm. We termed these approaches "rushes" to distinguish them from those which were formerly aggressive in origin and to which the female had accordingly responded. From what we could ascertain, rushes were initiated approximately 3 weeks prior to, and 7 weeks prior to the first spawning in Experiments 1 and 2, respectively.

Another change we observed was that the female frequently swam towards or rested in areas adjacent to the dominant, which had never occurred prior to this period. In Experiment 1 this behavior was often focussed around the habitat where the male was resting, with the female swimming close to (within 0.5 m) or settling at the base of the structure. At other times, as the male rested in the habitat, the female actually entered the structure and came to rest either within the same tube or in one at a different level. In cases where the female was just outside the shelter, as the male exited he frequently rushed her, after which she might follow after him at distances of approximately 0.5-1.5 m; her following him after a rush occurred in other areas of the tank as well. We also observed instances in which the female rested in the shelter while the male was outside, swimming 2-3 times around the shelter followed by his rushing her in the shelter or as she emerged. These all appeared to be early manifestations of the courtship behavioral repertoire.

In contrast to the termination of aggressive interactions between the dominant male and female during this period, the aggressions of the dominant

towards the subordinate male became progressively more vigorous with respect to the intensity, such that a bout of chasing which had previously lasted 5-10 sec, now could last from 20-35 sec, with the two fish covering anywhere from 1-3 circuits around the perimeter of the tank. Also reflective of this heightened intensity was the fact that the dominant began to nip and bite the subordinate. Whereas biting had rarely been observed prior to reproduction, now it frequently occurred. The most obvious manifestation of this was that as many as 30-40 wounds appeared over all the areas of the subordinate's body. Comparable wounding of the subordinate took place in both Experiments 1 and 2, during the reproductive periods. One further piece of evidence of this increased aggression was the fact that the subordinate male spent the majority of its time at either end of the aquarium, sculling at the wall between mid-depth and the surface. This position appeared to be one which least stimulated aggressions by the dominant male. The subordinate males of each study also ceased being aggressive towards the female.

Besides changes in the aggressive interactions of the fish, external changes in the appearance of the female were also occurring, suggesting the approach of the reproductive season. Enlargement of the gonads increased the girth of the female, resulting in a more rotund appearance. At the same time, we also noted changes in the female's pigmentation. While prior to this period she was generally a solid dark gray (Figure in preparation), now there was a thin, mottled white, vertical bar or stripe down the middle of each side of the body, which we termed a

"saddle". At this time, the saddle was in an early stage of development (Figure in preparation) of what was to be a progression of significant shading changes taking place prior to and during each spawning (see below for further explanation). Along with this, a pale, grayish-white patch developed in the inter- and supraorbital areas of the female, giving the appearance of "eyebrows".

Unlike the female, the male's appearance prior to and during spawning was altered very little. The only discernible shading changes were the development of a light gray shade covering the entire head and the opercula, and the transient appearance of faint white rays (approximately 2-4 cm long) extending outwards from the orbits of the eyes (Figure in preparation). Otherwise, the male's shading was unchanged, with the trunk of his body being a dark gray, the ventral portion of the maxilla and the entire mandible being a light, almost white shade of gray, with the exception of the dark pores of the mandibular lateral line canals.

The first spawning between the dominant male and the female occurred on April 21, 1975, in Experiment 1. From that point 37 spawnings were observed over 21 days of observations within a 6-week period. During this time the fish spawned at least once and as many as three times per day. During Experiment 2, the dominant male and the female first spawned on March 30, 1976. These fish completed 16 spawnings during 10 days of observations. In the latter group, spawnings were observed prior to an experiment in which we studied the effects of temperature on reproductive behavior, which will be reported elsewhere (Olla, unpublished). Eggs were collected on two occasions in Experiment 1 and on five occasions in Experi-

ment 2. Examination of these samples and comparison with previous work on the embryology of this species (Kuntz and Radcliffe 1917) indicated that spawnings were successful and the normal development of the fertilized eggs was proceeding.

Throughout a typical day when spawning was to occur, the dominant male was generally active, swimming about the tank, feeding and intermittently rushing the female. Aggression towards the subordinate male frequently occurred right up until and after each spawning. In both Experiments 1 and 2, the subordinate males continued to be restricted in their movements by the heightened aggression directed toward them and remained almost exclusively at either end of the tank, sculling in mid-water.

The female, besides showing changes in pigmentation as well as courtship behaviors preliminary to spawning, also engaged in activities which appeared not to be directly related to spawning, such as feeding, swimming (with no apparent interactions with the other animals) and resting.

While the female exhibited little response to the rushes of the dominant prior to this period, now at times, she responded with progressive shading changes of varying magnitude. For example, within several seconds after a particularly vigorous rush by the dominant male, the saddle oftentimes increased in depth and width. The anterior area of the dorsal fin became a mottled white, ending posteriorly at the same place as the white saddle. In addition, faint white vertical stripes became evident on the body, originating at the posterior edge of the saddle and extending just

past the caudal peduncle. The shading at this point could vary, with these stripes at times modified into a kind of checkerboard pattern (Figure in preparation).

Generally, unless spawning was imminent, i.e., would occur within 15-30 min, these shading changes were retrogressive. A particular pattern, once achieved in the morning, might not persist for more than 10-20 sec or several minutes, followed by a fading with only a thin saddle present.

As the day progressed and the time of spawning approached (30-45 min prior to spawning), the male was more responsive to the female as evidenced by the increased intensity of the rushes. In the 15-min period prior to a spawning, the number of rushes significantly increased. The highly developed shading pattern of the female, once achieved, now persisted. The saddle was almost maximally developed, appearing whiter and extending fully down to the abdomen. The checkerboard or caudal stripe pattern was now much more clearly defined (Figure in preparation).

As the rushes continued, the female's dorsal fin remained in an erect position during the 5-10 min period prior to spawning. Swimming only with the pectorals she also intermittently began to flex the caudal fin upward.

Beginning anywhere from 2-5 min before spawning, the female began swimming back and forth along the length of the tank at mid-depth in a series of activities which we term "runs". These runs were accompanied by the final shading development in which all of the white areas on her body (ie., the saddle, caudal stripes or white portions of the checkerboard

pattern, the "eyebrows" and the anterior half of the dorsal fin) were almost totally blanched. Then, either as a run was beginning or was in progress, her caudal fin was rigidly flexed upward, exposing the dilated vent, while at the same time the head was tilted downward (Figure in preparation). The female's swimming in this position seemed awkward resulting in her moving with a characteristic wobble or wiggle. These runs served to heighten the attraction of the dominant male, for he would break off other activities to follow her.

The male swam just slightly behind with his head close to the caudal peduncle (within 30 to 40 cm). Then suddenly, while increasing her speed by changing from pectoral swimming to caudal thrusts, the female swam toward the surface, with the male immediately accelerating in a similar manner to keep apace with her (Figure in preparation). The angle of their ascent was about 40 to 70°. When the fish were less than a meter from the surface and while still swimming rapidly, they turned their bodies so that their ventral areas faced toward each other (Figure in preparation). On occasions when the fishes' movements were perfectly coordinated, the pectorals of the male appeared to be circling the female. With the animals in contact and their bodies arched into U-shapes, they released the gametes either before reaching the surface or as they broke the surface. The pair then separated and swam downwards (Figure in preparation) with the female coming to rest on the sand where the male usually rushed her 2-3 times within 5-15 sec following spawning.

The spawning as we have described it appeared to comprise the prevalent mode of gamete release. However, there occurred slight variations in the

behavior which still resulted in gamete release. For example, as the female was rushing to the surface, rather than orienting the ventral area of her body toward the male, she bent her body into the U-shape with the result that her dorsal side faced the ventral side of the male. Gamete release still occurred as the fish flexed their bodies into U-shapes. The origin of this variation was usually due to the fact that on the upward rushing, the female was moving too rapidly to be in the proper alignment for the ventral-to-ventral release with the male.

While runs were always performed prior to spawning, there were some day-to-day variations in the total number as well as in the time span in which they occurred. For example, on some days there were as few as 2 runs prior to a spawning, while on other days there were as many as eleven. Similarly, the duration of a series of runs varied from 30 sec to 3.0 min.

One noteworthy aspect of the run sequence was that the runs were usually not performed in succession, but rather were interspersed with other behaviors which appeared to comprise additional courtship activities. For example, many times after completing one run, the pair began circling around each other in mid-water. In some cases they followed each other, head to tail, along the perimeter of an imaginary circle. In other cases as the male swam around the female, she either remained sculling in a fixed position or pivoting about her vertical axis, obviously orienting to the moving male. The total number of separate circling bouts during a run sequence ranged from 2 to 10 with the duration ranging from 2 to 40 sec.

Another behavior interspersed with the run sequence was a rush up to the surface which did not culminate in gamete release. Typically at the onset of these "false" spawning rushes, the female began the transition from pectoral swimming to caudal thrusts. Then moving rapidly upwards with the male alongside, the female broke away from him short of the surface and swam downwards. These incomplete spawning rushes were variable in number, sometimes occurring not at all, while in other cases occurring as many as six times.

It was apparent that for the release of gametes to occur, the continuity of the run sequence had to be maintained by both the male and the female. In instances when it was not maintained, the female turned away from the male and often came to rest on the sand. Of the 37 spawnings observed in Experiment 1, breakoffs occurred prior to 15 of them. While breakoffs did not occur during spawnings in Experiment 2 we have not completed tabulating the data.

One of the main causes in Experiments 1 and 2 for these breakoffs was due to the fact that the dominant male, instead of maintaining his attention toward the female, chased or displaced the subordinate male which had either (actively) moved too close to the pair or (passively) happened to be in areas where the courtship behavior was being carried out.

Another reason in Experiment 1 for the breakoffs which were initiated by the female appeared to be premature contact of the female by the male. The male's contacting her during a run or as she rapidly ascended (rather than at the apex of the pathway) would usually result in her breaking off the

entire pre-spawning sequence. The inappropriateness of the premature contact stimulus was substantiated by a retrogression in the female's shading pattern. One final causative factor for the breakoffs may have been related to the fact that there was a questionable release of gametes by one of the pair. This may have indicated that the non-spawning animal was not mutually interacting with its mate to sustain the continuous sequence in the final courtship repertoire.

Each time we observed the courtship behaviors, it became more and more apparent that the final release of gametes was not a haphazard event, but rather the culmination of a precisely coordinated and synchronized build-up of social and physiological factors.

D.

The Effect of Temperature on the

Behavior of Marine Invertebrates

The summer and part of the fall of 1976 were spent in the design and construction of apparatus systems in which to hold and observe blue crabs.

With the arrival of an invertebrate behaviorist in mid-October, observations of blue crab behavior began with efforts concentrated initially on describing the repertoire of the species under laboratory conditions. As certain components of the repertoire became known, the extent of blue crab activity required in their behavior was measured in order to establish activity budgets for various thermal conditions and the relation between the budgets and laboratory conditions, e.g. container shape, substrate, shelter, etc.

As water temperatures fell during the winter, we examined the influence of the naturally occurring lower range of temperature on the crab's activities. In particular we wished to see at what specific temperatures crabs would enter and emerge from dormancy as well as to characterize the dormant state.

INTRODUCTION

Our investigations on the effects of temperature on the behavior of marine invertebrates have begun with the blue crab, Callinectes sapidus. The summer and part of the fall of 1975 were spent in the design and construction of aquarium systems in which to hold and observe blue crabs.

With the arrival of an invertebrate behaviorist in mid-October, observations of blue crab behavior began with efforts concentrated initially on describing the repertoire of the species under laboratory conditions. As certain components of the repertoire became known, the amount of time crabs spent engaged in these behaviors was measured in order to establish activities budgets for various thermal conditions and the relation between the budgets and laboratory conditions, e.g. aquarium shape, substrate, shelter, diet.

As water temperature fell during the winter, we examined the influence of the naturally occurring lower range of temperature on the crabs' activities. In particular we wished to see at what specific temperatures crabs would enter and emerge from dormancy as well as to characterize the dormant state.

MATERIALS AND METHODS

Observations were made on crabs held mainly in two systems. The first 350-l aquarium was cube-shaped and had one side as a window. The second aquarium was an elliptic cylinder of 1200 l with four windows initially. Four more windows were added later to improve visibility and make the aquarium symmetrical. Both tanks contained seawater at a salinity of 20-25 o/oo and were maintained on a natural seasonal photoperiod by fluorescent light and a 15-w night light diffused through white translucent plastic. Live mussels in the aquaria provided food ad libitum. The sand was approximately 15 cm deep. Black drapes and cardboard were arranged about the aquaria to provide observation blinds.

The crabs observed were juvenile and adult crabs of both sexes collected from the Navesink River, New Jersey, with baited traps. Trawled crabs proved to have high mortality and were not used for observations.

In order to construct an activities budget, two adult female blue crabs were observed in the elliptic aquarium which was maintained at 18°C and under 11.5 h of daylight. The amount of time spent in various activities and zones was measured using a tape recording giving a timing mark every 4 s. A crab was watched and the observer upon hearing the 4-s mark noted in a shorthand code its activity and position. Over a block of 4 contiguous days, 9 observation sessions were made each day at hourly intervals from 0800. During each

session, each crab was observed for 100 intervals (about 7 min) and the distance between crabs estimated from interzone distances after noting the simultaneous positions of the crabs. Eleven zones of equal area had been marked in the aquarium.

A variety of statistical techniques were used to treat the activities data. The Sign Test (Conover 1971) allowed comparison of the crabs in each activity. To examine the independence of the distribution of time among activities from the day observed and from the individual observed, contingency tables were constructed and chi-squares and Pearson's contingency coefficient (Conover 1971) calculated after some activities were dropped and grouped in order to reduce the number of zero and near-zero calls. The contingency table thus contained the number of 4-s intervals spent in four activity groups: buried, standing in low posture, locomotion, and in the open. This type of analysis was repeated with the zone occupancy data.

From the cold dormancy study two juvenile female crabs were observed in the cubical aquarium, in which the temperature and photoperiod were made to follow seasonal changes until 6 February, 1976 when the photoperiod was fixed at 11 h. On 17 February a recirculating cooling unit connected to the aquarium stabilized the water temperature at 8°C. On 20 February we began dropping the water temperature 1°C over 8 h and continued to observe the crabs over the 4 subsequent days while the lower temperature was held constant. The procedure of lowering the temperature 1°C a day and observing for 4 more days continued until

both crabs remained dormant for 4 days. The temperature then continued to be held constant below 3.8°C for 11 additional days after which time it was raised. Raising the temperature 1 day and observing the 4 subsequent days continued until both crabs emerged and showed sustained activity.

Besides scan samples, which consisted of observing the crabs as simultaneously as possible, and noting position, activity, distances, and antennule flicking rate, activities timing primarily using the previously described method began on 21 February. Each day 35 observations, lasting 3 min per crab, were made at quarter hour intervals. The resulting time data led to an activities budget.

In the activities budgets in Table II we note no differences between the two crabs except that the larger crab spends more time resting than the smaller. Day-to-day variation has greater influence on the budget than variation from individual to individual (compare the contingency coefficients in Table IV).

Originally we expected the crabs to budget portions of each day among several activities so that a number of activities would appear each and every day. Instead the crabs remained buried for a whole day, or fed for a whole day, or simply moved about with little or no feeding. One implication of the fact that each day's budget is due to the activity or not act of related activities is that observations may be made over a number of days and still be useful.

RESULTS AND DISCUSSION

BEHAVIORAL REPERTOIRE

Table I gives a hierarchical arrangement of the blue crab's repertoire. The terms are, for the most part, self-explanatory and some of these behaviors are described elsewhere (Teytaud 1971; Jachowski 1974). Additions continue to be made as observation time increases and extends over the cycle of seasons. Consequently, the repertoire presented now is preliminary with the details and functional significance of the behaviors to be given later.

ACTIVITIES BUDGET

In the activities budgets in Table II one sees no difference between the two crabs except that the larger crab swims more but cleans less than the smaller. Day-to-day variation has greater influence on the budget than variation from individual to individual (compare the contingency coefficients in Table IV).

Originally we expected the crabs to budget portions of each day among several activities so that a number of activities would appear each and every day. Instead the crabs remained buried for a whole day, or fed for a whole day, or simply moved about with little or no feeding. One implication of the fact that crabs budget the bulk of day to one activity or one set of related activities is that observations must be made over a number of contiguous days in order

to ascertain a realistic budget.

The pattern of zone occupancy (Tables II and IV) reveals little or no evidence for territoriality in adult female crabs. Within any one day, one or two zones may dominate the budget, but the identity of the zones varies from day to day. The contingency coefficient values in Table IV reflect this high dependence of zone occupancy on day-to-day variation.

The next step is to obtain activities budgets over a range of temperatures and examine the budgets not only for change in the mean values but also for changes in the variability.

COLD DORMANCY STUDY

Because of Leffler's (1972) anecdotal observation that blue crabs below 13°C enter a dormant state, which he termed "stupor", we gradually chilled two juvenile female blue crabs, not only to specify the temperature at which dormancy began, but also to attempt defining quantitative behavioral measures of its extent and consequences.

From the end of December 1975 until mid-February 1976, the water temperature in the cubical aquarium fell from 10.5°C to about 8°C , as Sandy Hook Bay became colder. During this period half-hourly scan samples (Table V) showed that both crabs were still active but spent most, and sometimes all of the day, buried. No feeding was observed during December, January and February.

When the temperature was lowered to 6°C , dormant time increased sharply (Tables V and VI). On the day of sharply falling temperature a period of walking and digging occurred, but such periods became briefer with halting movements on the other days during which the temperature was lowered still further. Dormancy followed the burst of activity and continued for several days under constant temperature until broken intermittently by activity.

The bursts of activity may represent escape behavior ordinarily functioning to bring the crab to warmer water. During these bursts the digging motions appeared to be incomplete, and incomplete digging may explain the shift at the lowest temperatures from being buried to being at rest in a huddled posture.

When the temperature reached 3.8°C the crabs remained continuously dormant for 15 days. At the end of this period the temperature was raised from 3.8°C in order to discover at what temperature dormancy would end. Until the rising temperature reached 10.5°C , the crabs would become briefly active only to return to dormancy. At 10.5°C the crabs returned to sustained activity, and one even began to feed on mussels.

Dormancy, as we observed it, was not simply inactivity or some sort of impaired mobility but rather a definite behavior in which the crab is actively adapting to its situation. Crabs may normally bury or remain motionless in a depression in the sand for long time periods. While motionless they usually assume a huddled posture in which the

Ventrum rests on the substrate and the chelae and legs are drawn up against the body. Ordinarily while buried or huddled the crab is still alert with the antennae and eyestalks up and the antennules constantly flicking. As the temperature decreased, the crabs spent increasingly greater time buried or huddled with the antennules and eyestalks first partially, then completely, withdrawn into their sockets and the antennae folded flat. These preliminary observations now enable us to characterize cold dormancy as a behavior of indefinite duration in which the crab remains buried or huddled with its eyestalks, antennules and antennae continuously retracted.

During the experiment it became obvious that the sensory ability of the crab should be assessed in order to see whether any diminished responsiveness near and during dormancy is derived from impairment of the crab's sensors or its effects or both. At the end of the 4-day block of observations, attempts were made to test the crab's response to a solution of freeze-dried clam extract, but the results were inconclusive because of the nature of water circulation in the aquarium. We suspect that the crab is not numbed senseless while dormant, but we still need to measure the degree of change in several dimensions of sensory ability.

Table I. Hierarchical Arrangement of the Behavioral Repertoire of the Blue Crab (*Callinectes sapidus*).

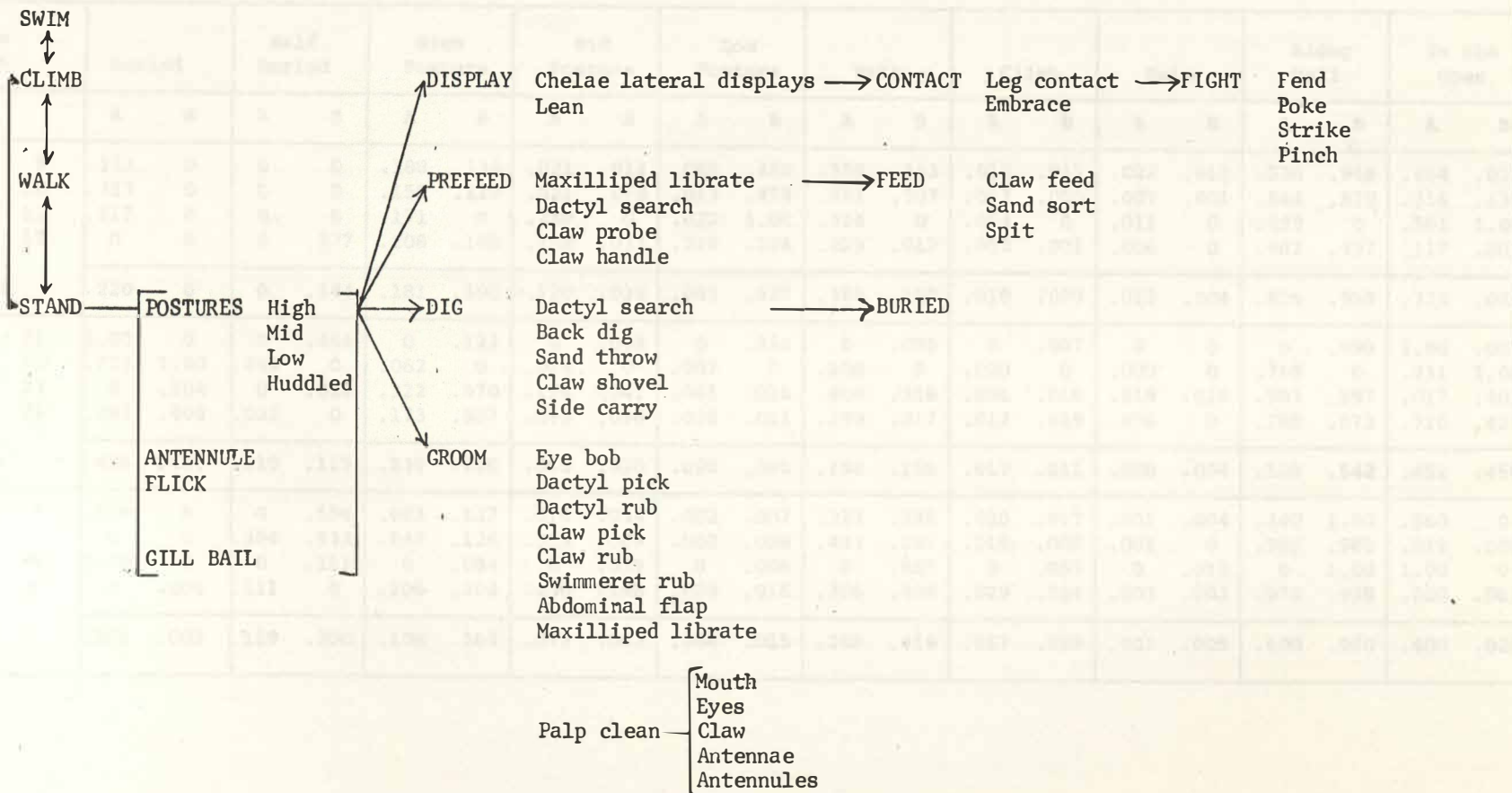


TABLE II. Activity Budget for Two Adult Female Blue Crabs Showing Proportion of the Day Spent in Various Activities.

Date 1976	Buried		Half Buried		High Posture		Mid Posture		Low Posture		Walk		Climb		Swim		Along Wall		In the Open	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Jan. 9	.333	0	0	0	.188	.134	.021	.012	.068	.450	.358	.343	.010	.017	.022	.013	.536	.968	.464	.032
10	.333	0	0	0	.158	.119	.021	.079	.013	.474	.451	.307	.017	.020	.007	.001	.644	.870	.356	.130
11	.217	0	0	0	.171	0	.240	0	.022	1.00	.324	0	.014	0	.011	0	.439	0	.561	1.00
12	0	0	0	.577	.208	.148	.198	.033	.228	.224	.329	.017	.032	.001	.006	0	.883	.997	.117	.003
Mean	.220	0	0	.144	.181	.100	.120	.039	.083	.537	.366	.167	.018	.009	.011	.004	.626	.959	.374	.041
Jan. 21	1.00	0	0	.444	0	.122	0	.003	0	.333	0	.070	0	.007	0	0	0	.998	1.00	.002
22	.222	1.00	.444	0	.062	0	.028	0	.007	0	.208	0	.020	0	.009	0	.769	0	.231	1.00
23	0	.204	0	.018	.322	.370	.154	.041	.061	.016	.408	.316	.036	.018	.019	.018	.983	.597	.017	.403
24	.481	.409	.033	0	.173	.307	.060	.038	.036	.011	.199	.217	.012	.019	.006	0	.280	.573	.720	.427
Mean	.426	.403	.119	.115	.139	.200	.060	.020	.026	.090	.184	.156	.017	.011	.008	.004	.508	.542	.492	.458
Feb. 3	.556	0	0	.556	.082	.137	.016	.034	.002	.007	.323	.246	.020	.017	.001	.004	.440	1.00	.560	0
4	0	0	.364	.533	.142	.126	.039	.009	.002	.028	.433	.297	.018	.008	.001	0	.988	.980	.012	.020
5	1.00	0	0	.111	0	.084	0	.059	0	.008	0	.645	0	.053	0	.013	0	1.00	1.00	0
6	0	.008	.111	0	.206	.304	.236	.146	.020	.016	.396	.489	.029	.034	.003	.003	.970	.938	.030	.062
Mean	.389	.002	.119	.300	.108	.163	.073	.062	.006	.015	.288	.419	.017	.028	.001	.005	.600	.980	.400	.020

Table II. (continued)

Date 1976	Display		Contact		Cleaning		Prefeed		Feed		Dig		Mean Dist. cm	Temp. °C
	A	B	A	B	A	B	A	B	A	B	A	B		
Jan. 9	.038	.027	.006	.002	.023	.017	.023	.003	.067	.002	.003	0	79.0	16.8°C
10	.022	.028	.019	.030	.012	.044	.010	.047	0	.061	0	0	52.8	15.9°C
11	0	0	.030	.030	.036	.012	.064	0	.265	0	.013	0	87.7	16.8°C
12	0	.013	.010	.031	.054	.091	.071	.002	.150	.081	.002	0	69.8	15.8°C
Mean	.015	.017	.016	.023	.031	.041	.042	.013	.120	.036	.005	0		16.3°C
Jan. 21	0	0	.002	0	.002	.076	0	0	0	0	0	0	45.7	15.8°C
22	0	0	.010	.046	.009	.074	.006	0	0	0	0	0	47.4	15.7°C
23	.009	.060	.022	.011	.102	.122	.168	.026	.224	.208	0	.007	66.6	16.7°C
24	0	.038	.001	.021	.037	.062	.102	.111	.071	.141	.029	0	73.4	16.7°C
Mean	.002	.024	.009	.020	.038	.084	.074	.034	.074	.087	.007	.002		16.2°C
Feb. 3	.017	.020	.032	.006	.012	.054	.002	.007	0	0	.001	.009	75.7	18.1°C
4	.032	.004	.009	.006	.047	.113	.004	0	0	0	.007	.007	61.2	18.1°C
5	0	0	0	0	.009	.063	0	0	0	0	0	.007	56.2	18.1°C
6	.049	.048	.020	.023	.092	.100	.020	.056	.123	.118	0	.017	53.2	18.1°C
Mean	.024	.018	.015	.009	.040	.082	.006	.016	.031	.030	.002	.010		18.1°C

TABLE III. Zone Occupancy of Two Adult Female Blue Crabs Showing Proportion of the Day Spent in Various Zones

ZONE		1		2		3		4		5		6		7		8		9		10		11		
Date		A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
Jan.	9	.098	.097	.053	.502	.031	.070	.401	.078	.051	.078	.082	.021	.077	.052	.120	.102	.087	0	0	0	0	0	0
	10	.101	.038	.097	.233	.056	.023	.111	.307	.412	.116	.059	.087	.066	.046	.097	.028	0	.111	0	.006	0	.004	
	11	.283	0	.033	0	.246	0	.118	0	.087	1.00	.053	0	.024	0	.043	0	0	0	0	0	.111	0	
	12	.130	0	.042	0	.056	.703	.132	.119	.410	.178	.141	0	.027	0	.062	0	0	0	0	0	0	0	
Mean	9-12	.153	.033	.056	.184	.098	.199	.190	.126	.240	.343	.084	.027	.049	.024	.080	.032	.022	.028	0	.001	.028	.001	
Jan.	21	0	0	0	.449	1.00	.009	0	.466	0	.056	0	.014	0	.007	0	0	0	0	0	0	0	0	0
	22	.508	1.00	.031	0	.223	0	.054	0	.052	0	.036	0	.022	0	.073	0	0	0	0	0	0	0	0
	23	.116	.210	.064	.081	.061	.042	.118	.103	.092	.122	.156	.051	.189	.176	.204	.202	0	.003	0	.001	0	0	0
	24	.038	.296	.039	.050	.042	.020	.063	.077	.583	.032	.021	.012	.021	.051	.023	.462	.001	0	.112	0	.056	0	0
Mean	21-24	.166	.376	.034	.147	.332	.018	.059	.162	.182	.052	.053	.019	.058	.058	.075	.166	.0002	.001	.028	.0002	.014	0	0
Feb	3	.084	.414	.047	.103	.032	.031	.088	.298	.051	.087	.021	.024	.032	.020	.422	.022	.222	0	0	0	0	0	0
	4	.492	.117	.066	.038	.044	.030	.147	.031	.097	0	.030	0	.036	.047	.089	.729	0	.008	0	0	0	0	0
	5	0	.221	0	.068	0	.154	0	.080	0	.150	0	.052	0	.097	0	.177	1.00	0	0	0	0	0	0
	6	.336	.138	.048	.038	.042	.297	.239	.128	.083	.104	.159	.024	.022	.172	.071	.098	0	0	0	0	0	0	0
Mean	3-6	.228	.217	.040	.062	.030	.128	.118	.134	.058	.085	.052	.025	.022	.084	.146	.256	.306	.002	0	0	0	0	0

TABLE IV. Results of Testing Independence.

Hypothesis

Distribution among activities
is independent of days

		χ^2	df	$R_2^{(1)}$
For Crab A	1st Block	1017.8*	9	0.448
	2nd Block	2724.6*	9	0.647
	3rd Block	1912.2*	9	0.551
	All Blocks	1181.5*	6	0.297
For Crab B	1st Block	3006.4*	9	0.693
	2nd Block	2363.8*	9	0.589
	3rd Block	1096.7*	9	0.528
	All Blocks	6386.4*	6	0.614

Distribution among zones is
independent of days

For Crab A	1st Block	1485.0*	24	0.540
	2nd Block	5168.5*	24	0.768
	3rd Block	3969.9*	24	0.724
For Crab B	1st Block	5216.1*	24	0.769
	2nd Block	4722.8*	24	0.753
	3rd Block	2287.8*	24	0.623

Distribution among activities is independent of individual crabs

1st Block	2623.0*	3	0.514
2nd Block	3410.6*	3	0.200
3rd Block	1262.4*	3	0.385
All Blocks	2057.2*	3	0.288

* Reject at .01 significance level

(1) Pearson's contingency coefficient

Table 11. Frequency of various activities during the day (1) for the day (2) and the night (3) for the day (4) and the night (5).

Activity	Day (1)	Night (2)	Day (3)	Night (4)	Total	Row Total	Col Total
Feeding	15	10	12	8	45	35	35
Resting	20	15	18	12	65	55	55
Other	5	5	5	5	20	20	20
Total	40	30	35	25	130	110	110

Table 12. Frequency of various activities during the day (1) for the day (2) and the night (3) for the day (4) and the night (5).

TABLE V. Frequency of Various Activities During the Day⁽¹⁾ for Two Juvenile Blue Crabs Subjected to Low Temperatures.

	DEC 30		DEC 31		JAN 2		JAN 7		JAN 9		JAN 10		JAN 11		JAN 12		JAN 15		JAN 21		
Temperature °C	10.2		10.2		9.9		9.8		8.9		8.6		9.2		8.5		8.8		9.1		
Crab	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
Buried				18	8		16	16	8	18		18		18	3	18	15	18		14	
1/2 Buried															1				10	1	
Huddled			6			2							12								
Low Posture	7	15	8			5			2		8			9		1			3	2	
Mid	6	3	2		2	2			1		2		1	2					2		
High	5		2			1			7		6		4	1		2			1	1	
Walk & Climb											2		1	2					2		
Intercrab Distance (2)	49.7 ± 9.6		35.0 ± 3.0		51.7 ± 6.3		17 ± 0		24.7 ± 8.5		51.9 ± 9.8		30.7 ± 12.5		55.3 ± 9.0		24.2 ± 5.8		36.4 ± 4.4		
Antennule Flicking Rate (3)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
																				32.2	15.4
																					+ 5.0 ± 9.2

(1) Sampling effort increased from 18 to 35 observations daily on 20 Feb. 76.

(2) With 95% confidence limits.

(3) Measurements began on 21 Jan. 76 and are for animals either buried or huddled. Given with 95% confidence limits.

TABLE V. (continued)

	JAN 22		JAN 23		JAN 24		FEB 3		FEB 4		FEB 5		FEB 6		FEB 17		FEB 18		FEB 19	
Temperature °C	7.8		8.1		8.1		8.4		8.4		8.4		8.2		9.4 to 8.0		7.7		7.9	
Crab	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Buried	18	18	18	18	18		18		18		17		18	16	17		17		18	
1/2 Buried							18		15		17			2	11	17	8			
Huddled									1										11	
Low Posture					18				1						5		3		2	
Mid															2		2		1	
High									1								4		1	
Walk & Climb																			3	
Intercrab Distance	34 ± 0		34 ± 0		74 ± 0		50 ± 0		50 ± 1.1		50 ± 0		48.5 ± 3.2		56.7 ± 4.4		41.6 ± 5.9		56.2 ± 2.7	
Antennule Flicking Rate	22.0 +4.8	12.7 +4.5	7.1 +4.6	8.7 +2.7	20.6 +3.6	24.5 +3.7	21.2 +2.6	(4)	26.0 +4.7	-	19.0 +2.1	-	23.4 +2.7	28.7 +6.0	31.1 +3.7	32.1 +4.3	25.0 +7.2	-	22.3 +4.8	-

(4) Antennules not visible enough for measurement.

TABLE V. (continued)

	FEB 20		FEB 21		FEB 22		FEB 23		FEB 24		FEB 25		FEB 26		FEB 27		FEB 28		FEB 29																					
Temperature °C	7.8 to 6.3		6.1		6.1		5.3		5.3		5.3		5.4 to 3.8		3.8		3.8		3.8																					
Crab	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B																				
Buried		35		35		35		32		35		35		34		18		34		27		35		35		35		35		35		35		35		35		35		35
1/2 Buried	17		35		27		32		35		34		18	34		27		35		35		35		35		35		35		35		35		35		35		35		
Huddled	10				4											4		6		1																				
Low Posture	3				3											4																								
Mid	3				1																																			
High	1															9																								
Walk & Climb	1															2																								
Intercrab Distance	44.9 ± 4.2		34 ± 0		49.7 ± 2.5		53 ± 0		53 ± 0		37.9 ± 5.2		25.5 ± 1.9		23 ± 0		23 ± 0		23 ± 0		23 ± 0		23 ± 0		23 ± 0		23 ± 0		23 ± 0		23 ± 0		23 ± 0		23 ± 0		23 ± 0			
Antennule Flicking Rate	17.1	-	0.076 ⁽⁵⁾		7.3	-	0	0	0	0	2.2	8.9	1.2	7.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	+3.0				+2.7					+2.2	+4.1	+2.0	+3.9																											

(5) Only one non-zero measurement.

TABLE V. (continued)

	MAR 1	MAR 2	MAR 3	MAR 4	MAR 5	MAR 12	MAR 13	MAR 14	MAR 15	MAR 16
Temperature °C	3.8	3.8	3.5	3.7	3.7	3.4	3.5 to 4.7	4.6	4.7	4.8
Crab	A B	A B	A B	A B	A B	A B	A B	A B	A B	A B
Buried	35	35	35	35	35	9	34	35	27	35
1/2 Buried						4	1		20	35
Huddled	35	35	35	35	35	13	35	35	2	35
Low Posture									4	
Mid										
High										
Walk & Climb									1	
Inter crab Distance	23 ± 0	23 ± 0	23 ± 0	23 ± 0	23 ± 0	23 ± 0	22.1 ± 0.7	17 ± 0	52.1 ± 7.2	59 ± 0
Antennule Flicking Rate	0 0	0 0	0 0	0 0	0 0	0 0	1.5 0 +2.3	0 0	0 7.4 +7.0	0 0

TABLE V. (continued)

	MAR 17		MAR 18		MAR 19		MAR 20		MAR 21		MAR 22		MAR 23		MAR 24		MAR 25		MAR 26	
Temperature °C	4.4		4.5		4.5 to 7.0		6.9		6.8		6.7		6.7		6.7 to 8.7		8.7		8.7	
Crab	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Buried											34		31		25		35			8
1/2 Buried												11		31	2	28		32	2	20
Huddled	34	33	34	34	35	30	35	25	35	35		11			4					2
Low Posture		1				3		4				6			1	1		2	27	2
Mid						1		2			6				1	5			6	1
High							1		1		6				2	1		1		2
Walk & Climb						1		3										1		
Inter crab Distance	59 ± 0		59 ± 0		52.7 ± 0.3		29.2 ± 2.1		16 ± 0		52.4 ± 1.0		23 ± 0		50.8 ± 2.6		18.0 ± 1.3		27.4 ± 2.6	
Antennule Flicking Rate	0	0	0	0	0	3.6	11.7	20.9	1.4	9.4	15.3	22.5	13.0	12.2	28.2	25.4	18.4	28.8	29.2	30.9
						+3.7	+3.6	+2.3	+1.8	+2.4	+1.7	+2.9	(6)	+3.3	+6.0	+5.9	+2.5	+3.5	+2.1	+4.4

(6) Only one observation.

TABLE V. (continued)

	MAR 27		MAR 28		MAR 29	
Temperature °C	8.7		8.8		8.7 to 10.8	
Crab	A	B	A	B	A	B
Buried						
1/2 Buried						
Huddled	14	35	34	34	17	26
Low Posture	5				3	3
Mid	14				4	2
High					12	4
Walk & Climb	2				1	
Intercrab Distance	31.8 ± 11.1		69 ± 0		49.9 ± 5.8	
Antennule Flicking Rate	39.0	26.2	20.4	30.2	25.3	47.1
	+6.2	+2.4	+1.7	+2.5	+5.2	+2.5

TABLE VI. Activities Budget for Two Juvenile Female Blue Crabs Showing Proportion of Observed Time in Various Activities.

	FEB 21 to 25	FEB 26	FEB 27 to 5	MAR 13	MAR 14 to 28	MAR 19	MAR 20 to 23	MAR 24	MAR 25 to 28	MAR 29										
Temperature °C	6.1	5.9 to 3.8	3.7	3.5 to 4.7	4.8	4.5 to 7.0	6.8	6.7 to 8.7	8.7	8.7 to 10.8										
No. of Days	4	1	9	1	4	1	4	1	4	1										
Crab	A	B	A	B	A	B	A	B	A	B	A	B								
Buried	0	.583	0	0	0	0	0	0	0	0	0	0								
1/2 Buried	.953	.335	1.00	0	1.00	0	0	0	0	.478	0	.693	0	.252	.058	0	0			
Huddled	.023	0	0	.783	0	1.00	.933	1.00	1.00	.957	1.00	.857	.508	.749	.057	.748	.115	.863	.428	.745
Low Posture	.018	.016	0	.193	0	0	.042	0	0	.014	0	.122	.012	.125	.123	.008	.274	.026	.124	.016
Mid	.006	.007	0	.024	0	0	.016	0	0	.022	0	.013	.002	.064	.040	.097	.286	.033	.104	.083
High	0	.059	0	0	0	0	0	0	0	0	0	0	0	.052	.072	.088	.061	.008	.317	.100
Walk	0	.001	0	0	0	0	.009	0	0	.007	0	.008	0	.009	.015	.059	.011	.012	.026	.053
Climb	0	0	0	0	0	0	0	0	0	0	0	0	0	.001	0	.001	0	.001	0	.002
Nondormant ⁽¹⁾	0	(2)	.029	.382	0	0	.057	0	0	.080	.078	.171	.249	.704	.400	.643	.986	.896	.998	.991
Partially Dormant ⁽¹⁾	.088	(2)	.147	.324	0	0	.022	0	.004	.011	.076	.188	.734	.296	.572	.304	.013	.103	.002	.006
Dormant ⁽¹⁾	.912	(2)	.824	.294	1.00	1.00	.921	1.00	.996	.908	.846	.640	.011	0	.028	.054	.001	.001	0	.003

(1) Dormant crabs have all eyestalks, antennules, and antennae retracted. Partially dormant crabs have at least one eyestalk, antennule, or antenna extended. Nondormant crabs have all these sensory appendages extended.

(2) Crab was not visible enough to discern position of antennulus.

... 40 x 40 x 120 cm) on a barren sand bottom. Two groups of 10 tautog 11.7 to 20 cm were released there and directly monitored by an underwater observer. In contrast to all previous ex-

E.

Shelter-Dependence of Young Tautog, Tautoga onitis and the Home Range of Juvenile Cunner, Tautogolabrus aspersus, under Natural Conditions.

... appeared to be a random pattern. It continued this random activity for 10 min. until locating a pile of bottom rubble covered with algae and supporting a small group of tautog (7 to 10 fish). The fish remained at this location during the 4 h of observation.

From these observations, it is obvious that the shelter-seeking response in young tautog is initiated by a complex of factors rather than merely the presence of physical hiding places. If predictions as to the capability of the organism to deal with natural events are to be made with any validity, the various components eliciting the shelter-seeking response must be defined.

Additional observations made this past summer have shown that juvenile cunner, Tautogolabrus aspersus 12.5 to 1.5 cm, after descending from the pelagic larval stage, occur in significant numbers in the mussel beds of Pile Island inlet. Over 100 h of underwater observations have enabled us to define basic survival patterns of behavior for this life stage.

Like the adult fish, at all times, the juveniles are apparently active and feed occasionally.

cial shelter (40 x 40 x 120 cm) on a barren sand bottom. Two groups of 10 tautog (12 to 20 cm) each were released there and directly monitored by an underwater observer. In contrast to all previous releases, these animals, within 5 min, swam away from the structure. In one case in which a tautog (22.5 cm) was tracked ultrasonically, the animal upon release immediately swam off in what appeared to be a random pattern. It continued this random swimming for 10 min, until locating a pile of bottom rubble overgrown with algae and supporting a small group of tautog (7 to 10 fish). The fish remained at this location during 24 h of monitoring.

From these observations, it is obvious that the shelter-seeking response in young tautog is mediated by a complex of factors rather than merely the presence of physical hiding places. If predictions as to the capability of the organism to deal with inimical events are to be made with any validity, the various components eliciting the shelter-seeking response must be defined.

Additional observations made this past summer have shown that juvenile cunner, Tautogolabrus adspersus (0.8 to 1.5 cm), after descending from the pelagic larval stage, occur in significant numbers in the macroalgae beds of Fire Island Inlet. Over 100 h of underwater observations have enabled us to define some normal patterns of behavior for this life stage.

Like the adults (Olla et al. 1975a), the juveniles are diurnally active and feed continually. Also as in the adults, they

appear to be visual feeders, moving towards and ingesting food items, while orienting into the current.

At this stage of maturity, these animals exhibit a home range of approximately 5 to 10 cm square adjacent to the algae which is utilized as shelter in the presence of predators. This area is aggressively defended against intrusion by conspecifics.

Observations on these juveniles are continuing to be made with special emphasis on the changes in their home range as a function of maturation. If throughout their first year, these fish continue to exhibit a home range which is significantly smaller than the adults', which also is limited (Green. 1975; Olla et al. 1975a), they would be highly susceptible to contaminants. Payne (1976) found the induction of benzopyrene hydroxylase in cunner when exposed to petroleum. This sublethal response in a fish possessing a small and limited home range, as in the cunner, has application as an indicator of petroleum contamination. By defining the limits of the cunner's movements through all life stages, we hope to provide a baseline with which the effect of point sources of pollution can be assessed.

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