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Behavioral Measures of Environmental Stress

Marine Fishes and Invertebrates

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TABLE OF CONTENTS

- I. Preface
- II. Detection threshold for naphthalene and other behavioral responses by the blue crab Callinectes sapidus.
(Pearson, W. H. and B. L. Olla, in journal review).
- III. Behavioral detection of a food extract by the hake, Urophycis chuss (Pearson, W. H., S. E. Miller, and B. L. Olla, ms in prep.)
- IV. Seasonal dispersal and habitat selection of cunner, Tautoglabrus adspersus and young tautog, Tautoga onitis.
(Olla, B. L., A. J. Bejda and A. D. Martin, in journal review).
- V. Effect of low temperature on the activity and distribution of juvenile bluefish, Pomatomus saltatrix. (Preliminary data report).

I. PREFACE

This report is divided into two sections, one dealing with the new direction of the program on the effect of petroleum on the behavior of both fish and invertebrates, and the other with the results from the final year of support for field work on juvenile labrids and temperature studies on young bluefish.

The first year's effort on petroleum hydrocarbons has gone exceedingly well. Based on the establishment of sensitivity to naphthalene for the blue crab, Callinectes sapidus (in press), accomplished at the end of the previous funding year, we have established a threshold of sensitivity to naphthalene and have been able to separate detection from higher order responses. This means we can predict what level of naphthalene the animals detect but do not avoid. The question of avoidance to much higher levels of naphthalene and to the water soluble fraction (WSF) of Prudhoe Bay crude oil, will be addressed during the coming year.

The results of the naphthalene detection threshold study are presented as a completed manuscript which has been submitted to a journal from which we are presently waiting to hear regarding its acceptance. Our research to date has established the base from which the next series of experiments dealing with sensitivity to the WSF of crude oil will begin. These results will, in turn, form the base for avoidance capability experiments.

Because of our prior experience in working with chemical detection thresholds in the blue crab, we have been able, in a relatively short time, to establish methodology to measure chemical detection based on behavioral responses in the hake, Urophycis chuss. Although the actual responses of these fish are obviously quite different than those of the blue crab, nevertheless there are types of behavior which transcend species differences, enabling us to apply similar methodology which has resulted in a highly quantitative behavioral assay for chemical detection. We are currently establishing detection thresholds to food extract and have presented the findings to date in this Report. The next step is to measure sensitivity to naphthalene and then to the WSF. Our eventual aim is to examine avoidance capabilities and the effect of petroleum hydrocarbons on chemical detection of food.

The next section of the Report is a manuscript that has been submitted to a journal for publication which presents findings on home range and shelter association in juvenile labrids.

Also included is a preliminary data report on the influence of thermal edges on the movements and distribution of young bluefish, Pomatomus saltatrix. The laboratory work which is still in progress will extend through mid-September. However, sufficient progress has been accomplished to present a significant portion of the results. A manuscript should be ready for journal submission sometime in mid-November.

II.

Detection Threshold for Naphthalene and Other Behavioral Responses by the Blue Crab, Callinectes sapidus.

Walter H. Pearson and Bori L. Olla

(Ms in Journal Review)

Abstract

Using behavioral criteria in the blue crab, Callinectes sapidus, developed in previous studies, the threshold for detection of the petroleum hydrocarbon naphthalene was 10^{-7} mg l^{-1} . Oriented locomotor activity and defensive displaying began at 2 mg l^{-1} naphthalene. No feeding behavior was observed. The absence of any activity other than detection at naphthalene concentrations less than 2 mg l^{-1} indicates that below that level the blue crab has no active behavioral strategy to mitigate any effects of naphthalene exposure. The possibility that the initial exploratory and defensive behavior leads to avoidance or other effective adaptive behavior above 2 mg l^{-1} naphthalene requires further examination.

Introduction

The behavioral repertoire of marine organisms contains behavior patterns, e.g., avoidance, that serve to mitigate any adverse effects of environmental perturbations. The occurrence and success of such adaptive behavior requires that the organism first detect the perturbation or its sequelae; secondly, recognize the condition as unfavorable; and, thirdly, take action adequate to eliminate or reduce the adverse effects.

Faced with chemical perturbations, such as, petroleum hydrocarbons, marine crustaceans can be expected to employ their primary sense, chemoreception, to fulfill the first prerequisite, detection. The present study measured the ability of the blue crab, Callinectes sapidus, to detect the petroleum hydrocarbon, naphthalene, and then went on to examine the occurrence and nature of behavior patterns over and above detection.

Previously, behavioral criteria were used to show that the blue crab detected a clam extract at 10^{-12} mg l⁻¹ (Pearson and Olla, 1977) and could also detect naphthalene (Pearson and Olla, in press). Here we report the results of two experiments concerning behavior of the blue crab under brief exposure to naphthalene. The first experiment employed the same behavioral criteria to determine the detection threshold for naphthalene. Pearson and Olla (1977) also found that the clam extract released food searching in the blue crab at levels 12 to 13 orders of magnitude higher than its detection threshold. With the expectation of an analogous situation and after the detection threshold for naphthalene was known, the second experiment was undertaken in order to discover what other behavior patterns in addition to detection were released at higher naphthalene levels.

Materials and Methods

Blue crabs, Callinectes sapidus, were trapped in Nacote Creek, Port Republic, New Jersey and transported to Sandy Hook Laboratory in an aerated 1700-liter fiberglass tank. The crabs were held in a rectangular 4300-liter tank with a partially recirculating seawater system. Seawater drawn from Sandy Hook Bay percolated through gravel and sand on the tank bottom and was recirculated through a filter of gravel, sand and oyster shell. The water was 21.5 ± 0.1 (SE) $^{\circ}\text{C}$ and 23.8 ± 0.1 o/oo during the first experiment and $21.6 \pm 0.3^{\circ}\text{C}$ and 14.7 ± 0.2 o/oo during the second experiment. Daylight-type fluorescent lights periodically adjusted to natural photoperiod provided lighting. An ad libitum diet of blue mussels, Mytilus edulis, was furnished. Molting or mating crabs were not tested.

The basic behavioral assay and apparatus have been described by Pearson and Olla (1977). The chemosensory testing apparatus was expanded to accommodate 24 testing chambers of 3.25 liters. Seawater passed through cellulose filters, a heat exchanger, and a head tank with gravel, sand and oyster shell before flowing into the individual chambers through two lengths of tubing at a rate totaling 1.0 l min^{-1} . Experimental solutions could be introduced through a valve in one of the seawater lines. A blind

with viewports enclosed the testing chambers.

Two experiments were performed. The first used methods employed by Pearson and Olla (1977) to measure the detection threshold of a food extract and was intended to determine the threshold concentration at which blue crabs detect seawater solutions of naphthalene. The second was intended to provide behavioral observations at higher concentrations than were achieved in the first experiment.

Because the second experiment required higher concentrations than the first, the two experiments differed in the manner in which the experimental solutions entered the testing chambers. In the first experiment an aliquot of 20 ml was injected within 10 sec into one seawater line. Dye studies (Pearson and Olla, 1977) had shown that the maximum concentration occurred in a testing chamber between 0.75 and 1.0 min after injection and was 5×10^{-3} times the concentration of the injected solution. In the second experiment, the experimental solution was continuously siphoned at a rate of 0.35 l min⁻¹ from a 20-liter glass Mariotte bottle (Einstrom-Heg, 1971) through one seawater line into a testing chamber. The flow in the other seawater line remained at 0.50 l min⁻¹. Dye studies revealed the time course of dilution within a chamber. Solutions of Azorubin Red were siphoned from the Mariotte bottle into a chamber and the optical densities of water samples taken from two positions

in the chamber were compared with those of standard dilutions of the dye solution in a spectrophotometer at 520 nm. The dye concentration in the chamber rose rapidly and leveled off at 4 min. After 6 min the dye solution had been diluted in the chamber by a factor of 0.388.

For the first experiment nearly saturated stock solutions were prepared by stirring for 4 h a weighted portion of ground naphthalene crystals (Matheson, Coleman & Bell) with seawater filtered through a 0.4-micron membrane. Approximately 3 h before their use each day dilutions of this stock solution were made with membrane-filtered seawater. This stock solution was refrigerated and not used after 4 days. For the second experiment 17 liters of a nearly saturated solution of naphthalene were prepared the day before use in the Marriotte bottle from which the solution would be drawn. A weighted portion of ground naphthalene crystals was added to 17 liters of seawater and the solution was heated to 30°C and stirred with a paddle stirrer for 6 h. The speed of the stirrer was adjusted to a point just below that that would produce a vortex. The naphthalene concentration of each stock solution was determined by Battelle Pacific Northwest Laboratories, Marine Research Laboratory, Sequim, Washington. A 750-ml sample of stock solution acidified with 1 ml of H₂SO₄, was extracted with 25 ml of hexane

(Burdick & Jackson) by shaking for 4 min. UV spectrophotometric analysis of the hexane extracts followed Neff and Anderson (1975). Some hexane extracts were further analyzed by capillary gas chromatography using a Hewlett-Packard Model 5840 with a 30 meter glass capillary column (OV101), and their naphthalene concentrations were calculated by comparison to external standards. For the first experiment stock solutions were $19.1 \pm 1.9 \text{ mg l}^{-1}$. The stock solutions decreased by 14% over the four-day holding period. In the second experiment the experimental solutions in the Marriotte bottles were $10.2 \pm 0.5 \text{ mg l}^{-1}$ for 4 days of testing, and $1.8 \pm 1.7 \text{ mg l}^{-1}$ for one day.

For the first experiment crabs were placed into individual testing chambers between 1300 and 1430 and tested the following morning between 0900 and 1300. For 8 days 24 crabs per day were tested. Each crab was presented first with a control solution of membrane-filtered seawater and then 2 h later with one of 5 dilutions of the naphthalene solution or a control of filtered seawater. The order of presentation and the choice of dilution were randomized except that crabs that were active were passed over until they became still. The observer was blind to the identity of the dilutions.

Observations on an individual crab began one min prior to injecting the experimental solution. The crab's behav-

ior was observed for 3 min after injection. The criteria used in scoring the behavior were the same as in Pearson and Olla (1977, in press) but expressed slightly more explicitly. Detection is indicated when within 1.5 min after injection and continuing for at least 1.0 min after onset, there is a sharp increase in the antennular flicking rate to above $120 \text{ flicks min}^{-1}$ accompanied by the abrupt onset of gill bailing as evinced by continuous rhythmic beating of the maxillipedal flagellae. Flicking rate was determined by timing the period necessary for 10 flicks of one antennule.

In the second experiment, for 5 days 12 crabs per day were placed into individual chambers between 1430 and 1600 and assayed the following day between 0930 and 1400. First, each crab was presented for 6 min with control seawater siphoning at a rate of 0.35 l min^{-1} from a Marriotte bottle. Before entering the chamber this solution from the Marriotte bottle mixed with uncontaminated seawater flowing from the head tank at 0.50 l min^{-1} . Secondly, two hours later each crab was presented for 6 min with the naphthalene solution siphoning from the Marriotte bottle under the same conditions as the control. A crab was observed for one min prior to switching to a control or experimental solution and for 6 min afterwards. Occasionally, when an interesting behavior began near the end of the observation period,

behavioral observations and the introduction of solution were continued for one additional minute. The behavioral criteria for detection were the same as in the first experiment.

Regression analysis (Draper and Smith, 1966) of data from both experiments was performed to calculate the threshold concentration at which 50% of the blue crabs detected naphthalene. The percentage of crabs detecting naphthalene was regressed against the logarithm of the maximum concentration of naphthalene to which the crabs were exposed in the chambers. For the first experiment the naphthalene concentration in the chambers was estimated by multiplying the concentration of the injected solution by 5×10^{-3} , the dilution factor derived from the dye studies. Similarly, for the second experiment, the naphthalene concentration in the Marriotte bottle was multiplied by 0.388, the dilution factor at 6 min.

Results

Blue crabs, Callinectes sapidus, detected low concentrations of naphthalene. From the regression equation (Fig. 1) the threshold concentration at which 50% of the crabs detected naphthalene was $8.5 \times 10^{-8} \text{ mg l}^{-1}$. Back calculation of the 95% confidence limits about the regression line

Fig. 1

indicated that the detection threshold fell between 10^{-4} and 10^{-10} mg l^{-1} .

In the second experiment where blue crabs were exposed to naphthalene concentrations ($3-5$ mg l^{-1}) considerably above the detection threshold, they showed other behaviors besides those indicating their detection of the naphthalene (Table 1). Detection behavior usually began within 20 sec of the addition of naphthalene and continued for the duration of the experimental period. Thirty-five percent of the crabs approached the inlet orifice and brought their antennules and buccal area as close to the inlet as possible given the configuration of the chamber. One individual manipulated the inlet with its chelae. Occasionally, a sequence of approach and retreat would be repeated several times. Leaning and shielding displays described by Jachowski (1974) were given in an upstream direction by 20.8% of the crabs. Approaching always preceded or accompanied the displaying. Grooming behavior occurred in 12.5% of the crabs and was not associated with displaying. None of the behaviors that are normally associated with feeding and that were seen in the experiments with the clam extract (Pearson and Olla, 1977) were observed in the presence of naphthalene. The one instance of chelae manipulation of the inlet orifice might be classi-

Table 1. The behavior of blue crabs (Callinectes sapidus) exposed to naphthalene for 6 minutes. Means are given with their standard errors. Parentheses enclose the number of data points.

	Control	Experimental	
Max. Concent. (mg l ⁻¹)	0	0.70 ± 0.66 (2)	4.0 ± 0.2 (8)
No. of crabs	60	12	48
Crabs detecting (%)	21.6	83.4	47.9
Crabs grooming (%)	8.3	8.3	12.5
Crabs approaching (%)	0 ^a	0	35.4
Crabs displaying (%)	0	0	20.8
Time of approach (sec)	0	0	188.9±22.9 (17)
Concentration at approach (mg l ⁻¹)	0	0	2.5±0.3 (17)
Time of display (sec)	0	0	214.5±26.7 (10)
Concentration at display (mg l ⁻¹)	0	0	2.9± 0.4 (10)

^a Two crabs (4.2%) walked but were not oriented to the inlet.

fied as a feeding behavior, but it was not preceded by any of the food searching behaviors typically accompanying chelae probing when a clam extract is present.

Knowing the time at which approaching or displaying were observed allowed the naphthalene concentration at which these behaviors occurred to be estimated by multiplying the naphthalene concentration in the Marriotte bottle by the dilution factor for the time at which the behavior occurred. Approaching occurred at $2.5 \pm 0.3 \text{ mg l}^{-1}$ naphthalene; displaying, at $2.9 \pm 0.4 \text{ mg l}^{-1}$ (Table 1).

Discussion

As previously noted (Pearson and Olla, in press) the changes in antennular flicking and gill bailing indicating when blue crabs detected a food extract also indicated when blue crabs detected the petroleum hydrocarbon, naphthalene, and, therefore, could be used to establish a detection threshold. The detection threshold for naphthalene ($10^{-7} \text{ mg l}^{-1}$) proved to be 5 orders of magnitude higher than that found for a freeze-dried clam extract (Pearson and Olla, 1977). The difference in the detection threshold between naphthalene and the clam extract may have derived in part from the difference in their chemical nature. Naphthalene was a single

compound while the clam extract was composed of a variety of organic chemicals. When single amino acids have been compared with complex synthetic mixtures or with extracts of natural food (Mackie, 1973; McLeese, 1974), the single amino acids have been found less effective in releasing feeding behavior than the more chemically complex mixtures. Laverack (1975) has suggested that all of the chemoreceptors of an animal are not alike in that different receptors are sensitive to different types of chemicals and that some receptors are specialized and others more general. It may be then that naphthalene being a single compound was only stimulating a subset of the blue crab's chemoreceptors and as a consequence would exhibit a higher detection threshold than a complex mixture stimulating a greater portion of the chemoreceptor population. This line of reasoning leads to the hypothesis that blue crabs would more readily detect whole oil than specific petroleum hydrocarbons because whole oil is a very complex mixture.

The function of the behavior seen at the higher levels of naphthalene is difficult to discern. The direct approaching of the water inlet appears to be exploratory in nature. The leaning and shielding displays appear to be more defensive than aggressive. Jachowski (1974) indicated that they are generally of short duration and given in less intensely threatening situations than other displays such as cheliped

extending or fending. The frequency of grooming in the experimental situation is low and does not differ much from that in the control situation so that it is questionable whether it is really an alternative response to the presence of naphthalene. The absence of the feeding behaviors that were released by high levels of clam extract (Pearson and Olla, 1977) indicates that the crab is not perceiving naphthalene as a food signal.

Other crustaceans appear to be both drawn to and repelled from petroleum hydrocarbons. Atema (1976) reported that after exposure lasting minutes to hours to various crude oils and their fractions, lobsters, Homarus americanus, and snails, Nassarius obsoletus, showed both attraction and repulsion. In the lobsters with some oil fractions there were aggressive postures and feeding upon oil-soaked material. The pattern of behavior appears to be a function of the specific type of oil fraction and the representation of fraction type in the crude oils. Percy's (1976) work with two arctic amphipods, Onisimus affinis and Gammarus oceanicus, gave similar results. These amphipods avoided fresh crude oil and oil-tainted food, but weathering caused two out of three crude oils to lose their ability to repel, presumably due to the loss of some specific volatile component.

Therefore, it appears that the initial reaction by the blue crab to the presence of naphthalene is detection followed by exploratory and defensive behavior. To resolve the question whether the initial attraction to the naphthalene source is sustained or oscillates between approach and withdrawal, or eventually leads to avoidance of the naphthalene requires a different assay apparatus.

The absence of any behavior other than detection at naphthalene concentrations less than 2 mg l^{-1} indicates that below that level the blue crab has no effective behavioral strategy for mitigating the effects of the hydrocarbon. This lack leads to the reasonable expectation that animals in the natural situation would not avoid water with less than 2 mg l^{-1} naphthalene and would, consequently, be exposed up to that level. This being the case, laboratory studies of acute and chronic effects that employ naphthalene concentrations below 2 mg l^{-1} would be entirely appropriate and useful.

Presently it cannot be stated whether the exploratory and defensive behavior released above 2 mg l^{-1} is part of any effective adaptive behavior. What can be stated is that naphthalene at a level above the detection threshold released oriented locomotor activity in the blue crab. Where this activity would take this crab remains to be examined.

In discussing an animal's behavior as the first defense against an environmental challenge, Slobodkin and Rapoport (1974) suggest that animals may be particularly vulnerable to environmental perturbations that are novel, i.e., not part of its evolutionary history, because novel events may not be detected. The blue crab can detect the presence of naphthalene but appears unable to evaluate its significance. In recent applications of decision theory to animal behavior (McFarland, 1977) there emerged two important variables, the utility and the probability. The utility is the evaluation of the attractiveness of various courses of action and the probability is the evaluation of the consequences of following each course. What the blue crab appears to be unable to do is to evaluate the consequences of moving into or out of the presence of naphthalene.

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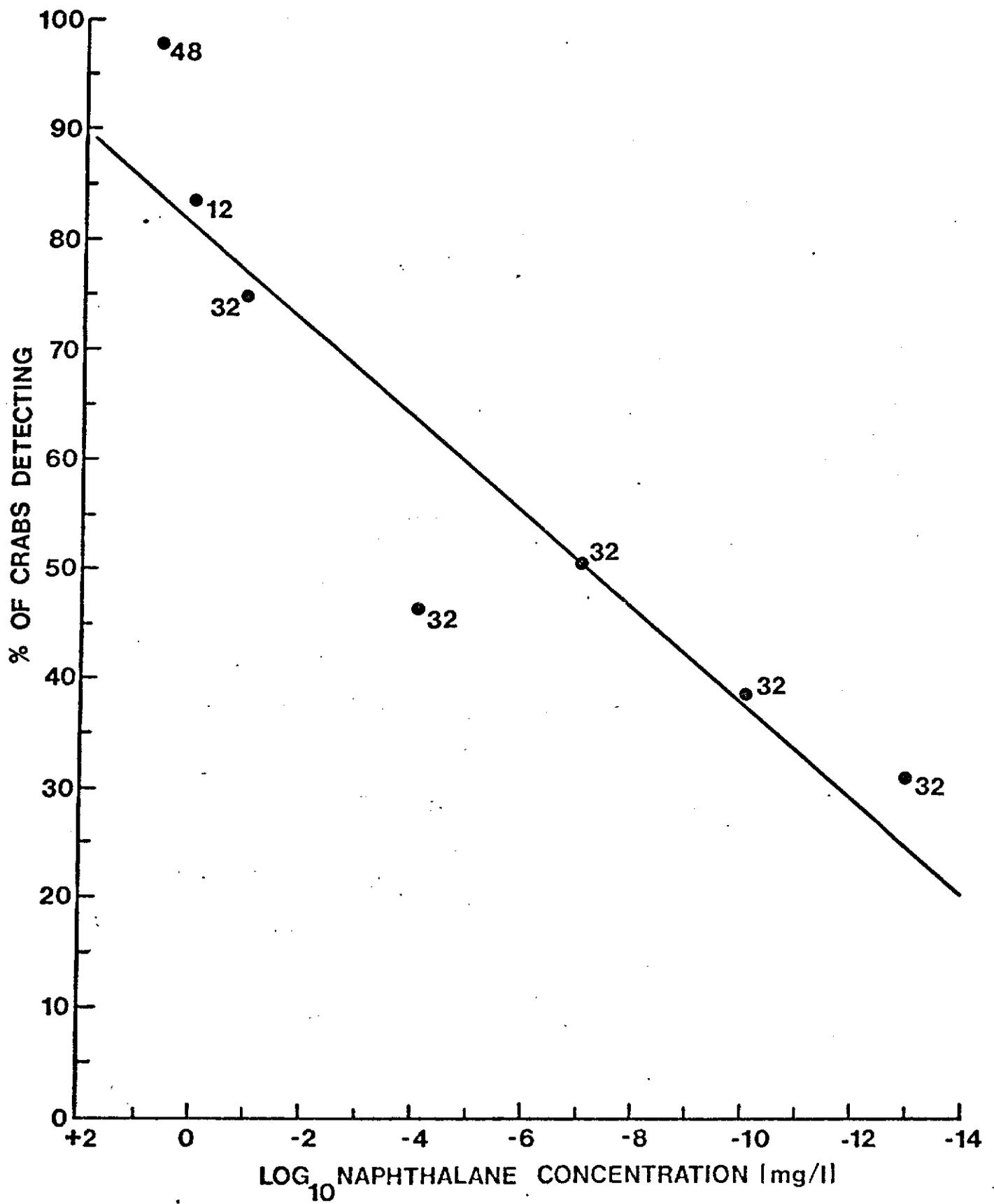
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Fig. 1 The percentage of blue crabs, Callinectes sapidus, detecting seawater solutions of naphthalene as a function of the logarithm of the maximum naphthalene concentration (mg l^{-1}) achieved in the chambers. The regression equation was $Y = 81.2 + 4.419 X$ with the 95% confidence limits for intercept and slope being ± 17.4 and ± 2.508 . Parentheses enclose the number of trials at each point. In the first experiment detection was 27.6% ($n = 192$) for the control solutions presented before the experimental ones and 25.0% ($n = 32$) for controls presented as one of the experimentals. In the second experiment detection of controls was 21.6% ($n = 60$).



III.

Behavioral Detection of a Food Extract

by the Hake, Urophycis chuss

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intended for citation or publication.

INTRODUCTION

For marine organisms the variety of life processes depending on chemoreception includes food detection and gathering, predator recognition and escape, establishment and maintenance of commensal, symbiotic, and parasitic relationships, induction of spawning, and courtship and mating (Grant and Mackie, 1974). One eventual aim of our research with the hake, Urophycis chuss, is to study the influence of petroleum hydrocarbons on behavioral patterns and selected life habits that are mediated by chemoreception. As a first step towards this aim we have examined the sensitivity of the hake to an extract of natural food utilizing behavioral criteria. The data reported here are still preliminary, and more trials, currently in process, are necessary to increase the statistical confidence in the detection threshold.

There are two indications that a particular organism depends heavily upon chemoreception. First, where a behavior necessary to fulfilling the life requirements of the organism needs chemical information, the acuity of chemoreception can be expected to be great. For example, some fish respond to odors when as little as two to several molecules are present in the nasal capsule (Bardach and Villars, 1974). Secondly, where there is high dependence on chemoreception, often there are also elaborated anatomical features, e.g., the nose trumpet of certain eels, that enhance signal-to-receptor contact (Bardach, 1975).

Hake have such elaborated anatomical structures, the modified pelvic fins, which Bardach and Case (1965) have shown to carry chemo-

receptors and to function in food gathering. Beyond their electrophysiological and behavioral confirmation of chemosensitivity in the pelvic fin, no quantitative assessments of chemosensory ability have been carried out for the hake.

In this work, observations of the feeding behavior of U. chuss led to the selection of particular behavioral patterns as criteria for assaying chemoreception in the hake. The aims of this work were not only to measure the threshold concentrations at which hake detected a food extract and began feeding behavior, but also to do so with methods similar to those previously employed for the blue crab, Callinectes sapidus (Pearson and Olla, 1977) so that the chemosensory abilities of a fish and a crustacean could be compared on as close to the same basis as possible. In later work the chemosensory testing techniques developed for the hake will be employed for petroleum hydrocarbons as was done for the blue crab (Pearson and Olla, 1979, in review).

MATERIALS AND METHODS

Experimental animals, Urophycis chuss (Walbaum), were collected by trawls of less than 10 min from Sandy Hook and Raritan Bays, New Jersey during April and May of 1978 and were transported immediately to the Sandy Hook Laboratory in aerated flow-through seawater tanks. The fish were held for several weeks prior to testing in a 1800-liter holding tank provided with a gravel and sand bottom and sections of PVC pipe as shelter. The hake readily used the shelter and began feeding on chopped clam within hours of capture. Chopped clam was provided three times a

week with the time of feeding given by a randomization technique. Temperature and salinity of the holding tank water were 11.3 (\pm 1.13 SD)°C and 21.6 (\pm 1.02) o/oo, respectively. Illumination on a natural photoperiod was provided by fluorescent lighting with a daylight spectrum. Fork length of fish used was 14.92 (\pm 1.43) cm.

The chemosensory testing apparatus was designed to present individual hake with experimental solutions and to observe the subsequent behavior and was essentially that used by Pearson and Olla (1977) except that the individual testing chambers were modified for the hake. From a head tank seawater was continuously siphoned to each 5.3-liter glass testing chamber at the rate of 1 liter/min. After passing through a glass funnel into an inlet manifold of plexiglass (12 mm dia) that was connected to the white translucent plexiglass cover clamped to each chamber, the seawater entered the testing chamber through three slits (1 x 30 mm) in the inlet manifold. Each testing chamber was provided with a sand substrate (500 ml) and a shelter of PVC pipe (10 cm long x 5 cm dia) that faced the inlet manifold at a distance of 6 cm. A blind with viewports surrounded the water table upon which seven to fourteen testing chambers, separated from each other by a partition, were arranged in a line.

From a buret calibrated to deliver 20 ml in 15 sec a 20-milliliter aliquot of an experimental solution was added to a chamber through the PVC pipe carrying seawater to the glass funnel. Dye studies were performed to obtain a dilution factor for estimating the effective concentration of an experimental solution within the testing chamber. Solutions

of azorubin red were introduced into testing chambers, and water samples taken at various times from six positions in the chamber were compared with standard dilutions of the dye solution in a spectrophotometer at 520 nm. The peak concentration within the chamber was found to occur between the inlet manifold and the shelter at 10 seconds after the start of solution introduction and was 1.86×10^{-2} ($\pm 5.2 \times 10^{-3}$ SD) times the concentration of the dye solution. The concentrations of experimental solutions were multiplied by the factor of 1.86×10^{-2} to obtain the effective concentration within the chamber.

The experimental solutions were seawater solutions of the freeze-dried extract of hard clam, Mercenaria mercenaria, used and described previously by Pearson and Olla (1977). Following their procedures stock solutions of the freeze-dried clam extract (FDCE) were prepared fresh on each day of testing with seawater filtered through a 0.4 micron membrane. The concentrations of this stock solution after correction for the FDCE retained in filtration averaged 1.11 (± 0.11) g/liter. Dilutions of the stock solution by 10^{-2} to 10^{-15} were made with membrane-filtered seawater shortly before each day's testing. A portion of the dilution water was set aside for use as a control solution. The control and experimental solutions were placed in a water bath to keep them at the same temperature as the seawater entering the testing chambers.

An individual hake, fed to satiation and then deprived of food for four days, was placed into each testing chamber 24 h before testing. The order in which the hake were observed and the choice of experimental dilution were given by a randomization technique. The observer was blind to the identity of the experimental solution. An in-

dividual fish was observed first for 2 min during which no solution was introduced, next for another 2 min after introducing the control seawater, and finally for 2 min after introduction of FDCE solution. An event recorder was used to measure the frequency and time duration of the following activities: resting in shelter, resting outside shelter, moving, backing, swimming along bottom, swimming in water column, moving modified pelvic fins forward of 90° angle with the body, yawning, coughing, and biting. Data from initially active fish (16.9%) were not included in subsequent analysis.

The behavior of fish observed after the introduction of a control or experimental solution was scored on the basis of criteria selected after observation of feeding behavior of hake in large aquaria and numerous trials in the chemosensory testing apparatus. A hake was considered to have detected an experimental solution if it began moving the the pelvic fins over the substrate after bringing the fins forward of a 90°angle with the body. Usually the fin movement was accompanied by moving forward and/or active swimming. A hake was considered to have begun feeding when it approached the inlet manifold and began biting.

Threshold concentrations for the detection of the FDCE and the onset of feeding were determined from the regressive equation relating the percentages of fish exhibiting the behavior of interest and the logarithm of the effective FDCE concentration in the testing chamber. This threshold concentration was taken to be that concentration at which 50% of the hake responded.

RESULTS

Observation of normal feeding behavior and selection of behavioral criteria.

Because the intent of this research was to establish thresholds for the searching and feeding behavior mediated by chemoreception, visual clues that may be involved in feeding were not emphasized. The following description deals mainly with behavior mediated by chemoreception.

Hake utilize their modified pelvic fins extensively in food searching. In the holding aquaria, resting and swimming hake typically had the pelvic fins folded back along the body. After the introduction of chopped clam, swimming increased in speed and duration. Food was approached and consumed after searching. During searching the fish swam with the fins extended laterally (90° to 120°). When a fish approached a clam piece, the pelvic fins were extended more anteriorly (150° to 180°) and the head was lowered so that the barbel was close to or contacting the substrate. The head was often moved from side to side. Commonly the fish swam past the food, and after contacting it with the barbel, backed to the clam with an anguillid swimming motion. Ingestion was accomplished by a gulping or biting motion in which the mandible was rapidly lowered and the opercula and branchiostegal rays were expanded. One to several bites were needed to ingest a clam piece, and several pieces could be ingested consecutively. Feeding would continue

until the gut was highly distended. Following periods of feeding to satiation, hake decreased activity and increased shelter association.

In the chemosensory testing apparatus, the initial state of hake was typically one of resting inside the shelter (57% of the animals tested). Fish resting outside the shelter (26%) were usually resting in the angles between the substrate and the shelter or between the substrate and chamber wall. The active fish (17%) were not used in measuring the chemosensory thresholds.

The number and time duration of behavioral patterns generally increased with FDCE concentration. At low FDCE concentrations (10^{-13} g/liter), hake exhibited general positional changes, e.g., moving forward and then backing (14.3%), occasional swimming (15.9%), pelvic fin movement (20.5%) and emergence from shelter (25.7%). At moderate concentrations (10^{-7} to 10^{-13} g/liter) more fish showed positional changes (25.8%), swimming (25.8%), fin movement (27.6%) and emergences (34.6%). At the high FDCE levels (10^{-2} to 10^{-7} g/liter) there were high levels of swimming (75.6%), emergences from shelter (87.9%) and fin movement (90.5%). Only at these high levels did fish approach the inlet manifold and exhibit biting (15.1%).

After the observations of normal feeding behavior and numerous trials in the testing apparatus the assay criteria described in detail in the Methods section were chosen. For 100 fish the amount of time spent with the pelvic fins extended was measured for the 2-minute periods when no control or experimental solutions were present. At the 95 percentile there was no pelvic fin extension. Thus, under the pre-

vailing test conditions the a priori probability of an instance of pelvic fin extension being spontaneous rather than a reaction to the control or experimental solution was less than 5%.

Threshold for detection of the clam extract

The percentage of hake detecting the FDCE fell with decreasing FDCE concentrations (Fig. 1). The regression equation was:

$$Y = 107.11 + 6.098 X$$

where Y equals the percentage of fish detecting and
X equals the logarithm of the FDCE concentration (g/liter)
within the testing chamber.

The 95% confidence limits of the intercept and slope were 38.58 and 2.756, respectively. The threshold concentration at which 50% of the hake detected the FDCE was 4.3×10^{-10} g/liter. Back calculation of the 95% confidence limits about the 50% point shows that the threshold fell between 10^{-7} and 10^{-12} g/liter. The percentage of hake detecting the control seawater was 3.9%.

The hake approached the inlet manifold and began biting only at the highest FDCE levels so that the number of data points was not adequate to construct a regression equation for feeding behavior. Graphical estimation (Fig. 1) suggested that the threshold for feeding behavior was on the order of 1 g/liter of FDCE.

DISCUSSION

In general comparison of chemosensory detection thresholds is difficult because the detection criteria, experimental chemicals, and other aspects of methodology differ, but the hake appears to be as sensitive as other fish. For example, the eel, Anguilla anguilla, detected phenyl ethanol down to 10^{-18} M (4×10^{-16} g/liter) (Teichmann, 1959). The lowest reported electrophysiological threshold for tests in any vertebrate was 10^{-11} M (8.9×10^{-10} g/liter) of L-alanine in the channel catfish, Ictalurus punctatus (Caprio, 1975). In the present study (Fig. 1) the hake detected the FDCE down to at least 10^{-17} g/liter.

In order to obtain as reliable a comparison as possible, the methodology used with hake followed that used with the blue crab (Pearson and Olla, 1977) as closely as behavioral and anatomical differences in the two species permitted. The hake appeared to have slightly less chemosensory acuity than the blue crab. For the same clam extract the detection threshold in the hake was 5 orders of magnitude above the one of 10^{-15} g/liter found for the blue crab. At present there is not enough data to indicate whether the feeding thresholds for the two species are distinct.

Although the detection criteria for the blue crab and the hake are both based on changes in the orientation and motion of chemosensitive appendages, the criteria may not be completely equivalent and, in consequent, the detection thresholds for the two species may not be measuring precisely the same phenomena. For the blue crab an abrupt

increase in the antennular flicking rate indicated detection (see Pearson and Olla, 1977 for detailed description) while for the hake changes in the orientation and movement of the modified pelvic fins indicated detection. The antennules of the blue crab and other decapods have been demonstrated to function as distance chemoreceptors (Hazlett, 1971). With the hake distance chemoreception may be mediated by the nares rather than the pelvic fins. Although it is generally believed that the olfactory apparatus mediates detection and arousal (Bardach and Villars, 1974), fish and, in particular, the hake (Bardach and Case, 1965) are capable of detecting the presence of food without the olfactory apparatus. With the increasing number of studies, such as that of Caprio (1975) showing that at least for the catfish gustatory chemoreceptors approach in sensitivity olfactory ones, the distinctions between the capabilities and functions of various chemosensitive anatomical structures become less clear.

Temperature may influence chemosensory thresholds, and the differences in the detection thresholds between the blue crab and the hake may derive from the differences in temperature. The blue crabs were tested at 20°C while the hake at 11°C. If both animals had been tested at the same temperature their detection thresholds could have been closer.

The high association with shelter shown by hake in both the holding tank and the testing chambers may be an extension of their

inquilism in the sea scallop, Placopecten magellanicus. Hake cease inquilism in the late winter and spring shortly before or upon reaching a length of 13 cm (Musick, 1969). The average size of the hake tested was 14.9 cm so that the hake in this study were probably captured shortly after leaving the sea scallops and migrating inshore. The readiness with which the hake utilized shelter during this study is not consistent with Musick's view that the cessation of inquilism is a function of the availability of large sea scallops as shelter.

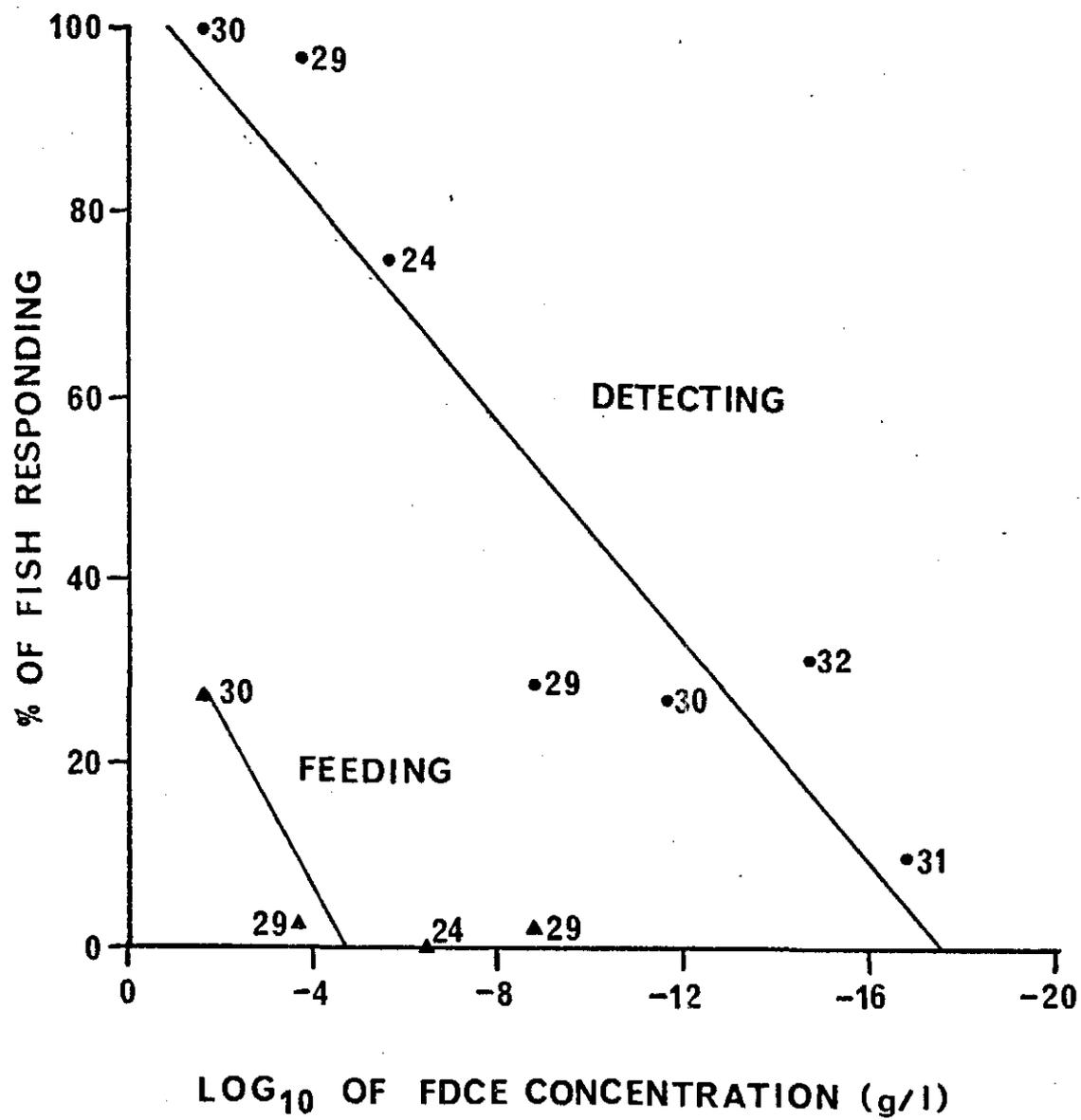
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Figure 1. The relation between the percentage of hake exhibiting detection (circles) and feeding (triangles) and the logarithm of the FDCE concentration (g/liter) within the chemosensory testing chamber. The regression equation is $Y = 107.11 + 6.098X$ ($R^2 = 0.866$). Control seawater was detected by 3.9% of the hake. The numbers of trials at each point are indicated.



IV.

Seasonal Dispersal and Habitat Selection of Cunner,
Tautogolabrus adspersus, and Young Tautog, Tautoga
onitis.

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(Ms in Journal Review)

ABSTRACT

Results of field observations examining seasonal movements in the cunner, Tautoglabrus adspersus, and young tautog, Tautoga onitis, showed a small portion of a resident population located off Fire Island, N.Y. to disperse seasonally. Dispersal was from habitats which provide cover for both species throughout the year to seasonal habitats occupied primarily during summer. While both species exhibit a high degree of association with cover, results of experimental transfers of young tautog, monitored either ultrasonically or directly with SCUBA, showed that fish will leave a suboptimal habitat even though cover is present. Dispersal and habitat selection are discussed in relation to seasonal changes in the environment and ecological requirements of the fish.

Association with and dependence on cover by marine fishes have been observed for a wide variety of species, exemplified by those which reside on coral reefs (for examples see: Hobson 1968, 1972, 1973; Sale 1969a, 1971, 1972, 1977; Smith and Tyler 1972, 1973). Although the number of species is much less, similar associations with cover also occur in temperate waters (for examples see: Hobson 1971; Bray and Ebeling 1975; Hobson and Chess 1976; Olla et al. 1974, 1975).

In both tropical and temperate regions a major behavioral trait of the family Labridae is that members show a strong association with cover. Field studies on two temperate-water labrids of the northwest Atlantic, cunner, Tautogolabrus adspersus (Olla et al. 1975), and young tautog, Tautoga onitis (Olla et al. 1974), have demonstrated their close association with cover. Under laboratory conditions similar associations have been observed for both species (cunner, Olla and Bejda unpubl. obs.; young tautog, Olla and Studholme 1975).

Over several years, incidental sightings of cunner and young tautog always found them in association with cover. However, it was apparent that a substantial number of fish were in areas in which cover was present only seasonally, e.g., macroalgae and mussel beds. This suggested to us that there must be movement to these areas sometime after emergence from winter torpor in March or April and movement away from these areas in the fall as the cover provided at these areas diminished. The possibility of seasonal dispersal and habitat selection appeared likely. At least for adult tautog changes in habitat requirements

with season have been established as evidenced by the fact the fish migrate offshore to over-winter (Cooper 1966; Olla et al. 1974).

In this study we have examined seasonal movements in cunner and young tautog, basing our observations on trapping and tagging, as well as surveying shelter sites seasonally by direct observation with SCUBA or mask and snorkel. We also performed a series of transfer experiments to examine certain aspects of habitat selection.

MATERIALS AND METHODS

Based on previous SCUBA observations, six study sites (A, B, C, D, E, and F; Figure 1) within Fire Island Inlet, Long Island, New York, were selected at which to monitor the seasonal movements of cunner, Tautogolabrus adspersus, and young tautog, Tautoga onitis. One site (A) was inhabited throughout the year and will be referred to as a perennial site. The five other sites (B, C, D, E, and F) were utilized by both species only during late April through October and will be referred to as seasonal sites. A description of each site is as follows:

Site A was the boat basin at the Fire Island Coast Guard Station, an open pentagon (110 x 52 x 47 cm), constructed of tongue-and-groove planks, steel sheeting, and piles (Olla et al. 1975). Along the outer perimeter was a zone of riprap (0.2- to 0.4-m diam), 3 m wide and 2 m high. The mean water depth ranged from 2.4 to 8.8 m. Beds of mussels, Mytilus edulis, were randomly distributed along the walls, piles and bottom.

Site B was a 20.3-cm diam drain pipe originating at the Fire Island water treatment plant. Located at a mean depth of 7.5 m, a 1.5-m section of the pipe was exposed and paralleled the bottom at a distance of 1 m. Beds of mussels surrounded the pipe for about 6-m radius.

Site C was one of the support piers for the Robert Moses Bridge, consisting of quarried stone and reinforced concrete. The mean water depth was 7.5 m. The perimeter of the pier for a distance of 2 m below the high water mark was incrustated with mussels.

Sites D and E each consisted of an exposed vertical mud bank about 6 m in length and 1 m high. Randomly spaced along the face of each bank were approximately 35 to 50 holes, apparently a result of erosion, varying in size from 12 to 20 cm in width and 5 to 15 cm deep. Small clumps of mussels were randomly distributed along the top of each bank. Site D was at a mean depth of 6.0 m and Site E at 7.6 m.

Site F was a grass bed which bordered a rocky shore line for 75 m and extended out from the shore 13 to 20 m. During the late spring and summer, the area typically consisted of dense growths of eel grass (Zostera marina) and algae (Codium spp., Enteromorpha spp., Polysiphonia spp., and Ulva spp.). Beds of mussels were interspersed between the vegetation. Water depth throughout the area varied from 0.3 to 1.5 m.

A seventh area, a small cove at the mouth of the Inlet, not designated in Figure 1, was the site of two transfer experiments involving experimental cover. This site consisted of a barren sand bottom, primarily dredge spoil, at a mean depth of 3.7 m.

Three methods, trapping, direct visual counts, and tagging were used to monitor, for both cunner and tautog, the periods and limits of movements as well as the types of habitats utilized. Fish traps were placed at Sites A, B, C, D, and E with two traps at Site A from March through November, one trap at Site B from May through November, and one trap each at Sites C, D, and E from June through November. Traps at each site were pulled at regular weekly intervals throughout the study and the number of cunner and tautog recorded. In order to compare the catch of the traps at the perennial site with the catch of the traps at the seasonal sites, the catch from all traps for each habitat type was combined

and then converted to the mean number caught per trap per week for each habitat type. Traps appeared efficient in catching cunner ranging in size from 3.9 to 25.0 cm ($\bar{X} = 14.5$ cm) and tautog from 7.3 to 35.0 cm ($\bar{X} = 16.9$ cm). The traps also provided the fish for the tagging portion of the study as well as one means of recapture.

Visual counts of cunner and tautog were made at Site F from the end of February through October. A series of six transects the length of the site and 3 m in width were swum by divers, counting all tautog and cunner observed within each transect with the sum of the six transects being the total count.

Cunner and tautog (>14.0 cm) trapped at Sites A, B, C, D, and E were tagged throughout the study with Floy-67C¹ anchor tags. Tags were consecutively numbered allowing identification of individual fish and their site of release. In addition each tag was printed with a request for fishermen catching tagged fish to return the tag, accompanied by information as to the location and date the fish was caught. Fish were recaptured either in our traps or by recreational fishermen.

Ultrasonic tracking and direct observation using SCUBA were employed for short term monitoring of movement and cover association of young tautog, both at their site of residency and at sites to which they were transferred. Nine fish were individually tracked using the same procedures previously described by Olla et al. (1974, 1975) for capturing, handling, and tracking. SCUBA was used in the transfer experiments in which fish were released in groups of ten. While lying motionless, 5 m from the shelter structure, the observer recorded at

1-min intervals the number of fish present. Fish were transferred by boat in 100-l barrels of aerated seawater with no more than five fish per barrel. The time to travel from capture to release sites ranged from 5 to 15 min.

In the portion of the study in which we provided the cover at the release sites, the structures were constructed from standard masonry cement blocks (20 x 20 x 40 cm), placed in a manner which exposed the central cavities (7 x 13 x 20 cm) of each block. The structure for the single fish release consisted of four blocks, arranged one block long and two blocks high and wide (40 x 40 x 40 cm). The two structures for the group releases consisted of 12 blocks, three blocks long and two blocks wide and high (120 x 40 x 40 cm).

RESULTS

Catch at Seasonal and Perennial Sites

There was a gradual decline in the catch of cunner in September and October and a sharp decline of tautog in October at sites B, C, D, and E, with no fish of either species being captured in November (Table 1). We made direct SCUBA observations of the sites in November and did not sight any fish. Transect data for Site F, using SCUBA or mask and snorkel, generally agreed with the results from Sites B, C, D, and E, indicating an absence of both cunner and tautog, but in this case, several weeks earlier (Table 2). From these observations we concluded that these sites (B-F) were utilized only on a seasonal basis. In contrast, as the catch was decreasing in the fall at Sites B, C, D, and E it was increasing at Site A (Table 1). Similar increases in catch of young tautog during the fall were observed in an earlier study at the Kismet artificial reef, located about 6 km from our study area (Briggs 1977).

The decrease in catch at Site A in November could be indicative of the reduction in movements related to the onset of winter torpor in the two species during late November or early December when the temperature drops below 5 to 6°C. Both species have been found at Site A during previous winters in a state of torpor (Olla et al. 1974, 1975).

Although traps were not in place at the seasonal sites earlier than May, visual sightings using SCUBA showed the absence of both species from these areas prior to mid or late April (Table 2). After their initial

arrival in the spring, both species inhabited the seasonal sites throughout the summer (Tables 1 and 2).

Tag Returns

Recaptures of tagged fish of both species showed limited movement, with 91.3% of the cunner and 73.2% of the tautog remaining at the same site at which they were released (Table 3). The remainder of the fish were Table recaptured at other sites. From September through November, all of these were at sites which could be considered perennial, including structures that were not one of our study sites (Table 3). On the other hand, from May through August, recaptures were at seasonal sites as well as perennial ones (Table 3). The figures from catch, recaptures and direct sightings are indicative of seasonal dispersal. The fish over-winter in torpor at perennial sites. Then, some small portion of the population disperses from this type of site in the spring, spending the summer at seasonal sites, returning to perennial sites in the fall. The site to which it returns to over-winter may not be the same site from which dispersal occurred in the spring.

Ultrasonic Tracking at Seasonal and Perennial Sites

In an earlier study, young tautog, tracked ultrasonically at Site A, showed restricted movement, remaining within several meters of cover (Olla et al. 1974). To confirm this earlier observation, two fish (no. 1 and 2; Table 4) were captured and released at Site A and monitored for Table 48 h each. They remained within 2 m of the structure, although ranging along its entire length. The results essentially agreed with those from the earlier study (Olla et al. 1974).

Then to test whether the same affinity was shown towards seasonal sites, two fish (no. 3 and 4; Table 4) were captured, released and ultrasonically tracked at Sites B and F. Again the fish exhibited limited movement, remaining within 3 to 6 m of cover, with the amount of area over which the animals ranged varying with the amount of the cover available. For example, Site F, comprised of algae, eel grass and mussels, extended about 15 m in width and 75 m in length. When fish no. 3 was released there, it moved freely throughout the entire area, but never more than several meters beyond its perimeter, comparable to the movements of fish released at Site A.

On the other hand, fish no. 4, released at Site B, ranged no more than 5 to 6 m, remaining in proximity to the submerged pipe which was the only available cover at this site.

Transfer Experiments

It was apparent from our results that at least a small percentage of cunner and young tautog dispersed and selected habitats other than those at which they over-wintered. To stimulate dispersal and examine how readily seasonal habitats were adopted by young tautog, fish affixed with ultrasonic tags were transferred from Site A (the perennial site) to Sites B or C. Three fish released at Site B (no. 5, 6, 7; Table 4), and tracked individually for 48 to 72 h, remained within several meters of the site. One fish released at Site C (no. 8, Table 4) and tracked for 48 h also remained within several meters.

The presence of conspecifics at both sites indicated that these were appropriate habitats for young tautog. On this basis, one might have predicted that the transferred animals would remain. However, it was also possible that the dependence on cover might be such that the fish would remain at any habitat that afforded cover.

To examine this question, a series of experimental releases were made at sites where we provided the cover. In one case the cover consisted of a cement block structure (40 x 40 x 40 cm) placed on a barren sand bottom 50 m from the nearest inhabited site (Site F). Cement blocks had been shown to be readily acceptable as cover by young tautog in the laboratory (Olla and Bejda unpubl. obs.). Using the same procedures as in all other ultrasonic tracks, a 22.5-cm fish (no. 9; Table 4) was transferred from Site A to the structure. During the first 5 min after being released, the fish randomly circled the structure, moving further away with each circuit, showing little, if any, attraction. When the fish had reached a distance of about 10 m from the structure, it began a shoreward movement which brought the fish to Site F. The fish remained at this site during the next 24 h, showing the same degree of movement exhibited by fish no. 3 (Table 4) which had been captured and released at this site.

To avoid any potential effect that the lack of species mates might have on the response to the structure and to insure that the animals were not homing to familiar sites, fish were next released in a group in an area well out of the fish's home range, approximately 4.5 km from Site A where they were captured. Two cement block structures (120 x 40 x 40 cm) were placed 10 m apart. The closest point where conspecifics could

be found was about 100 m away with only a barren sand bottom in between. Both structures were identical except around and under one we placed mussels and algae (Ulva spp.), naturally occurring food and shelter material. This was done to test whether these items influenced the acceptability of the structure. Two groups of 10 fish each (15-23 cm) were transferred from Site A, with one group released at each structure. Both groups responded similarly, leaving the area within 5 min of being released.

Each structure was then modified by the addition of a fish trap. To the structure, which was surrounded with mussels and algae, a trap was added which had been in the water for over a year and used throughout our studies to capture fish. It was colonized with various attaching organisms including mussels, and its attractiveness was obvious since it readily captured fish. The trap added to the other structure was new. Again, at each structure a group of 10 fish each (10-25 cm), captured at Site A, was released. As before, these fish also left the structures, but this time dispersal was slower with the last fish leaving 1 h after release. Although both structures provided cover and one even food, they were apparently not acceptable habitats, lacking some factor or factors sufficient to attract the animals.

DISCUSSION

It was clear from the results of trapping, tagging, and direct underwater observation that some portion of the cunner and young tautog populations dispersed in late spring. The dispersal was from the boat basin (Site A, which we termed a perennial habitat) to habitats that were utilized only seasonally. Once adopting a seasonal habitat, the fish appeared to remain there until fall. Then there was a general movement from these habitats back to a perennial habitat but, as was evident from the capture of tagged fish at perennial sites outside of the study area, not necessarily the one from which they dispersed in the spring. Once arriving at a perennial habitat, the fish remained to over-winter in torpor, not emerging until sometime in early spring when temperature reached 5° to 6°C.

Supporting our findings for seasonal movement, Briggs (1977) found a marked increase in the number of young tautog captured during the fall at the Kismet artificial reef, 6 km from our study area. This increase, we surmise, also reflects the movement of fish from seasonal habitats to one which appears to be perennial.

In attempting to define habitat requirements for both species, it is apparent that cover is a critical factor. During the day when these fish are active, they remain within several meters of cover and at night when quiescent and unresponsive, they are either in, against, or under cover (Olla et al. 1974, 1975). Once becoming torpid in winter, they remain under cover until spring. It seems reasonable to assume that dependence on cover is related to protection from predation. Large adult tautog, not as vulnerable to predation because of their size,

move away sometimes considerable distances, from cover each day to feed (Olla et al. 1974).

With such a strong tendency to remain in proximity to cover, the question arises as to what causes a portion of the population to disperse. It is clear that environmental factors are changing with season as are the requirements of the fish. Both species in the spring have emerged from three to four months of torpor, which has required them to live on stored energy reserves. The need for food arising from winter deprivation, coupled with the increased metabolic requirements resulting from the increase of temperature in late spring, would stimulate feeding and the competition for food.

At least until June, the major dietary component for both species is the mussel, Mytilus edulis (Olla et al. 1975). Thus prior to dispersal competition for food would be both intra- and inter-specific.

The spawning season for cunner also peaks during June (Dew 1976). Thus we can expect that competition for participation in either group spawning (Wicklund 1970) or pair spawning (Pottle and Green manuscript in preparation) would increase. This increase would relate either to participation in gamete release or male territoriality as related to pair spawning. The majority of tautog studied were immature and would generally not be involved in the reproductive competition.

Competition in both species is manifested through aggression (for tautog, Olla and Studholme 1975; Olla et al. 1977, 1978; for cunner, Olla and Bejda unpubl. field and laboratory obs.). The increase in aggression that may occur at the perennial habitat as a result of competition could cause this site to become suboptimal,

at least for some portion of the population. In all probability, the amounts of aggression which would cause dispersal would be related to the seasonally changing carrying capacity of the habitat.

Support for the idea that fish will leave a suboptimal habitat is reflected in the results of the transfer experiments where young tautog left the cement block structures provided for them. Similar results were obtained with juvenile cunner (*Olla unpubl. obs.*). In attempting to examine the mechanism for habitat selection in the manini, *Acanthurus triostegus sandvicensis*, Sale (1969b) performed a series of laboratory experiments and concluded from these that there was a higher intensity of exploratory behavior exhibited when animals were subjected to an inadequate environment. Similarly, it could be concluded that young tautog were showing greater exploratory behavior when they left the experimental cover provided for them. A portion of the fish that disperse will be lost, with the probability of survival decreasing as the amount of time taken to find a suitable habitat increases. Nevertheless, through this mechanism, fish are able to utilize seasonally optimal resources.

The return to perennial habitats from seasonal ones in the fall may also be related to these becoming suboptimal for the fish, but for different reasons than those which caused dispersal in the spring. At habitats which exist only seasonally, as in the case with macroalgae and eel grass beds, the actual cover that these beds provide begins to wane as they start to die back in the fall. Although some sites were structurally

more permanent, such as Site B (the submerged pipe), the animals did not use them as perennial habitats, and the changes which were occurring to render them suboptimal were not obvious. Besides changes in the environment, of prime importance for consideration is the change in the animal's requirements for cover. What served adequately in summer is not adequate for winter.

In observing cunner and young tautog in the field during winter torpor, both species were found in deep recesses and often buried under several millimeters of sand, further under cover than observed during night-time quiescence in summer. This afforded them greater protection during the long winter. The seasonal sites studied did not provide cover equivalent to that at perennial ones, which have numerous deep crevices and holes.

Laboratory studies on adult tautog confirm the change in cover requirements during winter torpor (Olla et al. 1977; Olla and Studholme 1978). As temperature declined, the fish began to show an affinity for those structures which would serve as cover during the winter at least one to two weeks before torpor was observed at which time the fish actually buried under them being almost completely covered by sand. These structures differed from the ones the fish used throughout the rest of the year at night. In the field, the offshore movement of the adults begins 4 to 8 weeks before they would encounter temperatures that would induce torpor, (Olla et al. 1974), indicating a change in habitat requirements with season. About the same time that adult tautog are

moving offshore, cunner and young tautog are moving to perennial sites.

Association with cover is no doubt a strongly motivated behavior for young tautog and cunner, but one for which there is a considerable range of adaptation. Under seasonally changing conditions or when habitats are simply suboptimal as in the transfer experiments, the animals will disperse, leaving cover at the risk of predation until alternate sites are found (as discussed earlier). On the other hand, a closer association results from some transient environmental causes. The presence of predators results in young tautog fleeing to cover (Olla et al. 1974). Similarly, elevated temperature stress also causes young tautog to associate more closely with cover at least under laboratory conditions (Olla and Studholme 1975). This strategy seems appropriate since exposure to naturally occurring elevated temperatures would be of a short duration (Olla and Studholme 1975, 1978).

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TEXT FOOTNOTES

- 1 Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

TABLE 1.- Mean monthly catch of cunner and young tautog at perennial (A) and seasonal (B, C, D and E) Sites (Figure 1).

Month	Mean catch/unit effort ¹			
	Cunner		Tautog	
	Perennial Site	Seasonal Sites	Perennial Site	Seasonal Sites
March	11.0		6.5	
April	36.0		2.7	
May	6.8	9.5	2.5	9.2
June	19.7	8.5	1.3	10.6
July	13.8	5.3	0.6	11.9
August	21.8	6.1	6.2	9.8
September	21.9	2.8	8.6	8.0
October	34.0	3.0	14.9	1.0
November	9.7	0	3.8	0

¹ Unit effort = one trap fished one week.

TABLE 2.- Visual counts using SCUBA or mask and snorkel of
 cunner and young tautog at seasonal Site F (Figure 1).

Date	Total number	
	Cunner	Tautog
February 28	0	0
March 4	0	0
12	0	0
20	0	0
25	0	0
April 2	0	0
29	17	3
May 20	29	11
22	74	20
29	60	15
June 5	65	14
11	79	19
18	10	0
26	69	12
July 2 ¹	53	7
8 ²	165	60
9 ²	93	27
10 ²	89	16
15	107	29
16 ²	42	13
29	44	24
August 12	63	20
13	169	71
September 3	42	7
24	34	6
October 2	0	0
20	0	0
29	0	0

¹ Mean of two counts.

² Mean of three counts.

TABLE 3.- Number and location of recaptures of cunner and young tautog tagged and released at perennial and seasonal sites (Figure 1).

Species	Release site	No. released	Total No. recaptured	No. recaptured at release site	No. recaptured at other sites			
					Spring and summer ¹		Fall ²	
					Perennial sites	Seasonal sites	Perennial sites	Seasonal sites
Cunner	A	875	176	166	5	1	4	0
	B	83	13	7	0	3	3	0
	C	15	0	0	0	0	0	0
	D	54	6	5	0	0	1	0
	E	10	0	0	0	0	0	0
	Total	1,037	195	178	5	4	8	0
Tautog	A	245	25	20	0	1	4	0
	B	283	29	18	0	5	6	0
	C	72	12	11	0	0	1	0
	D	123	3	2	0	0	1	0
	E	41	2	1	0	1	0	0
	Total	764	71	52	0	7	12	0

¹ May-August inclusive.

² September-November inclusive.

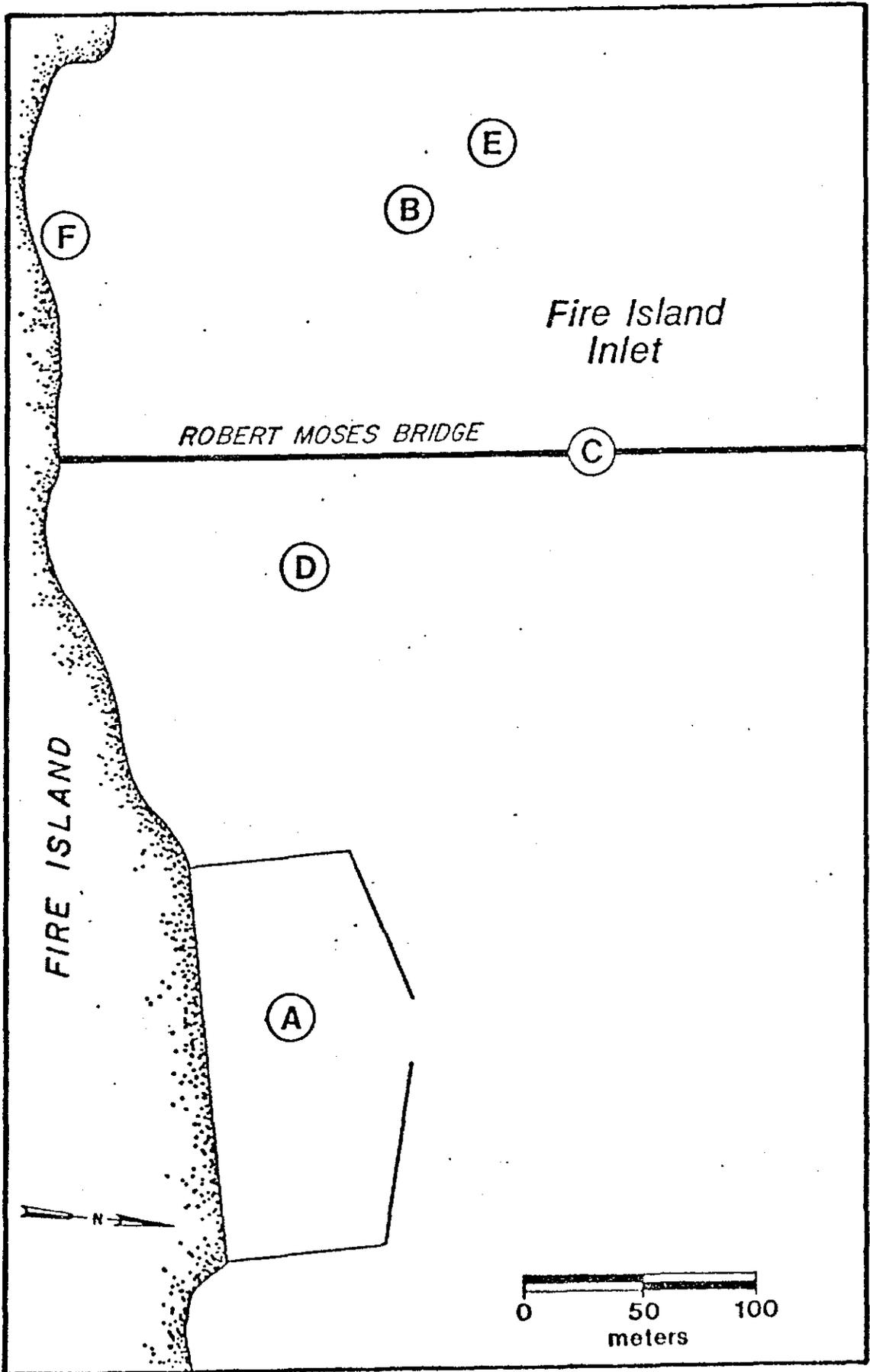
TABLE 4.- Size, capture and release sites (Figure 1), and period monitored for nine young tautog ultrasonically tracked.

Tautog no.	TL (cm)	Capture site	Release site	Tracking duration (h)
1	22.5	A	A	48
2	24.0	A	A	48
3	20.2	F	F	24
4	24.5	B	B	48
5	21.5	A	B	48
6	22.8	A	B	72
7	23.0	A	B	48
8	24.0	A	C	48
9	22.5	A	-1	24

¹ Experimental cover.

LIST OF FIGURES

Figure 1.--Location of study sites A, B, C, D, E, and F within Fire
Island Inlet, N. Y.



v.

Effect of Low Temperature on the Activity and
Distribution of Juvenile Bluefish, Pomatomus
saltatrix.

(Preliminary data report)

INTRODUCTION

Preliminary tests on the responses of young bluefish, Pomatomus saltatrix, showed that in a homeothermal system, when temperature decreased below acclimation within a preferred range, activity increased, indicating avoidance (ERDA Progress Report, 1977). A similar response had been observed previously when juvenile bluefish were subjected to increasing temperature (AEC Progress Report, 1974; Olla et al., 1975). This response, which had also been characteristic of adult bluefish (Olla and Studholme, 1971), was interpreted to reflect the capability of this species to regulate body temperature behaviorally by avoidance (Olla and Studholme, 1975; Olla, et al., 1975, 1978).

This past year, based on the results of our low temperature tests (ERDA Progress Report, 1977), we have continued to investigate the responses of juvenile bluefish to decreases in temperature in a heterothermal situation, i.e., a gradient where a choice is possible. The behavior of the fish in this type of environment differs somewhat from that observed in a homeothermal situation and is important in understanding the strategies the fish possess to deal with changing temperatures in the environment. Results of this type will also be applicable to problems arising at power plant outfalls to which fish may be attracted and subject to lethality.

In this report we are presenting preliminary results from the first 5 tests in this series which constitutes our final year of research on the responses of these fish to temperature. Further testing and data analysis should be completed within the next six months.

MATERIALS AND METHODS

Juvenile bluefish approximately 18-28 cm TL, were caught by hook and line in Sandy Hook Bay during late summer and early fall. These fish were maintained in the laboratory in a 3.2-kiliter fiberglass aquarium in filtered seawater at temperatures ranging from 15° to 20°C and a 12.0-h photoperiod for about 200 days until the first group of five was transferred to the experimental aquarium. During this holding period, all fish were fed at 3 to 4 day intervals on 0.5-g pieces of clam.

Based on the results of last year's preliminary experiments on the response of juvenile bluefish to low temperature (ERDA 1977) modifications were made in the experimental testing facility to allow more detailed analysis of their responses to thermal change.

Experimental System

The tests were conducted in a 1.5-kiliter fiberglass aquarium (2.48 x 0.88 x 0.96 m) with a single viewing window (2.29 x 0.81 m). Filtered seawater, maintained at an average of 20.0°C, was pumped at a rate of 1.5 to 1.9 liters/s into the bottom of the aquarium which was covered by a panel of fiberglass 0.5 cm in thickness. This sheet was perforated with 6-mm diameter openings to provide even distribution of incoming water. Two overflow outlets on opposite sides of the surface of the aquarium returned the water to an external sand, gravel and oyster shell filter during normal operation. (A series of dye studies confirmed that incoming water rose in an even layer across the tank with little variation between trials). Water quality was maintained by the continual addition of small amounts of new seawater with O₂ averaging 7.3 ppm; salinity, 22.2 o/oo and pH 7.2.

Daytime lighting was provided by fluorescent bulbs mounted above the aquarium with light levels averaging 200 ft-c at the water surface. Nighttime illumination of 0.05 ft-c was provided by a 7.5-w incandescent bulb. Photoperiod was held constant at 12 h (0600-1800) for all tests. The aquarium and lighting systems were screened from observers and recording equipment by a fiberboard enclosure with viewing windows.

Temperature was monitored remotely by means of 10 thermistors spaced vertically, 7 to 9 cm apart, along one corner of the aquarium from bottom to surface. During a temperature test, all probes were scanned sequentially every 20 s and temperatures recorded on a strip chart recorder.

To measure distribution of the fish throughout the aquarium during each test, exposures were made every 20 s with a 35-mm time-lapse camera mounted behind the fiberboard screen and focussed on the front of the aquarium. These exposures approximately coincided with the midpoint of each temperature scan. For additional time reference an L.E.D. digital clock (0.01 min) was mounted above the aquarium and included in each picture. Throughout each test, 16-mm motion pictures were made at regular intervals. Frame-by-frame analysis of these films will be made to record the frequency and duration of excursions by the fish into various thermal layers.

At the start of each test, 0° to 2°C water from a thermal exchanger was introduced through the bottom of the aquarium. During this time the overflow from the surface was diverted and not recirculated through the system. Introduction of chilled water was maintained for about 9 to 11 min, depending on the requirements of each test (i.e., until the desired

thermal profile was obtained). For the remainder of the test, normal circulation was discontinued.

At the conclusion of each test, normal circulation of 20°C water was restored, with temperature throughout the aquarium returning to 20°C in about 4 h.

Prior to the first test, a group of 5 bluefish, 23.0 to 28.5 cm TL, 128 to 265 g, was transferred to the experimental aquarium and held for 22 days at 19.6°C (+0.6°; -0.7°C). During this time they were fed in 3 to 4-day intervals using the following procedure: Weighed amounts (approximately 100-125 g) of 0.5-g pieces of clam were introduced, 3 to 4 pieces at a time through a feeding tube at the rear of the aquarium. Amounts ingested were recorded and feeding discontinued when ingestion fell below 100%.

Observations of activity and distribution at acclimation temperatures were begun 14 days after the fish were transferred. Five readings were made each hour (0800 - 1500) of swimming speed (the time for the fish to swim between two points 61 cm apart) with the median used as the hourly speed. In addition the average linear distance between fish (school gap) was estimated as follows:
$$\text{Length of school} - (\text{No. of fish in the school} \times \text{mean fish length}) / (\text{No. of fish} - 1).$$
 Note that in most instances where there is an overlap among the fish, this will be expressed in a negative distance (e.g. -10.0 cm). Horizontal distribution (estimated in height from the bottom using probe placements as indicators) within the aquarium was also recorded following each swimming speed reading. The medians of each set of observations were used for subsequent analysis.

Since the same group of fish were used for all five tests, the measures of activity and feeding recorded between each set of tests were used as the acclimation norms for each test (Table 1).

Test Procedures

As the chilled (0° - 2° C) water was introduced into the bottom of the aquarium, continual 20-s scans of the temperature probes were initiated, synchronized with each time-lapse exposure (see above). Swimming speeds and school gap were also measured approximately every 20 to 30 s. Filmed sequences of 25 ft each were made every 2 to 4 min depending on the nature of the test.

For analysis, temperature scans corresponding with the distribution (mean, range and standard deviation) of the fish, swimming speed and school gap, were averaged over minute intervals.

Test 1

Starting at 10.06 h, on the 23rd day after the fish were transferred to the experimental aquarium and held at 19.6° C, 1.6° C water was pumped into the aquarium at 1.5 liters/s for 9.80 min until the following thermal profile, as measured from bottom to surface, was established: 5.0 cm - 5.7° C; 12.0 cm - 6.9° C; 19.0 cm - 9.6° C; 26.0 cm - 11.2° C; 33.0 cm - 13.2° C; 40.0 cm - 14.3° C; 49.0 cm - 16.3° C; 58.0 cm - 17.4° C; 67.0 cm - 19.0° C; 76.0 cm - 20.0° C (see Fig. 1 for thermal profiles for the remainder of the test). The test was continued for 31 min before normal circulation of 20° C water was restored.

Test 2

Following the return to 20.0°C in Test 1, the group of five fish were held at 20.6° ± 0.2°C for 5 days (Table 1). Starting at 11.32 h on the 6th day, chilled 2.0°C water was pumped into the aquarium at 1.5 liters/s for 9.48 min until the following thermal profile was established: 5.0 cm - 7.2°C; 12.0 cm - 7.3°C; 19.0 cm - 7.9°C; 26.0 cm - 9.9°C; 33.0 cm - 10.3°C; 40.0 cm - 11.8°C; 49.0 cm - 15.7°C; 58.0 cm - 17.7°C; 67.0 cm - 18.4°C; 76.0 cm - 19.2°C (see Fig. 2 for thermal profiles for the remainder of the test). The test was discontinued after 29 min and normal circulation restored.

Test 3

Following completion of Test 2, the fish were held at 20.4° ± 0.3°C for 11 days. Starting at 11.30 h on the 12th day, 0°C water was pumped into the aquarium at 1.75 liters/s for 11.22 min until the following thermal profile was established: 5.0 cm - 5.1°C; 12.0 cm - 5.1°C; 19.0 cm - 5.7°C; 26.0 cm - 7.5°C; 33.0 cm - 8.6°C; 40.0 cm - 11.1°C; 49.0 cm - 15.4°C; 58.0 cm - 17.6°C; 67.0 cm - 19.3°C; 76.0 cm - 20.4°C (see Fig. 3a, b, c, d for thermal profiles for the remainder of the test). After 80 min the test was completed and circulation of 20°C water begun.

Test 4

The fish were held at 19.9° ± 0.3°C for 34 days. Starting at 8.58 h on the 15th day, 0°C water was pumped into the aquarium at 1.9 liters/s for 8.91 min until the following thermal profile was established: 5.0 cm - 1.0°C; 12.0 cm - 1.0°C; 19.0 cm - 1.0°C;

26.0 cm - 1.9°C; 33.0 cm - 5.2°C; 40.0 cm - 11.8°C; 49.0 cm - 16.0°C;
58.0 cm - 17.7°C; 67.0 cm - 18.4°C; 76.0 cm - 18.9°C (see Fig. 4a,b,c,d,e for
thermal profiles for the remainder of the test). Normal circulation
was restored after 90 min.

Test 5

The fish were held at $20.1^{\circ} \pm 0.4^{\circ}\text{C}$ for 17 days. Starting at
11.88 h on the 18th day, 0°C water was pumped into the aquarium at
1.6 liters/s for 10.24 min until the following thermal profile was
established: 5.0 cm - 4.6°C; 12.0 cm - 5.7°C; 19.0 cm - 8.7°C;
26.0 cm - 10.7°C; 33.0 cm - 13.1°C; 40.0 cm - 14.0°C; 49.0 cm - 14.4°C;
58.0 cm - 15.1°C; 67.0 cm - 17.0°C; 76.0-cm 18.6°C (see Fig. 5a, b for
thermal profiles for the remainder of the test). The test was discontinued
after 40 min and normal circulation restored.

RESULTS

Acclimation

Similar to activity patterns exhibited previously by groups of juvenile bluefish held in the laboratory at about 20°C, (AEC Progress Report, 1974; ERDA Progress Report, 1977) during the day the fish would swim parallel to one another in a typical schooling configuration, or as individuals, at average speeds ranging from 13.5 to 19.7 cm/s ($\bar{x} = 17.4$ cm/s) (Table 1). The short-term variation in swimming time (c.v.) ranged from 14.4% to 27.0% ($\bar{x} = 19.1\%$), also comparable to that of earlier groups (AEC Progress Report, 1974). Although no night readings were scheduled for this study, intermittent observations indicated that during the nighttime, activity was reduced, this group exhibiting the typical diurnal rhythm of activity which is characteristic of both young and adult bluefish (Olla and Studholme, 1972, in press).

The average distance between fish (school gap) tended to increase slightly as the fish were held in the aquarium, averaging -13.6 cm prior to the first test and -4.1 cm prior to the fifth one (Table 1).

Observations of distribution within the aquarium during acclimation indicated that the fish were usually swimming within the lower quarter of the water column from about 5-20 cm above the bottom (Table 1) with few excursions to the upper half except during feeding. This distribution pattern was similar to that of juvenile bluefish previously held in this system (ERDA Progress Report, 1977).

Feeding responses of these fish were also generally the same as those of other groups held previously (AEC Progress Report, 1974; ERDA Progress

Report, 1977). When small pieces of clam were introduced through the feeding tube normal patterns of grouping and orientation were disrupted as the fish responded individually, visually orienting toward the food, and increasing activity as they approached and ingested pieces of clam. As the fish became satiated and feeding motivation decreased, normal schooling and activity patterns were resumed. Amounts ingested per fish ranged from 14.5 to 27.2 g/fish ($\bar{x} = 23.1$ g/fish) (Table 1).

Temperature Tests

Test 1

During the first 4 min of introduction of 1.6°C water, the fish maintained their mean distribution between 18° and 20°C, shifting their position upward slightly and increasing activity as they avoided the cold water beneath them (Fig. 1; Table 2).

Although the fish continued to school back and forth across the length of the aquarium, their vertical distribution (as indicated by range lines, Fig. 1) began to increase as they made excursions to sample the water column. An excursion would begin with one or more fish angling the head and body about 45° toward the bottom, then swimming (body parallel to the bottom) into a colder layer for varying periods of time. Then, head and body angled toward the surface, the fish would return to warmer water. Detailed analysis of both the frequency and duration of these excursions as recorded by motion pictures remain to be completed.

For the last 4 min (6 through 9) of introduction of chilled water, although temperatures sampled ranged from 8.1° to 19.6°C, the fish continued to maintain their position in the lower half of the aquarium

in which temperature had decreased to 13.4°-14.7°C (Fig. 1; Table 2). During this initial period of the test, swimming speeds averaged 31.4 cm/s, nearly 62% higher than the mean daily activity of 19.4 cm/s recorded during acclimation at 20°C (Table 1). School gap averaged -10.1 cm, comparable to the mean (-13.6 cm) maintained during acclimation (Table 1).

For the next 4 min (10 through 13) although temperatures above 19°C were still available to the fish, mean distribution was recorded at 13.3°C, in approximately the middle of the water column, with individual fish making excursions into temperatures ranging from 6.9°C to 19.0°C (Fig. 1; Table 2). Although there was a decrease in mean swimming speed (23.9 cm/s), cohesiveness increased significantly as average school gap fell to -20.3 cm.

While the range of temperatures available to the fish remained approximately <6° and >19°C from 14 through 18 min (Table 2) mean distribution temperature rose slightly ($\bar{x} = 15.1^\circ\text{C}$) as the fish shifted their position into the upper third of the water column (Fig. 1), still not selecting the highest temperatures available although continuing to sample >18°C water (Table 2). The lower range of temperatures sampled also rose with no excursions recorded below 12.4°C (Table 2). Speeds were highly variable, ranging from 13.0 to 32.1 cm/s (Fig. 1) as the fish no longer moved continually as a school (school gap increasing to -7.6 cm) but often as individuals making vertical excursions to sample the water column.

By 19 min after the start of the test, there was a significant downward shift in spatial distribution (as well as in temperature to 13.3°C) which seemed to correspond to the expansion of the 12° to 14°C water layer. For the following 12 min, until the test was concluded, mean

distribution temperatures averaged 12.8°C although, at least through 28 min, temperatures 16°C were available and periodically sampled (Fig. 1; Table 2). Lower excursion temperatures ranged from 8.5° to 12.6°C limited in part at the conclusion of the test by the disappearance of temperatures less than 10°C. For min 11 through 24, where water temperatures of at least 10°C were available, the mean lower range sampled was 11.7°C. As the fish remained in 12°-13°C water, activity tended to decrease (Fig. 1) averaging only 16.4 cm/s, while cohesiveness decreased, school gap averaging -13.0 cm, comparable to the pre-test average (Table 1).

Test 2

As had been characteristic of the response of the fish in the first test, during the introduction of chilled 2°C water, the vertical distribution (i.e., range) of the fish began to increase while their position in the water column shifted upwards (Fig. 2). Although temperatures of 19° to 20°C continued to be available for the first 10 min, the temperatures at which mean distribution was recorded, varied but gradually decreased averaging 19.1°C for the first 5 min; 17.4°C for the next 5 min (Fig. 2; Table 3). Excursions recorded during this time indicated that the fish continually sampled the 19°-20°C water at the upper range, and with only 2 exceptions, in which they sampled water of 10.1°C and 10.3°C, did not go below 13°C to 14°C (Fig. 2; Table 3).

As the thermal gradient stabilized within the aquarium (temperatures available ranging from 7.9°C to about 17°C to 18°C for 11 through 17 min; Table 3) mean distribution temperatures continued to decrease (\bar{x} = 15.4°C) as the fish maintained their position in about the upper third of the

water column. During this period there were no excursions recorded into temperatures lower than 10.6°C.

For the first 17 min of the test, as the fish consistently continued to test temperatures differing by more than 5°C, mean swimming speeds were highly variable (c.v. = 35.5%) with activity averaging 23.2 cm/s, about 56% higher than that recorded during the acclimation period prior to the test (14.9 cm/s; Table 1). As had been apparent in Test 1, the increase in activity seemed to occur as the fish shifted distribution within the water column, tending to decrease as the distribution stabilized at somewhat colder temperatures. School gap, however, averaged -12.5 cm, comparable to the -12.7 cm recorded during acclimation (Table 1).

For the remainder of the test (min 18 through 29), temperatures throughout the water column, and correspondingly the range available, began to decrease (Table 3). Mean distribution temperature continued to drop, averaging 14.3°C until min 24, when, as the 12° to 14°C water layer expanded, the fish shifted distribution below 14°C (\bar{x} = 13.2°C; Fig. 2; Table 3). Testing of the water column continued but with only one exception (min 21; 10.2°C) no excursions were recorded below 11.4°-11.5°C. The mean low temperature sampled in this test, from min 11 until the test was completed, was 11.9°C.

As the fish remained in colder temperatures, there was a decrease of about 34% in activity with mean speeds averaging 15.4 cm/s.

It was evident from these first two tests that, as we had observed previously (ERDA Progress Report, 1977) as water temperature began to decrease, the initial response of the fish was to increase activity,

showing an avoidance response as they shifted their distribution in the water column then decreasing. Mean distribution was seldom at the highest temperature available (i.e., the one closest to the acclimation level) and it appeared that the fish had the capability to adapt to a range of temperatures 5° to 7°C below their acclimation level of 20°C since a sustained avoidance response did not occur.

Test 3

Based on the results of Tests 1 and 2 in which 11° to 12°C appeared to be limiting temperatures for the fish with respect to their distribution, the aim in this test was to establish a layer of water less than 12°C throughout the lower half of the aquarium while maintaining the temperature in the upper half at 16°C or higher. This would allow us to determine more accurately the limiting effect of 11° to 12°C and analyze in greater detail the behavior of the fish as they oriented to this particular thermal "edge". Consequently, the thermal profile in this test tended to differ from the first two with the range between bottom and surface temperatures averaging 12.4°C for the first 20 min as compared with 9.8°C for Test 1 and 8.9°C for Test 2 (Table 4).

During the first 10 min of the test, as 0°C water was introduced, the fish shifted their distribution upward in the water column, orienting, to a large extent, to the 20°C isotherm ($\bar{x} = 20.2^\circ\text{C}$) as it moved slowly toward the surface (Fig. 3a; Table 5). Although the time-lapse photographs did not record any excursions into temperatures lower than 14.6°C during this period (Table 5), preliminary analysis of motion pictures made intermittently during this time indicated that very rapid excursions

(lasting approximately 0.9 to 2.3 s) were occurring with 1 or more fish sampling cold temperatures ranging from 6.5° to 12.4°C. During the 0.5 min interval from 11.5 to 12.0 min, 11 excursions were recorded. In one instance, two fish in 17.1°C water, swam through two-thirds of the water column towards the bottom into temperatures of 5.9°C and returned to 17.1°C; one excursion lasting 2.7 s, the second 4.3 s. Fish were also observed making excursions down into the water column where the temperature differential was not as extreme. For example, a fish in 16.8°C water would swim only 8 to 10 cm, enter 13.4°C water and return in 2.5 s.

This type of analysis will be completed for each test in order to describe in greater detail the behavior of the fish to these thermal layers since the variability in their response is not always evident from the analysis of time-lapse pictures.

As compared with swimming speeds recorded during acclimation prior to the test (Table 1), average activity doubled ($\bar{x} = 27.3$ cm/s) for the first 13 min (Fig. 3a). The coefficient of variation, however, was only 22.3%, reflecting the consistent increase in activity as the fish showed sustained avoidance in response to the steadily rising 12°C isotherm. School gap averaged -9.5 cm, as the fish maintained somewhat closer distance than during acclimation (Table 1).

Similar to the responses observed in the first two tests, although water temperatures of 18°C and higher were available for min 16 through 21 (and in fact were included in the range tested by the fish), distribution temperature averaged 16.4°C (Table 5). There appeared to be a change in

the behavior of the fish, however, as they sampled the colder water. One filmed sequence at min 20 showed a fish beginning an excursion in 13.5°C water, entering 11.5°C and, instead of immediately returning to warmer temperatures, swimming, body aligned parallel to the bottom, back and forth along the 11.5°C isotherm. This type of excursion into temperatures of about 11.5° to 12.5°C in which the fish swam along a particular thermal edge for a longer time period (generally >5 s) seemed to become more frequent as the test continued. This is apparent when looking at the average lower ranges sampled during the test. For min 13 through 80, where temperatures of 8.5°C or lower were available, the average lower range was 12.2°C.

Through 34 min, the fish maintained their position in the upper two-thirds of the aquarium, even though water temperature decreased to 14°C (Fig. 3b). Although periodically swimming speed increased as high as 37.0 cm/s, average activity (min 14 through 34) decreased to 19.2 cm/s while cohesiveness continued to increase slightly, school gap averaging -14.4 cm.

As the temperature in the upper 50 cm of the water column began to decrease, and the range available diminished (i.e., became generally homeothermal; Figs. 3b, c, d), the fish consistently utilized only this section of the water column, avoiding the bottom 20-30 cm where water temperatures were below 10°-11°C. Consequently, mean distribution temperatures tended to be less variable, averaging 13.4°C for min 36 through 54; 12.5°C for the remaining 26 min when the test was concluded (Table 5). Activity recorded during these time periods was relatively

stable averaging 23.1 cm/s and 19.2 cm/s respectively. School gap increased from -11.8 to -3.4 cm, as schooling patterns became more variable, the fish becoming less cohesive.

Test 4

As in Test 3, our aim was to establish temperatures below 12.0°C in the lower half of the water column while maintaining warmer temperature in the upper half for as long as possible. In this test water temperatures >18°C were available for 13 min; >16°C for 24 min and >14°C for 45 min (Table 6). The temperature differential (i.e., gradient) in the water column through the first 20 min averaged 15.3°C, the largest established in any test (Table 4).

Typically, as chilled 0°C water was introduced for almost 9 min, the fish shifted their position upward in the water column maintaining mean distribution at 18.9°C (Fig. 4a) while continuing to sample both colder (5.2°C) and warmer (19°-20°C) water temperatures. As expected, activity during this initial shift in distribution, increased, averaging 31.0 cm/s, about 57% higher than levels recorded during the acclimation period prior to the test (Table 1). The mean school gap (-7.9 cm) was close to that recorded during acclimation (-7.3 cm; Table 1).

From min 10 through 18, although temperatures of 17° to 18°C were still available, as we had observed in the previous tests, distribution was not recorded in the warmest water available but at 16.1°C (Fig. 4a; Table 6). The lower range sampled averaged 11.9°C, only 0.4°C lower than the mean lower range of 12.3°C recorded for the test from min 10 through 90. This continued to confirm that 11.5° to 12.5°C temperatures

did constitute an important lower thermal behavioral limit. While from the preliminary analysis of the motion pictures it is evident that the fish do make excursions into water $<11.0^{\circ}\text{C}$, it does appear that these temperatures do represent a type of thermal edge which limits normal distribution. The continued sampling and attraction to this particular thermal layer in each of the tests, plus the apparent lack of any sustained distribution at temperatures lower than $11^{\circ}\text{-}12^{\circ}\text{C}$, is further indication of its importance.

While, generally, temperatures of $15^{\circ}\text{-}16^{\circ}\text{C}$ continued to be available in the upper third of the water column (Fig. 4b) the position of the fish was relatively stable through min 35 with mean distribution temperature (min 19-35) averaging 14.9°C . Activity decreased, averaging 20.9 cm/s but was still variable as the fish continued to sample temperatures from about 12°C to $15^{\circ}\text{-}16^{\circ}\text{C}$ (Fig. 4b; Table 6). By min 36 to 38, however, apparently corresponding to the expansion of 12°C to 14°C water, the fish shifted their position slightly downward in the water column and through min 55, mean distribution averaged 13.5°C (Table 6) with the fish primarily utilizing the top half of the water column (Fig. 4b, c). Swimming speed decreased to 19.6 cm/s while school gap remained at -7.6 cm.

For the remaining 35 min of this test, as water temperatures within the upper 50 cm of the water column became generally homeothermal (Fig 4d,e), mean distribution temperature averaged 12.4°C with activity remaining stable at 19.9 cm/s. The limiting nature of $11^{\circ}\text{-}12^{\circ}\text{C}$ water is clearly evidenced in this last section of the test, where, with one exception, (min 60, 10.8°C) no excursions were recorded below 11.4°C .

Test 5

During the first 5 min as 0°C water was introduced, the fish steadily increased activity, averaging 34.1 cm/s as they shifted distribution and followed the 18° to 20°C isotherm toward the surface (Fig. 5a). While activity increased by 42% as compared with acclimation levels, school gap decreased slightly averaging -9.7 cm as compared with a mean gap of -4.1 cm recorded prior to the test (Table 1).

At min 6, the fish moved down into 16°C water, although they continued to test nearly the entire water column with temperatures ranging from 9.0° to 19.4°C (Fig. 5a; Table 7).

For 7 through 18 min, although temperatures >17.5°C were available, distribution temperatures continued to decrease, averaging 14.5°C (Table 7). This is in contrast with Test 4 in which the fish maintained their position at temperatures >17.0°C for 18 min.

It appears from these tests that distribution within particular temperature ranges (which are not stressful) may, in fact, be related to the nature of the gradient established. In Tests 3 and 4, for the first 20 min, the gradients established were larger (12.4° and 15.3°C) and the 12°C isotherm higher in the water column (32.9 cm and 34.8 cm) than in Tests 1, 2 and 5 (Table 4). Correspondingly mean distribution temperatures (18.9°C and 17.3°C) as well as height in the water column (49.9 cm and 51.9 cm) were higher for these two tests (Table 4).

For min 12 through 21, where temperatures <10°C were still available, the mean lower range was 12.7°C, slightly higher than any previous test.

It should be noted, however, that the "cold" layer (i.e., $<12.0^{\circ}\text{C}$) never comprised more than the lower quarter of the water column.

As the mean and range in water temperature within the aquarium decreased, mean distribution temperature also decreased averaging 13.4°C for min 19 through 30; 12.8°C for min 31 through 40 (Table 7).

Similar to the previous tests, as the fish remained in colder water, activity decreased, averaging 24.5 cm/s at $12.8^{\circ}\text{--}13.0^{\circ}\text{C}$ (Fig. 5b). Inter-fish distance increased until school gap again measured -3.9 cm, comparable to acclimation (Table 1).

For the last 16 min of the test (25 through 40) with the range of temperatures in the aquarium continuing to diminish, the fish shifted distribution towards the bottom and tested the entire water column from bottom to surface in what was primarily a homeothermal system (Fig. 5b). This was the same behavior exhibited in previous tests last year where fish utilized the entire water column at 12.7°C when the gradient between surface and bottom was only 0.3°C (ERDA Progress Report, 1977).

DISCUSSION

The initial upward shift in distribution and corresponding increase in activity by juvenile bluefish as temperatures beneath them began to decrease were similar to the responses exhibited in previous tests in a heterothermal environment, i.e., a gradient where choice of temperatures was available (ERDA Progress Report, 1977). As the fish sampled the water column, apparently sensing the change, they would exhibit avoidance by increasing activity and shifting distribution, then decreasing activity as the temperature stabilized above 12°C. We had previously found that, when the temperatures reached stress levels (11°-12°C) throughout the water column (i.e., a homeothermal environment) and avoidance was not possible, increased activity would be sustained as the fish attempted to escape (ERDA Progress Report, 1977). Adult bluefish had shown a similar response as temperatures departed either upward or downward from preferred levels and no avoidance was possible (Olla and Studholme, 1971). We interpreted this response to reflect the ability of this species to regulate body temperature behaviorally by avoidance, i. e., behavioral thermo regulation (ERDA Progress Report, 1977; Olla and Studholme, 1975, in press; Olla et al., 1975, 1978).

Although the fish actively avoided the colder water layers, nevertheless, they did not maintain their position in the warmest water available, i.e., closest to their acclimation level. This, plus the variation in mean distribution temperatures among the tests suggests that the fish are not selecting a specific preferred temperature but rather are regulating their distribution within a non-critical range, with the 11° to 12°C

serving as the limiting temperature. This was similar to the lower limit established in the preliminary test series (ERDA Progress Report, 1977).

The upper limit of this range would appear to be about 27°-31°C based on the increase in activity (i.e., avoidance) exhibited by juveniles at these temperatures in previous tests (AEC Progress Report, 1974). It is probable, therefore, that distribution in the environment would generally be within these limits, with peak abundance in a middle range of about 15°-25°C. Although little information is available on juvenile bluefish distribution, Kendall (pers. comm.) reports that in April and May off Cape Hatteras, all juveniles sampled were taken at temperatures 13°-15°C; in June, most were found at temperatures above 18°C and in the fall, at 15°-17°C. Oven (1957) states that in the Black Sea, juvenile bluefish come inshore at 18° to 24.5°C and begin to leave when temperatures drop to 13° to 15°C in the fall. Adult bluefish distribution also appears to be within this temperature range. In the spring as water warms to 12° to 15°C they appear along the Middle Atlantic and New England coast, departing in the fall at 13° to 15°C (Lund and Maltezos, 1970). Peak abundance occurs at 18° to 22°C (Walford, unpublished).

During the shifts in distribution, the fish continued to sample the water column with the lower range in this series of tests averaging 11.7°-12.7°C. The continuous sampling (i.e., orientation) to those temperatures which are critical may be important in providing a spatial reference point as to the limits of the preferred environment. It can be hypothesized that a similar orientation to and sampling of temperatures would occur at the upper range (27°-31°C) in a heterothermal environment with distribution

not at any one preferred temperature but varying within the non-critical range depending on the nature of the gradient.

In the natural environment, species such as bluefish which are influenced in their distribution by temperature, food and undoubtedly other environmental parameters, are likely to encounter this type of edge or discontinuity, with gradients of 10°C not uncommon (Norcross et al., 1974). Although generally the distribution of the fish may be limited by 11°-12°C water, they obviously have the capability to move through temperature gradients of 10°-12°C (possibly to feed) even though temperatures encountered would be stressful and potentially lethal if exposure were prolonged.

Attraction of fish to discontinuities in temperature in the environment has been indicated by Neill (1976; as cited in Laurs and Lynn, 1977). Using a computer simulation model, he maintains that when large expanses of isothermal water are separated by narrow thermal discontinuities that the fish will tend to concentrate along these fronts.

As we had pointed out in the Discussion in last year's Report (ERDA Progress Report, 1977), young bluefish, instead of departing in the fall when temperatures begin to decrease, may remain in the warmer waters surrounding power plant outfalls, attracted by, in many cases, an abundance of forage species. Based on our findings it appears that by the time temperatures fall below 11°-12°C an effective thermal barrier would have been established and the fish "trapped" for the winter. This type of situation has been observed with young bluefish (Silverman, 1972). When a combination of wind and tides resulted in a decrease in outfall temperatures,

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TABLE 1. Activity (swimming speed), distance between fish (school gap) feeding and vertical distribution for juvenile bluefish, Pomatomus saltatrix, recorded during acclimation periods prior to each test.

Test	Days Held	Mean Holding Temperature (°C)	Mean Speed (cm/s)	Mean School Gap (cm)	Mean Amounts Ingested (g/fish)	Distribution Height (cm)
1	23	19.6	19.4	-13.6	14.5	5-16.6
2	5	20.6	14.9	-12.7	25.0	5-21.3
3	11	20.4	13.5	- 7.3	22.8	5-11.3
4	34	19.9	19.7	- 7.2	27.2	5-19.4
5	17	20.1	19.7	- 4.1	26.1	5-20.8

TABLE 2. Distribution (mean and range) with respect to temperature for juvenile bluefish, Pomatomus saltatrix, and temperatures available within the aquarium, averaged for 1-min intervals, in Test 1.

Time (min)	Distribution		Temp. available	Time (min)	Distribution		Temp. available
	Mean (°C)	Range (°C)	Range (°C)		Mean (°C)	Range (°C)	Range (°C)
1	20.0	20.0 - 20.1	20.0 - 20.2	17	15.3	13.3 - 18.1	8.0 - 18.1
2	19.0	18.9 - 19.5	18.9 - 20.2	18	15.0	12.4 - 18.6	6.5 - 18.6
3	18.0	17.6 - 18.8	17.6 - 20.2	19	13.3	12.6 - 15.5	7.8 - 18.7
4	18.0	16.5 - 20.0	16.5 - 20.2	20	12.5	10.9 - 13.9	6.2 - 17.4
5	16.5	13.1 - 18.1	13.1 - 20.2	21	12.7	8.5 - 14.1	8.5 - 17.6
6	14.7	9.5 - 18.5	9.5 - 20.2	22	13.2	11.2 - 16.3	9.4 - 16.3
7	13.4	8.1 - 16.6	8.1 - 20.2	23	11.9	11.0 - 13.8	10.6 - 16.8
8	13.4	9.1 - 18.1	6.9 - 20.2	24	13.3	12.2 - 18.0	9.1 - 18.0
9	14.6	12.0 - 19.6	7.6 - 20.2	25	13.4	12.4 - 16.6	11.1 - 16.6
10	13.2	6.9 - 19.0	6.3 - 20.2	26	13.0	11.5 - 17.7	10.6 - 17.7
11	13.8	10.4 - 15.2	5.7 - 19.7	27	12.4	11.4 - 13.2	10.8 - 17.1
12	12.7	9.7 - 18.6	6.9 - 19.8	28	12.7	11.8 - 13.5	11.5 - 16.3
13	13.7	11.4 - 18.1	7.8 - 19.4	29	12.9	12.3 - 14.7	11.0 - 14.7
14	14.9	12.9 - 19.6	6.6 - 19.6	30	12.8	12.0 - 13.5	11.8 - 13.5
15	15.3	13.3 - 18.8	6.3 - 18.8	31	12.8	12.4 - 14.6	12.0 - 14.6
16	15.0	14.4 - 18.1	7.3 - 18.1				

1/ Water inflow was discontinued between minutes 9 and 10.

TABLE 3. Distribution (mean and range) with respect to temperature for juvenile bluefish, Pomatomus saltatrix, and temperatures available within the aquarium, averaged for 1-min intervals, in Test 2.

Time (min)	Distribution		Temp. available	Time	Distribution		Temp. available
	Mean (°C)	Range (°C)	Range (°C)		Mean (°C)	Range (°C)	Range (°C)
1	20.3	20.3 - 20.5	20.3 - 20.6	16	15.3	12.0 - 17.2	7.9 - 17.2
2	18.8	17.6 - 20.1	17.6 - 20.5	17	15.0	12.5 - 17.2	7.8 - 17.2
3	18.9	15.4 - 20.5	15.4 - 20.6	18	14.6	12.5 - 16.7	7.9 - 16.7
4	19.4	18.9 - 20.2	11.7 - 20.6	19	14.7	11.7 - 16.1	7.9 - 16.1
5	18.2	15.1 - 20.5	11.3 - 20.6	20	14.4	13.0 - 16.2	8.2 - 16.2
6	17.9	10.1 - 20.6	10.1 - 20.6	21	13.6	10.2 - 16.1	8.3 - 16.1
7	18.6	14.0 - 19.9	9.3 - 19.9	22	14.0	11.5 - 15.9	8.3 - 15.9
8	16.7	14.3 - 19.9	7.6 - 19.9	23	14.7	13.1 - 16.3	8.3 - 16.3
9	17.7	13.2 - 19.8	7.6 - 19.8	24	13.4	12.1 - 16.1	8.8 - 16.1
10	^{1/} 16.2	10.3 - 19.2	7.1 - 19.2	25	13.6	12.2 - 15.9	8.1 - 15.9
11	17.0	13.0 - 18.9	7.9 - 18.9	26	13.0	11.4 - 15.8	8.9 - 15.8
12	15.1	10.6 - 18.2	7.9 - 18.2	27	13.0	11.9 - 15.9	8.9 - 15.9
13	15.3	10.6 - 18.2	7.9 - 18.2	28	12.7	12.2 - 15.4	9.0 - 15.4
14	16.5	12.5 - 17.8	7.9 - 17.8	29	13.5	12.4 - 15.2	9.0 - 15.2
15	13.3	10.6 - 16.8	7.9 - 17.7				

^{1/} Water inflow was discontinued between minutes 9 and 10.

TABLE 4. Distribution of juvenile bluefish, Pomatomus saltatrix, with respect to height in the water column and temperature; corresponding temperature gradient and position of the 12°C isotherm averaged for the first 20 min of each test in Tests 1-5.

Test	Mean distribution		Gradient (°C)	12°C isotherm height (cm)
	Height (cm)	Temperature (°C)		
1	35.2	15.1	9.8	26.0
2	47.0	16.7	8.9	30.4
3	49.9	18.9	12.4	32.9
4	51.9	17.3	15.3	34.8
5	42.0	15.6	9.6	20.8

TABLE 5. Distribution (mean and range) with respect to temperature for juvenile bluefish, Pomatomus saltatrix, and temperatures available within the aquarium, averaged for 1-min intervals, in Test 3.

Time (min)	Distribution		Temp. available	Time (min)	Distribution		Temp. available
	Mean (°C)	Range (°C)	Range (°C)		Mean (°C)	Range (°C)	Range (°C)
1	20.7	20.7 - 20.8	20.7 - 21.0	21	15.9	11.3 - 18.1	5.6 - 18.1
2	20.6	18.4 - 20.9	18.0 - 21.0	22	16.2	11.6 - 17.9	5.5 - 17.9
3	20.1	18.8 - 20.8	13.1 - 20.9	23	14.2	11.7 - 15.8	5.5 - 17.1
4	20.4	19.0 - 20.7	8.7 - 20.8	24	15.3	12.1 - 17.2	5.6 - 17.2
5	20.4	17.6 - 20.7	7.8 - 20.8	25	15.7	10.5 - 17.4	5.6 - 17.4
6	20.1	18.7 - 20.7	6.8 - 20.8	26	16.3	11.5 - 17.2	5.5 - 17.2
7	20.1	18.9 - 20.7	5.9 - 20.7	27	15.4	12.8 - 16.9	5.6 - 16.9
8	19.9	16.3 - 20.3	5.9 - 20.3	28	13.9	12.5 - 16.6	5.7 - 16.6
9	19.9	14.6 - 20.4	5.8 - 20.4	29	15.3	13.2 - 16.2	5.8 - 16.2
10	19.9	14.6 - 20.4	5.2 - 20.4	30	15.5	13.8 - 16.4	5.8 - 16.4
11	18.9	9.7 - 20.4	4.6 - 20.4	31	14.8	13.7 - 15.7	5.9 - 15.7
12 ^{1/}	19.7	17.6 - 20.4	5.1 - 20.4	32	14.7	12.3 - 15.9	5.9 - 15.9
13	18.3	10.0 - 20.4	5.0 - 20.4	33	14.6	13.5 - 15.7	6.0 - 15.7
14	18.2	14.2 - 19.2	4.7 - 19.2	34	14.9	13.5 - 15.1	6.0 - 15.1
15	18.1	10.5 - 19.1	4.9 - 19.1	35	14.5	13.0 - 15.1	6.2 - 15.1
16	17.5	10.5 - 18.8	5.1 - 18.8	36	13.5	9.8 - 15.0	6.3 - 15.1
17	15.6	12.1 - 18.7	5.3 - 18.7	37	13.3	12.9 - 14.7	6.3 - 15.0
18	15.5	12.4 - 18.5	5.3 - 18.5	38	13.8	10.9 - 14.9	6.3 - 14.9
19	17.2	13.6 - 18.1	5.5 - 18.1	39	13.4	12.6 - 14.5	6.5 - 14.5
20	17.0	11.2 - 18.1	5.6 - 18.1	40	13.4	12.2 - 14.4	5.9 - 14.4

^{1/} Water inflow was discontinued between minutes 11 and 12.

TABLE 5. (Continued)

Time (min)	Distribution		Temp. available	Time (min)	Distribution		Temp. available
	Mean (°C)	Range (°C)	Range (°C)		Mean (°C)	Range (°C)	Range (°C)
41	13.7	12.2 - 14.5	6.0 - 14.5	61	12.7	12.4 - 12.8	6.5 - 12.8
42	13.9	12.5 - 14.4	6.0 - 14.4	62	12.7	12.4 - 12.8	6.6 - 12.8
43	13.8	12.7 - 14.2	6.0 - 14.2	63	12.7	12.3 - 12.7	6.9 - 12.7
44	13.6	11.4 - 14.1	6.1 - 14.1	64	12.5	12.1 - 12.6	8.2 - 12.6
45	13.3	12.4 - 14.1	6.4 - 14.1	65	12.4	12.1 - 12.6	7.0 - 12.6
46	13.4	12.4 - 13.7	6.8 - 13.7	66	12.5	12.2 - 12.5	7.0 - 12.5
47	13.3	12.4 - 13.7	6.5 - 13.7	67	12.4	12.2 - 12.5	7.0 - 12.5
48	13.4	12.4 - 13.7	6.7 - 13.7	68	12.5	12.1 - 12.5	7.0 - 12.5
49	13.3	12.4 - 13.5	6.4 - 13.5	69	12.5	12.2 - 12.5	7.0 - 12.5
50	13.1	12.4 - 13.4	6.5 - 13.4	70	12.4	11.7 - 12.5	7.1 - 12.5
51	13.0	12.5 - 13.4	6.5 - 13.4	71	12.4	12.2 - 12.4	7.2 - 12.4
52	13.0	12.3 - 13.3	6.5 - 13.3	72	12.3	11.6 - 12.4	8.2 - 12.4
53	13.1	12.6 - 13.3	6.5 - 13.3	73	12.2	11.9 - 12.4	7.8 - 12.4
54	13.0	12.4 - 13.2	6.5 - 13.2	74	12.2	12.0 - 12.3	7.7 - 12.3
55	12.8	12.5 - 13.1	6.9 - 13.1	75	12.3	12.0 - 12.3	8.0 - 12.3
56	12.7	12.3 - 12.9	6.8 - 12.9	76	12.2	11.7 - 12.3	7.8 - 12.3
57	12.8	12.6 - 12.8	6.8 - 12.8	77	12.2	12.0 - 12.2	7.8 - 12.2
58	12.7	12.4 - 12.8	6.9 - 12.8	78	12.2	12.0 - 12.2	7.6 - 12.2
59	12.7	12.6 - 12.8	6.8 - 12.8	79	12.2	12.0 - 12.2	8.1 - 12.2
60	12.8	12.3 - 12.8	6.7 - 12.8	80	12.2	12.2 - 12.2	8.5 - 12.2

TABLE 6. Distribution (mean and range) with respect to temperature for juvenile bluefish, Pomatomus salatrix, and temperatures available within the aquarium, averaged for 1-min intervals in Test 4.

Time (min)	Distribution		Temp. available	Time (min)	Distribution		Temp. available
	Mean (°C)	Range (°C)	Range (°C)		Mean (°C)	Range (°C)	Range (°C)
1	20.0	20.0 - 20.1	20.0 - 20.1	21	15.2	13.8 - 17.0	1.0 - 17.0
2	19.7	15.6 - 20.1	15.6 - 20.1	22	15.7	14.2 - 16.8	1.0 - 16.8
3	19.7	18.3 - 19.9	7.9 - 20.0	23	15.9	15.0 - 16.4	1.0 - 16.4
4	18.9	15.9 - 19.8	3.9 - 20.0	24	15.0	12.6 - 16.2	1.0 - 16.2
5	19.1	10.4 - 19.9	2.8 - 19.9	25	14.8	12.6 - 15.9	1.0 - 15.9
6	18.5	13.6 - 19.9	2.3 - 19.9	26	14.7	13.0 - 15.9	1.0 - 15.9
7	18.4	17.1 - 19.4	1.4 - 19.4	27	14.3	13.9 - 15.7	1.0 - 15.7
8	18.0	15.3 - 19.6	1.2 - 19.6	28	15.0	13.9 - 15.4	1.0 - 15.4
9 ^{1/}	17.8	5.2 - 18.9	1.0 - 18.9	29	14.8	13.4 - 15.7	1.0 - 15.7
10	16.7	11.0 - 18.5	0.9 - 18.5	30	14.9	13.7 - 15.4	1.0 - 15.4
11	17.1	14.7 - 18.5	0.8 - 18.5	31	14.6	12.8 - 15.2	1.0 - 15.2
12	16.8	15.0 - 18.3	0.8 - 18.3	32	14.6	13.1 - 15.1	1.0 - 15.1
13	15.6	5.5 - 18.3	0.8 - 18.3	33	14.1	11.9 - 15.1	1.0 - 15.1
14	15.9	11.4 - 17.9	0.9 - 17.9	34	14.4	12.0 - 14.8	1.0 - 14.8
15	15.9	12.0 - 17.6	0.9 - 17.6	35	14.2	12.9 - 14.7	1.0 - 14.7
16	16.1	14.3 - 17.7	0.9 - 17.7	36	13.4	12.5 - 14.2	1.0 - 14.5
17	16.0	11.4 - 17.3	0.9 - 17.3	37	14.4	13.3 - 14.6	1.0 - 14.6
18	15.3	12.0 - 17.3	1.0 - 17.3	38	13.9	13.4 - 14.4	1.0 - 14.5
19	15.7	12.9 - 16.7	1.0 - 16.7	39	13.4	6.4 - 14.4	1.0 - 14.4
20	15.0	12.2 - 16.6	1.0 - 16.6	40	13.5	12.3 - 14.1	1.0 - 14.3

^{1/} Water inflow was discontinued between minutes 8 and 9.

TABLE 6. (Continued)

Time (min)	Distribution		Temp. available	Time (min)	Distribution		Temp. available
	Mean (°C)	Range (°C)	Range (°C)		Mean (°C)	Range (°C)	Range (°C)
41	13.6	6.4 - 14.2	1.0 - 14.2	61	12.7	12.2 - 13.1	1.4 - 13.1
42	13.8	13.3 - 14.1	1.0 - 14.1	62	12.8	12.6 - 12.9	1.4 - 13.1
43	13.9	12.4 - 14.1	1.1 - 14.1	63	12.7	12.4 - 13.1	1.4 - 13.1
44	13.6	12.2 - 14.1	1.1 - 14.1	64	12.7	12.5 - 12.9	1.4 - 12.9
45	13.6	12.9 - 14.1	1.1 - 14.1	65	12.6	12.3 - 12.9	1.4 - 12.9
46	13.4	12.9 - 13.8	1.2 - 13.8	66	12.7	12.4 - 12.9	1.5 - 12.9
47	13.3	13.1 - 13.7	1.2 - 13.7	67	12.6	12.3 - 12.9	1.5 - 12.9
48	13.4	13.0 - 13.6	1.2 - 13.6	68	12.6	11.8 - 12.9	1.5 - 12.9
49	13.2	12.7 - 13.6	1.2 - 13.6	69	12.4	12.3 - 12.7	1.5 - 12.7
50	13.5	12.4 - 13.7	1.2 - 13.7	70	12.4	12.3 - 12.7	1.5 - 12.7
51	13.2	12.6 - 13.6	1.2 - 13.6	71	12.5	12.2 - 12.7	1.5 - 12.7
52	13.1	12.6 - 13.4	1.3 - 13.4	72	12.5	12.1 - 12.7	1.5 - 12.7
53	13.2	12.9 - 13.4	1.3 - 13.4	73	12.4	12.1 - 12.7	1.5 - 12.7
54	13.1	12.8 - 13.3	1.3 - 13.4	74	12.4	12.1 - 12.7	1.5 - 12.7
55	13.1	12.3 - 13.4	1.4 - 13.4	75	12.4	12.1 - 12.6	1.5 - 12.6
56	12.7	11.3 - 13.2	1.4 - 13.3	76	12.2	12.0 - 12.4	1.5 - 12.5
57	12.9	12.3 - 13.2	1.4 - 13.2	77	12.3	12.0 - 12.4	1.6 - 12.4
58	12.9	12.6 - 13.2	1.4 - 13.2	78	12.3	12.2 - 12.4	1.6 - 12.4
59	12.8	12.6 - 12.9	1.4 - 13.2	79	12.2	11.4 - 12.4	1.6 - 12.4
60	12.7	10.8 - 12.9	1.4 - 13.2	80	12.2	12.1 - 12.4	1.6 - 12.4

TABLE 6. (Continued)

Time (min)	Distribution		Temp. available
	Mean (°C)	Range (°C)	Range (°C)
81	12.1	11.9 - 12.2	1.6 - 12.3
82	12.1	11.9 - 12.4	1.6 - 12.4
83	12.2	11.9 - 12.4	1.6 - 12.4
84	12.1	11.9 - 12.3	1.6 - 12.3
85	12.1	11.9 - 12.3	1.6 - 12.3
86	12.1	11.9 - 12.2	1.6 - 12.2
87	12.1	11.7 - 12.2	1.6 - 12.2
88	11.9	11.7 - 12.1	1.6 - 12.1
89	11.9	11.8 - 12.1	1.6 - 12.1
90	11.9	11.9 - 12.1	1.6 - 12.1

TABLE 7. Distribution (mean and range) with respect to temperature for juvenile bluefish, Pomatomus saltatrix, and temperatures available within the aquarium, averaged for 1-min intervals in Test 5.

Time (min)	Distribution		Temp. available	Time	Distribution		Temp. available
	Mean (°C)	Range (°C)	Range (°C)		Mean (°C)	Range (°C)	Range (°C)
1	19.8	19.8 - 19.8	19.8 - 20.0	21	13.7	13.2 - 15.5	9.9 - 15.5
2	18.9	18.7 - 19.4	18.0 - 19.9	22	13.7	13.3 - 14.2	10.7 - 14.2
3	18.6	17.2 - 19.1	17.2 - 19.7	23	13.5	12.9 - 14.2	10.9 - 14.2
4	17.9	16.0 - 19.2	13.2 - 19.8	24	13.3	12.9 - 14.2	11.6 - 14.2
5	18.3	15.9 - 19.8	12.4 - 19.9	25	13.3	13.1 - 13.6	12.2 - 13.6
6	16.3	9.0 - 19.4	8.9 - 19.6	26	13.2	12.7 - 13.6	12.4 - 13.6
7	14.6	9.4 - 19.7	9.0 - 19.7	27	13.1	12.6 - 13.6	12.6 - 13.6
8	15.6	11.4 - 19.0	7.4 - 19.1	28	13.1	12.7 - 13.4	12.7 - 13.4
9	14.5	10.5 - 17.2	3.6 - 19.1	29	13.1	12.7 - 13.4	12.7 - 13.4
10	15.1	13.2 - 18.8	3.9 - 18.8	30	13.0	12.9 - 13.4	12.7 - 13.4
11 ^{1/}	14.6	10.7 - 18.6	4.6 - 18.6	31	12.9	12.7 - 13.3	12.7 - 13.3
12	14.9	11.7 - 18.8	5.4 - 18.8	32	12.9	12.6 - 13.2	12.6 - 13.2
13	14.8	12.1 - 18.1	4.1 - 18.1	33	12.9	12.6 - 13.2	12.6 - 13.2
14	13.9	12.6 - 18.7	5.4 - 18.7	34	12.8	12.6 - 12.9	12.6 - 13.2
15	13.9	12.3 - 16.3	7.3 - 18.7	35	12.8	12.6 - 12.9	12.6 - 13.1
16	13.9	12.4 - 17.9	8.4 - 17.9	36	12.8	12.6 - 13.1	12.6 - 13.1
17	13.9	13.1 - 17.6	6.3 - 17.6	37	12.7	12.6 - 12.8	12.6 - 13.1
18	14.1	13.5 - 17.7	8.5 - 17.7	38	12.7	12.6 - 13.1	12.6 - 13.1
19	14.2	13.3 - 16.3	9.6 - 16.3	39	12.7	12.6 - 13.1	12.5 - 13.1
20	13.8	13.2 - 15.1	7.4 - 15.1	40	12.8	12.6 - 13.1	12.6 - 13.1

^{1/} Water inflow was discontinued between minutes 10 and 11.

LIST OF FIGURES

- Figure 1. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 1. Water inflow was discontinued between minutes 9 and 10.
- Figure 2. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 2. Water inflow was discontinued between minutes 9 and 10.
- Figure 3. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 3. a) Minutes 1-20; b) Minutes 21-40; c) Minutes 41-60; d) Minutes 61-80. Water inflow was discontinued between minutes 11 and 12.
- Figure 4. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 4: a) Minutes 1-20; b) Minutes 21-40; c) Minutes 41-60; d) Minutes 61-80; e) Minutes 81-90. Water inflow was discontinued between minutes 8 and 9.
- Figure 5. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 5: a) Minutes 1-20; b) Minutes 21-40. Water inflow was discontinued between minutes 10 and 11.

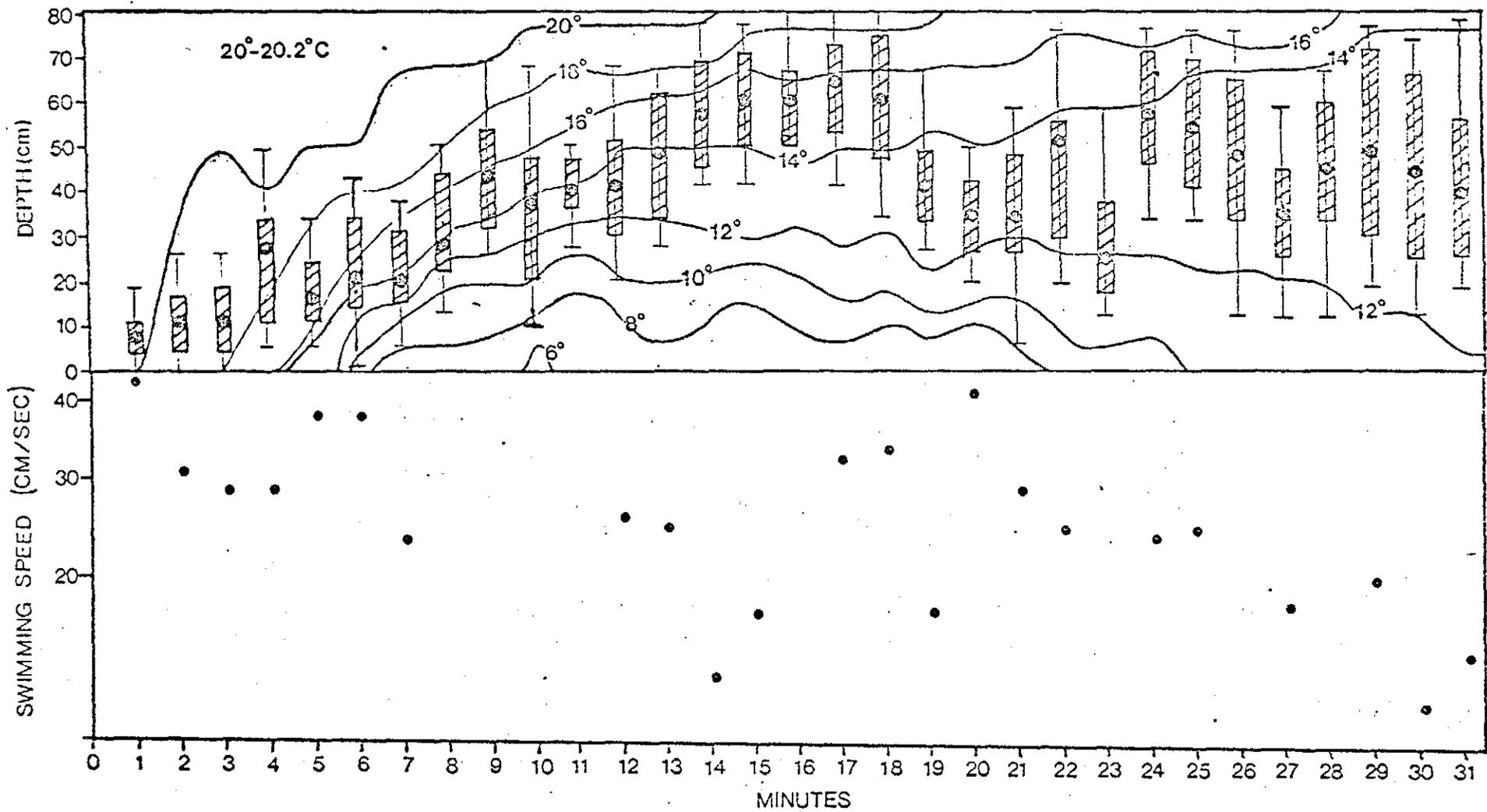


Figure 1. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 1. Water inflow was discontinued between minutes 9 and 10.

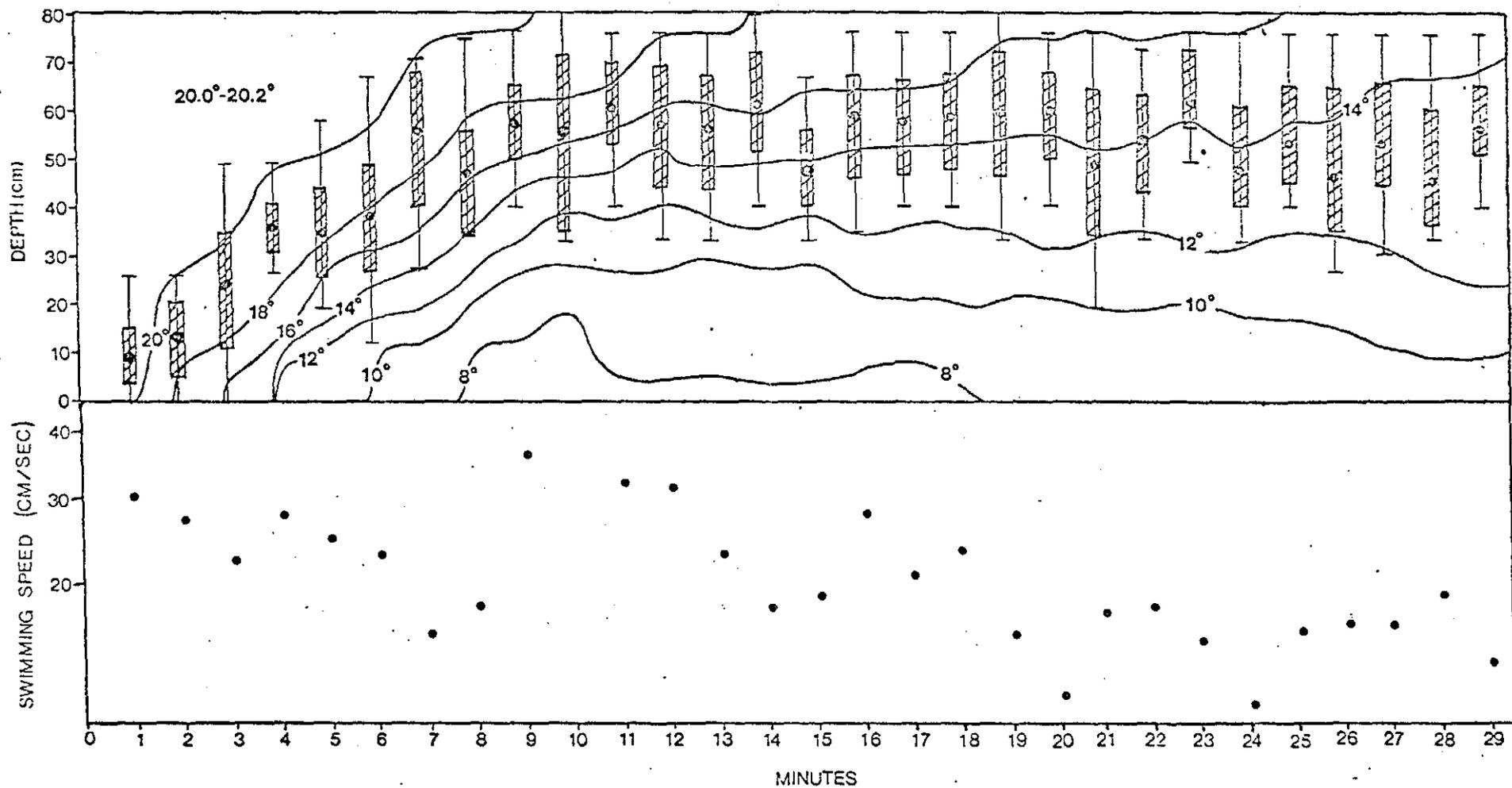


Figure 2. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 2. Water inflow was discontinued between minutes 9 and 10.

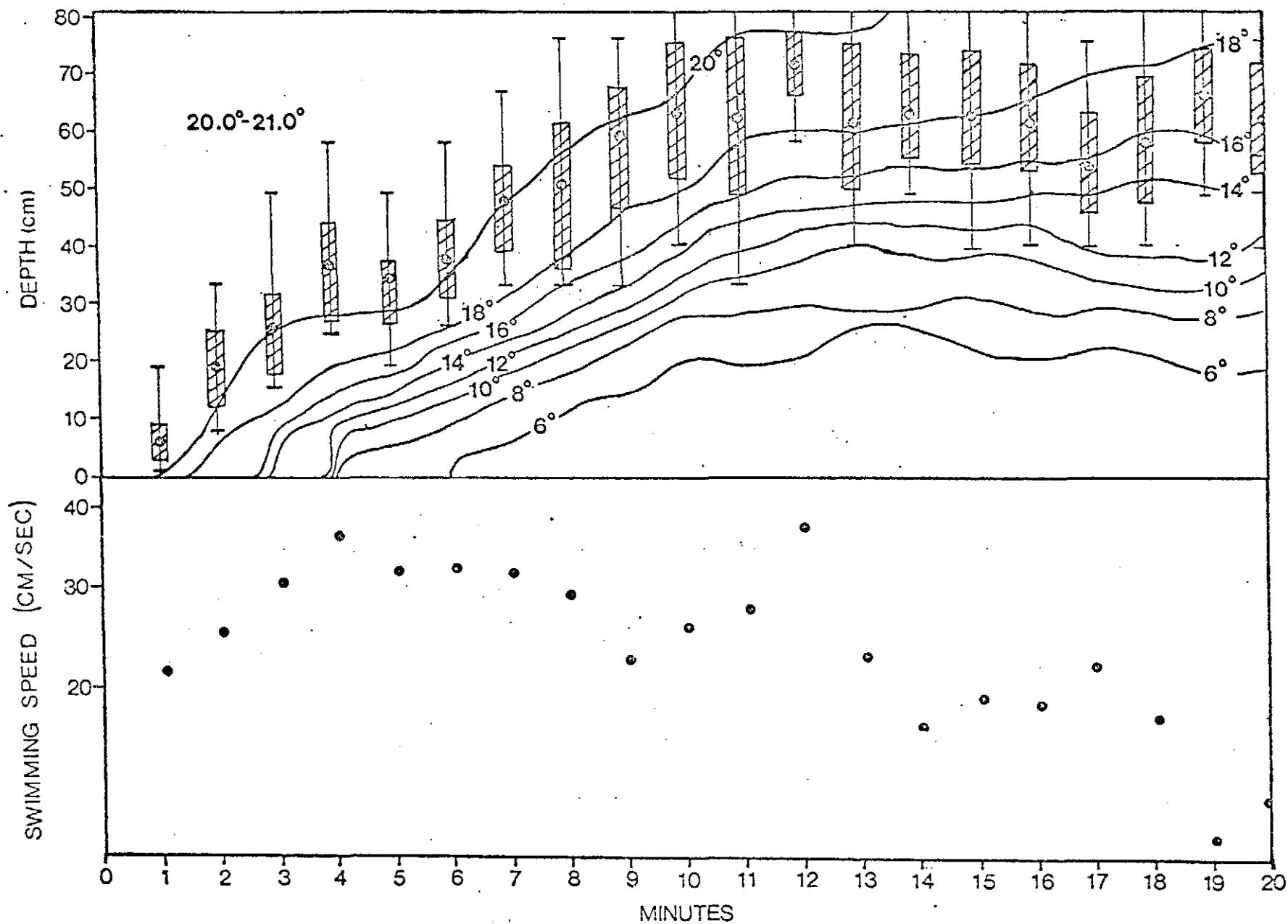


Figure 3a. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 3. a) Minutes 1-20. Water inflow was discontinued between Minutes 11 and 12.

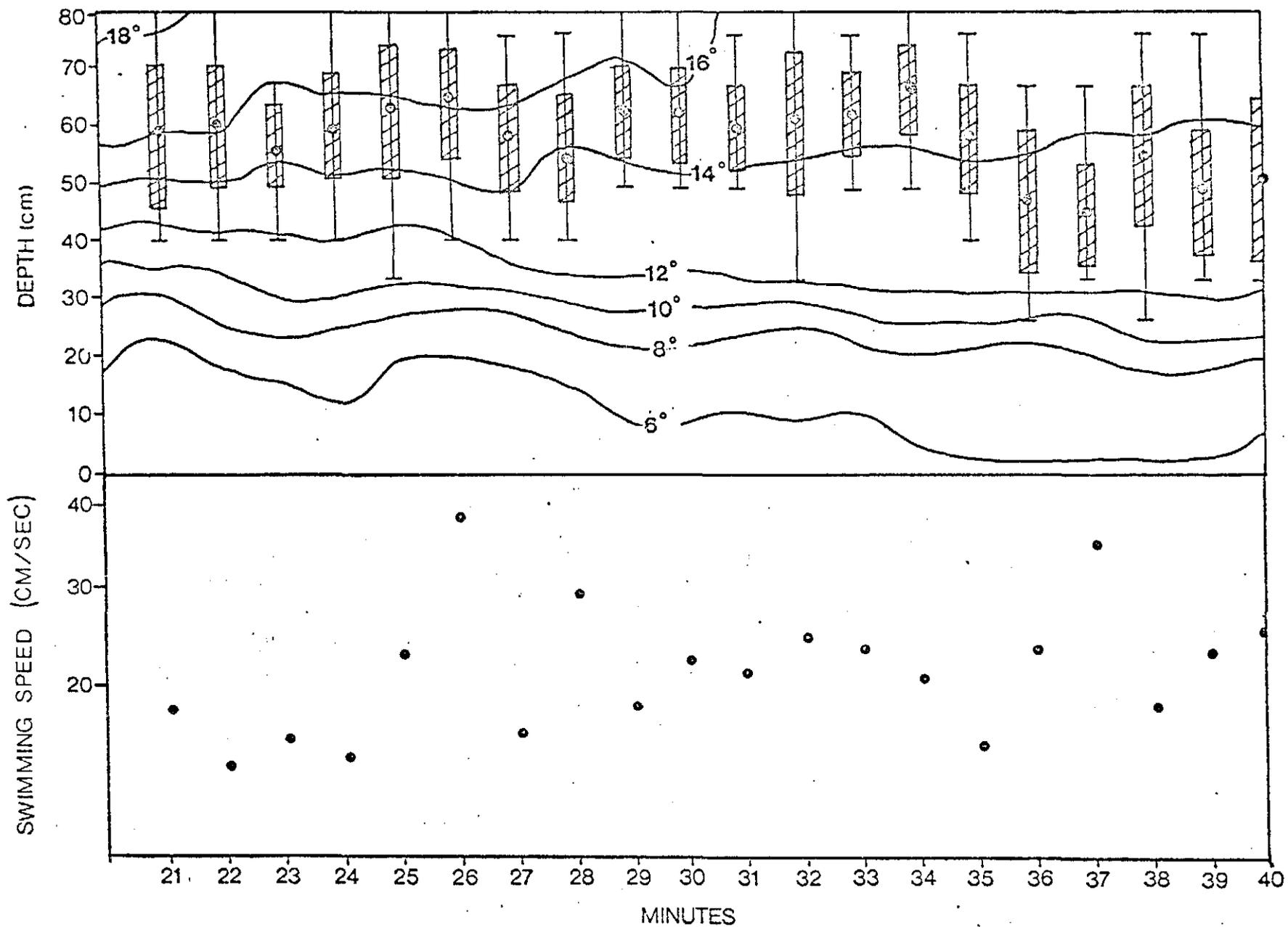


Figure 3b. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 3. b) Minutes 21-40.

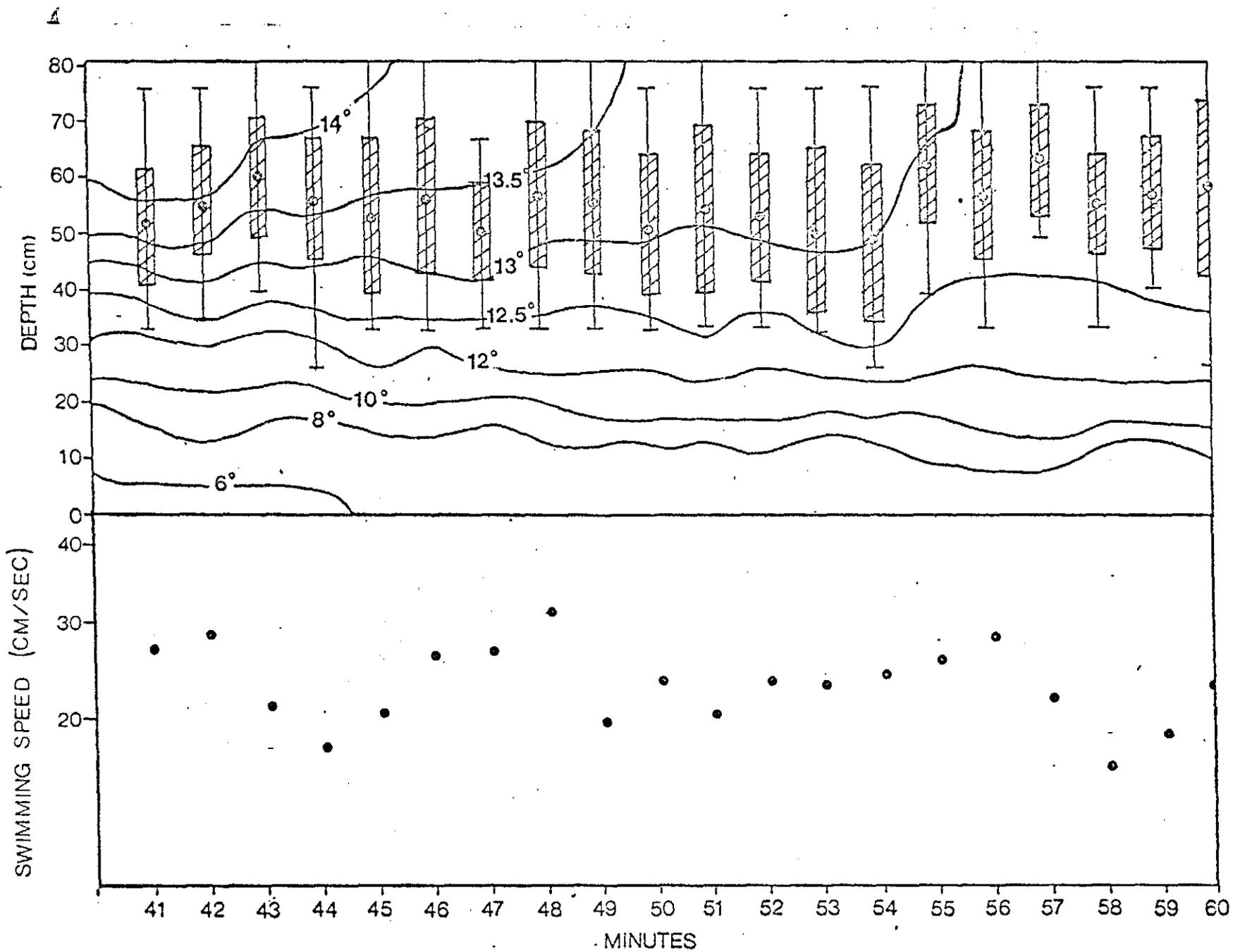


Figure 3C. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 3. c) Minutes 41-60.

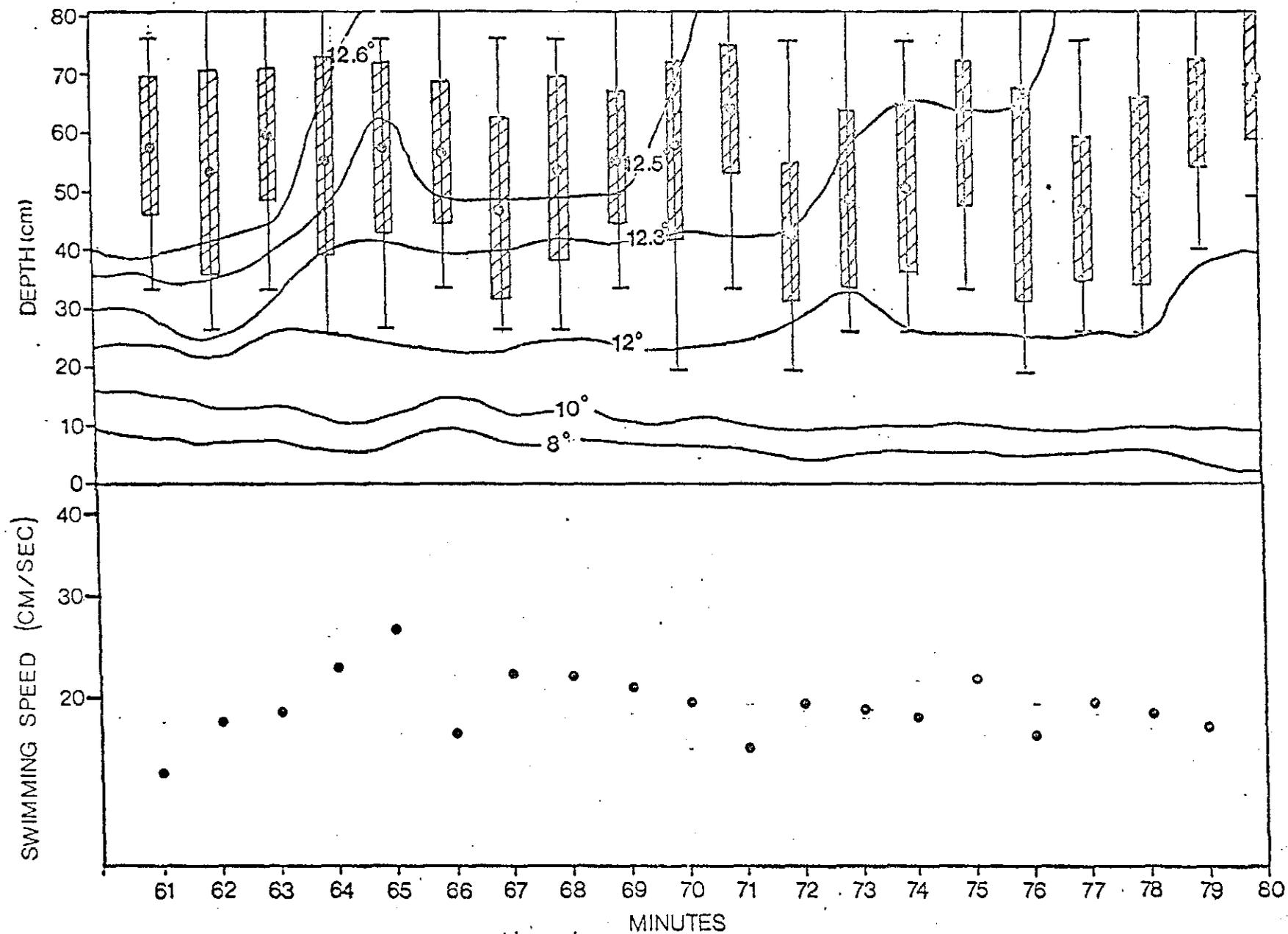


Figure 3d. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 3. d) Minutes 61-80.

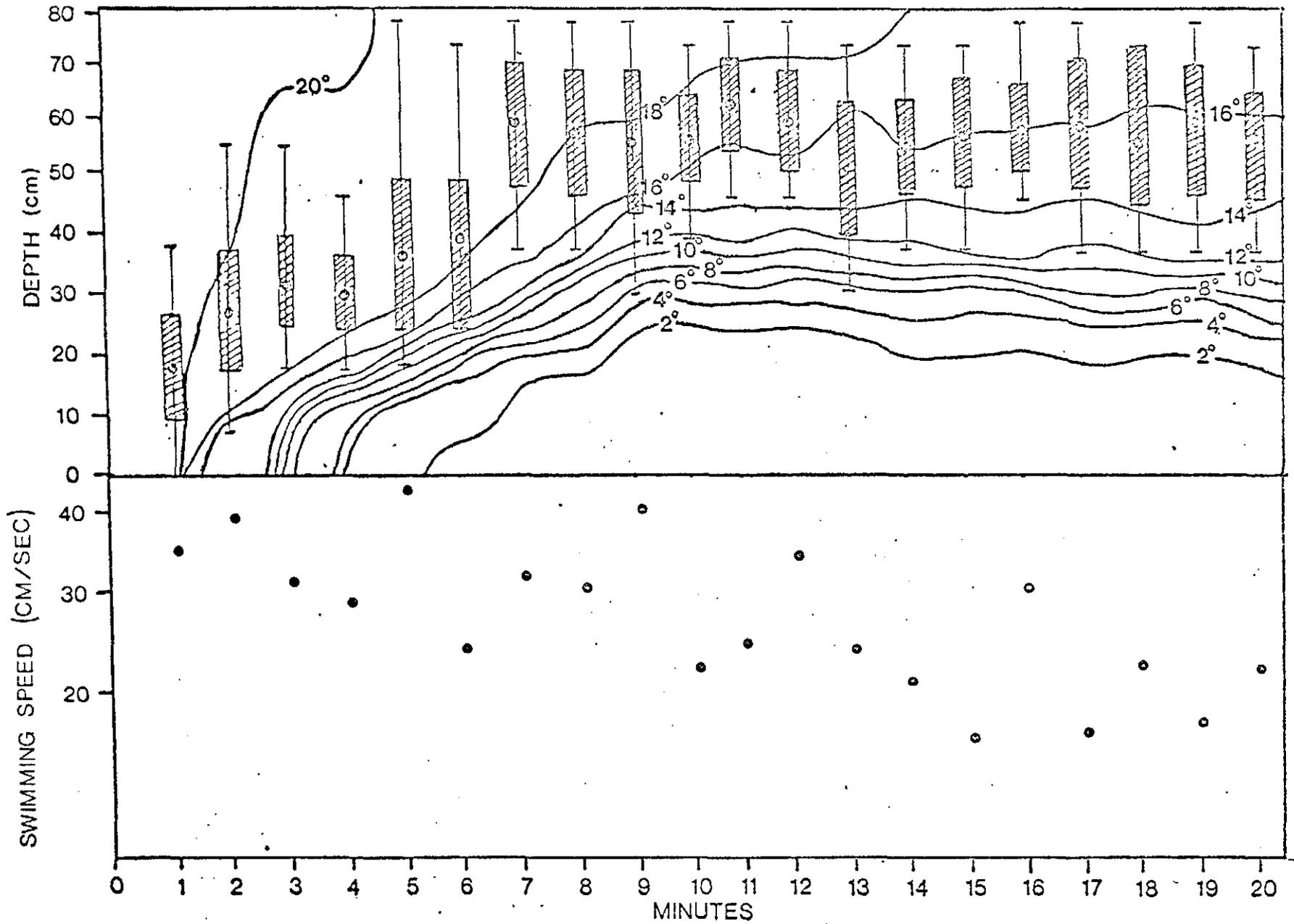


Figure 4a. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 4: a) Minutes 1-20. Water inflow was discontinued between Minutes 8 and 9.

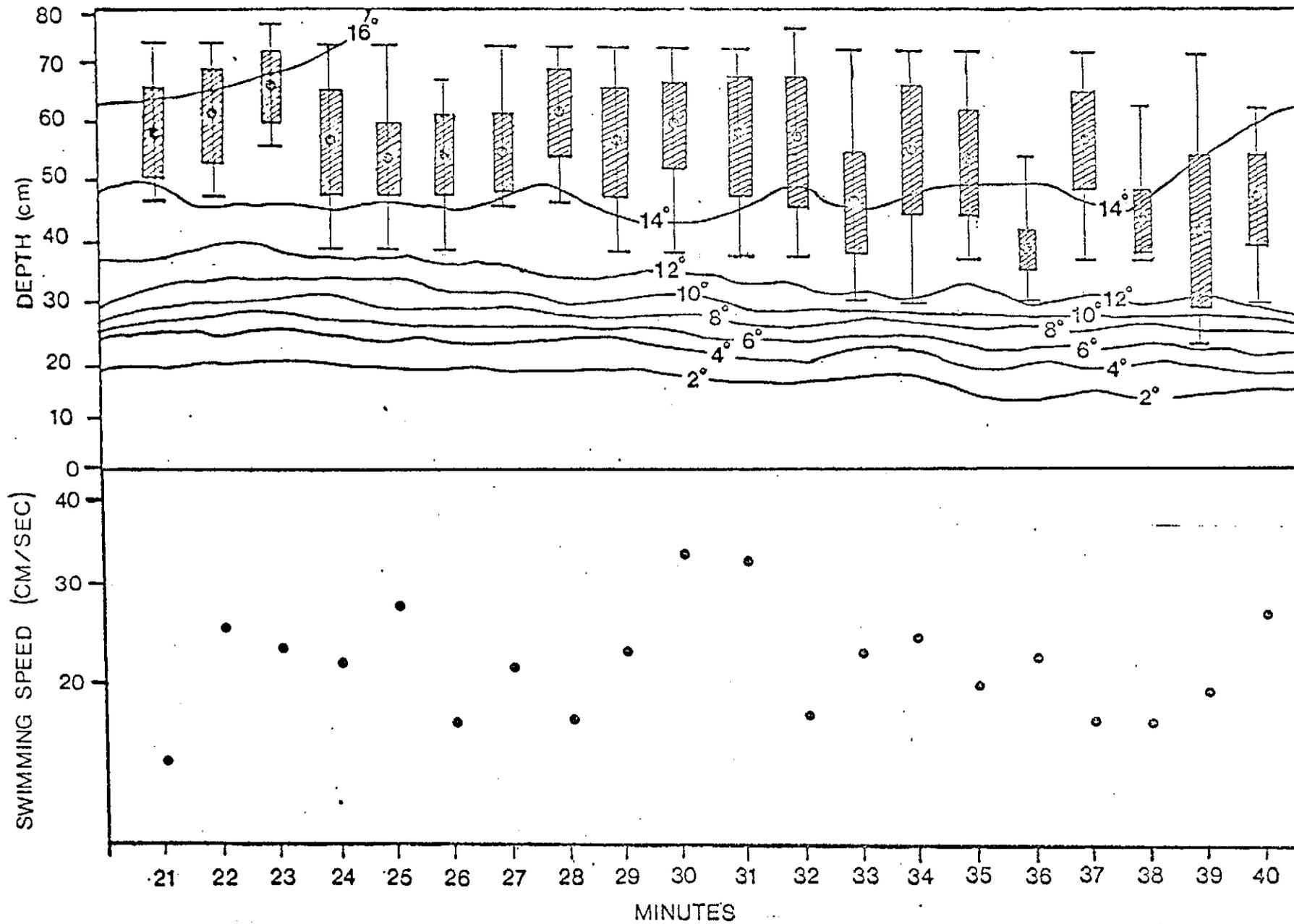


Figure 4b. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 4: b) Minutes 21-40.

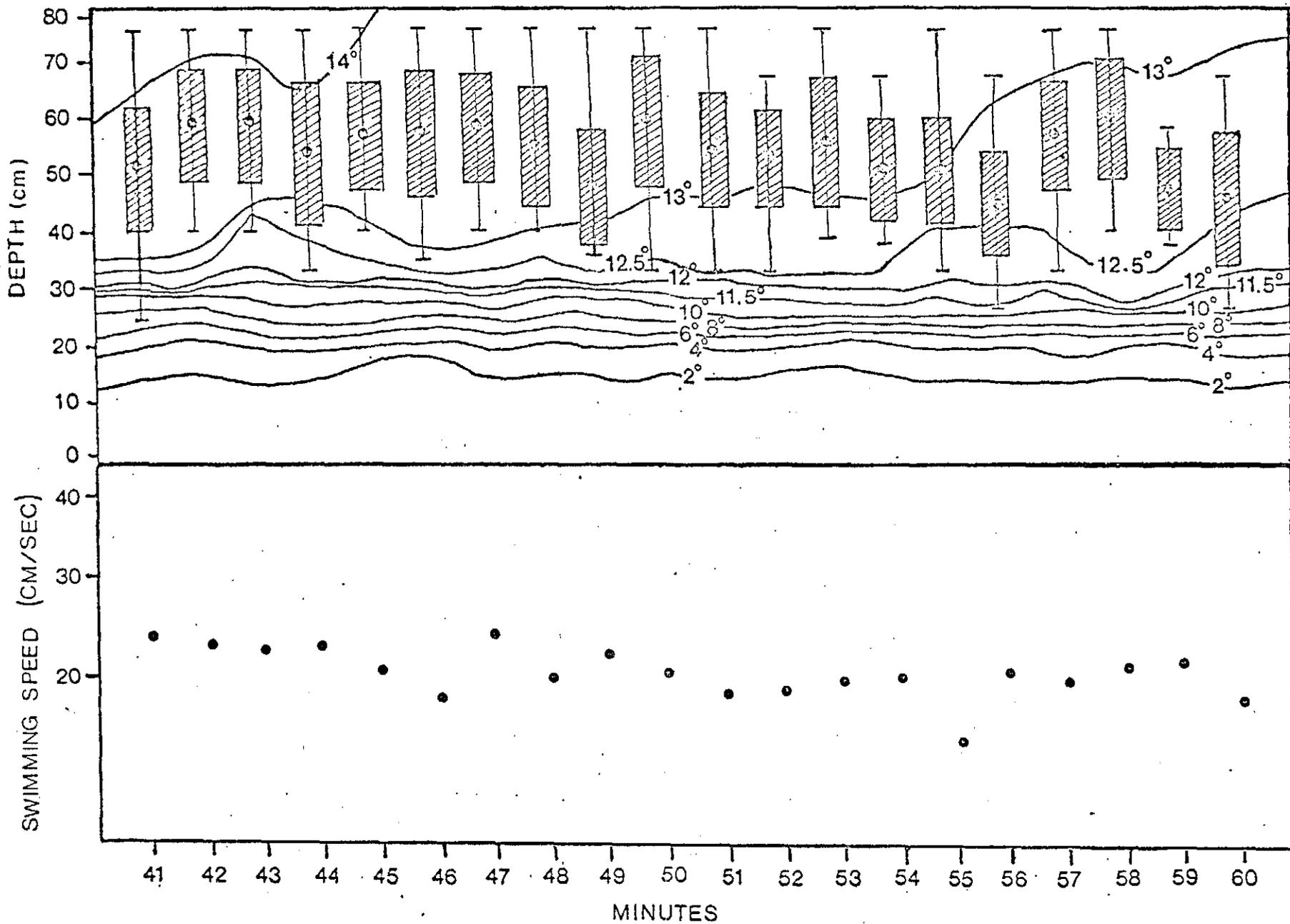


Figure 4c. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 4: c) Minutes 41-60.

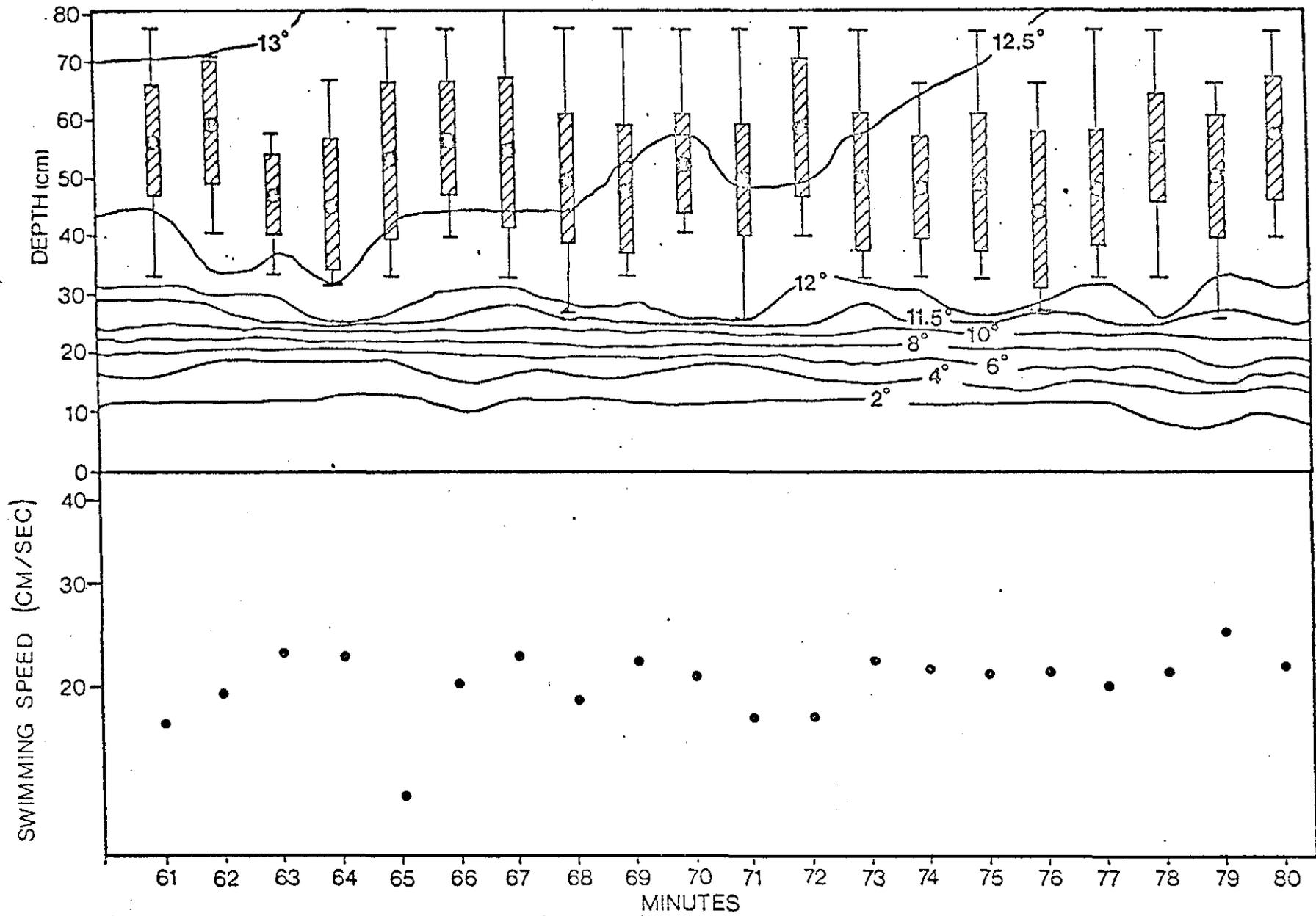


Figure 4d. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 4: d) Minutes 61-80.

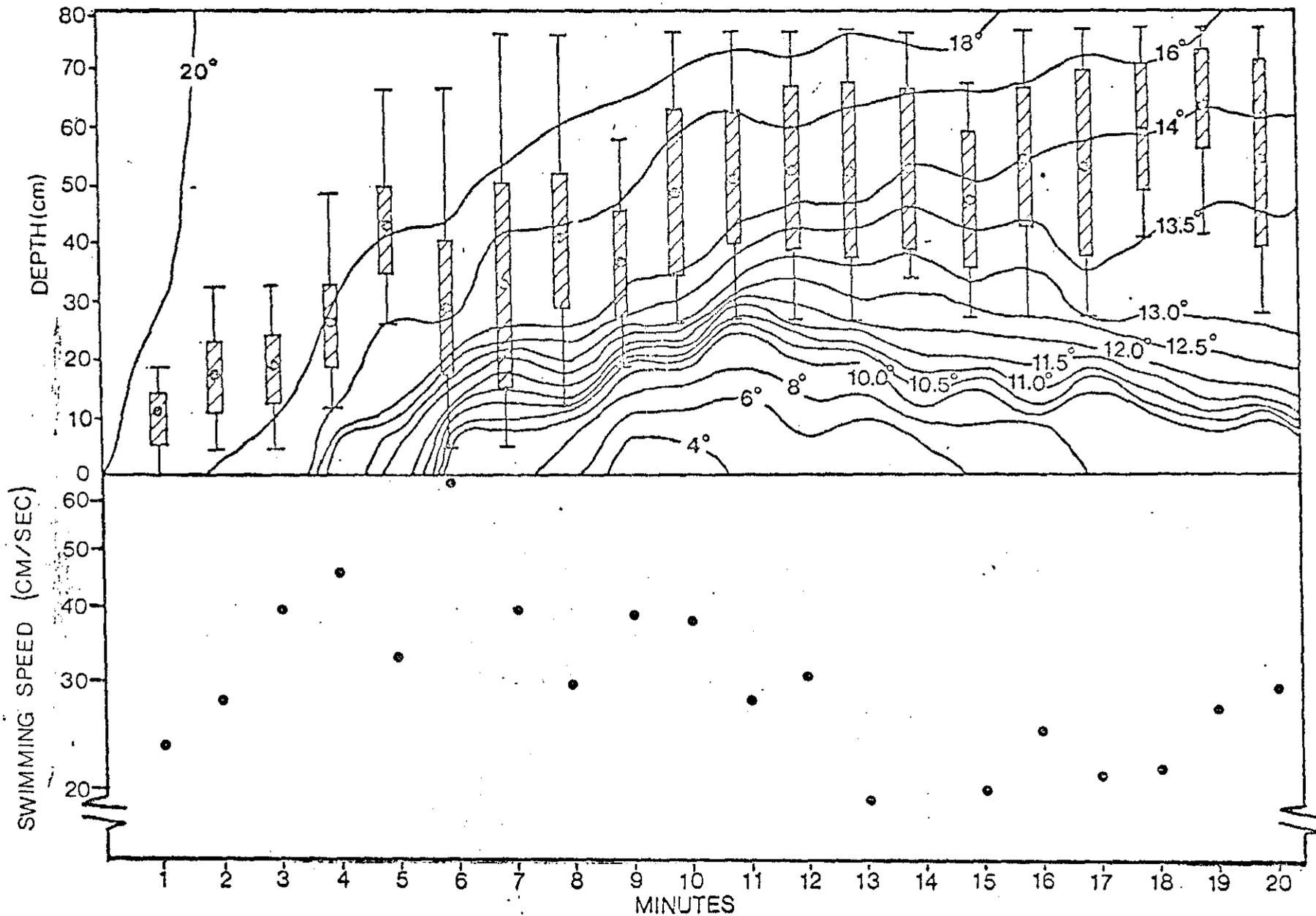


Figure 5a. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 5: a) Minutes 21-40. Water inflow was discontinued between Minutes 10 and 11.

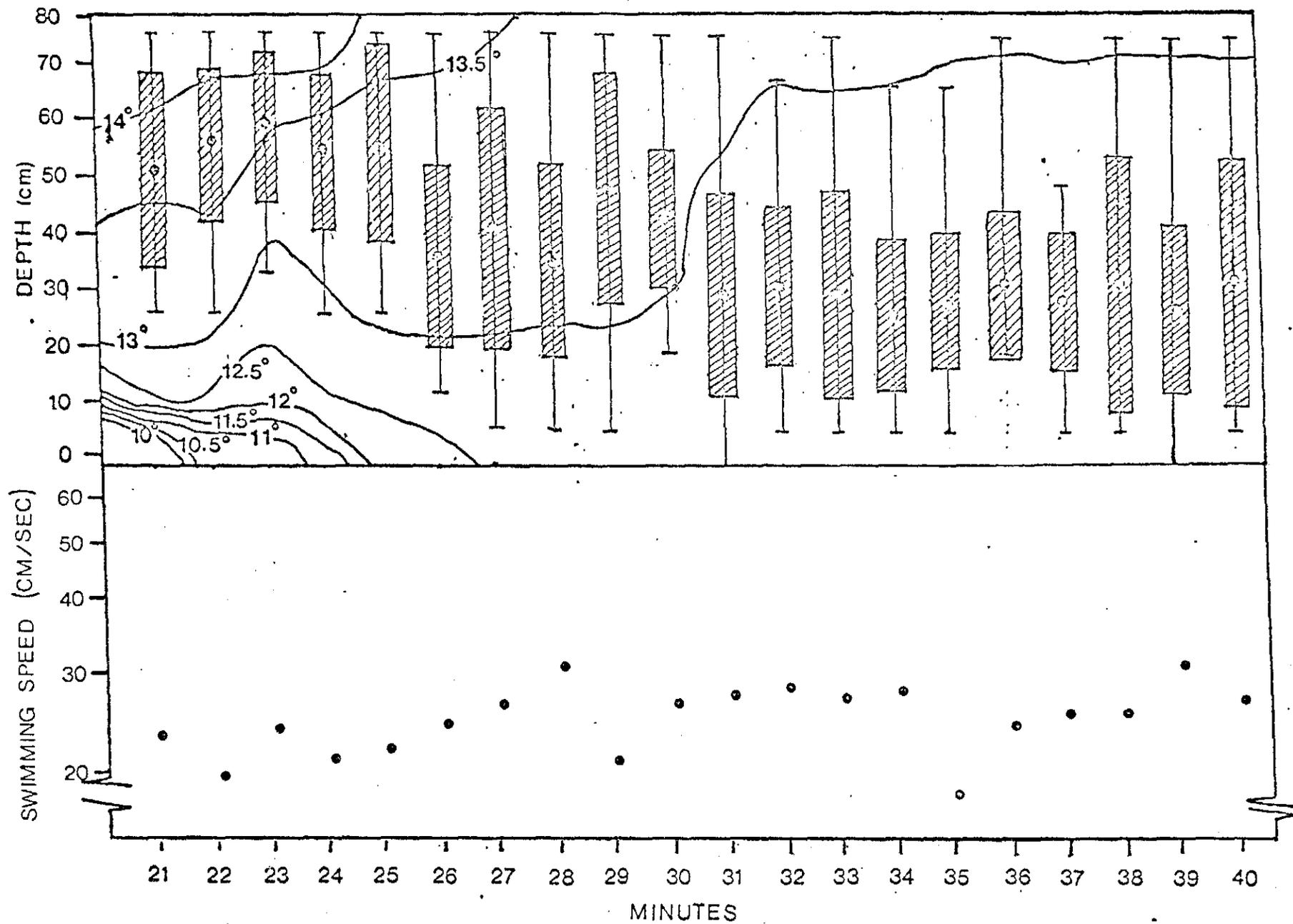


Figure 5b. Activity (swimming speed) and distribution (mean, standard deviation, and range) of juvenile bluefish in Test 5: b) Minutes 21-40.