THERMAL BEHAVIORAL RESPONSES OF
SELECTED CALIFORNIA LITTORAL FISHES

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ABSTRACT

Two horizontal temperature gradients were used to measure behavioral responses to temperature of various life stages of 16 species of temperate marine fishes from southern California, and we offer guidelines for standardization of collection, acclimation, preexperimental holding, and testing conditions. We classified behavioral responses to thermal gradients using eight experimental parameters: initial, mean, modal, and final selected temperatures; range of selected temperatures; skewness; kurtosis; and the degree of dispersion between individuals. We found four behavioral responses to changes in temperatures with time: 1) immediate—no general shift in selected temperature with time, 2) fast—a shift in selected temperature over the first 2 h of the experiment only, 3) slow—a shift in selected temperature over more than 2 h in the experiments, and 4) positioned—a wide range of selected temperatures and a tendency to remain in a given position in the gradient until conditions become extreme. Effects of preexperimental acclimation temperatures on thermal selection did not last longer than 4h. One day of food deprivation resulted in lower selected temperatures and changed the precision of selection and aggregating tendencies, although the direction of the change varied between species.

Over the last several decades, the behavior of fishes with respect to thermal gradients has been investigated by many workers (see review by Coutant 1977). Most studies in the literature, however, have dealt with freshwater or estuarine species that occur in large part in eastern North America. Little work has been carried out on temperate marine species, which, except for intertidal inhabitants, generally experience smaller natural diurnal and seasonal temperature fluctuations.

Our two horizontal gradients and experimental procedures were built on many of what appear to be the best attributes of previous studies. Variation in reported experimental techniques makes comparisons between studies difficult. We suggest guidelines for method standardization in this paper.

Horizontal gradients were chosen because they allowed experimentation with groups, permitted demersal fish to be in contact with a bottom and pelagic species to swim freely. This type of gradient also allowed us to combine some of the best attributes of spatial gradients (e.g., Norris 1963) and temporal ones (e.g., Beitinger 1976). Further, our study, in conjunction with a field survey, was designed to assess the effects of temperature on the distribution, behavior, and physiology of fishes found in King Harbor, Redondo Beach, Calif. This harbor, which receives the thermal discharge from an electricity generating station, as well as cold, upwelled water from the adjacent Redondo Submarine Canyon, contains a highly diversified thermal environment (Stephens 1972), including many horizontal gradients.

Our intent is to introduce a comprehensive approach to thermal response testing, including equipment design, preexperimental and experimental methodology and protocol, and to show representative examples of behavioral responses. We have examined to date the behavior of various life stages from larvae to adults of 16 fish species from 10 families. Comparative studies of laboratory and field results are in preparation.

EXPERIMENTAL CRITERIA

A wide range of experimental methodology exists in the literature (see review by McCauley 1977). McCauley and Tait (1970) stated, "Comparison of preference temperatures in the literature is

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questionable, because of differences in experimental techniques." Preexperimental feeding regimes differ significantly between studies. Cherry et al. (1975) discontinued feeding 2.5 to 3 days before testing; in contrast, Reynolds and Thomson (1974) fed fish approximately 2 h prior to experimentation. The time that the fish were allowed to adjust to the experimental chamber before initiation of data collection was also variable. Tat'yankin (1972) used a habituation period of only 0.5 h, while McCauley and Read (1973) used a period of 2 days. Length of time between observations was not consistent between studies. Ferguson (1958) observed fish hourly, but Norris (1963) recorded fish position every 6 s. Although most investigations used organisms once, Javaid and Anderson (1967) reused fish between successive experiments. Some of the differences in experimental techniques may have been due to species-specific problems; however, in many studies the primary concern was simply to provide a thermal gradient, to place test organisms in it, and to measure their response. Often, little attention was paid to factors relevant to the well-being of the fish (e.g., shock from capture and handling, nutritive condition) and to simulating natural intensities and quality of light.

General procedural recommendations have been made by Richards et al. (1977). Our methods build on techniques from past studies, including their best attributes. Some of the differences in experimental techniques are subtle, but important, especially since this investigation concerns marine species, on which little work has been done. The methods, procedures, and physical conditions of collection, handling, and experimentation in this study were chosen to minimize trauma to test organisms. The following methods and rationales that we employed are provided as suggestions toward standardization:

1) Our preferred methods of obtaining test organisms involved collecting by means of lift nets or traps or to rear them from eggs. These minimized damage to the fishes.

2) Fish feeding was established in the laboratory. We tested only fish that fed, as this indicated that they were most likely not in shock from collection.

3) We brought fish to desired acclimation temperatures, from that at which they were collected, at a rate of 1°C/day. The test specimens were held for at least 2 wk prior to testing. The length of the holding period was particularly important to assure acclimation to cold temperatures (Brett 1970).

4) We did not use anaesthetics in collections or preexperimental handling; Goddard et al. (1974) have shown that MS-222[4] can influence thermal behavioral responses for several weeks after treatment.

5) We fed the fish ad libitum just prior to their placement in the gradient. This standardized the feeding history, which has been shown to alter temperature selection (Ivlev and Leizerovich 1960; Javaid and Anderson 1967).

6) We placed the fish in the experimental chamber, adjusted to their acclimation temperature, on the evening preceding testing. This allowed adjustment to the new surroundings prior to experimentation. No fish were reused.

7) Testing fish in groups allowed us to assess the effects of temperature on populations, but we could only use this methodology to study gregarious species that did not display agonistic behavior.

8) We established the temperature gradient about the fish. Introduction of test organisms to an established gradient, even at the location of their acclimation temperature, can result in the fish darting to another part of the tank and experiencing a temperature shock.

9) We shifted isotherms during an experiment, and the hot and cold ends were reversed between experiments. This allowed us to attempt to partition any tendencies of the fish to select a particular compartment independent of temperature.

10) We shielded the test chamber from external light and observed the fish from above downward-directed experimental lights to insure that the fish would not respond to presence of the experimenter.

11) We used low levels of lighting, during the experiment, based on minimum intensities for schooling and larval feeding (Blaxter 1970). These levels of illumination did not appear to disturb the fish as was sometimes the case with brighter light. Additionally, Sullivan and Fisher (1954) reported increased precision of temperature selection at low light

intensities. We employed natural day lengths during preexperimental holding as well as during testing.

DESIGN OF GRADIENTS

We built two horizontal gradients: one for juveniles and adults and another, smaller one, for larvae and placed them in a sound-insulated and lightproof room. A differential of at least 10°C between the hot and cold ends of the gradient was established prior to collection of data used for behavioral analyses. We adjusted the size and position of the temperature gradient to keep the experimental fishes from the extreme end compartments; differentials of up to 25°C were employed for species with wide preferred temperature ranges.

Gradient for Juvenile and Adult Fishes

We divided this gradient (360 cm long × 60 cm wide × 60 cm deep, Figure 1) along its longitudinal axis to produce two experimental chambers (15 and 44 cm wide). The size of the test organisms determined which side of the gradient was used. Heating and cooling were controlled, primarily at the ends of the gradient. A rheostat connected to an immersion heater allowed us to minimize the frequency of the heater turning on and off, reducing fluctuations in heat production. A stainless steel (type 316) coil heat exchanger with cold freshwater coolant (1°C) chilled the seawater in the gradient. Two additional heat exchangers constructed of polyvinyl chloride and run along the bottom from the ends to the center of the experimental chamber served to produce a more even temperature gradient.

Formation of thermal currents can limit the temperature range and controllability of a horizontal gradient. Twelve pairs of surface and bottom baffles impeded thermal currents and divided the gradient into 11 experimental compartments.
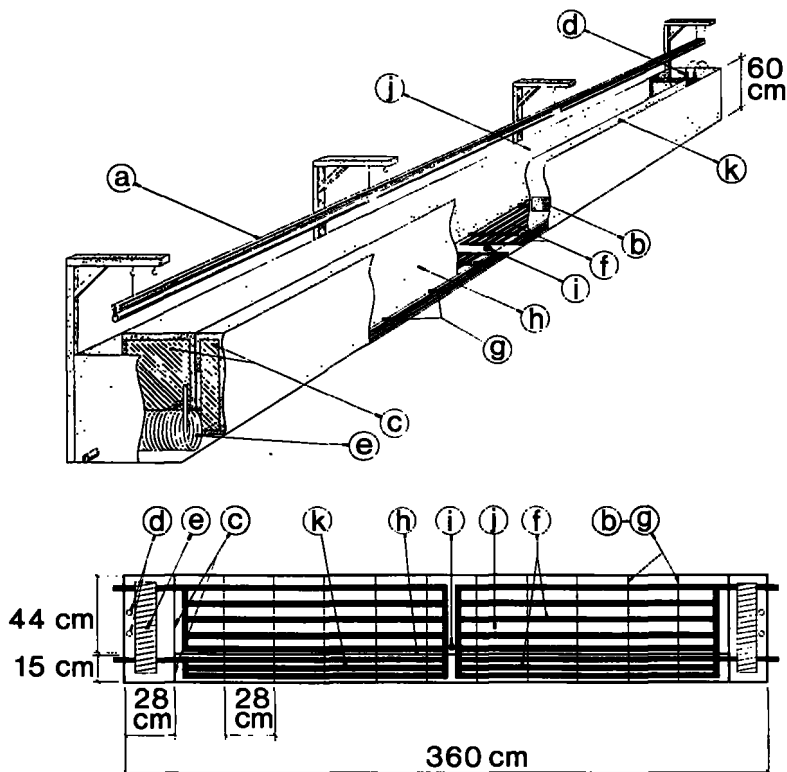

FIGURE 1.—Large experimental chamber for temperature selection measurement in fishes: a) daylight-simulating fluorescent light, b) surface baffle, c) screens separating experimental chambers (j and k) from the end heating and cooling compartments, d) 500-W heaters, e) stainless steel heat exchangers, f) polyvinyl chloride heat exchanger, g) bottom baffles, h) wall separating the large and small experimental chambers, i) drain, j) large experimental chamber, k) small experimental chamber.

The baffles could be lowered or raised with the water level so that they entered the water to a depth of 2 cm. Gentle aeration, from the bottom of each compartment, further eliminated vertical stratification. This also aided removal of any supersaturated gases that Gift (1977) reported to be potential problems in thermal gradients. A nylon screen prevented the test organisms from entering the area where the heating and cooling took place and also provided a flat surface over the bottom baffles. We subdivided the experimental gradient that consisted of 11 compartments each containing a centrally located thermistor probe into 21 visual units that were not visible to the test organisms, by forming an additional compartment centered midway between two thermistors. The mean temperature of two adjacent probes was used for these additional compartments. Daylight-simulating fluorescent fixtures (Duro-test Vitalites), with the use of diffusers, provided a light intensity of 60-70 fc at the water surface.

Gradient for Larval Fishes

The temperature gradient for larval fishes (Figure 2) operated on a counter-current principle. Alternation of hot and cold water entering the experimental chamber between replicate runs eliminated any potential rheotactic interference. The inner experimental trough (1.75 m long × 5 cm diameter; 0.8 mm wall thickness) contained two nylon screens 1.5 m apart that defined the experimental chamber. Seawater velocities of 0.1 to 0.9 mm/s were selected based on known larval swimming speeds (Blaxter 1969; Rosenthal and Hempel 1970; Hunter 1972), because velocities in this range would not present the larvae with any significant difficulty in maintaining a chosen position. Wilson (1974) successfully employed velocities of up to 10.8 mm/s with pelagic marine fish larvae in studying behavioral responses of pollutants.

Hunter and Thomas (1974) showed that larval anchovies aggregated at patches of food (*Gymnodinium splendens*). All entering seawater was filtered to 5 μm to rule out possible position selection by larvae based on presence of prey organisms. Eleven evenly spaced thermistor probes coupled to a telethermometer were used to monitor temperature. We subdivided the experimental chamber into 21 visual compartments and enclosed the trough in a lightproof box. A daylight-simulating fluorescent lamp, with the use of a diffuser, produced 10-15 fc at the water surface.

DEFINITIONS

The term "preferred temperature" has been used in various contexts in the literature (e.g., Brett 1952; Javaid and Anderson 1967; McCauley and Tait 1970; Tat'yankin 1972; McCauley and Read 1973). Much of the variation in the use of this
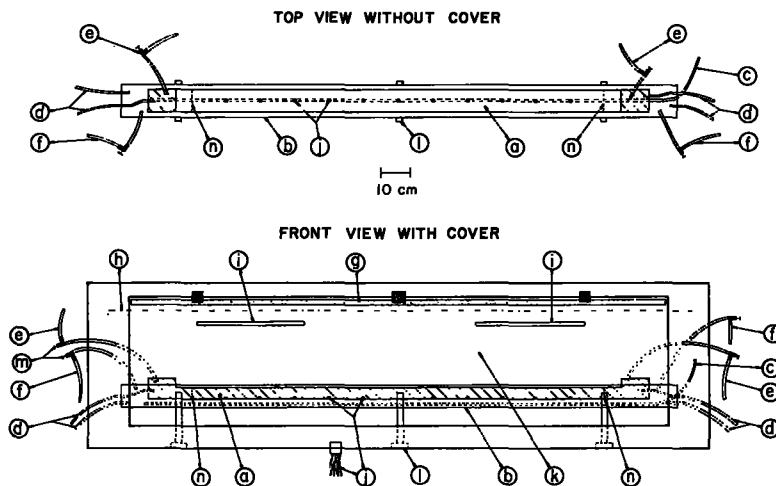

FIGURE 2.—Small experimental chamber for temperature selection measurements in larval fishes: a) experimental chamber, b) water jacket, c) air line, d) drains, e) seawater input line, f) freshwater input line, g) daylight-simulating fluorescent light, h) light diffuser, i) viewing slits, j) thermistor probes, k) door on lightproof cabinet, l) supports for water jacket, m) water flow control valves, n) nylon screen on ends of experimental chamber.

term can be attributed to different species exhibiting various behavioral patterns in a gradient tank, just as they do in their natural habitats. This makes it impossible to use only one procedure to determine the preferred range for all species under all conditions. We determined the preferred range and final perferendum by evaluating, on a case-by-case basis, the behavioral responses of a species subjected to known conditions such as acclimation temperature, feeding patterns, and captivity environment.

Experiments with larvae lasted 5-6 h, but juveniles and adults were tested for approximately 7-8 h. An "experiment," in this study, consisted of a set of individual runs, with each "run" being the observation of the position and water temperature selected by each fish in the gradient at a fixed point in time. We employed constant time intervals between runs for any experiment: 5 min for larvae and 15 min for juveniles and adults. Run selected temperatures were the primary data source, and we calculated their mean, mode, and variance prior to combining them with data from other runs to determine the preferred temperature.

DATA ANALYSES

Reynolds (1977) reported that skewness of temperature preference frequency distributions required a complete description of the distribution. We examined the following parameters to delineate thermal behavioral responses, the initial, mean, modal, and final selected temperatures, standard deviation about the mean, coefficients of skewness and kurtosis, and coefficient of dispersion. The first four parameters defined the preferred temperature range. The standard deviation about the mean selected temperature quantified movement through a range of temperatures and gave a measure of the degree of eury- or stenothermal preference. We used coefficients of skewness and kurtosis (Sokal and Rohlf 1969) in testing for normality and then to help define the shape of the temperature-specific fish frequency of occurrence distribution and to refine interpretation of behavioral types. The coefficient of dispersion quantified the tendency of a species to aggregate or school and gave the percentage of use of the experimental chamber by all fish within one standard deviation of the run selected temperature.

The frequency of occurrence of all experimental temperatures was not uniform due to the shifting of the gradient as well as having a variable number of degree intervals per run and generally fewer than the 21 compartments. This caused a bias in the number of fish observed at a particular temperature when summed over an entire experiment. To compensate for this, prior to calculation of the mean and modal selected temperatures, we adjusted the data by using the number of fish per total occurrence of a particular temperature in all experimental compartments rather than the actual number of fish at each temperature.

We defined the "initial selected temperature" as that chosen by the fish immediately following establishment of a gradient of 10°C. The modal selected temperature was determined from the percent occurrence frequency distribution derived from adjusted data. After an initial time of apparent searching and testing of water conditions the experimental animals selected a temperature or range of temperatures at which they remained for the duration of the experiment. We called this the final selected temperature (or temperature range) and determined it from plots of selected temperature against time. The mean selected temperature was derived by methods presented in Appendix Table 1.

EXPERIMENTAL TECHNIQUES AND BEHAVIORAL RESPONSES

Our experimental techniques and data interpretation methods are useful for a wide variety of behavioral types. There are three salient features of this methodology: 1) the shifting and reversal of the temperature gradient to partition position preference from thermal preference, 2) the extended duration of the experimental period and its relationship to the thermal history of the test organisms, and 3) the criteria for behavior evaluation.

Shifting and Reversal of Temperature Gradient

Hasler (1956) pointed out that fishes in experimental gradients can position themselves according to small deformities in the tank structure. We employed two methods to eliminate this factor: shifting the position of a given isotherm in the gradient during an experiment, and reversing the hot and cold ends between replicate experiments.

Shifting the isotherm position during an experiment required the fish to thermoregulate actively, similar to those studied by Beitinger (1976, 1977) in his temporal gradient. This technique demonstrated that the fish could follow an isotherm and did not necessarily arbitrarily select a position in the experimental tank. The precision with which a group of fish followed an isotherm varied between species and was related to the size of their preferred temperature range. Juvenile surfperch, *Damalichthys vacca*, for example, which preferred a narrow range of temperatures,

closely followed an isotherm (approximately 11°C) (Figure 3). In contrast, juvenile topsmelt, *Atherinops affinis*, after initially selecting approximately 22°C, remained within that compartment, and shifting the gradient did not cause them to move until the temperature reached 26°-27°C. This isotherm was then tracked (Figure 3). Topsmelt are physiologically eurythermal, at least during embryonic stages, and the upper limit for hatching of topsmelt eggs is 26.8°C (Hubbs 1965). Brett (1956) suggested that the preferred temperature may not be a strong enough directing force to move
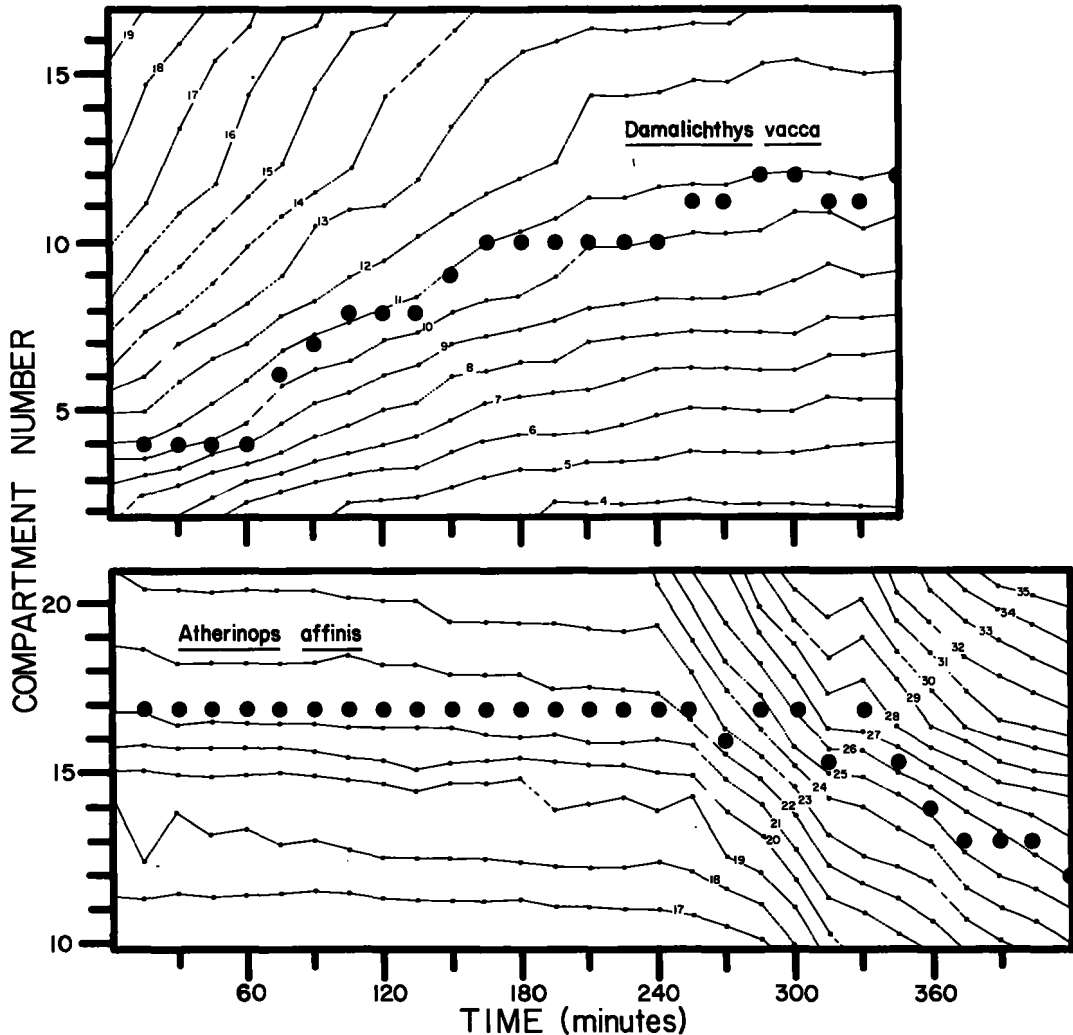
FIGURE 3.—Changes in fish and isotherm position in the experimental gradient. Juvenile *Damalichthys vacca* followed the 10°-11°C isotherms. Juvenile *Atherinops affinis* remained in the position they initially selected and moved very little until the temperature reached 26°-27°C. They then followed the temperature range of 25°-27°C. The small numbers indicate isotherms. Large dots indicate the mean temperature selected by nine individuals.

fish with wide temperature tolerances from a particular area until stress-inducing conditions are reached.

Temperatures Selected and Their Relationship to Thermal History

We classified the behavioral responses of the 16 species surveyed into four groups based on changes in temperatures selected throughout an experiment: 1) immediate response—no general shift in selected temperature over time, 2) fast response—a shift in selected temperature not exceeding the first 2 h of the run, 3) slow response—a shift in selected temperature over more than 2 h, and 4) positioned response—a broad preference and a tendency to remain in a given position in the gradient until conditions become extreme.

Shiner surfperch, *Cymatogaster aggregata*; pile surfperch, *Damalichthys vacca*; black surfperch, *Embiotoca jacksoni*; and black croaker, *Cheilotrema saturnum*, showed the first behavioral pattern of immediate response (Figure 4). These fishes moved most quickly from their preexperimental acclimation temperature to their final selected one or range, remaining there for the duration of the experiment. These fishes generally had the narrowest selected temperature ranges and also aggregated tightly (Table 1).

Fishes with a fast response to the temperature gradients included speckled sanddab, *Citharichthys stigmaeus*; señorita, *Oxyjulis californica*; spotted sand bass, *Paralabrax maculatofasciatus*;
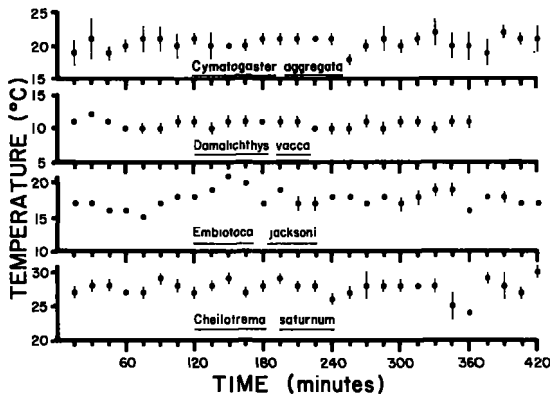
FIGURE 4.—Immediate response to temperature change. These species showed no trend in selected temperature with time. Dots are mean selected temperatures and vertical lines are 1 SD about the means. Results are for duration of one experiment.

and sculpin *Scorpaena guttata* (Figure 5). These species required up to 2 h to home in on a selected temperature and also generally did not aggregate as tightly, nor select as narrow a temperature range as those fishes that showed an immediate response to the temperature gradients (Table 1).

All larvae studied responded slowly under experimental conditions. These included topsmelt, *Atherinops affinis*; California grunion, *Leuresthes tenuis*; rockpool blenny, *Hypsoblennius gilberti*; and painted greenling, *Oxylebius pictus* (Figure 6). Four older fishes also showed this behavior: kelp bass, *Paralabrax clathratus*; olive rockfish, *Sebastes serranoides*; California halibut, *Para-*

TABLE 1.—Behavioral responses of larval and juvenile fishes in temperature selection experiments. Initial and final selected temperatures are taken from Figures 4-6 and other similar experimental data.

| Species	Experimental date	No. of fish	Mean Standard length (mm)	Mean Acclimation temperature (°C)	Selected temperatures (°C)					Coefficient of skewness (g_1)	Coefficient of kurtosis (g_2)	Coefficient of dispersion (%)
					Mean	SD	Mode	Initial	Final			
Immediate response:												
Cymatogaster aggregata	12 June 1975	8	109	18.2	19.9	2.1	19	18.7	21	0.22	2.87	24
Damalichthys vacca	6 June 1975	9	69	18.1	10.5	0.9	10	11.4	11	0.41	4.61*	12
Embiotoca jacksoni	13 Dec. 1974	7	118	16.7	18.0	1.6	18	17.0	18	−0.61*	4.54*	5
Cheilotrema saturnum	6 Oct. 1975	7	42	17.0	27.6	2.0	28	26.6	28	−0.79*	3.12	13
Fast response:												
Citharichthys stigmaeus	22 Dec. 1975	9	90	18.9	10.1	2.6	10	14.8	10	0.43	3.44	33
Oxyjulis californica	28 May 1975	6	120	17.2	15.5	1.9	15	15.0	16	−0.69*	5.44*	11
Paralabrax maculatofasciatus	31 July 1975	6	179	20.6	24.2	3.1	27	21.2	25	−0.83*	2.70	29
Scorpaena guttata	24 Nov. 1975	6	64	17.6	17.5	4.2	19	17.2	17	−0.63*	4.01*	35
Slow response:												
Atherinops affinis (larvae)	31 July 1975	6	14.5	21.5	25.2	2.9	27	21.9	27	−1.07*	4.12*	26
Leuresthes tenuis (larvae)	9 May 1975	6	8.1	16.5	25.2	4.1	26	19.2	27	−0.12	2.86	37
Hypsoblennius gilberti (larvae)	2 July 1975	6	4.4	19.4	22.2	3.1	19	19.7	26	0.39	2.10	36
Oxylebius pictus (larvae)	14 May 1975	6	3.4	16.0	26.8	3.3	27	19.7	29	0.82*	3.24	30
Paralabrax clathratus	28 July 1975	6	196	21.0	13.5	3.1	14	17.2	15	0.13	2.70	47
Sebastes serranoides	11 Dec. 1974	8	82	17.0	18.0	1.3	18	16 2	17	−0.21	2.44	4
Paralichthys californicus	15 Oct. 1975	5	94	20.5	20.8	6.6	24	20.3	22	−0.10	1.91*	65
Pleuronichthys coenosus	3 Dec. 1975	4	134	10.0	7.5	2.5	7	10.8	7	1.40*	5.15*	23
Positioned response:												
Atherinops affinis	14 Jan. 1976	9	60	15.0	23.3	3.2	26	16.4	26	−0.71*	2.41	4

*P<0.05.

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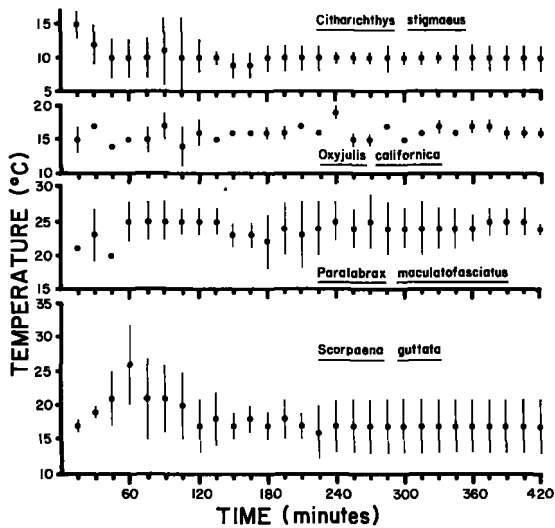
FIGURE 5.—Fast response to temperature change. These species changed their selected temperatures over the first 2 h of the experiment only. Symbols as in Figure 4.
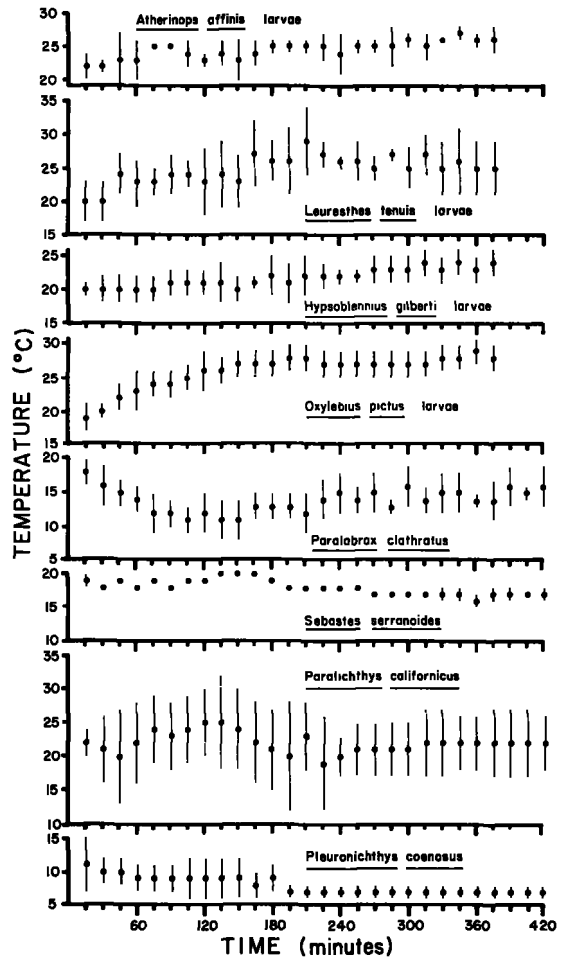

FIGURE 6.—Slow response to temperature change. These fishes changed their selected temperature over more than 2 h in the experiments. Symbols as in Figure 4.

lichthys californicus; and C-O turbot. *Pleuronichthys coenosus* (Figure 6). Members of this group required more time to stabilize their response than either the immediate or fast responders. The temperature selection acuity and aggregating tendencies of these fishes were similar to those of the second group (Table 1).

Juvenile topsmelt were the only species observed that showed a positioned response (Figure 3). Ehrlich et al. (in press) discussed this behavior in detail. California grunion are closely related to topsmelt, and we have observed them together, in the field, throughout larval, juvenile, and adult stages. Possibly juvenile California grunion, which were not tested, may show similar responses.

Preexperimental acclimation temperatures showed the greatest effect on thermal selection of the fishes during the first 2 h after establishment of the gradient (Figures 4-6). The short duration of the influence of thermal history on temperature selection has also been reported by Doudoroff (1938). Clearly, trying to determine a preferred temperature for these species or others with similar responses, during the transition period, would make data interpretation difficult. After this initial period, the fishes, in most cases, chose a final selected temperature, which may be synonymous with what Fry (1947) termed the "final preferendum." He defined this as the temperature range

that the fish would eventually select, independent of their acclimation temperatures. Topsmelt, however, did not show this pattern, for their initial selected temperature gave a good indication of their preference and was independent of their acclimation temperature (Ehrlich et al. in press). Doudoroff (1938) also found that fishes did not select the temperatures to which they had been acclimated but rather selected a common range of temperatures, which he suggested must have some physiological significance.

Figures 4-6 show that the final preferendum was reached within several hours after the establishment of the gradient. This is considerably less time than the approximately 24 h reported by

Reynolds and Thomson (1974) or Reynolds and Casterlin (1976). The differential, however, between the acclimation and the final preferendum must be considered. Reynolds and Thomson (1974) tested fish acclimated 17°C below their final preferendum. Crawshaw (1975) used a range of acclimation temperatures from 22°C below to 3°C above the final preferendum and found that as the temperature differential diminished so did the time required to reach the final preferendum. Differentials of 5°C required as little as 1 h and 3°C only 0.5 h (Crawshaw 1975). Based on the temperature differences between acclimation and the final preferendum (Table 1), Reynolds' and our results generally fit the pattern described by Crawshaw.

Behavioral Criteria

Most studies pertaining to behavioral responses of fishes to thermal gradients have been concerned with only one factor: the final preferendum. Additional information, however, can be obtained from examination of parameters associated with the frequency distribution of the selected temperatures, particularly: skewness (degree of distortion from symmetry) and kurtosis (peakedness). Ivlev and Leizerovich (1960) compared the percent of the area under the curve of number of fish per temperature against the mode of the distribution as well as the percentage of the curve on either side of the mode. Reynolds and Casterlin (1976) and Reynolds (1977) discussed the relationship between various measures of central tendency (mean, mode, and median) and skewness. They also improved descriptions of thermal behavioral responses by quantifying skewness but did not state the statistical significance of the skewness. Sokal and Rohlf (1969) stated that the absolute value of coefficients of skewness and kurtosis have little meaning and that they must be tested for statistical significance. We identified distinct behavioral types with respect to the frequency distribution of selected temperatures by examining skewness and kurtosis. The responses were, in part, species-specific but also varied with ontogenetic stage and nutritive condition. Reynolds and Casterlin (1976) showed that skewness also varied diurnally. Kurtosis can be used to assess whether the test organisms display eury- or stenothermal behavioral responses (Ivlev and Leizerovich 1960). A narrow preferred temperature range

will be overly peaked about the mean (leptokurtic), and a broad range of preferred temperatures will show no obvious mode or only a very slight one (platykurtic). The coefficient of kurtosis is particularly useful for quantifying the strength of the temperature selection response in populations that are not normally distributed where normal parameters such as mean and standard deviations are inappropriate.

A normal bell-shaped frequency distribution is representative of species with a wide preferred temperature range that is not close to lethal or avoided temperatures. Speckled sanddabs displayed this type of behavior (Table 1, Figure 7). Newly hatched larvae, however, of species such as California grunion showed little temperature selection acuity and preferred an even wider range of temperatures (g_1 = 0.003, 0.5<P), (g_2 = 1.75, 0.01<P<0.025). This behavior resulted in a platykurtic distribution (Figure 7). Reynolds and Thomson (1974) reported that newly hatched Gulf grunion, *Leuresthes sardina*, also showed no acute temperature preference. The precision with which larval California grunion selected temperatures increased by 2 days posthatching, producing a
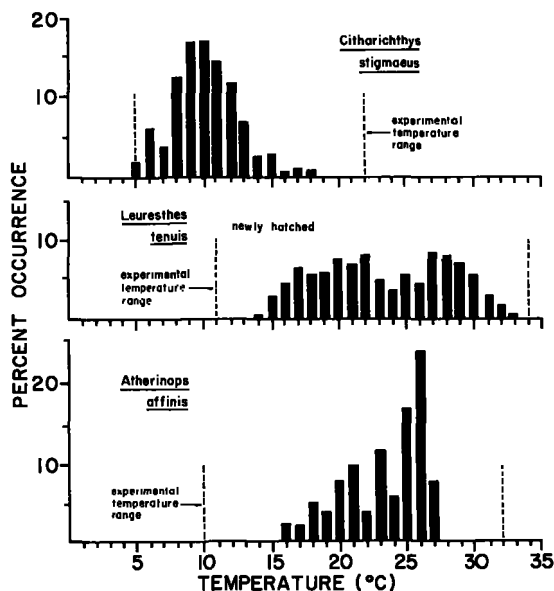

FIGURE 7.—Temperature-specific occurrences. Examples of three types of frequency distributions: normal (based on 220 fish observations), adult speckled sanddabs; platykurtic (based on 281 fish observations), newly hatched California grunion; and, skewed to the left (based on 241 fish observations), juvenile topsmelt.

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normal frequency distribution (Table 1), but subsequent food deprivation resulted in selection of colder water (mean 18.7°C) and a narrower distribution (SD 3.3°C). Selection of colder water during food deprivation may be a mechanism of energy conservation by poikilothermic organisms. Other mechanisms of energy conservation, both behavioral and biochemical, have been found during starvation of herring and plaice larvae (Blaxter and Ehrlich 1974; Ehrlich 1974). The increased precision of temperature selection during food deprivation coincides with the findings of Reynolds (1977) that stress can increase precision of temperature selection. This pattern, however, of lowered selected temperature but increased precision during food deprivation was not duplicated by all species.

Comparison of data from 2 consecutive days of observation of shiner surfperch demonstrated that the temperatures they selected, as well as their tendency to school or aggregate, varied between the 2 days. The selected temperatures decreased on the second day (means 19.9° to 15.6°C and modes 19° to 16°C), but unlike California grunion the standard deviation of the mean increased (2.1° to 2.6°C). School tightness also decreased as indicated by a larger coefficient of dispersion (24 to 37%). The major preexperimental difference between the first and second day runs was that the fish were not fed before the second day of experimentation. The lowering of the preferred temperature during food deprivation followed that of the California grunion and brook trout (Javaid and Anderson 1967). Furthermore, this selection of cooler water during food deprivation agrees with the findings of Brett et al. (1969) and Brett and Higgs (1970) who showed that a limited food supply resulted in a decrease in the optimal temperature for growth, which is coincident with the final preferendum for sockeye salmon (Brett 1971). The wider preferred temperature range and reduced aggregation may reflect increased searching by hungry fish. Hunger can cause fish to increase the distance between individuals (Hunter 1965) as well as disrupt fish school integrity (Blaxter and Holliday 1958).

Larval California grunion, topsmelt, rockpool blennies, and painted greenlings selected water that was often warmer than naturally available. This behavior has several adaptive advantages but also presents potential harmful consequences resulting from man's alteration of their natural habitat. Selection of warm water by larvae will reduce the duration of the highly vulnerable yolk-sac and larval stages. In King Harbor it kept many of these larvae in the back basins that contained the largest concentration of food organisms (McGowen[5]). Furthermore, in genera such as *Hypsoblennius* that become demersal following the planktonic larval stages, selection of warm water will help the larvae to remain in the nearshore environment where they must be when they leave the planktonic community. Marshall (1966) discussed similar mechanisms by which nearshore demersal species maintain their population integrity. Rockpool blenny larvae, however, that entered water warmer than 28°C lost their equilibrium, could not extricate themselves and eventually died. This same behavioral response of entering water above a lethal temperature and not leaving it has been reported for other species (e.g., Beitinger and Magnuson 1976). Similar behavior in the field near sources of hot water such as power plant effluents may significantly affect local populations. This could be magnified as a result of predation, for it has been shown that the vulnerability of fishes to predation is increased by sublethal heat shocks (Sylvester 1972; Coutant 1973; Yocum and Edsall 1974).

Various workers (Lowe and Heath 1969; Reynolds and Thomson 1974; Reynolds and Casterlin 1976; Beitinger 1977) have reported that the final preferendum is often close to the upper lethal temperature. Frequency distributions skewed to the left such as for topsmelt (Table 1, Figure 7) are reflective of this behavior. The mode occurrence for topsmelt was 26°C, and they sharply avoided warmer water. Coutant (1975) pointed out that the upper avoidance temperature is more sharply defined than the lower one for most species. Beitinger (1977) found bluegill. *Lepomis macrochirus*, tolerated less variation in avoidance temperature near their lethal limits.

Differences in group cohesion for individual runs between nonschooling species such as adult speckled sanddabs (Figure 5) and tightly aggregating ones such as olive rockfish (Figure 6) are illustrated by comparison of the standard deviations about the run selected temperatures. Although a low coefficient of dispersion may indi-

cate tighter aggregation, it could also result from individuals of a normally solitary species with a narrow preferred temperature range being compressed into a tight aggregation by a steep temperature gradient. Comparison of the coefficient of dispersion and the measures of eury- or stenothermal preference (the standard deviation about the mean selected temperature and the coefficient of kurtosis) (Table 1) helps to distinguish between behavioral aggregation and compression of individuals with stenothermal preferences. Juvenile topsmelt, for instance, aggregated closely, but the close association of the individual fish was not the result of thermal compression since they showed a wide temperature preference (Table 1). Greater caution, however, must be used in interpreting the coefficient of dispersion for species such as pile surfperch with a narrow (leptokurtic) range of preferred temperatures (Table 1). The occurrence of pile surfperch in the field at temperatures of 12°-18°C (Stephens[6]) shows that the close aggregation in the gradient was not due to thermal compaction of fish with an obligatory stenothermal preference. These fish in King Harbor were associated with the coolest water available (Stephens, see footnote 6). Coordinated laboratory and field studies provide greater understanding of the factors that affect fish populations and distributions than either investigation alone.

ACKNOWLEDGMENTS

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[6]Stephens, J. 1977. Effects of thermal effluent from Southern California Edison's Redondo Beach Steam Generating Plant on the warm temperate fish fauna of King Harbor marina. Field study report for Phase II. Annual Report for 1 March 1975-29 February 1976. Unpubl. manuscr., 111 p. Southern California Edison Res. Contract No. U0654902.

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APPENDIX TABLE 1.—Equations and an example from an artificial data set for calculation of mean selected temperature and coefficient of dispersion. An artificial data set was used to provide a more concise presentation of the mathematical techniques. The standard deviation of the mean selected temperature is 0.7°C, and the data are neither significantly skewed ($g_1 = 0.00$, $P > 0.05$) nor lepto- or platykurtic ($g_2 = 2.5$, $0.2 < P < 0.4$). Initial, mean, modal, and final selected temperatures were equal (13°C).

MEAN SELECTED TEMPERATURE (MST)

METHOD

STEP 1. Eliminate individual fish observations at the extreme ends of the gradient.

STEP 2. Determine the frequency of occurrence of individual temperatures $f(T_i)$ and the number of fish (F_i) at each temperature (T_i).

STEP 3. Define the valid experimental range (R) as the continuous interval in which the minimum occurrence of a temperature is at least 25% of the maximum observed temperature frequency.

STEP 4. When T_i is an element of R ($T_i \epsilon R$), calculate the relative number of fish (f_i) corrected for the variation in occurrence of each temperature.

STEP 5. When $T_i \epsilon R$, calculate the corrected number of fish (f') for the range of temperatures (R) analyzed.

STEP 6. Compute the percent occurrence of fish (P_i) for each $T_i \epsilon R$.

STEP 7. Determine the mean selected temperature (MST), when $T_i \epsilon R$.

EQUATIONS

$i = 1, \ldots, n$
$T_1 = $ minimum observed temperature
$T_n = $ maximum observed temperature

$f_i = \dfrac{F_i}{f(T_i)}$

$f' = \sum\limits_{i=1}^{n} f_i$

$P_i = \dfrac{f_i}{f'} \times 100$

$MST = \sum\limits_{i=1}^{n} P_i / 100 T_i$

EXAMPLE

Eliminate the one fish that occurred in Compartment 1 at 075 min (see Artificial Data Set).

See Data Analyses for Artificial Data Set.

$R = 8\text{-}16°C$
(See Data Analyses for Artificial Data Set.)

See Data Analyses for Artificial Data Set.

$f' = 4.97$
(See Data Analyses for Artificial Data Set.)

See Data Analyses for Artificial Data Set.

$MST = (0.20)(12°C) + (0.60)(13°C) + (0.20)(14°C) = 13.0°C$
(See Data Analyses for Artificial Data Set.)

COEFFICIENT OF DISPERSION (CD)

METHOD
First calculate the coefficient of dispersion for an individual run (cd_j) and then for the entire experiment (CD).

EQUATIONS

$$cd_j = \dfrac{2 \, sd_j}{T_{jmax} - T_{jmin}} \times 100$$

where
$j = 1, \ldots, m$
$m = $ number of experimental runs
$sd_j = $ standard deviation of the run selected temperature of the jth run

$$CD = \dfrac{\sum\limits_{j=1}^{m} cd_j}{m}$$

$T_{jmax} = $ maximum experimental temperature of the jth run
$T_{jmin} = $ minimum experimental temperature of the jth run

EXAMPLE

$$cd_{000 \, min} = \dfrac{(2)(0.9°C)}{15°C - 5°C} \times 100 = 18\% \qquad CD = \dfrac{(10)(18\%)}{10} = 18\%$$

(See Artificial Data Set.)

DATA ANALYSES FOR ARTIFICIAL DATA SET

i	T_i (°C)	$f(T_i)$	F_i	f_i	P_i
1	5	1	0	–	–
2	6	7	0	–	–
3	7	5	0	–	–
4	8	19	0	0	0
5	9	9	0	0	0
6	10	29	0	0	0
7	11	10	0	0	0
8	12	30	29	0.97	20%
9	13	10	30	3.00	60%
10	14	30	30	1.00	20%
11	15	10	0	0	0
12	16	25	0	0	0
13	17	7	0	–	–
14	18	13	0	–	–
15	19	3	0	–	–
16	20	2	0	–	–

$\Sigma f_i = 4.97 = f'$

ARTIFICIAL DATA SET

TIME (min)	COMPARTMENTS																						RUN SELECTED TEMP. (°C)		cd (%)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	MEAN	SD	
000																								
TEMP. (°C)	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	13.0	0.9	18
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0			
015																								
TEMP. (°C)	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	13.0	0.9	18
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0			
030																								
TEMP. (°C)	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	13.0	0.9	18
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0			
045																								
TEMP. (°C)	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	13.0	0.9	18
NO. OF FISH	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0			
060																								
TEMP. (°C)	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0	13.0	0.9	18
NO. OF FISH	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	0	0			
075																								
TEMP. (°C)	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0	19.5	20.0	13.0	0.9	18
NO. OF FISH	1	0	0	0	0	2	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0			
090																								
TEMP. (°C)	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0	13.0	0.9	18
NO. OF FISH	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	0	0			
105																								
TEMP. (°C)	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	13.0	0.9	18
NO. OF FISH	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	0			
120																								
TEMP. (°C)	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	13.0	0.9	18
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0			
135																								
TEMP. (°C)	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	13.0	0.9	18
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0			