ASPECTS OF ESTUARINE INTERTIDAL ECOLOGY OF JUVENILE STRIPED MULLET, *MUGIL CEPHALUS,* IN HAWAII[1]

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ABSTRACT

Behavior and distribution of schools of young striped mullet, *Mugil cephalus,* were examined in the field and laboratory. Prejuvenile fish approximately 20 mm standard length leave the open ocean to enter intertidal estuarine regions, where they select the shallowest water, areas with extensive diel temperature and salinity fluctuations. At about 50 mm standard length, the mullet move into deeper intertidal waters. It is at this size that mullet are thought to have completed their metamorphosis to juveniles. In a vertical thermal gradient, fish generally <50 mm standard length selected final mean temperatures of 30.0°-32.4°C at the salinities tested (0, 15, 34‰). In the field, they were found in water with high (34.0°-37.2°C), often near lethal (39.0°-42.5°C), temperatures in shallow pools with salinities of 2-30‰. Juveniles generally >50 mm experimentally selected final mean temperatures of 29.0°C at 34‰ salinity to 19.5°C at 0‰ salinity. In the field, fish ≥50 mm remained seaward of the tide line in water of lower and more uniform temperature and higher and more uniform salinity than those recorded for mullet <50 mm. Mullet <50 mm occur seasonally when there are a maximum number of low tides ≤0.0 mm and a minimum number of high tides ≥0.6 m. This allows the mullet increased time to feed undisturbed in areas where there are no predators and intraspecific and possible interspecific competitors for food and space. By the time fish reach 50 mm standard length, the tidal situation changes, allowing predators and competitors access to the shallow areas during low tide. When in the presence of predators, the schooling habit increases chances of survival for individual mullet.

The marine environment includes the highly complex estuarine and intertidal habitats, which undergo continuous fluctuation. Organisms dwelling within these areas must be able to tolerate or escape from the consequences of extreme temperature and salinity oscillations brought about by tidal and meteorological changes. Coral and rocky intertidal tidepools and the estuarine environment serve as nursery and feeding grounds for the young of many species of fishes (Randall 1961; Norris 1963; Lauff 1967; Carr and Giesel 1975).

The purpose of this study was twofold: to determine whether young striped mullet, *Mugil cephalus* Linnaeus, select specific environmental conditions, particularly with respect to temperature and salinity, as found in intertidal estuarine environments in Hawaii, and to explore the possible causal mechanisms that might lead to the selection of such conditions. An experimental vertical thermal gradient (use of such gradients was

reviewed by Mantelman 1958; Ivlev and Leizerovich 1960; Fry 1964) in a tank was used to study the relationship between salinity and temperature and the distribution of schools of young striped mullet, and field observations were made of the distribution, feeding, and predator-prey behavior of schooled mullet.

METHODS AND MATERIALS

Field Sites and Capture of Fish

Young striped mullet were observed and collected in estuarine intertidal habitats at a number of locations on the island of Oahu (Figure 1) in the Hawaiian Archipelago during 1972 and 1973. All experimental fish were captured with hand or beach seines near stream mouths or springs and on tidal mud flats in Maunalua Bay on the southeast side of the island. Schools were usually caught in the morning at low tide and transported <16 km to the Oceanic Institute, Makapuu, Oahu.

Observations were made along Wailupe Beach, Wailupe Stream, and Kuapa Pond Streams (Hawaii Kai Development drainage culverts) in Maunalua Bay, and along Kahana River and a silted Hawaiian fishpond in Kahana Bay on the east side
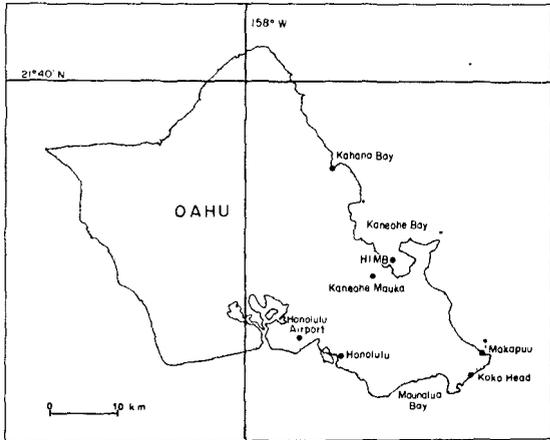
FIGURE 1.—The island of Oahu, Hawaii, showing the major study areas and the locations at which environmental data were collected.

of Oahu. Observations were made primarily during daylight hours, but a few night observations were made as well at Kahana River and Wailupe Beach. Field observations were recorded as I followed at a distance schools of mullet as they swam about estuarine intertidal regions and estuarine streams. Information about the distribution of mullet was also collected by using seines. Behavioral and distributional records were kept and the temperature and salinity of the water through which the fish passed were measured with a tele-

thermometer and compensated salinity refractometer, respectively.

Young *Mugil cephalus* were distinguished and differentiated from the young of a second sympatric species of mullet, *Chelon engeli,* an introduced species (Randall and Kanayama 1972), by differences in body pigmentation pattern and opercle coloration. In addition, young *C. engeli* ≤50 mm standard length (SL) occurred in the intertidal estuarine regions predominantly during the summer and fall, whereas, striped mullet predominated in the winter and spring months. Only observations of mullet that were unquestionably identified as striped mullet were used in this report.

Experimental Methods

Experiments were carried out at the Oceanic Institute during 1972 and 1973 (Table 1). An experimental thermal vertical gradient was established in a 566-l cylindrical Plexiglas[3] tank, 91 cm high and 89 cm in diameter, inside a lighttight enclosure (Figure 2). Epoxy-coated copper coils spiraled around the inside of the tank, having entered through the surface above and through the side at the bottom. These separate sets of coils exited at midtank through the side. Pumps con-

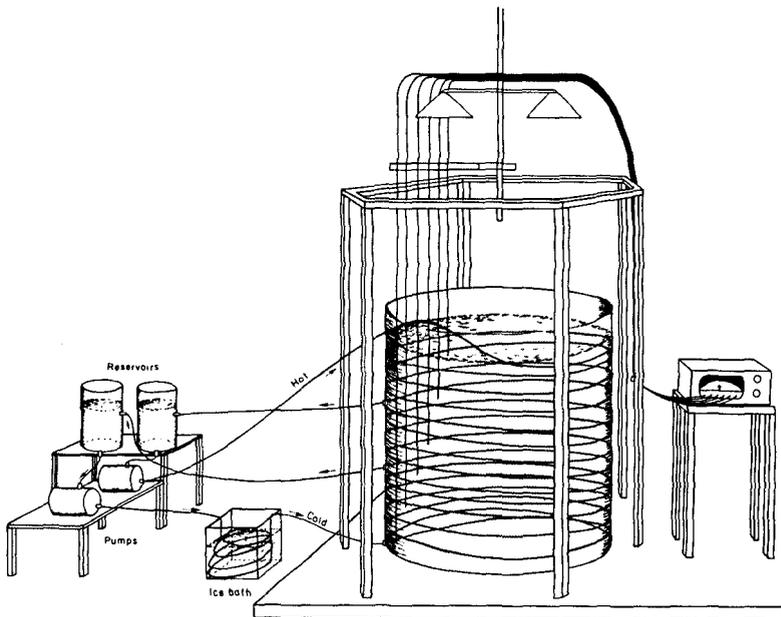[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

FIGURE 2.—Experimental apparatus (diagramatic). Light excluding sides and covering have been removed from frame.

TABLE 1.—Summary of experimental conditions and fish statistics.

Experimental salinity (‰) (actual test salinity)	Month and year of experiments	Min-max tank temp (°C)	Number fish in size range (mm SL)								Length to nearest mm Mean (range)	Total number fish	Experimental group code (see Figure 3)
			17-19	20-29	30-39	40-49	50-59	60-69	70-79	80-130			
34(32)	Feb. 1972	16.8-36.0	2	36							24 (19-28)	38	
32	Mar. 1972	15.1-38.6		39	11						27 (21-38)	50	A1, 2, 3
34	Mar. 1972	17.0-40.1		3	29	2					34 (29-43)	34	
			2	78	40	2					28 (19-43)	122	
34(33)	May 1972	17.8-40.8			7	29	2				42 (37-52)	38	
33	May 1972	17.5-41.0				14	17				51 (46-59)	31	B1, 2, 3
					7	43	19				46 (37-59)	69	
34(36)	July 1972	15.8-39.2					5	4	7	2	68 (55-83)	18	
34	July 1972	15.0-39.2					7	3	10	11	75 (56-98)	31	
32	Mar. 1973	15.0-37.8				1		5	9	22	80 (48-103)	37	C1, 2, 3
32	Mar. 1973	17.0-40.0								20	109 (82-129)	20	
						1	12	12	26	55	82 (48-129)	106	
15(16)	Jan. 1972	16.9-40.0		13	3						27 (24-31)	16	
(14)	Mar. 1973	13.0-39.0	1	39							26 (19-29)	40	D1, 2, 3
(15)	Mar. 1973	13.2-39.9		27	23						28 (20-39)	50	
			1	79	26						26 (19-39)	106	
15(14)	Aug. 1972	15.5-39.8						1	3	18	88 (69-114)	22	
15	Mar. 1973	14.1-39.8							1	10	98 (75-125)	11	E1, 2, 3
								1	4	28	92 (69-125)	33	
0	Feb. 1972	15.9-36.9		26	4						26 (22-34)	30	
.	Mar. 1972	16.4-38.9	2	36							22 (19-26)	38	
.	Mar. 1972	16.0-40.1	1	47	10						27 (17-34)	58	F1, 2, 3
.	Mar. 1973	14.8-39.0		35	2						26 (21-31)	37	
			3	144	16						24 (17-34)	163	
0	May 1972	17.0-38.5			10	19	4				43 (35-51)	33	G1, 2, 3
0	Jan. 1973	18.8-38.2							1	35	98 (76-118)	36	
.	Mar. 1973	16.2-38.6								16	102 (87-130)	16	H1, 2, 3
									1	51	99 (76-130)	52	

nected to reservoirs circulated water, chilled as it passed through a set of coils in an ice bath, before entering the bottom of the tank, and water heated by a braided glass heating tape wrapped around a section of the coil, before it passed into the tank at the surface. The reservoirs allowed air bubbles to escape and the addition of water to the coils.

Vinyl-coated thermistor probes (and leads), extending through plastic tubes to various levels in the tank, ran above the top of the tank and out to a telethermometer recorder.

Fine mesh plastic window screen was attached to the inside circumference of the coils to keep fish in the central area of the tank. The volume of water in the tank available to the fish was approximately 486 l, 88 cm in diameter and 80 cm deep. Observations were made through narrow eye-width slits cut at various levels in each side of the enclosure. A light-excluding cover surrounded the observer during observations. The viewing slits were closed when not in use.

Water samples were taken from the surface, middepth, and bottom before and after each experiment for oxygen, pH, and salinity analysis. Oxygen measurements could not be made con-

tinuously during the experiments, but oxygen measurements before and after each experiment did not change noticeably. In addition, respiratory movements of mouth and opercles, which might have been indicative of oxygen deficiencies, in the mullet did not change with increased heating. The above measurements were made primarily to ensure that mullet were not orienting to factors other than temperature.

Illumination was provided by two 15-W incandescent light bulbs fixed in reflectors 84 cm above the surface of the water. Due to the position and low wattage of the light sources, a light gradient was established in the tank. The behavioral and distributional responses of the fish in a continuously changing thermal environment indicated that orientation to temperature and not light gradients occurred. The same observations were used to control for any orientation to pressure gradients, which inevitably existed in the 80-cm deep tank.

One of three experimental salinity conditions, freshwater (range 0-2‰), 15‰ (range 14-16‰), and 34‰ (range 30-36‰), was established prior to placing the fish in the tank. Freshwater was

thoroughly mixed with seawater of 36‰ salinity until a desired salinity was obtained in the tank. Frequently, schools of fish in the field were not caught in water of identical salinity to that used experimentally. Before placing these fish in the experimental tank, freshwater slowly ran into the container of water in which the fish were transported to the laboratory. When the desired lower salinity was reached by dilution and overflow of the water in the container (this required about 60 min to accomplish), the fish were transferred by dip net to the experimental tank. The experimental tank had a water temperature within 1° or 2°C of the water in which the fish were caught and transported or in which dilution occurred.

Within 30-60 min after being placed in the tank, schools and individual mullet swam throughout the tank at relatively uniform speeds. Single and grouped individuals "grazed" along the sides and bottom of the screen in the tank. The behavior of the mullet at this time appeared to be similar to the behavior of undisturbed fish observed in the field.

The water in the tank was cooled and heated simultaneously after the fish demonstrated what appeared to be "normal" schooling and grazing behavior. At half-hour intervals the temperature at various levels was recorded and the behavior and depth and temperature distribution of the mullet were noted. The observations required about 1 or 2 min to complete. Observations continued until the vertical distribution of the mullet did not change with respect to specific water temperatures during two or three consecutive observations. This occurred between 4 and 8 h after commencing the experiments, when the maximum water temperature in the tank was between 36.0° and 40.8°C, and the minimum temperature was between 13.0° and 19.0°C. Upon termination of the observations, the heating and chilling equipment was turned off, water samples were collected, and one of the sides of the enclosure around the tank was slowly removed. The lights were dimmed slowly and turned off by a rheostat. The fish were left in the tank overnight, exposed to natural twilight conditions in the evening and morning, the room having a number of large windows. During the evening and overnight periods the tank temperature gradually became more uniform.

Well before a second series of observations was to be made during the next day, the side of the tank's enclosure was replaced, the lights having been turned on during the twilight period by a

rheostat. The tank was also oxygenated for approximately 30 min, followed by at least an additional 30-min period during which the tank was not disturbed. The second day of observations served to check on the experimental procedures and results obtained the first day, and to achieve higher tank temperatures than reached during the first day. Statistical comparisons between first and second day activity were not significant ($P \geqslant 0.05$), indicating that the fish did not change their depth or temperature distributions.

RESULTS

Experimental

Prior to the onset of heating and chilling, fish generally <50 mm SL (Table 1), with one exception, initially concentrated near the surface or in the upper half (40-80 cm) of the tank. Fish in the 30- to 50-mm SL size ranges in 0‰ salinity were initially concentrated in the lower half (0-40 cm) of the tank. Fish generally ≥50 mm SL initially concentrated near or on the bottom, or in the lower half of the tank. However, fish of all sizes continuously moved throughout the 80-cm deep tank, indicating that the light and pressure gradients and the depth of water were not limiting. When left for hours in the tank at constant temperature conditions at each test salinity, the mullet exhibited the same behavior, distribution patterns, and movements as those observed in mullet before heating and chilling were initiated during the experiments. These observations served as a control for the distributional patterns of mullet observed under test conditions.

Experimental results were grouped and analyzed according to test salinities (0, 15, and 34‰) and mullet size ranges (20-30, 30-50, and ≥50 mm SL) (Table 1). There was overlap and occasional fish outside of specific size ranges in some experiments due to the size composition of the individual mullet caught in schools in the field and subsequently put into the experimental tank. The experimental time period was divided for analysis into five observation intervals, each consisting of three observations (i.e., 1 complete hour of observation with observation being made each half hour). Only data for observation intervals 1, 3, and 5 are presented in Figure 3. Each graph consists of open histograms for the temperature and depth distributions for fish of specified size ranges, test salinity, and observation interval. Observations of

depth distribution were made to within 5-cm intervals; the means given in the graphs being the mean of a given interval (e.g., 47.5 cm for 45-50 cm).

Statistical comparisons for depth or temperature distributions were significant (analysis of variance, $P \leqslant 0.001$) in all but a few cases. The following comparisons were made, the exceptions to $P \leqslant 0.001$ values being noted in parentheses: 1) between observation intervals for given fish size ranges and test salinity (no exceptions), 2) between salinities for given fish size ranges and observation interval (depth distribution for fish $\geqslant 50$ mm SL in observation interval 5 and salinities 15 and 34‰ ($P = 0.27$); depth distribution for fish 20-30 mm SL in observation interval 1 and salinities 0 and 15‰ ($P < 0.003$); temperature distribution for fish $\geqslant 50$ mm SL in observation interval 1 and salinities 0 and 15‰ ($P < 0.002$)), and 3) between size ranges for a given test salinity and observation interval (depth distribution for a salinity of 34‰ in observation interval 5 and fish size ranges 30-50 and $\geqslant 50$ mm SL ($P < 0.004$); temperature distribution for salinity 34‰ in observation interval 5 and fish size ranges 20-30 and 30-50 mm SL ($P = 0.46$)).

Changes in depth distribution of fish are readily discernable in the histograms in Figure 3. At each test salinity, with the exception of 30-50 mm SL fish at 0‰ salinity, mullet $\leqslant 50$ mm SL moved downwards in the tank to a mean depth of 47.5 or 52.5 cm by the last observation interval. Fish $\geqslant 50$ mm SL moved up to mean depths of 32.5 to 42.5 cm. Fish 30-50 mm SL at 0‰ moved from an initial distribution in the bottom half of the tank to a mean of 52.5 cm during the remainder of the experiments (observation intervals). As test salinities decreased so did the final depth distribution for given fish size ranges, except for 30- to 50-mm SL fish.

Changes in fish depth distribution were directly related to tank temperature, since water temperature decreased with depth. However, temperature values changed rapidly between depths 60 and 20-30 cm and were relatively isothermal and cold between 20-30 cm and the bottom of the tank, and isothermal and hot above 60 cm. As a result only small differences in final depth distribution corresponded with relatively large differences in final temperature distribution.

The mean selected temperature tended to increase between observation intervals 1 and 5

at each test salinity for given fish size ranges. The exception to this tendency was fish $\geqslant 50$ mm SL at 0‰ salinity (20.9°-19.5°C). Fish $\leqslant 50$ mm SL (20-30 and 30-50 mm) tended to select higher final observation interval 5) mean temperatures (30.0°-32.3°C) than did fish $\geqslant 50$ mm SL (20.0°-19.5°C) at each test salinity. For all fish size ranges the final mean selected temperature tended to decrease as the test salinity decreased. This decrease was greatest for fish $\geqslant 50$ mm SL (29.0°-19.5°C).

The depth and temperature distribution results taken together indicate that temperature selection was the more important, depth distribution being secondarily related. Other gradients such as light, pressure, and oxygen, if present, did not appear to influence the distribution of the mullet at least to the extent that temperature did. Fish $\leqslant 50$ mm SL appeared to have a predilection towards the surface whereas fish $\geqslant 50$ mm SL appeared to be predisposed towards the bottom. This was evident before the initiation of heating and chilling in each experiment and during constant temperature control experiments. As the experiments progressed it also appeared as if mullet $\leqslant 50$ mm SL, in most instances, were "forced" downwards by rising temperatures. Similarly, mullet $\geqslant 50$ mm SL were "forced" upwards by decreasing water temperature, and then downwards by rising temperature, such that their final temperature and depth distributions were somewhat lower than those for fish $\leqslant 50$ mm SL in similar conditions.

Just how important the actual temperature and depth distribution values selected by mullet are is unknown. What does appear to be important is the relative difference between distributions for fish generally < 50 mm SL as compared with those for fish generally > 50 mm SL at each salinity, and the relative changes which occurred between salinities for each fish length interval. The predisposition of fish < 50 mm SL towards the surface (and higher temperatures) may be adaptive in the field. Warm water rises and the warmest (hottest) water is usually on the surface. By moving in the surface layer fish < 50 mm SL may be able to orient towards the shallowest water inshore, which at low tide should also be the warmest. The predisposition of fish > 50 mm SL towards the bottom of the tank (and cooler temperatures) may similarly be adaptive in the field. In this case movement away from areas subjected to tide pool formation may be important for survival.

A $\left\{\begin{array}{l}34°/oo\ \text{Salinity}\\20 - 30\ \text{mm SL}\end{array}\right\}$1
n = 698
$\overline{X}D$ = 67.5 cm
$\overline{X}T$ = 25.8° C

A2
n = 734
$\overline{X}D$ = 62.5 cm
$\overline{X}T$ = 31.2° C

A3
n = 542
$\overline{X}D$ = 52.5 cm
$\overline{X}T$ = 32.3° C

B $\left\{\begin{array}{l}34°/oo\ \text{Salinity}\\30 - 50\ \text{mm SL}\end{array}\right\}$1
n = 414
$\overline{X}D$ = 52.5 cm
$\overline{X}T$ = 28.2 °C.

B2
n = 414
$\overline{X}D$ = 57.5 cm
$\overline{X}T$ = 32.9°C

B3
n = 76
$\overline{X}D$ = 47.5 cm
$\overline{X}T$ = 32.2 °C

C $\left\{\begin{array}{l}34°/oo\ \text{Salinity}\\\geq 50\ \text{mm SL}\end{array}\right\}$1
$\overline{X}D$ = 32.5 cm
$\overline{X}T$ = 24.6° C
n = 599

C2
$\overline{X}D$ = 47.5 cm
$\overline{X}T$ = 28.5° C
n = 581

C3
$\overline{X}D$ = 42.5 cm
$\overline{X}T$ = 29.0° C
n = 362

D $\left\{\begin{array}{l}15°/oo\ \text{Salinity}\\20 - 30\ \text{mm SL}\end{array}\right\}$1
$\overline{X}D$ = 57.5 cm
$\overline{X}T$ = 26.5° C
n = 636

D2
n = 546
$\overline{X}D$ = 57.5 cm
$\overline{X}T$ = 30.4° C

D3
n = 573
$\overline{X}D$ = 47.5 cm
$\overline{X}T$ = 30.0° C

E $\left\{\begin{array}{l}15°/oo\ \text{Salinity}\\\geq 50\ \text{mm SL}\end{array}\right\}$1
$\overline{X}D$ = 27.5 cm
$\overline{X}T$ = 23.2° C
n = 198

E2
n = 187
$\overline{X}D$ = 37.5 cm
$\overline{X}T$ = 24.2° C

E3
n = 44
$\overline{X}D$ = 42.5 cm
$\overline{X}T$ = 24.8° C

F $\left\{\begin{array}{l}0°/oo\ \text{Salinity}\\20 - 30\ \text{mm SL}\end{array}\right\}$1
n = 771
$\overline{X}D$ = 57.5 cm
$\overline{X}T$ = 25.2° C

F2
n = 829
$\overline{X}D$ = 62.5 cm
$\overline{X}T$ = 30.0° C

F3
n = 925
$\overline{X}D$ = 47.5 cm
$\overline{X}T$ = 30.8° C

G $\left\{\begin{array}{l}0°/oo\ \text{Salinity}\\30 - 50\ \text{mm SL}\end{array}\right\}$1
$\overline{X}D$ = 17.5 cm
$\overline{X}T$ = 28.0° C
n = 156

G2
n = 99
$\overline{X}D$ = 52.5 cm
$\overline{X}T$ = 29.4° C

G3
n = 99
$\overline{X}D$ = 52.5 cm
$\overline{X}T$ = 30.3° C

H $\left\{\begin{array}{l}0°/oo\ \text{Salinity}\\\geq 50\ \text{mm SL}\end{array}\right\}$1
$\overline{X}D$ = 22.5 cm
$\overline{X}T$ = 20.9° C
n = 99

H2
n = 156
$\overline{X}D$ = 27.5 cm
$\overline{X}T$ = 21.3° C

H3
n = 32
$\overline{X}D$ = 32.5 cm
$\overline{X}T$ = 19.5° C

FREQUENCY DISTRIBUTION (%)

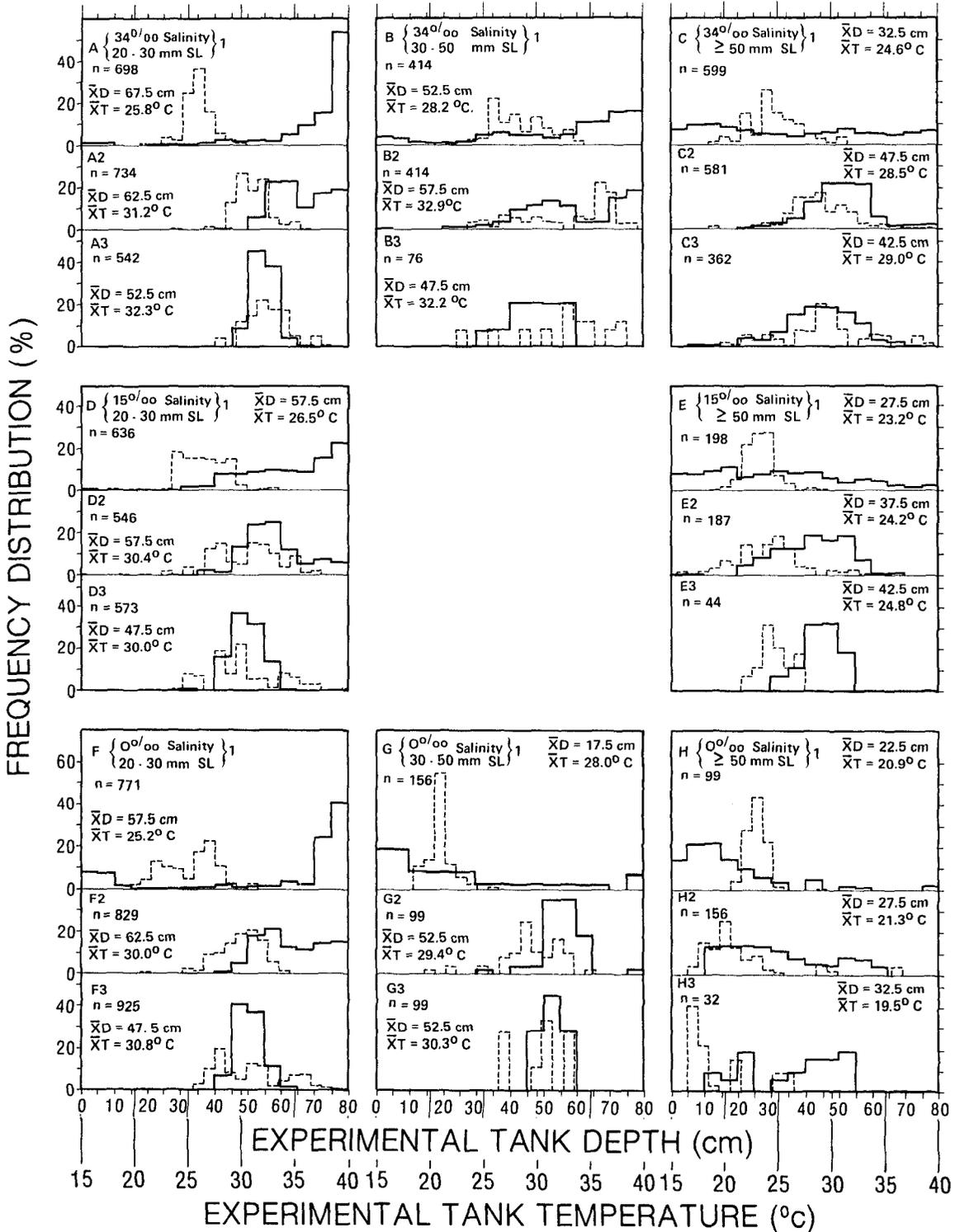EXPERIMENTAL TANK DEPTH (cm)

EXPERIMENTAL TANK TEMPERATURE (°c)

FIGURE 3.—Experimental temperature (dashed line) and depth (solid line) distributions for indicated mullet size ranges in the 80-cm deep tank at the indicated salinity (34, 15, or 0‰). No experiments were conducted with fish 30-50 mm SL at 15‰ salinity. Each of the eight salinity-fish size range "conditions" are subdivided into three observation intervals: 1) observation interval 1, corresponding to the first three experimental observations (1-3); 2) observation interval 3 (7th-9th observations); and 3) interval 5 (13th-15th observations). Also presented are mean depth ($\overline{X}D$) and temperature ($\overline{X}T$) data. Sample size (n) is based on the pooled data for the number of times each fish was observed within the observation interval for all experiments at a given salinity and for a given fish size range. Experiments varied in duration and number of observations made. Thus, the sample size fluctuates. See Table 1 for the actual (maximum) number of fish and experiments for each salinity-fish size range condition.

Field

Mullet Distribution

The initial appearance of the 17- to 35-mm SL mullet prejuveniles, a distinct silvery, countershaded pelagic stage (Hubbs 1958), in the estuarine intertidal regions varied between 1972 and 1973. In 1972 they were observed and collected along the tide line (the most shoreward edge of falling or rising water, which is contiguous with deeper offshore water) in sand and mud flat tide pools and around freshwater streams and springs at the end of January. In 1973 they did not appear in these areas until the end of February. Prejuveniles were particularly abundant in areas with the finest silt, mud, and/or sand particles near the outlets of freshwater rivers, streams, or springs.

Fish ≥50 mm SL could be seen year around in the intertidal areas. The main body of this study concentrated on those fish that entered the intertidal in 1972. Also observed were juveniles of the 1971 year class, fish ≥80 mm SL, in the intertidal in early 1972, and prejuveniles and juveniles of the 1973 year class, ≤50 mm SL, in early 1973. The disappearance of prejuveniles-juveniles from the low tide intertidal swash zone (Hedgpeth 1957) and tide line regions appeared to be completed by the end of June each year, although occasional schools were seen as late as August. However, these schools were composed of fish usually about 40 mm SL or larger, that moved with the tide line.

Prejuvenile mullet undergo metamorphosis to juveniles after entering the estuarine intertidal region. The most evident change is the loss of the pelagic silvery coloration with a general darkening of all surfaces, especially the dorsal side. However, a general countershaded pattern remains. Other less obvious changes include: the elongation and convolution of the intestine, development of adipose eyelids, transformation of the third anal element from a soft ray to a spine, and changes in the morphology of lips and teeth. Metamorphosis is thought to be completed at about 50 mm SL (Jacot 1920).

During metamorphosis, diet and feeding habits change. I found copepods in the stomach contents of some prejuveniles in Hawaii in the estuarine intertidal regions. Other prejuveniles and juveniles had plant and animal material as well as mud or silt in their stomachs. I found that sediments constituted the bulk of the diet of juvenile mullet in some localities in Hawaii. In the estuarine intertidal region around the island of Oahu, the sizes of these injested particles ranged from 0.02 to 0.60 mm in diameter. Odum (1968) showed that fine particulate materials are a source of adsorbed organic matter and microorganisms, and are important in the diet of *Mugil cephalus* along parts of the east coast of the United States. The change in diet from copepods to plant material and mud or silt presumably occurs concurrently with changes in intestinal length, lips, and teeth. After metamorphosis is completed, the juvenile fish move into somewhat deeper intertidal water.

Prejuveniles and juveniles of all sizes formed schools ranging in size from tens to hundreds of individuals. Prejuveniles and juveniles <50 mm SL were always observed in the shallowest, warmest water near shore wherever they occurred (Table 2). At low tide they were located along the tide line, the shallowest water along estuarine streams, and trapped in shallow mud flat and occasionally sand tide pools (the swash zone). Intense continuous feeding activity was usually observed. The substrate in the areas in which the small mullet occurred was covered usually by the finest inorganic sediment (sand and silt 0.02-0.60 mm in diameter).

Salinity and temperature values changed daily depending on tide level (water depth), wind, bottom type (particle size, color, etc.), insolation, and the location of springs and streams. Often a spatial as well as temporal kaleidoscope of temperature and salinity values was recorded, especially along Wailupe Beach.

On 15 March 1972 the last hour (1200-1300 h local time) of a natural fish kill was observed in

TABLE 2.—Summary of field data collected during observations of prejuvenile and juveniles *Mugil cephalus* in Hawaii during 1972-73.

Locality	Habitat	Size (mm SL)	Month	Tide	Temperature range (°C)	Salinity range (‰)	Water depth (cm)	School size	Remarks
Wailupe Beach, Maunalua Bay[1]	Inshore of tide line in swash zone, tide pools, freshwater springs	<50	Feb. to May	Low	19.8-37.2 (22.0-26.9 in center of springs)	2-29.5	0.6-15	10's-100's	Mullet trapped in tide pools. No predators observed. No mullet ≥50 mm SL observed or collected.
	Coral rock/rubble tide pools with open connections/channels to deeper water	≥50	Feb. to May; Dec.	Low	23.0-35.1 (22.0-26.9 in springs)	2-35 (2-10 in springs)	2.5-30	10's-100's	Seaward of tide line. Occasionally attacked by predatory fish.
	Mud/sand flats, sandy beach, coral rock/rubble	<50	Feb. to June	High	26.1-30.1	10-35	5-30	10's-100's	In wave wash (tide line); attacked by predators.
		≥50	Feb. to June; Dec.	High	26.1-30.1	10-35	2.5-90	10's-100's	Feeding. Attacked by predators.
Wailupe Stream, Maunalua Bay[1]	Tidal stream	20-200	May	Low/high	27.8	—	1.8-200	10's-100's	In shallowest water. Feeding during low tide. Attacked by predators at high tide.
Kaupa Pond, Maunalua Bay[1]	Cement drainage culverts	<50	Feb. to July	Low	21.9-36.2	0-32	0.6-13	10's	Tideline. Feeding in shallowest water.
	Mud bottomed channel	≥50	Feb. to July	Low	21.6-30.1	15-32	13-30+	10's	Feeding on surface. Unable to see below surface.
		<50	Feb. to July	High	28.1-34.0	15-32	0.6-13	10's	Along tide line—shallowest water.
		≥50	Feb. to July	High	28.1-34.0	15-32	30+	10's	Feeding.
Kahana Bay[1]	Silted areas, fishpond	<50	May	Low	—	—	0.6-5	10's	Feeding. No predators observed.
	Fishpond channels	30-200	May	Low	24.0-26.5	2-15	0.6-15+	10's	Feeding. No predators observed.
	River; mud/sand spits (bars)	<50	May	Low	24.1-29.6	2-30	0.6-5	10's	Feeding in tide line/shallowest water.
		≥50	May	Low	24.1-29.6	2-31	2.5-7.5	3-5	Feeding.
		<50	May	High	20.0-25.0	—	2.5-15	10's	Feeding in tide line/shallowest water amongst mangrove roots.
Kahana Bay[2]	River; mangrove vegetation	<50	May	Low/high	—	—	2.5-15	—	In shallowest water. Individuals spread out motionless on bottom.
Wailupe Beach, Maunalua Bay[2]	Mudflats; coral rocks/rubble	<50	Feb. to July	Low/high	—	—	2.5-15	—	In shallowest water. Spread out or in compact groups motionless on bottom.
		≥50	Feb. to Aug.	Low/high	—	—	7.5+	—	In shallowest water. Individuals spread out motionless on bottom.

[1]Daylight observations of mullet.
[2]Night observations of mullet.

one of the cement culverts in Kuapa Pond (Hawaii Kai), Maunalua Bay. The tide was low and just starting to turn and flood. Prior to this day heavy rains washed down large amounts of silt, rocks, and debris to a depth of about 0.2-0.5 m. A narrow channel was cut through the mud by the trickling stream, and isolated "tide pools" or pockets of water were common. An estimated several thousand prejuvenile and juvenile mullet 18-80 mm SL were found dead along the bottom of the culvert. Although it appeared that the fish had a free exit at higher tide levels, via the shallow (1 cm deep at low tide) channel to the cooler tidal region (26°-30°C), the fish were presumably trapped physi-cally by the debris and/or by a very rapid increase in water temperature. Dead mullet were found in the pockets with water temperatures of 39.5°-42.5°C. The only survivors observed were mullet 20-35 mm SL slowly swimming in small pockets at temperatures as high as 39.0°-41.1°C. Salinity measurements were not made, but would be expected to be low.

Juvenile mullet ≥50 mm SL were not observed or collected in tide pools at low tide. At low tide these larger fish occurred beyond the tide line in tide pools with open connections to deeper water or along sills and sand/mud flats which sloped into deeper water. These areas were characterized by

higher but more uniform salinities and lower but more uniform temperatures than areas in which fish <50 mm SL were generally found.

At high tide, water temperature and salinity values were nearly uniform throughout a given location. Mullet <50 mm SL were concentrated along the tide line on the beach or along the sides of rivers in the shallowest water available. Schools were dense and often composed of more individuals than found in schools at low tide in the same area. Little feeding occurred; evasion of predators was seen more commonly. At high tide, schools of mullet with individuals ⩾50 mm SL moved into the former tide line and tide pool areas, and were observed feeding in the areas from which the smaller mullet retreated.

The results of the experiments and field observations demonstrate that dynamic differences occur in the behavior and distribution of schools of mullet composed of individuals generally <50 mm SL as compared with schools with juveniles of greater length. In the field young mullet <50 mm SL prefer and select areas characterized by minimal water depth, tide pool formation, relatively high fluctuating temperatures, and relatively low fluctuating salinities. Juveniles ⩾50 mm SL, on the other hand, seek somewhat deeper water and tide pools with lower more uniform temperatures and higher more uniform salinities.

Experimentally, a wide range of temperature values (13°-40.8°C) was available to the fish. However, mullet <50 mm SL tended to concentrate in water of higher temperature near the surface of the tank and fish >50 mm SL tended to occur deeper in the tank at lower temperatures for each test salinity. Although the experimental tank al-

lowed fish a means of behaviorally escaping lethal or near lethal conditions (as presumably did deeper tide pools for mullet ⩾50 mm SL in the field), entrapment in shallow intertidal tide pools in the field did not. Fish <50 mm SL appeared to actively seek such near lethal conditions in the field (and experimentally), and as observed in a Kuapa Pond stream culvert, occasionally perished as a result.

Predators

Most predators observed interacting with mullet during this study were solitary stalking or stationary "sit-and-wait" species (Table 3). Attacks by predators upon schools of mullet with individuals <50 mm SL were almost nonexistant at low tide.

Where deeper water was immediately contiguous with a shallow water shelf (e.g., along Kahana River), predators (e.g., barracuda) in the deeper water were observed orienting towards and paralleling the movements of schools of the small mullet feeding in the shallower water. When mullet strayed off the shelf into deeper water, they were attacked. Predation upon mullet ⩾50 mm SL during low tide was occasionally observed as schools moved and fed in the deeper intertidal region.

At high tide, schools of these larger mullet continued to be attacked by predators, as they were at low tide. Similarly, during high tides and ebb and flood periods, predators attacked mullet schools with individuals <50 mm SL.

At night, along Wailupe Beach and the Kahana River (Table 2), mullet schools broke up and individuals spread out and remained relatively motionless near the bottom. The fish slowly moved

TABLE 3.—Predatory fish observed interacting with schools of mullet.

Location	Species	Standard length (mm)	Water depth (cm)	Tide	Remarks
Wailupe Beach	Lizardfish Saurida gracilis	60-175	5-23	Low/high	In tide pools with open connections and channels to deeper water. Attacked and chased juveniles of all sizes.
	Needlefish Tylosurus crocodilus	100-300	30-75	High	A possible predator, moved in with flood tide. Observed following schools of mullet near surface.
	Great barracuda, Sphyraena barracuda	50-225	30-75	Low/high	Moved inshore with flood tide; attacked and chased individuals of all sizes in schools. Followed feeding individuals in schools. Swam slowly along the shoreline at high tide.
Wailupe Stream	Great barracuda	40-600	30-90	Low/high	Mullet <50 mm SL usually in shallowest water 1.8-75 cm deep. Barracuda in deeper water followed or paralleled movements of mullet in shallow water and attacked when the mullet strayed into deeper water.
Hawaii Kai (Kuapa Pond) culverts	Great barracuda	30-250	15-75	High	Moved in with flood tide. Water turbid; caught in seines with juvenile mullet. No mullet found in stomach contents.
Kahana Bay River	Great barracuda	125-500	15-60	Low/high	At low tide mullet <50 mm SL in shallowest water 15 cm deep, barracuda followed (paralleled) schools of mullet in shallower water (see above).
	Eleotris sandwichensis	78	7.5-30	Low	Single unsuccessful attack on school of mullet of individuals about 40 mm SL. Caught after attack.

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(drifted) with the tides. The break up of schools may have been a result of reduced predation and/or lowered visual sensitivity thresholds (Munz and MacFarland 1973).

When a school was attacked, it usually split into two or more segments and passed around behind the predator to reform a single school again. When a predator was successful in separating an individual from a school, a chase occurred, the results of which were seldom observed. Of the approximately 50 lizardfish stomach contents analyzed, one contained a juvenile mullet. None of the 10 barracuda stomach contents analyzed contained juvenile mullet.

Potential invertebrate predators were abundant in the various habitats where mullet occurred. However, only individuals of a single crab species, *Thalamita crenata,* were observed stalking and extending their chelipeds toward passing mullet. In one instance an individual crab did capture a juvenile mullet, but only after it had been wounded by and escaped from a barracuda.

DISCUSSION

Mugil cephalus is a worldwide (lat. 42°N-42°S, Thomson 1966) inhabitant of the estuarine intertidal as well as freshwater and coastal marine environments (Broadhead 1953, 1955; Hendricks 1961; Thomson 1963, 1966; Johnson and McClendon 1970). In Hawaii, selective pressures appear to have favored prejuvenile and juvenile mullet that are able to survive in the shallowest, warmest estuarine intertidal waters, waters that are characterized by temporal and spatial heterogeneity with respect to temperature, salinity, and depth. Before discussing the adaptations evolved by striped mullet making possible survival in estuarine intertidal regions, a discussion of the environmental variables important to young mullet in Hawaii might be in order.

The monthly occurrence of mullet <50 mm SL observed in 1972 and 1973 in Hawaii is presented with data for 12 consecutive years (1962-73) of recorded (skycover, rainfall, seawater temperature) and predicted (tidal) data in Figure 4. These appear to be the most important environmental factors that bear directly upon the lives of mullet in the estuarine intertidal region. Indirectly, the length of daylight (time from sunrise to sunset) may also be important; it is shortest (about 10.9 h) about 22 December each year, and longest (13.3 h) about 21 June each year.

Visual observations and collections of mullet <50 mm SL indicate that these mullet occur in the Hawaiian intertidal estuarine regions during the months when there are a maximum number of low tides ≤0.0 m (mean tide level at Honolulu is 0.2 m (0.8 ft)). Perhaps of greater importance is the occurrence of mullet when there is a minimum number of high tides ≥0.6 m (2.0 ft). In Maunalua Bay, tide pools begin to form when the tide level is approximately 0.06 m (0.2 ft). The number of tides that would result in tide pool formation at noon (1000-1400 h local time) begins to decrease during the time of the year mullet are undergoing metamorphosis in the intertidal estuarine region, but is still maximal when prejuveniles first enter the inshore areas. Thermal and salinity stresses should be maximal during the noon time period. It is not known whether this tidal-estuarine intertidal situation is unique to Hawaii or of more widespread occurrence. Also unknown is whether the peak occurrence of young mullet during such tidal relationships is fortuitous, or whether selection pressures have resulted in a shift of the peak occurrence from either earlier or later in the winter-spring season to its present "position" in April.

The extent to which stress occurs in the intertidal estuarine region may be ameliorated by low ambient (oceanic) seawater temperatures and maximum cloud cover. During the time mullet <50 mm SL are found in the intertidal estuarine region in Hawaii, seawater temperatures are minimal and increasing, and average cloud cover is seasonally maximal. During the late winter-spring, the lowest seasonal seawater temperatures occur in the tropical-temperate Northern Hemisphere, and increase until maximum levels are reached about September.

The average maximum amount of cloud cover, which occurs in Hawaii during April (when young

FIGURE 4.—The relative abundance of mullet <50 mm SL in the Hawaiian estuarine intertidal tide pools compared with environmental data collected (seawater temperature, rainfall, and sky cover) and predicted (tides). The monthly means (connected by horizontal lines), ranges (vertical lines), and standard deviations (vertical boxes) were derived from data for the 12-yr period, 1962-73. Mullet abundance data were from field observations and collections in 1972-73. Sky cover data were derived from monthly average values. Sky cover and rainfall data were taken from *Climatological Data, Hawaii,* U.S. Weather Bureau, NOAA; tidal information from *Tide Tables,* West Coast of North and South America including the Hawaiian Islands, National Ocean Survey, NOAA; seawater temperature data were collected by the National Marine Fisheries Service, Honolulu.
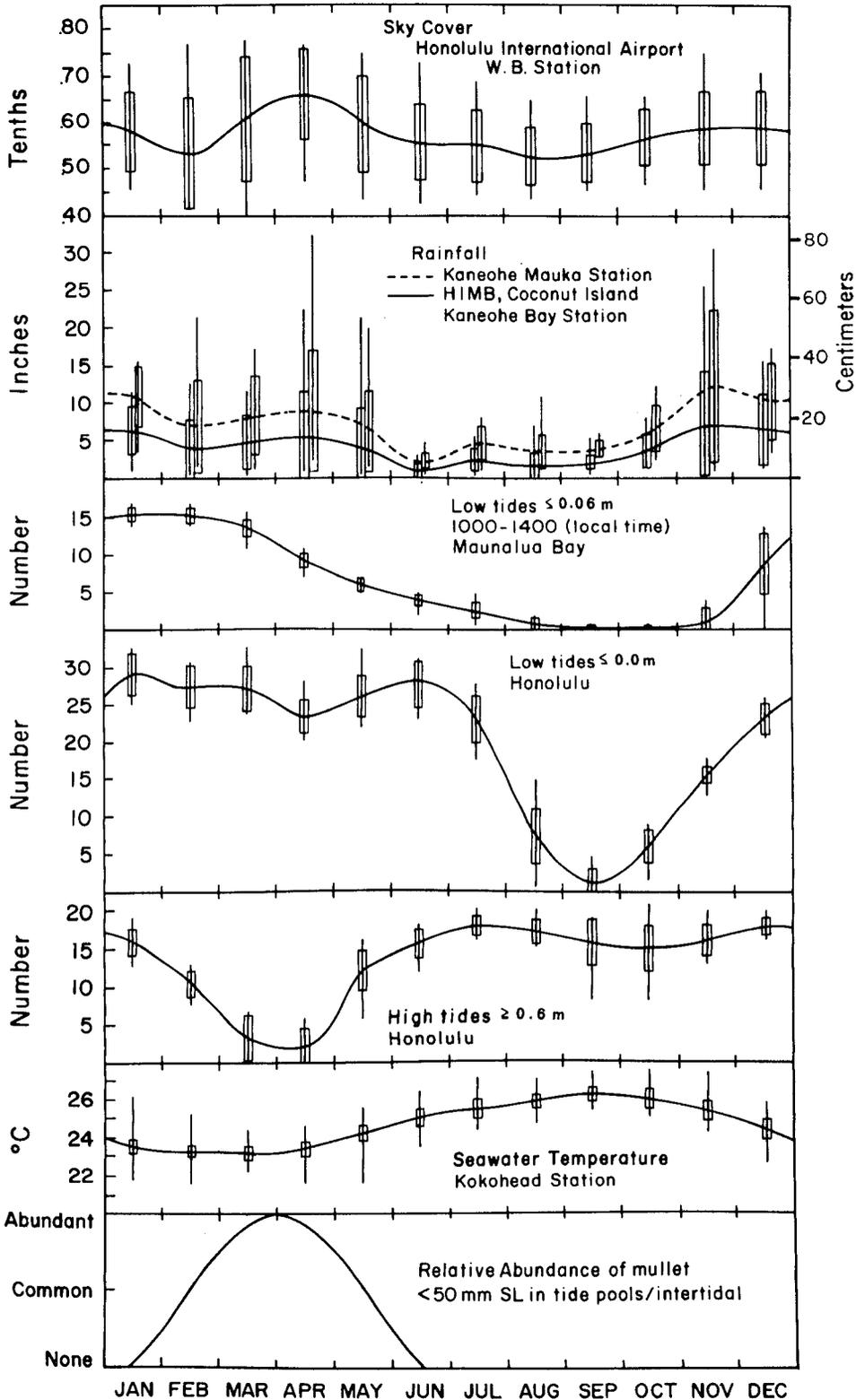
mullet are most abundant), reduces insolation and thus reduces the potential for the attainment of lethal conditions in tide pools. These relationships are particularly important since young mullet congregate in areas of springs and freshwater run-off. However, cloud cover during February through May varies more than during any other period of the year and points to the fact that the environment in which mullet <50 mm SL occur fluctuates tremendously within a season and from year to year.

Seasonal rainfall is maximal during winter-spring in Hawaii. Rainfall in the mountains (Kaneohe Mauka Station) exceeds that in nearby shore regions (Hawaii Institute of Marine Biology Station). Fluctuations in rainfall from month to month and year to year are great and appear to be unpredictable, particularly during the season when mullet <50 mm SL are abundant in the intertidal estuarine region. Run-off is maximal during this season due to the heavier mountain rainfall. This run-off could contribute to potentially lethal or near lethal conditions in the intertidal region by reducing its salinity, particularly during periods when low tides occur during noon. Intertidal spring water temperatures, on the other hand, were recorded to be as much as 10° cooler than surrounding water of higher salinity (Table 2). This cooler water may serve to reduce overall intertidal estuarine temperatures, at least during nontide-pool forming tide levels, but at the same time it increases the thermal and salinity heterogeneity of the environment.

Returning to a discussion of adaptations of mullet, experimental studies indicate that temperature acclimation is important in the ability of striped mullet (at least larger juveniles) to survive higher temperatures (Heath 1967; Sylvester 1974, 1975; Sylvester et al. 1974). Heath, although not providing fish length or salinity data at which tests were made, reported critical thermal maxima (CTM) of 42.4°-43.1°C for mullet in the northern Gulf of California. Sylvester (1974, 1975) and Sylvester et al. (1974) demonstrated increased CTM (29.0°-41.6°C) with increasing acclimation temperatures at a salinity of 32‰ for juvenile striped mullet, 70-125 mm SL, in Hawaii. At a lower acclimation temperature, and a salinity of 0‰, the CTM's were reduced. In general, CTM's were lower at lower salinities. Sylvester (1974) also found that juveniles adjusted or acclimated faster at higher temperatures, and that their thermal resistance to lethal temperatures de-

creased slightly when they were exposed to fluctuating low, rather than constant, temperatures.

Sylvester (1975) also demonstrated the existence of increased CTM at noon and lower CTM in the morning and afternoon for fish 78-122 mm SL.

There is good evidence that underlying biochemical changes are responsible for acclimation to changing thermal regimes (reviews in Hochachka and Somero 1971, 1973; Haschemeyer 1973; Somero 1975). Hochachka and Clayton-Hochachka (1973) provided some evidence that this may also be the case for striped mullet about 120 mm long in Hawaii.

Whether the ability of mullet to tolerate increasingly higher temperatures, seasonally and daily, is a result of interacting endogenous factors (biological rhythms) as is indicated in other animals (Sweeney and Hastings 1960; Wilkins 1965), and/or exogenous factors (direct exposure to increasing temperatures) is not known.

Sylvester's (1974, 1975) studies were conducted between August and January and those of Heath (1967) in March and September. As the discussion above and Figure 4 indicate, ambient seawater temperatures are highest during August to October and lowest during February to April in the tropical-temperate Northern Hemisphere. Although the seasons varied during which the experiments of Sylvester and Heath were conducted, the CTM data obtained were similar for the experimentally acclimated fish. Doudoroff (1957) and Allen and Strawn (1971) reported that relatively brief exposure to high nonlethal temperatures usually increased heat resistance in a number of species of fish. This increased resistance was not readily lost when fishes were subsequently exposed to low temperatures. This also appears to be true for striped mullet as Sylvester's (1974) study indicates. Thus, striped mullet appear to have an ability to modify their thermal tolerance in direct response to prevailing environmental conditions (exogenous factors). The ability to increase their heat resistance even after a brief exposure to high nonlethal temperature would be especially advantageous to mullet in the estuarine intertidal, at least in Hawaii.

If exogenous factors are solely responsible for the ability of striped mullet to survive high temperatures, it is difficult to explain the differences in the distribution of striped mullet presented in this report.

Prejuveniles enter the intertidal estuarine regions from the far more environmentally uniform

oceanic waters, and appear to be "preadapted" to the near lethal conditions inshore. This may indicate the existence of an ontogenetic biological rhythm (cued by slight monthly changes in photoperiod or water temperature?) in these mullet, which biochemically and physiologically preadapts these fish for life in the intertidal estuarine regions, while they are still in oceanic waters. Seasonal and daily acclimation to existing thermal and salinity regimes may then occur after the prejuveniles arrive inshore.

Factors affecting the distribution of striped mullet ≥50 mm SL are more complex. In Hawaii, field acclimated fish behaviorally select or prefer water temperatures well below their experimental CTM. The natural fish kill observed in March also indicates that the larger juveniles (and most prejuveniles) were not able to survive exposure to high temperatures (at least for relatively long periods of time). Behavioral selection of temperature regimes well below CTM has also been observed in the estuarine goby, *Gillichthys mirabilis* (de Vlaming 1971).

Mullet ≥50 mm SL in Hawaii moved seaward to pools with open connections to deeper water with ebbing tides during the spring. During the non-tide-pool forming low tides in the late summer, the larger juveniles may be acclimated to tolerate higher ambient seawater temperatures in Hawaii as they are in the northern Gulf of California. In Hawaii, however, intertidal waters reach their maximum temperatures during the period from late winter to early summer when shallow tide pools are formed, although ambient oceanic temperatures are higher during late summer. Heath (1967) indicated that inshore water temperatures in the northern Gulf of California are highest during the late summer-early fall period. It is not known whether CTM's are similar for field acclimated striped mullet ≥50 mm SL in the spring in Hawaii and in the late summer in the northern Gulf of California, or whether mullet from both locations have CTM's paralleling seasonal changes in ambient (oceanic) seawater temperature.

Selected temperatures are lower for young mullet ≥50 mm SL compared with smaller fish at each salinity, and much lower at decreasingly lower salinities (Figure 3). Presumably, physiological changes mediated hormonally/biochemically occur during metamorphosis, resulting in a preference for reduced temperatures by the larger juveniles. This decrease in temperature "toler-

ance" with metamorphosis (age) is somewhat contrary to the discussion thus far. It may only be a behavioral trait not directly correlated with CTM (i.e., CTM may actually be increasing). Behavioral selection of lower temperatures appears to be adaptive in the field during the period between April and August. In addition to having widely varying salinity values, many of the tide pools formed during this period may have been too shallow for larger juveniles to feed and swim. Many of the pools were shallower than the body depth of the older juveniles. Thus, those individuals that remained seaward of the tide line as they completed metamorphosis may have reduced or escaped the possibility of entrapment and exposure to lethal conditions in tide pools and shallow water; conditions observed once during this study.

These relationships may indicate the existence of an endogenous rhythm involved in the movement of (behavioral selection by) juvenile mullet towards deeper, relatively cooler, more saline water during or after metamorphosis. This rhythm may be acting in opposition to the presumably increased acclimation to higher ambient (oceanic) seawater temperatures. The change in behavior with metamorphosis may be a result of endogenous rhythms perhaps coupled with exogenous factors, such as the slight monthly changes occurring in seawater temperature and/or photoperiod, or it may be due directly to these exogenous factors. The reproductive cycle of striped mullet appears to be coupled with both these environmental variables (Kuo et al. 1974; Kuo and Nash 1975), so presumably younger individuals could use these same cues as well. It is difficult to separate cause from effect, but the shallowness and volume limitations of tide pools may be critical. Thus, selection may have favored those metamorphosed individuals with reduced physiological tolerance to high fluctuating temperatures and low fluctuating salinities as found in the estuarine intertidal (i.e., those individuals that behaviorally moved away from such conditions).

If selection favored those metamorphosed (metamorphosing) individuals that moved into deeper intertidal waters, what selection pressures may have favored individuals able to survive the kaleidoscopic conditions of the estuarine intertidal tide pools?

Experimental and field evidence demonstrate the importance of refugia for species from their competitors and/or predators (Gause 1934; Crombie 1946; Connell 1961; Paine 1969). Connell

proposed that intertidal species are limited in their upper distributional range by physiological (and presumably biochemical) adaptive abilities to environmental stress. At the lower end of the range, organisms are limited by biotic factors such as competition and predation. Field observations indicated that there was essentially no predation, including that by birds, of mullet <50 mm SL when they occupied the intertidal estuarine tide line and swash zone areas at low tide (Tables 2, 3). At high tide, and during ebb and flood, mullet <50 mm SL were exposed to predators, but the potential for being attacked and caught was reduced by occupying the shallowest tide line waters and by the schooling habit.

The absence of predatory fishes in the shallow intertidal estuarine regions at low tide may be related to 1) a subminimal depth or area of water in which to maneuver, and 2) possibly, although data are lacking, an inability of predators to adjust to rapidly fluctuating thermal and salinity regimes. Predators escaped entrapment by remaining seaward of the tide line during ebbing tides just as juvenile mullet ≥50 mm SL did. In addition, potential invertebrate predators were absent from the shallow intertidal areas presumably escaping seaward and/or, as often observed or caught, burrowing to a level below the surface of the mud/sand substrate.

Juvenile mullet ≥50 mm SL as well as adult mullet appear to be competitors with individuals <50 mm SL for food resources in the intertidal estuarine region. At high tides the larger fish moved into and fed in the areas used by the younger fish during low tides. With the incoming tide, the younger fish moved shoreward with the tide line. In addition, other species of fishes moved in with the flood tides. It is not known whether these fishes utilized the same food resources as the young mullet.

Space also may be at a premium in the shallow intertidal estuarine regions, particularly in tide pools. As discussed previously, the volume of water in the tide pools as well as the depth of pool water may be critical. Formation of large schools is characteristic of larger juvenile mullet as it is for the species as a whole and inter- and intraspecific competition for space may occur. Other species of fishes, as well as the larger juvenile mullet, were not observed in the shallowest water during low tide. The ability of small mullet to occupy the shallowest, warmest water may also occur in the northern Gulf of California (Heath

1967), where they (no length data) are one of two species penetrating the farthest up seawater drainages along the margin of the desert.

Mullet <50 mm SL formed loose schools with individuals constantly feeding during low tides, particularly in tide pools. At high tides, or in more exposed environments, feeding often ceased and tight dense schools were formed. This was evident when predators were nearby, approaching, or attacking. When exposed to predators at high tides and changing tides, the schooling habit confers an increased advantage to the mullet in terms of survival (Major 1977, in press). Most of the attacks by predators on schools that I observed, failed. The formation of schools appears to be yet another adaptive feature in the behavioral repertoire of mullet. The schooling habit increases the ability of individual mullet to survive as prejuvenile and juveniles in the intertidal estuarine region and presumably as prejuveniles in oceanic waters.

Prejuvenile and small juvenile mullet have presumably evolved the necessary biochemical and physiological adaptations to exist successfully in the fluctuating, often near lethal, intertidal estuarine environment in the spring months. In Hawaii, this has allowed them to use this intertidal refugium to escape their predators and competitors for food and space, making possible undisturbed feeding activity. Kinne's (1960) work with *Cyprinodon macularius* and Norris's (1963) study of *Girella nigricans* suggest that high temperatures increase the rate of food uptake and digestion. Food conversion (to growth) efficiencies are highest at lower temperatures, however. De Silva and Perera (1976) experimentally determined that young mullet grow more rapidly at 20‰ salinity than at salinities of 30, 10, or 1‰. This was comparable to Kinne's (1960) work with *C. macularius*.

The widely fluctuating environmental variables in the estuarine intertidal in Hawaii may provide the necessary conditions for rapid growth in mullet. This would allow metamorphosis to be completed in all mullet by the time the tidal situation becomes less favorable, as predators gain access to the small mullet and intra- and interspecific competitors gain access to their feeding areas as well. The formation of large schools during all stages of life appears to be important in reducing predation and possibly also in competing with other species for food and space in the estuarine intertidal region.

It is interesting to note that the environmental conditions and the behavior of prejuveniles and juvenile striped mullet in Hawaii appear to be very similar in many instances to those of various species of western U.S. desert pupfish, *Cyprinodon* (Barlow 1958, 1961; Kinne 1960; Lowe and Heath 1969; Brown and Feldmeth 1971; Deacon and Minckley 1974), and to the African cichlid, *Tilapia grahami* (Coe 1966). Daily and seasonal changes in water temperature and possibly salinity (ionic) regimes in the low tide, tide pools in Hawaii and desert springs and pools appear very similar. The pupfish and *T. grahami* young live in the shallowest, hottest water often at near lethal temperatures. Adults, generally, did not occur in these areas at the same time as the young. Feeding appeared to be continuous and was directed at the substrate, as it was in mullet <50 mm SL. The shape, size, and length of the pupfish and *T. grahami* also appear to be very similar to those of the small mullet.

The changes occurring in the behavior and distribution of mullet prejuveniles transforming to juveniles is also very similar to the changes occurring in prejuvenile and juveniles opaleye, *Girella, nigricans,* in the intertidal areas along southern California and Baja California, Mexico (Norris 1963).

The ability of certain life history stages of these diverse species of fishes to tolerate fluctuating conditions and/or near lethal thermal and ionic (salinity) regimes in shallow water possibly indicates convergence of adaptations to similar environments. The physiological adaptations may be mediated biochemically (hormonally) and may be a result of the interaction of both endogenous and exogenous factors or cues. The evolutionary driving or selection forces operating appear to include predation and at least intraspecific competition for food and space.

ACKNOWLEDGMENTS

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