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Title: INFLUENCE OF TEMPERATURE AND SALINITY ON THE ADAPTATION OF *ANOPLARCHUS PURPURESCENS* AND *PHOLIS ORNATA* TO AN INTERTIDAL HABITAT

Abstract approved: Redacted for Privacy
Carl Bond

The influence of physical factors, namely temperature and salinity, on the distribution of two coexistent species of blennioid fish in Yaquina Bay was evaluated. The two species, *Anoplarchus purpurescens* (family Stichaeidae) and *Pholis ornata* (family Pholididae) exhibited distributional differences. Only *Pholis* inhabited rocky intertidal substrates in the upper part of the bay while *Anoplarchus* predominated in the intertidal zone at the mouth of the bay closer to oceanic influence. Measurements of the microhabitat temperatures and salinities reveal only slight environmental fluctuations which were further minimized by exploitation of the insulating capacity of the rock and cobble habitat. The critical thermal maxima of the two species were similar, 29.5°C for *Anoplarchus* and 31.0°C for *Pholis*, but administration of thermal stress in a cycled program simulating tidal exposure and inundation sharply differentiated the thermal tolerances of the two species. Salinity influenced the thermal capacities of the species in a manner which reflects their distribution in the bay. The thermal tolerances of both were sharply reduced when exposed to salinities of 0, 56, and 75 ppt, yet Pholis had a greater tolerance to dilute salinities at temperatures representative of natural conditions (5-15°C). Studies on the osmoregulatory capabilities of these species indicate that both are efficient osmoregulators with fluctuation in serum osmolality restricted to about 300 mOsm over a range of salinities from 0 to 56 ppt (1800 mOsm). Comparison of temperatures and salinities measured in the field with laboratory determined tolerances revealed that temperature is not a limiting factor in the comparative distribution of the species in estuaries; dilute salinities may restrict the distribution of one species, Anoplarchus purpurescens, in the intertidal zone.

# Influence of Temperature and Salinity on the Adaptation of *Anoplarchus purpurescens* and *Pholis ornata* to an Intertidal Habitat

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# INFLUENCE OF TEMPERATURE AND SALINITY ON THE ADAPTATION OF _ANOPLARCHUS PURPURESCENS_ AND _PHOLIS ORNATA_ TO AN INTERTIDAL HABITAT

## INTRODUCTION

Fishes of the suborder Blennioidei are among the most abundant and diverse groups of benthic fishes inhabiting the littoral and sublittoral regions of the north Pacific Ocean. Blennioids of the families Stichaeidae (pricklebacks) and Pholididae (gunnels) and sculpins of the family Cottidae are the predominant fishes in the northeast Pacific intertidal zone. Miller and Lea (1972) list 17 species of stichaeids and pholidids off the California coast and Hart (1973) lists 20 species in Canadian waters of the Pacific coast. The high cockscomb prickleback, _Anoplarchus purpurescens_ (family Stichaeidae), and the saddleback gunnel, _Pholis ornata_ (family Pholididae), are two species of northern blennioids common to Oregon coastal waters. Both species have been observed in abundance in Yaquina Bay on intertidal substrates consisting of muddy sand and loose cobble. Pricklebacks and gunnels, being long and slender, are able to obtain shelter in the numerous crevices and pockets available in loose cobble. While other families of intertidal fishes must restrict themselves to tidepools at low tide, a greater surface area of intertidal substrate is available as permanent habitat for northern blennioids since they are capable of withstanding complete emersion as the tide retreats as long as shelter in the form of loose rocks or vegetation is available. This preference for sheltered habitats regularly exposed to atmospheric conditions indicates abilities to utilize atmospheric oxygen (Riegle, 1976) and resist desiccation; such adaptations have enabled the northern blennioids to be among the most successful inhabitants of the intertidal zone both in terms of species abundance and diversity.

As early as 1924, Klugh observed the influence of physical limiting factors on the distribution of tide-pool biota. Doty (1946) recognized that critical tide levels could result in sharp changes in exposure to environmental fluctuation characteristic of the intertidal zone and that this physical control exhibited a profound influence on the distribution of intertidal flora and fauna. Wolcott (1973) and Bannister (1976) have provided insight into the importance of physiological tolerance limits in governing the intertidal vertical distribution of limpets. While both Wolcott and Bannister have documented that limpets occurring higher in the intertidal zone have greater thermal tolerance, it is much more difficult to determine the extent to which the distribution of limpets or any other species is, in fact, governed by physical factors such as temperature. Thompson and Lerhner (1976) claim that physical control rather than biological accommodation governs intertidal fish community structure in areas of strong seasonal fluctuation. Norris' (1963) ambitious study of the broad implications of temperature in the life history of a California littoral fish Girella nigricans, underscores the importance of this ecological variable in the lives of temperate, nearshore fishes. Studies on the distribution of intertidal fishes (c.f. Williams, 1954; Gibson, 1972; Sasaki and Hattori, 1972; Barton, 1973) indicate that fish species that reside in the intertidal zone can often be differentiated with respect to their vertical ranges. While the vertical distribution of fishes is not as sharply defined as that of sessile intertidal organisms, owing to the greater mobility of fishes (Gibson, 1969), differences in this distribution may reflect differences in the extent of eurythermicity or euryhalinity as fishes living higher in the intertidal zone might be shown to possess a greater tolerance to temperature and salinity extremes. Miles (1918) has shown that intertidal blennioid species are more tolerant to salinity changes than offshore, non-blennioid species. Within the intertidal zone, cohabitant species may be shown to possess slight but significant differences in physiological capacities reflecting their height of occurrence in the intertidal zone. Nakamura's (1976) study supports this contention indicating temperature as the chief mechanism governing the vertical distribution of two species of intertidal sculpins of the genus Oligocottus.

Bays and estuaries in the northeast Pacific appear to act as a biological "filter" in restricting the inhabitation of intertidal areas by blennioid species. Of the approximately 20 species of northern blennioid fishes which may be encountered in open coastal situations, only two species, Anoplarchus purpurescens and Pholis ornata, are abundant in the intertidal zone of Yaquina Bay. This may be a direct response to decreased salinities present in estuarine habitats. Kinne's (1963, 1964) extensive reviews emphasize the importance of salinity in influencing the distribution of littoral species. Kinne (1963) points out that the biological effects of temperature and salinity are correlated in various ways--a particularly important consideration in studies on the physiological ecology of rocky shore and estuarine species. Temperature and salinity can be subject to extreme, long term seasonal fluctuation as well as to sudden, tidally induced fluctuations, particularly in a relatively small, north Pacific estuary such as Yaquina Bay.

Since A. purpurescens and P. ornata are such cryptic species, closely associated with particular substrates in the intertidal zone, they might be less capable of rapid locomotor responses to temperature and salinity changes than more mobile, open water species. The influence of such physical factors as temperature and salinity on fish distribution might be more readily shown in those species which are less able to modify rapidly habitat ranges in response to environmental changes.

The purpose of this study was to determine whether these two species of blennioids exhibit spatial and temporal differences in distribution in Yaquina Bay and, if they do, to evaluate the influence of physical factors, namely temperature and salinity, in the maintenance of these distribution patterns. Specifically, this study attempted to determine if temperature and/or salinity act as limiting factors in the distribution of these two species in the bay. This question was evaluated by measurement of the temperature and salinity in the microhabitat of the two species and relation of the temperature and salinity experienced in the field with laboratory studies on temperature and salinity tolerances.

Two basic considerations were dealt with in studies on the temperature and salinity tolerances of these two species of fish. The first concerned the combined effects of environmental variables acting in concert. A comprehensive analysis of thermal tolerances was attempted by evaluation of the effect of salinity upon tolerance to temperature extremes. Physiological responses to salinity extremes were further investigated through studies on the comparative osmoregulatory capacities of Anoplarchus and Pholis. The second consideration is that slight differences in thermal tolerance may be meaningful when one considers the manner in which thermal stress is administered. Thermal responses were studied by exposure of each species to a cyclic regime of thermal extremes in a manner simulating tidal exposure and inundation at times of extreme differences between atmospheric and aquatic environmental temperatures. Essentially then, this study attempted to relate certain aspects of the ecology of these two species of fish, specifically their comparative distribution in an estuary with physiological capacities relevant to changes in the two environmental factors recognized to be most influential in the lives of estuarine organisms--temperature and salinity.

# MATERIALS AND METHODS

## Field Studies

Field collections of fishes in rocky intertidal areas immediately north and south of Yaquina Bay, and within the bay, were made in order to assess the relative abundance of blennioid species, particularly Anoplarchus purpurescens and Pholis ornata along the coast. Collections were made at Yaquina Head 2.5 miles north of the mouth of Yaquina Bay and at a reef 3.3 miles south of Neptune Beach State State Park 18 miles south of the mouth of the bay. In Yaquina Bay, the intertidal distribution of the two species of fish was determined from collections of fishes within quadrats along a 10 m transect at three different sites (fig. 1-4). The sample sites within the bay were all characterized by large amounts of loose rock and cobble scattered over a substratum of soft, porous mudstone. An accumulation of clamshell (chiefly Mya arenaria) fragments covered much of the substrate at site 1 (fig. 2). Sparse patches of eelgrass (Zostera) were observed in the lower intertidal zone at this site. That portion of the substrate affording the greatest amount of shelter, in the form of loose boulders, was selected for sampling. Site 2 was located approximately mid-bay adjacent to Sawyers Landing (fig. 3). This sample site was on a steeper slope resulting in a greater height range sampled along the transects. At this intermediate site, abundant

Figure 1. Yaquina Bay and Estuary, Oregon. Numbers indicate locations of three sampling sites.

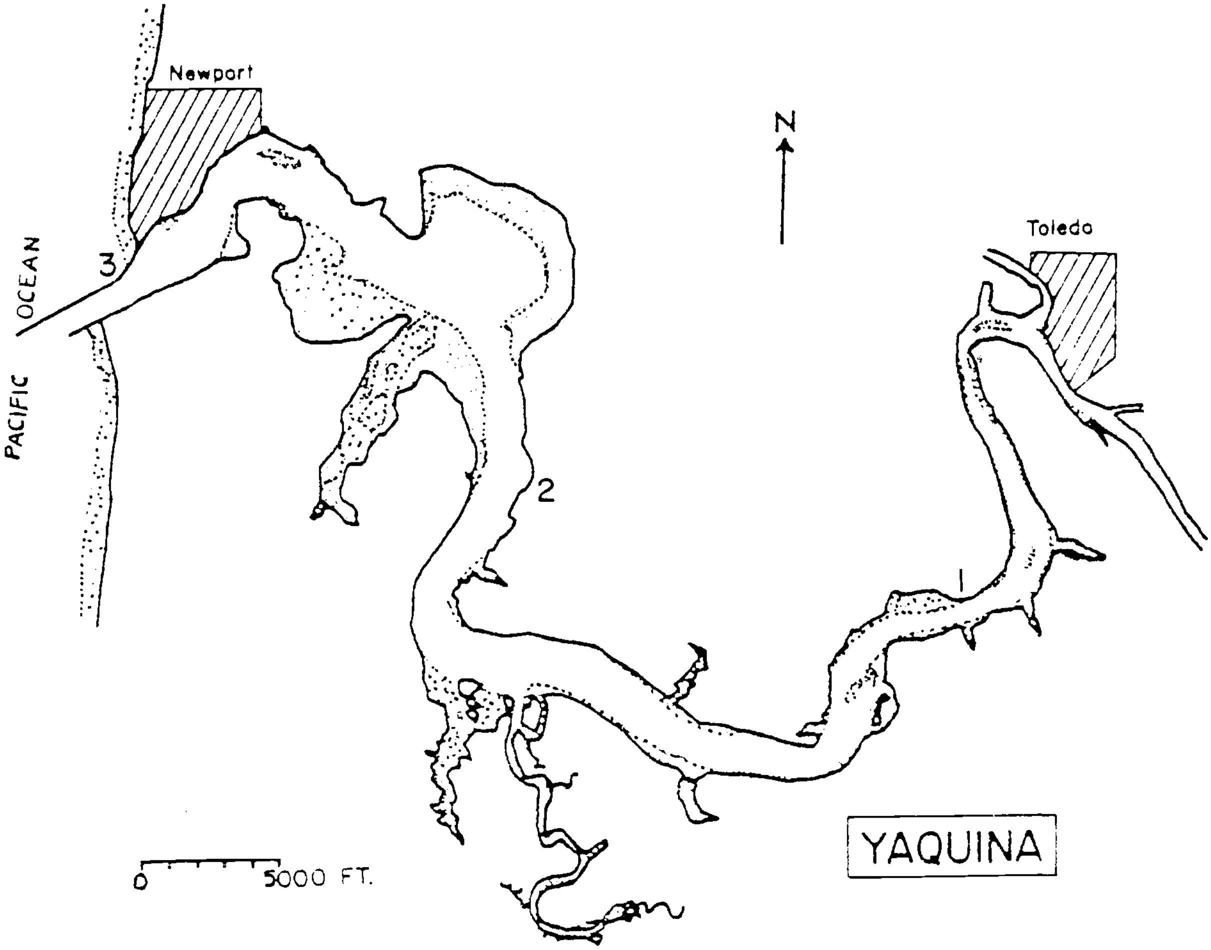


Figure 1.

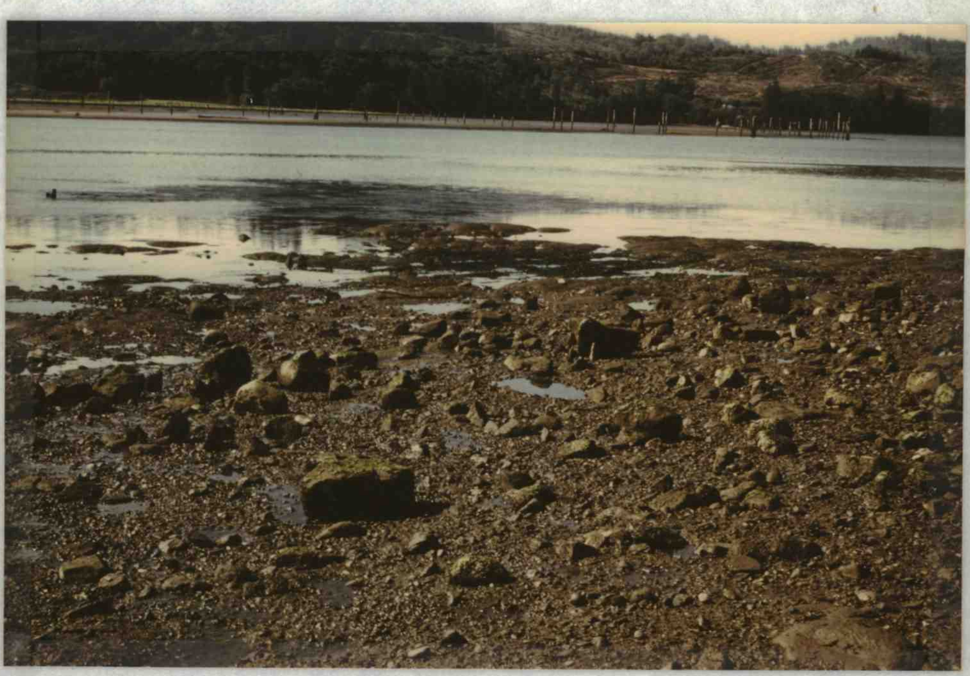


Figure 2. Photo of site 1.

Figure 3. Photo of site 2.

cover was available in the form of loose cobble and scrap metal refuse from the adjacent marina. Low intertidal eelgrass beds, fucoids, and seasonally abundant Ulva were the predominant flora. A considerably greater abundance and diversity of invertebrates were observed at this site than at site 1. Site 3 (fig. 4) was located in one of several trenches carved in the mudstone substratum beneath the north end of the Yaquina bridge at the mouth of the bay. This trench was one of the last parts of the intertidal zone to drain at low tide and was filled with loose cobble and large boulders. While the drainage of sites 1 and 2 left very little standing water in the intertidal zone, several pools of water were formed among these trenches. The diversity of plant and animal life at site 3 most closely approximated that found in open coastal situations.

Samples were taken twice a month over a two year period from July, 1974 to July, 1976 at site 2. During the first year, samples were taken in 1 $m^2$ quadrats along transect lines set parallel to the shoreline, but during the second year, transects were set normal to the shoreline to determine the vertical range of the two species in the intertidal zone. In both sites 1 and 3 the amount of substrate habitable by fishes was much more restricted and transects were set without regard for orientation relative to the shoreline. The position of the transect was dictated by attempts to maximize the amount of habitable substrate sampled. Since the vertical

Figure 4. Photo of site 3.

distribution of the two species was determined from site 2 samples only, the position of the transect was not as important for sites 1 and 3. For purposes of comparison of relative abundances within the same time period, five transect samples were taken at each of the three sites from April, 1977 to July, 1977.

At the site of each transect sample, a 1 x 10 m area was laid out and subdivided into ten 1 m square quadrats. Within each quadrat all loose stones and vegetation were moved and the fishes collected and counted. Care was taken to replace the rocks in their original position to minimize topographical disturbances which might be perceived by the fishes. Once collected and identified, the fishes were replaced. The exact same location was never sampled successively at site 2 in order to allow at least one month recovery from the disturbances caused by sampling. This was not possible in sites 1 and 3 due to the limited amount of habitable substrate; as a result, there was much overlap of successive transect samples.

The date of transect sampling was determined by consideration of both time and duration of low tide. Samples were taken on those days in which measurement of microhabitat temperatures and salinities could be considered at their most extreme. Therefore, during spring and summer months, samples were taken during minus tides occurring latest in the morning, and, during the fall and winter months, samples were taken during minus tides occurring latest at night. By this method, measurement of the range of microhabitat temperatures and salinities experienced by these fishes was maximized. The range of air temperature, surface water temperature in the bay, and temperature beneath rocks inhabited by fishes was measured with mercury thermometers and a thermistor telethermometer (Yellow Springs$^{R}$ model no. 43 TD). Air temperature was measured in the sun 0.5 m above the substrate sampled. Microhabitat temperatures were determined by placing the thermometer probe among rocks inhabited by fishes. The salinity of the bay surface water and water retained in small pockets among the rocks was measured with a refractometer (A/O$^{R}$ temperature compensated). Temperatures and salinities were measured every half hour beginning at the time of low tide and continuing until immersion of the habitat. Remote sensing of microhabitat temperature with the telethermometer was used to determine the rate of temperature change upon reimmersion. A simple apparatus consisting of a piece of plastic tubing connected to a one-way squeeze bulb and placed beneath a rock in a water pocket enabled remote monitoring of salinity change upon tidal advance as well. Intertidal height of each sample site was determined by the method outlined by Barton (1973). Essentially, this method involved sighting, through a transit level, a rod place at the height to be determined. Height of the sample sight was determined by addition of the height change increment measured on the rod to the height of the low tide.

## Laboratory Studies

Fishes collected for laboratory studies were held in tanks of continuously circulating seawater until needed. No collections were made in areas where field studies were underway. Prior to each experiment, fishes were acclimated at least seven days at 15°C in a 160 liter fiberglass tank. Water was aerated and recirculated through charcoal filters. Salinity was maintained at 32 ppt. Acclimation and all experimental procedures were performed under a 24-hour constant light regime. Fish were fed every other day with a commercially prepared flake food (Tetramin$^{R}$).

### Determination of Critical Thermal Maxima

The determination of critical thermal maximum (CTM) was accomplished by exposure of test animals to a relatively rapid and constant rate of temperature increase. Five individuals of each species were placed in each of two aerated 2800 ml flasks containing seawater at acclimation temperature and salinity. Species were tested together such that no variation in tolerance due to variation in exposure could occur when exposures were replicated. These two flasks, containing a total of 20 individuals, were placed in a water bath at 36°C. This permitted a rate of increase of .53°C/min.

Thermometers placed through the stopper on top of each flask permitted constant monitoring of temperature change. Before fish were tested, the consistency of rate of temperature change using this method was evaluated. Rates of increase were very consistent ranging from .50 to .57°C/min. for a mean rate of .53°C/min. The critical thermal maximum was the mean temperature at which no opercular beat was observed and the fish did not respond to mechanical stimulation. In order to determine if recovery was possible from this comatose condition, fishes which failed to respond to prodding were removed and returned to seawater at 15°C. Seasonal variations in tolerance levels were assessed by repeating this experimental procedure four times for each species, twice in the winter, 1976, and twice in the summer, 1977.

## Effects of Short Term Exposures to Lethal Temperatures

An apparatus was constructed to test the effects of potentially lethal temperature exposures administered in six hour doses once every 24 hours in a manner simulating temperature changes which might accompany tidal exposure and inundation. Six hour temperature doses were selected as this represented the maximum recorded exposure of fish habitats at low tide. The apparatus (fig. 5) consisted of two 100 l plastic containers connected via float valves to the

Figure 5. Diagram of cycled temperature apparatus.

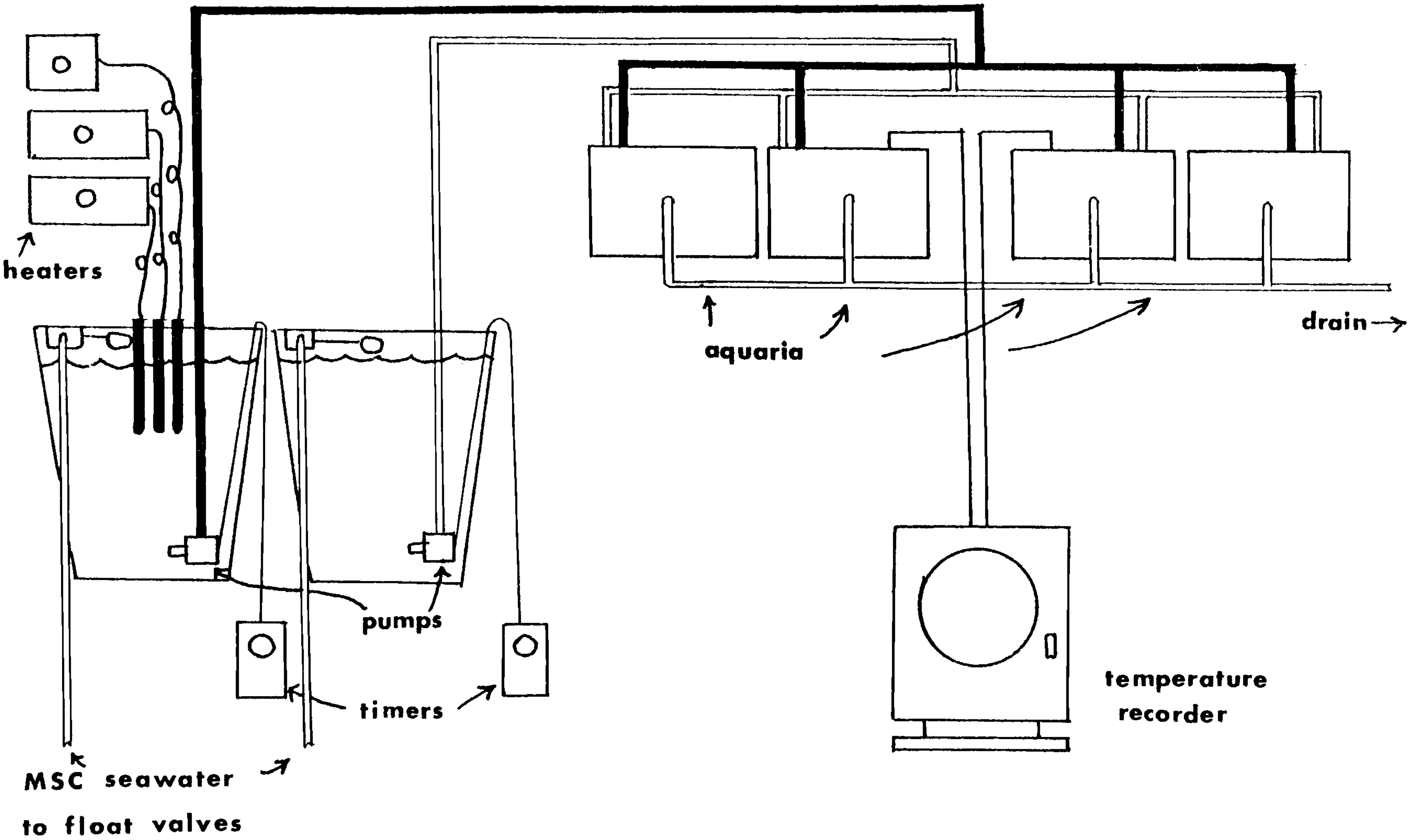

heaters
aquaria
drain
pumps
timers
temperature recorder
MSC seawater to float valves

Figure 5.

Marine Science Center seawater system. One of these tanks was heated with two 1000-watt Napco$^{R}$ heaters and with a 500-watt Versa Therm$^{R}$ temperature controller to obtain precise control. The other container held seawater at ambient temperature. Water of the desired temperature was pumped via submersible electric pumps from the 100 l containers into four foam insulated 14 l glass aquaria. The temperature cycle was monitored in the aquaria with a Taylor$^{R}$ recorder. The tested cycles had peak temperatures of 31°, 29°, 27°, and 25°C. Operation of the pumps, and thus the nature of the thermal regime, was governed by Paragon$^{R}$ no. 4001-0 timers. The exposure period was characterized by a gradual heating period up to the predetermined temperature followed by rapid cooling to the ambient conditions. The daily thermal experience thus consisted of a six-hour heating phase followed by 18 hours at ambient temperature (fig. 11a-c). The total time course for each experiment was five days, one six-hour exposure each day. Fish were not fed during the course of the experiment. Experiments were terminated after five days regardless of the mortality in order to avoid complicating effects which might arise due to food deprivation. Cycled temperature experiments were performed in June and July, 1977. Ten *Anoplarchus* were placed in each of two of the aquaria and ten *Pholis* were placed in the other two aquaria so that replicate exposures were obtained for each species. The fish were introduced to the tanks when the heating cycle reached the acclimation temperature (15° C). Each aquarium was continuously checked during the heating cycle and intermittently checked while at ambient temperature. Salinity was monitored throughout the course of each experiment. Fluctuation was minimal ranging from 29-32 ppt. Time to death was recorded.

### Determination of Combined Effects of Temperature and Salinity

In order to assess the effects of salinity on temperature tolerance, fishes acclimated at 15° C and 32 ppt were placed in 28 liter glass aquaria with water recirculated and filtered through charcoal filters. Aquaria were held in a cold room and heated by opposition with Versa-Therm$^R$ electronic temperature controllers sensitive to .005° C. Temperatures of 0° C were achieved by heating aquaria held in a small chest freezer. The desired salinity of the water in each aquarium was obtained by dilution with tap water (dechlorinated) or addition of Instant Ocean$^R$ synthetic sea salts to full strength seawater. In this manner, 48 combinations of temperatures of 0, 5, 10, 15, 20, 25° C and salinities of 0 (distilled water), 1, 3.2, 10, 32, 42, 56, 75 ppt were obtained. These salinities were selected in accordance with bioassay techniques outlined by Doudoroff (1951). Ten fish of each species were tested at each combination of temperature and salinity. Each group of fish was placed in a beaker containing

600 ml of water at acclimation temperature and salinity. These beakers were aerated and floated in the experimental aquaria until equilibration of temperatures (approximately 20 minutes) after which the fish were released into the experimental aquaria. The fish were observed at intervals of 0.25, 0.50, 1, 2, 4, 8, 16, 24, 32, 40, 48, 72, and 96 hours. The criteria for death was again cessation of opercular movements and failure to respond to prodding. Cumulative percent mortality at the end of each observation interval was plotted on semilog paper with the percent mortality converted to probits. The median resistance time (MRT - time to 50% mortality) and the standard deviation (±1 probit) were interpolated from the graphs. Cumulative percent mortality after 96 hours exposure was also evaluated using response surface estimation techniques outlined by Alderdice (1972).

### Determination of Osmotic Response to Salinity Changes

Several acclimated (15°C, 32 ppt) individuals of each species were placed in aquaria with salinities of approximately 0 (dechlorinated tap water), 3.2, 10, 32, 42, and 56 ppt. Temperature was maintained at 15°C. After 48 hours, blood was taken from five individuals of each species at each salinity by severing the caudal artery. Blood was collected in 5 μl heparinized capillary tubes and centrifuged for four minutes. The osmolality of the serum was determined using a Wescor$^R$ no. 5100 Vapor Pressure Osmometer. The osmolality of the blood of fishes held at 0 and 56 ppt was determined also after 24 and 72 hours in order to assess the rate of change in serum osmotic concentration at salinities considered to be extreme by environmental standards.

# RESULTS

## Field Studies

Collections made at the two open coastal sites adjacent to Yaquina Bay included several species of blennioid fish. Among the most abundant species were *Anoplarchus purpurescens*, *Xiphister atropurpureus*, *Xiphister mucosus*, *Apodichthys flavidus*, and *Xererpes fucorum*. Occasionally, *Phytichthys chirus*, *Chirolophus nugator*, and *Pholis laeta* were collected. No *Pholis ornata* were observed yet C. E. Bond (pers. comm.) has taken them at Yaquina Head. Barton (1978) has reported the presence of a closely related species of *Anoplarchus*, *A. insignis*, in collections from Yaquina Head. Blennioid species encountered in intertidal collections within the bay were almost exclusively *Anoplarchus purpurescens* and *Pholis ornata*. A few *Apodichthys flavidus* were noted. Another species of blennioid fish, the Pacific snakeblenny (*Lumpenus sagitta*) is reported to be common in Yaquina Bay (Beardsley and Bond, 1970), yet this species was never observed in collections from intertidal rocky substrates.

Results of the two-year sampling program at site 2, adjacent to Sawyers Landing, reveal a considerably greater abundance of *Anoplarchus purpurescens* (fig. 6). The relative abundance of the species at successively increasing heights in the intertidal zone

Figure 6. Seasonal changes in number of individuals and relative percent abundances of *Anoplarchus* and *Pholis* at site 2 measured from July, 1974 to July, 1976.

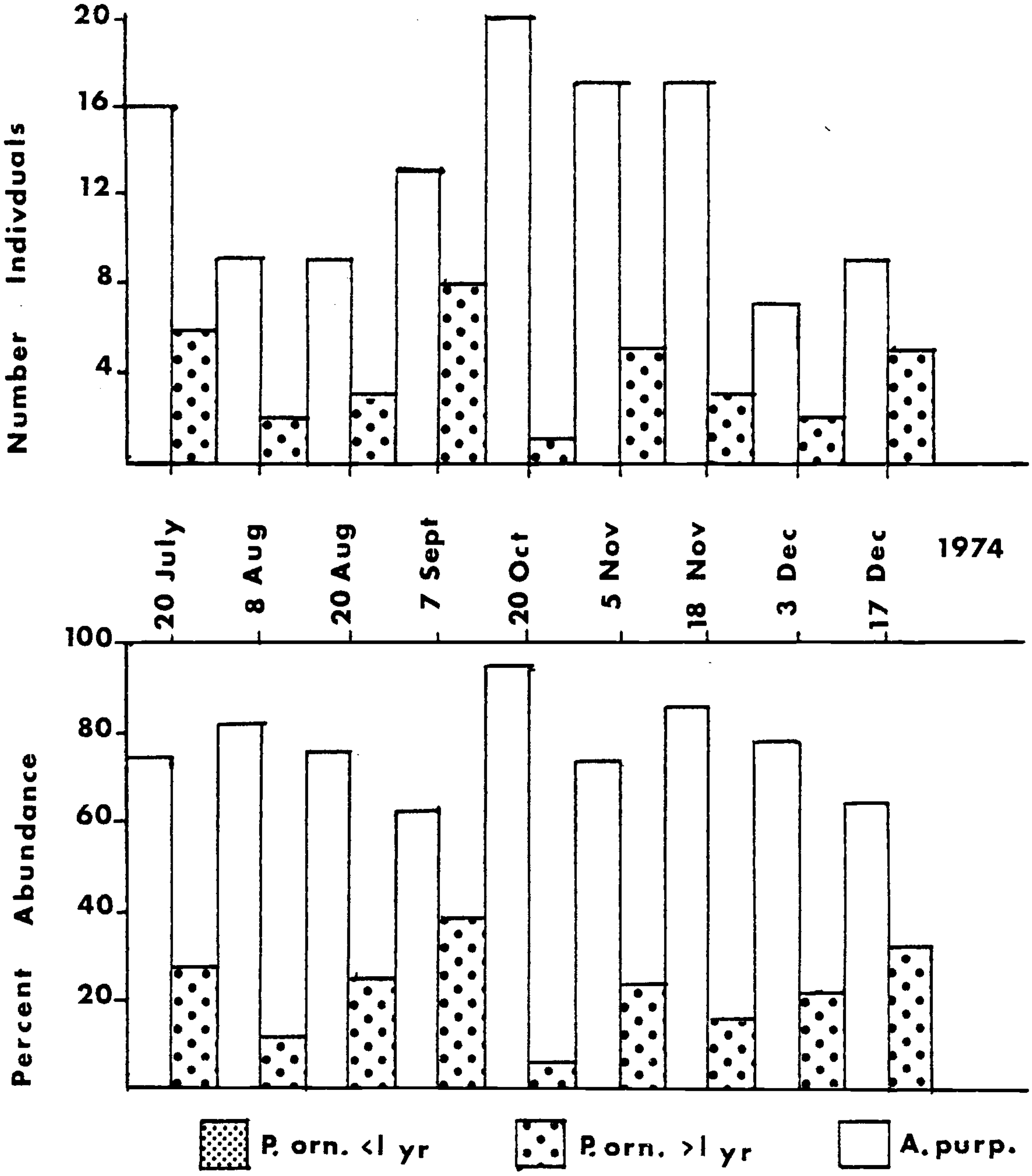

Number Indivduals
20
16
12
8
4
20 July
8 Aug
20 Aug
7 Sept
20 Oct
5 Nov
18 Nov
3 Dec
17 Dec
1974
Percent Abundance
100
80
60
40
20
P. orn. <l yr
P. orn. >l yr
A. purp.

Figure 6.

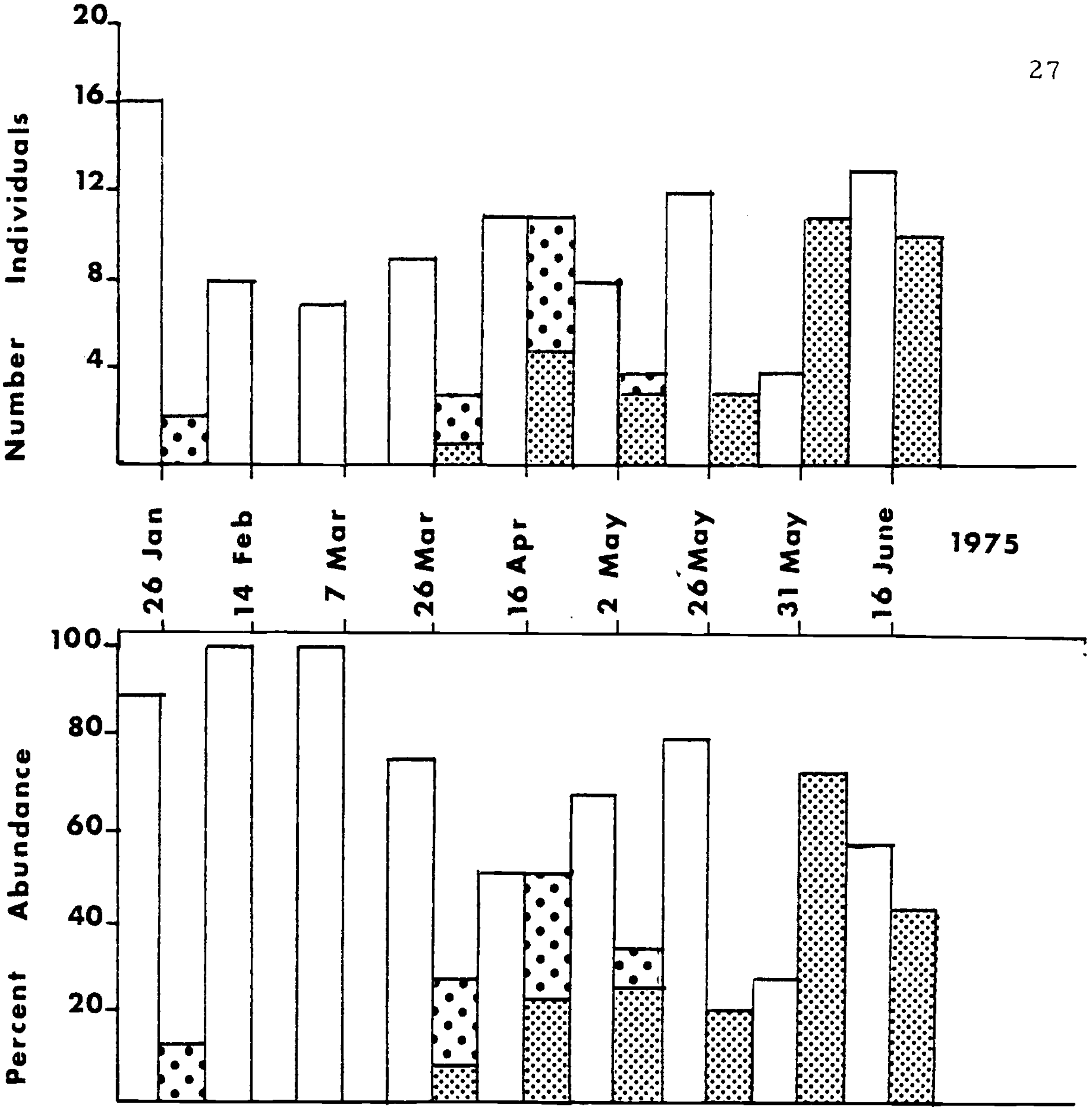

Number Individuals
20
16
12
8
4
26 Jan
14 Feb
7 Mar
26 Mar
16 Apr
2 May
26 May
31 May
16 June
1975
Percent Abundance
100
80
60
40
20

Figure 6.

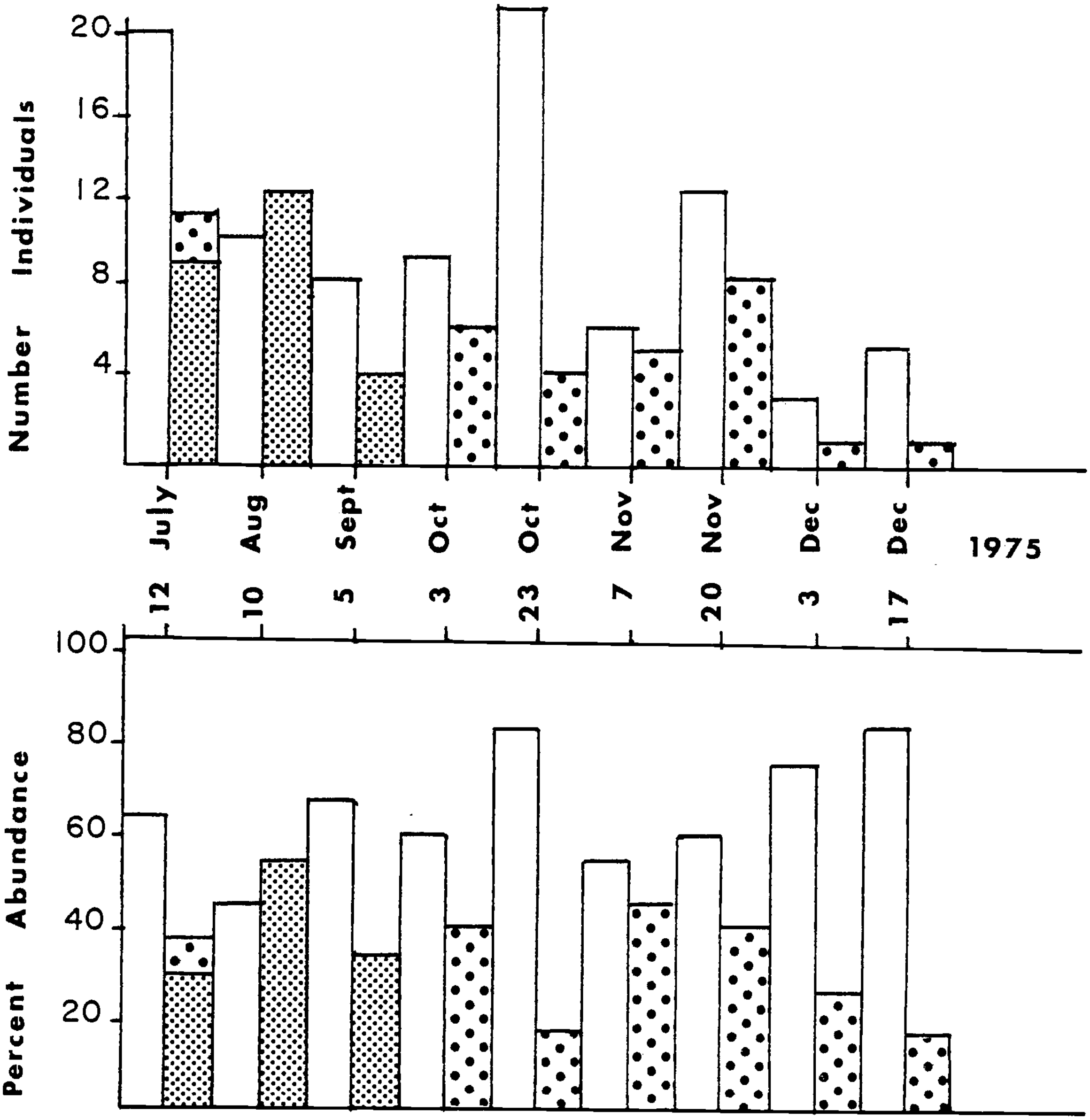

Number Individuals
20
16
12
8
4
12 July
10 Aug
5 Sept
3 Oct
23 Oct
7 Nov
20 Nov
3 Dec
17 Dec
1975
Percent Abundance
100
80
60
40
20

Figure 6.

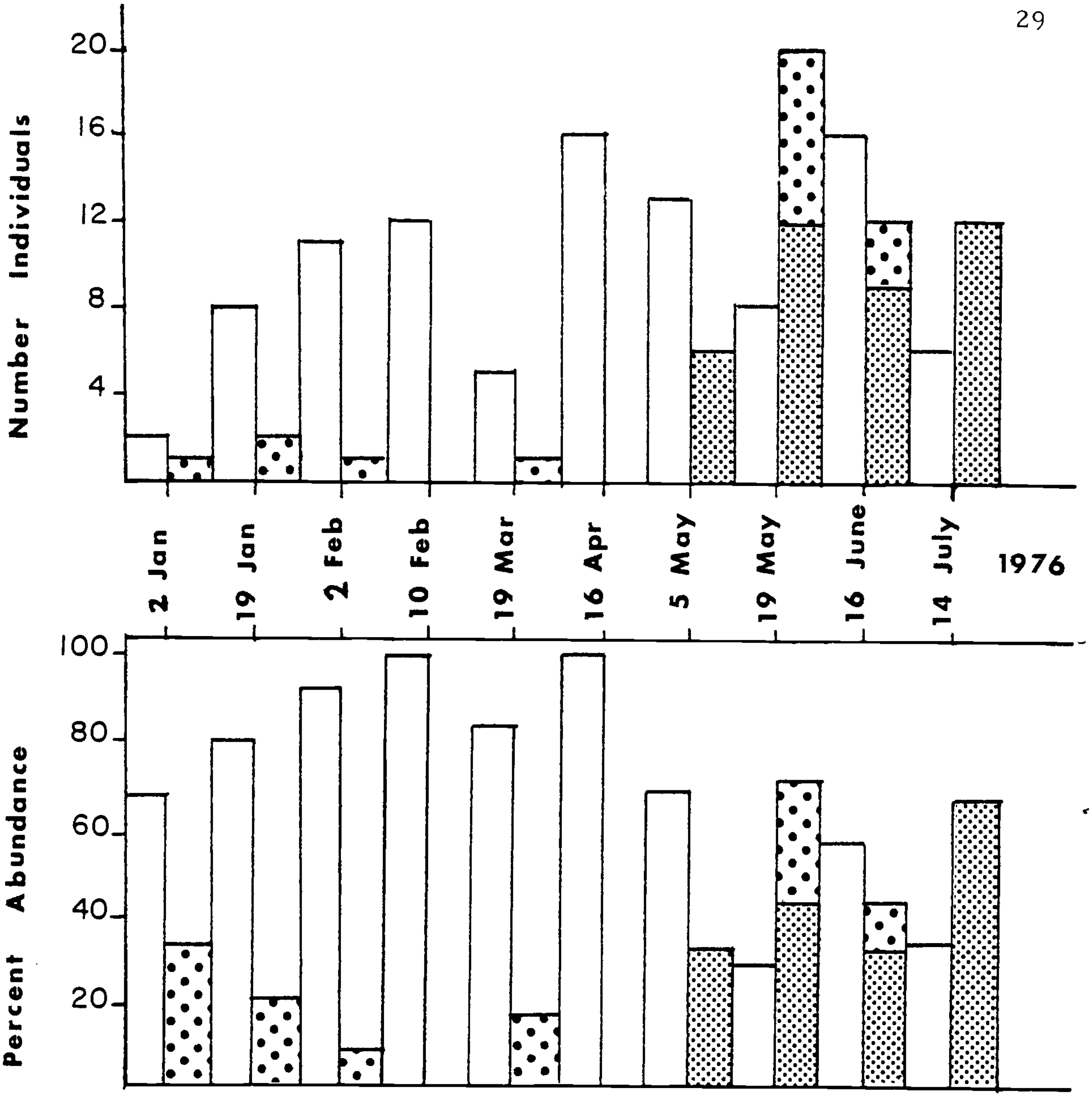

Number Individuals
20
16
12
8
4
2 Jan
19 Jan
2 Feb
10 Feb
19 Mar
16 Apr
5 May
19 May
16 June
14 July
1976
Percent Abundance
100
80
60
40
20

Figure 6.

was determined from those sample transects set normal to the shoreline (table 1). No sharp differences in the vertical ranges of the species is apparent, yet the total abundance of Pholis, measured as the number of fish/m$^2$, seems to increase with increasing height in the intertidal zone up to the third quadrat station (table 1). Anoplarchus, on the other hand, is most abundant at the lowest station sampled and decreases in abundance with increasing height. Neither species was present above the fifth quadrat station at an intertidal height of .76 m above mean lower low water (MLLW). No fish were present below .24 m at this sample site as this height represented the lower boundary of habitable rocky substrate. No shelter was available from the .24 m level to the water line at low tide as only a muddy substratum with sparse patches of eelgrass (Zostera) was present. Fish were observed among the vegetation when this area was covered with water but no fish were found there at low tide.

No differences in microhabitat preferences were observed between the two species when found coexisting. Both species could be found sharing the same crevice or residing beneath the same rock. Therefore, the range of temperatures and salinities experienced by coexistent species in the intertidal zone is assumed to be the same. There are striking differences in the overall habitat preferences however. Pholis will readily invade vegetative cover and was young-of-year individuals from older ones difficult in the late summer after about six months of growth. Seasonal variation in the relative abundance of the two species could only be attributed to heavy settling of post larval Pholis as no seasonal variation was noted in the total abundance of Anoplarchus in the intertidal zone. While post-larval Anoplarchus were occasionally observed, their total numbers did not merit comparative quantification of young-of year vs. older individuals as did Pholis.

Striking differences in the relative abundance of the two species were observed at different parts of the bay (table 3). In the rocks and cobble of the uppermost bay site (site 1) the only blennioid species observed was Pholis ornata. The height of the intertidal substrate sampled here was .46 m; since the sample site was oriented approximately parallel to the shoreline, there was very little variation in height above the MLLW throughout the entire 1 x 10 m area sampled. Striking seasonal variation in the abundance of Pholis at this height in site 1 was observed (fig. 7). Fish were plentiful in April, but their numbers declined in May--the month in which most of the samples were taken. In July, no fish were observed at this height but they were still present near the sample site lower in the intertidal zone (approximately -.5 m). In November, they were again abundant higher in the intertidal zone. At site 2 the relative abundance determined from the two-year sampling program resembled that determined

Figure 7. Seasonal changes in total abundance of *Pholis* at site 1 measured from April to November, 1977.

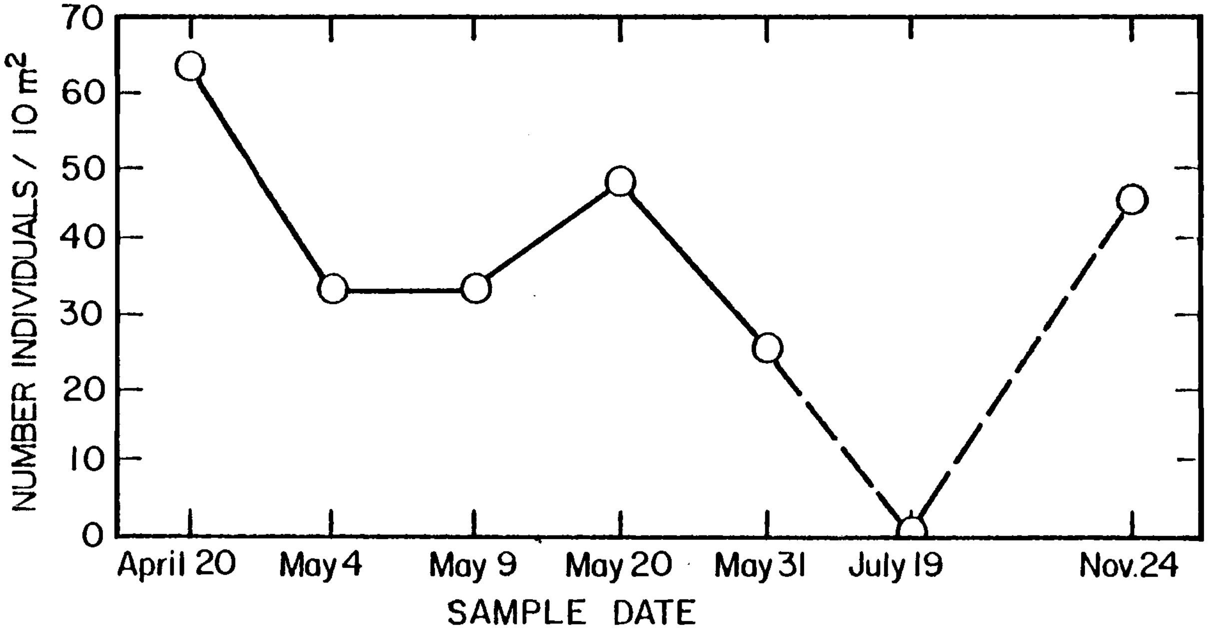

70
60
50
40
30
20
10
0
NUMBER INDIVIDUALS / 10 $m^2$
April 20
May 4
May 9
May 20
May 31
July 19
Nov. 24
SAMPLE DATE

Figure 7.

frequently observed in mudflats in the summer and fall months when vegetative cover is heaviest. Anoplarchus was never observed in any other habitat than that provided by loose rocks and cobble. Analysis of variance in two factor tests of the significance of species abundance and season indicates the significantly greater (P=.01) abundance of Anoplarchus at site 2. In addition, significant seasonal variation in abundance (P=.05) is also evident. This was attributed to a widespread settling of post-larval Pholis in the intertidal zone in the early spring. The significance of the species x season interaction indicates that seasonal variation is due to changes in total abundance of one species--Pholis ornata (table 2, fig. 6). In reporting the total and relative abundances of the two species (fig. 6), individuals of Pholis were separated into two groups, young of year and older than one year. This separation was made in order to reveal the effect of seasonal post-larval settling of young Pholis on the total abundance of this species in the intertidal zone. The comparison of young-of-year Pholis and older individuals was made only during the spring and summer months when the size of the post larval settling young permitted them to be distinguished from older age groups. Post larval Pholis ranged from 20 mm when first settling in early spring to approximately 40 mm in late summer when no distinction between them and older age groups was attempted. The lack of data on age and growth of Pholis made distinguishing from the more limited sampling done in conjunction with sampling at sites 1 and 3.

Most of the individuals encountered at site 2 were *Anoplarchus* (table 3). At the mouth of the bay closest to oceanic influence (site 3), the vast majority of the blennioids collected in the intertidal zone were *Anoplarchus*. The few *Pholis* collected at this site were invariably young of year.

Measurements of the salinity at these three sample sites clearly show the freshwater influence of the Yaquina River; the uppermost site consistently had the lowest salinities recorded during sampling of the three sites in the spring and summer of 1977 (table 4). In order to minimize variation due to precipitation, this series of transect samples and associated microhabitat measurements were taken in moderate weather conditions in which no rain had fallen at least 24 hours prior to sampling. The influence of salinity was also apparent in the intertidal distribution of fishes of the family Cottidae. At site 1, only sculpins of the freshwater genus *Cottus*, specifically *C. asper*, were observed. At site 2, the most abundant sculpin was *Oligocottus maculosus* with *Clinocottus acuticeps* occasionally collected in freshwater runoff from an adjacent culvert. At the lower bay site, site 3, *O. maculosus* and *Artedius harringtoni* were collected beneath rocks in small water pockets. *Gobiesox meandricus* (family Gobiesocidae) was also observed under rocks at site 3.

The temperatures and salinities of the microhabitat of Anoplarchus purpurescens and Pholis ornata, measured over the course of a low tide exposure during the two year sampling program. at site 2, are given in tables 5 and 6 and figs. 8 and 9. The greatest range of temperature was measured in air with very little fluctuation noted at the adjacent water's edge or under rocks (fig. 8). Examples of the changes in microhabitat temperature and salinity during the latter half of the low tide interval were plotted, one for summer and one for winter (fig. 10). These were selected because they represent the effects of a relatively broad range of atmospheric temperatures on the temperature and salinity of the under-rock microhabitat. The mean fluctuation of temperature measured in air was 2.8°C, but was only .83 and .85°C at the adjacent water's edge and under rocks respectively (table 5). The seasonal fluctuation in temperature was moderate and, at no time were the fishes observed to be thermally stressed in their microhabitat. Extreme temperatures, resulting in heat kills of some intertidal organisms, have been recorded along the Oregon coast however (J. J. Gonor, pers. comm.).

Seasonal fluctuation in microhabitat salinity at site 2 ranged from 0 ppt during winter to just above 30 ppt in summer (fig. 9). The range of salinities at low tide was considerably greater in the pockets of water retained among the rocks and cobble (mean

Figure 8. Mean and range of temperatures measured at site 2 from July, 1974 to July, 1976.

*Fig. 8 - Mean and range of temperatures measured at site 2 from July, 1974 to July, 1976.*

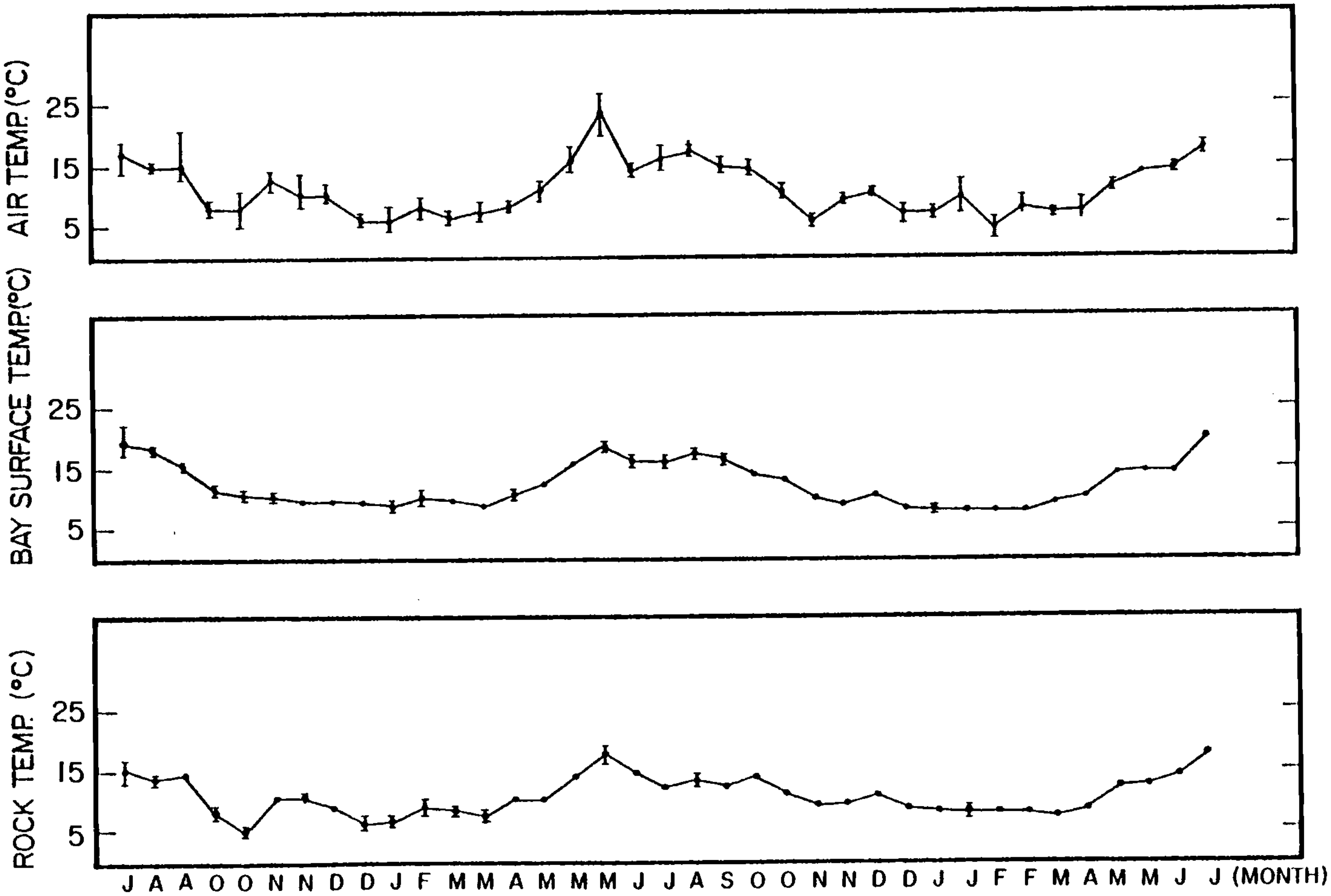


Figure 9. Mean and range of salinities measured in site 2 from July, 1974 to July, 1976.

*Fig. 9- Mean and range of salinities measured at site 2 from July, 1974 to July, 1976.*

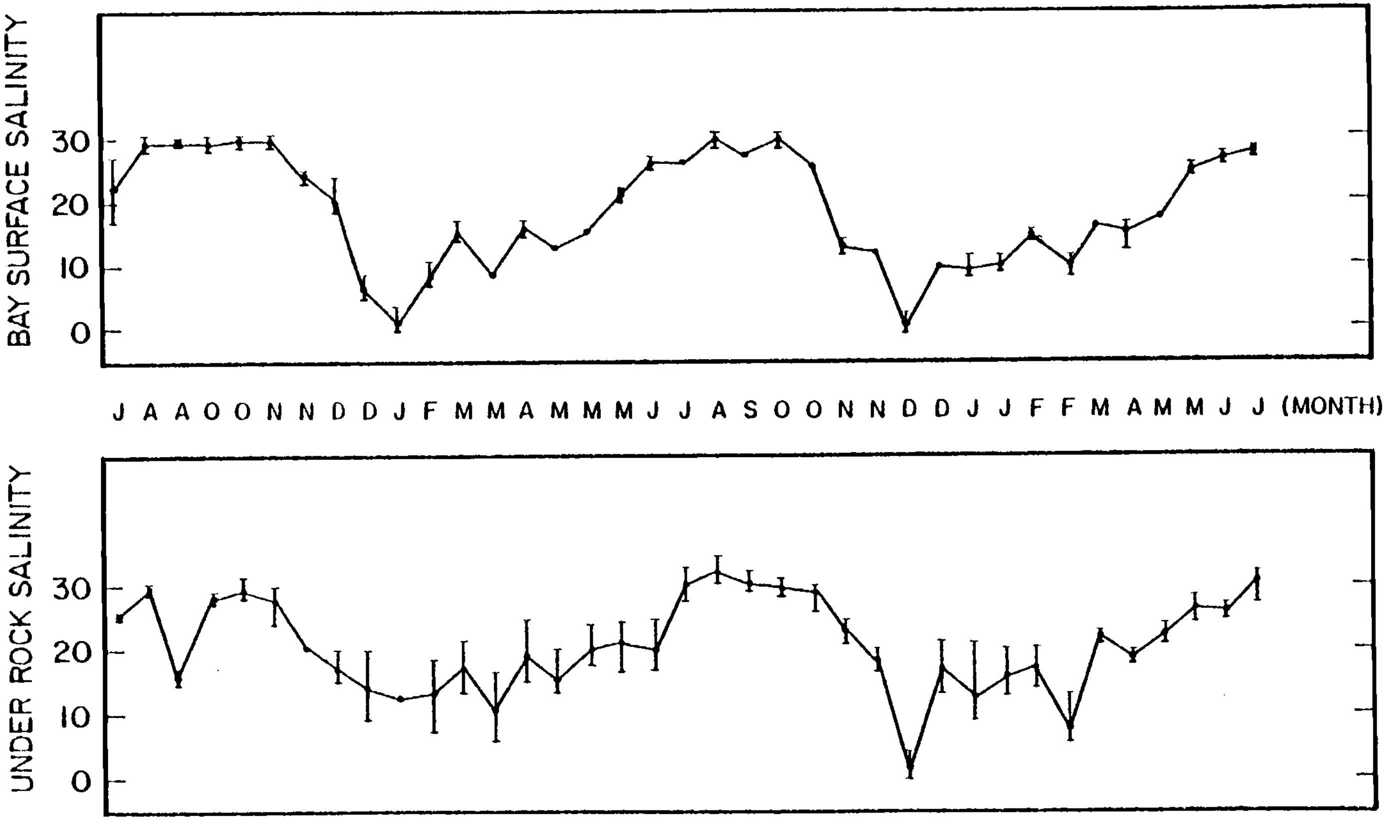


Figure 10. Selected examples of changes in microhabitat temperature and salinity at site 2 during a low tide interval.

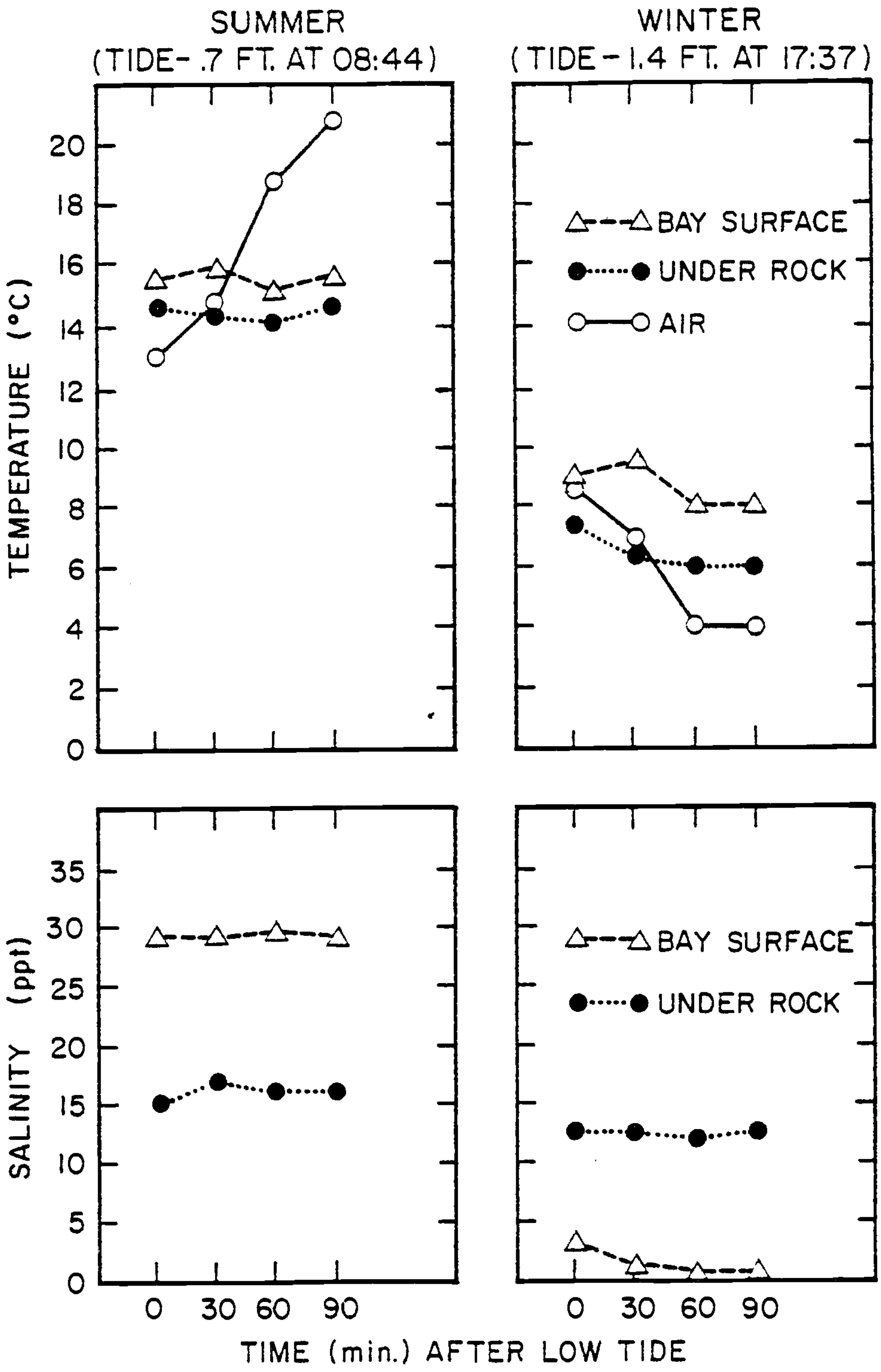

SUMMER
(TIDE- .7 FT. AT 08:44)
WINTER
(TIDE - 1.4 FT. AT 17:37)
TEMPERATURE (°C)
0
2
4
6
8
10
12
14
16
18
20
BAY SURFACE
UNDER ROCK
AIR
SALINITY (ppt)
0
5
10
15
20
25
30
35
BAY SURFACE
UNDER ROCK
0
30
60
90
0
30
60
90
TIME (min.) AFTER LOW TIDE

Figure 10.

fluctuation of 4.8 ppt) than at the adjacent water's edge (mean fluctuation of 1.7 ppt, table 6). The difference between salinities under rocks and at the adjacent water's edge was sometimes as great as 10 ppt. Measurements of the rate of change of temperature and salinity upon reimmersion with the rising tide indicate very rapid flushing of the under-rock habitat with temperatures and salinities equilibrating approximately three minutes after immersion.

In order to evaluate fully the extent of influence of atmospheric conditions upon the microhabitat of these fishes, estimations of the maximum and minimum temperatures and salinities, which could be experienced during the low tide intervals sampled, were made by calculating the rate of change of temperature and salinity and duration of exposure at low tide (table 7). These were used to estimate extreme environmental conditions which could be experienced. The equation used to calculate maximum or minimum temperature and salinity is:

$$\begin{array}{c} \text{Estimated} \\ \text{Temp }(^\circ\text{C}) \end{array} = \begin{array}{c} \text{Mean} \\ \text{Temp} \end{array} \pm 1/2 \; \begin{array}{c} (\text{duration exposure}) \\ (\text{hrs}) \end{array} \begin{array}{c} (\text{rate of temp chg}) \\ (^\circ\text{C/hr}) \end{array}$$

or or or

$$\begin{array}{c} \text{Estimated} \\ \text{Salinity (ppt)} \end{array} = \begin{array}{c} \text{Mean} \\ \text{Salinity} \end{array} \pm 1/2 \; \begin{array}{c} (\text{duration exposure}) \\ (\text{hrs}) \end{array} \begin{array}{c} (\text{rate of salinity chg}) \\ (\text{ppt/hr}) \end{array}$$

The estimated exposure duration was twice the length of sampling period because temperatures and salinities were recorded from the time of low tide to the time of reimmersion by the advancing tide. Because temperatures and salinities were monitored every half hour, a measure of the rate of change of these two variables in the latter half of the exposure period was determined. The mean temperatures and salinities are calculated from the measurements made in the latter half of the sampling period and are therefore not as precise as if they were calculated from measurements made over the entire course of exposure of the habitat at low tide. The rate of change in temperature and salinity is minimal, especially in the under rock microhabitat of the fishes (table 7). Because of the very small rate of change in temperature and salinity in the under rock microhabitat, the calculated extremes of temperature and salinity are also quite small. Maximum and minimum calculated temperatures were 20.9 and 3.1°C respectively; maximum and minimum salinities were 35.2 and 1.3 ppt respectively.

Callaway et al. (1969) and Karentz (1975) have monitored salinities at stations within one mile of site 1. Both recorded prolonged exposure to extremely dilute conditions. In Karentz' study, salinities recorded at low tide between December and April never exceeded 5 ppt.

## Laboratory Studies

Laboratory studies were performed on the temperature and salinity tolerance of Anoplarchus and Pholis in order to evaluate more accurately the role that these environmental factors play in governing the distribution of these two species. The critical thermal maxima of the two species were similar (within 2°C) and showed no seasonal differences (table 8). A most striking feature in the thermal tolerances was the ability of several individuals of each species to recover from a heat-induced comatose state if replaced in water at acclimation temperature and salinity. A slight seasonal effect was observed with greater numbers recovering during the summer experiments. Fish exposed to 0°C would lose equilibrium and, aside from a few convulsive spasms, fail to move or respond to prodding. Doudoroff (1942) termed this state "primary chill coma." The percent recovery from this condition depended on duration of exposure (table 8) and, in all trials, Anoplarchus exhibited a consistently greater percentage of recovery from chill exposure.

Exposure to a cyclic regime of high temperatures emphasizes the differences in thermal tolerances between the two species (fig. 11a-c). Fishes were exposed to cyclic thermal regimes in which the peak temperature exceeded that which the fish could withstand for a period of 96 hours of continuous exposure. The total thermal exposure, measured in degree-minutes (°C min.), was determined by calculation of the area above the acclimation temperature recorded by the thermograph. A lethal amount of thermal exposure was determined by measuring the total area of exposure experienced up to the median resistance time (MRT). The total thermal exposure that each species could withstand sharply increased with a decrease in peak temperatures from 29°C to 27°C. At peak temperatures of 29°C and 31°C, neither species survived the first 6 hour thermal exposure; but Pholis appeared capable of withstanding a slightly greater amount of exposure (fig. 11a, b). Peak exposure temperatures of 27°C resulted in a sharp differentiation of tolerance to thermal exposure (fig. 11c). The total amount of thermal exposure experienced up to the MRT was 7176°C min. or two complete cycles for Anoplarchus. For Pholis, the total was greater than 17940°C min.; fewer than half of the individuals had died before the end of the experimental period. No deaths were recorded at peak temperature pulses of 25°C.

The median resistance time was determined for each combination of temperature and salinity tested (table 9), and the MRT at each temperature was plotted for each salinity (fig. 12). For each species, a scope for thermal tolerance was calculated from the areas enclosed in each of the plotted polygons in fig. 12. In order to quantify this tolerance scope within the experimental period of 96 hours (5760 min.),

Figure 11 a-c. Thermal exposure cycles and percent mortalities of *Anoplarchus* and *Pholis* at 31, 29, and 27°C.

*Fig. 11a-c. Total thermal exposure, measured in °C min. and percent mortalities of each species at peak temperatures of 31.0 and 29.0 °C.*

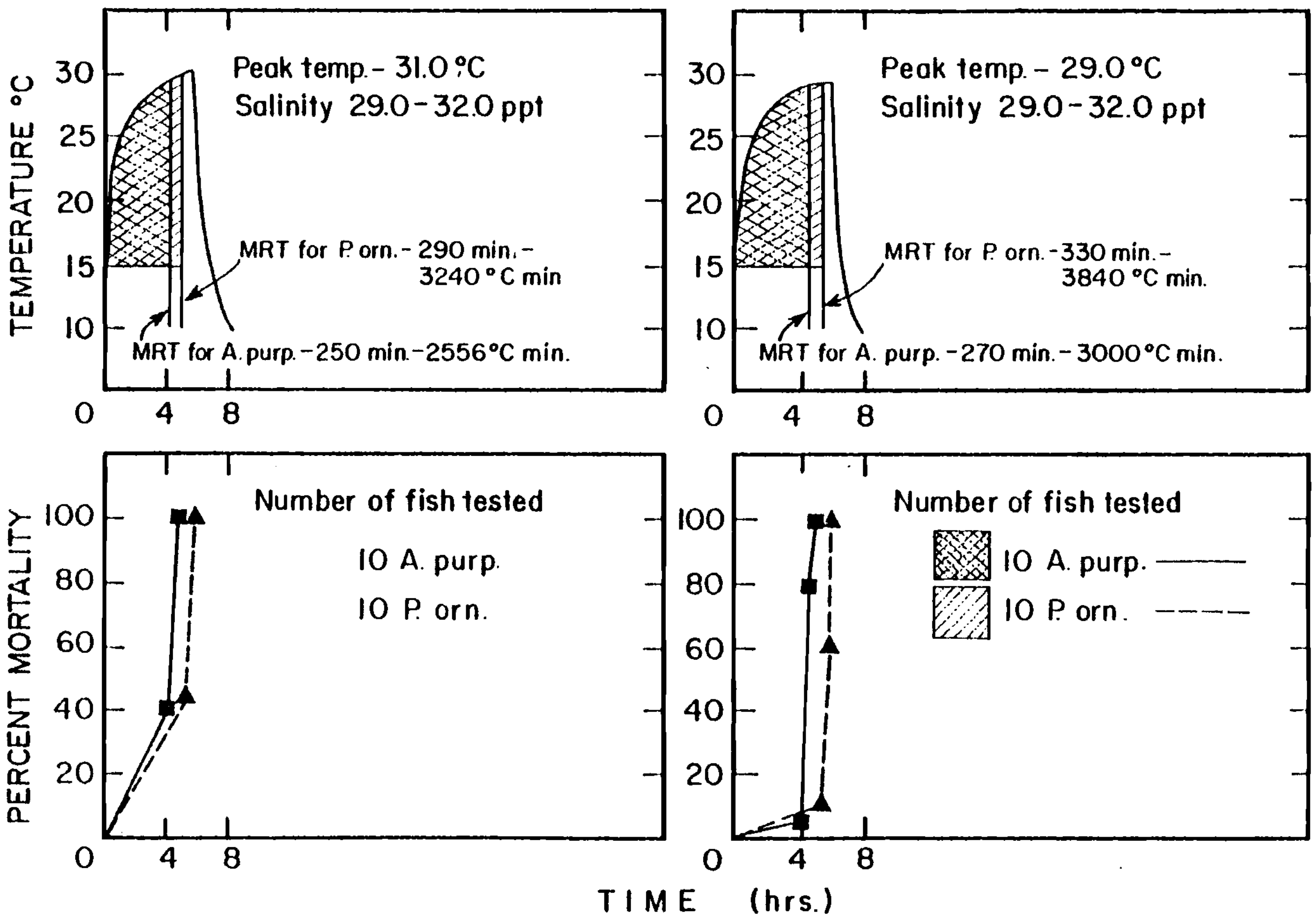


Fig. 11a

Fig. 11b

*Fig. 11c – Total thermal exposure, measured in °C min, and percent mortalities of each species at peak temperatures of 27.0 °C.*

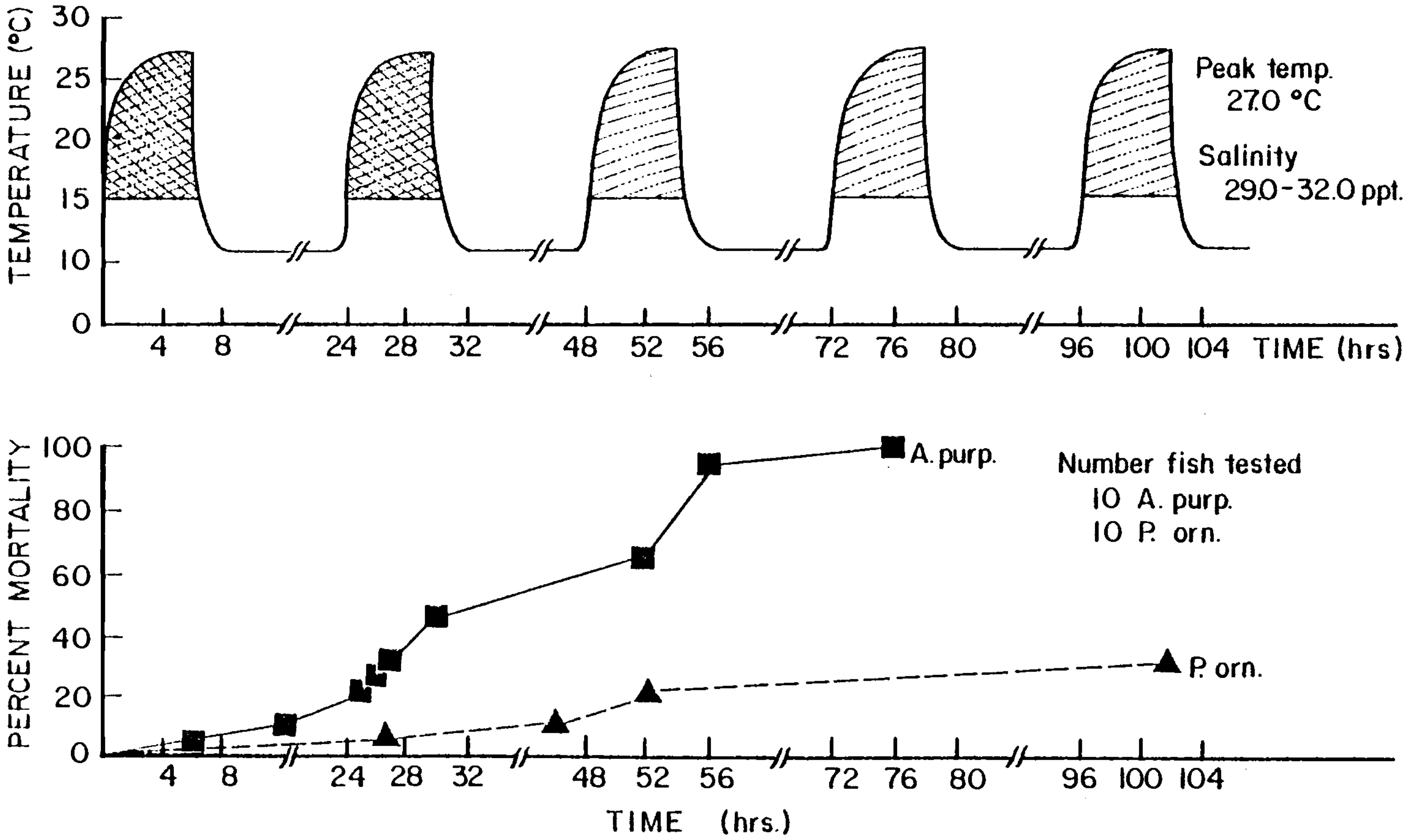
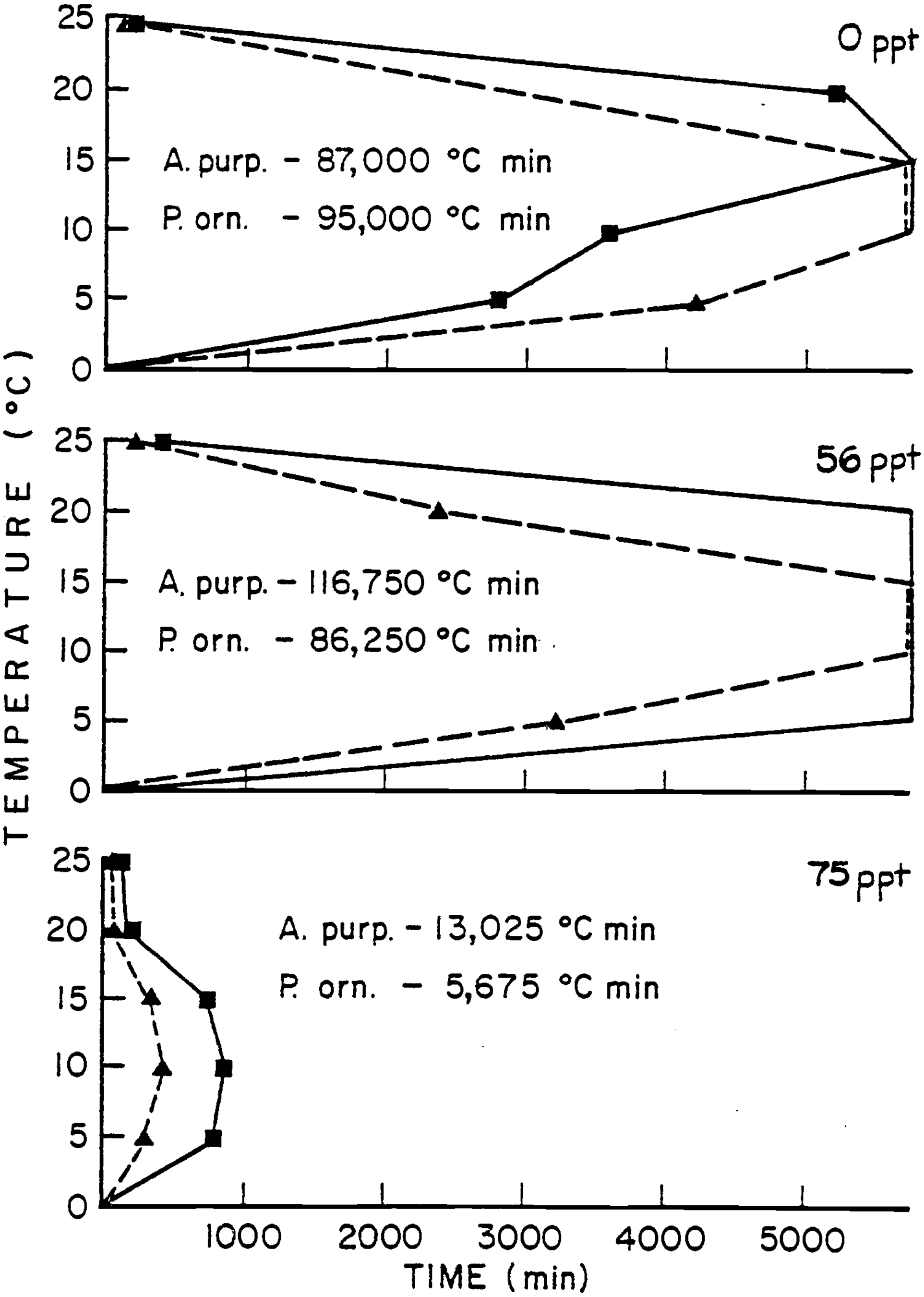


Figure 12. Plots of median resistance time vs. temperature at each salinity. Areas of enclosed polygons determine total thermal exposure in °C min.

*Fig. 12 - Plots of median resistance time vs. temperature at each salinity - Areas of enclosed polygons determine total thermal exposure in °C min. Ten individuals of each sp. tested at each salinity.*



the upper boundary of the scope, and hence the maximum MRT, was placed at 5760 min. If more than 50% of the fish lived beyond the duration of a particular experiment, their MRT was defined as 5760 min. Hence the calculated scopes only serve to measure relative tolerances to 96 hour exposures to the different combinations of temperature and salinity. By this method, a measure of the influence of salinity on the scope for thermal tolerance in each species was obtained (fig. 13). At 75 ppt the thermal scope of both species is sharply reduced yet the scope of *Anoplarchus* is still approximately twice that of *Pholis*. At 56 ppt *Anoplarchus* still has a greater thermal scope but, at 0 ppt, the reverse is obtained with *Pholis* having a slightly greater thermal scope. The combined influence of temperature and salinity on MRT is indicated in three-dimensional plots (fig. 14, 15). These plots essentially portray in three dimensions those polygons used to calculate tolerance scopes (fig. 12). Here, the greater tolerance of *Anoplarchus* to higher salinities over a broad range of temperatures and the greater tolerance of *Pholis* to temperature extremes in more dilute media is revealed. This is most readily observable at 25°C where the MRT of *Pholis* is greater than *Anoplarchus* except at 56 and 75 ppt (fig. 14, 15). Response surface estimations of the cumulative percent mortality after 96 hours are given in fig. 16 with the range of habitat temperatures and salinities superimposed. The equations used to generate these surfaces are

Figure 13. Effect of salinity on tolerance scope of *Anoplarchus* and *Pholis*.

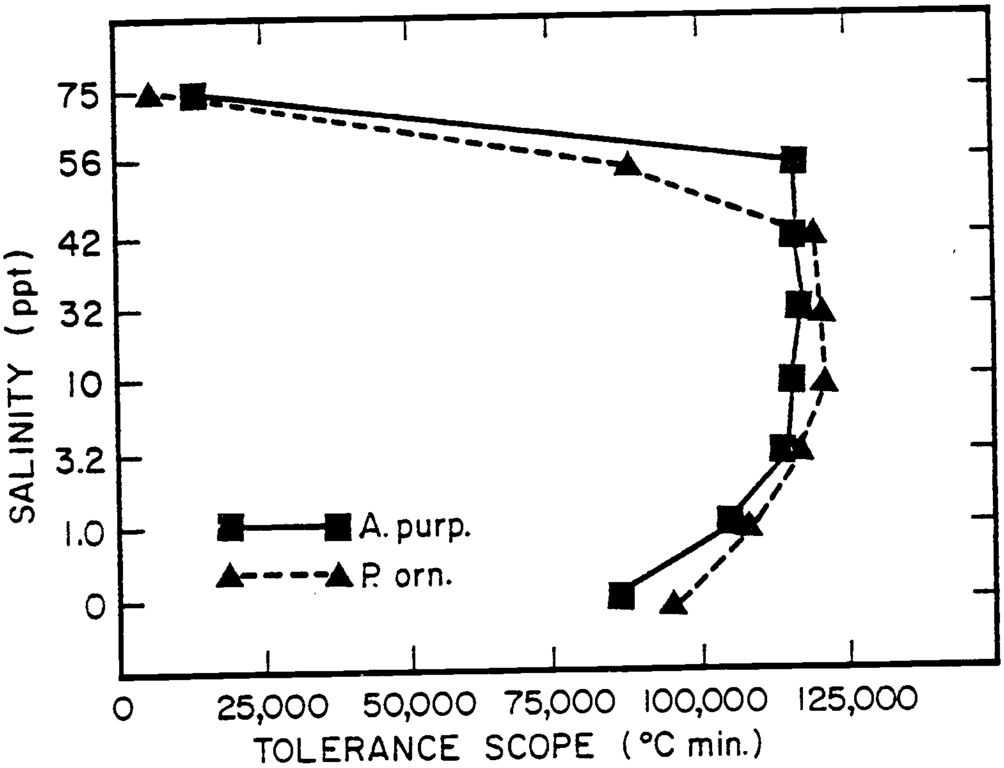

SALINITY (ppt)
75
56
42
32
10
3.2
1.0
0
A. purp.
P. orn.
0
25,000
50,000
75,000
100,000
125,000
TOLERANCE SCOPE (°C min.)

Figure 13.

Figure 14. Thermal tolerance surface for *Anoplarchus*.

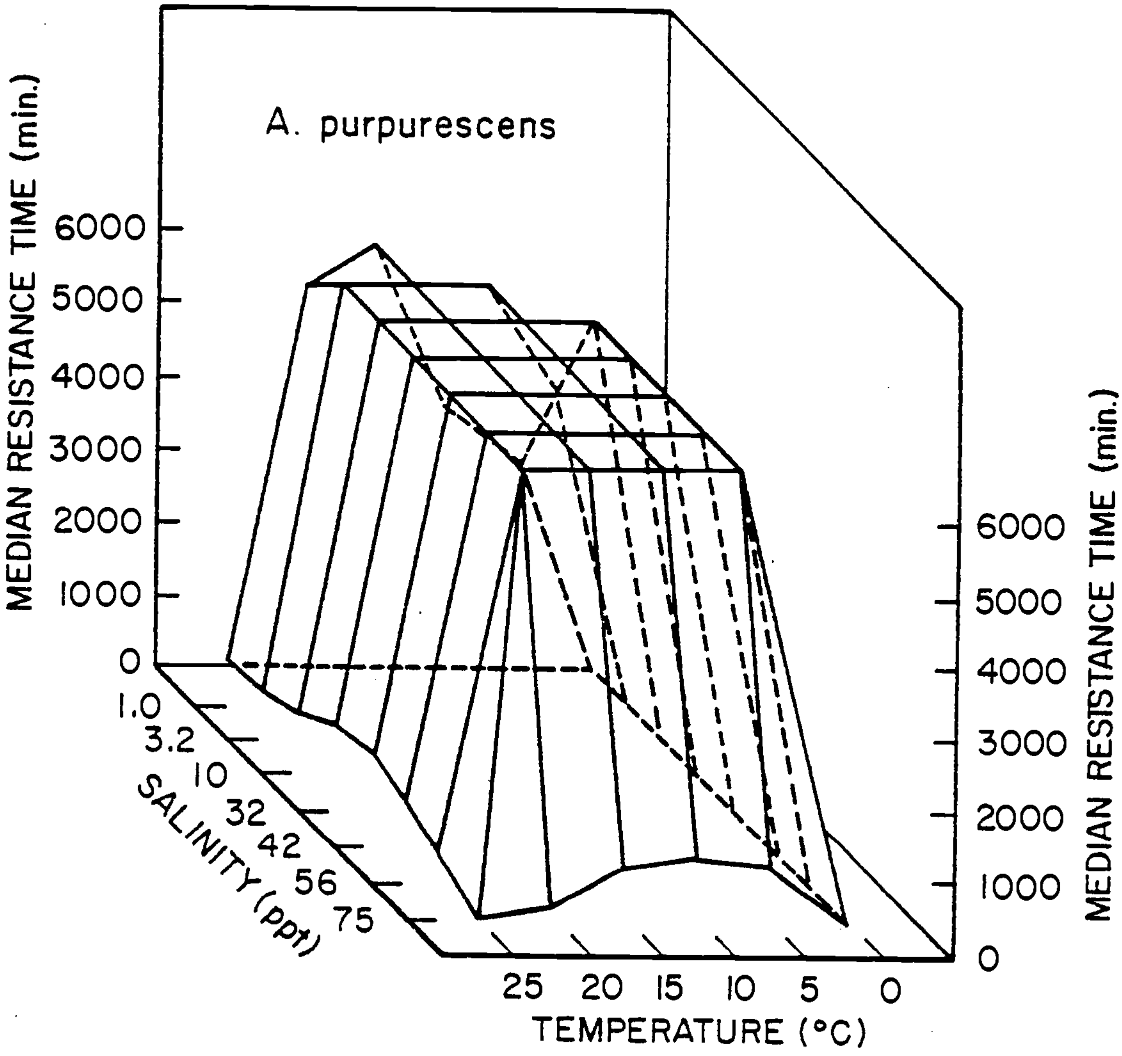

A. purpurescens
MEDIAN RESISTANCE TIME (min.)
6000
5000
4000
3000
2000
1000
0
SALINITY (ppt)
1.0
3.2
10
32
42
56
75
TEMPERATURE (°C)
25
20
15
10
5
0
MEDIAN RESISTANCE TIME (min.)
6000
5000
4000
3000
2000
1000
0

Figure 14.

Figure 15. Thermal tolerance surface for *Pholis*.

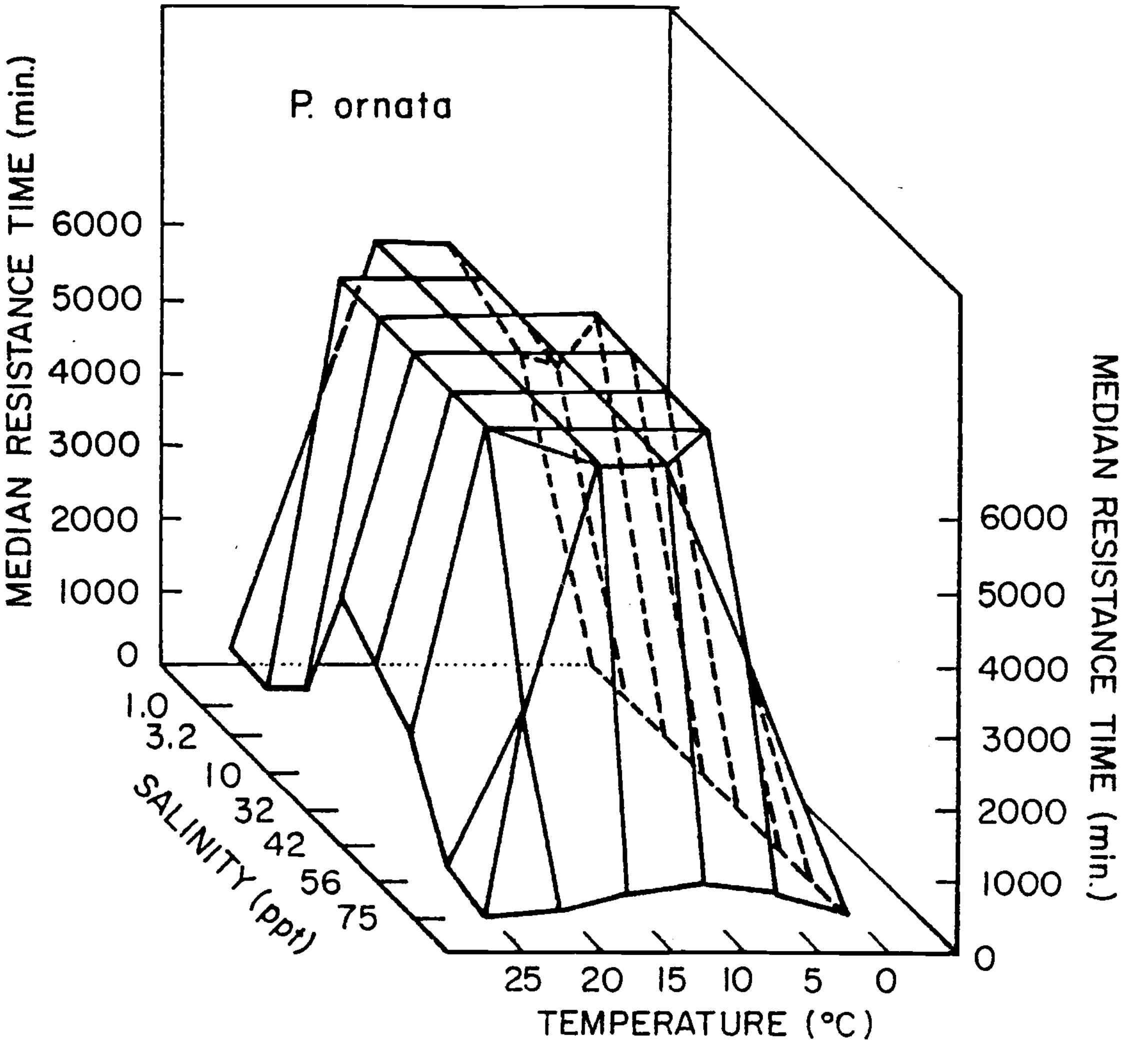
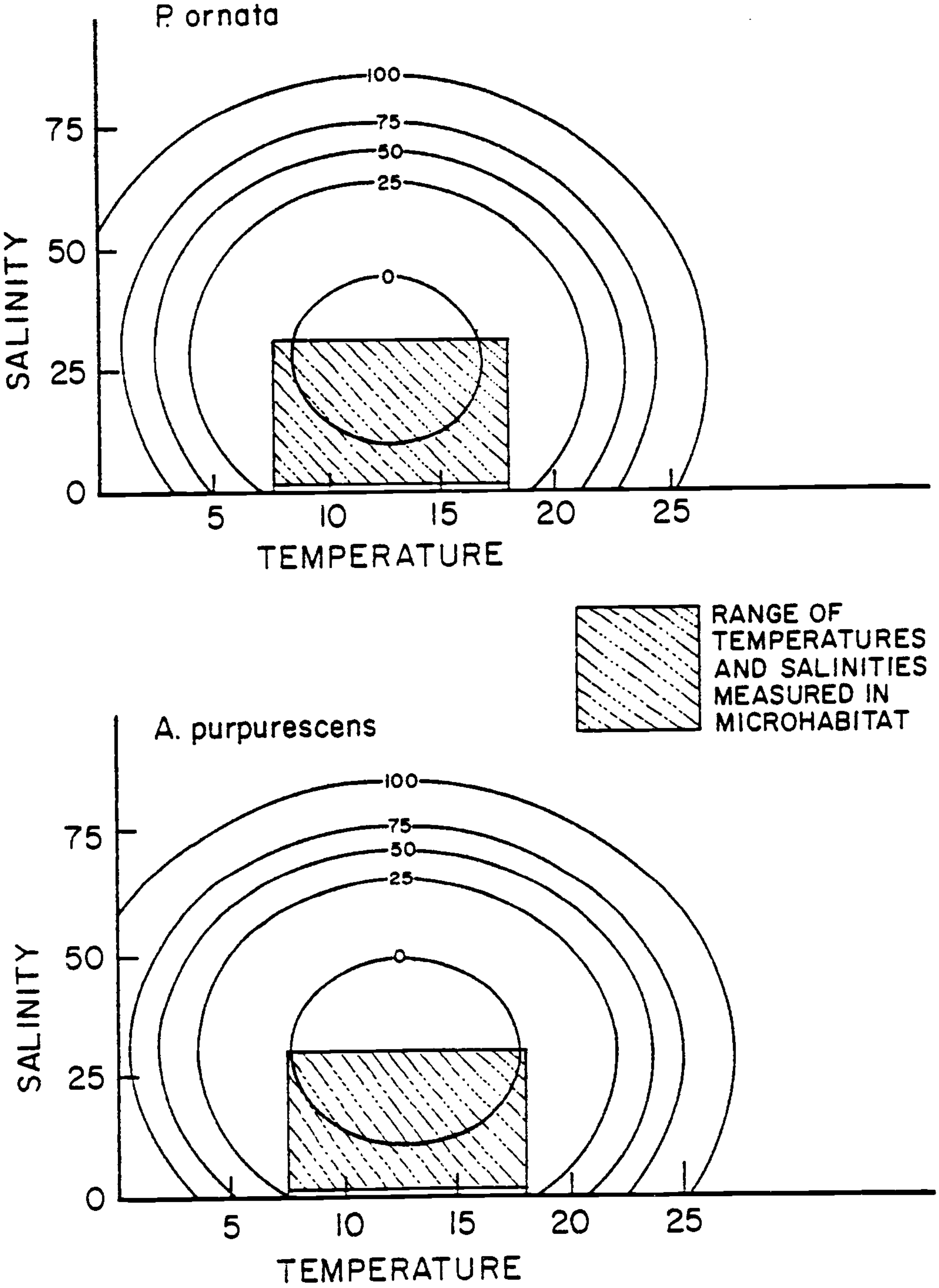

P. ornata
MEDIAN RESISTANCE TIME (min.)
6000
5000
4000
3000
2000
1000
0
SALINITY (ppt)
1.0
3.2
10
32
42
56
75
TEMPERATURE (°C)
25
20
15
10
5
0
MEDIAN RESISTANCE TIME (min.)
6000
5000
4000
3000
2000
1000
0

Figure 15.

Figure 16. Response surface estimations of percent mortality after 96 hours for *Anoplarchus* and *Pholis*.

*Fig. 16 - Response surface estimations of percent mortality after 96 hours.*



given in table 10. These response surfaces provide a graphic portrayal of the combined effects of temperature and salinity but are not precise enough to indicate the slight differences in tolerance between the two species.

Analysis of the blood serum osmolality of both species after exposure for 48 hours to salinities ranging from 0 to 56 ppt emphasize the euryhaline nature of these fishes with both species capable of efficient osmoregulation over a broad range of salinities (fig. 17). At 32 ppt, both species maintain blood osmolality between 350 and 390 mOsm. After 24 hours' exposure to hypersaline conditions, serum osmolality increases in both species with *Anoplarchus* showing a greater resistance to change. Exposure to essentially fresh water for the same time period decreases the serum osmolality in both species (fig. 18). Both species are capable of limited recovery of normal extracellular osmotic concentrations after three days' exposure to 56 ppt.

Figure 17. Serum osmolality of <u>Anoplarchus</u> and <u>Pholis</u> following 48 hours exposure to salinities ranging from 0 ppt to 56 ppt. Each dot represents the mean of five measurements and each vertical bar indicates the range of measured values.

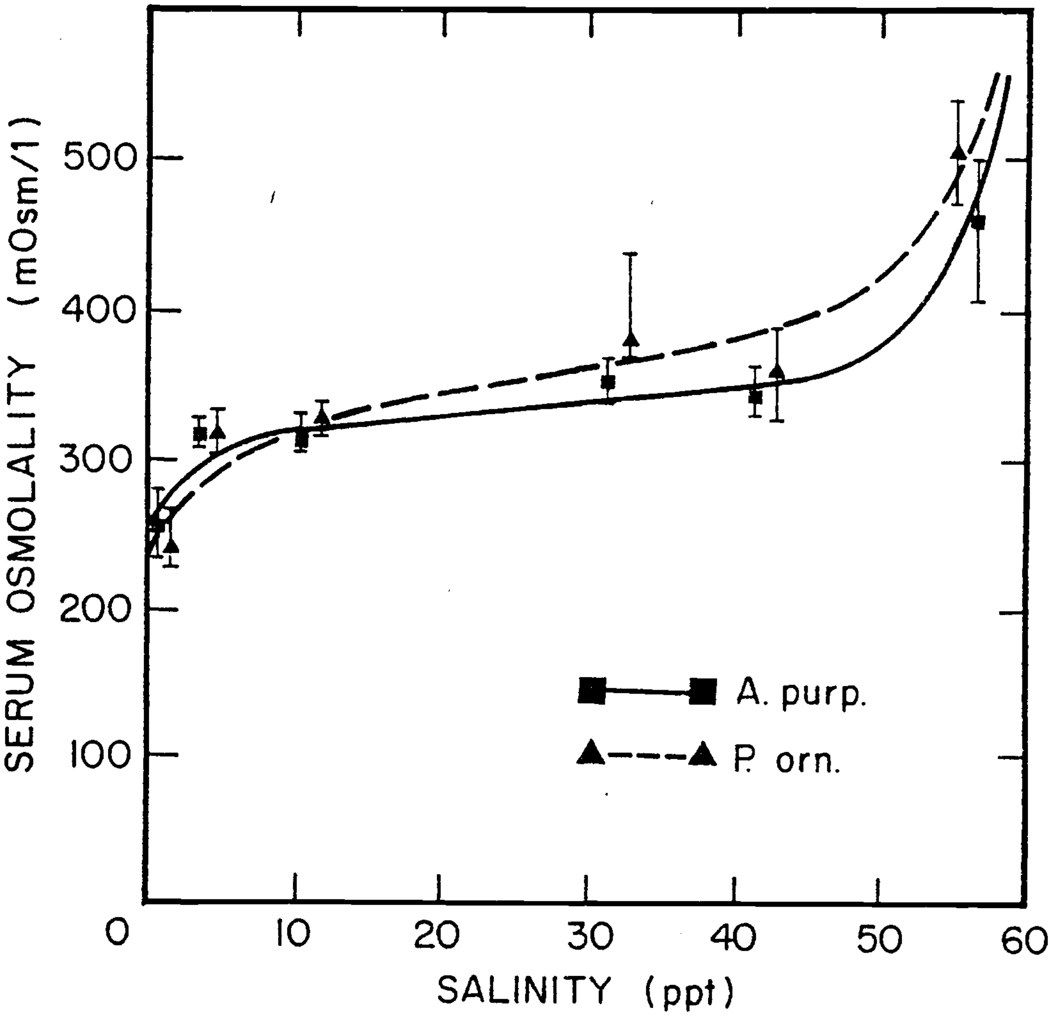

SERUM OSMOLALITY (mOsm/1)
500
400
300
200
100
0
10
20
30
40
50
60
SALINITY (ppt)
A. purp.
P. orn.

Figure 17.

Figure 18. Serum osmolality measured at 24 hour intervals over the course of a 72 hour exposure to 0 and 56 ppt. Vertical bars indicate range of five measurements with the means of measurements at each interval connected by solid or broken lines.

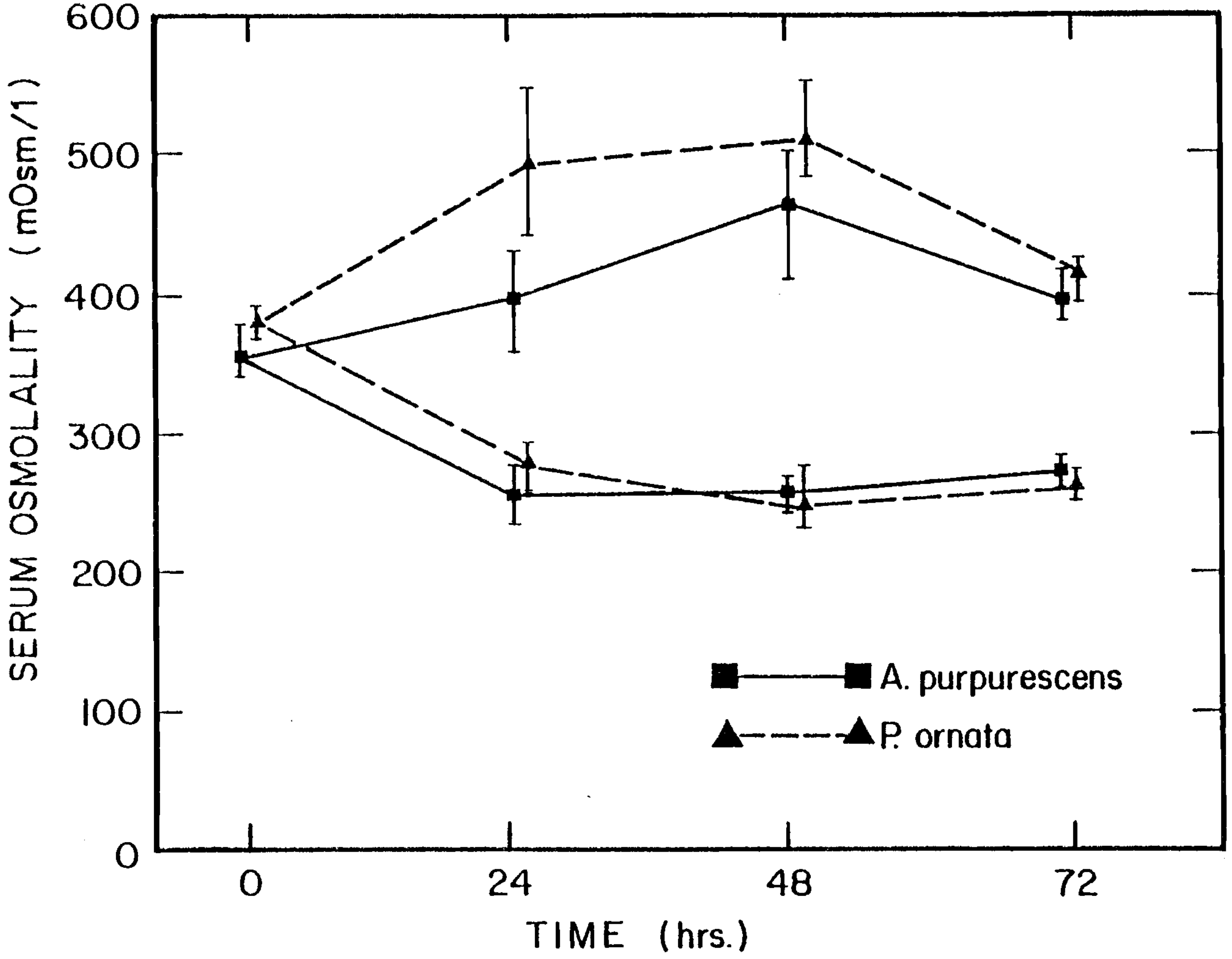

600
500
400
300
200
100
0
SERUM OSMOLALITY (mOsm/1)
0
24
48
72
TIME (hrs.)
A. purpurescens
P. ornata

Figure 18.

Table 1. Relative densities of each species in quadrats of increasing intertidal height

| height above MLLW (m) | quadrat number | mean no. fish/m$^2$<br>A. purp. | <br>P. orn. |
|---|---|---|---|
| .24 | 1 | 2.6 | .4 |
| | 2 | 2.4 | 1.0 |
| | 3 | 2.0 | 2.0 |
| | 4 | 1.7 | 1.4 |
| .76 | 5 | .7 | .6 |
| | 6 | 0 | 0 |
| 1.96 | 10 | 0 | 0 |

*Ten quadrats were sampled in each of 18 transects from VIII:19:1975 to VII:14:1976

Table 2. Analysis of variance in two factor test of significance of species abundance and season

| Source | d.f. | M.S. | S.S. | F |
|---|---|---|---|---|
| Treatments | 3 | 741.8 | 247.3 | 12.33** |
| species | 1 | 533.5 | 533.5 | 26.61** |
| season | 1 | 127.9 | 127.9 | 6.38** |
| Species x season | 1 | 80.3 | 80.3 | 4.00 |
| Error | 68 | 1363.3 | 20.05 | |
| Total | 71 | 2105.1 | | |

**highly significant (p=.01)
*significant (p=.05)

Table 3. Total numbers and relative percent abundance of *A. purpurescens* and *P. ornata* from transect collections taken at upper, mid, and lower sites from April to July, 1977

| Site | Date | number collected | | percent abundance | |
|---|---|---|---|---|---|
| | | A. purp. | P. orn. | A. purp. | P. orn. |
| 1 | IV:20:1977 | 0 | 55/9* | 0 | 100 |
| | V: 4:1977 | 0 | 18/16 | 0 | 100 |
| | V: 9:1977 | 0 | 21/13 | 0 | 100 |
| | V:20:1977 | 0 | 31/18 | 0 | 100 |
| | V:31:1977 | 0 | 16/10 | 0 | 100 |
| 2 | IV:20:1977 | 10 | 3/3 | 62 | 38 |
| | V: 4:1977 | 12 | 3/2 | 71 | 29 |
| | VI:17:1977 | 19 | 0/0 | 100 | 0 |
| | VI:23:1977 | 11 | 10/9 | 37 | 63 |
| | VIII: 1:1977 | 20 | 1/0 | 95 | 5 |
| 3 | V: 8:1977 | 50 | 0/0 | 100 | 0 |
| | V:18:1977 | 36 | 1/0 | 97 | 3 |
| | VI:17:1977 | 30 | 0/1 | 97 | 3 |
| | VI:23:1977 | 29 | 0/3 | 91 | 9 |
| | VII:29:1977 | 22 | 0/7 | 76 | 24 |

*one year or older/young-of-year

Table 4. Mean temperatures and salinities measured during transect sampling from April to July, 1977

| Site | Date | bay temp (°C) | under-rock temp. (°C) | bay salinity (ppt) | under-rock sal. (ppt) |
|---|---|---|---|---|---|
| 1 | IV:20:1977 | 11.7 | 14.0 | 4.0 | 12.2 |
| | V: 4:1977 | 11.8 | 13.5 | 10.0 | 17.0 |
| | V: 9:1977 | 11.5 | 13.5 | 10.0 | 17.5 |
| | V:20:1977 | 14.0 | 16.0 | 8.0 | 13.9 |
| | V:31:1977 | 13.7 | 15.0 | 6.0 | 14.8 |
| 2 | IV:20:1977 | 11.3 | 12.0 | 14.0 | 25.8 |
| | V: 4:1977 | 9.9 | 12.0 | 19.5 | 21.5 |
| | VI:17:1977 | 12.8 | 14.5 | 24.0 | 28.0 |
| | VI:23:1977 | 12.0 | 12.0 | 32.0 | 32.0 |
| | VIII: 1:1977 | 13.4 | 17.5 | 30.0 | 33.8 |
| 3 | V: 8:1977 | 13.3 | 15.5 | 29.0 | 31.2 |
| | V:18:1977 | 10.8 | 11.0 | 30.0 | 28.5 |
| | VI:17:1977 | 11.1 | 12.0 | 32.0 | 32.0 |
| | VI:23:1977 | 14.6 | 20.5 | 33.0 | 32.8 |
| | VII:29:1977 | 11.8 | 11.5 | 33.5 | 33.7 |

Table 5. Mean and range of temperatures measured in air, at bay surface at low tide and under rocks in habitats

| Date | mean air temp. (°C) | range | mean sea temp. (°C) | range | mean rock temp. (°C) | range |
|---|---|---|---|---|---|---|
| VII:20:1974 | 17.3 | 14.0-19.0 | 19.0 | 17.2-22.5 | 15.2 | 13.2-17.0 |
| VIII: 3:1974 | 14.8 | 14.0-15.5 | 18.0 | 17.4-18.5 | 13.3 | 13.0-14.0 |
| VIII:20:1974 | 14.5 | 13.0-21.0 | 15.6 | 15.2-16.0 | 14.5 | 14.2-14.8 |
| X: 7:1974 | 8.0 | 7.0- 9.5 | 11.9 | 10.8-12.5 | 8.3 | 7.0- 9.0 |
| X:20:1974 | 7.5 | 5.5-10.5 | 10.3 | 10.0-11.0 | 4.8 | 4.0- 5.5 |
| XI: 5:1974 | 12.5 | 11.0-14.0 | 10.3 | 10.0-10.5 | 10.5 | 10.5 |
| XI:18:1974 | 10.3 | 8.0-14.0 | 9.5 | 9.5 | 10.8 | 10.5-11.0 |
| XII: 3:1974 | 10.7 | 9.0-12.5 | 9.5 | 9.5 | 9.1 | 9.0- 9.5 |
| XII:17:1974 | 5.5 | 5.0- 7.0 | 9.2 | 9.0- 9.5 | 6.4 | 5.0- 8.0 |
| I:26:1975 | 5.9 | 4.0- 8.5 | 8.6 | 8.0- 9.5 | 6.5 | 6.0- 7.5 |
| II:24:1975 | 8.2 | 6.5- 9.5 | 10.0 | 9.5-11.5 | 8.9 | 8.0-10.0 |
| III: 2:1975 | 6.2 | 5.5- 7.0 | 9.2 | 9.0- 9.5 | 8.2 | 7.5- 9.0 |
| III:26:1975 | 6.7 | 6.0- 8.5 | 8.8 | 8.5- 9.0 | 7.5 | 7.0 - 8.0 |
| IV:16:1975 | 8.3 | 8.0- 9.0 | 10.6 | 10.0-11.0 | 10.0 | 10.0 |
| V: 2:1975 | 11.0 | 9.5-12.5 | 12.6 | 12.6 | 10.3 | 10.0-10.5 |
| V:26:1975 | 15.1 | 14.0-18.0 | 15.9 | 15.5-16.0 | 14.1 | 14.0-14.5 |
| V:31:1975 | 23.5 | 20.5-26.5 | 18.7 | 18.0-19.0 | 17.6 | 17.0-19.0 |
| VI:16:1975 | 16.1 | 13.8-15.0 | 16.2 | 15.0-17.0 | 14.3 | 14.0-15.0 |
| VII:12:1975 | 16.2 | 14.0-18.0 | 16.0 | 15.5-17.0 | 12.2 | 12.0-12.5 |
| VIII:10:1975 | 17.7 | 17.0-18.0 | 17.5 | 17.0-18.0 | 13.3 | 12.5-14.0 |
| IX: 5:1975 | 14.8 | 14.0-16.0 | 16.2 | 15.5-17.0 | 12.5 | 12.5 |
| X: 3:1975 | 14.2 | 13.5-15.5 | 14.0 | 14.0 | 14.0 | 14.0 |
| X:23:1975 | 10.5 | 9.5-12.0 | 13.0 | 12.5-13.5 | 11.0 | 10.5-12.0 |
| XI: 7:1975 | 6.2 | 5.0- 7.0 | 10.2 | 10.0-10.5 | 9.0 | 9.0 |
| XI:20:1975 | 9.2 | 9.0- 9.5 | 8.5 | 8.5 | 9.5 | 9.5 |
| XII: 3:1975 | 10.7 | 10.5-11.0 | 10.7 | 10.5-11.0 | 11.0 | 11.0 |
| XII:17:1975 | 7.5 | 5.0- 8.5 | 8.0 | 8.0 | 8.4 | 8.0- 8.5 |
| I: 2:1976 | 7.0 | 6.5- 8.0 | 7.8 | 7.5- 8.5 | 8.0 | 8.0 |
| I:19:1976 | 9.8 | 7.5-12.5 | 8.0 | 7.5- 9.0 | 8.2 | 7.5- 9.0 |
| II: 2:1976 | 4.5 | 3.0- 6.5 | 7.8 | 7.5- 8.0 | 7.8 | 7.5- 8.0 |
| II:10:1976 | 8.0 | 7.0-10.0 | 7.8 | 7.5- 8.0 | 8.0 | 8.0 |
| III:19:1976 | 7.3 | 6.5- 8.0 | 9.5 | 9.5 | 7.5 | 7.0- 8.0 |
| IV:16:1976 | 7.3 | 5.5-10.0 | 10.2 | 10.0-10.5 | 8.3 | 8.0- 9.0 |
| V: 5:1976 | 11.5 | 11.0-12.5 | 14.2 | 14.0-14.5 | 12.2 | 12.0-12.5 |
| V:19:1976 | 14.5 | 14.5 | 14.3 | 14.0-14.5 | 12.5 | 12.5 |
| VI:16:1976 | 14.5 | 14.0-15.0 | 14.5 | 14.5 | 14.2 | 14.0-14.5 |
| VII:14:1976 | 17.5 | 17.0-18.5 | 20.0 | 20.0 | 18.0 | 18.0 |
|  |  | $\overline{X}$ =2.8* |  | $\overline{X}$ = .83* |  | $\overline{X}$ = .85* |

*X = mean fluctuation of temperature

Table 6. Mean and ranges of salinity measured at bay surface at low tide and under rocks in microhabitats

| Date | mean bay salinity (ppt) | range | mean under-rock salinity (ppt) | range |
|---|---|---|---|---|
| VII:20:1974 | 22.6 | 17.2-26.0 | 26.0 | 25.5-26.5 |
| VIII: 3:1974 | 29.5 | 28.0-30.0 | 29.5 | 29.0-30.0 |
| VIII:20:1974 | 29.1 | 29.0-29.5 | 16.0 | 15.0-17.0 |
| X: 7:1974 | 29.5 | 29.0-30.0 | 29.4 | 29.0-29.5 |
| X:20:1974 | 30.2 | 29.5-31.0 | 29.2 | 28.0-31.0 |
| XI: 5:1974 | 30.0 | 30.0 | 28.0 | 24.0-30.0 |
| XI:18:1974 | 24.5 | 24.0-25.5 | 21.0 | 21.0 |
| XII: 3:1974 | 20.8 | 19.0-24.5 | 17.0 | 15.5-20.0 |
| XII:17:1974 | 6.4 | 5.0- 8.0 | 13.6 | 8.5-20.0 |
| I:26:1975 | 1.0 | 0.0- 3.0 | 12.4 | 12.0-12.5 |
| II:24:1975 | 7.7 | 7.0-10.0 | 13.1 | 8.0-18.0 |
| III: 2:1975 | 15.0 | 14.0-16.0 | 17.5 | 15.0-20.0 |
| III:26:1975 | 8.7 | 8.5- 9.0 | 10.8 | 6.0-16.0 |
| IV:16:1975 | 12.9 | 10.0-15.5 | 19.4 | 15.0-24.0 |
| V: 2:1975 | 13.5 | 12.0-15.0 | 15.2 | 13.0-20.0 |
| V:26:1975 | 15.4 | 15.0-16.0 | 20.5 | 17.0-23.0 |
| V:31:1975 | 21.2 | 21.0-21.5 | 21.5 | 16.0-23.0 |
| VI:16:1975 | 26.5 | 26.0-27.0 | 20.2 | 16.0-25.0 |
| VII:12:1975 | 26.0 | 26.0 | 30.4 | 28.0-32.0 |
| VIII:10:1975 | 29.5 | 28.5-30.0 | 32.0 | 31.0-34.0 |
| IX: 5:1975 | 27.8 | 27.5-28.0 | 30.8 | 29.5-32.0 |
| X: 3:1975 | 29.5 | 29.0-30.5 | 29.3 | 29.0-31.0 |
| X:23:1975 | 25.5 | 25.0-26.5 | 29.2 | 27.0-30.0 |
| XI: 7:1975 | 12.5 | 12.0-13.0 | 22.7 | 21.0-25.0 |
| XI:20:1975 | 12.0 | 12.0 | 18.3 | 17.0-20.0 |
| XII: 3:1975 | .5 | 0.0- 1.0 | 1.3 | 0.0- 2.0 |
| XII: 7:1975 | 10.0 | 10.0 | 17.0 | 15.0-21.0 |
| I: 2:1976 | 9.0 | 8.0-11.0 | 13.0 | 9.0-21.0 |
| I:19:1976 | 10.0 | 9.5-10.5 | 15.9 | 12.5-20.0 |
| II: 2:1976 | 14.7 | 14.0-15.0 | 17.0 | 14.0-20.0 |
| II:10:1976 | 10.1 | 8.8-11.0 | 7.8 | 6.5-13.0 |
| III:19:1976 | 16.0 | 16.0 | 22.5 | 22.0-23.0 |
| IV:16:1976 | 15.0 | 12.5-16.0 | 19.7 | 18.0-22.0 |
| V: 5:1976 | 18.0 | 18.0 | 22.7 | 21.0-24.0 |
| V:19:1976 | 24.3 | 24 0-25.0 | 26.4 | 24.0-28.0 |
| VI:16:1976 | 26.3 | 26.0-26.5 | 25.6 | 25.0-27.0 |
| VII:14:1976 | 27.8 | 27.0-28.0 | 30.4 | 27.0-32.0 |
|  |  | $\overline{X} = 1.7$* |  | $\overline{X} = 4.8$* |

*mean fluctuation of salinity

Table 7. Rate of change of temperature and salinities at site 2 during sampling from July, 1974 to July, 1976

| Date | time of low tide | hours of exposure | $\Delta T_a$ ($^oC$/hr.) | $\Delta T_b$ ($^oC$/hr.) | $\Delta T_r$ ($^oC$/hr.) | $\Delta S_b$ (ppt/hr.) | $\Delta S_r$ (ppt/hr.) |
|---|---|---|---|---|---|---|---|
| VII:20:1974 | a. m. | 6 | +2.5 | +2.6 | +1.9 | +4.4 | + .5 |
| VIII: 3:1974 | a. m. | 4 | + .9 | + .6 | + .5 | +1.0 | +1.0 |
| VIII:20:1974 | a. m. | 4.5 | -4.0 | 0.0 | + .1 | 0.0 | + .5 |
| X: 7:1974 | p. m. | 4.0 | -1.6 | - .9 | -1.3 | - .7 | - .3 |
| X:20:1974 | p. m. | 1.5 | -4.0 | -0.0 | - .5 | -1.5 | -3.0 |
| XI: 5:1974 | p. m. | 4.0 | -3.0 | + .4 | - .1 | 0.0 | -6.0 |
| XI:18:1974 | p. m. | 3.0 | -6.0 | 0.0 | + .5 | +1.5 | 0.0 |
| XII: 3:1974 | p. m. | 3.5 | -2.0 | 0.0 | - .3 | -5.5 | 0.0 |
| XII:17:1974 | p. m. | 3.5 | -2.0 | - .5 | -1.9 | -1.3 | +4.0 |
| I:26:1975 | p. m. | 4.5 | -3.0 | - .7 | - .9 | -1.5 | -0.0 |
| II:24:1975 | p. m. | 5.0 | -2.0 | -1.3 | -1.3 | -1.5 | +3.6 |
| III: 2:1975 | p. m. | 2.5 | -2.0 | - .7 | -2.0 | -2.6 | -6.9 |
| III:26:1975 | p. m. | 4.5 | -1.6 | - .3 | - .3 | - .6 | +3.6 |
| IV:16:1975 | a. m. | 4.5 | - .7 | 0.0 | 0.0 | 0.0 | +2.2 |
| V: 2:1975 | a. m. | 2.0 | -6.0 | 0.0 | -1.0 | -6.0 | -1.0 |
| V:26:1975 | a. m. | 3.0 | -2.6 | + .3 | + .3 | - .3 | +2.3 |
| V:31:1975 | a. m. | 3.5 | -3.0 | +1.0 | -2.0 | 0.0 | +1.0 |
| VI:16:1975 | a. m. | 3.0 | + .7 | -1.5 | -1.0 | + .5 | + .5 |
| VII:12:1975 | a. m. | 6.0 | +3.0 | + .6 | + .3 | 0.0 | 0.0 |
| VIII:10:1975 | a. m. | 4.0 | 0.0 | - .5 | +1.0 | +1.5 | 0.0 |
| IX: 5:1975 | a. m. | 5.5 | 0.0 | + .4 | 0.0 | 0.0 | +1.6 |
| X: 3:1975 | p. m. | 2.5 | -2.0 | 0.0 | 0.0 | -1.5 | - .8 |
| X:23:1975 | p. m. | 2.5 | -2.6 | -1.0 | -1.5 | -1.5 | + .3 |
| XI: 7:1975 | p. m. | 2.5 | - .5 | 0.0 | 0.0 | - .5 | 0.0 |
| XI:20:1975 | p. m. | 2.5 | 0.0 | 0.0 | 0.0 | 0.0 | -1.0 |
| XII: 3:1975 | p. m. | 6.0 | -1.0 | -1.0 | 0.0 | -1.0 | 0.0 |
| XII:17:1975 | p. m. | 4.5 | -3.0 | 0.0 | - .5 | 0.0 | + .6 |
| I: 2:1976 | p. m. | 5.0 | -1.5 | -1.0 | 0.0 | -3.0 | -1.0 |
| I:19:1976 | p. m. | 3.5 | -5.0 | -1.5 | -1.5 | + .5 | -1.5 |
| II: 2:1976 | p. m. | 2.0 | -3.5 | - .5 | - .5 | -1.0 | -0.0 |
| II:10:1976 | p. m. | 2.5 | -3.0 | - .5 | 0.0 | +2.2 | - .7 |
| III:19:1976 | a. m. | 4.0 | +3.0 | 0.0 | 0.0 | 0.0 | +2.0 |
| IV:16:1976 | a. m. | 6.0 | +4.5 | + .5 | +1.0 | -4.0 | + .8 |
| V: 5:1976 | a. m. | 3.0 | +1.5 | - .5 | - .5 | 0.0 | 0.0 |
| V:19:1976 | a. m. | 3.5 | 0.0 | + .5 | 0.0 | -1.0 | 0.0 |
| VI:16:1976 | a. m. | 3.0 | -2.0 | 0.0 | -1.0 | -1.0 | 0.0 |
| VII:14:1976 | a. m. | 5.0 | 0.0 | 0.0 | 0.0 | +1.0 | - .3 |

$\Delta T_a$ - rate of change of air temperature

$\Delta T_b$ - rate of change of bay surface water temperature

$\Delta T_r$ - rate of change of under-rock microhabitat temperature

$\Delta S_b$ - rate of change of bay surface water salinity

$\Delta S_r$ - rate of change of under-rock microhabitat salinity

Table 8. Critical thermal maxima, percent recovery from heat coma, and percent recovery from chill coma of *A. purpurescens* and *P. ornata* tested in different seasons

| Season | Winter | | | | Summer | | | |
|---|---|---|---|---|---|---|---|---|
| Species | A. purp. | | P. orn. | | A. purp. | | P. orn. | |
| no. tested | 5 | | 5 | | 5 | | 5 | |
| trial no. | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 |
| CTM (°C) | 30.0 | 29.5 | 31.0 | 31.0 | 30.0 | 29.5 | 31.5 | 31.0 |
| Pct. recovery from heat coma | 50 | 70 | 50 | 40 | 70 | 90 | 90 | 90 |
| Pct. recovery from chill coma | | | | | | | | |
| 4 hour exposure | 80 | 100 | 0 | 20 | 100 | 100 | 40 | 40 |
| 8 hour exposure | 0 | 60 | 0 | 0 | 80 | 60 | 20 | 10 |

Table 9. Median resistance times ±1 standard error (±1 probit) for *A. purpurescens* and *P. ornata* at different combinations of temperature and salinity

| Temperature (°C) | Salinity (ppt) | A. purpurescens MRT | A. purpurescens Std. error | P. ornata MRT | P. ornata Std. error |
|---|---|---|---|---|---|
| 0 | 0 | 0 | -- | 0 | -- |
| 5 | 0 | 2800 | 1500-5200 | 4200 | 2700-6400 |
| 10 | 0 | 3600 | 1900* | > 5760 | ** |
| 15 | 0 | > 5760 | ** | > 5760 | ** |
| 20 | 0 | 5200 | 3500* | 3200 | 1000* |
| 25 | 0 | 120 | 66-220 | 190 | 150-310 |
| 0 | 1 | 0 | -- | 0 | -- |
| 5 | 1 | 4320 | 2700-7200 | 4600 | 3000* |
| 10 | 1 | > 5760 | ** | > 5760 | ** |
| 15 | 1 | > 5760 | ** | > 5760 | ** |
| 20 | 1 | > 5760 | ** | > 5760 | ** |
| 25 | 1 | 145 | 118-180 | 155 | 130-190 |
| 0 | 3.2 | 0 | -- | 0 | -- |
| 5 | 3.2 | > 5760 | ** | > 5760 | ** |
| 10 | 3.2 | > 5760 | ** | > 5760 | ** |
| 15 | 3.2 | > 5760 | ** | > 5760 | ** |
| 20 | 3.2 | > 5760 | ** | > 5760 | ** |
| 25 | 3.2 | 340 | 22-540 | 670 | 480-960 |
| 0 | 10 | 0 | -- | 0 | -- |
| 5 | 10 | > 5760 | ** | > 5760 | ** |
| 10 | 10 | > 5760 | ** | > 5760 | ** |
| 15 | 10 | > 5760 | ** | > 5760 | ** |
| 20 | 10 | > 5760 | ** | > 5760 | ** |
| 25 | 10 | 680 | 420-1100 | 2475 | 1400-3450 |
| 0 | 32 | 0 | -- | 0 | -- |
| 5 | 32 | > 5760 | ** | > 5760 | ** |
| 10 | 32 | > 5760 | ** | > 5760 | ** |
| 15 | 32 | > 5760 | ** | > 5760 | ** |
| 20 | 32 | > 5760 | ** | > 5760 | ** |
| 25 | 32 | 810 | 740-920 | 2050 | 1900-2200 |
| 0 | 42 | 0 | -- | 0 | -- |
| 5 | 42 | > 5760 | ** | > 5760 | ** |
| 10 | 42 | > 5760 | ** | > 5760 | ** |
| 15 | 42 | > 5760 | ** | > 5760 | ** |
| 20 | 42 | > 5760 | ** | > 5760 | ** |
| 25 | 42 | 680 | 350-1600 | 1525 | 680-3700 |

Table 9. (Continued)

| Temperature (°C) | Salinity (ppt) | A. purpurescens MRT | A. purpurescens Std. error | P. ornata MRT | P. ornata Std. error |
|---|---|---|---|---|---|
| 0 | 56 | 0 | -- | 0 | -- |
| 5 | 56 | > 5760 | ** | 3250 | 2200-4800 |
| 10 | 56 | > 5760 | ** | > 5760 | ** |
| 15 | 56 | > 5760 | ** | > 5760 | ** |
| 20 | 56 | > 5760 | ** | 2400 | 1750-3600 |
| 25 | 56 | 430 | 270-700 | 210 | 105-410 |
| 0 | 75 | 0 | -- | 0 | -- |
| 5 | 75 | 760 | 680-860 | 310 | 250-380 |
| 10 | 75 | 860 | 580-1300 | 440 | 320-610 |
| 15 | 75 | 740 | 460-1050 | 340 | 250-440 |
| 20 | 75 | 200 | 150-300 | 94 | 58-150 |
| 25 | 75 | 42 | 36-48 | 37 | 30-46 |

*upper limit of std. error greater than 5760 minutes

**std. error not determined since MRT greater than 5760 minutes

Table 10. Regression equations describing response surface estimations of percent mortality at different combinations of temperature and salinity for *A. purpurescens* and *P. ornata*

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Anoplarchus purpurescens

$$Y = 1.6904 - .2208x_1 - .0349x_2 + .0036x_1^2 + .0001x_1x_2 + .0006x_2^2$$

Pholis ornata

$$Y = 1.6889 - .2261x_1 - .0292x_2 + .0087x_1^2 + .0001x_1x_2 + .0005x_2^2$$

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$$Y = \arcsin\sqrt{\frac{\%\ \text{mortality}}{100}}$$

$x_1$ = temperature

$x_2$ = salinity

# DISCUSSION

## The Physical Environment

The abundance of suitable rocky nearshore habitat in the northeast Pacific has accommodated the development of a diverse intertidal ichthyofauna. Amphibious fishes, chiefly blennioids, are particularly abundant along exposed coasts of the northeast Pacific, but estuarine intertidal areas appear to be restricted habitats in terms of the number of blennioid species which inhabit them. Studies which characterize the physical environment of blennioid habitats and attempt to relate this environment to individual species' own tolerance levels may provide information on the extent to which physical, as opposed to biotic, control governs animal diversity in a given area.

Measurements of temperature in Yaquina Bay indicate that the overall thermal habitat of littoral fishes residing there is quite uniform. In Yaquina Bay, salinity is lowest and most variable during the winter because of periodic heavy precipitation. Temperature is most variable during the summer owing to coastal upwelling and local heating (Frolander, 1964; Frolander et al., 1973). Very little fluctuation of temperature was observed as a result of tidal exposure and inundation. As a result, the fishes are not likely to experience both extremely high or low temperatures or rapid changes in temperature as tides advance and retreat. If temperature is as influential in governing the lives of organisms as some believe (i. e., Norris, 1963), the consistency of the thermal environment in the northeast Pacific littoral zone probably is the chief factor enabling the development of biologically accommodating mechanisms, i. e., resource partitioning, among several species. Barton (1973) has revealed biological accommodation in the form of habitat and food partitioning in several coexistent species of central California blennioids. While biological accommodation may be the chief mechanism governing the ecological interactions of intertidal fishes, the habitats selected by the species may still be indicative of their tolerance scopes. Sculpins of the genus Oligocottus are thermally restricted in that one species, O. maculosus, living higher in the intertidal zone has a greater thermal capacity than another species of the same genus living lower in the intertidal zone (Nakamura, 1976). Freezing temperatures are rarely encountered on the Pacific coast at this latitude and were never recorded in the intertidal zone during the course of this study. Whether or not temperature regimes can be considered moderate or extreme cannot be adequately evaluated without determination of the thermal scope of the affected organism. In comparing the thermal habitat of the western versus the eastern Pacific coast, Gislen (1949) concluded that the marine flora and fauna in the northeast Pacific is more exclusive, uniform, and stenothermic than at the same latitude in the western Pacific. The combination of low tides occurring at early or late hours in the day, and the amount of precipitation in the form of fogs or rain tend to minimize tidally induced thermal fluctuation. This is not to say that extreme thermal conditions do not occur; heat kills have been recorded on this coast, yet blennioid fishes, by virtue of their cryptic nature, exploit the insulation provided by rock and cobble habitats. They are therefore less prone to be affected by extreme temperatures. Accurate assessment of the influence of rare, non-periodic thermal events, such as heat kills, on the distribution of animals is most difficult. Fishes, being mobile, probably are less affected by thermal events in the intertidal zone than sessile invertebrates.

Salinity fluctuation was more influenced by seasons than tides. In the winter, fishes were frequently exposed to freshwater flushing during heavy rainstorms that drove local salinities to near 0 ppt. The intertidal habitat did tend to minimize tidally induced salinity fluctuations. As the tide dropped, the freshwater influence increased and salinities recorded adjacent to the rocky shoreline were consistently lower than those in pockets in the intertidal zone. This condition persisted until the return of the tide when a rapid flushing equilibrated the salinities of the under-rock habitat and the less saline, overlying water. These conditions probably persist for only a short time because the salinities increase with the advancing tide. The overall effect was to minimize the amount of dilution experienced by fishes living in the intertidal zone. Amphibious fishes, such as the northern blennioids, are not dependent on pockets of water retained in the intertidal zone; they are frequently found out of water and thus are probably capable of a considerable amount of resistance to desiccation. Salinity fluctuation is therefore not as influential as it might be for another commonly encountered coexistent species, Oligocottus maculosus. This species was invariably found in small water pockets left by the receding tide, only rarely being collected completely emergent from water. The nature of salinity fluctuation, like the thermal regime, cannot be adequately evaluated without an assessment of the tolerance to salinity fluctuation in these species.

## Distribution of Pholis and Anoplarchus

Along the northeast Pacific coast, the blennioid fish fauna is less diverse in estuaries than on the open coast. Many of the 20 or so species which live on the open coast are rarely encountered but only a few of the most abundant species inhabit the rocky intertidal substrates of estuaries. The comparative distribution and associated tolerances of the two species studied here is made more interesting by the fact that one species, Anoplarchus purpurescens, inhabits both open coastal and estuarine situations while the other species, *Pholis ornata*, is most abundant in bays and estuaries. Exposed shores of estuaries are subject to the same reduction in salinity that open coastal habitats experience when exposed to seasonally heavy rainfall, but estuaries may also experience lowered and more variable salinity due to the amount of freshwater runoff entering them. The effect of salinity in restricting the inhabitation of estuarine substrates may differ between those species in which estuaries are at the limit of their habitable range, such as *Anoplarchus*, and those in which estuaries represent the preferred habitat, such as *Pholis*. In order to evaluate the effect of salinity, it is first necessary to establish whether or not distributional differences are present along the salinity gradient present from lower to upper bay.

The influence of temperature on the intertidal distribution of these two species would be more apparent were the two species more sharply differentiated with respect to the height to which they occur in the intertidal zone. As it is, no obvious differences exist and no direct thermal limitations can be inferred. *Pholis* appears in slightly greater abundance at higher levels but I believe this is due mainly to the heavy settling of young of year individuals over a greater range of habitats than those occupied by adults. Young *Pholis* appear less selective in habitat requirements than older individuals as indicated by their settling in substrates chiefly inhabited by *Anoplarchus*. Either they are subject to greater predation in less favorable habitats or they actively seek out more suitable sites as they get older because fewer young were observed in fall and winter on substrates chiefly occupied by Anoplarchus. In studies on the settling behavior of several species of northeast Pacific inshore species, including two species of blennioids, Marliave (1977) concluded that the physical substrate for settling included some features of adult habitat but was not always the same substrate preferred by adults. Stephens et al. (1970) work on nearshore blenniids suggests non-random recruitment. The settling larvae of Pholis ornata appear to exercise some selectivity as Marliave (1977) observed for Pholis laeta. The broad settling of young P. ornata in rocky substrates indicates a more general habitat preference that becomes more specific with age.

While Anoplarchus and Pholis were found to coexist broadly in the intertidal zone, and when coexisting, were found to share the same microhabitat, there are striking differences in the overall habitat preferences of the two species. While Anoplarchus is restricted to rocky substrates, Pholis readily invades vegetative cover. Seasonal changes in vegetative cover in the mudflats result in seasonality of occurrence of Pholis. R. Bayer (pers. comm.) has confirmed the seasonality of occurrence of Pholis in the mudflats of Yaquina Bay from samples taken throughout the year. When fishes leave the mudflats in the winter, no concomitant increase in abundance of Pholis is noted in collections in intertidal rocky substrates.

Therefore, the bulk of the population utilizing mudflats as summer and fall habitat probably move into the subtidal zone. Forsberg *et al.* (1977) observed seasonal changes in the distribution of *Pholis* in Tillamook Bay with the fish being restricted to lower and mid bay sites during winter and early spring and extending their distribution into the lower portion of rivers emptying into the bay during summer and fall. This seasonality may be a direct response to salinity fluctuation or it may be a behavioral response to the presence or absence of vegetative cover. Similar seasonal changes in intertidal abundance, i.e., fish moving into deeper water in winter months have been observed in other species of *Pholis*, particularly where periodic freezing in the intertidal zone occurs (Quasim, 1956; Sawyer, 1967 - *P. gunnellus*; Smith and Paulson, 1977 - *P. laeta*). *Pholis ornata* was also observed to modify its vertical range seasonally at one site in Yaquina Bay. Fewer fish were observed at a given height as spring progressed into summer. During summer, no *Pholis* were found at this height but their numbers increased during fall and winter. This may be a direct response to changes in temperature or it may be a response to the increased threat of desiccation. The relative mobilities of *Anoplarchus* and *Pholis* appear to be quite different. While *Anoplarchus* is restricted to rocks and cobble and is not often found far from this type of habitat, *Pholis* readily modifies both its vertical and horizontal ranges in response to seasonal environmental changes. Conventional sampling techniques used in studies of bay and estuarine fishes probably do not indicate the true abundance of *Anoplarchus* present because of this species' close association with rocky substrates.

Striking differences in the relative abundances of the two species were observed in Yaquina Bay. The two species broadly coexist at mid-bay, yet, in the upper bay close to freshwater influence, only *Pholis* was observed. At the mouth of the bay closest to oceanic influence, the vast majority of the fishes were *Anoplarchus*. This implies a greater tolerance to dilution by *Pholis*. Bond (1973) has reported its occurrence in freshwater in Oregon. Callaway *et al.* (1969) have measured the seasonal variation in salinity at a station about one mile upriver from the upper bay sample site of this study. Their continuous monitoring of salinities reveal frequent exposures to prolonged dilution (0-5 ppt) in this vicinity. Since individuals of *Pholis* reside here throughout the year, they must be well adapted to periodically dilute conditions. Such increased tolerances to dilute conditions suggests that the modification in the horizontal range of *Pholis* recorded by Forsberg *et al.* (1977) were behavioral responses to changes in vegetative cover rather than physiological responses to increased dilution.

## Studies on Thermal Tolerance

Studies on the critical thermal maxima and 96 hour exposures to different combinations of temperature and salinity indicate that Pholis can tolerate slightly higher temperatures than Anoplarchus. Slight differences in thermal capacity may, however, result in sharp distribution differences if temperature is of primary influence in governing animal distribution. Periodic, repeated, short-term exposures to temperatures beyond the 96 hour lethal level (25°C), a condition which might exist during low tide series on very warm days, sharply differentiate the thermal capacities of the two species. Heath (1967) was able to differentiate the lethal exposures of sympatric species of Gulf of California shore fish with a cycled temperature program with different peak temperatures in each cycle. DeHart (1974) determined that effects leading to lethality accumulate over a period of several days in some species of temperate freshwater fish. Exposure of the two species of blennioid fish to cyclic temperature regimes also suggested cumulative effects, but this cannot be ascertained unless comparison of MRT's are made between short term exposures and long term exposures at the same temperature. A greater heat tolerance might facilitate summer existence among vegetation in intertidal mud flats that lack the insulation afforded to individuals living secreted in rocks and cobble.

The relative plasticity of thermal tolerance levels is widely known--acclimation temperature can sharply influence the range of thermal tolerance in animals. When the blennioid species were acclimated to 15°C, they experienced chill coma at 0°C and survived several hours exposure to 25°C. One group of ten individuals of both species was acclimated at 5°C, and these showed no discernible changes in activity at 0°C. The MRT at 25°C was less than one hour. Brett (1956) observed that fish species that show similar upper lethal limits may be characterized by quite different lower levels of tolerance. Exposure of pupfish (Cyprinodon nevadensis amargosae) to cycling temperatures show that at least this species can simultaneously compensate to warm and cold temperatures (Feldmeth et al., 1974). Fishes appear to acclimate to warm and cold temperatures at different rates with cold acclimation taking considerably longer (Brett, 1956). Because the fishes in this study were always laboratory acclimated to temperatures higher than ambient conditions, I assumed that the one week period of acclimation was sufficient. Many species of fish have been shown to exhibit an endogenous, seasonal rhythm in the acclimation state. If this condition, sometimes referred to as the "acclimatized state" (c.f. Graham, 1970, 1972), existed, the CTM for summer tested fish would be assumed to be significantly higher than winter tested fish. Also, fewer winter tested fish might die after experiencing chill coma. Aside from a slightly greater percentage of recovery from heat coma in the summer, no seasonal differences in temperature tolerance were observed. Graham (1972) observed no seasonal compensation for temperature in Panama Bay fishes, but has observed seasonal adjustments in temperature tolerance levels in southern California intertidal fishes (Graham, 1970). The variability of summer water mass temperature, strongly influenced by cold water upwellings off the coast of Oregon, may act to minimize seasonal thermal differences experienced by estuarine fishes, especially since there is an approximately 70% exchange of water between the estuary and the ocean with each complete tidal cycle (Goodwin _et al._, 1970). The range of thermal conditions experienced throughout the year, especially in the under rock microhabitat, does not seem broad enough to select for an endogenous rhythm actively adjusting the range of thermal tolerance. This does not imply that seasonally induced endogenous changes in the physiological state of these fishes are never present. Seasonal events, such as reproduction, always are accompanied by changes in the physiology of an organism. One temperature adaptation in the circa-annual rhythmicity of _Anoplarchus_ has been studied in some detail--that of the capacity to produce macromolecular antifreezes. Duman and DeVries (1975) showed that Alaskan populations of _Anoplarchus purpurescens_ could be acclimated to -1.5°C and that the production of serum antifreeze compounds was influenced by temperature and photoperiod regimes (Duman and DeVries, 1974). In addition, they detected a genetic difference between Alaskan populations and San Simeon, California populations with the latter unable to produce antifreezes. Populations of *Anoplarchus* in Yaquina Bay are assumed to resemble those of San Simeon as freezing conditions are rarely encountered and no overt seasonal effects on temperature tolerance were observed. Both *Pholis* and *Anoplarchus* are remarkably hardy in their ability to recover from the effects of prolonged chill coma. *Anoplarchus* was, in this aspect, substantially more tolerant than *Pholis*.

## Effect of Salinity on Temperature Tolerance

Fry (1947) recognized the importance of considering the effects of interaction of what he termed "controlling factors" in governing the metabolism of an organism. The most obvious factor interactions to consider are those which influence osmotic and ionic regulation over the range of thermal tolerance of the organism. As early as 1912, Loeb and Wasteneys showed that the resistance of fish to high temperature was affected by the salinity of the medium. Exposure of *Anoplarchus* and *Pholis* to different combinations of temperature and salinity reveal *Anoplarchus* to be slightly more tolerant of high salinities over the range of temperatures tested but not as tolerant of dilution as *Pholis*. This difference in tolerance is reflected in the relative abundance of the two species in Yaquina Bay; the uppermost site closest to freshwater influence is uninhabitable by Anoplarchus. The prolonged dilution of this upper bay habitat during months of heavy precipitation, as recorded by Callaway et al. (1969) and Karentz (1975), is the most readily observable instance of physical factors which might influence the comparative distribution of these two species. Short term exposures, lasting up to 96 hours, revealed slight, but consistent differences in tolerance to decreased salinities. Longer exposures would certainly more strongly differentiate these tolerances by exhibiting chronic effects on such biological activities as growth, feeding behavior, and reproductive function.

The three dimensional graphic depiction of the effect of salinity on the thermal scope of each species, as well as the response surface estimation of the 96 hour percent mortality, provide ample evidence that survival in variable environments is strongly influenced by these environmental factors acting in concert. This presents a complication of the thermal physiology of these organisms that is most difficult to deal with both conceptually and logistically. Is the absence of Anoplarchus in the upper bay site directly due to the influence of salinity or is it due to its indirect influence by limiting thermal tolerance? Morris (1960) showed that environmental salinity affects the temperature tolerance of three species of cottid fishes. Other inshore temperate marine species shown to exhibit combined effects of temperature and salinity include *Limanda limanda* (Lowthion, 1974) and *Oligocottus maculosus* (Courtright and Bond, 1969) Blaber's (1973) study indicated very little influence of salinity on temperature tolerance of juvenile *Rhabdosargus holubi*, a South African estuarine species. Experiments with euryhaline fishes, particularly of the order Cyprinodontiformes, suggest maximal survival from thermal stress at salinities isosmotic to body fluids (Garside and Chin-Yuen-Kee, 1972; Garside and Jordan, 1968; Strawn and Dunne, 1967; Whitfield and Blaber, 1976) but the work of Arai *et al*. (1963) indicates that relief from osmotic stress may not be the only factor governing thermal tolerance regimes at various salinities. While the effect of salinity on the thermal tolerance of fishes has been well documented, in no case have the interactive effects of these two factors been shown to combine to produce an effect greater than the sum of their separate actions. Studies on the survival and growth of striped bass (*Morone saxitalis*) by Otwell and Merrimer (1975) show a high degree of additivity in the combined effects of temperature and salinity yet their combination does not produce an effect greater than the summed effect of the two factors. Some confusion exists in the literature over the use of the term "interaction" with respect to multifactoral studies of environmental effects. In the strictest sense, temperature and salinity exhibit interactive effects only if their combined effect is greater than the sum of their individual effects. Interactive effects are well known in studies of the effects of toxicant mixtures in which one toxicant affects the biological action of another. The above mentioned studies have dealt with the influence of one factor, such as salinity, on the organism's response to another, such as temperature.

Fry's concept of "scope for activity" (1947, 1971) as a function of different types of environmental influences provides a basis for quantification of relative thermal capacities in aquatic organisms. Theoretically determined curves for scope enclose surface areas which may be experimentally quantified as a means of comparing thermal capacities. Brett (1956) has defined a "zone of tolerance" to indicate the effect of acclimation on thermal tolerance, the unit of tolerance equal to an area bounded by 1°C and thus expressed as "degrees-centigrade-squared." Brett's technique gives a measure of the eurythermicity of an organism. This study of the comparative tolerances of the two species of blennioids extends this concept of comparison of surface areas to evaluate the thermal scope of each species (a function of MRT at each experimental temperature and thus expressed as degrees-centigrade-minutes) at different salinities. Analysis of response surfaces is another method of comparison of surface area as a means of defining tolerance scopes. Alderdice (1972) has proposed detailed techniques emphasizing response surface analysis methods developed by Box and Youle (1955) as a means of quantifying the response of an organism. Wallis (1967a, b), Lough and Gonor (1973a, b) and Lough (1974, 1975) have employed response surface techniques in studies of embryonic growth and survival of bivalves while Hicks (1973) and Biggs and McDermott (1973) have used it in analysis of tolerance of littoral crustaceans. In addition to Alderdice's extensive application of response surface analysis to the determination of temperature and salinity tolerances in fishes (c.f. Alderdice, 1972), response surface contours have been used to describe the tolerances of the previously mentioned Limanda limanda (Lowthion, 1974) Rhabdosargus holubi (Blaber, 1973) as well as several species of Texas marsh fishes (Strawn and Dunne, 1967). Application of this technique is especially relevant to studies on intertidal fishes that naturally experience fluctuations in temperature and salinity in the littoral zone. Comparison of the estimated response surfaces for Anoplarchus and Pholis with the three dimensional graphic interpretation of the combined effects of temperature and salinity on the MRT indicate the conservatism present in this response surface estimation of percent mortality. In this case, the estimated surfaces are not sufficiently precise so that the differences in tolerance regimes of the two species can be detected. Such conservatism is desirable in analyses of tolerance to temperature and salinity extremes because such extremes, while not directly affecting the tolerance of these species, may account for more chronic and secondary environmental effects on biological function. Fish exposed to non-lethal thermal stresses were observed to exhibit less cryptic behavior. Such thermal extremes experienced in nature may not be directly lethal, but may expose the fish to greater incidence of predation. In Yaquina Bay, a variety of birds, including crows, egrets, mergansers, gulls, herons, and grebes have been observed feeding on gunnels (R. Bayer, pers. comm.).

## Osmotic Responses to Changes in Salinity

The understanding of organismic response to environmental influences is enhanced by the ability to monitor a variety of biological functions. In order to understand further the effects of salinity on these fishes, which were experimentally determined to be extremely eurythermal and euryhaline, measurements of the osmoregulatory responses were made. Parry (1966) mentions that the physiological response of fishes to changing environmental osmotic stress can be most easily followed by measurement of osmotic changes in body fluids, especially blood. Both species of blennioid fish are very efficient in blood serum osmoregulation. While this regulation appears taxed at 56 ppt and 0 ppt, both species seem capable of at least partial recovery of "normal" osmoconcentrations after three days' exposure to 56 ppt. Regulation at this salinity is probably not achieved without great metabolic cost and probably could not be maintained indefinitely. Such osmoregulatory powers reflect the general trend in temperature and salinity tolerance of these species--experimental conditions that the animal is exposed to far exceed that which could be encountered in nature. Salinity conditions of 42 and 56 ppt are virtually unheard of in the northeast Pacific temperate shores, yet these fishes do appear to have the capacity to adapt to these conditions at least for limited durations. Periodic exposure to essentially fresh water is much more frequent, and both these species show strong osmotic resistance to this as well. Most impressive is the ability, especially in _Pholis_, to tolerate a limited exposure to distilled water. Those marine species capable of withstanding hypersaline conditions are invariably shallow water, warm temperate and tropical species in habitats where high evaporative rates drive salinities up. Lui (1969) determined that atherinids of the species _Taeniomembras microstomus_ tolerate salinities from 3.3 to 108 ppt with remarkable osmoregulatory abilities. The most impressive group of fishes, both in terms of their eruythermicity and euryhalinity, are the cyprinodonts. Rao (1975) determined that newly hatched cyprinodont larvae of the species _Fundulus parvipinnus_ are tolerant of salinities ranging from freshwater to 70 ppt. Feldmeth and Waggoner (1972) determined that adult _F. parvipinnus_ can tolerate salt concentrations up to 128 ppt by assuming an increase in blood osmolality of over 100 mOsm and a tissue water loss of 5%.

The blennioid species *A. purpurescens* and *P. ornata* possess one of the broadest ranges of salinity tolerance measured in temperate species with cold water affinities. This tolerance is reflected in the extent to which the fishes are capable of regulating extracellular osmolality. As the osmoconcentration of the exposure medium varies through approximately 1800 mOsm, variation in the blood osmolality is less than 300 mOsm in both species--indication of a high degree of physiological adaptation to euryhaline conditions. Both species are tolerant of a broader range of salinities than that reported for the cohabitant *Oligocottus maculosus* (Courtright and Bond, 1969). Measurements of the water permeability of *Lumpenus lampreteaformis* by Evans (1969) suggest that this ability to regulate ion content is coupled with an extremely low permeability to water in the northern blennioids. Evans (1967) indicates that *Xiphister atropurpureus*, an open coast blennioid, cannot tolerate salinities below 10% seawater. This observation, together with the experimentally determined euryhalinity and osmotic resistance of *Anoplarchus* and *Pholis*, provides strong evidence for tolerance to extreme dilution being a prerequisite for estuarine inhabitation by blennioid species. *Pholis ornata*, the species presumed to be most adapted to estuarine salinites owing to its widespread distribution in bays and estuaries in the northeast

Pacific, appears less resistant to osmotic stress imposed by high salinities than the species which is more abundant in open coastal situations, Anoplarchus purpurescens.

The rate of adjustment of blood osmolality in fishes seems to vary from a few minutes to several days (Parry, 1966). The response of the two blennioid species studied is similar to that reported in cyprinodont fishes by Schmidt-Nielson (1977) and Renfro and Hill (1971). In studies on the cyprinodonts, fish were transferred from freshwater to saltwater which resulted in a rapid increase in blood osmotic pressure followed by a decline several hours later. Both species of blennioids exhibited a rapid (within 24 hours) increase in osmotic pressure but the ensuing decline took place much later than that reported for the cyprinodonts. House (1963) also determined a very rapid response to salinity change, on the order of several minutes, for the littoral blenniid, Blennius pholis, but did not record a later attempt at osmotic recovery. The response to extremes in salinity was observed within the first day after exposure but a considerably longer period of exposure to hypersaline conditions seems necessary to effect an attempted recovery of "normal" osmoconcentration. This is a rather striking adaptation and somewhat difficult to explain when one considers that exposure to hypersaline conditions of the kind tested rarely, if ever, happens in nature; and, if it does, would not persist for a period longer than a tidal cycle.

# CONCLUSIONS REGARDING THE INFLUENCE OF TEMPERATURE AND SALINITY ON THE ADAPTATION OF BLENNIOIDS TO ESTUARINE HABITATS

This study dealt with three basic considerations: 1) whether differences in the intertidal distribution of two sympatric species of blennioid fish could be determined, 2) whether estuarine intertidal inhabitation by Anoplarchus purpurescens and Pholis ornata was affected by temperature and salinity, and 3) whether the extent of experimentally determined eurythermicity or euryhalinity would indicate the presence of specific limiting temperatures or salinities measured in the field for these two species. Because of the nature of the temperature and salinity regimes that might be experienced in the intertidal zone, I assumed that, at some point within the estuary, the environment becomes physically limiting, and that these two species would exist up to the limit of their tolerable range. Because only two of the nearly twenty species of blennioids that inhabit the outer coast were observed in intertidal habitats in estuaries, rocky intertidal shores within Yaquina Bay were assumed to be a habitat in which physical limitations might be elucidated. Identification of a limiting temperature or salinity, or combination of both, would depend upon a comprehensive evaluation of the extent of eurythermicity and euryhalinity in these fishes.

Striking differences in the relative abundances of the two species at different sites in the bay demonstrated the potential for determining physical factors influencing distribution patterns. Measurements of the temperature and salinity regimes in the field indicate that the under-rock microhabitat effectively insulates against tidally induced environmental fluctuation. Minimal differences between air and water temperatures also facilitate intertidal inhabitation. I hypothesized that this uniformity of thermal habitat, a function of the combined influences of climatic and tidal conditions, and a basically cryptic behavior, in which fishes further minimize thermal fluctuation, facilitate the occupation of the rocky intertidal zone by several families of fishes. Included among these are several amphibious species, chiefly in the suborder Blennioidei. Within Yaquina Bay, the absence of sharp differences in the vertical distribution of the two species indicates that their distribution cannot be differentiated on the basis of temperature or its corollary effect, resistance to desiccation. Because of the overall absence of sharp thermal differences between the microhabitat of these fishes and the atmosphere, both species may be limited in the maximum height to which they can occur by their abilities to resist desiccation--a conclusion reached also by Wolcott (1973) in studies on limpet ecology. While short term, tidally influenced fluctuations in salinity do not appear to affect the intertidal abundance of either species, seasonal fluctuation in salinity probably is the chief factor excluding Anoplarchus from the upper bay.

Both species of blennioids exhibit broad tolerances to temperature and salinity, much broader than those measured in the field. The overall tolerance scopes of Anoplarchus and Pholis were very similar with slight differences noted in tolerance to extreme conditions. These slight differences may result in substantial differences in distribution as observed in the upper bay intertidal zone. Within naturally experienced thermal ranges (5 to 10°C), Pholis is capable of greater dilution tolerance; only this species was present in the upper bay intertidal zone. The breadth of tolerance of the two species further suggests that physical factors do not directly affect the distribution of these fishes. The main exception would be the restriction of the distribution of Anoplarchus to mid and lower bay sites where prolonged dilution is not encountered as in the upper bay. While the differences in tolerance to temperature and salinity observed to exist between these species could not be directly correlated to any field measurements of temperature and salinity, the tolerances were in the direction of those experienced in the field, i.e., Anoplarchus was less tolerant of dilution while being more tolerant of higher salinities. I suggest that the increased tolerance of Pholis to high temperatures may reflect an increased tolerance to the potentially higher temperatures in mudflat habitats lacking the insulation provided in rocky shores. Slight differences in tolerance may be significant in view of the observation that cycling the thermal exposures sharply differentiated the tolerances of the two species. Temperature and salinity exert a combined influence on the tolerance level even in strongly eurythermal and euryhaline species such as these blennioids. While field measurements of temperature indicate no direct influence on the maximal range of habitation, the seasonal adjustment of vertical range by Pholis strongly suggests a response to seasonally changing thermal regimes. Seasonal changes also exhibit secondary influences on the distribution of this species by affording a greater amount of cover in the form of increased vegetation in the mudflats in summer and fall. Wolcott's (1973) hypothesis that range limits of animal populations should not be expected to be limited solely by physical factors is applicable to these two coexistent species of fish, yet seasonal changes in the vertical distribution of Pholis and the absence of Anoplarchus in the upper bay sites of decreased salinity indicate that these fishes have expanded their ranges near the limits of their physiological tolerances, i.e., the limits at which the cost of metabolic expenditure in a marginal habitat outweigh any ecological benefits derived from habitation in that area. The responses of organisms to physical changes in habitat is extremely complex and difficult to determine, however, due to the intricate manner in which environmental factors may exhibit combined influences.

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