METABOLIC RESPONSES OF SPOT, *LEIOSTOMUS XANTHURUS*, AND ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, LARVAE TO COLD TEMPERATURES ENCOUNTERED FOLLOWING RECRUITMENT TO ESTUARIES

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ABSTRACT

The larvae of marine fishes that spawn during fall-winter in coastal North Carolina waters experience a decrease in temperature as they enter estuarine nursery areas. To determine the effect of changes in temperature on larval metabolism, the oxygen consumption of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, was measured and their QO_2 and Q_{10} values were determined. Atlantic croaker respiration decreased with temperature at rates that would be expected if no compensation or stress were involved. Spot showed unexpectedly high respiration rates at low temperature. The increased respiration is apparently due to stress. Based on laboratory feeding and growth data, we concluded that spot are subject to an energy deficit at $\leqslant 10°C$. We infer the timing of larval immigration corresponds with environmental temperatures reaching tolerable levels. Atlantic croaker larvae immigrate earlier in the winter and are exposed to cold water for longer periods than spot larvae. Our conclusion is that stress and energy loss experienced by early immigrating spot larvae may result in increased mortality.

The larvae of fishes that spawn during fall and winter in offshore North Carolina waters experience a decrease in both temperature and salinity as they enter estuarine nursery areas (Fig. 1). The spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, two sympatric species of Sciaenidae, are representative of winter spawning species off the North Carolina coast.

Previously, we have examined the effects of increased temperature on the oxygen and food consumption of the postlarval stages of these two species (Hoss et al. 1971, 1974; Peters and Kjelson 1975). In this paper we continue our research on the early life history of these species and evaluate how decreasing water temperature, encountered following recruitment into estuarine waters, might affect oxygen consumption, food consumption, and ultimately survival.

Crawshaw et al. (1981) stated that young fish typically select warm shallow water because 1) it permits more rapid growth owing to higher metabolism, given an adequate food supply, and 2) the predation by larger fish is less in shallow water. For some fish this explanation is plausible, but this does not apply to the larvae of many winter-spawning marine fishes which begin life in relatively warm coastal waters and then enter colder estuarine waters. For these species we expect that metabolism and growth of the estuarine immigrants should be reduced (Brett 1956). The specific objective of this paper is to describe how decreasing temperature affects the metabolism of larval fish as they are moved from warm to cold water by a combination of passive and active transport mechanisms that are not, as yet, completely understood. Oxygen consumption is a common method of estimating metabolic activity, which frequently changes in response to environmental conditions (O'Hara 1968). In this study we measured routine oxygen consumption which is the amount used by fish whose only movements are spontaneous.

STUDY AREA AND METHODS

Spot and Atlantic croaker spawn off the North Carolina coast inshore of the Gulf Stream over the continental shelf (Hildebrand and Cable 1930; Dawson 1958; Powles and Stender 1978). Here, spot spawn from October to February, but principally from December to January while Atlantic croaker spawn from September to May but principally between October and December (Lewis and Judy 1983). After between 30 and 60 days in coastal

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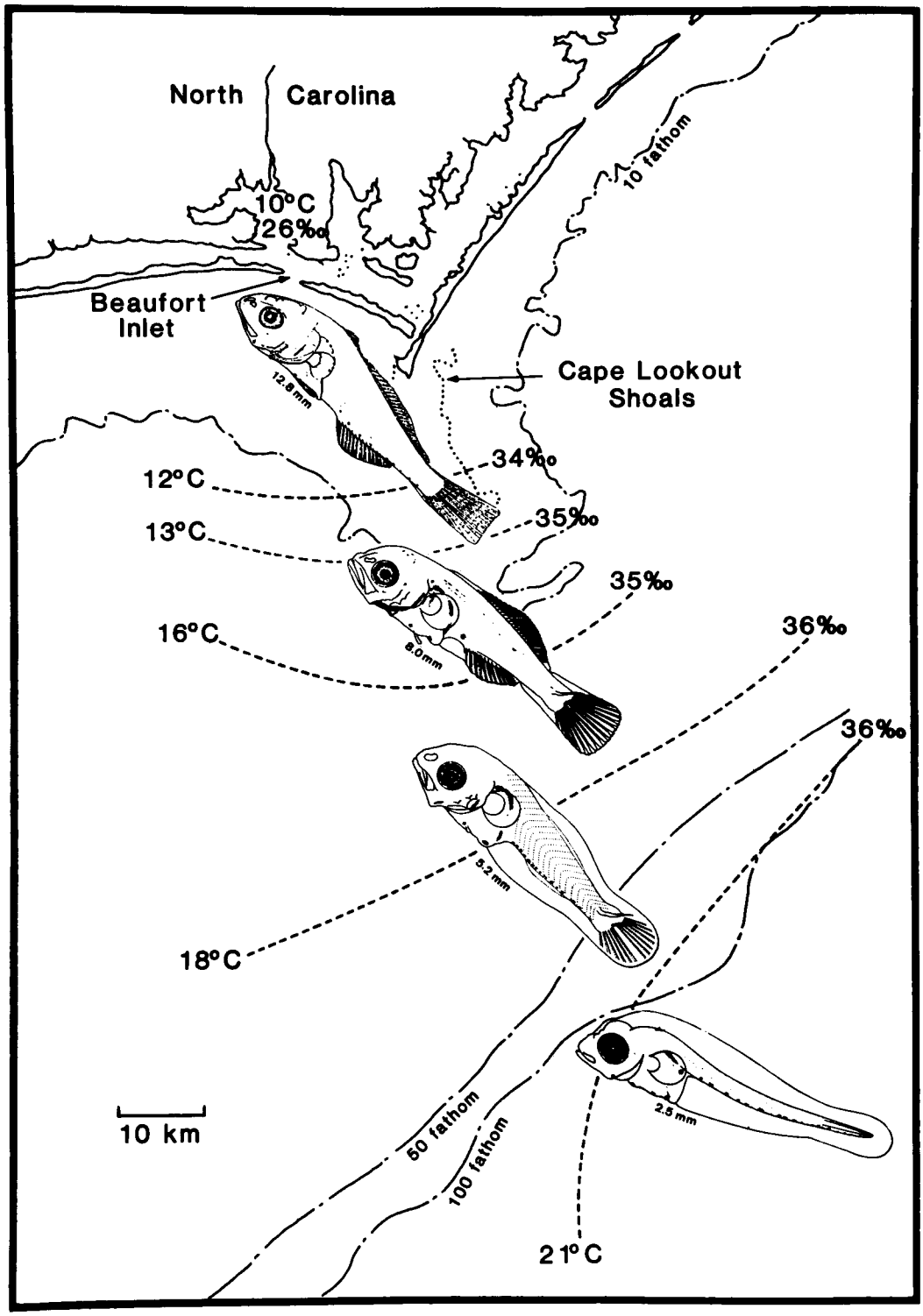

FIGURE 1.—Representative winter temperatures, salinities, and developmental stages of larval spot from the spawning area to Beaufort Inlet, North Carolina. Drawings from Powell and Gordy (1980) and Lippson and Moran (1974).

waters (Warlen 1982; Warlen and Chester 1985), the larvae enter estuaries where they develop into juveniles. In the spawning area, water temperatures are usually between 18° and 25°C (Fahay 1975; Hettler and Powell 1981). The fish encounter decreasing temperatures as they move inshore to the estuarine nursery areas. In the lower Newport River estuary, for example, mean water temperatures between November and March may range from 14° to 6°C with the highest temperatures during this period occurring in November and the lowest in January (Hoss 1974).

Larvae of Atlantic croaker and spot were obtained from both field collections and eggs spawned in the laboratory. Older larvae were captured in a bridge net (Hettler 1979) and held in the laboratory for no more than a week prior to use. First feeding larvae were obtained from spawned fish, reproduced by the methods of Hettler and Powell (1981), and then were reared at experimental temperatures.

Oxygen consumption was measured with a differential respirometer (Umbreit et al. 1964), following procedures used by Hoss, Hettler, and Coston (1974). Fish were transferred to 15 mL respiration flasks and, following a 2-h acclimation period, their oxygen consumption was measured. Numbers of larvae per flask varied between 1 and 30, depending on the size of the larvae. Acclimation temperatures were 10°, 15°, and 20°C. Notochord or standard lengths and dry weights were obtained for individual fish.

The metabolic equation $Q = aW^k$, was used to describe the relation between oxygen consumption and dry weight of fish acclimated at 10°, 15°, and 20°C. In this equation, W is the weight of the fish, and a and k are constants for the species obtained from least-squares regression of the log of oxygen consumption on the log of weight (Winberg 1956). A k value of 0.67 implies that oxygen consumption varies in proportion to surface area, whereas a value of 1 indicates that respiration varies in proportion to weight.

We used the metabolic equation to estimate oxygen consumption of larvae of equal weight at different temperatures. We compared larvae of 4 mg dry weight because this is the realistic estimate of their weight as they are transported from coastal to estuarine waters (Warlen 1982; Warlen and Chester 1985).

Growth and feeding rates of small spot (≈20 mm SL) collected from the Newport River were calculated from data collected in the laboratory at several temperatures. Wet weights (≈15–30 mg) were recorded to the nearest milligram, and 10 fish were randomly assigned to 4 L test and control containers. Control fish were dried to determine the dry/wet weight ratio, which was then used to estimate initial dry weight of experimental fish. One experiment was conducted at 6°, 8°, 10°, 12°, and 16°C, and two experiments were conducted at 18°C. In all cases fish were fed newly hatched brine shrimp several times a day to assure an ad libitum food supply. After 4–6 days all food was removed; larvae were allowed time to clear their guts and then were dried and weighed.

Growth and feeding rates were expressed as percent of body weight per day. Growth rate was calculated from the expression:

$$\text{Growth rate} = 100\,[(Wn/Wo)^{1/n} - 1]$$

where Wn = dry weight of all fish in a tank at day n
Wo = estimated original dry weight of fish
n = number of days fed.

Calculation of feeding rates required the assumption of constant growth rates. Using original dry weights and calculated growth rates we determined the total dry weight of fish in each container at the beginning of each day. Dry weights of brine shrimp eaten each day divided by the calculated dry weights of fish gives proportion of body weight ingested. These proportions were then summarized as average daily percent of dry body weight ingested.

In order to compare metabolic parameters, i.e., oxygen consumption, feeding, and growth rates, the following conversion factors were used: 1.0 mg dry wt = 5.0 cal (Thayer et al. 1973; Paffenhöffer 1967); 1.0 mg O_2 = 3.38 cal (Phillipson 1966) and 0.7 mg O_2 = 1 mL O_2 at STP. One tenth calorie per fish per day was added to all the rates so that measured zeros could be shown on a log scale.

RESULTS AND DISCUSSION

The regression equations relating oxygen consumption to weight at several temperatures are shown in Table 1. Higher coefficient of determination (R^2) values were found at higher temperatures, a trend best explained by differences in the size range of fish measured at different temperatures. Values for k, were generally comparable to values reported by other investigators for fish of a similar size and at comparable temperatures—Hoss (1974), pinfish; Houde and Schekter (1983), bay anchovy, sea bream, and lined sole; Almatar (1984), herring; and Laurence (1978), cod and haddock.

TABLE 1.—Metabolic equations relating oxygen consumption to body size. $Q = aW^k$ where Q = oxygen consumption ($\mu L\ O_2 \cdot h^{-1}$), *a* and *k* are regression coefficients, W is dry wt in mg, N is the number of observations, T the temperature, and R_2 the coefficient of determination.

Species	T	N	W	*a*	*k*	R^2
Atlantic croaker	10	52	1.50 - 6.43	1.80	0.66	0.42
	15	65	1.90 -11.71	2.00	1.02	0.65
	20	81	0.013- 9.31	3.59	0.86	0.94
Spot	10	37	1.82 - 8.01	3.63	0.70	0.54
	15	48	2.18 -10.27	3.15	0.64	0.63
	20	79	0.014- 8.91	4.07	0.92	0.97

Comparing between measured oxygen consumption rates at 10° and 15°C and those predicted from Van't Hoff's equation (Vernberg and Vernberg 1972), we conclude that Atlantic croaker show no sign of regulating their oxygen consumption as water temperature is decreased. The difference between oxygen consumption rates based on Q_{10} values of 2 and 3 (Fig. 2) is an expected range. For every 10°C change in temperature, the rate of a chemical reaction typically changes by a factor of 2 to 3. A Q_{10} value of appreciably <2 or more than 3, indicates that some process other than a chemical one is involved (e.g., a change in cell membrane permeability). A Q_{10} of one indicates temperature independence (Vernberg and Vernberg 1972). Our conclusion that Atlantic croaker did not display thermal stress is based on the fact that measured respiration rates at reduced temperatures (10° and 15°C) were within the range expected (Fig. 2A).

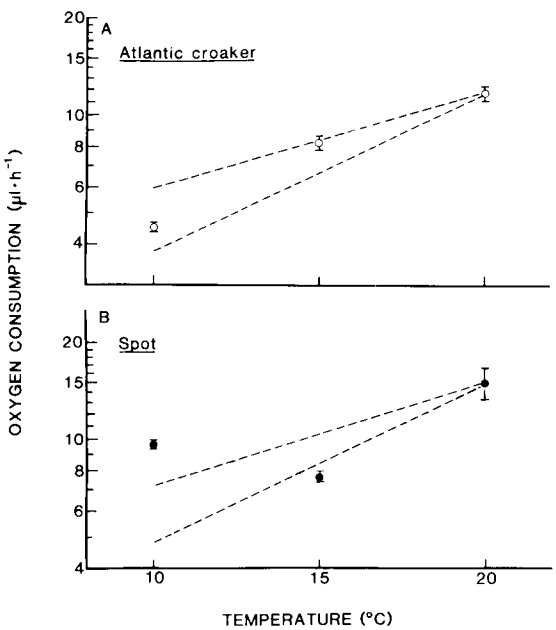

FIGURE 2.—Oxygen consumption rates for 4 mg Atlantic croaker (A) and spot (B) at three temperatures estimated from equations in Table 1. The bars indicate standard errors from regressions in Table 1. Broken lines are estimates of the rates expected based on Van't Hoff's equation, the rate measured at 20°C, a Q_{10} of 2 (upper line) and a Q_{10} of 3 (lower line).

For spot a decrease in temperature from 20° to 15°C resulted in a decrease in oxygen consumption of approximately the amount expected for a Q_{10} of 3. A further decrease in temperature to 10°C, however, caused an increase in the respiration rate. The changes in oxygen consumption at low temperatures could be interpreted either as adaptive, i.e., maintaining a high metabolic rate even at the lower temperature, or inadaptive, i.e., a metabolic breakdown.

Based on feeding, growth, and survival data, however, we think the increase in respiration by spot at 10°C is a result of cold stress, not adaptation. In Figure 3 we present three measures of metabolic rate, ad libitum feeding rate, maximum growth rate, and routine oxygen consumption for spot, all as a function of temperature. Feeding, growth, and oxygen consumption rates decrease with decreasing temperature and the rates are similar over a limited range of the conditions tested (Fig. 3). The rates of decline in feeding and growth from 18° to 12°C approximates that of oxygen consumption from 20° to 15°C. At lower temperatures stress appears to become important. For example, it was not possible to measure growth at 10°C or below because only a fraction of the larvae survived. At 8° and 10°C some of the larvae did not eat and at 6°C none of them did. This agrees with Dawson (1958) who concluded that the lethal minimum temperature for spot is in the 4.0°-5.0°C range and probably varies with size. The intersection of ad libitum feeding rate and routine oxygen consumption occurs at approximately 10°C (Fig. 3). At this temperature there is just enough energy available for routine metabolism. Below this temperature there is not enough energy available even at the ad libitum feeding rate to maintain the larvae, and spot held at this temperature for any length of time would be unlikely to survive.

We conclude from our data on metabolic responses to temperature that spot and Atlantic croaker larvae differ in their response to cold temperatures which prevail at the time of their recruitment to the estuary and that this difference may have important implications for their survival. Both species spawn in warm waters of the continental shelf where the eggs hatch. As the larvae grow they are

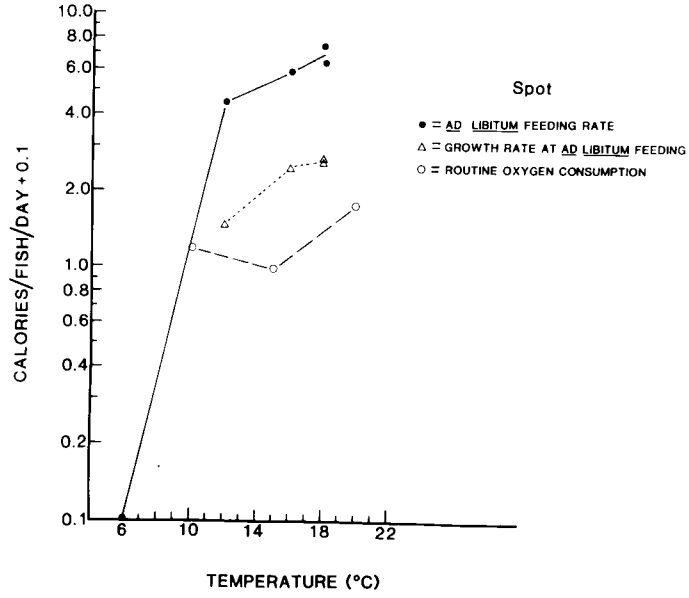

FIGURE 3.—Ad libitum feeding rate, growth rate at ad libitum feeding rate, and routine oxygen consumption for 4 mg dry wt spot at various temperatures between 6° and 20°C.

transported from warm coastal waters into cold estuarine waters. Atlantic croaker are capable of enduring low winter temperatures with decreased metabolic rates that allow for balanced energy intake. Spot, in contrast, show signs of thermal stress manifested as increased respiration rate (at 10°C). This increased metabolism along with no attendant increase in feeding results in an energy deficit and in eventual mortality of the larvae. Species specific differences in the time of entry to the estuary serves as ecological evidence supporting our contention that spot are more susceptible to cold weather. Most spot enter the estuary after the peak in Atlantic croaker immigration and generally after the coldest weather.

Our findings have important implications with respect to recruitment of estuarine-dependent fish which spawn in the ocean during winter. It may be that during severe winters, many of the larvae of cold sensitive species (e.g., spot) that reach the estuary early are killed by cold water temperatures (10°C or less). Thus, only the late arriving larvae survive to recruit into the fishery. The difference in survival between severe and normal winters may help to explain in part the difference between good and poor year classes of certain fish.

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