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EFFECTS OF TEMPERATURE AND SALINITY ON YOLK UTILIZATION IN *BAIRDIELLA ICISTIA* (Jordan & Gilbert) (PISCES: SCIAENIDAE)

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Abstract: The effects of nine different combinations of temperature and salinity on yolk utilization of the eggs and larvae of the sciaenid fish, *Bairdiella icistia* (Jordan & Gilbert) have been investigated. The rate of yolk absorption was accelerated at higher temperatures, but salinity had only a slight effect. Increased water content resulted in larger yolk sacs at hatching in low salinities and at low temperatures. In all treatments, functional eyes and jaws were formed before the yolk had been completely exhausted. Yolk was utilized most efficiently at the intermediate temperature (24 °C) and lowest salinity (20 ‰).

INTRODUCTION

The rate and efficiency with which a fish embryo or larva utilizes its supply of yolk may influence its chances of survival. The sooner the yolk is exhausted, the sooner a larva will need an external source of food and the sooner it will be faced with starvation when none is available. A higher efficiency of conversion of yolk into body tissue will presumably result in a stronger larva with a greater chance of survival (Blaxter, 1969). The main purpose of the experiments described in this paper was to determine whether combinations of temperatures and salinities within the zone of tolerance for the bairdiella, *Bairdiella icistia* (Jordan & Gilbert) could influence yolk utilization in such a way that survival of the early stages might be affected. *B. icistia* is primarily a marine fish, and the present work is part of a broader study of the effects of temperature and salinity on early development in this species (May, in press).

A number of previous studies have shown that yolk is utilized faster at higher temperatures (*e.g.*, Blaxter, 1956; Lasker 1965; Ryland & Nichols, 1967; Flüchter & Pandian, 1968). The effect of temperature on the efficiency of yolk utilization has been studied less often, especially in marine fishes (see Blaxter, 1969), and there are few data on the effects of salinity or temperature–salinity combinations on yolk utilization in fishes. Only the recent work of Alderdice and his colleagues has touched upon this subject (Alderdice & Forrester, 1971; Alderdice & Velsen, 1971); in their studies, salinity seemed to have a relatively slight effect on the rate of yolk absorption. They point out that a different size of yolk sac in different salinities might reflect increased water content in lower salinities rather than a greater amount of yolk, a fact which emphasizes the need for dry weight or caloric measurements when the effect of salinity on yolk utilization is being studied.

Lasker (1962) found that during the final stages of yolk absorption, when functional eyes and jaws are still lacking (and hence external feeding is impossible), larval sardines (*Sardinops caerulea*) have a greater catabolic demand than can be supplied by their yolk and so incur an energy deficit which is made up by tissue resorption, so that the period of final yolk absorption is an especially sensitive time for sardine larvae, and it suggests that external food must be found very quickly once feeding is possible. Hayes, Pelluet & Gorham (1953) showed that temperature could affect the order of appearance of several developmental features, such as hatching and eye pigmentation, in salmon (*Salmo salar*) embryos and larvae. One of the objectives of the present experiments was to determine whether certain combinations of temperature and salinity would alter the relation between yolk exhaustion and the development of eyes and jaws in bairdiella larvae, making the initiation of external feeding more precarious.

Methods

A 3 × 3 factorial design was used, incorporating three levels of temperature (21°, 24°, and 27 °C) and three of salinity (20, 30, and 40‰), all of which reasonably cover the ranges of these two factors within which normal embryonic development takes place; in nature, bairdiella may spawn over this range of temperature or even beyond it. Eggs used in this experiment were obtained by hormone-induced spawning of captive bairdiella as described elsewhere (May, in press). Eggs and semen from a single pair of fish were mixed in each of the nine different combinations of temperature and salinity, and the fertilized eggs were transferred to incubators at the same temperature and salinity as during fertilization. After hatching, larvae were kept in static water in 400 ml Pyrex beakers at the same temperature and salinity which obtained during fertilization and embryonic development. All media had been treated with antibiotics (for details, see May, in press).

As a measure of the amount of yolk, the dimensions of the yolk sac were recorded as follows. At the approximate time of 50 % hatching in each combination of temperature and salinity, five larvae were sampled, anaesthetized with MS-222 (tricaine methane sulfonate) at 100 mg/l, placed on the stage of a Nikon overhead projector and the outlines of their yolk sacs and oil droplets traced on tracing paper. Similar tracings of yolk sacs were made on larvae from all treatments at intervals of 5 to 15 h until the yolk was completely exhausted, the intervals being smaller at the higher temperatures where yolk was absorbed more quickly; larvae were used only once. The yolk sac at hatching was approximately spheroidal and its volume was estimated by measuring the major (L) and minor (H) axes of the yolk on the tracings, converting to original dimensions by applying a calibration factor, and calculating the volume of a spheroid with these dimensions as Blaxter & Hempel (1963) did for herring larvae. The volume of the oil droplet at hatching was calculated from the formula for the volume of either a spheroid or a sphere, depending on which

resembled more closely. At later stages of development, the irregular shape of the yolk made calculation of yolk and oil volumes impossible. Ryland & Nichols (1967) used the changing area of the silhouette of the yolk as an index of the amount of yolk present at various times after hatching, and this seemed best in the present case. Yolk areas of bairdiella larvae were measured from the tracings by means of a planimeter.

Samples of unfertilized eggs, of newly hatched larvae, and of larvae at the time of complete yolk absorption in all treatments were taken for dry weight measurements. Thirty five unfertilized eggs were placed in seven groups of five on a glass microscope slide, dried at 60 °C and stored over silica gel. Similarly, seven groups of five newly hatched larvae and larvae at yolk exhaustion from each combination of temperature and salinity were rinsed briefly in distilled water, placed on microscope slides, dried and stored. Poor survival in stressful combinations of temperature and salinity reduced the number of larvae available at yolk exhaustion: at 24 °C–40‰, only five groups of four larvae each were sampled, and at 27 °C–40‰ too few healthy larvae were available to allow any sampling. Within a week of sampling, the groups of four or five dried eggs or larvae were weighed to the nearest 0.1 μg on an electrobalance, and the weights were converted to a per-egg or -larva basis.

In a subsequent experiment the chorions of unfertilized eggs from another hormone-induced spawning were dissected off, weighed, and expressed as a proportion of the total dry weight. The amount of yolk in unfertilized eggs of the present experiments was then calculated by assuming that there was the same proportion of chorion to total dry weight, and subtracting the chorion weight from the total egg dry weight. The percentage efficiency of yolk utilization was calculated by dividing the mean dry weight of the larva at yolk exhaustion by the mean dry weight of the original yolk and multiplying by 100.

Homogeneity of variance was tested for sets of data by Bartlett's test (Sokal & Rohlf, 1969), and normal statistics were applied only to homoscedastic sets of data. Nonparametric techniques were used in other cases.

Results

YOLK AND OIL VOLUMES AT HATCHING

The yolk volume at hatching decreased with increasing salinities and was greater at 21 °C than at higher temperatures in all salinities (Fig. 1). The values had a much greater variance at 21 °C which could not be eliminated by a logarithmic transformation; the Friedman rank test for two-way classifications (Tate & Clelland, 1957) was, therefore, applied, first to salinity, considering temperature as blocks, then to temperature, considering salinity as blocks. By this test, the effects of both temperature and salinity on yolk volume at hatching were highly significant ($P < 0.01$).

The volume of the oil droplet was slightly smaller at 30‰ than at either 20 or

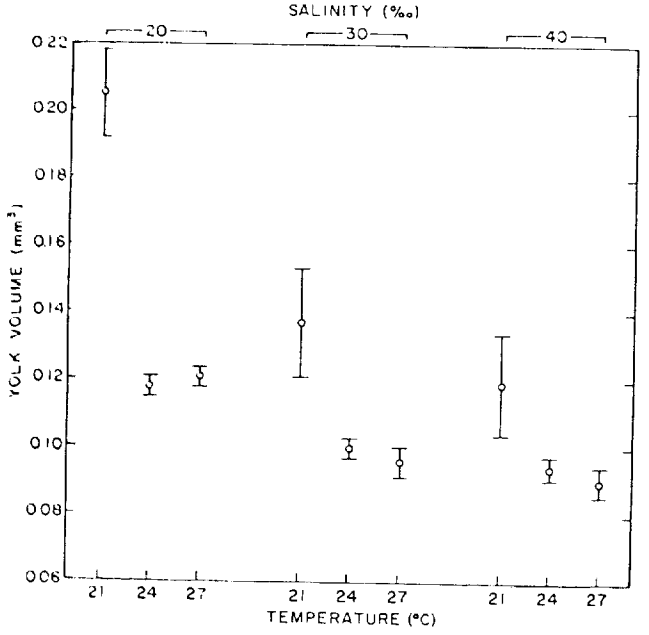

Fig. 1. *Bairdiella icistia*: yolk volumes at hatching (mean ±S.E.). The number of measurements in each case was five.

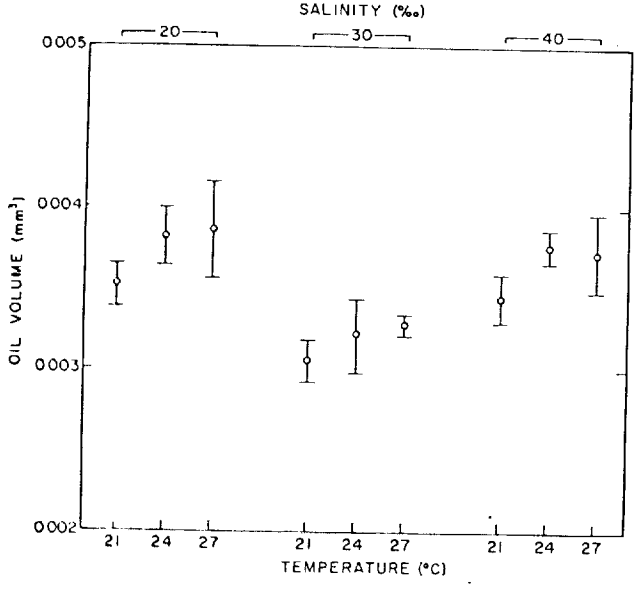

Fig. 2. *Bairdiella icistia*: volume of oil droplet at hatching (mean ±S.E.). The number of measurements in each case was five.

40 $^{0}/_{00}$ (Fig. 2). A factorial analysis of variance showed that the effect of salinity was highly significant ($P < 0.01$), the temperature effect and interaction being nonsignificant ($P > 0.05$). The mean volumes ranged from 0.00304 to 0.00386 mm^3 over the range of experimental conditions.

YOLK ABSORPTION

The size of the oil droplet decreased at a slower rate than the total yolk and made up a larger and larger proportion of the yolk as time progressed, its area equalling between 6 and 10 % of the total yolk area at hatching and up to 50 % at the final sampling shortly before the yolk was entirely consumed. It may be that only a tiny droplet of oil remained in the final stages of yolk absorption, but in gross examination it was virtually impossible to distinguish from the rest of the viscera because of its small size. No differences attributable to treatment effects were apparent in the relation between the rate of disappearance of oil and that of total yolk.

The area of the total yolk decreased exponentially, while the area of the oil droplet (which is included in the total yolk area) decreased more gradually. The oil droplet measurements were somewhat more irregular than the measurements of total yolk, probably reflecting real differences between larvae as well as experimental error in measuring small areas.

Because of the exponential nature of the decrease in yolk area, this has been plotted, along with oil droplet area, semi-logarithmically against time for all nine treatments (Fig. 3a, b, c). Ryland & Nichols (1967) found that a similar plot yielded straight lines for various temperatures in plaice larvae. For bairdiella, the more rapid rate of yolk absorption at higher temperatures was obvious, but the effect of salinity was more subtle. At all temperatures there was a slight tendency for yolk to be absorbed more slowly at 40 $^{0}/_{00}$ during the first few hours, but for most of the yolk sac stage the rates tended to be similar at different salinities within each temperature. This was true both of the total yolk area and of the area of the oil droplet. In the final hours of yolk absorption, yolk disappeared more rapidly at the higher salinities. At 27 °C the size of the oil droplet decreased much more slowly at 20 $^{0}/_{00}$ than at the higher salinities during the final three observations. The end of each line in Fig. 3a, b, c indicates that on the subsequent observation no yolk was detectable; thus, at 24 °C there was a small amount of yolk present at 53 h in all salinities, but at 27 h yolk was present only in the 20 $^{0}/_{00}$ group (Fig. 3b). There was similar effect at 27 °C, with yolk present only in the 20 $^{0}/_{00}$ group at 47.5 h (Fig. 3c).

The times required for 95 % of the yolk to be utilized were interpolated graphically from a semilogarithmic-probability plot of mean percentages of the original yolk areas against time, which helped to linearize the data. These values (Table 1) show that at all temperatures the 95 % point was reached soonest in 30 $^{0}/_{00}$. At 21 °C, yolk absorption was slowest in 40 $^{0}/_{00}$, at 24 °C slowest in 20 $^{0}/_{00}$, and at 27 °C the rates were almost the same at 20 and 40 $^{0}/_{00}$. The accelerating effect of high salinities (see Fig. 3a, b, c) was not apparent until after 95 % of the yolk had been consumed.

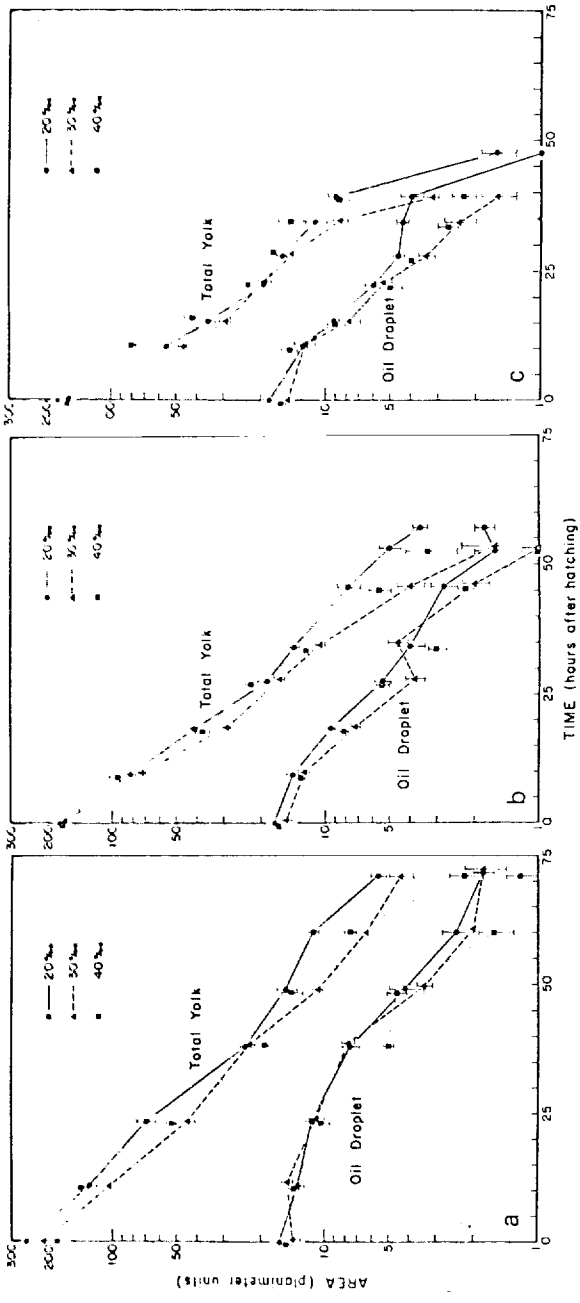

Fig. 3. Total yolk and oil droplet areas (mean ±S.E.) plotted semi-logarithmically against time for three salinities at different temperatures: in some cases the symbol representing the mean covers the standard error: each mean based on measurements from four or five different larvae: one planimeter unit corresponds to 0.0018 mm² in terms of the original dimensions of the larvae: a, 21 °C; b, 24 °C; c, 27 °C.

Regression equations for the logarithm of total yolk area against time were calculated for each treatment, but the majority of the nine lines showed deviations from linearity at either the 5 % or the 1 % level of significance. This was true even when only the first four samples in each treatment were considered. For this reason the data were not subjected to a covariance analysis.

TABLE I

Bairdiella icistia: yolk absorption and eye and jaw formation.

Temperature (°C)	Salinity (‰)	Time of 95 % yolk absorption (h after hatching)	Time of functional eye and jaw formation[1] (h after hatching)	Yolk left at time of eye and jaw formation (% of original yolk)
21	20	54.5	71.0	2.2
	30	49.8	71.0	2.1
	40	57.0	71.0	1.3
24	20	42.5	45.5	4.4
	30	37.0	45.5	2.4
	40	39.5	45.5	3.3
27	20	39.0	34.3	6.3
	30	34.8	34.3	5.4
	40	39.5	39.0	5.5

[1] The figure given is the time of the first observation on which pigmented eyes and a movable jaw were noted, rather than the exact time of development of these features.

The development of pigmented eyes and a movable jaw probably marks the time when external feeding becomes possible. The time at which functional eyes and jaws were first noted decreased with increasing temperature (Table I) but was the same for all salinities at 21° and 24 °C; at 27 °C, eyes and jaws were formed at 34.3 h in the 20 and 30 ‰ groups but did not develop completely until sometime between 34.3 and 39 h in the 40 ‰ group. In general there was more yolk left when the eyes and jaws were formed in the lower salinities and higher temperatures (Table I).

DRY WEIGHT

The average dry weight per unfertilized egg was 19.1 μg (S.D., ±0.8 μg), and the chorion constituted 10.6 % of the total dry weight, leaving an average of 17.1 μg of yolk per unfertilized egg. The dry weight of larvae at hatching was higher at 30 and 40 ‰ than at 20 ‰ (Fig. 4). The Friedman test showed that salinity had a highly significant effect on dry weight at hatching ($P < 0.01$), whereas the effect of temperature was not significant ($P > 0.05$). The larger yolk volumes at low salinities and low temperatures (Fig. 1) must, therefore, have been due to a greater water content under these conditions. The dry weight at yolk absorption was lower in 21 °C–40 ‰ than other treatments (Fig. 5). No dry weight samples were taken at yolk absorption in 27 °C–40 ‰ because of poor survival under these conditions. A

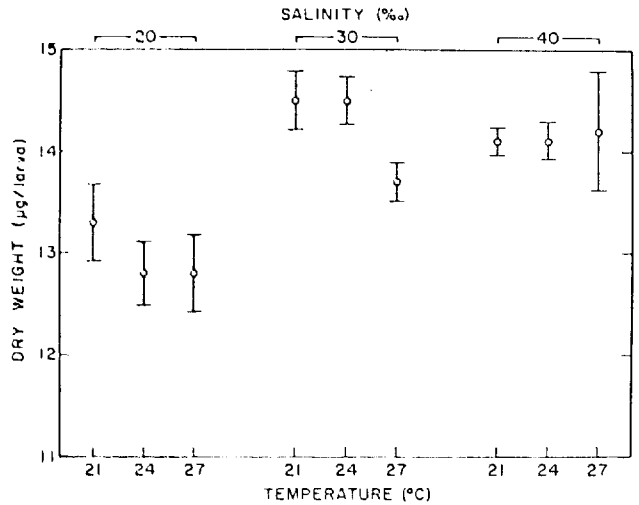

Fig. 4. Dry weight of larvae at hatching (mean ±S.E.). The number of measurements in each case was seven.

one-way analysis of variance showed that the experimental treatments had a significant effect ($P < 0.05$) on dry weight at yolk absorption. Multiple comparisons among means by the Student–Newman–Keuls multiple range procedure for unequal sample sizes (Sokal & Rohlf, 1969, p. 242) showed that the two 40 $^{0}/_{00}$ samples along with the 27 °C samples and that from 21 °C–30 $^{0}/_{00}$ formed a group without significant differences and that none of the treatments other than 21 °C–40 $^{0}/_{00}$ were significantly different from one another (Table II).

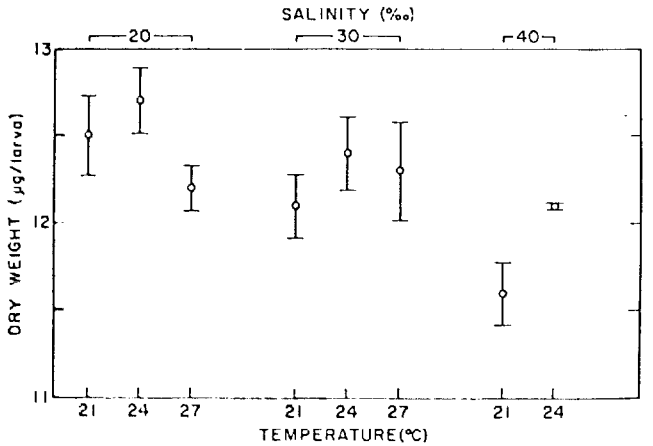

Fig. 5. Dry weight of larvae at the time of complete yolk absorption (mean ±S.E.). The number of measurements was seven in each case except for the 24 °C–40 $^{0}/_{00}$ group, which involved only five measurements.

TABLE II

Bairdiella icistia: multiple comparisons of mean dry weight at yolk absorption by the Student-Newman-Keuls procedure: means not underscored by a common line differ significantly at the 5 % level.

Temperature (°C)	21	21	24	27	27	24	21	24
Salinity (‰)	40	30	40	20	30	30	20	20
Mean dry weight (μg)	11.6	12.1	12.1	12.2	12.3	12.4	12.5	12.7

TABLE III

Bairdiella icistia: the % efficiency of yolk utilization from fertilization to complete yolk absorption, as 100 × dry weight of larva at yolk exhaustion/dry weight of original yolk.

Temperature (°C)	Salinity (‰)	Percentage efficiency
21	20	73.1
	30	70.8
	40	67.8
24	20	74.3
	30	72.5
	40	70.8
27	20	71.4
	30	71.9

In all salinities, there was maximum efficiency of yolk utilization at the intermediate temperature, 24 °C (Table III). At 21 °C and 24 °C, efficiency declined with rising salinity, but at 27 °C there was a slight increase between 20 and 30 ‰ (Table III).

DISCUSSION

There is accelerating influence of temperature on the rate of yolk absorption. A change from 21° to 24 °C increased the rate considerably but the increase between 24° and 27 °C was less pronounced, in accordance with the fact that, in general, Q_{10} decreases at higher temperatures (Johansen & Krogh, 1914; Bělehrádek, 1935). At 40 ‰, a rise in temperature from 24° to 27 °C gave no detectable increase in the rate of development to 95 % yolk absorption. In this case osmotic stress may have interfered with the normal response to temperature.

Salinity appears to have only a small effect on the rate of yolk absorption, but high salinities produced a slight acceleration of yolk utilization during the final hours of yolk absorption. Hatching is also completed more rapidly at the higher salinities (May, in press). For Pacific herring (*Clupea pallasi*) larvae, Alderdice & Velsen (1971) found only small differences in the times required for yolk exhaustion and the initiation of feeding behavior at different salinities whereas temperature had a strong influence. The dry weight of newly-hatched bairdiella larvae was affected by salinity, but not by temperature. At all temperatures the dry weight of newly hatched bairdiella

larvae was lowest in the lowest salinity, even though this salinity was the closest to being isosmotic with the body fluids of the embryo.

The results on dry weight show that the larger yolk volumes at hatching in low temperatures and salinities must be due to higher water content. This correlates with the larger subdermal space found in larvae from low salinities (May, in press). Larger yolk sacs have commonly been found in larvae hatching in lower salinities (Holliday & Blaxter, 1960; Westernhagen, 1970; Alderdice & Velsen, 1971), while Holliday & Blaxter (1960) showed that the body fluids of herring larvae hatching in lower salinities had smaller freezing point depressions and hence more water. Alderdice & Forrester (1971) found the opposite trend (larger yolk sacs at higher salinities) in petrale sole (*Eopsetta jordani*) but they only investigated a narrower range of salinities. Increased body dimensions are usually found in larvae kept in low salinities (see *e.g.*, Battle, 1929; Sweet & Kinne, 1964; Holliday, 1965) probably, in part, because of an increased water content.

The weights at yolk exhaustion were highest, and hence the calculated yolk utilization efficiencies also highest, at low salinities and an intermediate temperature. Efficiency would be expected to be highest at 24 °C since the two other temperatures (21° and 27 °C) are near the lower and upper limits, respectively, for normal embryonic development (May, in press). Wood (1932) found that above and below the normal temperature range for brown trout (*Salmo fario*) embryos, respiration increased relative to growth and a smaller embryo resulted. Blaxter's (1969) review shows that maximum efficiency of yolk utilization usually occurs at intermediate temperatures when a wide range of this variable is considered. Conversion efficiencies for older fishes are also usually maximal at intermediate temperatures (Kinne, 1960; Warren & Davis, 1967; Brett, Shelbourn & Shoop, 1969).

In the case of sole (*Solea solea*) embryos between fertilization and hatching, Flüchter & Pandian (1968) found decreasing conversion efficiencies with increasing temperature over the range of 10° to 20 °C; the eggs used, however, were collected from water at 8 °C and a lowered efficiency at the unusually high experimental temperatures might have been expected.

In the present study, the efficiency of yolk utilization at 21° and 24 °C was lower in the higher salinities, the highest value being in 20 $^{0}/_{00}$, *i.e.*, closest to being isosmotic with the larvae. At 27 °C, however, efficiency was nearly identical in 20 and 30 $^{0}/_{00}$. No data are available for other species concerning yolk utilization efficiencies in different salinities, but Kinne (1960) found that after the yolk-sac stage the desert pupfish (*Cyprinodon macularius*) had a higher conversion efficiency in 15 $^{0}/_{00}$ than in 30 $^{0}/_{00}$ or freshwater, and Vallet *et al.* (1970) found that adult mullet (*Mugil auratus*) grew well in 12 and 20 $^{0}/_{00}$ but lost weight in 5 and 37.5 $^{0}/_{00}$, despite comparable levels of food intake at all salinities.

Brocksen & Cole (1972) found that juvenile bairdiella kept at 25 °C had a lower maintenance requirement (the ration necessary to maintain a constant weight) in Salton Sea water with a salinity of 37 $^{0}/_{00}$ than in other salinities within the range,

29–45 ‰. At high feeding levels, however, bairdiella grew best at 29 ‰ and least well at 33 and 37 ‰, which is in better agreement with the present results for yolk utilization efficiencies, but the authors suggest that experimental difficulties may have biased their results at high levels of food consumption. It is possible that there is a real difference between the optimal salinity for bairdiella eggs and larvae and that for juveniles. It should be remembered, however, that the present work on early stages was conducted in ordinary sea water, whereas Brocksen & Cole used water from the Salton Sea, which has an unusual ionic composition and an effect on early survival very different from that of sea water (May, 1972). The effect of the ionic composition of Salton Sea water on the physiology of adult fishes has yet to be determined.

Holliday (1965) postulated that lower activity levels (presumed to be a result of negative buoyancy), coupled with decreased osmotic demands on metabolism, account for the enhanced survival of starving herring larvae in low salinities. Unfed bairdiella larvae also survive longest in low salinities (May, in press); this fact, along with the greater dry weight at yolk exhaustion at 20 ‰, may reflect a lower rate of metabolism in the lower salinities. Although there is no general agreement as to the effects of salinity on overall fish metabolism (see Gordon, 1964), several recent studies based on oxygen consumption indicate that the energetic cost of osmoregulation in adult fish is lowest in a salinity isosmotic to the body fluids (Rao, 1968, 1971; Farmer & Beamish, 1969; Job, 1969). The few published investigations of embryonic and larval oxygen consumption in different salinities (Lasker & Theilacker, 1962; Holliday, Blaxter & Lasker, 1964) report no marked salinity effects, except after abrupt transfer between salinities. No studies appear to have been made of salinity effects on the oxygen consumption of embryos at elevated temperatures.

Ryland & Nichols (1967) discuss some of the ramifications of higher conversion efficiencies in yolk-sac larvae. They point out that various temperatures within the annual range could produce plaice larvae differing in length by as much as 10 % at the time of first feeding, with a corresponding 10 % difference in swimming and escape speeds; in herring, the difference in speed might be 25 %. Such changes could no doubt influence a larva's ability to capture food and avoid predators and thus might affect survival and ultimately year-class strength. In the case of bairdiella larvae, there is ≈ 10 % difference in mean dry weight at yolk absorption over the range of temperatures and salinities considered here. In addition to increased swimming ability, larger larvae may have a significantly greater ability to resist starvation, as Blaxter & Hempel (1963) have shown for herring; however, a simple direct correlation between the efficiency of yolk utilization and survival potential may not be valid in all cases. Blaxter & Hempel (1966) have noted that reduced activity, which would be reflected in a higher efficiency value, could be detrimental to survival if it persisted until the time of first feeding.

Bairdiella larvae develop functional eyes and jaws before the yolk is entirely exhausted. At this time more yolk is left at the higher temperatures. In salmon, Hayes, Pelluet & Gorham (1953) also found that relative to other developmental parameters,

eye pigmentation was precocious at high temperatures. Higher salinities tended to decrease the amount of yolk present in bairdiella at eye and jaw formation. The ecological significance of these slight differences is not clear. There is no evidence that any combination of temperature and salinity affects the temporal relation between yolk exhaustion and the ability to begin feeding in such a way as to decrease the chances for survival in this species. Whether, as in the sardine (Lasker, 1962) there is an energy deficit in bairdiella larvae just prior to first feeding, and whether such a deficit would be influenced by varying temperature-salinity combinations, cannot be deduced from the present results; information on oxygen consumption under different conditions is needed.

In conclusion, temperatures within the range encountered by bairdiella eggs and larvae do affect their rate of yolk absorption and the efficiency of yolk utilization and may, to some extent, influence their chances for survival. The effects of salinity on the rates are less pronounced, but salinity may significantly alter yolk utilization efficiencies. Within the rather narrow zone of tolerance, the sublethal effects of temperature and salinity on yolk absorption rates and efficiencies in bairdiella are relatively small.

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