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EFFECT OF FEEDING HISTORY AND EGG SIZE ON THE MORPHOLOGY OF JACK MACKEREL, TRACHURUS SYMMETRICUS, LARVAE

GAIL H. THEILACKER

National Oceanic and Atmospheric Administration National Marine Fisheries Service Southwest Fisheries Center La Jolla, California 92038, U.S.A.

INTRODUCTION AND OBJECTIVES

Starvation of marine fish larvae after volk absorption may be one of the principal causes of larval fish mortality (Hunter, 1976a). Past studies showed that starvation in fish larvae could be detected by using morphometric criteria (Arthur, 1976; Ehrlich et al., 1976; Nakai et al., 1969; Kostomarova, 1962), histological criteria (Ehrlich et al., 1976; O'Connell, 1976; Umeda and Ochiai, 1975), and chemical criteria (Ehrlich, 1974a, 1974b). Use of histological criteria has several advantages over use of morphometric and chemical criteria. Histological criteria describe condition of individual larvae, indicate early starvation, and are independent of size; the disadvantage is that histological analyses are time consuming. Although morphometric paramenters require less time, past studies (Arthur, 1976; Ehrlich et al., 1976; Nakai et al., 1969; Kostomarova, 1962) show that they were not sensitive enough to indicate early starvation or to estimate condition of individual larvae.

In a recent laboratory study, Theilacker (1978) identified early starvation in individual jack mackerel, *Trachurus symmetricus*, larvae using either histological or morphometric criteria by comparing starved larvae to those fed at a constant food density. Larvae in the ocean are subject to widely varying food concentrations including no food (Lasker, 1975); hence, wild larvae may grow at different rates and sizes of body parts may change at different rates. Thus, histological and morphometric characteristics are needed that assess condition of larvae with variable feeding histories.

The objective of this study was to develop a sensitive morphometric technique that identified individual larval condition and was independent of egg size and feeding history. To accomplish this, the condition of jack mackerel larvae reared in the laboratory was investigated when initial feeding was delayed or when food type or density varied. Also, because the size of jack mackerel eggs varied, the condition of fed and starved larvae from large and small eggs was compared. In addition, the rate of recovery of tissues degenerated from starvation (Theilacker, 1978) was determined.

METHODS

COLLECTING AND REARING

Jack mackerel eggs were collected 20–30 miles off the coast of San Diego, California, in June and July 1977, by towing a 1/2 m diameter net with a plastic cod end just below the sea surface. These jack mackerel eggs were smaller than those collected in the earlier study (Theilacker, 1978). Thus, to test for effect of egg size, results from Theilacker (1978) were used in this study.

The larvae were reared in 100-liter black circular tanks at $15.5^{\circ} \pm 0.1^{\circ}$ C using rearing techniques described by Lasker et al. (1970), Theilacker and McMaster (1971), and Hunter (1976b). The foods used were rotifers, *Brachionus plicatilis*, (66 to 182 m μ wide; Theilacker and McMaster, 1971) and *Gymnodinium splendens*, a dinoflagellate (53 m μ diameter; Scura and Jerde, 1977). All rearing experiments were conducted with early, post-yolk-sac larvae of less than 4.0 mm standard length; wild jack mackerel at this size select prey between 50 and 200 m μ in width (Arthur, 1976).

Four feeding treatments were used: (1) high food density (50 *Gymnodinium* and 30-50 rotifers per ml) given at the time yolk is nearly absorbed and feeding begins, Day 5 (Group I, Table 1); (2) high food density

| Small-egg larvae | | | | Standard length (mm) | | Head length (mm) | | Eye diameter (mm) | | Body depth at pectoral (mm) | | Body depth at anus (mm) | |
|-------------------|-----------------|-------|-----|----------------------------|------|------------------------|------|-------------------------|------|-----------------------------------|------|-------------------------------|------|
| Treatment | Group | n | Day | mean | SD | mean | SD | mean | SD | mean | SD | mean | SD |
| Fed | 1 | 11 | 6 | 3.318 | .185 | .703 | .051 | .267 | .015 | .430 | .028 | .198 | .011 |
| | | 14 | 7 | 3.318 | .154 | .737 | .041 | .277 | .017 | .441 | .029 | .192 | .020 |
| | | 15 | 8 | 3.360 | .148 | .749 | .054 | .278 | .024 | .448 | .043 | .201 | .018 |
| | | 11 | 9 | 3.450 | .211 | .825 | .079 | .303 | .027 | .519 | .055 | .213 | .021 |
| | | 5 | 10 | 3.520 | .110 | .877 | .015 | .333 | .009 | .554 | .023 | .235 | .014 |
| Feeding delayed | 11 | 23 | 7 | 3.285 | .112 | .718 | .036 | .267 | .014 | .403 | .027 | .191 | .016 |
| one day | | 38 | 8 | 3.243 | .139 | .739 | .040 | .276 | .018 | .436 | .040 | .191 | .016 |
| · | | 29 | 9 | 3.317 | .136 | .767 | .054 | .284 | .020 | .445 | .055 | .202 | .019 |
| | | 15 | 10 | 3.290 | .126 | .785 | .051 | .291 | .018 | .477 | .037 | .202 | .017 |
| | | 5 | 11 | 3.390 | .074 | .831 | .038 | .316 | 0.33 | .487 | .052 | .206 | .013 |
| | | 3 | 12 | 3.450 | .229 | .827 | .052 | .312 | .026 | .476 | .071 | .204 | .017 |
| Feeding delayed | 111 | 19 | 8 | 3.147 | .120 | .721 | .033 | .268 | .011 | .423 | .025 | .196 | .012 |
| two days | | 22 | 9 | 3.173 | .127 | .749 | .028 | .274 | .011 | .430 | .043 | .185 | .017 |
| · | | 10 | 10 | 3.140 | .117 | .751 | .058 | .270 | .023 | .462 | .052 | .190 | .016 |
| | | 2 | н | 3.050 | .071 | .774 | .145 | .293 | .054 | .501 | .165 | .191 | .054 |
| Starved | IV | 28 | 6 | 3.248 | .121 | .687 | .034 | .251 | .013 | .390 | .027 | .185 | .013 |
| | | 6 | 7 | 3.075 | .147 | .663 | .056 | .249 | .021 | .368 | .032 | .173 | .007 |
| Large | egg larvae | ь | | | | | | | | | | | |
| Fed | v | 14 | 6 | 3.375 | .075 | .704 | .031 | .252 | .016 | .458 | .022 | .208 | .016 |
| | | 15 | 7 | 3.483 | .126 | .736 | .038 | .259 | .014 | .476 | .031 | .204 | .016 |
| | | 15 | 8 | 3.560 | .132 | .770 | .030 | .286 | .015 | .519 | .040 | .218 | .016 |
| | | 10 | 9 | 3.826 | .237 | .845 | .056 | .316 | .020 | .590 | .039 | .250 | .013 |
| | | 15 | 10 | 3.717 | .203 | .851 | .074 | .306 | .029 | .576 | .061 | .235 | .022 |
| Starved | VI | 14 | 6 | 3.311 | .109 | .655 | .036 | .236 | .016 | .413 | .032 | .179 | .016 |
| | | 15 | 7 | 3.355 | .131 | .688 | .020 | .248 | .013 | .417 | .023 | .183 | .012 |
| · | VII | 19 | 8 | 3.041 | .175 | .646 | .035 | .232 | .014 | .419 | .025 | .174 | .015 |
| Small | -egg-larvae | ¢ | | | | | | | | | | | |
| High-low density | VIII | 11 | 6 | 3.186 | .092 | .657 | .027 | .244 | .009 | .405 | .023 | .167 | .010 |
| | | 15 | 7 | 3.190 | .171 | .702 | .036 | .271 | .010 | .418 | .033 | .194 | .013 |
| | | 14 | 8 | 3.257 | .160 | .714 | .024 | .270 | .017 | .414 | .041 | .183 | .017 |
| | | 11 | 9 | 3.082 | .261 | .680 | .059 | .270 | .019 | .423 | .041 | .185 | .016 |
| | | 2 | 10 | 3.025 | .318 | .731 | .024 | .281 | .012 | .425 | .024 | .187 | .024 |
| Fed wild plankton | IX ^d | 5 | 6 | 3.360 | .152 | .717 | .052 | .269 | .008 | .435 | .015 | .197 | .015 |
| | | 5 | 7 | 3.280 | .277 | .700 | .066 | .265 | .019 | .445 | .035 | .190 | .014 |
| | | 6 | 8 | 3.383 | .133 | .793 | .051 | .289 | .022 | .456 | .036 | .210 | .009 |
| | | 8 | 9 | 3.450 | .160 | .814 | .052 | .291 | .021 | .459 | .030 | .210 | .018 |
| | | 6 | 10 | 3.617 | .216 | .861 | .085 | .315 | .030 | .558 | .073 | .232 | .026 |
| | | 5 | 11 | 3.510 | .074 | .870 | .046 | .320 | .019 | .530 | .039 | .224 | .019 |

Table 1. Daily means of five body measurements of Trachurus symmetricus larvae subjected to various feeding treatments.

^a Day 7, Group II larvae were not included in morphometric SWDA (see text).

^b Data from Theilacker (1978). Days 8, 9 and 10, Group V larvae are not included in morphometric SWDA. Size class selected for SWDA = 3.0-3.5 mm.

^c Condition of larvae in Treatments VIII and IX was compared by morphometric and histological analyses; treatments were not included in morphometric SWDA.

^d Larvae reared by Kim Devonald, Scripps Institution of Oceanography.

beginning on the day after yolk absorption, Day 6 (Group II); (3) high food density beginning 2 days after yolk absorption, Day 7 (Group III); (4) no food (Group IV). Measurements of larvae sampled from these four treatments were used to develop the morphometric criteria that identify larval fish condition.

Beginning on day six, 5-30 larvae were sampled daily and preserved in Bouin's fixative. After preservation, the standard length (SL, tip of upper jaw to perpendicular at end of notochord), head length (HL, tip of upper jaw to cleithrum), eye diameter (ed), body depth at the pectoral (bd-1), and body depth at the anus (bd-2) were measured. After measurement larvae were prepared for histological examination using standard techniques (Theilacker, 1978).

MORPHOMETRIC ANALYSIS

Morphometric analysis of larval fish condition was based on a stepwise discriminant analysis (SWDA). This technique finds the best set of variables (body measurements) that discriminate satisfactorily between known groups of larvae; by using the variable set, this technique predicts the group to which the individual larvae appear to belong. A known group in this study usually means a group of animals pooled by treatment (Table 1); however, there was one exception, Group II, that is explained in Results. The variables (body measurements) in which the feeding and starving groups were expected to differ were: (1) HL; (2) ed; (3) bd-1; (4) bd-2; (5) HL/SL; (6) ed/SL; (7) bd-1/SL; (8) bd-2/SL; (9) ed/HL; (10) bd-1/HL; (11) bd-2/HL. To classify individual larval condition all 11 variables were entered into the SWDA.

Larvae of between 3.0 and 3.5 mm standard length were selected for morphometric SWDA.

HISTOLOGICAL ANALYSIS

Condition ("healthy", "recovering", "intermediate", or "starved") of all larvae in each treatment was determined by examining the histological characteristics of the pancreas, liver, and gut (Theilacker, 1978).

Because the SWDA selects discriminating variables (larval body measurements) based on all cases within a group, it was desirable that most larvae within each group have similar nutritional conditions, i.e., have the same histological grade. Therefore, for the SWDA all larvae were not retained in Group II (see Results). The dominant histological condition of the larvae within each group (feeding treatment) was used to define the group.

RESULTS

GROWTH

Jack mackerel eggs collected for this study were 0.90 \pm 0.03 mm live diameter (n = 32) and larvae hatched at

 2.1 ± 0.05 mm live SL (n = 20). These eggs were 0.08 to 0.10 mm smaller than eggs collected in an earlier study (Theilacker, 1978), the results of which are used in this study. During a 4-day period after the first day of feeding, fed larvae (Group 1, Table 1) grew at 0.051 mm/day and 1-day delay-fed larvae (Group II) grew at 0.026 mm/day (Fig. 1). Larvae that were starved 2 days before feeding (Group III) did not grow over the 4-day experiment.

The relationship between body depth and standard length was similar between larvae fed continuously on rotifers and larvae fed rotifers for two or more days following 1-day delay in feeding. This relationship held only for larvae of the same length but not for those of the same age (Groups I and II, Table 1). Starved larvae were usually smaller than unstarved larvae of the same age.

HISTOLOGICAL ASSESSMENT OF LARVAL GROUPS

In many of the larvae given food, histological evidence existed for both feeding and starving. In these larvae the liver, pancreas, and gut tissues appeared normal and there were inclusions in the hindgut that indicate digestion; however, there were also separations between midgut mucosal cells, indicating the larvae had starved at some time.

This condition was between the histological conditions defined in the earlier study of large-egg larvae (Theilacker, 1978) as "healthy" (feeding larvae) and "intermediate" (early-starved larvae, usually larvae that starved 1 or 2 days). In discussions of larval fish histology that follow, reference to this condition is "recovering". "Recovering" larvae are eating and digesting food but have starved at some time.

In "recovering" larvae that were starved 2 days before feeding, vacuoles were visible within the midgut cells. The appearance of these large vacuoles was unusual, and it suggests that the gut epithelium may be a site for intracellular digestion (Iwai, 1968) or storage. The liver cells of these larvae also had very large





intracellalar spaces, probably areas for storage of glycogen. Both the condition in the midgut and the liver were unique to larvae feeding after 2 days of starvation.

The dominant histological condition of larvae within a group (I-VIII, Table 1) was used to define group condition (Fig. 2A). For Group I, continuously fed larvae, 76% were graded histologically as "healthy". However, some larvae given food did not eat; 7% of the larvae in Group I were starving and graded "inter-



Figure 2. Comparison of larval classification by histological and morphological methods. (A) Using histological methods, larvae in each feeding treatment were divided into "Healthy", and "Reccovering", "Intermediate", and "Starved" categories. (B) Using morphometric methods, larvae were matched to their feeding treatment. The distribution of larvae was similar to histological groupings although the categories into which they are distributed are not exactly parallel, see text.

mediate" and 17% of the larvae were graded "recovering", i.e. larvae were eating but had starved at some time. Hence, 93% of the larvae belonging to Group I were eating. In Group II, tissue degeneration caused by 1 day of starvation had completely regenerated in 48% of the larvae that ate for 1 day and in 89% of the larvae after eating 2 days. Because at least 2 days of feeding were required before most larvae were "healthy", only larvae that fed 2 or more days after 1 day of starvation were included in Group II for the morphometric SWDA. As a result, 75% of Group II larvae were "healthy" and 20% were "recovering", therefore, 95% were eating. Tissue regeneration was never complete in larvae that fed 1-4 days after 2 days of starvation (Group III), 54% of the larvae were "recovering" and 44% were "intermediate". Therefore, about half of these larvae were eating and half were starving; no single histological condition dominated. For Group IV, larvae that were starved 1 or 2 days (early-starved), the majority, 78% received the "intermediate" grade and 19% were graded "starved", hence 97% were starving.

To simulate field conditions, both larvae from large and small egg groups were included in the morphometric SWDA (Fig. 2A) because egg size in the sea is unknown. The dominant histological condition of larvae hatching from large eggs (Theilacker, 1978) was as follows: fed larvae in Group V (Table 1), 85%"healthy", larvae starved 1 and 2 days (early-starved) in Group VI, 44% "intermediate" and 37% "starved" (hence 81% starving), larvae starved 3 days (latestarved) in Group VIII, 80% "starved" and 7% "intermediate" (hence, 87% starving).

MORPHOMETRIC SWDA

The SWDA was run with the same larval groups, -VII (Table 1) used for histological analysis. Eleven morphometric variables (see Morphometric Analysis)

Table 2. Morphological classification of *Trachurus symmetricus* larvae. The number of larvae in the actual, predetermined group is compared with the predicted group membership determined by the stepwise discriminant analysis.

| A - 4 I | | Egg | | Predicted group membershi | | | | ip | | |
|-----------------------|------------------------------|------|-----|---------------------------|----|----|-----|----|----|-----|
| group | Treatment | (mm) | n | v | I | II | III | IV | VI | VII |
| v | Fed | 1.00 | 26. | 23 | 2 | 0 | 0 | 0 | 1 | 0 |
| I | Fed | 0.90 | 46. | 1 | 20 | 11 | 3 | 4 | 5 | 2 |
| 11 | Feeding delayed ^b | 0.90 | 86. | 2 | 23 | 26 | 26 | 9 | 0 | 0 |
| 111 | Feeding delayed ^e | 0.90 | 52 | 1 | 3 | 14 | 31 | 2 | 0 | 1 |
| IV | Starved; 1 and 2 days | 0.90 | 32. | 0 | 0 | 2 | 2 | 20 | 6 | 2 |
| VI | Starved; 1 and 2 days* | 1.00 | 29. | 4 | 1 | 0 | 0 | 6 | 17 | 1 |
| VII | Starved 3 days | 1.00 | 15. | 1 | 0 | 0 | 2 | 1 | 3 | 8 |

Data from Theilacker (1978).

Feeding delayed 1 day. Includes larvae fed 2 or more days after 1 day of starvation (see text).

Feeding delayed 2 days.

1

were entered into the SWDA. The analysis selected a set of seven variables as the best set to discriminate between the predetermined groups. The variable set, listed in order of selection, was: (1) HL/SL; (2) HL; (3) bd-1/HL; (4) ed; (5) bd-2/HL; (6) bd-1; and (7) bd-1/SL.

The SWDA (Table 2) allowed differentiation between fed and starved larvae that hatched from large and small eggs, in particular Groups V vs. I and Groups VI vs. IV. SWDA classified larvae hatching from small eggs as belonging not only to their own feeding treatment but to several treatments; classification of larvae hatching from large eggs was more precise (Table 2).

COMPARISON OF HISTOLOGICAL AND MORPHOLOGICAL METHODS

The distribution of larvae to feeding treatment by SWDA was similar to that based on histological criteria (Fig. 2), although the four categories into which they are distributed are not exactly parallel. For example, all "healthy" larvae (first category, Fig. 2A) were reared in feeding treatments V, I, and II (with several exceptions for larvae hatching from large eggs), however, all larvae in treatments V, I, and II (first category, Fig. 2B) were not "healthy" - some larvae given food did not eat. In Results (Histological Assessment of Larval Groups), feeding treatments V, I, and II were called "healthy" treatments, i.e., the majority of the larvae reared with these treatments were "healthy". Even though it is not accurate to compare the histological and morphological distributions of larvae as shown in Figure 2A vs. 2B, the comparison does allow a relative assessment of the sensitivity of the SWDA.

The SWDA assigned a reasonable proportion of larvae to correct feeding treatment. To summarize Figure 2, 77% of the larvae belonging to three feeding groups, Groups V, I, and II, were histologically graded "healthy"; the SWDA matched 66% of the larvae taken from Groups V, I, and II correctly to their feeding treatment. For larvae that were starved 1, 2 or 3 days, Groups IV, VI, and VII, 89% received the starved histological grades ("intermediate" and "starved"); the SWDA matched 84% of the starved larvae taken from Groups IV, VI, and VII correctly to their feeding treatment.

EVALUATION OF MORPHOMETRIC SWDA AS A CLASSIFICA-TION TECHNIQUE

The discriminant analysis, SWDA, can now be used as a classification technique since a set of variables, combination of body measurements, has been found that satisfactorily discriminates larvae with known feeding histories. To test the power of the SWDA as a classification technique, a discrimination function derived from the variable set was used to classify condition of larvae with "unknown" feeding histories. In this application of SWDA the independent variables were not selected but entered directly into the analysis. To evaluate the accuracy of this test, all larvae were examined histologically.

Two groups of larvae, reared in experiments where food density and type were varied, were treated as the "unknown" sampled. The treatments for the two groups of larvae that hatched from small eggs were: (1) high-low rotifer density, 30-50/ml given on first day of feeding and 6-12/ml for the next 5 days and temperature at 15.5° C (Group VIII, Table 1); and (2) wild plankton diet of one copepod/ml, nauplius or copepodite $80-200 m\mu$ width, given at time of first feeding and temperature at 17° C (Group IX, Table 1).

Larvae fed rotifers at high-low densities, Group VIII, grew at 0.036 mm/day for 2 days and then began to shrink after the rotifer density was decreased (Fig. 3). In contrast, larvae fed wild plankton at low densities, Group IX, grew at 0.064 mm/day (Fig. 3), about the same rate as larvae fed rotifers at high densities, Group 1, (Fig. 1).

All larvae sampled from both "unknown" groups, Groups VIII and IX (Table 1), were retained for the SWDA classification. Size range for larvae fed rotifers at high-low density, Group VIII, was 2.7-3.5 mm. Larvae fed wild plankton at low density, Group IX, were larger, 3.0-3.8 mm (Table 1), and in better condition (Table 3) than larvae fed rotifers at low density, Group VIII.

Table 3 compares the use of histological and morphometric criteria to classify individual larvae. For the wild plankton treatment, SWDA classified 28 larvae as belonging to the three feeding groups labelled as "healthy", Groups V, I, and II (see Histological



Figure 3. Growth of small-egg *Trachurus symmetricus* larvae with means and standard deviations. Feeding treatments are indicated, and sample size is in Table 1.

| Table 3. | Small-egg Trachurus symmetricus larvae were fed wild plankton at a low density (Group IX) or a varied density of rotifers (Group |
|----------|--|
| VIII). | Each larva in both treatments was classified with the morphometric SWDA and the histological method. Larvae classified incorrectly |
| with th | e SWDA are underlined. Total number of larvae within each experiment does not agree with Table 1, as several larvae were lost during |
| the mi | crotechnique procedure. |

| | Morphometric classification and predicted group membership | | | | | | | | | |
|--------------------|--|--------------------|-----------------------|-----------------------|--------------------------------|--------------------------------|---------------------------------|--|--|--|
| Histological grade | Fed 1.0 mm | Fed 0.9 mm | Delay 1 day 0.9 mm | Delay 2 day 0.9 mm | Starved I and 2 days 0.9 mm | Starved 1 and 2 days 1.0 mm | Starved 3 days 1.0 mm VII | | | |
| | •••••• | | | | IV | VI | | | | |
| | | Plankton Treatment | | | | | | | | |
| Healthy. | 3 | 10 | 7 | 0 | 0 | 0 | 1 | | | |
| Recovering | 1 | 0 | 3 | 0 | 1 | 0 | 1 | | | |
| Intermediate | 0 | 2 | 2 | 1 | 0 | 0 | 0 | | | |
| Starved | 0 | 0 | 0 | 0 0 | | 0 | 0 | | | |
| | Density Treatment | | | | | | | | | |
| Healthy | 0 | 3 | 1 | 0 | 0 | 0 | 0 | | | |
| Recovering | 1 | 7 | 4 | 5 | 6 | 0 | 1 | | | |
| Intermediate | 0 | 0 | 1 | 1 | 7 | 6 | 3 | | | |
| Starved | 0 | 0 | 0 | 0 | 2 | 0 | 1 | | | |

Assessment of Larval Groups), 20 of these larvae, 71% were histologically graded "healthy" and four were graded "recovering" (Table 3). A "recovering" larva had eaten and was digesting food; the SWDA classification of these four larvae into the "healthy" groups was not unreasonable. Twenty-four of the 28 larvae, 86%, identified as belonging to the "healthy" groups by SWDA were identified as eating by histology. SWDA predicted that three larvae were starving; these larvae were classified as belonging to the three starving groups, Groups IV, VI, and VII. These allocations were incorrect; histologically there were no starving larvae.

In the high-low rotifer density treatment, SWDA classified 17 larvae as belonging to the three "healthy" feeding groups, Groups V, I, and II, four of these larvae received the "healthy" histological grade and 12 were graded "recovering". Therefore, 94% of the larvae classified by SWDA as belonging to a feeding group were eating. SWDA classified 26 larvae into the three starving groups, Groups IV, VI, and VII, nineteen, 73%, of these larvae received the "starving" histological grades ("intermediate" and "starved").

The SWDA classifications in Table 3 that were unreasonable are underlined. In sum, 88% of morphometric SWDA classifications of larvae to feeding treatments were reasonable, as verified by a histological examination of all larvae.

DISCUSSION

The purpose of these experiments was to document a morphological method that can be used to identify probable feeding condition of field-collected larvae. Analysis of early, post yolk-sac jack mackerel larvae reared in the laboratory with various feeding regimes showed that larvae of the same size which were "healthy" according to histological analysis can differ in other body measurements and age. It was found that body proportions differed between larvae of the same size that hatched from large (Theilacker, 1978) and small eggs. For example, body depth of fed small-egg larvae was deeper than fed large-egg larvae of the same size, though this relationship did not hold when larvae were the same age (Table 1). Growth rate of larval body parts may vary because larvae experienced different feeding conditions.

Growth and condition of jack mackerel hatched from small eggs were assessed in this study for a variety of feeding treatments. Small-egg larvae, fed either high rotifer densities or low copepod densities, grew at about the same rate and were "healthy", but larvae fed a low density of rotifers grew more slowly and were in poor condition. Therefore, at low densities, the quality of copepods as a food for larval jack mackerel was superior to rotifers. When fed at high rotifer densities, growth rate of small-egg larvae was less than the growth rate of large-egg larvae (Fig. 4).

In general, egg size appears to be an important factor that affects resistance to starvation and influences growth (Ware, 1975). In the jack mackerel experiments, large-egg larvae starved more slowly and lived 1 day longer without food (Theilacker, 1978) than small-egg larvae (Fig. 4). These results agree with studies by Blaxter and Hempel (1963) on herring, and Stanley (1977), however collected conflicting data, indicating that there was no influence of egg size on I



Figure 4. Comparison of fed and starved, large- and small-egg Trachurus symmetricus larvae with means and standard deviations. Sample size is in Table 1. Data for large-egg larvae from Theilacker (1978); data for small-egg larvae is the same as in Figure 1.

survival time during starvation for Japanese medaka, Oryzias latipes. Blaxter and Hempel (1963) also found that, with a large difference in herring egg size, the duration of the yolk-sac stage differed. This was not the case with jack mackerel, the difference in egg size was small and the time from hatching to first feeding was the same, 5 days at 15.0° to 15.5° C.

Both large- and small-egg jack mackerel larvae, which were starved for 1 and 2 days after yolk absorption, ate immediately after the addition of food. This behavior was similar to most other fish larvae (Hunter, in press). A 1-day period of starvation preceding the feeding of larvae from small eggs slowed the onset of growth. Growth did not proceed until the internal tissues that had deteriorated during starvation, had recovered. The energy for growth may have been diverted to tissue repair. In larvae starved for 2 days before feeding, evidence of cellular deterioration in the gut, pancreas and liver remained after feeding commenced. About half of these larvae appeared to be storing or digesting material in the gut epithelium. Although the larvae were feeding and "recovering" after 2 days of starvation, there was no growth during the experiments. These findings differ from results of May (1971) He found that grunion, Leuresthes tenuis, larvae were extremely resistant to starvation and that growth of larvae proceeded at the same rate when starved up to 16 days before feeding.

Evidence of morphometric differences between laboratory-reared and sea-collected larvae indicate that it may be difficult to transfer laboratory-collected data to the sea (Blaxter, 1975). Most data substantiating this hypothesis were collected during long-term laboratory experiments. An attempt was made to avoid this objection by restricting (1) the time of my experiment to 5 days; and (2) the size class selected for SWDA analysis to 3.0-3.5 mm SL.

Recently developed morphological criteria that identify larval fish condition were applied in this study. It was expected that complex relationships in larval fish morphology would occur between larvae fed at various food densities, including no food, delayed initial feeding, and between feeding and starving larvae that had hatched from different egg sizes. However, by using a combination of several larval fish body measurements, the SWDA, it was possible to correctly assign most larvae into feeding groups; allocations were corroborated by a histological examination of individual fish. Morphological criteria for assessment of condition of wild larvae are most useful than histological criteria because they take much less time to determine, cost less, and can be used routinely. The morphometric technique should allow reasonable estimates - independent of egg size and feeding history — of condition of early, post yolk-sac wild larvae. These estimates may be useful for detecting the incidence of starvation in sea-caught larvae and for predicting larval survival in the field.

SUMMARY

Because starvation of marine fish larvae after yolk absorption may be an important factor influencing larval survival, there is a need to recognize starvation in wild larvae. The primary purpose of this study was to develop morphometric criteria sensitive enough to identify condition of larvae that hatched from large and small eggs and were subjected to varying feeding treatments. Morphometric criteria for assessing larval condition are not as precise as histological criteria; however, morphometric criteria are more useful than histological criteria because they take less time to determine (measuring body parts is relatively easy) and therefore could be used routinely in analyses of wild larvae.

In this study a multivariate statistical analysis (SWDA) was used to assess the condition of jack mackerel larvae. The criteria used in the analysis were based on measurements of larvae hatched from large and small eggs and raised under conditions in which availability of food and time of feeding (delayed by 1 or 2 days) were varied. The larvae were divided into seven groups, according to their feeding treatment and egg size. Using the SWDA, larvae were classified in each controlled feeding group according to probable feeding history. All larvae in the seven groups were examined histologically to assess the power of the morphometric technique to properly classify condition of individual larvae. The histological analysis graded 77% of the larvae belonging to three feeding groups as "healthy" and SWDA matched 66% of the larvae taken from these feeding groups correctly. In the three starving groups, 89% received the histological "starved" grades and SWDA matched 84% of the starved larvae correctly to the three starved treatments. Hence, SWDA assigned a reasonable proportion of larvae to correct feeding treatment. Classification of larvae by SWDA was more precise for larvae hatching from large eggs than for larvae hatching from small eggs.

Histological analysis of larvae showed that tissue degeneration caused by 1 day of starvation after yolk absorption completely regenerated in 89% of the larvae after feeding for 2 days. However, the 1-day period of starvation slowed the onset of growth. Tissues never completely regenerated in feeding larvae following 2 days of starvation after yolk absorption.

Growth rate of larval body parts was found to vary because larvae hatched from different size eggs or because larvae experienced different feeding conditions. Resistance to starvation was 1 day longer for larvae hatching from large eggs than for larvae hatching from small eggs.

To test the sensitivity of the morphometric criteria selected by SWDA, SWDA criteria were used to classify condition of larvae raised in two independent experiments in which type of food (wild vs. laboratory cultured) and density of food were varied. SWDA classification of each larva was evaluated by examining each larva histologically. Eighty-eight percent of the larvae raised in independent experiments had similar condition classifications by SWDA method and histological method. It was concluded that the morphometric method should allow reasonable estimates — independent of egg size and feeding history — of condition of early, post yolk-sac wild larvae.

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