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Causes of mortality in young jack mackerel

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ABSTRACT: Field and laboratory experiments were conducted with the purpose of partitioning jack mackerel *Trachurus symmetricus* larval mortality into portions due to starvation and to predation. Field collections were made to determine larval condition, growth, net retention and production; laboratory experiments were conducted to determine growth and body shrinkage due to preservation treatment. Age-specific starvation and total mortality rates were estimated and predation was inferred as the difference between the two. In the offshore oligotrophic part of the spawning habitat, larvae suffered a high rate of mortality which rapidly declined as they developed. Predation was the major source of mortality of yolk-sac larvae. As the yolks were absorbed and the larvae began to feed, starvation became a significant source of mortality. As the larvae further developed, starvation rapidly declined and predation again became the dominant source of mortality, although at a much lower rate.

INTRODUCTION

Survival of young fish is limited by predation and starvation (Hunter 1984). Furthermore, these 2 sources of mortality may interact if starving larvae are more vulnerable to predation (Shepherd & Cushing 1980). The magnitude of mortality is influenced by endogenous factors (e.g. quality and quantity of yolk) and exogenous factors (transport, predator abundance and food supply). These factors act in concert on development and growth of young fish through the most hazardous phase of their life history. Above-average parental endowment and environmental conditions assure rapid, healthy growth and minimize mortality; on the other hand, poor parental endowment and adverse environmental conditions lengthen the period of extreme vulnerability. To link larval survival to recruitment of fish into the adult population, early mortality must be quantified. To understand the causes of mortality, a distinction must be made between that fraction due to starvation and that due to predation.

Earlier evidence points to predation as the major cause of larval mortality (Methot & Kramer 1979, O'Connell 1980, Ellertsen et al. 1981, Hunter 1984). In this field study we assess the mortality due to starvation and subtract it from total mortality rate to determine the rate of predation and the relative importance of these sources of mortality. We designed a field study to give us information on total mortality and starvation-induced mortality of young jack mackerel *Trachurus symmetricus*. We intensively sampled a small portion of jack mackerel spawning habitat, over a period of 4 d, off the coast of southern California. Total mortality of young jack mackerel was inferred from size-specific catch rates and the duration of growth within size categories (Hewitt 1981, Hewitt & Brewer 1983). Starvation mortality was determined using laboratory-developed histological criteria for characterizing jack mackerel condition (Theilacker 1978, 1981, in press). We then partitioned total mortality into the fraction due to starvation and the fraction due to predation.

METHODS

The sample area (Fig. 1) was chosen because it was well outside coastal and island influences and yet still within the spawning habitat of jack mackerel. In the first experiment, 3 ichthyoplankton samples were obtained over a close-spaced grid of stations: 1 sample was preserved in a formalin solution and used to estimate the size-frequency distribution of jack mackerel larvae; a second sample was preserved with Bouin's fixative and used for histological analysis of larval tissue condition; a third sample was preserved in alcohol and was the source of otoliths used to describe the growth of larvae. In 1983, a second collection was made using various net meshes for the purpose of quantifying the fraction of larvae extruded through the nets. Laboratory experiments were conducted to deter-

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mine the degree of larval body shrinkage that may be expected with various preservation treatments.

The size-specific larval catch curve was adjusted for extrusion losses and divided by the duration of growth to yield an age-specific production curve; the slope of this curve measures the total mortality rate. Growth of jack mackerel larvae was obtained from laboratory experiments (Theilacker 1978) and from daily growth increments in the otoliths of field-collected larvae. Larval condition and starvation mortality were estimated for each of 4 larval size categories (yolk-sac, < 3.5 mm, <4.0 mm and <4.5 mm). Field collections, estimation of total mortality, larval condition, growth, extrusion and shrinkage are described in more detail in the following sections.

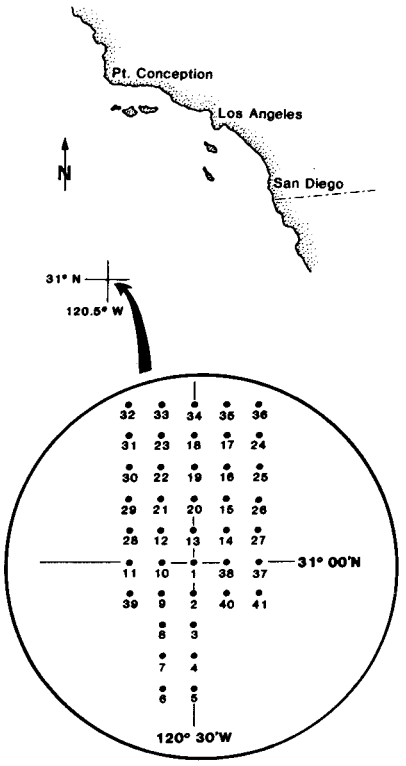

Fig. 1. The study area was a closed-spaced grid of stations 4 n mile apart and approximately 350 km southwest of San Diego, California

Field collections. In May 1980 jack mackerel eggs and larvae were sampled 350 km off the coast of California (Fig. 1) aboard the NOAA ship *David Starr Jordan.* A grid of 41 stations was established with 4 n mile spacing; stations were occupied over a 4 d period with 19 stations occupied twice to test for possible transport. At each station an oblique Bongo (60 cm mouth diameter) tow and an oblique 1 m ring tow, both fitted with 0.505 mm mesh nylon nets, were conducted (see Smith & Richardson 1977 for a description of these sampling gears). The Bongo tow yielded 2 samples; 1 was preserved in 10% buffered formalin and the other was preserved in an 80% alcohol solution. The 1 m ring tow sample was immediately preserved in Bouin's solution to avoid autolysis of larval tissues; after 2 d the Bouin's solution was replaced with a 70% alcohol solution. In addition 28 vertical profiles of temperature and 3 of salinity profiles were obtained.

A second collection was made in April 1983 at 31°N, 121°W (approximately 30 n mile from the first collection) aboard the NOAA ship *Townsend Cromwell.* These catches were used to estimate extrusion of jack mackerel larvae through 0.333 mm and 0.505 mm mesh nets. Fifty oblique Bongo tows were conducted with paired nets made of 0.333 mm and 0.505 mm mesh nylon. Another 50 paired tows were conducted with nets made of 0.333 mm and 0.150 mm nylon mesh; these tows were made with a small-mouth (25.23 cm mouth diameter) apparatus (PAIROVET) retrieved vertically to the surface from a depth of 70 m. Both samples were preserved in a 10% buffered formalin solution.

Total mortality. Jack mackerel larvae were sorted from the formalin-preserved plankton samples and counted by size. Catches were adjusted for extrusion losses using size-specific estimates of net retention (see 'Extrusion' section below).

To determine the mortality of the larvae we assumed that the size-specific abundance of larvae, measured at one time, is representative of the fate of a cohort as it ages through time. The assumption implies constant daily production of eggs and negligible transport of larvae into or out of the study area. Jack mackerel are serial spawners, spawning over several months. Because the experiment was conducted in the middle of the spawning season, it is not unreasonable to expect that the production of eggs was constant. We were unable to detect a change in the spatial distribution of the larvae over the 4 d sampling period. In areas where sampling was repeated, larval densities were similar. Southerly transport in May is commonly 0.2 kn in this locality (Hickey 1979); all southern stations, including those that were repeated (Stations 1 to 14), showed low larval densities (0 to 5 tow^{-1}), implying negligible transport to larvae to the south over the 4 d.

If we accept that relative abundances, measured at one time, are representative of a cohort's history through time, then larval mortality is the change in abundance. Larval growth may vary with size; thus size-specific catches must be standardized by dividing each catch by the duration of growth through the size

Table 1. *Trachurus symmetricus.* Histological condition of 4 size classes (preserved size) of field-collected jack mackerel larvae (from Theilacker in press)

	Dying	Starving	Recovering	Healthy	Total	Dying % d^{-1}
Yolk-sac	–	–	–	15	15	0
3.2 to <3.5 mm						
Number	43	74	45	38	200	
Duration (d)	1	3	2	6		
Number d^{-1}	43	24.7	22.5	6.3	96.5	45
3.5 to <4.0 mm						
Number	2	16	38	54	110	
Duration (d)	1	3	2	3.3		
Number d^{-1}	2	5.3	19	16.4	42.7	5
4.0 to <4.5 mm						
Number	0	2	12	45	59	
Duration (d)	–	3	2	3.3		
Number d^{-1}	–	0.7	6	13.6	20.3	0

category. The quotients may be referred to as production rates, and when plotted against the age of each category, they define the production curve (Hewitt & Brewer 1983). The slope of the production curve measures the larval mortality rate.

Larval condition. For our estimate of starvation-induced mortality, we used the results reported by Theilacker (in press). She used a histological technique to diagnose condition of individual jack mackerel larvae (Theilacker 1978, 1981).

Special samples were taken during our study for histological analyses. These samples were preserved rapidly (in less than 8 min) to minimize tissue decomposition. Theilacker examined tissue condition of individual, ocean-caught larvae and classified each larva into a health category. Health categories corresponded to the dominant tissue condition found in larvae which were exposed to various feeding treatments in the laboratory. The number of ocean-caught larvae belonging to each health category was totaled and then adjusted for duration, which is the number of days a larva, given its state of health, is expected to remain within the size interval. For healthy larvae, the duration is simply the size interval divided by growth rate in mm d^{-1}. For example, jack mackerel belonging to the smallest size category (< 3.5 mm, Table 1) begin to eat at 3.2 mm (preserved length) and grow at .05 mm d^{-1}. The size interval for this category is 0.30 mm, and at a growth rate of 0.05 mm d^{-1}, the duration is 6 d for healthy larvae. Older larvae grow at 0.15 mm d^{-1} (see 'Larval growth'). The durations for the Dying, Starving, and Recovering categories depend on the persistence of the histological criteria used to identify these categories. In the laboratory, larvae deprived of food show the histological indicators of starving for 3 d before dying; young larvae that eat after a period of starvation show the histological criteria that identify the Recovering condition for 2 d, subsequently appearing healthy (Theilacker 1978, 1981). After the total numbers were adjusted for duration, the calculated relative proportions of larvae belonging to each health category showed that 45% of larvae less than 3.5 mm were dying per day due to starvation. This mortality rate decreased to 5% for 3.5 to 4.0 mm larvae, and no starvation-induced mortality was observed in jack mackerel larger than 4.0 mm (Table 1).

Larval growth. We based growth estimates on both laboratory and field data. First-feeding jack mackerel grow slowly (0.05 mm d^{-1}), and this rate of growth is difficult to discern by reading otoliths. Therefore, for first-feeding jack mackerel, we used laboratory-determined growth rates (Theilacker 1978, unpubl.), and we estimated growth of older jack mackerel by counting daily growth increments in otoliths (sagittae) of ocean-caught fish (Brothers et al. 1976).

Standard length of all larvae collected in the Bongo samples was measured and converted to 'live' size using preservative and time-in-net shrinkage correction factors (see 'Shrinkage' below). Otoliths dissected from these larvae were mounted on a slide in clear fixative (Protex) diluted with xylene. After drying for 24 h on a slide warmer, daily increments were counted under oil immersion at a magnification of 1500× using a compound light microscope. All increments from the focus to the outer edge of the otolith were included in the counts. The focus is the central area of the otolith that forms during yolk absorption and is usually void of rings. In the laboratory, jack mackerel absorb most of their yolk and begin to eat 5 d after hatching at 15°C (Theilacker 1978). We assumed development in the

field at 15.5 to 16.5 °C was the same; thus to obtain jack mackerel age, we added 5 to the number of increments. The radius of each otolith was measured to the nearest micron.

To test for differences in growth rates, larvae were grouped by sample density, high or low, and the average growth rates were compared by using an analysis of covariance. We assumed for the analysis of covariance that growth was linear (the size range of larvae collected in these samples was limited). Larvae used in the growth analysis were collected in standard Bongo hauls and preserved in alcohol. To obtain quantitative samples, Bongo nets are thoroughly hosed down before preservation. This abrasion damages larvae, causing loss of eyes and otoliths. Thus the number of larvae that could be aged was small. A total of 221 larvae were aged, 61 taken from low density samples and 160 from high density samples.

Extrusion. The length-specific catch ratio of 0.333 and 0.150 mm meshes from PAIROVET tows together with the catch ratio of 0.505 and 0.333 mm meshes from the Bongo tows was used to compute the catch ratio for

Table 2. *Trachurus symmetricus.* Size-specific sample mean and retention rates of jack mackerel larvae in 0.333 mm mesh (Column 4) and 0.505 mm mesh (Column 8) nylon nets

Preserved size	PAIROVET Sample mean			Bongo Sample mean			
	0.150 mm mesh	0.333 mm mesh	Retention rate	0.333 mm mesh	0.505 mm mesh	Retention rate	Retention rate
(mm) (1)	(2)	(3)	(4)=(3)/(2)	(5)	(6)	(7)=(6)/(5)	(8)=(4)×(7)
1. All tows							
2.0	0	0	–	0.10	0	–	–
2.5	0.02	0.04	2.00	1.54	0.06	0.04	0.08
3.0	0.18	0.16	0.89	2.00	0.84	0.42	0.37
3.5	0.06	0.06	1.00	0.98	1.04	1.06	1.06
4.0	0	0	–	1.76	1.68	0.95	–
4.5	0	0	–	0.72	0.72	1.00	–
5.0	0	0	–	0.98	0.90	0.92	–
5.5	0	0	–	0.26	0.32	1.23	–
6.0	0	0	–	0.06	0.14	2.33	–
6.5+	0	0	–	0.06	0.04	0.67	–
Total	0.26	0.28	1.08	8.50	5.74	0.68	
n	50	50	50	50	50	50	
2. Tows with at least 1 mesh having a positive catch							
2.0	0	0	–	0.102	0	–	–
2.5	0.05	0.10	2	1.57	0.06	0.04	0.08
3.0	0.45	0.40	0.89	2.04	0.86	0.42	0.37
3.5	0.15	0.15	1.00	1.00	1.06	1.06	1.06
4.0	0	0	–	1.80	1.71	0.95	–
4.5	0	0	–	0.73	0.73	1.00	–
5.0	0	0.05	–	1.00	0.92	0.92	–
5.5	0	0	–	0.27	0.33	1.22	–
6.0	0	0	–	0.06	0.14	2.33	–
6.5+	0	0	–	0.06	0.04	0.67	–
Total	0.65	0.70	1.08	8.63	5.85	0.68	
n	20	20	20	49	49	49	
3. Tows with both meshes having a positive catch							
2.0	0	0	–	0.12	0	–	–
2.5	0	0	–	1.76	0.07	0.04	0.03
3.0	0.75	0.50	0.67	2.36	0.98	0.42	0.28
3.5	0.50	0.50	1.00	1.00	1.17	1.06	set = 1.0
4.0	0	0	–	2.05	1.88	0.92	set = 1.0
4.5	0	0	–	0.86	0.83	0.97	set = 1.0
5.0	0	0	–	1.05	1.05	1.00	set = 1.0
5.5	0	0	–	0.24	0.38	1.58	set = 1.0
6.0	0	0	–	0.07	0.17	2.39	set = 1.0
6.5+	0	0	–	0.07	0.05	0.70	set = 1.0
Total	1.25	1.00	0.80	9.71	6.57	0.68	
n	4	4	4	42	42	42	

0.505 mm mesh compared to 0.150 mm mesh. The latter mesh was considered to be extrusion-free (Lo 1983).

From each tow, jack mackerel larvae were measured and grouped into 0.5 mm preserved length classes from 2.0 to 6.5+ mm. The sample mean catch of larvae in each length class was computed for both PAIROVET (0.150 and 0.333 mm mesh) and Bongo (0.333 and 0.505 mm mesh) for tows grouped in 3 ways: (1) all 50 tows, n = 50 for PAIROVET and Bongo respectively; (2) tows in which at least 1 net had a positive catch (number of total larvae greater than 0), n = 20 for PAIROVET and 49 for Bongo; (3) tows in which both nets had positive catches, n = 4 for PAIROVET and 42 for Bongo (Table 2). The results from Group 3 were used to estimate the length-specific retention rate of jack mackerel larvae. Although the sample size from Group 3 was extremely small for PAIROVET tows, the estimated retention rate of jack mackerel was in agreement with that of northern anchovy *Engrualis mordax*. For jack mackerel larvae, the 0.333 mm mesh retained 0.67 of the 0.150 mm mesh catch of larvae $\leq$ 3.00 mm and retained all larger larvae, whereas for anchovy larvae, the 0.333 mm mesh retained 0.63 of the 0.150 mm mesh catch of larvae $\leq$ 4.0 mm and retained all larger larvae (Lo 1983). Because few larvae of 2.0 mm length class were caught in this experiment, the catches of larvae of 2.0 mm and 2.5 mm were combined to obtain 1 retention rate for larvae $\leq$ 2.5 mm. Retention rates of jack mackerel larvae in 0.505 mm mesh compared to 0.333 mm mesh were 0.04, 0.42 and 1.00 for larvae of length classes $\leq$ 2.5, 3.0 and $>$ 3.0 mm. Products of catch ratios from PAIROVET (0.150 and 0.333 mm mesh) and Bongo (0.333 and 0.505 mm mesh) were used as estimates of retention rates of 0.505 mm mesh: 0.03, 0.28 and 1 for larvae of length classes $\leq$ 2.5, 3.0, and $>$ 3.0 mm.

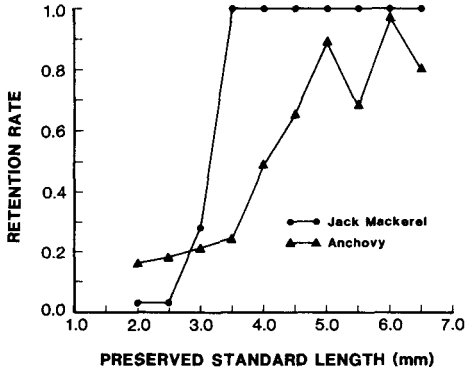

Fig. 2. *Trachurus symmetricus* and *Engrualis mordax*. Length-specific retention rates of jack mackerel and northern anchovy larvae estimated for 0.505 mm nylon mesh net

The functional relation of retention rate and length of jack mackerel was different from that of anchovy. Because there is little morphological difference between these 2 species before first feeding ($<$ 3.0 mm), the apparent difference in retention of these larvae is probably due to the small sample size of the jack mackerel catch (Table 2; Fig. 2). The 50 % retention point is reached earlier by jack mackerel because of their greater body depth (Fig. 2).

Shrinkage. All length measurements were adjusted to be equivalent to 'live' size. Both handling and preservation cause shrinkage of larval fishes, and the amount of shrinkage is dependent on handling time (which is different for laboratory and field) and type of preservative used (Blaxter 1971, Theilacker 1980, Hay 1981). In this study, net tows for histological analyses were 5 min, and subsequent preservation in Bouin's fixative was within 3 min; Bongo tows were 20 min and subsequent net wash and preservation in formalin (fish used for size-frequency) or alcohol (fish used for aging) was within 8 min. Larval jack mackerel standard length was adjusted for shrinkage due to handling using an equation developed by Theilacker (in press):

$$y = 1.0109 - 0.0105x \quad (1)$$

where y = the ratio of net-capture size/live size; x = net tow time.

Additional shrinkage of standard length in preservative after collection in the net was 9 % for Bouin's, 4 % for formalin, and assumed to be zero for 80 % alcohol; shrinkage of standard length for jack mackerel preserved in Bouin's in the laboratory was 8 %. Northern anchovy do not shrink in 80 % alcohol (Theilacker 1980), and we assumed that jack mackerel did not.

RESULTS

Field conditions

A temperature variation of approximately 1.5 C° was evident across the surface of the study area (Fig. 3). Zooplankton volumes and abundance of jack mackerel larvae described similar variations, more abundant at the cooler northern stations and less abundant at the warmer southern stations (Fig. 3). (Volume of zooplankton preserved in jars was checked and classified as high, low and very low.) Satellite imagery suggests that the study area may have coincided with the edge of a warm water tongue extending into cooler coastal water (Fig. 4). A temperature-salinity curve drawn from data collected within the study area agreed well with a curve obtained on an inshore station with the exception of the warm water portion of the curves (Fig. 5), suggesting a thin, warm layer of oceanic water

intruding coastward over deeper coastal water. Coastal zooplankters were sampled at depths of 40 m and greater but not in the surface waters, further supporting this interpretation. Similar hydrographic features are known to persist for several weeks (P. Fiedler pers. comm.) which supports the assumption of negligible larval transport.

Growth

Larval growth rates may vary with larval condition. If larvae are competing for food in areas where the density of larvae is high, condition of some larvae may be poor, and thus average growth rates would be slower than expected. Within the sample area, a larval density gradient was apparent; densities ranged from 100 to 300 larvae per tow in the northeast quadrant to about 0 to 45 per tow in the remaining area.

The growth rate for larvae collected in areas of low larval density areas was 0.166 mm d^{-1} and for larvae collected in high density areas was 0.147 mm d^{-1}. We could not reject the null hypothesis that daily growth rates are equal ($p = 0.20$). Thus we concluded that there was no difference in growth rates of jack mackerel within the sample area, and to estimate mortality rates, we combined all samples. For larvae older than 14 d of age since fertilization, growth rates of the ocean-caught jack mackerel and laboratory-raised jack mackerel were the same (Fig. 6; Theilacker 1978, unpubl.).

Mortality

Larvae were enumerated by 0.2 mm preserved size classes; sizes were converted to live size (i.e. adjusted for shrinkage), and the results were expressed as average catch by live size category (Table 3). Catches were further adjusted for net retention and divided by the duration of growth (Fig. 7) to estimate age-specific production rates (Table 3). The duration of growth

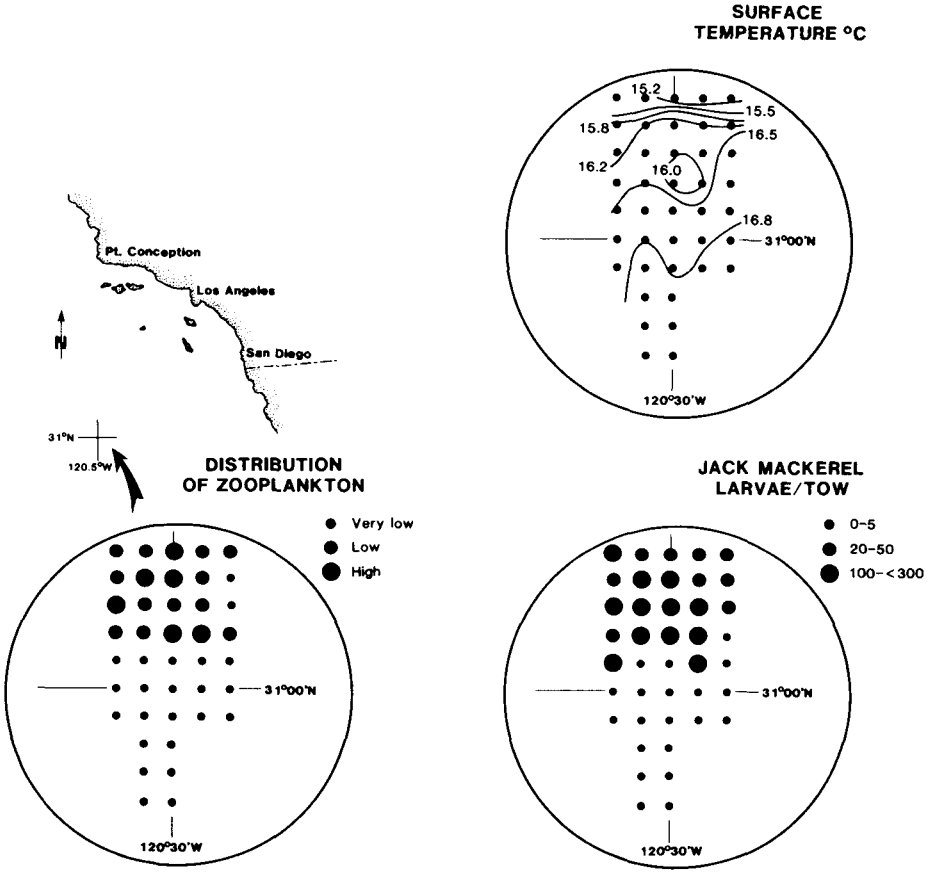

Fig. 3. Temperature, zooplankton and jack mackerel distributions over the study area. All showed north-to-south gradients

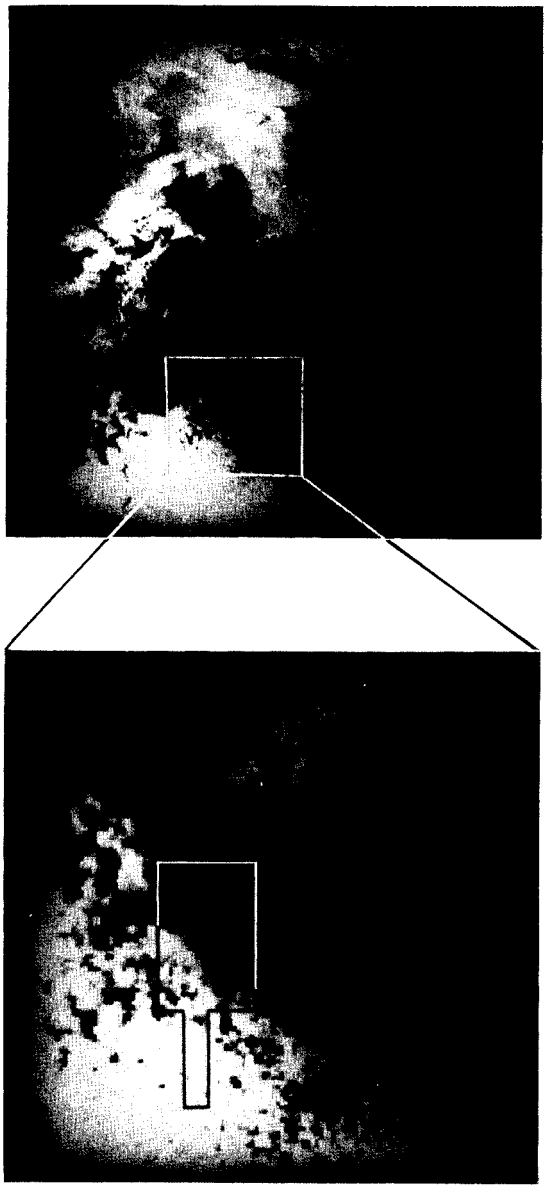

Fig. 4. NOAA 6 weather satellite imagery of sea surface temperature obtained during study period (P. Fiedler); light shading indicates warm water and dark shading indicates cool water. Upper image: prevailing surface thermal structure over the Southern California Bight; lower image: enlargement of study area with station grid outlined

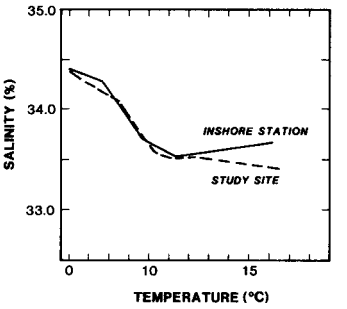

Fig. 5. Temperature/salinity curves drawn from profiles obtained from the study area and from 30 km off the coast

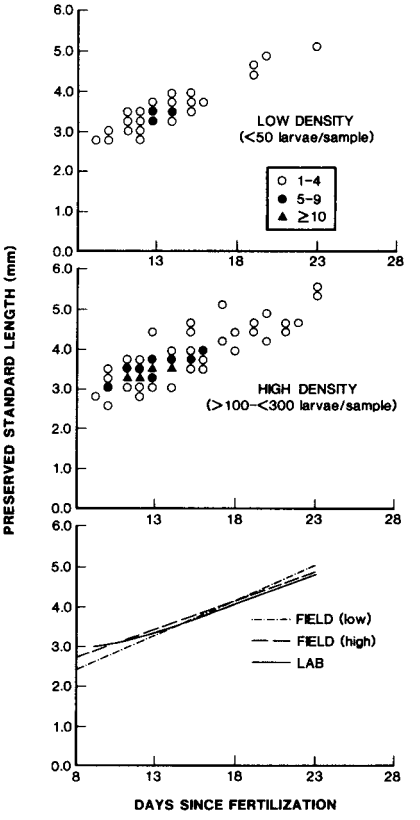

Fig. 6. *Trachurus symmetricus*. Growth of jack mackerel at low and high density stations compared to growth observed in the laboratory. Symbols in the insert show number of larvae examined

through the size categories was estimated directly from the growth curve (Fig. 7). The plot of production rate on age defines the production curve (Fig. 8) as very steep through the yolk-sac stage with survival rapidly improving as the larvae develop. Instantaneous daily mortality rate Z(t) was modeled as continuously declining with age using a Pareto-type function, $Z(t) = 1/P_t(dP_t/dt) = -\beta/t$ (Hewitt & Brewer 1983), where P_t = production at age t, measured from the moment of fertilization; β = larval mortality coefficient (Fig. 9).

Table 3. *Trachurus symmetricus.* Size-specific average catch and production rates of jack mackerel larvae. Duration of growth estimated from Fig. 7

Preserved size (mm)	Live size (mm)	Age since fertilization (d)	Retention rate	Duration of growth (d)	Catch[a] (larvae tow^{-1})	Production rate (larvae [tow d]$^{-1}$)
2.6	3.30	4.25	0.03	1.0	5.27	175.67
2.8	3.56	6.67	0.28	3.25	12.36	13.57
3.1[b]	3.94	11.63	0.28	7.25	26.86	13.25
3.4	4.32	16.37	1.00	2.25	7.32	3.25
3.6	4.57	18.63	1.00	2.25	4.55	2.02
3.8	4.83	20.87	1.00	2.25	1.64	0.73
4.0	5.08	23.12	1.00	2.25	0.68	0.30

[a] Larvae tow^{-1} = larvae (unit m^3)$^{-1}$ (m depth)$^{-1}$
[b] Size Groups 3.0 and 3.2 mm combined due to insufficient data

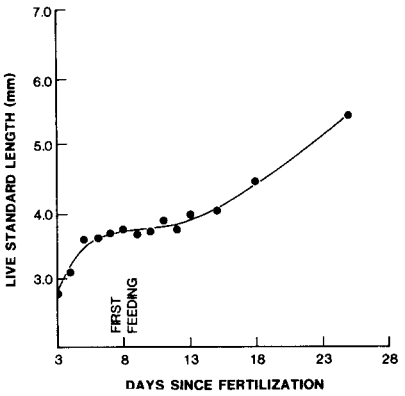

Fig. 7. *Trachurus symmetricus.* Growth of jack mackerel larvae as observed in the laboratory (Theilacker 1978, unpubl.) Curve fitted by eye

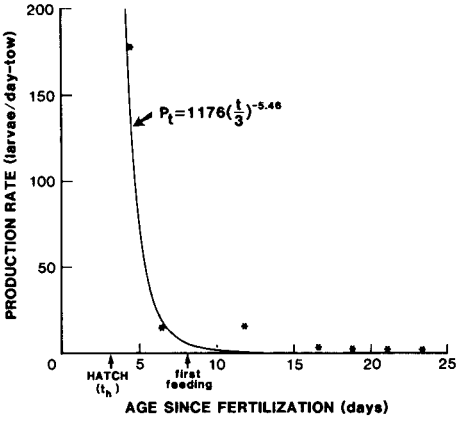

Fig. 8. *Trachurus symmetricus.* Production curve of jack mackerel larvae. Data from Table 3

By integrating Z(t) from the time of hatch (t_h), the production curve may be expressed as:

$$P_t = P_h\,(t/t_h)^{-\beta} \text{ for } t > t_h \qquad (2)$$

For t_h = 3 d, P_h = 1176 and β = 5.46.

After linearization by logarithmic transformation on both sides of the equation, the Pareto-type mortality curve fitted to jack mackerel data yields r^2 = 0.88. This high r^2 indicates that the Pareto-type mortality curve is an appropriate model to describe the mortality process of jack mackerel. Total instantaneous daily mortality rate and daily starvation mortality rates (percent dying per day) are compared in Fig. 9. The total mortality rate is the sum of starvation and predation mortality rates. In this study, the total mortality rate and the starvation mortality rate were estimated by 2 different procedures. Due to small sample size and the difference in estimation procedures, it is possible to observe an estimated starvation rate greater than the total mortality as shown for the larvae of 11 to 12 d old in Fig. 9. In

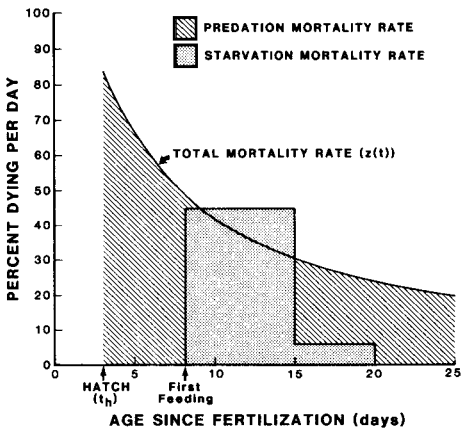

Fig. 9. *Trachurus symmetricus.* Total mortality rate of larval jack mackerel as a function of age since fertilization. Mortality due to predation + mortality due to starvation = total mortality (see text)

this case, one could conclude that the starvation constitutes the major portion of the total mortality. For yolk-sac larvae (prior to first feeding), starvation is not a source of mortality and the large losses (50 to 80 % d^{-1}) are due to predation. As larvae absorb yolk and begin to search for food, starvation becomes a significant source of mortality with losses at this life stage being about 45 % d^{-1}. As larvae develop further, their ability to capture food rapidly improves and predation again becomes the major source of mortality, although at a much reduced rate (20 % d^{-1}).

DISCUSSION

By comparing starvation mortality with total mortality, we have shown that starvation was a significant cause of death for first-feeding larval jack mackerel in a relatively oligotrophic portion of the spawning habitat. Theilacker (in press) estimates approximately 4-fold reduction in starvation rate of first-feeding larvae near islands and banks, where food is more abundant. However, we have no estimate of total mortality for jack mackerel larvae in the nearshore zone. It is unreasonable to expect starvation to account for all of the mortality at the time of first feeding (as indicated in Fig. 9). Because of the small sample size, there may be considerable errors associated with the estimates of total and starvation mortality. We are, however, confident about the qualitative content of our conclusions.

In terms of numbers removed, predation appeared to be the most important source of mortality. Predation was most severe during the yolk-sac phase. From the production curve (Fig. 8), we estimate that 99 % of hatching larvae were removed prior to yolk-absorption. Predation may be even more harsh during the early embryonic period prior to hatching. Estimated losses from fertilization to yolk-sac absorption range from 99.5 % to 99.9 %. Predation was the dominant source of mortality, but at a much reduced rate, once larvae had successfully fed and developed motility. Dramatic reduction in the vulnerability of actively feeding larval anchovy to predation has been reported by Lillelund & Lasker (1971), Theilacker & Lasker (1974) and Webb (1981). Hunter (1981, 1984) lists crustacea, chaetognaths, medusea, ctenophores and planktivorous fish as known predators of fish eggs and larvae. But sibling cannibalism may be the main source of mortality on clusters of eggs and yolk-sac larvae; Grave (1981) estimates that Atlantic mackerel *Scomber scombrus* larvae constitute 83 % of the diet of larger mackerel larvae.

The size-specific larval production (P_l) used in modelling the mortality curve was corrected by an extrusion factor (Table 3). The extrusion study indicated that 0.505 mm mesh net retained 3 % of larvae < 2.5 mm. If in fact the true retention is greater than 3 %, the mortality for yolk-sac larvae, which is due to predation, would be overestimated. However, subsequent partitioning of total mortality into starvation and predation would remain the same.

In our computation of total mortality rate, we assumed a steady state, i.e. that daily egg production was constant and that each cohort experienced the same daily mortality rate. Even though jack mackerel are serial spawners, egg production may vary due to adults moving into and out of the area, and age-specific daily mortalities may vary between cohorts. We realize that our data are insufficient to test these assumptions. However, we believe our approach of partitioning the total mortality of young fish into starvation and predation provides useful information for future studies. Despite sparse data, our results give a good indication of when each of the 2 causes of mortality dominate during the life stage. Future studies are recommended to verify our results and to test the assumptions that we made.

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LITERATURE CITED

Blaxter, J. H. S. (1971). Feeding and condition of Clyde herring larvae. Rapp. P-v. Réun. Cons. int. Explor. Mer 160: 128–136

Brothers, E. B., Mathews, C. P., Lasker, R. (1976). Daily growth increments in otoliths from larval and adult fishes. Fish. Bull. U. S. 74 (1): 1–8

Ellertsen, B., Mokness, E., Solemdal, P., Tilseth, S., Westgard, T., Oiestad, V. (1981). Growth and survival of cod larvae in an enclosure. Experiments and a mathematical model. Rapp. P.-v Réun Cons. int. Explor. Mer 178: 45–57

Grave, H. (1981). Food and feeding of mackerel larvae and early juveniles in the North Sea. Rapp. P-v. Réun. Cons. int. Explor. Mer 178: 454–459

Hay, D. E. (1981). Effects of capture and fixation on gut contents and body size of Pacific herring larvae. Rapp. P-v. Réun. Cons. int. Explor. Mer 178: 395–400

Hewitt, R. P. (1981). The value of pattern in the distribution of young fish. Rapp. P-v. Réun. Cons. int. Explor. Mer 178: 229–236

Hewitt, R. P and Brever, G. D. (1983). Nearshore production of young anchovy. Calif. Coop. Ocean. Fish. Invest. (CalCOFI) Rep XXIV: 235–245

Hickey, B. M. (1979). The California Current System – hypotheses and facts. Prog. Oceanogr. 8: 191–279

Hunter, J. R. (1981). Feeding ecology and predation of marine fish larvae. In: Lasker, R. (ed.) Marine fish larvae: morphology, ecology and relation to fisheries. Wash. Sea Grant, Univ. Wash. Press, Seattle, p. 33–77

Hunter, J. R. (1984). Inferences regarding predation on the early life stages of cod and other fishes. Flodevigen rapportser. 1, The propagation of cod, *Gadus morhua* L.: 533–562

Lillelund, K., Lasker, R. (1971). Laboratory studies on predation by marine copepods on fish larvae. Fish. Bull. U. S. 69: 655–667

Lo, N. C. H. (1983). Re-estimation of three parameters associated with anchovy egg and larval abundance: temperature dependent incubation time, yolk-sac growth rate and egg and larval retention in mesh nets. National Oceanic and Atmospheric Administration, La Jolla, NOAA-TM-NMFS-SWFC-31: 1–33

Methot, R. D. Jr., Kramer, D. (1979). Growth of northern anchovy, *Engraulis mordax,* larvae in the sea. Fish. Bull. U. S. 77: 413–423

O'Connell, C. P. (1980). Percent of starving northern anchovy larvae *(Engraulis mordax)* in the sea as estimated by histological methods. Fish. Bull. U. S. 78: 475–489

Shepherd, J. G., Cushing, D. H. (1980). A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. Cons. int. Explor. Mer 39: 160–67

Smith, P. E., Richardson, S. (1977). Standard techniques for pelagic fish egg and larva surveys. FAO, Fish. Tech. Pap. 175: 100

Theilacker, G. H. (1978). Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus,* larvae. Fish. Bull. U. S. 76: 403–414

Theilacker, G. H. (1980). Changes in body measurements of larval northern anchovy, *Engrualis mordax,* and other fishes due to handling and preservation. Fish. Bull. U. S. 78: 685–692

Theilacker, G. H. (1981). Effect of feeding history and egg size on the morphology of jack mackerel, *Trachurus symmetricus,* larvae. Rapp. P-v. Réun. Cons. int. Explor. Mer 178: 432–440

Theilacker, G. H. (in press.) Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus,* determined with histological and morphological methods. Fish. Bull. U. S. 84

Theilacker, G. H., Lasker, R. (1974). Laboratory studies of predation by euphausid shrimps on fish larvae. In: Blaxter, J. H. S., (ed.) The early life history of fish. Springer-Verlag, Berlin, p. 287–299

Webb, P. W. (1981). Responses of northern anchovy, *Engraulis mordax,* larvae to predation by a biting planktivore, *Amphiprion percula.* Fish. Bull. U. S. 79: 727–735

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