STARVATION-INDUCED MORTALITY OF YOUNG SEA-CAUGHT JACK MACKEREL, *TRACHURUS SYMMETRICUS*, DETERMINED WITH HISTOLOGICAL AND MORPHOLOGICAL METHODS

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ABSTRACT

Young jack mackerel, *Trachurus symmetricus*, living offshore are starving while those living nearshore are healthy. These results for sea-caught jack mackerel were determined by using histological and morphological criteria that reliably diagnosed the viability of laboratory-raised jack mackerel. Both the histological and morphological indices indicated that 350 km offshore about 70% of the first-feeding jack mackerel were starving. In contrast, 12% of the fish collected near islands and banks were starving. In both habitats, mortality rates decreased to zero for jack mackerel at 2 weeks of age. The accuracy of the techniques for prediction of the nutritional state of wild larvae is discussed and evaluated.

Jack mackerel, *Trachurus symmetricus*, hatch with yolk reserves that last for 5 d at 15°-15.5°C. After the yolk is absorbed, they must eat within 3 d or die of starvation. In addition, growth is retarded in larvae that have experienced only 1 d of starvation, and resumption of normal growth does not occur until 2-3 d after the starvation period (Theilacker 1978, 1981). Thus, in the laboratory, availability of food at the time of first feeding affects growth and survival of young jack mackerel. In the field, the relative importance of starvation as a source of mortality of jack mackerel is unknown. It was first suggested by Hjort (1914) (reviewed by May 1974) that the strength of the year class is determined early in life by the availability of food for larvae at the time of first feeding (the critical period hypothesis). But only recently (O'Connell 1980) has the presence of starving ocean-caught larvae been documented. In this study I give evidence that starvation may be a major cause of natural mortality of young jack mackerel at sea. I use two techniques, developed in the laboratory, to determine the incidence of starvation (Theilacker 1978). The potential use of these techniques to monitor sea samples for larval survival is discussed.

METHODS

Collection

In May 1980 a concentration of jack mackerel eggs and larvae was located 350 km off the coast of California (lat. 31°00'N and long. 120°30'W). A 400 mi^2 grid was established which contained 41 stations, 4 mi apart; it took 4 d to sample all stations (Fig. 1). At each station, a standard oblique bongo net tow (Smith and Richardson 1977) and a 1 m net sample were taken. The bongo samples will be used in another study to estimate growth and mortality of jack mackerel larvae (Hewitt et al. in press). The 1 m net (505 μm mesh) was used to sample larvae qualitatively from the upper 50 m of water. Ahlstrom (1959) found that 88% of the larval jack mackerel collected off California were in the upper 50 m, and all the jack mackerel collected by Devonald (1983) were above 42 m. A special collection procedure was used for the samples taken for histological and morphological analyses. Immediately after the net tow, the sample was preserved in Bouin's solution to avoid autolysis of larval tissues (elapsed time was usually 8 min) (Theilacker 1978). The collecting net was not washed down (a procedure required for quantitative samples), and the cod end containing the sample was placed directly into Bouin's solution. The preserved sample was removed from the cod end within an hour. After 2 d, Bouin's solution was replaced by 70% alcohol.

In addition to jack mackerel collections taken in the open ocean 350 km offshore, a few special tows (n = 24) for assessment of starvation were made during routine cruises in 1978, 1979, and 1980 near the Channel Islands (Anacapa, Santa Barbara, and San Clemente) and Tanner Bank.

Preparation of Fish

More than 2,000 jack mackerel were collected in

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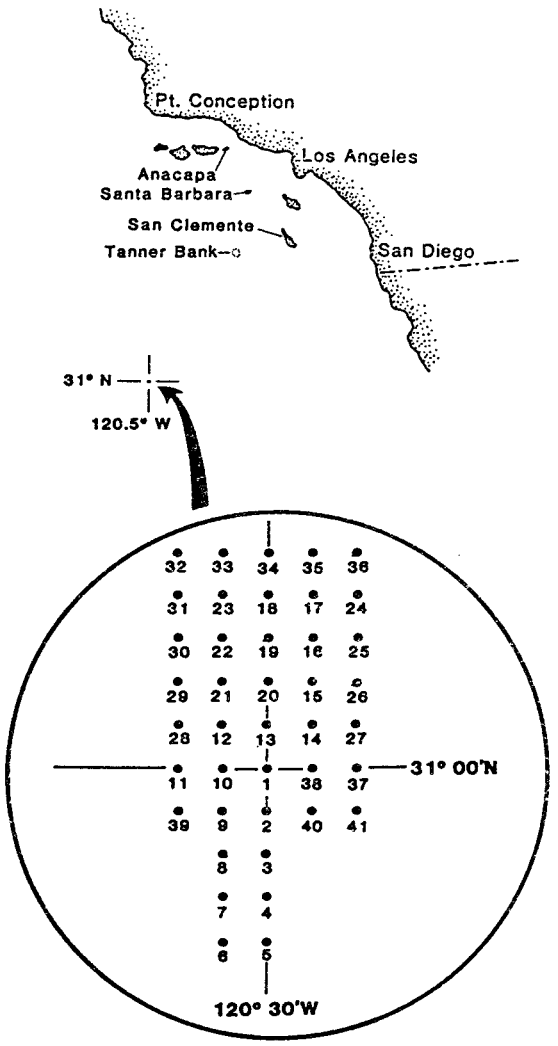


FIGURE 1.—Location of jack mackerel, *Trachurus symmetricus*, collections off the coast of California. Nearshore stations were at Anacapa, Santa Barbara, and San Clemente Islands and at Tanner Bank. The grid of open-ocean stations was 350 km offshore; stations were 4 mi apart.

samples taken offshore; from 0 to 262 fish were caught per sample (Table 1). Larvae sorted from the samples (n = 445) were counted and five body measurements taken: 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). After measurement, some larvae (n = 369) were prepared for histological examination. When samples contained fewer than 50 jack mackerel, most larvae were examined, but when samples contained more than 100 jack mackerel, about 25% of the fish were examined histologically. Jack mackerel size distribution in the offshore study area (determined for 400 fish taken from stations 16, 23, 34, and 35) was similar among stations and ranged between 2.6 and 4.7 mm SL. To ensure analysis of all ages in the larger samples, fish were taken equally from each of four length classes: <3.0; 3.0–<3.5; 3.5–<4.0; 4.0–<5.0 mm. These larvae were imbedded in paraffin, sectioned at 6 μm, and stained with Harris hematoxylin and eosinphloxine B (Theilacker 1978). In my analysis of histological data I combined the first two size classes because the size at first feeding was 3.2 mm.

The prevalence of starvation was assessed for 371 jack mackerel selected from 20 of the 32 positive stations (Table 1). In addition, I analyzed 41 jack mackerel taken in 14 hauls from the inshore stations near the Channel Islands and Tanner Bank.

Histological Analysis

The histological assessment of nutritional state is based on distinct cellular changes that occur in tissues when larval jack mackerel were deprived of food; these changes are well documented by Umeda and Ochiai (1975), O'Connell (1976), and Theilacker (1978). To determine the condition of individual ocean-caught jack mackerel, I used the histological criteria I developed in the laboratory by starving jack mackerel except I did not grade the pancreas. Grades were assigned to 11 histological characteristics of the brain, digestive tract, liver, and musculature (Theilacker 1978, 1981). Fish identities were unknown during this examination. I classified jack mackerel larvae into four categories (healthy, recovering, starving, and dying) according to their histological scores (the summation of the grades for each of the 11 histological characteristics).

Tissues of jack mackerel from the sea which had tissues similar in appearance to the tissues of feeding, laboratory-raised fish were classified as healthy; sea-caught jack mackerel which resembled laboratory fish that had fasted before eating were classified as recovering (these fish showed signs of feeding and digestion, but also showed signs of starvation); sea-caught larvae which were classified as starving resembled larvae that had been starved in the laboratory for 1-3 d (Theilacker 1978, 1981). I did not observe the dying category in laboratory-starved larvae; this category is described in Results.

Morphological Analysis

To detect starvation I used a set of morphological

TABLE 1.—Number of jack mackerel collected and the condition of those that were analyzed histologically.

Station No.	Number of fish					
	Sampled	Analyzed	Dying	Starving	Recovering	Healthy
Offshore						
1	0	0				
2	2	1	0	0	1	0
3	0	0				
4	2	0				
5	0	0				
6	0	0				
7	2	1	0	1	0	0
8	2	2	0	0	2	0
9	1	1	1	0	0	0
10	0	0				
11	3	3	3	0	0	0
12	0	0				
13	1	0				
14	1	0				
15	>200	0				
16	>200	0				
17	20	13	0	8	5	0
18	>125	0				
19	43	35	7	0	1	27
20	242	64	8	19	13	24
21	>250	0				
22	>175	0				
23	150	32	1	0	4	27
24	1	0				
25	23	0				
26	4	3	3	0	0	0
27	0	0				
28	262	58	3	36	14	5
29	11	11	1	4	4	2
30	250	57	4	13	18	22
31	32	9	7	1	0	1
32	109	25	0	2	20	3
33	31	23	1	3	10	9
34	38	0				
35	43	0				
36	31	24	3	4	1	16
37	7	5	2	1	2	0
38	2	2	1	0	0	1
39	0	0				
40	1	0				
41	0	0				
Total (Offshore)	>2,264	369	45	92	95	137
Around Islands						
Anacapa	12	12	0	1	0	11
Santa Barbara	3	3	0	0	2	1
San Clemente	17	17	0	1	5	11
Tanner Bank	9	9	0	1	0	8
Total (Nearshore)	41	41	0	3	7	31

characteristics that successfully diagnosed the extent of starvation in 85% of the laboratory-reared jack mackerel (Theilacker 1978). The technique is based on a stepwise discriminant analysis (SWDA) using 11 body part measurements. The analysis allowed me to distinguish between individuals belonging to fed and starved treatments, given a set of morphological measurements that describe the characteristics of the individuals in each feeding treatment. The 11 body part measurements used to distinguish between groups of fed and starved jack mackerel were 1) head length, 2) eye diameter, 3) body depth at the pectoral, 4) body depth at the anus, 5) head length/standard length, 6) eye diameter/standard length, 7) body depth at the pectoral/standard length, 8) body depth at the anus/standard length, 9) eye diameter/head length, 10) body depth at pectoral/head length, and 11) body depth at anus/head length. Standard length was used in the ratios but not as a unit to allow discrimination between feeding and starving fish of the same length.

Adjustment for Shrinkage

In order to use morphological measurements to diagnose starvation of jack mackerel, it is essential to adjust for shrinkage of body measurements. Both handling and preservation cause shrinkage of larval fishes, and the amount of shrinkage varies among body parts. Final fish size is dependent not only on initial size but also on the handling time (which is different for the laboratory and the field) and the type of preservative used (Blaxter 1971; Theilacker 1980a; Hay 1981). The shrinkage of laboratory specimens of jack mackerel preserved in Bouin's solution is known (Theilacker 1980a), but for field-collected specimens the shrinkage caused by the net tow and the subsequent effect of Bouin's preservative must be evaluated.

I conducted laboratory experiments to estimate the amount of shrinkage caused by handling (net retention) and by preservation. Live jack mackerel were pipetted individually (time = 0) onto a slide, and four body measurements were taken before placing the fish into a net container through which 15°C seawater circulated. Standard length, head length, eye diameter, and body depth at the anus were measured. Body depth at the pectoral fin was not measured because it was difficult to measure quickly on live jack mackerel. During net treatments, I usually remeasured each fish four more times at 5-7 min intervals, replacing the fish in the net between each set of measurements. After 25-30 min, the fish were preserved in either Bouin's fixative (used for histological analyses) or 5% buffered Formalin[2] (as per shipboard procedures; Smith and Richardson 1977). Remeasurements after preservation were taken in 3-4 wk.

Shrinkage of net-captured larval fish has been shown to decrease with increasing fish size. For example, shrinkage of northern anchovy decreased from 19% at 4 mm SL to 8% at 18 mm SL (Theilacker 1980a). The jack mackerel tested in this study ranged between 3.35 and 4.10 mm SL, and within this restricted length group shrinkage was proportional to size. Thus for the shrinkage analyses, all jack mackerel were combined into one group.

For the combined size group, length of the jack mackerel body (Fig. 2) and the head continued to shrink for the duration of the net treatment. Width of the body (Fig. 3) and the eye shrank initially, and then remained relatively constant during additional treatment. To account for positive correlation between body parts, a multivariate analysis (Table 2) was used to relate the ratio of net-treated size to live size (for each body part) with treatment time. Individual shrinkage was highly variable; for example, shrinkage of body depth varied between 0 and 23% for treatment times between 5 and 20 min (Fig. 3). However, since these were the best estimates of average shrinkage for body parts, the regressions (Table 2) were used to calculate the adjustment factors needed for this study. Factors for each body part

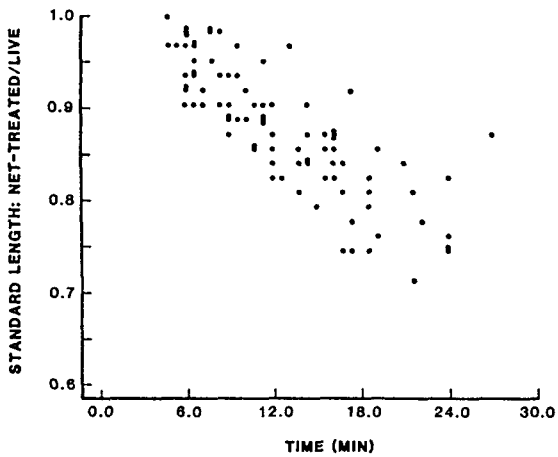


FIGURE 2.—Shrinkage of standard length, shown as the ratio of net-treated size to live size, of individual *Trachurus symmetricus* larvae as a function of net-treatment time; estimated parameters are in Table 4.

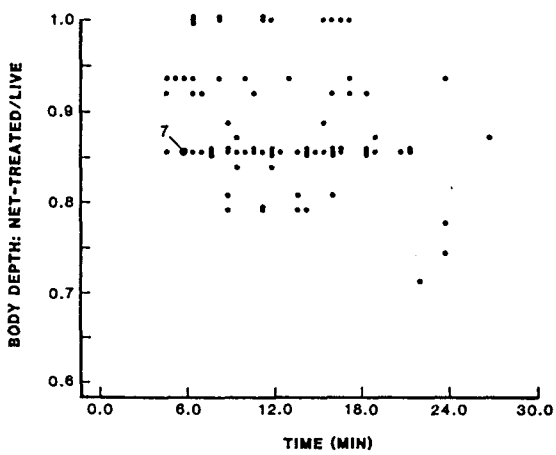


FIGURE 3.—Shrinkage of body depth, shown as the ratio of net-treated size to live size, of individual *Trachurus symmetricus* larvae as a function of net-treatment time; estimated parameters are in Table 4.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Shrinkage of jack mackerel larvae. Parameters estimated from multivariate linear equations relating the ratio of the net-treated size of a mackerel body part to its live size (y) with the net-treatment time (x).

Net-treated size/ live size[1]	a	(SE)	b	(SE)	P^2	r^2
Standard length (SL)	1.0109	(0.0117)	−0.0105	(0.0008)	<0.001	0.66
Head length (HL)	0.9281	(0.0157)	−0.0038	(0.0011)	0.001	0.12
Eye diameter (ED)	0.9360	(0.0168)	−0.0027	(0.0012)	0.031	0.06
Body depth (BD-2)	0.8980	(0.0177)	−0.0014	(0.0013)	0.280	0.02

[1]n = 89.
[2]Probability that slopes differ from zero.

were calculated by 1) combining the shrinkage ratio at 8 min (average elapsed time for field collections, see Methods) with 2) the average shrinkage in Bouin's preservative after the net treatment, and 3) comparing the combined shrinkage with results from shrinkage determined in the laboratory study (Theilacker 1980a; Table 3). Also given in Table 3 are average shrinkage ratios calculated for specified time intervals.

Adjustment factors for standard length, head length, and eye diameter (Table 3) support the view that shrinkage of field-collected fishes is greater than shrinkage of fishes preserved in the laboratory. Shrinkage of BD-2 was an exception to this pattern, however, as less shrinkage occurred under simulated field conditions (20-23%) than in the laboratory (25%). I (Theilacker 1980a) reported a similar paradox for northern anchovy where simulated-field net treatments caused 8% shrinkage of BD-2 as compared with 10% shrinkage for standard laboratory preservation. Jack mackerel shrinkage was greater in Bouin's solution than in Formalin, results which are consistent with studies on northern anchovy. Also, as with northern anchovy, Formalin preservation caused a slight increase in the size of the jack mackerel eye (Table 3).

I adjusted the body measurements of the ocean-caught jack mackerel with the shrinkage factors (ratio R_8, Table 3). Use of these adjustments should equate the morphology of preserved, ocean-caught jack mackerel (this study) with the morphology of preserved, laboratory-raised jack mackerel that were used to develop the morphological SWDA (see Methods: Morphological Analysis). It was necessary to reestimate the SWDA function for this study, although nearly the same analysis was made previously (Theilacker 1978). A new estimate was required because pectoral body depth was not included in the shrinkage measurements in this study; hence, an SWDA function that excluded this measurement was needed. Elimination of pectoral body depth from the analysis reduced the level of predictability from 35% to 78%. This new function was used here to classify the condition of ocean-caught jack mackerel

TABLE 3.—Shrinkage of jack mackerel larvae[1]. Treatment ratio (R) is treated size divided by previous size (1.00 = no shrinkage).

Treatment ratio	R	n	Mean time	Ratios: Standard length	Head length	Eye diameter	Body depth
8 min net/live size	[2]R_1	89	8	0.93	0.90	0.91	0.89
5-10 min net/live size	R_2	36	7.3	0.94	0.90	0.92	0.89
11-15 min net/live size	R_3	22	12.6	0.87	0.88	0.88	0.86
16-28 min net/live size	R_4	27	19.4	0.81	0.86	0.89	0.88
Bouin's fixative/ net-treated size	[3]R_5	15	—	0.91	0.84	0.93	0.91
Formalin fixative/ net-treated size	[3]R_6	13	—	0.96	0.93	1.08	0.91
Laboratory-preserved in Bouin's fixative live size	[4]R_7	45	—	0.92	0.82	0.90	0.75
Calibration factor = $R_7/R_1 \times R_5$	[5]R_8	—	—	1.09	1.08	1.06	0.93

[1]Range in standard length 3.35-4.10 mm.
[2]Calculated from regression (Table 2); ocean-caught fish preserved within 8 min; see text.
[3]Shrinkage in fixative after net treatment.
[4]Data from Theilacker (1980a).
[5]Adjustment factor to equate measurements of field-collected mackerel (this study) with measurements of laboratory-raised mackerel (Theilacker 1978).

after the size of their body parts was adjusted for shrinkage.

RESULTS

Habitat Conditions

A larval-density gradient was apparent in the open ocean study area. High densities of jack mackerel larvae (100-<300/sample) were found in the central stations and in stations near the western boundary of the grid; lower densities (20-50) were found to the north and east, and densities of larvae approached zero at the southern stations that were occupied at the beginning and again at the end of the 4-d observation period (Fig. 4). Larval densities in the south did not change during this period.

The study area was chosen because temperature, viewed on satellite thermal image of the sea surface, corresponded to the temperature range (15°-16°C) associated with jack mackerel spawning (Farris 1961). Surface temperature in the study area increased from 15.2°C in the north to 16.8°C at the southern stations, with the majority of jack mackerel found in water temperatures of 16.1°-16.6°C. Water temperatures inshore of the grid were about 14°C.

A temperature-salinity curve obtained at station 19 (Fig. 1) agreed well with the curves obtained from inshore stations with the exception of the warm-water portion of the curve, which appeared to be a thin, warm lens of open ocean water intruding coastward over deeper coastal water.

Histological Assessment of Fish Condition

I used the tissue characteristics of laboratory fish (raised at 15.0°-15.5°C) of known feeding history as the criteria to determine the nutritional condition of the sea-caught jack mackerel. Photomicrographs of the diagnostic tissue characteristics were documented by Theilacker (1978). Many of these characteristics are shown also for wild fish (Fig. 5, see also Figures 6-14). In addition, the wild fish exhibited four tissue conditions that were not observed in the laboratory: lesions in the brain; luminal vacuoles in the midgut; total degeneration of the midgut mucosal cells; and a wavy configuration of the muscle fibers. Each of these conditions will be considered in the following section that describes the tissues of ocean-caught fish. My emphasis will be on those tissue characteristics that diagnose starvation in young jack mackerel.

Brain

The brain of an ocean-caught jack mackerel was considered normal when the neurons were distinct, round, and closely spaced. In these fish, brain cell division was common, but it was not graded. One percent of the jack mackerel examined had brain lesions of the type (Fig. 6) induced by ultraviolet light in larval northern anchovy, *Engraulis mordax*, and Pacific mackerel, *Scomber japonicus* (Hunter et al. 1979). The grading system classified these jack mackerel (n = 3) into the healthy category. In a

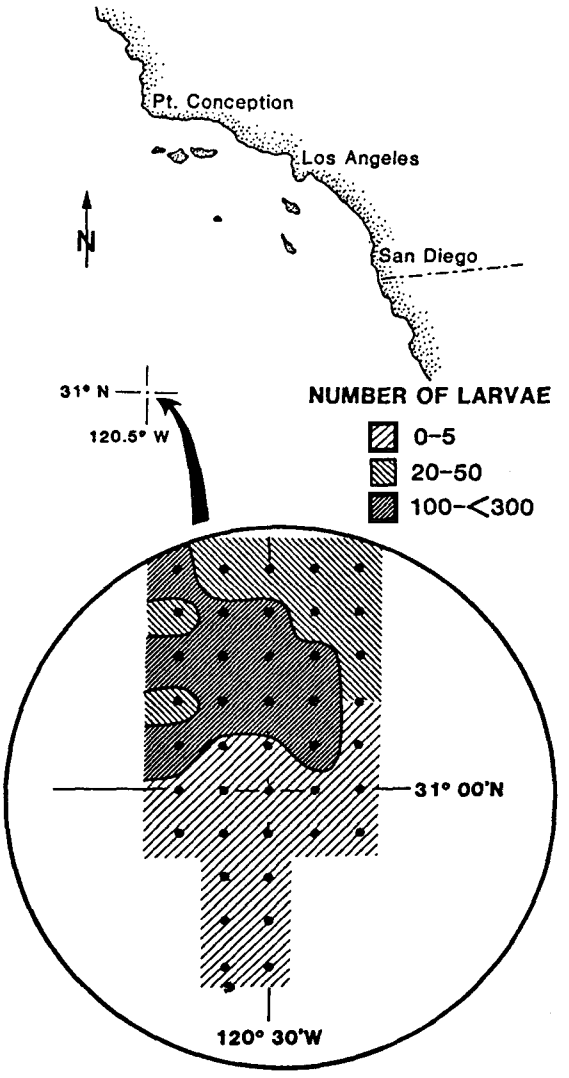


FIGURE 4.—*Trachurus symmetricus* larval density gradient shown as number of larvae collected per sample (not quantitative). Station grid located 350 km off the coast of California.

single specimen, lesions were present not only in the brain but throughout the spinal cord (Fig. 7) as well. In addition, the gut and associated glands had deteriorated to the extent that this fish was considered starving.

An abnormal central nervous system of a jack mackerel larva consisted of vacuolar degeneration and shrinkage of neurons. The degenerating neurons exhibited increased staining (Fig. 8).

Digestive Track and Associated Glands

The midgut mucosa of young jack mackerel is composed of a single layer of columnar epithelial cells. Older fish (3.7-4.0 mm) showed increased mitotic activity in the basal layer. Microvilli bordered the midgut lumen only in fish that appeared healthy. Mucosal cells were closely united in the fish considered to be normal (Figs. 9, 10). Basal separations between these cells were common, not only in fish that appeared to be starving but also in fish that showed signs of feeding and digestion (Fig. 11). O'Connell (1980) also reported that sea-caught northern anchovy exhibited basal separations between mucosal cells while the apical portions were well joined.

All wild jack mackerel categorized as recovering had basal separations between midgut mucosal cells. Laboratory fish that were artificially starved for 1-2 d before feeding showed these separations for several days after feeding resumed. In the laboratory, larvae did not grow while their tissues were regenerating (Theilacker 1981).

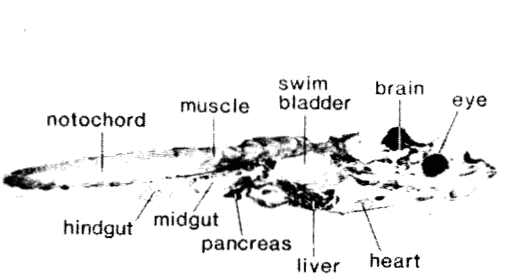
Many sea-caught jack mackerel of all ages had intracytoplasmic vacuoles in the midgut epithelium. Basal and membrane lined, these vacuoles resembled the vacuolar condition found in some recovering, laboratory fish (Theilacker 1981). In addition, many sea-caught larvae had smaller, luminal vacuoles that were found in the laboratory fish (Fig. 12). These luminal vacuoles may indicate a degenerative condition. In higher vertebrates a metabolic imbalance can cause vacuolar degeneration. Vacuolation appears first as numerous small, clear vacuoles dispersed throughout the cytoplasm. As the condition becomes more severe, these minute vacuoles coalesce to form large (sometimes single) clear spaces that displace the nucleus (Anderson 1971). On the other hand, the numerous luminal vacuoles can secrete mucous into the lumen or store fat. Use of a routine mucicarmine staining was negative for the presence of mucous cells. Unfortunately, the presence of fat in the vacuoles could not be tested because fat is removed during tissue preparation by clearing agents. Neither vacuolar condition was graded.

Another unusual condition of the midgut occurred in many of the smaller wild jack mackerel. In these fish, the margin of the lumen had lost its integrity, microvilli were absent, and the sloughing of the mucosal cells into the lumen (a condition common in starved laboratory jack mackerel) appeared to have progressed until the lumen contained masses of undefinable, cellular material (Fig. 13). O'Connell (1980) described a comparable condition which he found in the midgut of a single, northern anchovy specimen, the smallest examined. All jack mackerel exhibiting this condition were smaller than the size attained at first feeding, indicating shrinkage had occurred. The hindgut also contained necrotic debris, and other diagnostic tissues were in poor condition. These jack mackerel were classified as dying.

Hindgut mucosal cells of wild jack mackerel typically showed eosin-staining inclusions that are reported to be sites of intracellular digestion (Iwai 1968, 1969; Iwai and Tanaka 1968; Watanabe 1981). Inclusions in the wild jack mackerel varied in intensity; in healthy specimens the intensity appeared to be related to time of day (feeding period), increasing during daylight hours and decreasing during the night. Although the presence and intensity of hindgut inclusions were noted, they were not graded. Inclusions were not present in larval teleosts deprived of food in the laboratory (Theilacker 1978; Umeda and Ochiai 1975; O'Connell 1976). However, in many wild jack mackerel showing signs of starvation the presence of pale inclusions indicated that the fish had eaten at some time in the past.

The key diagnostic characteristics of the pancreas were obscure in ocean-caught jack mackerel because of the intensity of staining. In laboratory fish, the pancreas was very sensitive to food deprivation. For example, a breakdown in the symmetry of the acinar secretory unit was detectable after 1 d of food deprivation (Theilacker 1978). In the wild fish, the intensity of the staining of the pancreas was difficult to control (see Fig. 12), and I was not able to obtain consistent results, hence the condition of the pancreas was not evaluated.

The jack mackerel liver was considered normal when hepatocytes had clear, distinct nuclei (Fig. 9). The appearance of the cytoplasm was quite variable; in some larvae very few intracellular spaces existed in the cytoplasm of the hepatocytes whereas in others extensive intracellular spaces existed. Presumably these spaces are areas where glycogen and fat are stored within the cell. This presumed incorporation of stores was most marked in healthy



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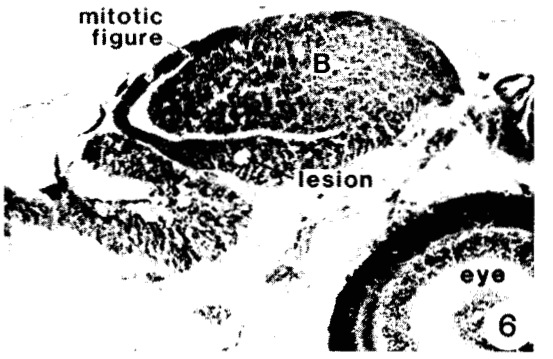

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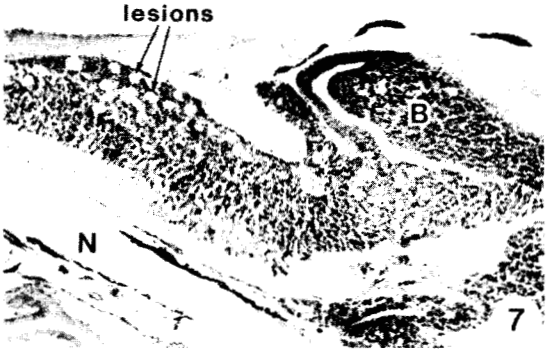

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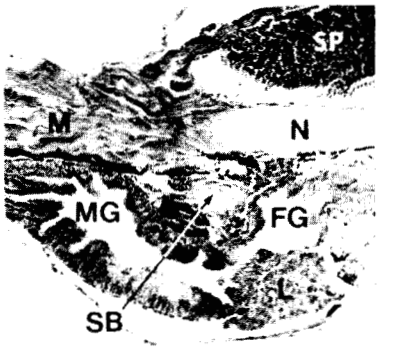

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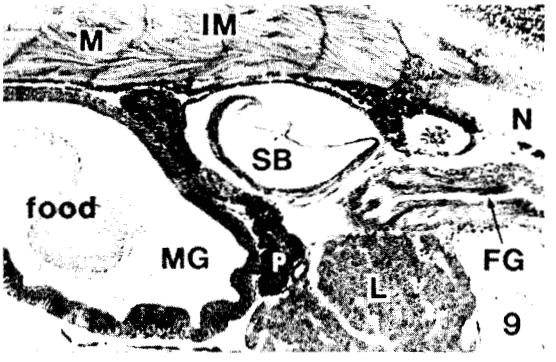

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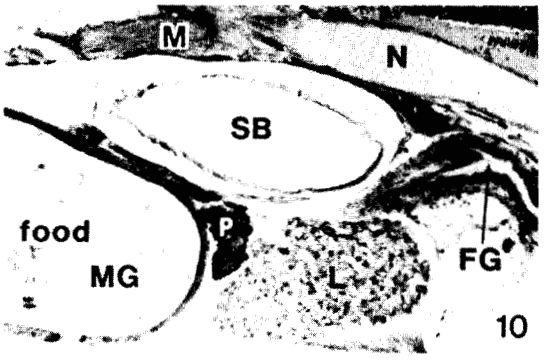

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FIGURE 5.—*Trachurus symmetricus* larva, 3.75 mm SL. All 11 histological criteria graded as healthy. Bar = 281 μm.

FIGURE 6.—Head of *Trachurus symmetricus* larva graded healthy. Mitotic activity and the location of brain lesions are indicated. Bar = 47 μm. B = brain.

FIGURE 7.—*Trachurus symmetricus* larva graded as starving. Lesions present throughout brain and spinal cord. Bar = 47 μm. B = brain, N = notochord.

FIGURE 8.—Pectoral area of a dying *Trachurus symmetricus* larva showing darkly stained primitive nerve cells, wavy muscle fibers, necrotic and atrophied liver, and loss of integrity of midgut mucosal cells. Bar = 47 μm. FG = foregut, L = liver, m = muscle, MG = midgut, N = notochord, SB = swim bladder, SP = spinal cord.

FIGURE 9.—Pectoral area of healthy *Trachurus symmetricus* larva collected offshore showing parallel muscle fibers and abundant intermuscular tissue, distinct nuclei in liver and midgut, and good cellular integrity. Note deflating swim bladder. Bar = 47 μm. FG = foregut, IM = intermuscular tissue, L = liver, M = muscle, MG = midgut, N = notochord, P = pancreas, SB = swim bladder.

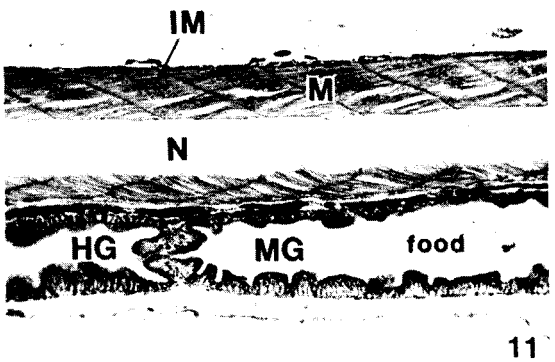
FIGURE 10.—Pectoral area of healthy *Trachurus symmetricus* larva collected near San Clemente Island showing abundant glycogen reserves in the liver. Bar = 47 μm. FG = foregut, L = liver, M = muscle, MG = midgut, N = notochord, P = pancreas, SB = swim bladder.

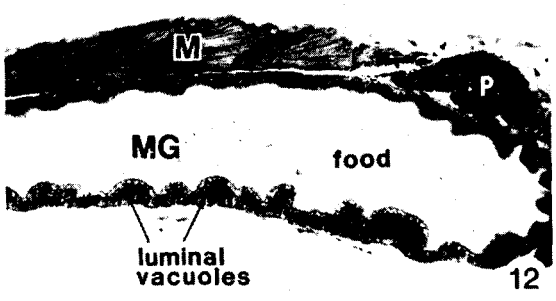
jack mackerel collected near islands and banks (Fig. 10) whereas healthy jack mackerel collected offshore showed moderate to little storage (Fig. 9).

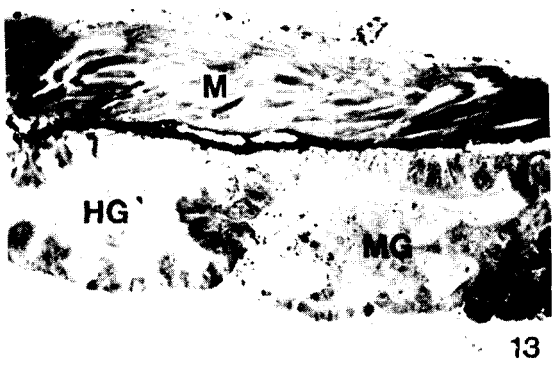
At the other end of the grading scale, the shrunken livers of jack mackerel considered to be starving contained darkly stained hepatocytes composed of evenly stained cytoplasm with indistinct, irregular nuclei.

Musculature

Healthy muscle tissue in jack mackerel had the following characteristics: few spaces between the muscle fibers; distinct and parallel, striated myofibrils; and abundant, basophilic and nucleated intramuscular tissue (Fig. 9). Nourishment was considered inadequate in fish exhibiting separated (Figs. 11, 14) and hyaline muscle fibers (Fig. 13) and a reduction (Figs. 11, 14) or absence (Fig. 13) of intramuscular tissue. In some sea-caught jack mackerel, muscle fibers were wavy (Fig. 8). Presence of wavy muscle fibers in wild fish was considered abnormal because it was always associated with the poor condition in the other diagnostic tissues, but this characteristic was not used in classification. In starved laboratory fish, nonparallel fibers were reported (Theilacker 1978, 1981), but the wavy pattern was unusual. There were fish with intermediate spaces between muscle fibers that, according to the scores of the other diagnostic tissues, appeared healthy. The







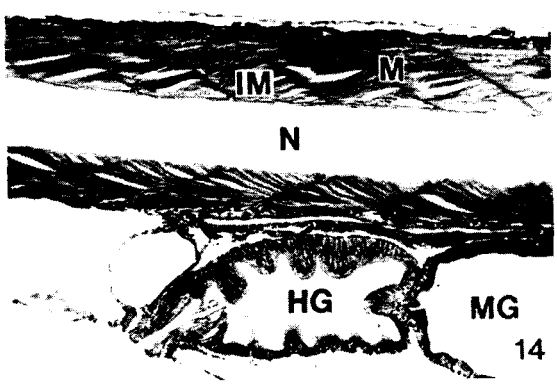


FIGURE 11.—*Trachurus symmetricus* larva graded recovering. Prominent separations between midgut and hindgut epithelial cells, slight muscle fiber separation and intermediate intermuscular tissue containing distinct nuclei. Bar = 47 μm. HG = hindgut, IM = intermuscular tissue, M = muscle, MG = midgut, N = notochord.

FIGURE 12.—Healthy *Trachurus symmetricus* larva showing luminal vacuoles in the midgut. This histological characteristic was not graded. Bar = 47 μm. M = muscle, MG = midgut.

FIGURE 13.—*Trachurus symmetricus* larva graded dying. No intermuscular tissue; hyaline muscle fibers; total degeneration of midgut mucosa. Bar = 34 μm. HG = hindgut, M = muscle, MG = midgut.

FIGURE 14.—Recovering *Trachurus symmetricus* larva showing slight muscle fiber separation and slight reduction of intermuscular tissue. Bar = 47 μm. HG = hindgut, IM = intermuscular tissue, M = muscle, MG = midgut, N = notochord.

grading system usually classified these fish into the recovering category.

General Histological Observations

In jack mackerel that were considered healthy, swim bladder inflation was first noted at 3.4 mm. Swim bladders were inflated in larvae taken at night whereas they were deflated in those taken in the day. The swim bladders of 72% of the fish were deflated by 0700 (n = 81) except for fish scored in the starving category where inflation was common at any time of day, which was possibly a symptom of starvation or an additional energy-sparing function of the swim bladder (Hunter and Sanchez 1976).

Theilacker (1978) pointed out that the gallbladder was always enlarged in jack mackerel that were deprived of food in the laboratory, and this condition occurred in sea samples of starved larvae taken in the day. On the other hand, gallbladder enlargement was also found in the healthy fish as well as starved fish collected at night. According to Love (1970), the gallbladder discharges its contents when stimulated by food. Jack mackerel do not eat at night, so the gallbladder of healthy fish may remain distended during the night. Thus enlargement of the gallbladder was not used to diagnose starvation. Theilacker's (1978) samples of fed and unfed fish were taken only during the day, when feeding occurs.

Mitotic figures in the brain of jack mackerel occurred in fish collected at all times of day and night. On the other hand, mitosis of mucosal cells in the midgut was restricted to the night. It seems that mucosal cells of northern anchovy also divide late at night, when the digestive tracts are empty (O'Connell 1981).

Evidence for Starvation in the Sea

Results of the histological analysis showed that starvation was a major source of mortality for the smallest jack mackerel larvae (<3.5 mm) as 59% appeared to be dying of starvation, 23% were eating but had fasted previously, and only 19% were classed as healthy. The incidence of starving larvae decreased to 16% in the 3.5-4.0 mm size class and was 3% in the older larvae (Table 4). The numbers of fish used for the histological assessment of starvation was adequate for the smallest (<3.5 mm SL) larval size class (coefficient of variation ranged between 0.09 and 0.15 for the four condition categories), but larger samples would be needed to give a reliable estimate of the fraction starving for the older larvae (>3.5 mm SL) because of the low incidence of starvation.

Despite the fact that jack mackerel abundance decreased from west to east and north to south (Fig. 4), I found no consistent differences in the incidence of starvation between fish taken from areas of high larval density and those taken from areas of low larval density (Fig. 15). Therefore, to estimate mortality due to starvation, I combined all samples collected in the offshore area. To estimate mortality rates on a daily basis, the observed number of fish belong-

TABLE 4.—Histological condition of jack mackerel collected 350 km off the coast of California.

	Dying	Starving	Recovering	Healthy	Total	Daily percent Starving[1]	Daily percent Dying[2]
Yolk sac	—	—	—	15	15	0	0
<3.5 mm							
Number	43	74	45	38	200		
Duration (d)	1	3	2	6			
Number/d	43	24.7	22.5	6.3	96.5	70	45
3.5-<4.0 mm							
Number	2	16	38	54	110		
Duration (d)	1	3	2	3.3			
Number/d	2	5.3	19	16.4	42.7	17	5
4.0-<4.5 mm							
Number	0	2	12	45	59		
Duration (d)	—	3	2	3.3			
Number/d	—	0.7	6	13.6	20.3	3	0

[1] $\frac{\text{Number dying/d + starving/d}}{\text{Total}}$

[2] $\frac{\text{Number dying/d}}{\text{Total}}$

ing to each size and health category was divided by the duration—the number of days jack mackerel are expected to remain in each category (Table 4). Durations spanned 1 to 6 d depending on age and condition. For healthy fish, duration is simply the size-class interval divided by the growth rate. Healthy fish belonging to the smallest size group (<3.5 mm) grow at 0.05 mm/d (Theilacker 1978) and begin to eat at 3.2 mm SL. Thus duration for this size interval (0.3 mm) was 6 d. Growth rate for older fish was 0.15 mm/d; the rate was determined for this study by counting daily growth increments in otoliths (Hewitt et al. in press). The duration that a larva remains in one of the starvation states is a function of the persistence of the histological criteria. Young jack mackerel deprived of food in the laboratory show signs of starvation for 3 d before dying, and larvae recovering from a period of starvation show these signs for 2 d (Theilacker 1978, 1981). Older fish may be more resistant to starvation, but as I had no information for older jack mackerel, I used the durations for younger larvae.

For the smallest jack mackerel living 350 km offshore, 45% were dying of starvation per day. Daily mortality dropped rapidly to 5% to zero for older larvae (Table 4). Increasing the durations for the older larvae in the starving and recovering categories (Table 4) decreases this estimate of daily mortality.

Results of the histological examination of jack mackerel collected near islands and banks allow a preliminary assessment of the effects of different habitats on starvation (Table 5; Fig. 16). A large difference existed in the daily larval mortality caused by starvation between the open ocean and island and bank habitats. In areas near the islands, none of the first-feeding larvae were dying of starvation whereas 45% from the open ocean were dying of starvation. In addition, healthy larvae taken near islands were apparently more fit than healthy larvae captured in the open ocean, as the larvae from the island habitats had abundant quantities of glycogen in the liver (Fig. 10), whereas livers of larvae from the open ocean rarely contained glycogen stores (Fig. 9). This indicates that food must have been much more abundant in the island habitat because not only were fewer fish starving but the healthy fish were able to store glycogen. The healthy fish from the open sea may have been just able to meet their daily metabolic requirements.

The morphological data gave essentially the same results as did the histological method. On the basis of morphometric evidence, 70% of the first-feeding jack mackerel (<3.5 mm SL) were starving and the number decreased to zero for older jack mackerel (Table 6). Although the results were similar, the morphological categories used to classify the fish were different from the histological ones. In particular, there was no morphological category for dying fish. For the morphometric SWDA, larvae were grouped by feeding treatment (Table 6), and the histological categories (Table 4) were based on the dominant larval tissue conditions determined to characterize a nutritional state. Thus the morphometric SWDA cannot be used to estimate the number of larvae dying per day due to starvation.

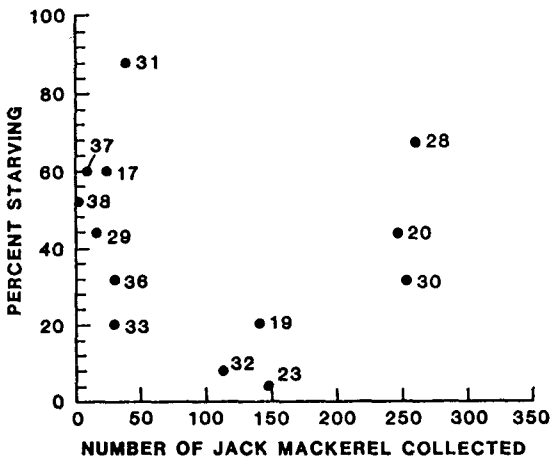


FIGURE 15.—Percentage of starving *Trachurus symmetricus* larvae (number starving/number analyzed) related to the number of larvae collected at each offshore station; station number is indicated.

DISCUSSION

Larval Starvation and Recruitment

Both histological and morphological criteria indicate that starvation is probably a major source of larval jack mackerel mortality at the time of first-feeding but that the survivors of this 6-d period are much less vulnerable to starvation. Prey (mainly young stages of copepods) are more abundant at the nearshore islands and banks off the coast of California than offshore (Beers and Stewart 1967, 1970; Arthur 1976, 1977; Devonald 1983), and survival of first-feeding jack mackerel was higher in the nearshore habitats than offshore. Thus selection of spawning sites may have a great effect on survival. Eggs and larvae of jack mackerel are very widely distributed; they occur from Baja California to British Columbia and up to 400 mi off the coast of

TABLE 5.—Histological condition of jack mackerel collected near islands and banks off the coast of California.

	Dying	Starving	Recovering	Healthy	Total	Daily percent Starving[1]	Daily percent Dying[2]
Yolk sac	—	—	—	—	0		
<3.5 mm							
Number	0	2	6	12	20		
Duration (d)	1	3	2	6			
Number/d	—	0.7	3	2	5.7	12	0
3.5-<4.0 mm							
Number	0	1	1	12	14		
Duration (d)	1	3	2	3.3			
Number/d	—	0.3	0.5	3.6	4.4	7	0
4.0-<4.5 mm							
Number	0	0	0	7	7		
Duration (d)	1	3	2	3.3			
Number/d	—	—	—	2	2	0	0

[1] $\frac{\text{Number dying/d + starving/d}}{\text{Total}}$

[2] $\frac{\text{Number dying/d}}{\text{Total}}$

TABLE 6.—Predicted condition of field-collected jack mackerel larvae determined with the morphometric technique.

	Starved 3 days	Starved 1 & 2 days	Fed	Total	Daily percent Starving[1]
<3.5 mm					
Number	48	66	150	264	
Duration (d)	[2]2	2	6		
Number/d	24	33	25	82	70
3.5-<4.0 mm					
Number	0	1	121	122	
Duration (d)	2	2	3.3		
Number/d	—	0.5	36.7	37.2	1.3
4.0-<4.5 mm					
Number	0	0	59	59	
Duration (d)	2	2	3.3		
Number/d	—	—	17.9	17.9	0

[1] $\frac{\text{Number starved/d}}{\text{Total}}$

[2] Unfed jack mackerel larvae die in 4 d.

California and up to 1,000 mi off Oregon and Washington (reviewed by MacCall and Stauffer 1983). In addition, jack mackerel have a protracted spawning season which extends from March through September. The bank and island habitat must be a very small fraction of the total spawning habitat; thus despite the higher survival in inshore areas, the offshore zone may be the most important. In addition, better feeding conditions around islands may be offset by a greater abundance of predators. Whether the large concentration of starving larval jack mackerel found offshore was an isolated case or a general condition in offshore areas is unknown.

Given that relative recruitment strength of jack mackerel year classes varies greatly and is rarely "average" (Fig. 17; MacCall and Stauffer 1983), the daily mortality rate of about 45% found in this study is not unrealistic. Considering the relatively long lifetime (i.e., 30+ yr) and high fecundity of jack mackerel, one can deduce that the overall mortality may be very high. This study certainly indicates that starvation at the onset of feeding may be an important factor influencing recruitment variation in jack mackerel.

O'Connell's (1980) study of northern anchovy is the only other study in which starvation in the sea has

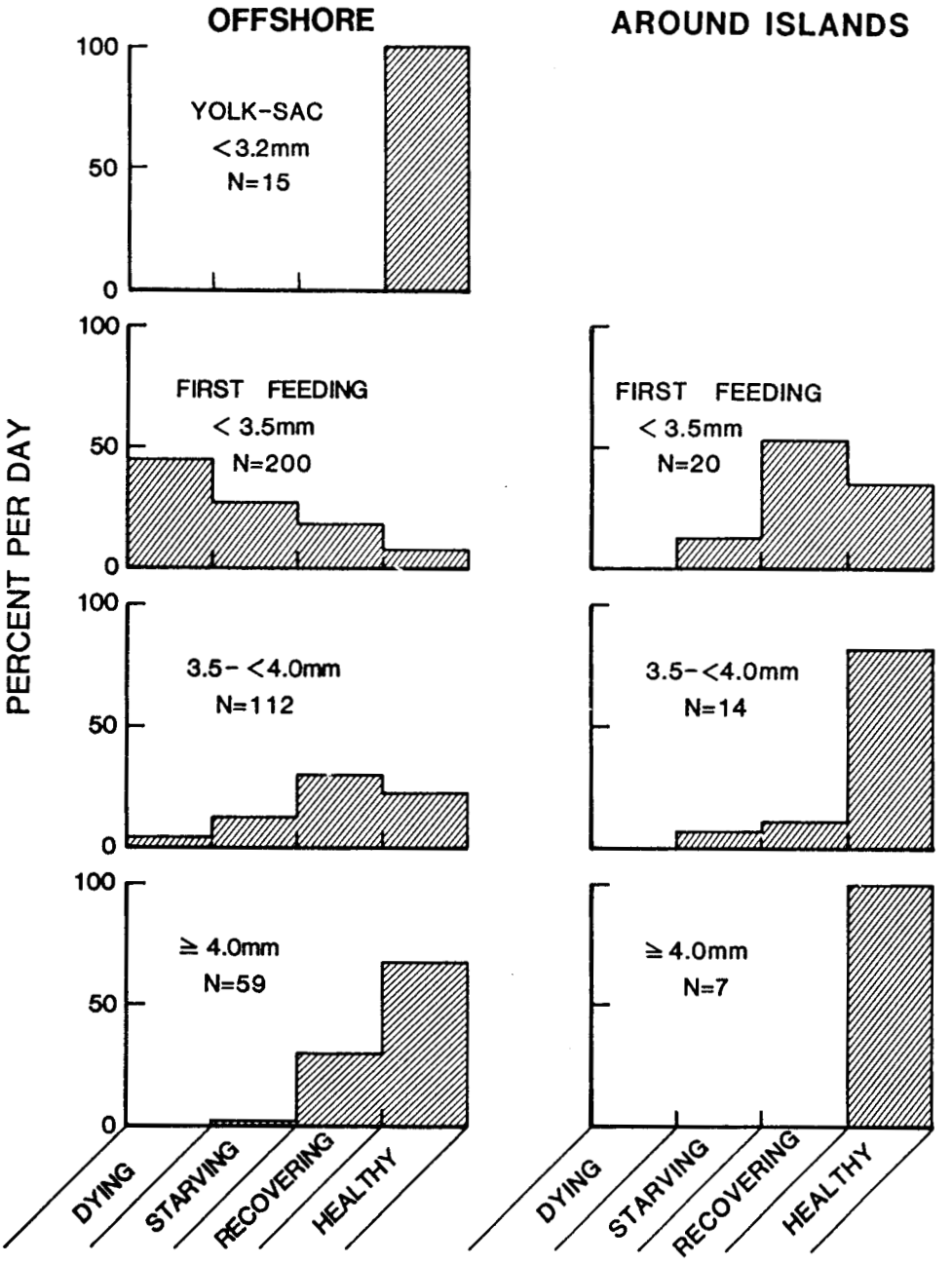


FIGURE 16.—Comparison of the nutritional condition of young *Trachurus symmetricus* collected from offshore and nearshore habitats. Daily percents taken from Tables 2 and 3.

been assessed using histological criteria. O'Connell examined 318 northern anchovy larvae from 64 stations that extended over a large area, 20-350 km off the coast of California. To compare the mortality of northern anchovy with the daily rates I found for jack mackerel, I calculated size-specific daily mortality of northern anchovy by using 1) O'Connell's (1980) histological evaluation, 2) information on time to irreversible starvation to determine durations (Lasker et al. 1970; Hunter 1981; Theilacker and Dorsey 1981), 3) information on shrinkage of ocean-caught northern anchovy to determine size at first

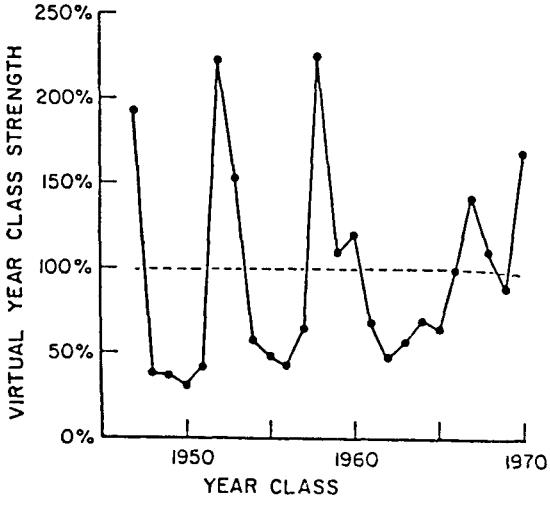


FIGURE 17.—Relative recruitment strengths of jack mackerel year classes in southern California. Virtual year-class strength is measured by the sum of percentage contributions to seasonal landings over the lifetime of the year class. The dashed line indicates average strength (from MacCall and Stauffer 1983; Fig. 4).

feeding (Theilacker 1980a), and 4) a growth rate of 0.37 mm/d for healthy sea-caught northern anchovy (Methot and Kramer 1979). Although the number of first-feeding larvae was low in O'Connell's data (n = 23), I calculated a starvation-induced mortality rate of between 35 and 46%/d. Thus my calculations indicate that substantial numbers of northern anchovy larvae as well as jack mackerel larvae are dying at the time of first feeding. This loss rate for northern anchovy is similar to estimated total mortality rate at this stage, 39%/d (Lo in press; 1978 data), which suggests that starvation is the major source of mortality at first feeding. This conclusion for northern anchovy could not be drawn at the time that O'Connell did his work because the data on net shrinkage were not known. The average rates estimated by O'Connell were much lower because he combined larval size classes.

Attempts to assess larval starvation in the sea using morphological criteria are more common (Shelbourne 1957; Honjo et al. 1959; Nakai et al. 1969; reviewed by May 1974; Ehrlich et al. 1976), but they have seldom been successful, probably because of the biases introduced by failure to correct adequately for shrinkage (see next section). Recently Devonald (1983) used a morphometric index with shrinkage adjustments to assess jack mackerel feeding regimes off California. She found good correspondence between jack mackerel condition and prey availability and concluded that feeding conditions were better near islands than in the area between islands. Several of her samples and my samples were taken concurrently (San Clemente and Tanner Bank; Table 1), and I found that 92% of the jack mackerel from the island habitat were healthy. Thus, my results obtained using histological criteria confirm Devonald's conclusion.

Other techniques used in the past to assess food availability include RNA/DNA (Buckley 1980), food in gut (Rojas de Mendiola 1974; Ciechomski and Weiss 1974; Arthur 1976; Ellertsen et al. 1981), and otoliths. Of course otolith work is critical because estimates of growth rates are essential for assessment of mortality, but it is of no value for assessing growth at the onset of feeding (Methot 1981).

Arthur (1976) conducted the only other study on the feeding of jack mackerel off the coast of California. He found, after examining the stomach contents of 750 specimens from 65 offshore samples, that 60% of the first-feeding jack mackerel and 10% of the older larvae (7 mm) had empty stomachs. This observation lends additional credence to my histological evaluation of jack mackerel collected offshore that shows 59% of the first-feeding fish and 3% of the older fish (>4 mm) were starving.

I believe my estimates of jack mackerel mortality due to starvation are conservative. The assumptions I made about the persistence of starvation and the duration of growth were based on extensive laboratory studies (Theilacker 1978, 1981). Because the majority of jack mackerel were collected at sites warmer (16.1°16.6°C) than the culture temperature (15°15.5°C), the durations for growth and starvation may be altered, but the final estimate of mortality due to starvation is higher after the appropriate changes to the durations are made. Furthermore, if net retention of robust fish is greater than retention of thin fish of the same length, starvation may be underestimated. In addition, the selection of unhealthy larvae by predators would also increase the starvation estimate.

Previous evidence supporting the occurrence of starving fish larvae in the ocean has been mainly circumstantial (reviewed by May 1974; Jones and Hall 1974; Lasker 1975). Evidence from this study and O'Connell's (1980) study shows that starvation does occur and that the young stages of jack mackerel and northern anchovy are highly vulnerable.

Comparison of Morphological and Histological Criteria for Starvation Diagnosis

The incidence of starvation based on mor-

phological criteria was essentially the same as that based on histological criteria. Owing to the relative ease, and low cost of measuring fish compared with a histological examination, the morphological analysis is an attractive approach. On the other hand, histological analysis defines a cause and effect relation between structure and starvation whereas gross morphological measurements provide an index of starvation which is highly vulnerable to errors and biases in calibration and interpretations. Because of the importance of these measurements in recruitment studies, it is appropriate to consider the merits of and potential errors in these techniques in some detail.

The morphometric approach relies on measurements of fish to compare reared and wild animals at the same developmental stage. Thus shrinkage adjustments are needed to intercalibrate laboratory measurements and field measurements. Fish shrink when collected in a net and preserved, and shrinkage of the size of all body parts is dependent on the time in the net, size of fish, and type of preservative used (Blaxter 1971; Theilacker 1980a; Hay 1981). In this study, tow time was controlled at 5 min and samples were preserved within 8 min. Thus damage to the fish and shrinkage were minimal, but the samples were not quantitative. It is doubtful that the morphometric technique will work with jack mackerel taken in standard, quantitative collections. Quantitative net tows are 20 min, and they include an additional hosing down of the nets before sample preservation (Smith and Richardson 1977). The procedure damages the larvae, causing extensive shrinkage which makes accurate measuring difficult. Further, a long tow time decreases confidence in time-specific shrinkage estimates because fish can be collected at any time during the towing period. Increasing the tow time also causes both the magnitude of the shrinkage correction factor and the standard error of its estimate to increase. For example, in this study, standard length of jack mackerel shrank by an average of 6.0 $\pm$ 0.6% in 8 min and 19.0 $\pm$ 1.0% in 20 min.

While laboratory calibration is absolutely essential for the morphometric analysis, no shrinkage calibration is needed for the histological analysis, and it might be possible to use the histological observations on other fishes. Diagnostic criteria for the starving condition of jack mackerel (Theilacker 1978), northern anchovy (O'Connell 1976), and yellowtail, *Seriola quinqueradiata*, (Umida and Ochiai 1975) were similar. In addition, important biological information is gained while using the histological approach whereas gross morphological indices provide no such information. For example, histological analysis of jack mackerel has revealed a pattern of diel swim bladder inflation and a disruption of this rhythm, accumulation of glycogen reserves, and brain lesions presumably produced by UV radiation (Hunter et al. 1979). There is just no substitute for this extensive biological information. On the other hand, population work requires large samples, and morphological indices are probably the only practical means for working with very large samples. Thus, the optimal experimental design for population work on starvation is probably the use of morphological criteria (calibrated for shrinkage) combined with a smaller subsample of fish which are graded histologically. All work requires special net tows, preservation, procedures, and laboratory calibration.

Caution needs to be exercised when transferring information obtained in the laboratory to the field. Raising larval jack mackerel in small containers is known to affect growth, nutritive condition, and possibly activity (Theilacker 1980b). Additionally, there is evidence that wild fish tend to be thinner than their laboratory counterparts (larval herring, Blaxter 1971; juvenile herring, Balbontin et al. 1973; larval northern anchovy, Arthur 1976). My use of the morphometric SWDA assumes that the morphometric criteria I developed in the laboratory for larval jack mackerel raised in large tanks are applicable to ocean-caught jack mackerel.

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