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MORPHOLOGICAL EVIDENCE FOR STARVATION AND PREY SIZE SELECTION OF SEA-CAUGHT LARVAL SABLEFISH, *ANOPLOPOMA FIMBRIA*

One of the major causes of larval mortality is starvation, this being related to the patchiness of food resources (Hunter 1981). While starvation has been induced under laboratory conditions [e.g., herring, *Clupea harengus*, and plaice, *Pleuronectes platessa* (Ehrlich et al. 1976); northern anchovy, *Engraulis mordax* (O'Connell 1976); jack mackerel, *Trachurus symmetricus* (Theilacker 1978, 1981)], starved larvae have rarely been observed in nature (northern anchovy, O'Connell 1980; jack mackerel, Theilacker 1986). Various methods have been used to characterize starvation in fish larvae, including condition factor (Blaxter 1971), chemical analyses (Ehrlich 1974), histological analyses (Umeda and Ochiai 1975; O'Connell 1976, 1980; Theilacker 1978, 1986), and morphological analyses (Shelbourne 1957; Nakai et al. 1969; Ehrlich et al. 1976; Theilacker 1978, 1981, 1986). While histological and chemical analyses are based on qualitative changes in tissues that result from starvation, their methodologies require special preservation techniques, negating their application to samples preserved without these techniques in mind. To characterize starvation in samples that have not been specially preserved, measures of morphology and/or condition factor are more appropriately applied. In the present study, in the absence of special preservation techniques, the occurrence of starvation in sea-caught larval sablefish, *Anoplopoma fimbria*, was examined using morphological measures.

The sablefish inhabits the continental shelf of the North Pacific Ocean and is the subject of an intensifying fishery off the west coast of North America, yet little is known about the early life history of the species. Recent evidence obtained off Canada suggests that sablefish spawn in water deeper than 300 m, with spawning activity peaking in February. Eggs (1.8-2.2 mm in diameter) descend while developing, and hatching probably occurs at depths in excess of 400 m (Mason et al. 1983). Although size at hatching and the size at first feeding have not been clearly defined, Mason et al. (1983) reported collecting recently hatched larvae of 5-6 mm. After hatching, larvae ascend to surface waters and become neustonic (Kendall and Clark 1982[1]). Juveniles apparently remain in shallow water until they mature. Beyond reports of distribution (Kendall and Clark fn. 1; Clark 1984[2]) and descriptive work (e.g., Kobayashi 1957; Ahlstrom and Stevens 1976), studies of larval and early juvenile sablefish have concentrated on aging and growth (Boehlert and Yoklavich 1985; Shenker and Olla in press).

Our aim in the present study was to detect the possible occurrence of starvation in larval sablefish collected off Washington and Oregon during April and May 1980 (Kendall and Clark fn. 1), using selected morphological measurements to determine variability in larval condition. Further, to elucidate the possible relationship between larval condition and feeding requirements, prey size-selection and diet were analyzed.

Methods

Sablefish larvae were collected by using a 0.5 m neuston net (Sameoto and Jaroszynski 1969) with 0.505 mm mesh, towed for 10 min from the RV *Tikhookaenskiy*, during the first cooperative U.S.-U.S.S.R. ichthyoplankton survey off the Washington and Oregon coast in 1980 (Kendall and Clark fn. 1). Larvae from stations 20, 24, 25, 34, 38, 50,

[1]Kendall, A. W., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon and Northern California, April-May 1980. Processed Rep. 82-11, 44 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

[2]Clark, J. B. 1984. Ichthyoplankton off Washington, Oregon and Northern California, May-June 1981. Processed Rep. 84-11, 46 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

54, 70, and 71 (Fig. 1), collected between 22 April and 4 May 1980, formed the basis for this study. All larvae were preserved in 10% Formalin[3] at sea. After sorting, larvae were switched into 5% Formalin, where they remained until their examination in 1983.

The following body measurements were recorded: standard length (SL), head length (HL), eye diameter (ED), body depth at pectoral (BD.P), and body depth at anus (BD.A) (after Theilacker 1981). Standard length was measured to the nearest 0.1 mm. All other measurements were made to the nearest 0.05 mm using an ocular micrometer. Because body proportions change dramatically with size of larvae, it was necessary to restrict any comparisons to samples which were not statistically different in terms of the distribution of SL values. Also, to minimize ambiguities attributable to slight differences in size, comparisons of body measurements were made using a ratio of the body measurement to SL (e.g., HL/SL) as well as the absolute measurement (mm). Because a number of larvae were damaged prior to the time measurements were made (e.g., eyes were missing, the gut was separated from the body) the sample size (n) varied within a station. To classify larval condition, statistical comparisons of the body measurements were made using the Mann-Whitney test (Zar 1974), a nonparametric rank procedure.

Food particle-size selection was examined by measuring the widths of prey items ingested by 84 larvae from stations 24, 34, 50, 70, and 71. Soft-bodied prey items were not measured due to the difficulty in accurately assessing their effective width. All measurements were made using an ocular micrometer at 40×. Prey widths were originally plotted for five size classes of larvae: 8.2-12.5, 12.6-16.5, 16.6-20.5, 20.6-24.5, and 24.6-28.5 mm SL. The prey-size selection curve of larvae 12.6-16.5 mm closely approximated the curve of larvae 16.6-20.5 mm, and so these size classes were combined. Similarly, the curves of larvae 20.6-24.5 mm and 24.6-28.5 mm were essentially superimposed one upon the other, and as a result these size classes were also combined. This yielded three functional sablefish size classes for particle-size analysis: 8.2-12.5, 12.6-20.5, and 20.6-28.5 mm SL.

The incidence of empty guts was recorded, and diet was analyzed in terms of numerical percent composition and frequency of occurrence of copepod nauplii.

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

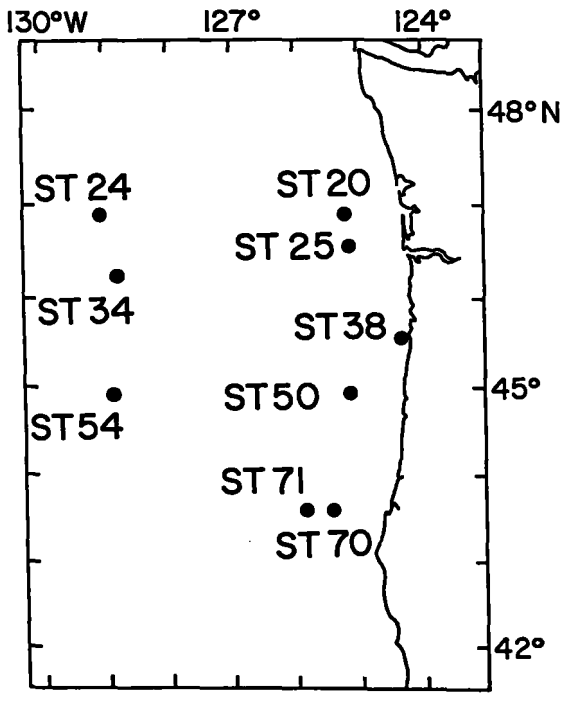

FIGURE 1.—Map of the Washington and Oregon coast where larval sablefish were collected in 1980.

Results

Morphological Measurements

Out of a total of 56 larvae collected at station 25, 48% (27 larvae) appeared emaciated, in marked contrast to larvae collected at all other stations. This emaciated condition, which we interpreted as evidence of starvation, was present in 82% of the larvae <12.5 mm SL (27 out of 32) collected at this station but was absent in fish larger than 12.5 mm SL. To test whether this interpretation, which was based on a gross visual examination of these larvae, was statistically verifiable, the morphology of the emaciated larvae from station 25 was compared with larvae of the same size from stations 20, 24, 34, 38, 50, 54, 70, and 71. The size range, 8.2-12.5 mm SL, was selected as the broadest range over which the distributions of SL values of these two groups were equivalent, and excluded the two smallest larvae collected at station 25 from the comparisons. Significant differences were observed in seven of eight body measurements, indicating that distinct differences were present in the larvae from station 25 when compared with larvae of similar size from all other stations (Table 1).

TABLE 1.—A comparison of median values of body measurements of *Anoplopoma fimbria* larvae from station 25 with larvae from stations 20, 24, 34, 38, 50, 54, 70, and 71. The size range was 8.2-12.5 mm SL.

	Station 25	Stations 20, 24, 34, 38, 50, 54, 70, and 71	P[1]
Standard length, SL (mm)	10.0	10.25	>0.20
95% Confidence Interval, C.I.	(9.2-10.4)	(10.0-10.5)	
n[2] =	25	118	
Head length, HL (mm)	1.5	2.1	<0.001
95% C.I.	(1.4-1.8)	(2.0-2.1)	
HL/SL	0.165	0.200	<0.001
95% C.I.	(0.147-0.177)	(0.194-0.206)	
n =	25	114	
Eye diameter, ED (mm)	0.7	0.85	<0.001
95% C.I.	(0.6-0.7)	(0.8-0.9)	
ED/SL	0.069	0.082	<0.001
95% C.I.	(0.066-0.073)	(0.081-0.084)	
n =	23	113	
Body depth at pectoral, BD.P (mm)	1.0	1.3	<0.001
95% C.I.	(0.9-1.15)	(1.3-1.3)	
BD.P/SL	0.109	0.128	<0.001
95% C.I.	(0.098-0.118)	(0.125-0.131)	
n =	13	100	
Body depth at anus, BD.A (mm)	1.0	1.2	<0.005
95% C.I.	(0.7-1.2)	(1.15-1.25)	
BD.A/SL	0.104	0.116	>0.10
95% C.I.	(0.082-0.139)	(0.112-0.118)	
n =	11	84	

[1] P = probability that body measurements of station 25 larvae were equivalent with larvae from stations 20, 24, 34, 38, 50, 54, 70, and 71, as determined by the Mann-Whitney test.
[2] The sample size was not constant within each group because some larvae were damaged prior to the time measurements were made (e.g., some had lost eyes, the gut was separated from the body).

Analysis of Gut Contents

Examination of the gut contents of larvae <12.5 mm SL provided further evidence as to the starved condition of the larvae at station 25. At this station 75% of the larvae (24 out of 32) had no food in their guts, and 9% (3 larvae) had ingested 2 or fewer prey items. In addition to being empty, the guts of larvae collected at station 25 were shrunken, which is reflective of poor feeding conditions (Nakai et al. 1969). At all other stations the incidence of empty guts for larvae <12.5 mm SL was <1%, as was the incidence of larvae ingesting 2 or fewer prey items.

Circumstantial evidence as to the cause of starvation comes from food analyses. It was apparent that while sablefish larvae selected increasingly larger prey as they grew larger, the minimum size of prey eaten did not increase appreciably. By examining the widths of all prey items ingested by larvae of different lengths (Fig. 2), three general patterns emerged: 1) Larvae 8.2-12.5 mm SL principally ingested the narrowest prey (0.01-0.10 mm in width), 2) larvae 12.6-20.5 mm SL ingested slightly larger prey (0.11-0.20 mm in width), and 3) sablefish 20.6-28.5 mm SL primarily ingested the largest prey (0.21-0.30 mm in width), although they also ingested a broad range of prey sizes.

Copepod nauplii were the dominant small prey, and were all <0.20 mm wide. They accounted for 88.3% of the diet (by number) of small larvae (≤12.5 mm). Based on prey-size selection alone (Fig. 2), it appears that copepod nauplii may have also contributed substantially to the diet of larvae 12.6-20.5 mm SL, but not to the diet of fish 20.6-28.5 mm SL. Dietary analysis confirmed this, with nauplii comprising 26.9% of the diet of larvae 12.6-20.5 mm, but merely 1.4% of the diet of fish 20.6-28.5 mm SL.

Considering the relative importance of copepod nauplii in the diet of larvae 12.6-20.5 mm SL and the fact that this size class continued to ingest nauplii although capable of ingesting larger prey, the frequency of occurrence of copepod nauplii in the guts of these larvae was examined at each station as inferential evidence of the abundance or availability of copepod nauplii (Table 2). At station 25 only 27% of larvae 12.6-20.5 mm SL ingested nauplii compared with 60-100% at all other stations; the low frequency of occurrence of nauplii in guts of these larvae at station 25 was obtained even though no guts were empty. These data indicate that copepod nauplii may not have been abundant or

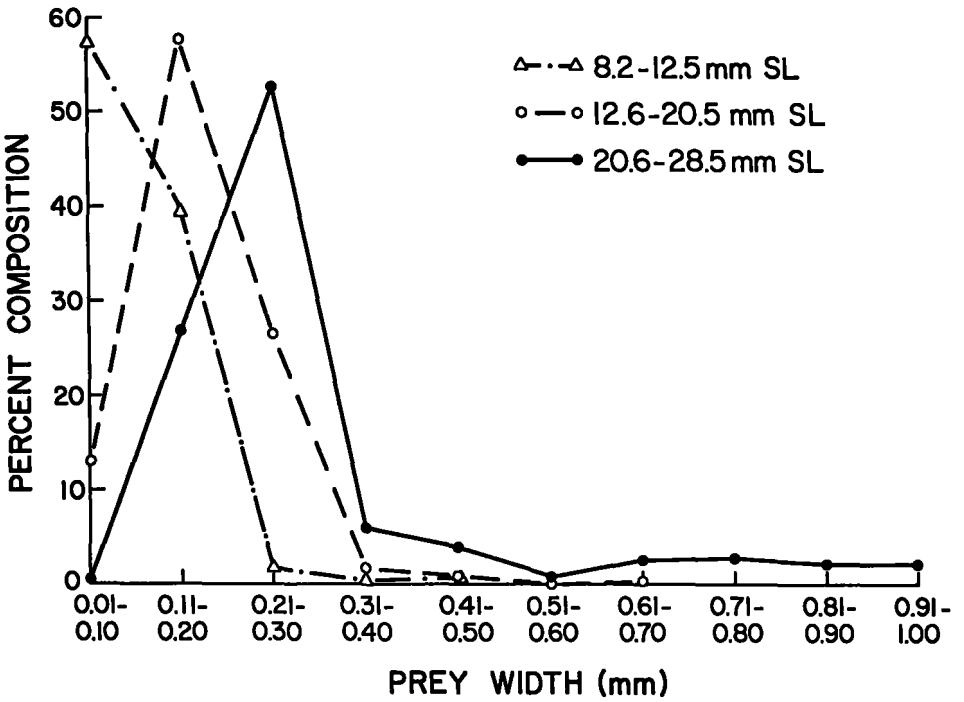

FIGURE 2.—The size of prey selected by larval sablefish, plotted for three size classes of larvae: 8.2-12.5 mm SL (n = 43), 12.6-20.5 mm SL (n = 25), and 20.6-28.5 mm SL (n = 16).

TABLE 2.—Frequency of occurrence of copepod nauplii found in the guts of larval sablefish, by size class and station.

	Station number								
Size class	20	24	25	34	38	50	54	70	71
≤12.5 mm	38/38	6/6	[1]7/32	9/9	32/32	6/6	15/16	10/10	11/12
	100%	100%	22%	100%	100%	100%	94%	100%	92%
12.6-20.5 mm	6/10	2/2	4/15	8/8	11/11	1/1	3/3	10/11	2/3
	60%	100%	27%	100%	100%	100%	100%	91%	67%

[1]This includes 24 larvae ≤12.5 mm SL with empty guts.

readily available at station 25, with the high incidence of starvation at this station suggesting a cause-and-effect relationship between these two factors.

Discussion

There is no definitive way of discerning whether the sablefish larvae that we categorized as starving had starved to the "point of no return". To ascertain whether sea-caught larvae have starved beyond recovery requires rearing larvae from eggs in the laboratory under different feeding regimes, and using these as standards of comparison for sea-caught specimens. Unfortunately, this has been done in only a few cases. For example, O'Connell (1976) established histological criteria for starvation under laboratory conditions for the northern anchovy. These criteria were then employed to identify starving larvae collected in the Southern California Bight (O'Connell 1980). The proportion of starving larvae was estimated to be 8%, for larvae <7.5 mm SL, with this representing 40% of the daily rate of mortality. In a more recent and comprehensive study, Theilacker (1986) utilized both histological and morphological criteria (Theilacker 1978, 1981) to examine starvation of sea-caught first-feeding jack mackerel in the Southern California Bight. She determined that starvation varied with habitat. In the open ocean, the number of larvae <3.5 mm dying

of starvation per day was 57-70%, whereas only 6-12% of the first-feeding larvae collected near islands and banks were starving.

Until techniques are developed for rearing sablefish from eggs, we are limited to utilizing comparisons of sea-caught larvae to infer the importance of starvation in the early life history of this species. While starving larvae were observed at only one station, our finding confirms that sablefish larvae do encounter suboptimal environmental conditions in the sea. However, neither the transience nor geographic extent of this phenomenon can be assessed in the absence of an intensive sampling scheme designed specifically to answer these questions.

Although definitive plankton composition data are lacking, the occurrence of starving larvae at station 25 appears to reflect a paucity of copepod nauplii. While appropriate prey concentrations (Laurence 1974; Lasker 1975; Houde 1978), particle size (Lasker 1975; Hunter 1981), and prey species composition (Lasker 1975; Scura and Jerde 1977) all relate to the survival and growth of marine fish larvae, not all larvae are able to maintain associations with suitable prey patches. Lasker (1975) emphasized the transient nature of optimal feeding conditions in the sea, noting that northern anchovy larvae which had been associated with a good feeding patch (a bloom of *Gymnodinium splendens* that persisted for 18 d) would probably die of starvation after a wind storm broke up the bloom. Patchiness of food resources has also been suggested by the station-to-station variability in growth rates of northern anchovy (as determined from daily increments of otoliths) (Methot and Kramer 1979). Similarly, after monitoring larval development in both good and bad plankton patches, Shelbourne (1957) reported that a scarcity of appropriate food resulted in a deterioration of the physical condition of plaice larvae.

Where morphological measurements of larvae are concerned, changes in body measurements which result from handling and preservation techniques must be considered. Net abrasion results in mechanical damage to the larvae (Blaxter 1971) as well as shrinkage (Blaxter 1971; Theilacker 1980), with the amount of shrinkage depending on whether death preceded fixation (Blaxter 1971), and the extent of handling (Theilacker 1980). The type of fixative used (Theilacker 1980), its concentration, salinity, and temperature (Hay 1982) also affect the degree of shrinkage. In the present case, shrinkage most likely occurred during the 3 yr these larvae were held in Formalin. However, absolute lengths may not be critical to evaluating the significance of our findings, and the differences that were seen between stations could not have resulted simply from differences in shrinkage. This was clear from the qualitative differences in gut appearance seen between stations (i.e., shrunken and empty guts versus guts filled to distention). Further, since the sablefish larvae we examined were all caught and preserved during the same cruise, we assumed that whatever shrinkage that may have resulted from handling and preservation techniques is constant throughout the samples.

Larval fishes are limited in the prey that they consume by their ability to capture and process it. As they grow, larvae become very successful predators, caused in part by an increase in mouth size. As a result, the size of prey selected increases as development proceeds. Prey width was used to examine prey-size selection because prey width appears to be the critical dimension for the successful ingestion of oblong prey by larval fishes (Blaxter 1965; Arthur 1976; Hunter 1981). For sablefish, definitive shifts in the size of prey consumed occurred at about 12.5 and 20.5 mm SL. The diet of the larger larvae was more diverse than the diet of small larvae. This expansion of the range of prey selected is not uncommon (e.g., Hunter 1981) and is adaptive inasmuch as it enables larvae to ingest suboptimal prey items at times when optimal or preferred prey are not available. Smaller fish appear limited in the size of prey they can exploit. This limitation, combined with larvae $\leq$12.5 mm SL being associated with an unsuitable prey patch at station 25, may have been responsible for the high incidence of empty guts and starvation.

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