EFFECTS OF AN EL NIÑO EVENT ON THE FOOD HABITS OF LARVAL SABLEFISH, ANOPLOPOMA FIMBRIA, OFF OREGON AND WASHINGTON

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ABSTRACT

The effect of El Niño conditions on the food habits of larval sablefish, Anoplopoma fimbria, was examined by comparing the diet of larvae collected off Oregon and Washington during the 1983 El Niño event and during 1980, a year in which conditions were not anomalous. While differential utilization of appendicularians, pteropods, and amphipods was seen in the 2 years, the most notable difference was that small copepods contributed significantly more to the diet in 1983 than in 1980. Dietary data for 1983 were generally supported by independent plankton observations, especially with respect to the predominance of *Paracalanus parmus*, a small calanoid copepod. Because adult sablefish live and spawn in deep water, changes in the food habits of neustonic larvae may represent one of the principal effects of the El Niño conditions on this species.

Larvae represent a precarious stage in the life history of marine fishes as they are highly vulnerable to fluctuations in oceanographic conditions and food resources. Their survival is dependent on successful feeding, avoidance of predation, and favorable transport (Sinclair et al. 1985). The relative importance of these factors is difficult to assess since each varies with species, developmental stage (Hewitt et al. 1985), and environmental conditions. Additionally, these sources of mortality are interactive insofar as the transport of larvae into areas with suboptimal feeding conditions may result in starvation, and starving larvae are at greatest risk for predation. Because survival past the larval and early juvenile stages clearly depends on successful feeding, understanding the success of larval populations requires a thorough knowledge of feeding ecology. As a result, in recent years a number of studies have provided detailed descriptions of the food habits of marine fish larvae (e.g., Laroche 1982; Cohen and Lough 1983; Govoni et al. 1983; Gadomski and Boehlert 1984; Brewer and Kleppel 1986), and a few studies have documented the occurrence of starvation under natural conditions (O'Connell 1980; Hewitt et al. 1985; Grover and Olla 1986; Theilacker 1986). The present study examined the food habits of larval sablefish, Anoplopoma fimbria,

collected during 2 years of differing oceanographic conditions.

As oceanographic conditions are manifested through changes in zooplankton assemblages, between-year comparisons of the diet of larval fishes can reflect differences in oceanic conditions. Such comparisons are of particular interest when they include periods characterized by highly anomalous conditions. One such oceanographic anomaly, an El Niño event, occurred in the eastern Pacific Ocean off North America from the fall of 1982 through late summer 1983.

The magnitude of El Niño-induced anomalies in physical conditions appears to be greatest in surface waters, with anomalous conditions having the greatest effect on those life stages of fishes that occupy the upper water column. Adult sablefish inhabit deep slope waters and spawn at depths in excess of 300 m (Mason et al. 1983), and therefore may be relatively insulated from El Niño conditions (Bailey and Incze 1985). Their eggs may also be insulated, as they hatch in water deeper than 400 m (Mason et al. 1983). However, larvae ascend to surface waters where they reside through early juvenile stages (Shenker and Olla 1986; J. M. Shenker^s). During this neustonic phase they are most vulnerable to anomalous oceanographic conditions. While El Niño con-

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ditions may affect fish larvae in several ways, Bailey and Incze (1985) speculated that sablefish may be particularly sensitive to altered food production.

The aim of the present work was to examine the effect of an El Niño event on the food habits of larval sablefish, through a comparison of their diet off Oregon and Washington during the 1983 El Niño event and 1980, a year in which oceanographic conditions were not anomalous⁴. Since an earlier study showed that prey size-selection was a function of larval size (Grover and Olla 1986), ontogenetic differences in diet were also considered.

METHODS

Sablefish larvae were collected by the cooperative U.S.-U.S.S.R. ichthyoplankton survey off Oregon and Washington, during 1980⁵ and 1983⁶, using a 0.5 m neuston net (Sameoto and Jaroszynski 1969) with 0.505 mm mesh towed for 10 min. Collections were made from 22 April to 4 May 1980 by the RV Tikhookaenskiy and from 22 April to 30 April 1983 by the RV Ekvator (Fig. 1). Samples with a minimum of 10 specimens were examined. A total of 267 larvae collected from 10 stations in 1980 and 136 larvae from 6 stations in 1983 were examined. In each year the number of larvae that were examined represented more than 45% of the total number of sablefish that were collected. In conjunction with neuston sampling surface water temperatures were recorded along major transects.

All larvae were preserved in 10% Formalin⁷ at sea. Upon sorting they were switched into 5% Formalin, where they remained until their examination.

After the standard length (SL) of each larva was measured, the digestive tract was removed. Contents of the entire digestive tract were evaluated. Only larvae with all or a large portion of the gut intact were examined. Gut contents were teased out, and prey items were identified: invertebrate eggs, pteropods, copepod nauplii, copepods, amphipods, euphausid larvae, appendicularians, and other prey



FIGURE 1.—Map of the stations off Washington and Oregon where larval sablefish were collected. Dots represent 1980 collections and crosses represent 1983 collections.

items. When possible copepods were identified to species.

Lengths of all prey items were recorded. After the study was begun, it became clear that prey widths should also be measured. From that point on, both lengths and widths were recorded for all prey that were not dorsoventrally or laterally flattened. A conservative approach was taken with prey dimensions, i.e., prey widths excluded appendages and cephalothorax lengths were measured for copepods. Both measurements were recorded for a total of 7,508 prey items.

Diet was analyzed in terms of numerical percentage composition (%N), percent frequency of occurrence (%FO), and volumetric percentage composition (%VOL). Prey volumes were calculated from prey dimensions, assuming a spherical shape for invertebrate eggs, while all other prey were more appropriately described by a cylindrical shape. For a comparison, volumes were also calculated assuming a spheroidal shape, following Gadomski and Boehlert (1984). Regardless of whether a cylindrical or spheroidal shape was assumed, the relative contri-

⁴Sea Surface Thermal Analysis. Dates of issue: 8 May 1980 – 6 May 1986. Northwest Ocean Service Center, NOAA, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115. ⁵Kendall, A. W., and J. Clark. 1982. Ichthyoplankton off

⁵Kendall, A. W., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon and Northern California, April-May 1980. Processed Rep. 82-11, 48 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98112.

Clark, J., and A. W. Kendall. 1985. Ichthyoplankton off Washington, Oregon, and Northern California, April-May 1983. Processed Rep. 85-10, 48 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

⁷Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

bution of each prey type was essentially the same, except that invertebrate eggs contributed slightly more (in all cases $\leq 0.1\%$) to the total volume when the spheroidal shape was assumed. After the volume of each individual prey was calculated, a median volume for each prey type was determined. Median values were used because they are free from implicit assumptions regarding the normality of these data. Each median volume was then multiplied by the raw data from the numerical percentage composition analysis to produce corresponding volumetric percent composition data. Data were examined by size group and year.

The three analyses (%N, %FO, and %VOL) were coalesced to yield a more comprehensive assessment of prey importance, the index of relative importance (IRI = (%N + %VOL) × %FO) (Pinkas et al. 1971). For this combined analysis copepods were classified by size. Copepods <1 mm in length (TL) included *Corycaeus anglicus*, *Oithona similis*, *Oncaea* sp., *Paracalanus parrus*, and copepodites. Broken copepods of an indeterminable size were classified as unidentified small copepods. Copepods 1-2 mm long included *Pseudocalanus* sp., *Clausocalanus* spp., *Ctenocalanus vanus*, *Aedideus* sp., *Scolecithricella minor*, and *Acartia* spp. *Calanus* spp. and *Metridia lucens* were the only copepods >2 mm that were ingested.

RESULTS

Composition of the Diet of Small Larvae (≤12.5 mm SL)

During 1980, copepod nauplii comprised over 80% of the prey items ingested by number, although copepods <1 mm long contributed slightly more to the diet in terms of volume (Table 1, Fig. 2). The index of relative importance, IRI, (Pinkas et al. 1971) indicated that nauplii were more important than copepods (Table 1, Fig. 3). Many of the copepods <1 mm that were ingested by small larvae were in pieces and impossible to identify. Of those that could be identified, *Oithona similis* was the dominant species, followed by *Paracalanus parvus* (Table 2). The only noncopepod prey of much consequence was pteropods (Figs. 2, 3), locally comprising as much as 45.7% of the diet, by number.

In 1983, copepod nauplii were again the dominant prey in terms of number, but copepods represented more than twice as much in volume as they did in 1980 (Table 1, Fig. 2). While both were significant components of the diet, copepod nauplii had a slightly larger IRI value than copepods <1 mm (Fig. 3). Although the proportion of *O. similis* in the diet was similar in both years, *P. parvus* contributed more to the diet during 1983 (Table 2). A comparison of the sizes of copepods ingested during 1980 and 1983 (Table 3) showed that more small copepods were eaten in 1983, both in terms of the number of copepods ingested ($\chi^2 = 8.46$, 1 df, P < 0.005) and volume ($\chi^2 = 755.32$, 1 df, P < 0.001).

Composition of the Diet of Medium-Sized Larvae (12.6-20.5 mm SL)

While copepods ranked first in all analyses in 1980, other major prey items varied with method of analysis (Table 1, Fig. 2). From the IRI it is clear that copepods <1 mm were the most important prey, with O. similis the dominant species by number (Table 2), and P. parvus dominant by volume. In addition, sizable numbers of 1-2 mm copepods, especially Acartia longiremis, were ingested at several stations. Copepod nauplii ranked second in IRI value. Of noncopepod prey items pteropods, euphausid larvae, and appendicularians were all of consequence in the diet.

In 1983, while copepods <1 mm were again the principal prey, they comprised a greater portion of the diet than in 1980, with *P. parrus* dominating both in terms of number (Table 2) and volume. Copepod nauplii ranked second by number, but accounted for little prey volume, while euphausid larvae, the only noncopepod prey to contribute substantially to the diet, ranked higher than nauplii both in terms of volume and IRI. Of the copepod species ingested, the most striking difference between the years was the increased contribution of *P. parrus* in 1983 (Table 2).

Copepods >1 mm contributed more to the diet in 1980 than 1983 while small copepods comprised a greater portion of the diet during 1983 (Table 3), both in terms of number ($\chi^2 = 130.25$, 1 df, P < 0.001) and volume ($\chi^2 = 9906.86$, 1 df, P < 0.001).

Composition of the Diet of Large Larvae (20.6-28.5 mm SL)

While ranking second to small copepods by number and second to large copepods by volume, appendicularians comprised more than 30% of the diet by number and volume during 1980, and ranked highest in IRI value, slightly ahead of copepods <1 mm (Table 1, Fig. 3). In contrast, euphausid larvae and amphipods were the most important noncopepod prey items in the diet during 1983, although each contributed <15% to the diet. In 1983 the diet

TABLE 1.—Composition of the diet of larval sablefish in terms of the Index of Relative Importance (IRI) and its components: numerical percent composition (%N), frequency of occurrence (%FO), and volumetric percent composition (%VOL), by size class and year, with n = sample size and $\%\Sigma$ IRI = the contribution of each prey type to the total IRI.

| Prey type | %N | %FO | %VOL | IRI | %ΣIRI | RI Prey type | | %FO | %VOL | IRI | %ΣIRI |
|----------------------|------|----------|---------------|-----------|--------------------------|-------------------|------|---------|------------|------------------|-------|
| Larval size ≤12.5 mm | | | - Larval size | | 12.6-20.5 mm-Continued - | | | | | | |
| 1980 | | | | | | 1983 | | | | | |
| Invertebrate eggs | 0.5 | 7.9 | 0.1 | 4.7 | <0.1 | Invertebrate eggs | 0.2 | 1.5 | 0.1 | 0.5 | 0.1 |
| Pteropods | 5.8 | 25.5 | 11.2 | 433.5 | 3.1 | Pteropods | 0.3 | 9.1 | 0.1 | 3.6 | 0.1 |
| Copepod nauplii | 84.0 | 96.4 | 27.1 | 10,710.0 | 77.7 | Copepod nauplii | 9.9 | 60.6 | 0.6 | 636.3 | 3.6 |
| Copepods <1 mm | 7.4 | 66.1 | 27.8 | 2,326.7 | 16.9 | Copepods <1 mm | 83.3 | 100.0 | 71.6 | 15 ,490.0 | 88.3 |
| 1-2 mm | 0.8 | 14.5 | 8.0 | 127.6 | 0.9 | 1-2 mm | 3.7 | 48.5 | 10.1 | 699.3 | 3.8 |
| >2 mm | | | | | | >2 mm | <0.1 | 1.5 | 1.1 | 1.8 | <0.1 |
| Amphipods | | | | | | Amphipods | 0.1 | 4.5 | 0.2 | 1.4 | 0.1 |
| Euphausid larvae | 0.4 | 6.7 | 15.3 | 105.2 | 0.8 | Euphausid larvae | 2.3 | 40.9 | 15.7 | 736.2 | 4.2 |
| Appendicularians | 0.6 | 7.3 | 7.2 | 56.9 | 0.4 | Appendicularians | 0.2 | 7.6 | 0.5 | 5.3 | <0.1 |
| Other prey | 0.5 | 4.2 | 3.3 | 15.6 | 0.1 | Other prey | | | | | |
| n = | 165 | | | | | <i>n</i> = | 66 | | | | |
| 1983 | | | | | | | | - Larva | al size 20 | .6-28.5 mm | |
| invertebrate eggs | 0.5 | 8.2 | <0.1 | 4.9 | <0.1 | 1980 | | | | | |
| Pteropods | 2.1 | 14.3 | 2.7 | 68.6 | 0.4 | | • • | | | | |
| Copepod nauplii | 74.3 | 91.8 | 15.9 | 8,280.4 | 51.6 | Invertebrate eggs | 2.9 | 13.0 | <0.1 | 39.0 | 0.2 |
| Copepods <1 mm | 21.7 | 85.7 | 66.2 | 7,533.0 | 46.9 | Pteropods | | | | | |
| 1.2 mm | 1.0 | 18.4 | 5.8 | 125.1 | 0.8 | Copepod nauplii | 1.4 | 30.4 | <0.1 | 45.6 | 0.3 |
| >2 mm | | | | | | Copepods <1 mm | 40.6 | 95.7 | 13.2 | 5,148.7 | 33.1 |
| Amphipods | | | | | | 1-2 mm | 11.0 | 87.0 | 10.0 | 1,827.0 | 11.8 |
| Euphausid larvae | 0.4 | 4.1 | 9.3 | 39.8 | 0.2 | >2 mm | 4.1 | 69.6 | 42.0 | 3,208.6 | 20.6 |
| Appendicularians | | | | | | Amphipods | 0.5 | 17.4 | 0.4 | 15.7 | 0.1 |
| Other prey | | | | | | Euphausid larvae | 0.9 | 17.4 | 2.2 | 53.9 | 0.3 |
| n = | 49 | | | | | Appendicularians | 38.4 | 73.9 | 32.0 | 5,202.6 | 33.5 |
| | | | | | | Other prey | 0.2 | 8.7 | 0.1 | 2.6 | <0.1 |
| | | - Larval | size 12. | 6-20.5 mm | | n = | 23 | | | | |
| 1980 | | | | | | 1983 | | | | | |
| Invertebrate eggs | 0.3 | 5.1 | <0.1 | 4.7 | < 0.1 | Invertebrate eggs | 0.2 | 9.5 | <0.1 | 2.8 | <0.1 |
| Pteropods | 9.4 | 38.0 | 3.7 | 497.8 | 3.9 | Pteropods | 0.5 | 14.3 | <0.1 | 8.6 | <0.1 |
| Copepod nauplii | 25.8 | 70.9 | 1.7 | 1,949.7 | 15.3 | Copepod nauplii | 0.4 | 19.0 | <0.1 | 9.5 | <0.1 |
| Copepods <1 mm | 48.2 | 93.7 | · 37.7 | 8.048.8 | 63.2 | Copepods <1 mm | 71.3 | 95.2 | 24.1 | 9,082.1 | 57.6 |
| 1-2 mm | 7.9 | 49.4 | 19.3 | 1,343.7 | 10.5 | 1-2 mm | 9.6 | 76.2 | 12.3 | 1,668.8 | 10.6 |
| >2 mm | 0.2 | 3.8 | 5.0 | 19.8 | 0.2 | >2 mm | 4.0 | 66.7 | 41.6 | 3,041.5 | 19.3 |
| Amphipods | | | | | | Amphipods | 8.1 | 47.6 | 7.2 | 728.3 | 4.6 |
| Euphausid larvae | 2.4 | 25.3 | 18.3 | 523.7 | 4.1 | Euphausid larvae | 5.5 | 61.9 | 14.3 | 1,225.6 | 7.8 |
| Appendicularians | 5.4 | 17.7 | 13.7 | 338.1 | 2.7 | Appendicularians | 0.4 | 14.3 | 0.4 | 11.4 | <0.1 |
| Other prey | 0.4 | 3.8 | 0.5 | 3.4 | <0.1 | Other prey | | | | | |
| D = | 79 | | | 2 | | n = | 21 | | | | |

shifted towards smaller copepods (Table 3), especially *P. parvus*, so that copepods <1 mm ranked highest in IRI value. Evidence for this shift came from numerical data ($\chi^2 = 27.30, 2$ df, *P* < 0.001) as well as volumetric data ($\chi^2 = 1928.73, 2$ df, *P* < 0.001).

A comparison of the diet of medium-sized and large larvae showed that despite other dietary differences, the number of copepods in the diet of medium-sized larvae equalled the number of copepods ingested by large larvae in 1980 ($\chi^2 = 0.13$, 1 df, P > 0.75). However, large larvae ingested a greater volume of copepods in 1980 than did medium-sized larvae ($\chi^2 = 148.09$, 1 df, P < 0.001). In 1983 the numbers of copepods ingested by medium-sized and large larvae were again equivalent ($\chi^2 = 2.93$, 1 df, P > 0.05), although copepods contributed more, volumetrically, to the diet of medium-sized larvae ($\chi^2 = 657.22$, 1 df, P < 0.001).

Comparison of Oceanographic Conditions

Because 1983 was a year of anomalous El Niño conditions, differences in diet between 1980 and 1983 may have been due to differing oceanographic conditions in the 2 years. Surface water temperatures taken during the ichthyoplankton surveys, were used as an indicator of oceanographic conditions. As the two surveys followed the same transects, station coordinates corresponded for the 2 years. Temperatures recorded from 20 April to 5 May 1980 averaged $10.67^{\circ}C(s = 0.783)$, while those from 23 April to 6 May 1983 were significantly higher (P = 0.001) averaging $11.78^{\circ}C(s = 0.772)$.



FIGURE 2.—Relative importance of prey items in the diet of larval sablefish, by size class and year, expressed as numerical percent composition (%N), volumetric percent composition (%VOL), and percent frequency of occurrence (%FO). The area of each block represents the Index of Relative Importance (IRI) of a given prey (IRI = (%N + %VOL) × %FO). Sample sizes are as listed in Table 1.

Comparisons with other years revealed that thermal patterns off Oregon and Washington were similar for 1980 through 1982 and 1984 through 1986 (fn. 4). In contrast, 1983 was markedly different, being the only year among those compared when a 13°C isotherm developed and when surface temperatures ≤ 10 °C were not found between the coast and long. 130°W during the first week in May.

TABLE 2.—Species composition of copepods consumed by sablefish larvae. Data are expressed as numerical percentages of all copepods that were ingested by each size class in each year.

| | Larval size class (mm) | | | | |
|--|------------------------|-----------|------------|--|--|
| Copepod species | ≤12.5 | 12.6-20.5 | 20.6-28.5 | | |
| 1980 | | | | | |
| <1 mm | | | | | |
| Corycaeus anglicus | | 0.6 | 8.5 | | |
| Oithona similis | 27.4 | 38.7 | 16.8 | | |
| Oncaea sp. | 0.2 | 0.2 | 0.5 | | |
| Paracalanus parvus | 9.4 | 19.5 | 35.8 | | |
| unidentified | 38.5 | 19.5 | 8.0 | | |
| copepodites | 14.5 | 7.1 | 3.3 | | |
| 1-2 mm | | | | | |
| Pseudocalanus sp. | 1.8 | 1.7 | 3.1 | | |
| Clausocalarius spp. | 1.2 | 2.6 | 2.4 | | |
| Ctenocalanus vanus Aetideus sp. | 5.1 | 1.1 | 4.7 | | |
| Scolecithricella minor | | 0.1 | | | |
| Acartia sp. | 1.4 | 7.8 | 4.9 | | |
| unidentified | 0.5 | 0.8 | 4.7 | | |
| >2 mm | | | | | |
| Calanus spp. | | 0.2 | 5.4 | | |
| <i>Metridia lucens</i> unidentified | | 0.1 | 0.2 1.7 | | |
| 1983 | | | | | |
| <1_mm | | | | | |
| Corycaeus anglicus | 0.3 | 0.3 | 1.5 | | |
| Oithona similis Oncaee sp. | 24.8 | 28.7 | 17.1 | | |
| Paracalanus parvus | 39.2 | 47.5 | 45.3 | | |
| unidentified | 23.7 | 13.2 | 15.8 | | |
| copepodites | 7.5 | 5.9 | 4.1 | | |
| 1-2 mm | | | | | |
| Pseudocalanus sp. | 0.8 | 0.7 | 1.4 | | |
| Clausocalanus spp. | 0.5 | 0.7 | 3.6 | | |
| Ctenocalanus spp. | 2.9 | 1.3 | 1.5 | | |
| Aetideus sp. | | 0.1 | | | |
| Scolecithricella minor | | | | | |
| Acartia spp. | 0.3 | 0.4 | 0.7 | | |
| unidentified | | 1.1 | 4.2 | | |
| >2 mm | | | | | |
| Calanus spp. | | <0.1 | 3.4 | | |
| <i>Metridia lucens</i> unidentified | | | 1.4 | | |

TABLE 3.—Size selection of copepods by sablefish larvae. Data are expressed as a percentage of all copepods that were consumed by each size class of larvae in each year.

| | Larval size class (mm) | | | | | | | | |
|-----------------|------------------------|---------------|---------------|-------|---------------|---------------|--|--|--|
| | | 1980 | | 1983 | | | | | |
| Copepod size | ≤12.5 | 12.6- 20.5 | 20.6- 28.5 | ≤12.5 | 12.6- 20.5 | 20.6- 28.5 | | | |
| A. By num | ber | | | | | _ | | | |
| <1 mm | 90.0 | 85.6 | 72.9 | 95.5 | 95.6 | 83.8 | | | |
| 1-2 mm | 10.0 | 14.1 | 19.8 | 4.5 | 4.3 | 11.4 | | | |
| >2 mm | 0.0 | 0.3 | 7.3 | 0.0 | <0.1 | 4.8 | | | |
| B. By volu | me | | | | | | | | |
| <1 mm | 77.8 | 61.0 | 20.3 | 91.9 | 86.5 | 30.7 | | | |
| 1-2 mm | 22.2 | 31.0 | 15.5 | 8.1 | 12.1 | 15.9 | | | |
| >2 mm | 0.0 | 8.0 | 64.2 | 0.0 | 1.4 | 53.4 | | | |

DISCUSSION

A comparison of the diet of sablefish larvae in 1980 and 1983 revealed several differences. Most notably, for larvae of all sizes, copepods <1 mm contributed significantly more to the diet in 1983 than in 1980. Appendicularians were the dominant prey for large larvae in 1980, but were negligible in the diet during 1983. Amphipods were only of consequence in the diet of large larvae in 1983. Pteropods comprised a substantial portion of the diet of small and medium-sized larvae in 1980, but made a trivial contribution to the diet in 1983 although ingested by larvae of all sizes.

Although concurrent zooplankton data are lacking in this study, judging from the diet, prey populations were probably quite different in 1980 and 1983. As a result of the anomalous conditions during 1983, a separate study extensively sampled zooplankton off the Oregon coast (Miller et al. 1985), where almost half (48%) of the sablefish larvae from 1983 were collected.

In both 1980 and 1983, the timing of sablefish larvae collections corresponded to the spring transitional period off Oregon reported for previous years (Peterson and Miller 1976, 1977). During this period winds and currents shift, upwelling develops, and the zooplankton is transitive between a winter assemblage that is dominated by southern species of copepods and a summer assemblage that is dominated by copepods with northern affinities. During 1980, 8% of the copepods that were ingested were northern species, representative of the spring transition, i.e., Pseudocalanus sp. and Acartia spp., especially Acartia longiremis. In contrast, during 1983 as a result of the El Niño event manifested through increases in surface water temperatures. sea level, and poleward currents, reductions in salinities and coastal upwelling, and a depression of the thermocline (Fiedler 1984; Huyer and Smith 1985; McGowan 1985), only a partial spring transition occurred, with southern (winter) species, especially P. parvus continuing to dominate the plankton through July (Miller et al. 1985). The diet during 1983 reflected this same trend with P. parvus being paramount in importance while northern species accounted for <1.5% of the ingested copepods.

The fact that the pteropod *Limacina helicina*, a species with northern affinities which is the dominant pteropod species off Oregon, was not very abundant in 1983 (C. B. Miller⁸) correlates well with

⁸C. B. Miller, College of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. December 1985.



FIGURE 3.—Indices of relative importance (IRI values) of dominant prey items in the diet of larval sablefish, by size class and year. Only IRI values >100 are included. In each case the sum of IRI values <100 accounted for <1% of the sum of all IRI values.

our dietary observations which showed a marked decrease relative to 1980. Plankton data regarding the relative abundance of appendicularians and amphipods are less correlative with diet.

Preliminary analyses of collections made off Oregon in the spring and summer of 1983 (Miller et al. 1985) indicated that zooplankton density was reduced, possibly as low as 30% of that found in a non-El Niño year. Indirectly lending support for this was data from satellite imagery which monitored phytoplankton pigment images and which indicated that primary productivity was substantially reduced during 1983 (Fiedler 1984).

Fulton and LeBrasseur (1985) suggested that while interannual fluctuations in zooplankton biomass affect planktivorous fish living in the open ocean off the west coast of North America, major shifts in the particle size of zooplankton may have a greater effect. In particular, the extreme northward shifting of the subarctic Pacific boundary, which occurred during the 1957-58 El Niño event, resulted in the replacement of large copepods with small copepods off North America from lat. 40°N to 52°N. They hypothesized that the absence of large copepods and decreased biomass in these waters during a warm El Niño year would result in reduced growth and perhaps reduced survival of juvenile salmonids.

Ontogenetic changes in the diet of sablefish larvae included the diminution of small prey such as copepod nauplii and pteropods, and the increasing contribution of larger prey such as amphipods, euphausid larvae, and appendicularians as larvae grew. These observations parallel earlier findings on prey size-selection of larval sablefish (Grover and Olla 1986) and agree with trends seen in many other marine fish (Hunter 1981). All size classes of larvae showed some flexibility in the prey they ingested. from year to year as well as from station to station, with large larvae ingesting the widest range of prey items. The expansive range of prev ingested by large larvae may have enabled them to ingest large numbers of small copepods during 1983, when larger prey of high caloric value may not have been readily available.

From all indications, 1983 was a year of reduced planktonic productivity off Oregon and Washington (Fiedler 1984; Miller et al. 1985). It was also a year when *P. parvus*, a small copepod, was dominant both in the plankton (Miller et al. 1985) and in the diet of larval sablefish. As low productivity and the predominance of small copepods were also observed during a previous El Niño year (Fulton and LeBrasseur 1985), these planktonic conditions may be fairly typical of El Niño events off Oregon and Washington. A comparison of the diet in 1980 and 1983 suggests that a decrease in the size of copepods ingested by sablefish larvae in 1983 may be one of the principal effects of El Niño conditions on the diet of this species. While it is possible that some energetic deficit may be imparted because of this dietary shift, the actual effects on the growth of larval sablefish are at present unknown. Although the diet in 1983 was reflective of the plankton, corresponding plankton data were not available for 1980, thus it is unclear how closely the diet resembled the plankton in 1980. However, if we assume that the copepods that were ingested by larvae are indicative of the copepods that were available, as was the case in 1983, then we may infer that larger copepods were more readily available during 1980, in the absence of anomalous conditions.

While a reduction in zooplankton biomass might affect sablefish larvae of all sizes, a paucity of large copepods would likely have the greatest effect on larvae >20.6 mm for two reasons: 1) large larvae repeatedly ingested the largest prey (Grover and Olla 1986) and 2) they were the only size class that ingested a substantial volume of large copepods.

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LITERATURE CITED

- BAILEY, K. M., AND L. S. INCZE.
- 1985. El Niño and the early life history and recruitment of fishes in temperate marine waters. In W. S. Wooster and D. L. Fluharty (editors), El Niño north: Niño effects in the eastern subarctic Pacific Ocean, p. 143-165. Washington Sea Grant Program, Univ. Wash., Seattle.

BREWER, G. D., AND G. S. KLEPPEL.

1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Mar. Ecol. Prog. Ser. 27:217-226.

COHEN, R. E., AND R. G. LOUGH.

1983. Prey field of larval herring Clupea harengus on a con-

tinental shelf spawning area. Mar. Ecol. Prog. Ser. 10:211-222.

FIEDLER, P. C.

- 1984. Satellite observations of the 1982-1983 El Niño along the U.S. Pacific Coast. Science 224:1251-1254.
- FULTON, J. D., AND R. J. LEBRASSEUR.
- 1985. Interannual shifting of the subarctic boundary and some of the biotic effects on juvenile salmonids. In W. S. Wooster and D. L. Fluharty (editors), El Niño north: Niño effects in the eastern subarctic Pacific Ocean, p. 237-247. Washington Sea Grant Program, Univ. Wash., Seattle.

GADOMSKI, D. M., AND G. W. BOEHLERT.

- 1984. Feeding ecology of pelagic larvae of English sole Parophrys vetulus and butter sole Isopsetta isolepis off the Oregon coast. Mar. Ecol. Prog. Ser. 20:1-12.
- GOVONI, J. J., D. E. HOSS, AND A. J. CHESTER.
 - 1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: Brevoortia patronus, Leiostomus xanthurus, and Micropogonias undulatus. Mar. Ecol. Prog. Ser. 13:189-199.
- GROVER, J. J., AND B. L. OLLA.

1986. Morphological evidence for starvation and prey size selection of sea-caught larval sablefish, Anoplopoma fimbria. Fish. Bull., U.S. 84:484-489.

- HEWITT, R. P., G. H. THEILACKER, AND N. C. H. LO.
- 1985. Causes of mortality in young jack mackerel. Mar. Biol. Prog. Ser. 26:1-10.
- HUNTER, J. R.
 - 1981. Feeding ecology and predation of marine fish larvae. In R. Lasker (editor), Marine fish larvae: morphology, ecology, and relation to fisheries, p. 34-77. Washington Sea Grant Program, Univ. Wash., Seattle.
- HUYER, A., AND R. L. SMITH.
 - 1985. The signature of El Niño off Oregon, 1982-1983. J. Geophys. Res. Sec. C(Oceans) 90:7133-7142.

1982. Trophic patterns among larvae of five species of sculpins (family: Cottidae) in a Maine estuary. Fish. Bull., U.S. 80:827-840.

MASON, J. C., R. J. BEAMISH, AND G. A. MCFARLANE.

- 1983. Sexual maturity, fecundity, spawning, and early life history of sablefish (Anoplopoma fimbria) off the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 40:2126-2134. McGowan, J. A.
 - 1985. El Niño 1983 in the Southern California Bight. In W. S. Wooster and D. L. Fluharty, (editors), El Niño north: Niño effects in the eastern subarctic Pacific Ocean, p. 166-184. Washington Sea Grant Program, Univ. Wash., Seattle.
- MILLER, C. B., H. P. BATCHELDER, R. D. BRODEUR, AND W. G. PEARCY.
 - 1985. Response of the zooplankton and ichthyoplankton off Oregon to the El Niño event of 1983. In W. S. Wooster and D. L. Fluharty (editors), El Niño north: Niño effects in the eastern subarctic Pacific Ocean, p. 185-187. Washington Sea Grant Program, Univ. Wash., Seattle.
- O'CONNELL, C. P.
 - 1980. Percentage of starving northern anchovy, *Engraulis* mordax, larvae in the sea as estimated by histological methods. Fish. Bull., U.S. 78:475-489.

PETERSON, W. T., AND C. B. MILLER.

- 1976. Zooplankton along the continental shelf off Newport, Oregon, 1969-1972: distribution, abundance, seasonal cycle, and year-to-year variations. Oregon State Univ. Sea Grant College Program Publ. No. ORESU-T-76-002, 111 p.
- 1977 Seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. Fish. Bull.,

LAROCHE, J. L.

U.S. 75:717-724.

- PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.
 - 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game Fish. Bull. 152: 1-105.
- SAMEOTO, D. D., AND L. O. JAROSZYNSKI.
 - 1969. Otter surface sampler: a new neuston net. J. Fish. Res. Board Can. 26:2240-2244.

SHENKER, J. M., AND B. L. OLLA.

- 1986. Laboratory feeding and growth of juvenile sablefish,
- Anoplopoma fimbria. Can. J. Fish. Aquat. Sci. 43:930-937. SINCLAIR, M., M. J. TREMBLAY, AND P. BERNAL.
- 1985. El Niño events and variability in a Pacific mackerel (Scomber japonicus) survival index: support for Hjort's second hypothesis. Can. J. Fish. Aquat. Sci. 42:602-608.

THEILACKER, G. H.

1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull., U.S. 84:1-17.