

AN ABSTRACT OF THE THESIS OF

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Title: Feeding Ecology of Pelagic larvae of Two Pleuronectids  
(English Sole, *Parophrys vetulus*, and Butter Sole, *Isopsetta*  
*isolepis*) off the Oregon Coast

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Abstract approved: \_\_\_\_\_

Dr. G. W. Boehlert

The feeding habits of the two dominant larval pleuronectids off the Oregon coast, English sole (*Parophrys vetulus*), and butter sole (*Isopsetta isolepis*), were analyzed. Larval specimens were collected primarily during April of 1971 and March and April of 1973. *Isopsetta* larvae ingested a variety of prey, changing with increasing fish size, a pattern typical of larval fishes. Small *Isopsetta* fed predominantly on tintinnids, invertebrate eggs, and nauplii, whereas large larvae consumed more copepodite and adult copepods. In contrast, the diet of *Parophrys* larvae is very specific; appendicularians (*Oikopleura* spp.) comprised 97% of the total number of food items consumed in 1973. Thus, although larval *Parophrys* and *Isopsetta* co-occur in Oregon coastal waters during part of the year, they are not competing for food resources.

Both Parophrys larvae and appendicularians are most abundant during fall and winter months when total zooplankton concentrations off Oregon are low. Isopsetta larvae are most abundant during spring months when productivity (and thus larval feeding conditions) is enhanced. Isopsetta larval feeding requirements are relatively broad due to their more varied diet. In contrast, Parophrys larvae may depend upon high densities of a specific prey, appendicularians, as a winter food source. A mismatch of Parophrys and appendicularian abundance peaks could cause increased larval starvation.

In 1971, seasonal peaks of Parophrys larvae and appendicularians did not coincide. During this year, larvae fed less on appendicularians than in 1973 (66% of the total number of food items), and more on food sources such as tintinnids, invertebrate eggs, and nauplii. Larvae were less robust in 1971 than in 1973, and more had empty guts, indicative of increased starvation. In addition, fewer large larvae were present in 1971, perhaps due to high mortality rates.

Feeding Ecology of Pelagic Larvae of  
Two Pleuronectids (English Sole, Parophrys vetulus, and  
Butter Sole, Isopsetta isolepis) off the Oregon Coast

by

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## DEDICATION

I dedicate this thesis to my father, mother, and sister for their support and encouragement.

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FEEDING ECOLOGY OF PELAGIC LARVAE OF  
TWO PLEURONECTIDS (ENGLISH SOLE, PAROPHRYS VETULUS, AND  
BUTTER SOLE, ISOPSETTA ISOLEPIS) OFF THE OREGON COAST

INTRODUCTION

Marine fishes with very high fecundities are characterized by great mortality between egg and adult stages. It is generally agreed that most of this mortality occurs during the first few months in the pelagic larval phase due to starvation and predation (Hunter 1976). This stage in the life history, termed the "critical period," is very important because it is the time in which year-class strength may be determined (May 1974). Hjort (1914; 1926) believed that the most critical factor for larval survival is the availability of planktonic food at the time of complete yolk absorption. It is essential that high concentrations of an appropriate food be present or first-feeding larvae may die of starvation after just a few days (Blaxter and Hempel 1963; May 1974; Hunter 1981). In addition, starving larvae are more susceptible to predation, disease, parasites, and unfavorable environmental conditions. They are also less

efficient at catching prey due to impaired swimming abilities (Laurence 1972).

Many factors affect the coincidence in timing of abundances of larval fishes and their food sources. Many marine fishes spawn when chances of optimal conditions for larvae are greatest (Cushing 1975). Maximal food density, however, is not the only critical factor in optimizing larval conditions. Survival is also influenced by currents which may transport planktonic larvae away from favorable areas. Productivity associated with upwelling, for example, may result in high larval food densities but coincide with detrimental offshore transport away from coastal nursery grounds (Parrish et al. 1981). In the Oregon coastal region, however, Laroche and Richardson (1979) have suggested that offshore larval drift is probably not an important factor in year-class strength because much of the time alongshore currents are dominant.

Parophrys vetulus and Isopsetta isolepis are the second and third most abundant species in the Oregon nearshore larval fish assemblage (2-28 km from the coast) as described by Richardson and Percy (1977). Parophrys has an extended spawning season, with peaks from January to March, though spawning may also occur as early as September (Kruse and Tyler 1983; Mundy 1984). Isopsetta spawns from February through May (Richardson et al.

1980); thus the larvae of these two species only co-occur during part of their pelagic phases.

The development of both species from egg to benthic juvenile is similar. Larval Parophrys hatch from pelagic eggs in 4 to 12 days, depending upon temperature (Alderdice and Forrester 1968). Newly hatched larvae are 2.7 to 2.9 mm standard length (SL). Metamorphosis occurs between 50 and 120 days, during which the larvae settle out and assume the benthic form (Laroche et al. 1982; Rosenberg and Laroche 1982). Standard length at this time remains relatively constant (18 to 22 mm SL) and extensive morphological changes occur, such as the migration of the left eye to the right side of the body. Isopsetta larvae hatch about six days after fertilization, also ranging in size from 2.7 to 2.9 mm SL (Richardson et al. 1980). The yolk disappears four days after hatching (3.4 to 4.0 mm SL). Eye migration begins at 12 or 13 mm SL and transformation into the benthic juvenile is complete at about 21 mm SL.

Laroche and Richardson (1979) observed year-to-year temporal and spatial variations in larval abundance which may be related to fluctuating year-class strengths (Hayman and Tyler 1980). These variations are due in part to changes in peak spawning times and durations, but also are due to biotic and environmental factors which influence larval survival. During winter months

off the Oregon coast, one of the most important of these factors may be food availability. In this region, summer upwelling (strongest from June through August) causes increased nutrient concentrations in surface waters, which, combined with greater light intensity, results in increased primary production and greater summer larval food abundances (Small et al. 1972; Peterson and Miller 1977). Because Parophrys spawns during fall and winter months, larval food availability may be the most critical factor affecting subsequent year-class strength. In addition, the morphologically similar larvae of Parophrys and Isopsetta may compete for food resources when they co-occur during winter months. Therefore, it is necessary to understand the feeding ecology of the pelagic larval stages of these two species in order to better understand the causes of variability in year-class strength.

## METHODS

### Sample Selection

Larvae were selected from curated ichthyoplankton survey samples collected off the coast of Oregon during the Sea Grant Early Life History project (1971-1975) conducted by Oregon State University School of Oceanography. From January 1971 through August 1972, collections were made along the Newport Hydrographic (NH) line (on  $44^{\circ}40'N$ ), 2-111 km off Newport, Oregon (Figure 1; Richardson and Pearcy 1977). The hydroline number (NH1, NH3, etc.) refers to the number of nautical miles from the coast.

During March and April of 1972 and 1973, and during March of 1974 and 1975, samples were taken on a coastal grid 2 to 56 km offshore from the Columbia River to Cape Blanco, Oregon (Figure 1; Laroche and Richardson 1979). In all cruises, plankton was collected by a 70 cm (mouth diameter), non-closing bongo net with 0.571 mm Nitex mesh. Tows were stepped or straight oblique from the bottom or 150 meters to the surface. Samples were preserved in 5% formalin buffered with sodium borate. See Richardson and Pearcy (1977) and Laroche and Richardson (1979) for details.

Initially, 380 Parophrys larvae and 361 Isopsetta larvae

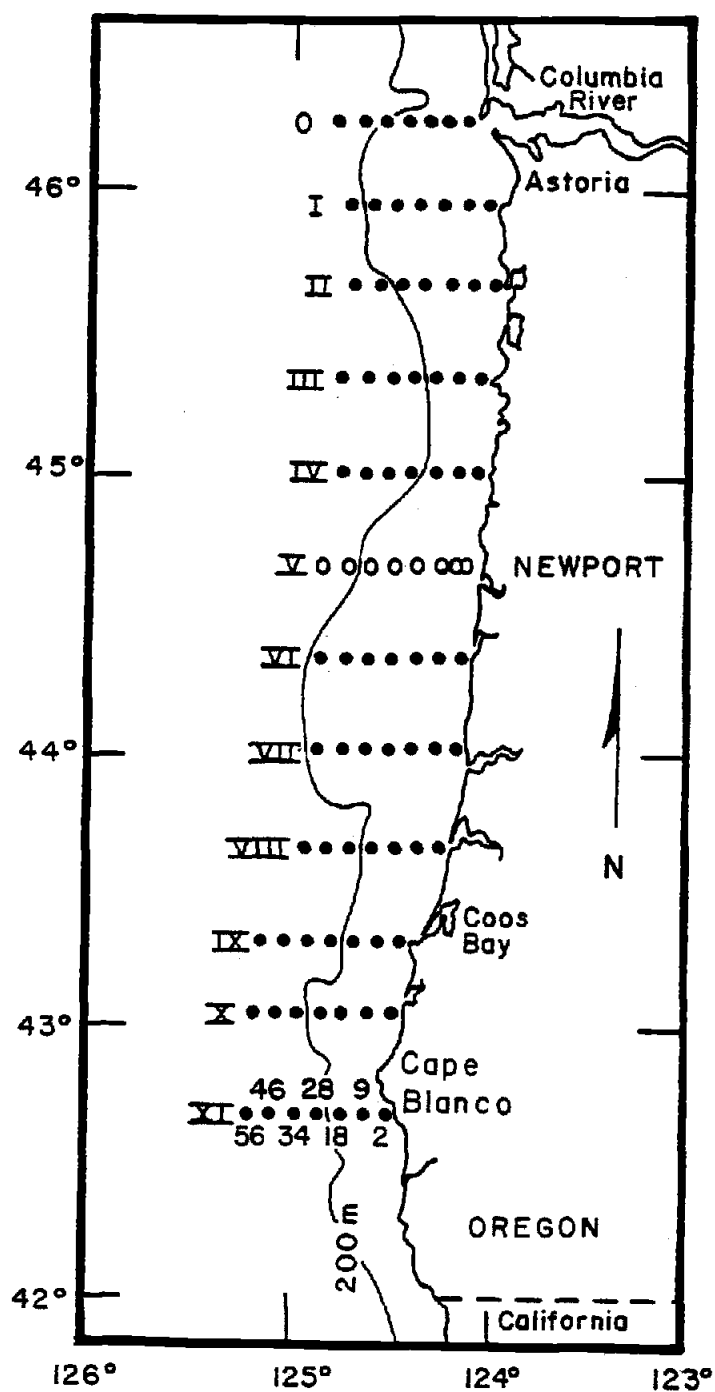


Figure 1. Sampling stations off Oregon. Numbers along transect XI are kilometers from shore. Open circles at transect V are the Newport Hydroline (from Laroche and Richardson 1979).

were examined from March and April of 1973. That year was chosen because there were sufficient larvae of both species in relatively broad size ranges. Information obtained from these larvae provided the major data base for analysis. For comparison, however, 183 Parophrys larvae from January through April 1971, 52 Isopsetta from June 1971, and 27 Isopsetta from June 1972 were also examined. This increased the number of small Parophrys and large Isopsetta, since these two size categories were limited in the 1973 samples.

A sample was selected for examination if it was recorded to contain at least ten specimens of Parophrys or Isopsetta larvae. Usually, about ten Parophrys and/or ten Isopsetta larvae from each selected sample were examined. Less than ten were examined from some samples, however, because of deterioration or more than ten were examined if they were available. When sorting a sample, usually the first ten larvae encountered with intact guts were removed. In some cases, however, larvae were selected with respect to larval size in order to obtain the broadest possible size spectrum from each sample.

Parophrys larvae examined from 1973 were from 38 samples from 13 days (17 March to 20 April). Isopsetta larvae from 1973 were from 30 samples from 13 days (17 March to 26 April). Isopsetta and Parophrys larvae co-occurred in 19 of these



samples. All samples (except one) were collected at stations 1, 5, 10, 15 and 20 nautical miles off the Oregon coast. Samples examined from 1973 were collected at a variety of day and night times to investigate diel feeding patterns. All other larvae examined were chosen from day collections (0800-1800) to maximize feeding incidence. Parophrys larvae from 1971 were from 13 samples during seven days (6 January to 22 April), all taken from the hours of 1000 through 1400 at NH1, NH3, NH5, NH10, and NH15. Isopsetta larvae from 1971 were from five samples from one day (28 June) at NH3 and NH5 from 1044 through 1224. Isopsetta from 1972 were from three samples also during one day (11 June) at NH3, NH5, and NH10 from 1104 through 1314. Isopsetta larvae from 1971 and 1972 were selected from only one day each because these were the only days that large larvae were taken during daylight hours.

#### Laboratory Techniques

Specimens were placed in glycerin and soaked overnight. Glycerin clears the animal and results in the gut being more pliable and thus easier to work with. A specimen to be examined was placed facing to the right in a drop of glycerin on a microscope slide. The following morphological measurements were made after Richardson et al. (1980) using an ocular micrometer

on a dissecting microscope: (1) standard length (SL): snout tip to notochord tip or the edge of the hypurals; (2) head length: snout tip to cleithrum; (3) eye diameter: anterior to posterior; (4) mouth width: horizontal distance from a frontal view; (5) body depth at the base of the pectoral fins: vertical distance excluding finfold or fins; (6) body depth at the anus: vertical distance excluding finfold or fins; and (7) posterior body depth: vertical distance posterior to the anus excluding finfold or fins.

The complete intestinal tract was removed from the body and placed on a separate slide in a drop of glycerin. Small Parophrys and Isopsetta larvae have a straight gut, which begins to coil at about 4 mm SL. Discrete esophagus and rectal regions are not discernible until the larva matures, but the gut can be roughly divided into fore, mid, and hindgut areas. The entire gut was teased open and the contents removed, noting the location of major food items. Food items were counted, measured, and identified to the lowest possible taxon.

#### Gut Content Analysis

To facilitate analysis, food items were classified into categories characterized by taxon and/or size. For example,

copepodites-copepods were classified as a species with a known size (Pseudocalanus sp., Oithona spp., etc.), or as unidentified but of a certain size range (cephalothorax length about .25, .50, .75, or 1.00 mm). Since in many cases, an animal was dorsal-ventrally or laterally flattened, and only length could be accurately measured, a cephalothorax length to width (widest part of the carapace excluding appendages) ratio was calculated for major copepod species. Unidentified copepodites-copepods were assumed to have a width one-third of their cephalothorax length.

Three parameters were quantified subjectively as follows: (A) stomach fullness: 0: empty, 1: 1/4 full, 2: 1/2 full, 3: 3/4 full, and 4: full; (B) digestive stage: 1: food present in excellent condition, 2: food somewhat digested, and 3: food very digested; and (C) gut diameter: 1: narrow, 2: average, and 3: distended.

For the various larval length groups, percent by number (%N) and percent frequency of occurrence (%F) were tabulated. %N is the percentage of the total number of prey items, while %F is the percent frequency of occurrence of a food item among larvae with food in their guts. The volume of a prey item was calculated assuming it to be a spheroid, by the formula  $1/6[\pi(\text{length})(\text{width})^2]$ . The mean prey width for each larval length group was calculated by summing the individual widths of

each prey item ingested in that length group, and dividing by the total number of prey items ingested. Mean prey volume was calculated in a similar manner.

### Appendicularians

One common prey item, appendicularians, were studied in more detail. Appendicularians are usually found in the gut almost completely digested except for characteristic spheroid fecal pellets. In order to establish a relationship between appendicularians and their fecal pellets, 202 appendicularians (Oikopleura spp.) randomly chosen from nearshore Oregon plankton samples were examined. The mean number of fecal pellets per appendicularian was calculated. The results were used to determine the number of appendicularians ingested from the number of fecal pellets found in a larval fish gut by dividing the number of gut fecal pellets by the mean number of fecal pellets per plankton appendicularian, after Shelbourne (1962). In addition, fecal pellet length to appendicularian trunk length and width were regressed, and confidence limits were determined using a predictive model (Neter and Wasserman 1974). Fecal pellets from larval fish guts were measured and classified into eight .05 mm length groups with median lengths of .05, .10, .15, .20, .25, .30, .35, and .40 mm, and the results were used to calculate ingested appendicularian size, following Shelbourne (1962).

### Morphometrics

For Parophrys and Isopsetta from 1973 and Parophrys from 1971, linear regressions of larval head length, eye diameter, mouth width, pectoral body depth, and posterior body depth on larval standard length were performed. Body depth at the anus was not used because of the limited number of successful measurements; in many cases the gut was somewhat separated from the body, although intact. Logarithmic and exponential fits were also tested. However, only the relationship between Parophrys 1971 posterior body depth and standard length was best fit by a nonlinear function.

Larval mouth width and prey size were compared for Parophrys and Isopsetta larvae from 1973. In addition, morphological measurements for Parophrys from 1971 and 1973 were compared in two ways. First, the slopes and intercepts of morphological regression lines were compared between the two years using the method of indicator variables described by Neter and Wasserman (1974). Secondly, the ratios: (head length/SL), (pectoral body depth/SL), and (posterior body depth/SL), were calculated for individual fish and the means of four length groups (9.0-9.9, 10.0-10.9, 11.0-11.9, 12.0-12.9 mm SL) with adequate numbers of representatives were compared between years using Student's t-test for unequal sample size and standard deviations.

The possibility that slope and intercept differences were artifacts of the different larval size frequencies examined in 1971 and 1973 was investigated by standardizing the length ranges between years; morphological regressions were compared for only larvae less than 15 mm SL. The same results were obtained, however; regression lines had the same equations as when full larval length ranges were analyzed.

Morphological and food item data were analyzed using SPSS (Statistical Package for the Social Sciences) and SIPS (Statistical Interactive Program, Oregon State University).

## RESULTS

### Variations in Feeding

More Parophrys and Isopsetta larvae from daytime samples had food in their guts than did those from nighttime samples (Figures 2 and 3). After midnight, the percentage of larvae with empty guts increases rapidly, particularly for Parophrys. In addition, food found in Parophrys and Isopsetta guts during early morning hours was always very digested and often in the posterior portion of the gut. Many larvae which had empty guts between 0200 and 0600 had very narrow guts, although empty but distended guts were also found. After 0600, the percentage of larvae with food in their guts increases rapidly and remains over 80% throughout the day.

In both 1973 and 1971, there were ontogenetic variations in gut fullness; smaller larvae had higher incidences of empty stomachs than larger larvae (Figure 4). For clarity, only larvae from daytime samples (0800-1800) were considered in this analysis since larvae of all sizes from nighttime samples have more empty guts than from daytime samples. More Parophrys larvae collected

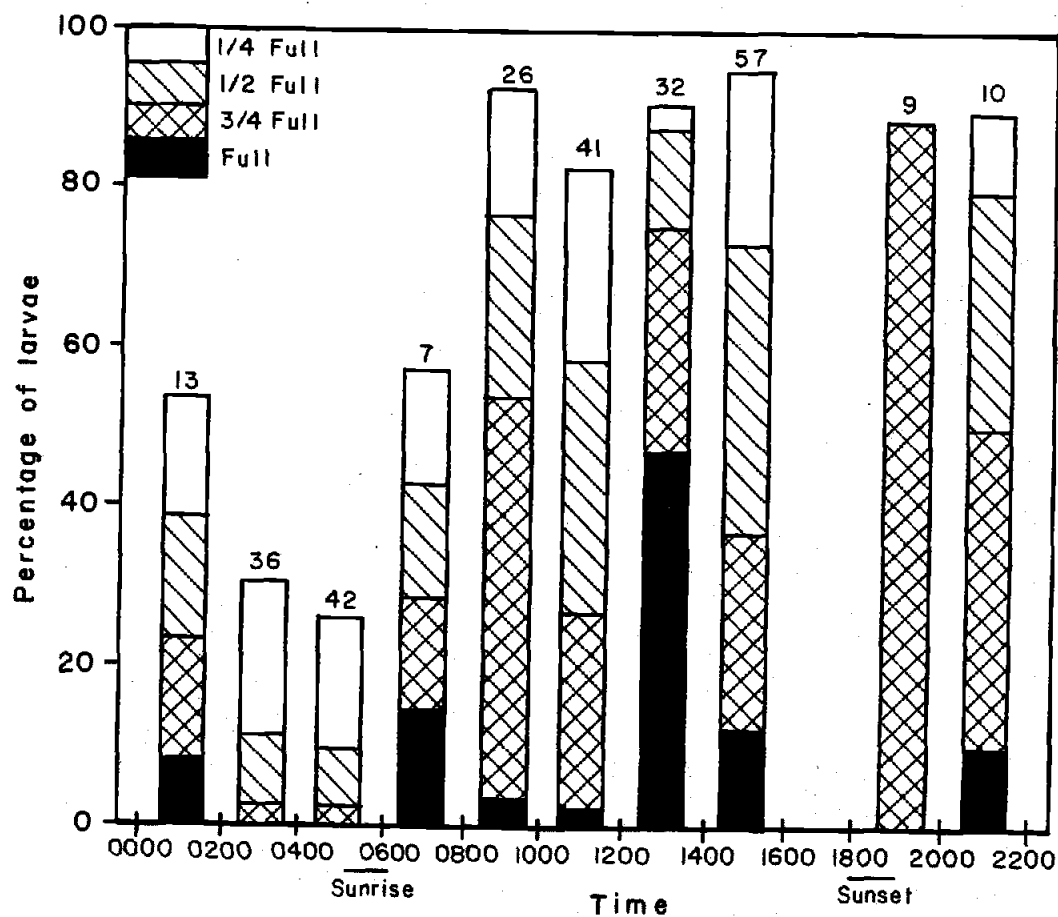


Figure 2. Diel variations in gut fullness of *Isopsetta isolepis* larvae from March and April, 1973. From the top of a bar to 100% represents the percentage of empty guts. The numbers above the bars are the numbers of larvae examined from that time period. Only larvae 6.0-17.9 mm SL are considered in this figure because smaller larvae have a higher percentage of empty guts which would bias the results.



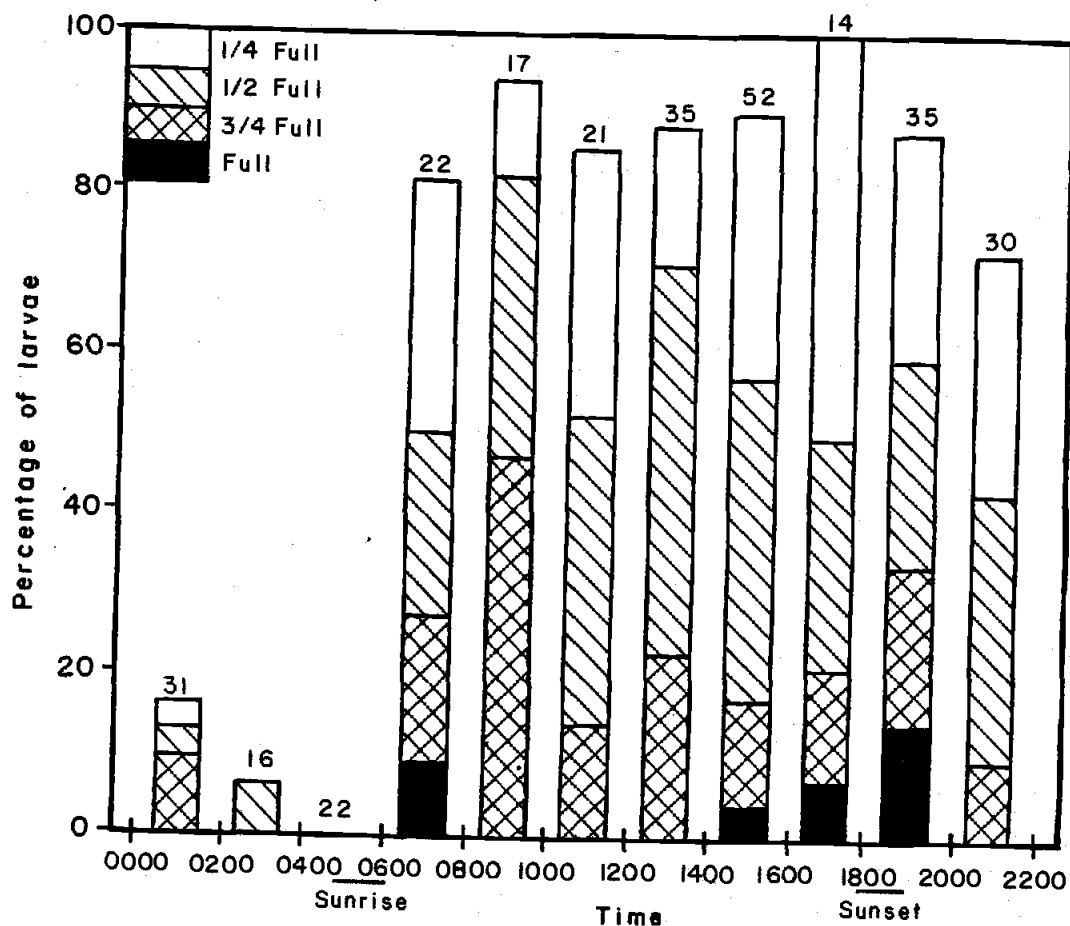


Figure 3. Diel variations in gut fullness of *Parophrys vetulus* larvae from March and April, 1973. From the top of a bar to 100% represents the percentage of empty guts. The numbers above the bars are the numbers of larvae examined from that time period. Only larvae 6.0-17.9 mm SL are considered in this figure because smaller larvae have a higher percentage of empty guts which would bias the results.

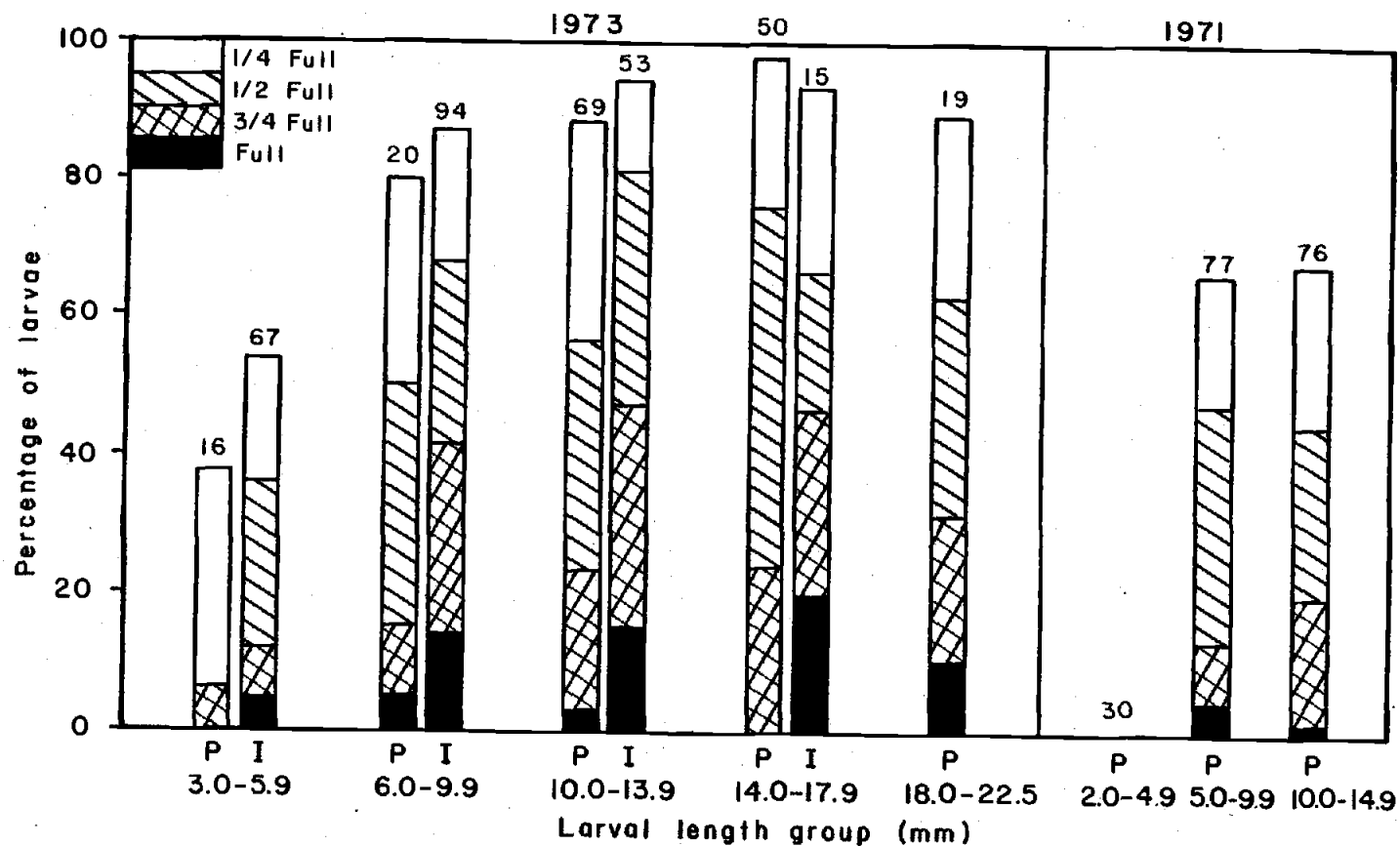


Figure 4. Ontogenetic variations in gut fullness of *Parophrys vetulus* (P) and *Isopsetta isolepis* (I) larvae from 1973 and 1971. From the top of a bar to 100% represents the percentage of empty guts. The numbers above the bars are the numbers of larvae examined from each length group. Only larvae from daytime samples (0800-1800) are considered in this figure.

during 1971 had empty guts than in 1973, and in fact, all Parophrys larvae below 5 mm SL examined from 1971 had empty guts. All Isopsetta larvae examined from 1971 and 1972 were greater than 10 mm SL, and almost all had food in their guts (Table 2). In addition, the mean numbers of food items per feeding larva were high in these years compared to Isopsetta from 1973 (Table 1). In all years, Isopsetta larvae have a higher maximum and mean number of items in their guts than do Parophrys larvae (Tables 1, 2, and 3), but an ontogenetic trend is not evident in either species.

#### Diet Composition

Isopsetta isolepis. Food items in the guts of Isopsetta larvae were usually in good condition, although often crushed. Crustaceans usually had exoskeletons intact, but tissues digested. Only rarely did prey appear to have been "just eaten" (with inside tissues remaining) or extremely digested and crushed (except in early morning hours, about 0200-0600). Food was rarely found in the esophagus or foregut region, but was usually found throughout the midgut and hindgut (or rectal) regions. Food in the hindgut did not generally appear to be more digested than in the midgut. Although there were differences in diet between years, no consistent differences were detected between stations

Table 1. Diet composition of Isopsetta isolepis larvae from 1973. The numbers in parentheses are percentages by number of a prey species in the previous major category (capitalized). %N = percentage of the total number of prey items. %F = percent frequency of occurrence.

	LARVAL LENGTH GROUPS (mm)								18.0-
prey items	2.7-5.9		6.0-9.9		10.0-13.9		14.0-17.9		21.1
	%N	%F	%N	%F	%N	%F	%N	%F	%N
TINTINNIDS	45.5	47.5	10.0	15.4	1.2	3.8	.9	4.3	
INVERTEBRATE EGGS	10.0	35.0	25.0	46.2	22.1	33.3	24.0	21.7	
unidentified	(50.0)		(40.8)		(80.6)		(100)		
<u>Calanus marshallae</u>	(50.0)		(59.2)		(19.4)				
NAUPLII	42.6	70.0	46.6	73.6	32.7	44.9	4.2	13.0	
COPEPODITES-COPEPODS	1.0	5.0	12.6	16.5	27.4	60.3	49.3	60.9	87.8
unidentified	(100)		(87.1)		(55.1)		(37.7)		(41.3)
Calanoid									
<u>Pseudocalanus</u> spp.			( 6.5)		(32.1)		(56.8)		(55.2)
<u>Paracalanus</u> spp.			( 3.2)		( 2.2)		( 1.8)		( 3.4)
<u>Ctenocalanus</u> spp.					( .7)		( 1.8)		
Cyclopoid									
<u>Oithona</u> spp.			( 3.2)		( 9.9)		( 1.8)		
APPENDICULARIANS			5.0	8.8	8.4	10.3	15.0	21.7	3.0
POLYCHAETE LARVAE			1.0	3.3	5.3	17.9	5.1	13.0	9.1
EUPHAUSIID CALYPTOPIS					1.4	7.7	1.7	8.7	
UNIDENTIFIED					2.7	5.5			
No. of larvae examined	73		124		114		37		13
No. with prey	40		86		75		22		5
Maximum no. of prey items per larvae	19		29		24		20		18
Mean no. of prey items per feeding larvae from day samples	5.3		9.4		6.4		7.2		7.0

Table 2. Diet composition of Isopsetta isolepis larvae from 1971 and 1972. The numbers in parentheses are percentages by number of a prey species in the previous major category (capitalized).

%N = percentage of the total number of prey items.

%F = percent frequency of occurrence.

prey items	LARVAL LENGTH GROUPS (mm)							
	1971				1972			
	10.0-13.9		14.0-17.9		18.0-20.9		15.0-20.9	
	%N	%F	%N	%F	%N	%F	%N	%F
INVERTEBRATE EGGS	68.0	80.0	61.3	50.0	40.0	22.7		
NAUPLII	18.2	60.0	14.9	57.1	2.7	9.1	15.2	58.3
COPEPODITES-COPEPODS	7.6	53.3	1.6	28.6	22.2	40.9	84.5	100.0
unidentified							(59.0)	
Calanoid								
<u>Acartia longerimis</u>	(100)		(75.0)		(58.6)		(15.7)	
<u>Pseudocalanus</u> spp.							( 6.2)	
<u>Paracalanus</u> spp.							( .3)	
Cyclopoid								
<u>Oithona</u> spp.							(18.8)	
Harpacticoid								
<u>Microsetella rosea</u>			(25.0)		(41.4)			
LAMELLIBRANCH LARVAE	4.4	20.0	17.3	35.7	8.1	18.2		
PTEROPODS			.4	7.1	10.8	31.8		
POLYCHAETE LARVAE	1.3	20.0	3.2	50.0	9.7	59.1		
CUMACEANS			.8	7.1	2.7	13.6		
APPENDICULARIANS	.4	6.7			.5	4.5	.3	8.3
WORMS			.4	7.1	2.2	9.1		
AMPHIPODS					.5	4.5		
No. of larvae examined	15		14		23		25	
No. with prey	15		14		22		23	
Maximum no. of prey items per larva	44		45		62		39	
Mean no. of prey items per feeding larva from day samples	15.0		17.7		8.4		25.5	

Table 3. Diet composition of Parophrys vetulus larvae from 1971 and 1973. The numbers in parentheses are percentages by number of a prey species in the previous major category (capitalized). %N = percentage of the total number of prey items. %F = percent frequency of occurrence.

prey items	LARVAL LENGTH GROUPS (mm)									
	1971					1973				
	2.7-4.9 %N	5.0-9.9 %N %F	10.0-15.9 %N %F	3.6-9.9 %N %F	10.0-13.9 %N %F	14.0-17.9 %N %F	18.0-22.4 %N %F			
APPENDICULARIANS		56.5 75.5	76.1 96.2	80.8 84.6	100.0 100.0	97.2 98.6	100.0 100.0			
INVERTEBRATE EGGS		6.2 18.9	5.4 11.3	5.6 3.9		1.1 2.7				
unidentified		( 8.3)	(10.0)	(100)		(100)				
<u>Calanus marshallae</u>		(91.7)	(90.0)							
NAUPLII		23.8 41.5	16.8 13.2	14.0 15.4						
COPEPODITES-COPEPODS		1.6 3.8	1.1 1.9							
TINTINNIDS		11.9 3.8				1.1 1.4				
POLYCHAETE LARVAE			.5 1.9			.6 1.4				
No. of larvae examined	30	77	76	44	148	122	66			
No. with prey	0	53	53	26	110	73	34			
Maximum no. of prey items per larva		23	14	5	6	16	11			
Mean no. of prey items per feeding larva from day samples		3.6	3.5	1.7	1.1	2.3	3.4			

within a year. Most guts contained a variety of prey types.

Isopsetta larvae had a varied diet in 1973 (Figure 5). Small larvae ingested primarily tintinnids (.05 mm) and nauplii (.10-.35 mm, mainly of copepods). With increasing larval size, tintinnids rapidly lost importance as a prey item, and larger prey, copepodites and copepods (.25-1.20 mm cephalothorax length) gained importance. The major copepod species ingested was Pseudocalanus (Table 1). Nauplii lost importance in the diet above 14 mm SL. Invertebrate eggs (.05-.30 mm), many of them Calanus marshallae (.20 mm), were frequently consumed throughout ontogeny. Appendicularians are also a significant prey item, particularly at larger sizes.

Since only five Isopsetta larvae greater than 18 mm SL with stomach contents were available for examination from 1973 (Table 1), larger Isopsetta larvae were examined from two other years, 1971 and 1972 (Figure 6 and Table 2). During 1971, invertebrate eggs were the dominant food source for all larvae examined. As in 1973, nauplii were important in the diet of smaller larvae, and copepodites and copepods gained importance with increasing larval length. The two species of copepod ingested in 1971, however, were Acartia longerimis and a harpacticoid, Microsetella rosea. Also in contrast to 1973, in 1971 lamellibranch larvae and pteropods were important diet items. During 1972, Isopsetta

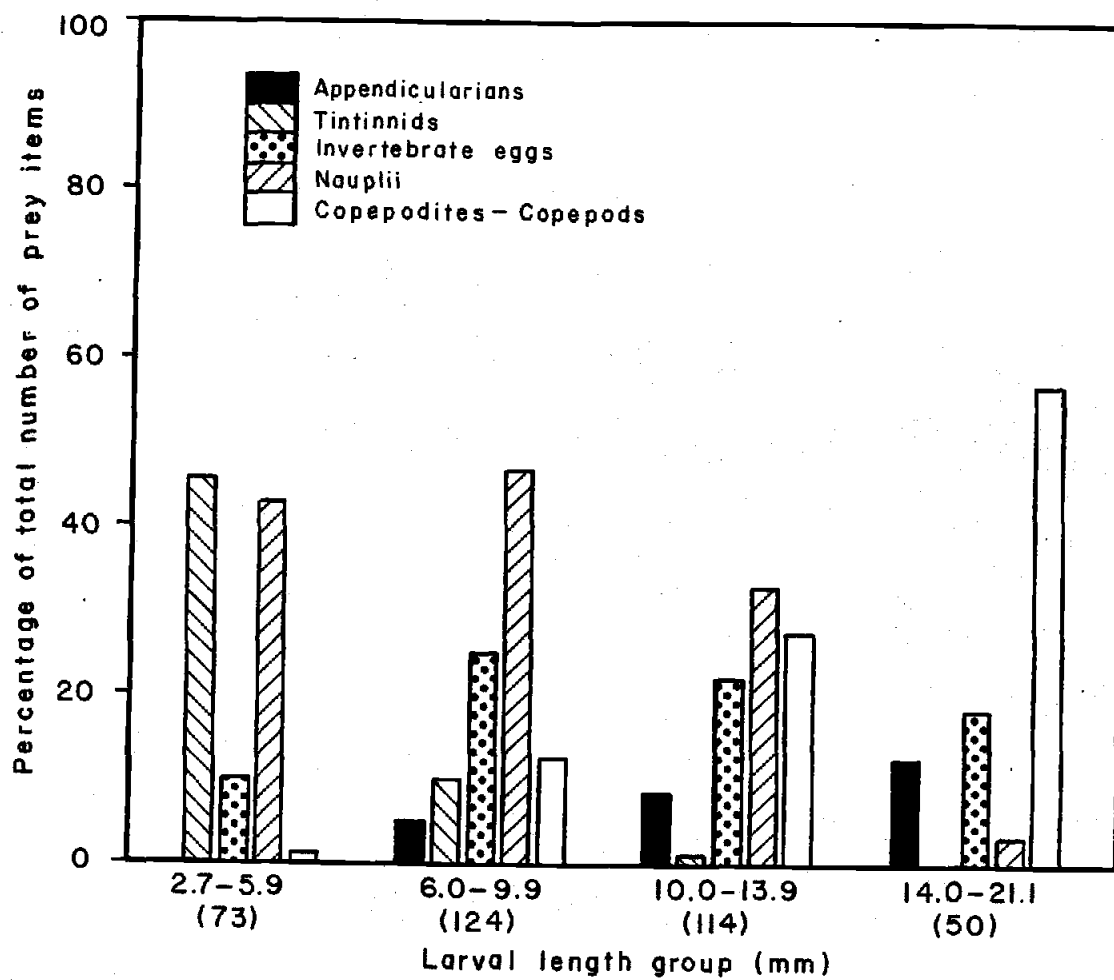


Figure 5. Diet composition of major prey items of *Isopsetta isolepis* larvae from 1973. The numbers in parentheses are the numbers of larvae examined from each length group.



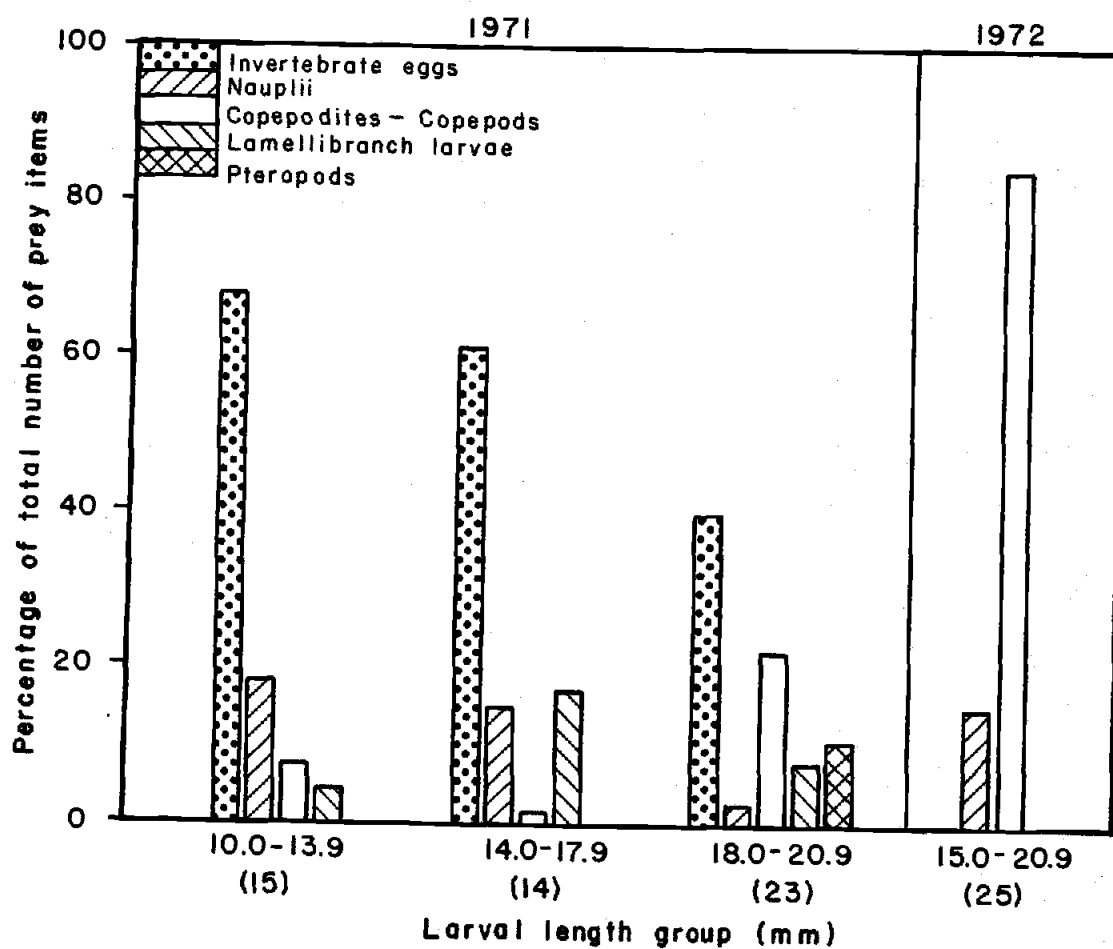


Figure 6. Diet composition of major prey items of *Isopsetta isolepis* larvae from 1971 and 1972. The numbers in parentheses are the numbers of larvae examined from each length group.

larvae greater than 15 mm SL had a less varied diet than in both 1971 and 1973, ingesting almost exclusively nauplii, copepodites, and copepods (mainly Acartia longerimis, Pseudocalanus sp., and Oithona spp.).

Parophrys vetulus. The diet of Parophrys larvae in 1973 was very different from that of Isopsetta larvae (Figure 7 and Table 3). Appendicularians, probably Oikopleura spp., were consumed almost exclusively. Only larvae less than 10 mm SL ingested a few nauplii and invertebrate eggs. Appendicularians were almost always found in the gut as highly digested remains, which consisted of spheroid oblong brown fecal pellets surrounded by a clear matrix and sometimes the trace of a tail. At times the gut contained only a clear mushy substance, with little or no structure. Only rarely were appendicularians in perfect, undigested condition; in these cases they were in the esophagus. Generally, however, food items were not found in the esophagus or foregut region, and were instead located throughout the mid and hindgut regions.

In 1971 (Figure 8 and Table 3), appendicularians still dominated the diet of Parophrys larvae greater than 5 mm SL. Tintinnids, invertebrate eggs and nauplii, however, were ingested to a greater extent than in 1973. There were no differences in diet in relation to station for Parophrys larvae collected from both years.

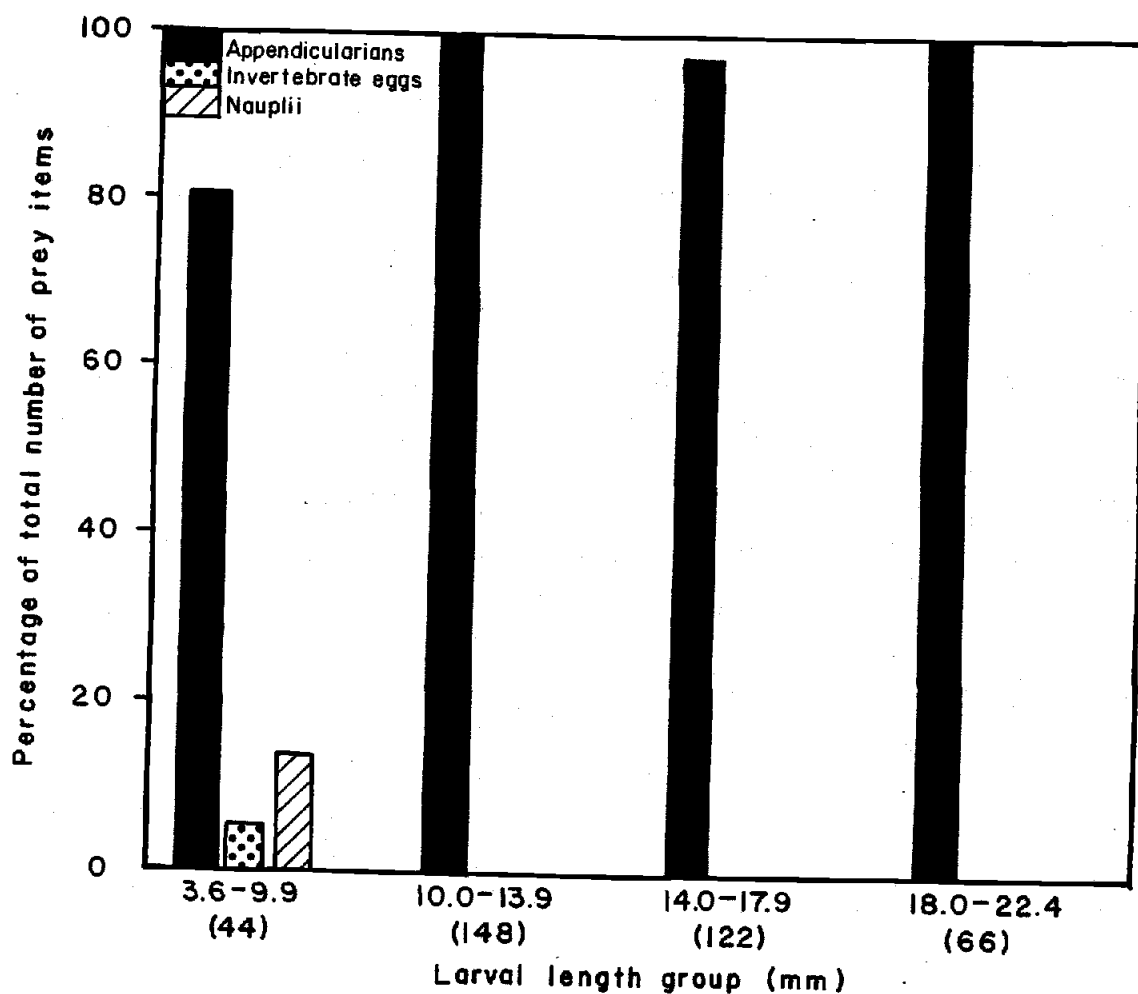


Figure 7. Diet composition of major prey items of *Parophrys vetulus* larvae from 1973. The numbers in parentheses are the numbers of larvae examined from each length group.

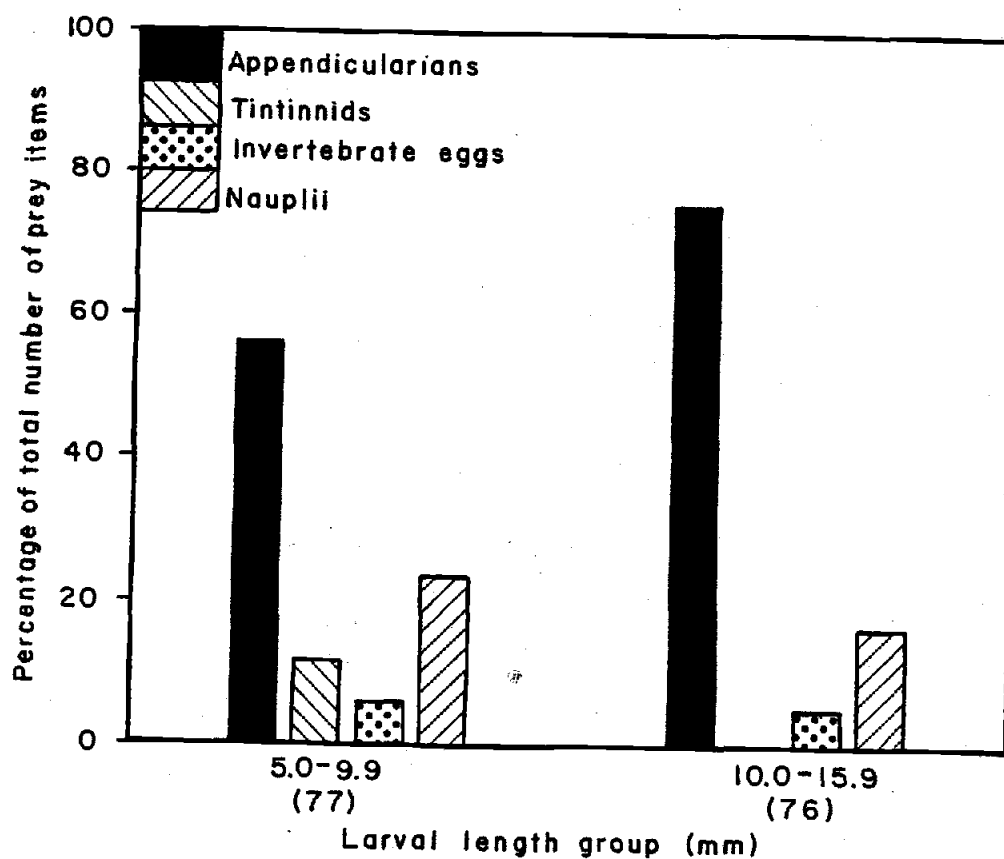


Figure 8. Diet composition of major prey items of Parophrys vetulus larvae from 1971. The numbers in parentheses are the numbers of larvae examined from each length group.

### Larval-Prey Size Relationships

The maximum size prey which can be ingested is determined by larval mouth size (Shirota 1970). Prey width, not length, is the critical measurement in determining prey size limitations since fish larvae usually engulf oblong prey (such as copepods) head first (Hunter 1981). Mean prey width increased with larval fish size increase for both Isopsetta (Figure 9) and Parophrys (Figure 10). The minimum width food ingested remains relatively constant for Parophrys and Isopsetta, as does the maximum width food for both species above 14 mm SL. For both species, the maximum prey size ingested was less than the size of prey the larvae apparently could have engulfed, particularly at larger fish sizes, as is indicated by the difference between fish mouth width and maximum prey width.

For Isopsetta, however, mean prey size increases more than mean prey width indicates, since prey items change ontogenetically from primarily sphere-like forms (tintinnids, invertebrate eggs, nauplii) to more elongated spheroids (copepodites-copepods). Thus, mean prey volume increases more with larval length increase than does mean prey width (Figure 9).

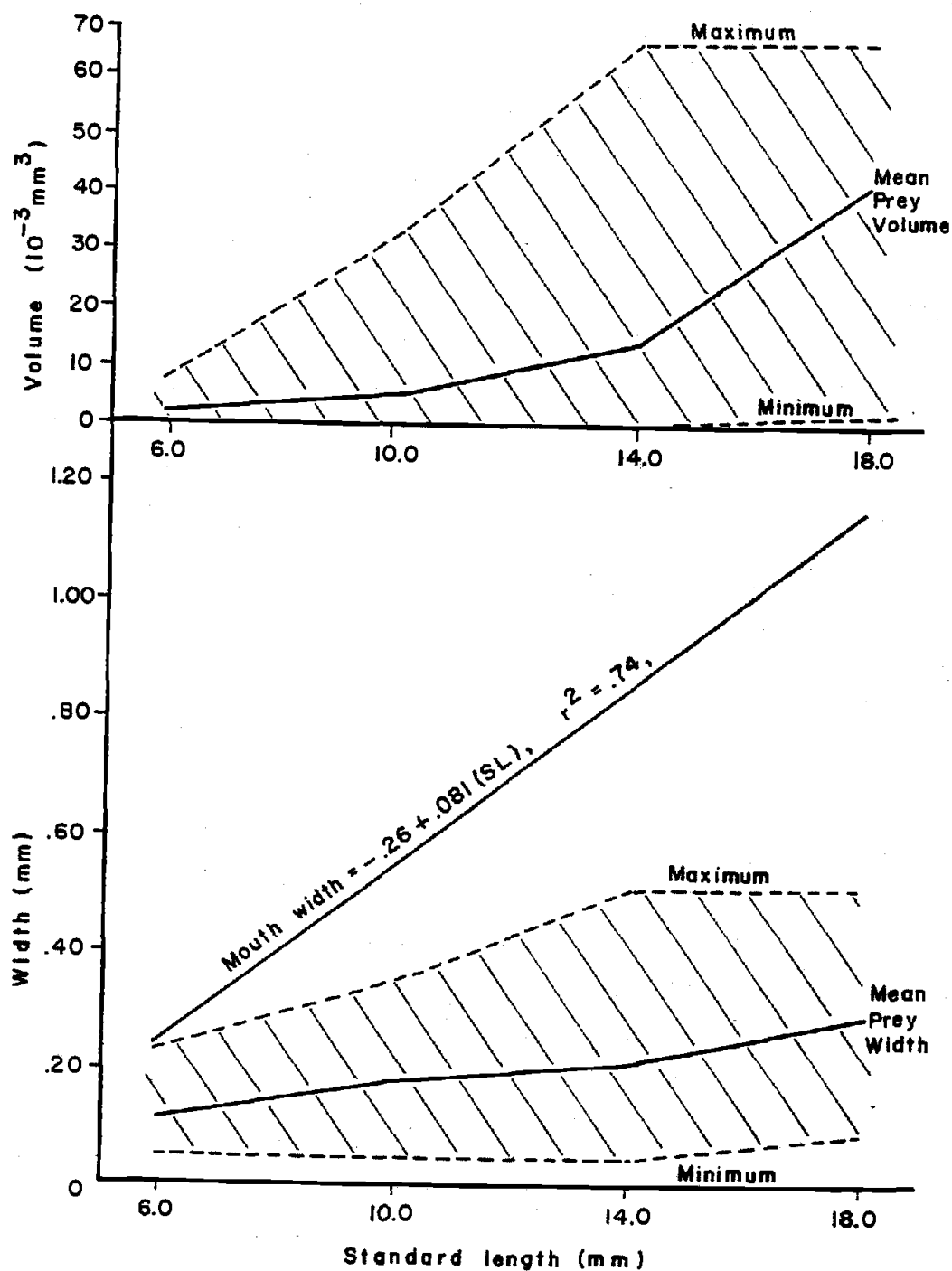


Figure 9. Larval-prey size relationships for Isopetta isolepis from 1973 (n = 361 Isopsetta).

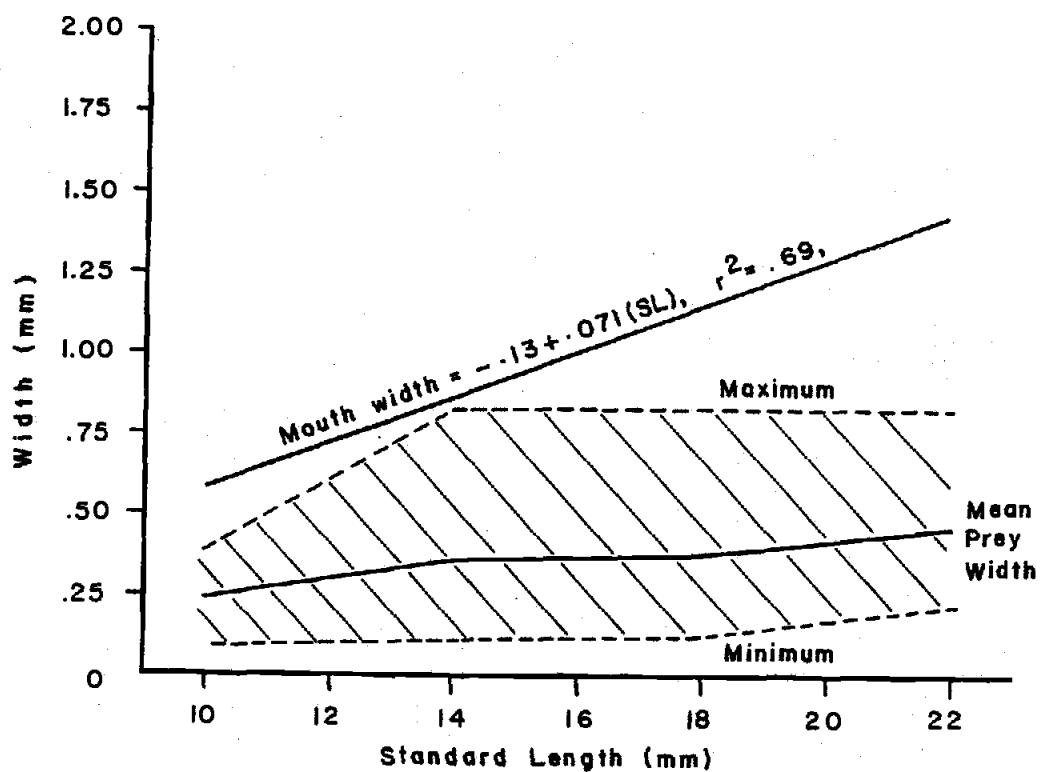


Figure 10. Larval-prey size relationships for *Parophrys vetulus* from 1973 ( $n = 380$  *Parophrys*).

### Appendicularian Size Relationships

The 202 appendicularians (Oikopleura spp.) examined from plankton net collections had a mean of 2.67 fecal pellets with a maximum of five. This was similar to Shelbourne's (1962) value of 2.65. Only five of the 202 appendicularians had no fecal pellets, and 78% had two or three. A relationship was established between size of Oikopleura and size of its fecal pellets. Generally, the larger the appendicularian, the larger the fecal pellets (Figure 11). There is a wide spread of variability, however, because some small fecal pellets were also found within larger appendicularians. In addition, large variability in the model is the result of its being predictive (Neter and Wasserman 1974). Prediction intervals are wider than confidence intervals because specific values, not mean values, are being predicted.

Smaller Parophrys from 1973 ingested a greater percentage of small appendicularians, as indicated by size frequencies of fecal pellets found in the guts of Parophrys larvae (Figure 12). Mean fecal pellet size, and thus mean size of appendicularian ingested (and mean prey width, see Figure 9), increased with larval size. Larvae larger than 10 mm SL, however, contained a range of fecal pellets from the smallest (.05 mm) to the largest (.40 mm).



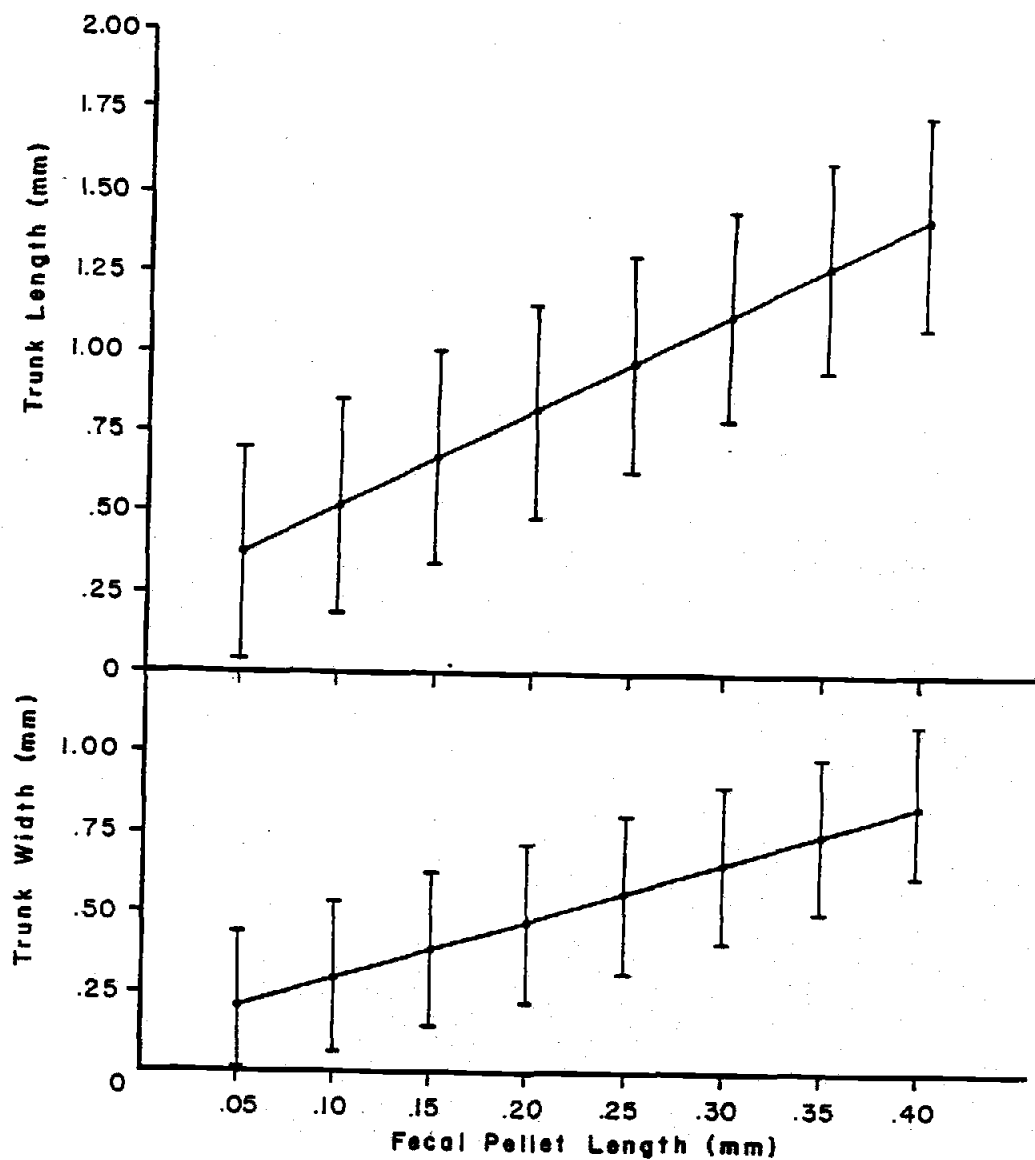


Figure 11. Appendicularian-fecal pellet size relationships ( $n = 202$  appendicularians, with a mean of 2.67 fecal pellets each):

$$\begin{aligned} \text{trunk length} &= .23\text{mm} + 2.98(\text{fecal pellet length}), r^2 = .78 \\ \text{trunk width} &= .12\text{mm} + 1.79(\text{fecal pellet length}), r^2 = .70 \end{aligned}$$

The vertical bars are .95 prediction intervals.

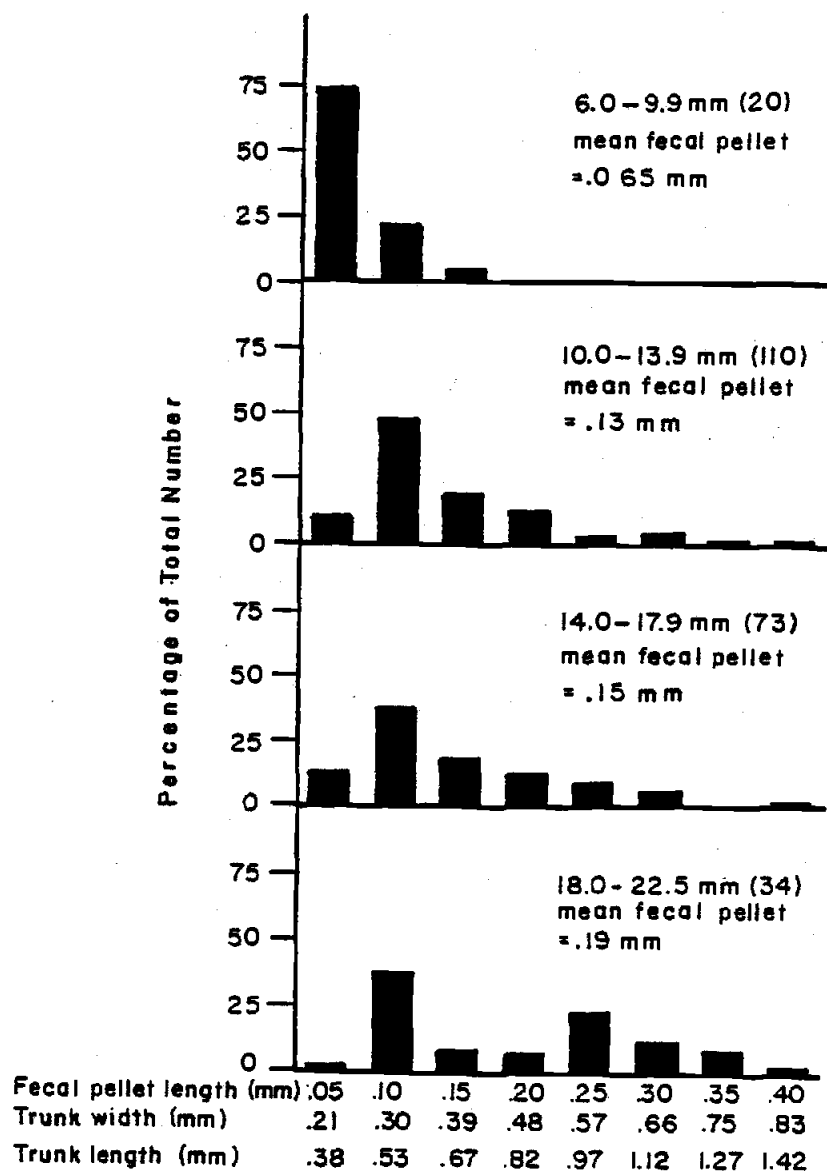


Figure 12. Gut fecal pellet size frequencies for four length groups of *Parophrys vetulus* larvae from 1973. Corresponding appendicularian trunk widths and lengths are below. The numbers in parentheses are the numbers of larvae examined from each length group.

### Morphometrics

All morphometric relationships for Parophrys and Isopsetta larvae were linear, except for Parophrys posterior body depth-SL in 1971, which fit best to a natural log function (Figures 13 and 14). Regressions of Parophrys eye diameter, head length, and pectoral body depth on standard length were compared between 1971 and 1973 (Figure 13). The slopes of all three relationships differed significantly between years, with 1973 increasing more rapidly in all cases. In addition, the intercept of pectoral body depth-SL differed between years, with a greater value in 1971. All mean ratios (head length/SL, pectoral body depth/SL, and posterior body depth/SL), differed significantly between 1971 and 1973, with 1973 having greater values in all cases (Table 4).

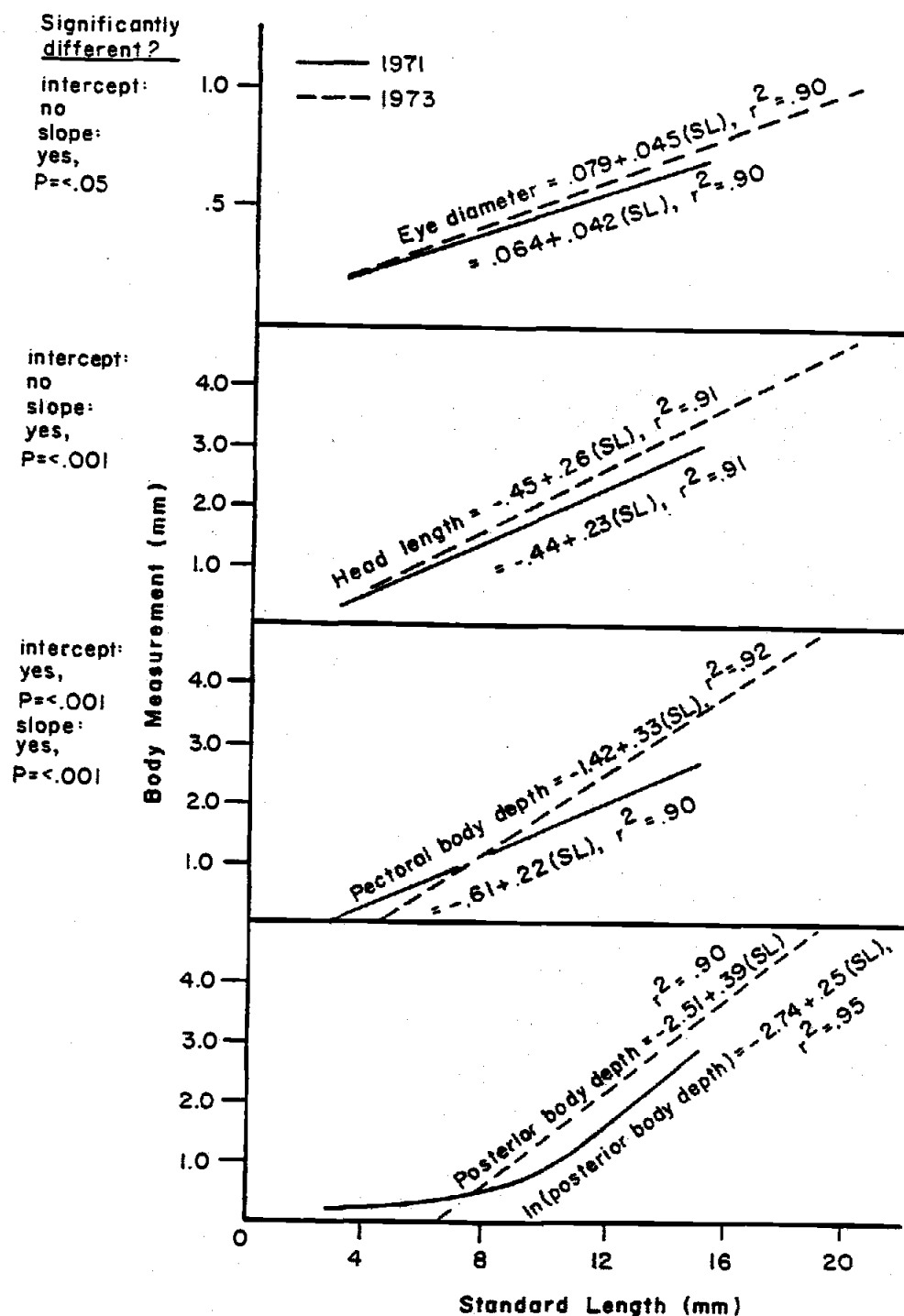


Figure 13. Morphometric relationships for Parophrys vetulus larvae from 1971 ( $n = 183$ ) and 1973 ( $n = 380$ ).

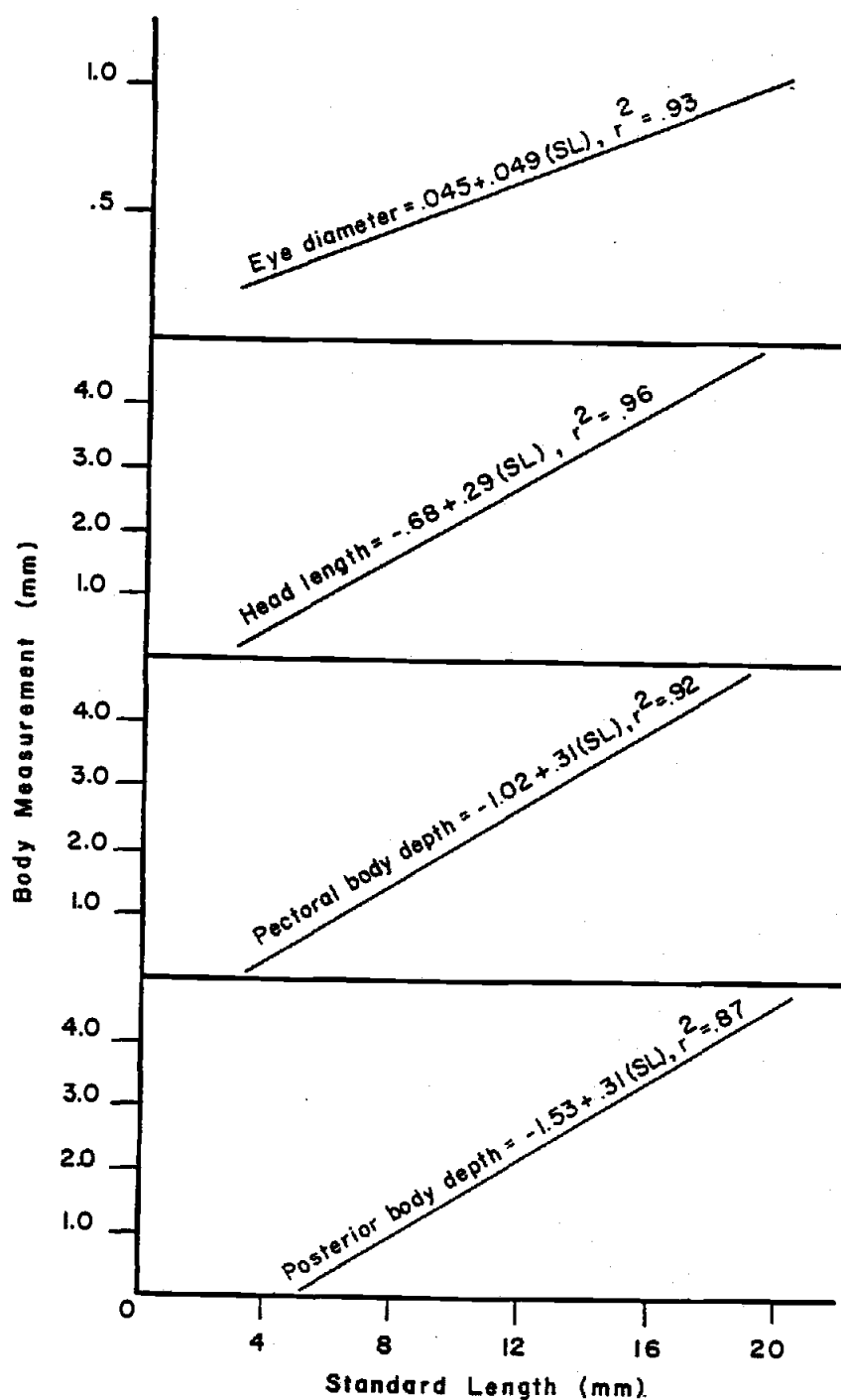


Figure 14. Morphometric relationships for Isopsetta isolepis larvae from 1973 (n = 361).

Table 4. Morphometric ratios for Parophrys vetulus larvae from 1971 and 1973.

length group (mm)	number of larvae		mean standard length (mm)		MEAN RATIOS					
					head length SL		pectoral body depth SL		posterior body depth SL	
	71	73	71	73	71	73	71	73	71	73
9.0- 9.0	18	12	9.66	9.61	.171	.189*	.141	.162*	.072	.095*
10.0-10.9	16	31	10.43	10.58	.174	.213**	.141	.187**	.074	.124**
11.0-11.9	27	30	11.34	11.47	.185	.220**	.159	.203**	.090	.151**
12.0-12.9	20	43	12.26	12.40	.202	.222**	.177	.213**	.117	.175**

\*significantly different ratios between years,  $P = < .05$

\*\* $P = < .001$

## DISCUSSION

### Variations in Feeding

Both Parophrys and Isopsetta larvae displayed a pattern of diurnal feeding typical of larval fish (Figures 2 and 3), which generally are visual feeders (Bainbridge and Forsyth 1971; Arthur 1976; Last 1978 a,b; 1980; Cohen and Lough 1983). More Parophrys than Isopsetta guts were empty during early morning hours (0200-0600), probably because of the higher digestibility of their prey; appendicularians lack the hard exoskeletons of copepods. Food in larval guts from early morning samples was very digested, indicating that it was from the previous day. Stomach fullness and digestive state did not vary significantly during the daylight period for either species. Thus, both species feed at relatively constant rates throughout daytime until darkness. At this time, feeding ceases and food present in the gut digests almost completely during the night. At daybreak, feeding commences; most larvae had food in their guts very soon after dawn.

Ontogenetic variations in feeding were also observed for

both Parophrys and Isopsetta. A higher percentage of small larvae had empty guts during daylight hours, a typical feeding pattern of larval fish (Last 1980; Cohen and Lough 1983). One possible explanation of this pattern is that upon capture and fixation regurgitation is more common at small sizes of larval flatfishes due to the straight gut. The more complex coiled gut at larger sizes could hinder regurgitation. To examine the effects of capture and preservation on larval gut contents, Hay (1981) released ten day old lab reared herring (Clupea harengus pallasii) larvae into the mouth of a towed plankton net at sea. After recovery and preservation in 4% formalin, the towed larvae had 63% empty guts, in contrast to 3% for the control group. All sizes of C. harengus larvae have straight guts, as do young Parophrys, whose gut begins to coil at about 4 mm SL. It is possible that some regurgitation by larger Parophrys and Isopsetta larvae also occurred upon collection in this study because prey items were rarely in the foregut or esophagus region. Extensive regurgitation was not evident, however, because prey were almost never only in the hindgut region if collected during daylight hours.

Another explanation for fewer prey in small larvae is an ontogenetic change in feeding success. Small larvae, particularly first feeding larvae, require higher prey concentrations of a more limited size range (.04-.10 mm) than



larger larvae (Hunter 1981). Small larvae have a shorter perceptive distance, often less than a body length (Blaxter and Staines 1971), which, combined with slower swimming speeds, results in low searching rates, usually less than a liter of water per hour (Hunter 1972; Houde and Schekter 1981). In addition, small larvae are handicapped by a lower percentage of capture success and longer handling times.

#### Larval Morphology

Body measurements of larval fish change due to preservation. Plaice, Pleuronectes platessa, had a 2.6% shrinkage in length when placed in 4% buffered formalin; after two weeks no further shrinkage occurred (Lockwood 1973). Herring, Clupea harengus, larvae shrunk about 5% in standard length after preservation in a 4% formalin in seawater solution; newly hatched C. harengus may continue to shrink up to 10% (Schnack and Rosenthal 1978; Hay 1982). Northern anchovy, Engraulis mordax, shrunk 8% in formalin, independent of size; an additional 3% shrinkage occurred if the larvae had been net damaged (Theilacker 1980). Laroche et al. (1982) found that 4 to 5 mm SL Parophrys larvae shrunk 5.1% after four months in 10% seawater diluted formalin. Parophrys and Isopsetta larvae in this study undoubtedly have shrunk to some degree, although more robust flatfish larvae

probably are not as susceptible as long slender C. harengus and E. mordax. Sampling and preservation techniques were the same in all the study years, however, and therefore shrinkage should be the same in all years, thus allowing valid morphological comparisons.

During starvation, larval fish undergo characteristic morphological changes. Larval length continues to increase, but the total body mass decreases, resulting in a thin larvae with abnormal body proportions. This has been observed for herring (Clupea harengus) and plaice (Pleuronectes platessa) (Ehrlich et al. 1976), pike (Esox lucius) and carp (Cyprinus carpio) (Kostomarova 1962), northern anchovy (Engraulis mordax) (O'Connell 1976), Japanese anchovy (Engraulis japonica) (Nakai et al. 1969), and jack mackerel (Trachurus symmetricus) (Theilacker 1978). The first structure to deteriorate is the digestive tract, resulting in a decrease in the size of the epithelial cells, and thus a reduction in the gut diameter. With continued starvation, all body tissues atrophy and deteriorate. One result is that the head may look disproportionally large because of the breakdown of the gut and reduction in the trunk musculature. Damage may be irreversible after only a few days, particularly for young larvae; death from starvation may occur even if food is then available (May 1974).

There have been attempts to identify poorly fed larvae by defining various condition factors; the higher the value of a condition factor, the better fed the larvae. Hempel and Blaxter (1963) defined a condition factor for C. harengus as  $\text{weight/length}^3$ . Ehrlich et al. (1976) used a similar condition factor for C. harengus and P. platessa larvae. Wyatt (1972), working with P. platessa, defined an index of condition, H/L, as the ratio of the height of the body musculature (H) to body length (L). This was a quantitative measure of Shelbourne's (1957) earlier qualitative description of P. platessa larval condition. Shelbourne compared larval P. platessa from high and low density plankton patches. Those from high density patches were more robust with a heavy trunk musculature, conspicuous gut, and thus greater body depth to length ratio.

Theilacker (1978; 1981) analyzed the condition of fed and starved jack mackerel (Trachurus symmetricus) larvae using a stepwise discriminant analysis. This method chose the set of body measurements (standard length, head length, eye diameter, body depth at the pectoral, body depth at the anus) that best described larval condition, since no single body measurement (plotted against standard length) was adequate to satisfactorily discriminate between the fed and starved larval groups.

In my study, however, single body measurements did

discriminate between larval groups. To compare Parophrys larval conditions between the years of 1971 and 1973, regressions of eye diameter, head length and pectoral body depth on standard length were examined (Figure 13). All three relationships had significantly different slopes, indicating that eye size, head length, and pectoral body depth all increased more in relation to standard length in 1973 than in 1971, all signs of greater robustness in 1973. The intercepts of the pectoral body depth regressions are also different, which is difficult to interpret. Perhaps egg sizes were different between the two years, which could result in different size larvae at hatching (Ware 1977). Egg size has been known to vary within a fish species dependent upon the date of spawning, parent size, and other factors (Bagenal 1971).

Posterior body depth is an especially important parameter to compare, because it is an indication of the condition of body musculature, which is reduced on thin, starving larvae. The relationships between posterior body depth to standard length, however, were not statistically compared because the 1971 relationship was logarithmic whereas the 1973 relationship was described better by a linear fit. This points out a problem with the current linear fit for all parameters. At very small sizes, the distributions level out, although not enough for a logarithmic or exponential fit to be better for any relationship

except for that of 1971 posterior body depth. Perhaps the best fitting curve would be two phased, logarithmic at smaller sizes and linear above about 10 mm SL.

To avoid this problem, ratios of head length, pectoral body depth, and posterior body depth to standard length were compared for four length ranges that were adequately represented in both 1971 and 1973, 9.0-9.9, 10.0-10.9, 11.0-11.9, and 12.0-12.9 mm SL (Table 4). The results show the same trends as above; larvae from 1973 are more robust. This suggests that 1973 was a year of better feeding conditions for Parophrys larvae than 1971.

#### Diet Composition

Isopsetta isolepis. Isopsetta larvae had a varied diet (Figures 5 and 6, Tables 1 and 2), as is typical of larval fishes. The major food sources of Isopsetta are various copepod life stages, which is also true for the larvae of Pacific hake (Merluccius productus) (Sumida and Moser 1980), Pacific sardine (Sardinops sagax), northern anchovy (Engraulis mordax) and jack mackerel (Trachurus symmetricus) (Arthur 1976), cod (Gadus morhua) (Last 1980), herring (Clupea harengus) (Bainbridge and Forsyth 1971), and others (Last 1980). An ontogenetic change in diet composition, with smaller larvae ingesting more small prey

items, such as tintinnids and nauplii, is also displayed by these species, and by Isopsetta larvae in this study. As size increases, ingestion of larger prey is necessary for the growth and survival of fish larvae (Howell 1973; Hunter 1977).

The maximum size of prey ingested is well below the maximum possible size as determined by mouth width (Figure 9). Although it is mechanically possible for Isopsetta to consume larger species of copepods, they did not. This is a trend commonly observed in other species of larval fish (de Mendiola 1974; Arthur 1976; Last 1978 a,b; Sumida and Moser 1980). Perhaps they are limited by other factors such as prey capture and handling abilities. Carapace width of copepods may not be a good functional measurement because appendages, in particular long spiny antennae, are not considered. Larvae may be able to ingest a large copepod if it was placed inactive within its reach, but to capture a fast moving live prey and maneuver it to the necessary head first position would be difficult and energy consuming. Thus, small easily captured prey may be preferable to faster moving large prey, resulting in size selectivity due to differential capture probabilities (Drenner et al. 1978). In addition, prey abundances in the plankton influence larval diet. Large prey may not be sufficiently abundant to be selected for. Plankton availability off Oregon will be discussed in a later section.

The two major copepod species ingested differed between years (Tables 1 and 2), but were of similar sizes, about one millimeter cephalothorax length. In 1973, the primary species was Pseudocalanus, whereas in both 1971 and 1972, Acartia longerimis was dominant, along with Microsetella rosea in 1971 and Oithona spp. in 1972, both smaller species. M. rosea is a pelagic harpacticoid species, so there is no indication of benthic feeding (Newell and Newell 1977). Also unique to 1971 was the ingestion of lamellibranch larvae and pteropods, both also pelagic. Since Isopsetta larval specimens examined from 1971 and 1972 are only from one day of sampling each, however, it is not possible to make generalizations concerning overall trends for these years. Differences may be due to differences in prey availability, which will be discussed further.

Parophrys vetulus. In contrast, Parophrys larvae have a very specific diet, composed of 97% appendicularians in 1973 (Figure 7, Table 3). In 1971, a greater percentage of other food items was ingested, but appendicularians still dominated the diet (Figure 8, Table 3). In both years, smaller larvae consumed more non-appendicularian food items. This could be due to the feeding limitations of small larvae, previously discussed in the section on variations in feeding. There also may not be adequate concentrations of very small appendicularians to support small

larvae.

Last (1980), in his study of the food of twenty species of fish larvae in the west-central North Sea, states that there are two distinct types of diet, "...one, that of pleuronectiform larvae, is based on appendicularia; the other, that of larvae of the other species, is based primarily upon copepods...". This is a broad generalization; of the twenty larvae studied, six were pleuronectiform, and only the following four of these had appendicularians as a major diet component: Glyptocephalus cynoglossus (75.3% of the total number of food items); Arnoglossus laterna (72.3%); Pleuronectes platessa (49.7%); and Microstomus kitt (39.6%). The other two species, Limanda platessa and Buglossideum luteum, only consumed 4.2% and 2.0% appendicularians, respectively. In other work by Last (1978a) on food of four species of pleuronectiform larvae (Pleuronectes platessa, Platichthys flesus, Limanda limanda and Solea solea) only Pleuronectes platessa had a diet based upon appendicularians (86.0%), S. solea consumed none, and Platichthys flesus and L. limanda ingested a variable, although usually low, percentage. All these species ingest a higher percentage of appendicularians at larger sizes, as do Parophrys vetulus larvae.

Some species of non-pleuronectiform larvae also ingest appendicularians. Appendicularians often are a major component



of the diet of larval sand eels, Ammodytes marinus, in the North Sea (Ryland 1964; Wyatt 1974). In addition, larvae of the chub mackerel, Scomber japonicus, were found to ingest 63.7 to 100% appendicularians in the southeastern Pacific (Lipskaya 1982).

The species that has most consistently been reported to ingest primarily appendicularians (notably Oikopleura dioica) as larvae is the plaice, Pleuronectes platessa (Shelbourne 1953; 1957; 1962; Ryland 1964; Wyatt 1974; Last 1978a). As with Parophrys vetulus larvae, Pleuronectes platessa gut contents composed of appendicularians were almost always digested, consisting of "...black cigar-shaped pellets, always associated with transparent, indigestible matrix vesicles." (Shelbourne 1953). The diet of larger P. platessa larvae is composed of a larger percentage of appendicularians, often as high as 100%. Similar to the current work, Shelbourne (1962) showed a size relationship between the larval predator and appendicularian prey.

### Appendicularians

Appendicularians are common tunicates in the upper 100 meters of nearshore waters (Alldredge 1976 a,b; 1977; Alldredge and Madin 1982). Members of the Oikopleuridae, the most common

family off Oregon, have an oblong spheroid trunk and a long thin tail. They construct a mucus house around their body through which they filter food particles by beating their tail and setting up currents of water. When the mucus house becomes clogged and inefficient at collecting food, it is abandoned and a new one built. In the laboratory at 13°C, mean generation time of Oikopleura dioica was 9.5 days (Paffenhofer 1973). Each female spawned 51 to 577 eggs. Almost all eggs hatched, and 26 to 73% of the young survived to reproductive age. Thus, Oikopleura may be a good prey in terms of population growth potential.

Very high densities of the appendicularian Oikopleura longicauda have been observed by Owen (1966) and Alldredge (1982). Owen inferred that these aggregations were maintained by a thermohaline driven vortex system, whereas Alldredge suggested that the parallel slicks, called windrows, were the result of "wind-wave interaction" causing Langmuir vortices. In both cases, O. longicauda are carried along surface waters to a convergence area, where they maintain themselves by swimming upward. During April 1981, Alldredge (1982) observed appendicularians in densities as high as 3565 per liter, one to eight centimeters deep. All were sexually mature and free swimming without their mucus house. On days of more intense winds, O. longicauda were more dispersed due to wind induced chop, suggesting that water column stability is an important

factor in maintaining high densities of appendicularians.

The means by which larval fish ingest appendicularians is unknown, since most mucus houses are larger than many larval fish mouths. Larvae may crush the house and engulf house and appendicularian together. Abandoned appendicularian houses have been reported as a food source for Oncaea spp. copepods and the sergeant major Abudefduf sp. by Alldredge (1972; 1976 a,c). Copepods feed on phytoplankton from the mucus house, but this is not generally a good larval fish food source (Scura and Jerde 1977). Although Abudefduf feed on the houses, adult fish have a more advanced digestive system than larval fish. Mucus houses and associated phytoplankton and fecal pellets may be largely indigestible to larval fish (and thus their ingestion would be an inefficient waste of digestive energy). In this study, there was no evidence of mucus houses within Parophrys guts, but most gut contents were very digested and perhaps the houses would be indiscernible among the amorphous material. Undigestible phytoplankton remains (diatom frustules, dinoflagellate and radiolaria tests), however, were not found in guts. Thus, the evidence from gut contents suggests that Parophrys larvae feed on appendicularians without houses.

Since appendicularians are without their houses only a very small percentage of the time, it would be necessary for larvae to

extract the appendicularian in some way if they did not eat the house. Perhaps larval fish simply break through the mucus and seize the appendicularian. Force would be necessary, since appendicularians do not easily abandon their houses due to the energy expenditure required to build a new one, and because of their vulnerability to predation outside of it (Alldredge 1976a). Four Oikopleura species observed by Alldredge (1976a) in the field required a mean of 2.8 to 6.6 gentle prods to force house jettisoning.

In this study, a relationship was established between appendicularian size and fecal pellet size; larger appendicularians have larger fecal pellets (Figure 11). This appendicularian-fecal pellet size relationship was used to determine predator-prey relationships for Parophrys larvae. As expected, smaller larvae have a larger percentage of small fecal pellets in their guts than larger larvae (Figure 12); because of mouth size limitations they are unable to ingest larger appendicularians. Larger Parophrys may be selecting larger prey, but they are still ingesting appendicularians of all sizes. The upper limit in fecal pellet size (.40 mm) corresponds to an appendicularian size of 1.42 mm length and .83 mm width, which reflects the upper size boundary of appendicularians abundant off Oregon.

Shelbourne (1962) developed a similar predator-prey size relationship for plaice larvae (Pleuronectes platessa) feeding on the appendicularian Oikopleura dioica in the North sea. He found a linear size relationship between Oikopleura from the plankton and its fecal pellets, and used the information to determine the size composition of Oikopleura ingested by P. platessa larvae based on fecal pellets in the gut. His results are similar to those of this study; small larvae are restricted to small appendicularians, but larger larvae eat a range of appendicularian sizes. Shelbourne concludes that "...competition for food will therefore be keenest in the early larval stage, when prey-size restriction prevails."

Ryland (1964) conducted a similar study in the North Sea and found the same predator-prey size relationship between P. platessa larvae and appendicularians as did Shelbourne, but found a different relationship between Oikopleura and their fecal pellets. Ryland's results, however, basically agree with the results of this study; pellet length is about one-third appendicularian trunk length (Shelbourne: trunk length =  $4.4(\text{fecal pellet length})$ ; Ryland:  $t.l. = -.017\text{mm} + 2.96 \text{ f.p.l.}$ ; this study:  $t.l. = .23\text{mm} + 2.98 \text{ f.p.l.}$ ). This relationship probably varies due to different species compositions of appendicularians in the plankton at different locations and times.

### Zooplankton Abundances and Seasonality

Patchiness. Larval fishes may require high food concentrations to survive, particularly at small sizes when densities as high as 20 food items per ml may be necessary (Theilacker and McMaster 1971). More common food density requirements for high survival in the laboratory are on the order of .5-5.0 microcopepods per ml (Houde 1978; Houde and Schekter 1981). Food density requirements are variable and dependent upon both fish size and species and prey size and type. Average densities in the open sea (13-40 nauplii/liter, 1-7 copepodites/liter, Hunter 1981), however, are well below these requirements.

This discrepancy may be due to problems in relating laboratory to field results, but an additional explanation is the patchy nature of the plankton. Plankton aggregations may result in patches with densities much higher than conventional integrating sampling gear indicates (Haury and Wiebe 1982). Recently, the occurrence of small-scale patchiness has been demonstrated by Owen (1981) who vertically sampled at twenty centimeter intervals.

Ocean stability may be a major factor in increasing patch

densities during certain times of the year. Upwelling is necessary to replenish surface nutrients, but upwelling and storms may disrupt larval food aggregations, resulting in homogeneous, but lower densities (Lasker 1975; 1978). In addition, upwelling may disperse food sources and result in diatom blooms, which are inadequate larval food sources. Lasker (1978) has shown that in the southern California Bight, stable oceanographic conditions are essential for the development of chlorophyll maximum layers in which dinoflagellates reach densities higher than 30 per ml. The co-occurrence of first feeding northern anchovy, Engraulis mordax, and high densities of this food source is critical to their survival (Lasker 1975).

Zooplankton off Oregon. It is impossible to determine if larval feeding trends in this study are due to selectivity or availability without coincident sampling of Parophrys and Isopsetta larvae and their food sources. It is possible to speculate, however, using information from general zooplankton surveys conducted by Peterson and Miller (1975; 1976; 1977) off the Oregon coast from June 1969 through July 1972. The smallest zooplankton ingested by larval fish (tintinnids; small nauplii, invertebrate eggs and appendicularians) were not sampled during these surveys because of mesh size (.24 mm). Samples were taken about every two weeks at NH1, NH3, NH5, and NH10. The hydrography of this area is seasonal. Winds during winter months are

generally from the southeast, resulting in ocean flow northward and toward shore. In contrast, during summer, winds are often from the north, causing surface transport to the south and away from shore, resulting in coastal upwelling. Thus, zooplankton species composition is also seasonal, with summer species having northern affinities and winter species having southern affinities.

Copepods are the most abundant component of the zooplankton at all times. The most common species in winter months in order of rank are Pseudocalanus sp. (a mean of 28.6% of the total zooplankton catch), Oithona similis (16.0%), Paracalanus parvus (14.2%), Ctenocalanus vanus (8.6%), Acartia longiremis (8.5%), Corycaeus anglicus (10.1%), and Calanus marshallae (4.8%). Corycaeus anglicus and Calanus marshallae were never ingested by Parophrys or Isopsetta larvae, although Calanus marshallae eggs were common prey items for Isopsetta larvae. This is due to the large size of Calanus marshallae (cephalothorax length 3.2-3.6 mm) and perhaps the sharp pointed posterior thorax of Corycaeus anglicus. Except for Calanus marshallae and Oithona similis (cephalothorax length of .5 mm), all the listed species have a cephalothorax length of about one millimeter. In contrast, in summer months, Pseudocalanus sp. still ranks first (46.7%), but next in rank are Acartia longiremis (20.7%), Calanus marshallae (9.0%), Acartia clausii (11.4%), and Oithona similis (6.8%).



Appendicularians, mainly Oikopleura spp., are most abundant in fall and winter months (Figure 15), ranking in abundance just after Acartia longiremis, and consisting of a mean of 5.7% of the total numbers of zooplankton caught. The presence of Oikopleura in summer samples was positively correlated with low surface salinities (below 33.0‰). Oikopleura were rarely observed in areas of active upwelling with surface salinities above 33.5‰ (Peterson and Miller 1976). Alldredge and Madin (1982) have suggested that upwelling may be detrimental to appendicularian abundances because the resultant high phytoplankton densities may quickly clog their mucus houses.

Total zooplankton abundances are lowest during winter from November through April, although the extreme low occurs only through January or February. Abundances are highest during upwelling, from June through August, often remaining high through autumn. Abundances may be higher closer to shore, but there are few definite winter spatial patterns as compared to summer months when upwelling maintains species gradients (Peterson and Miller 1976).

Peaks of zooplankton abundance may occur during the winter months of February or March due to reduced cloud cover (and thus increased light) and reduced wind speeds (resulting in increased water column stability). This winter abundance peak occurred in

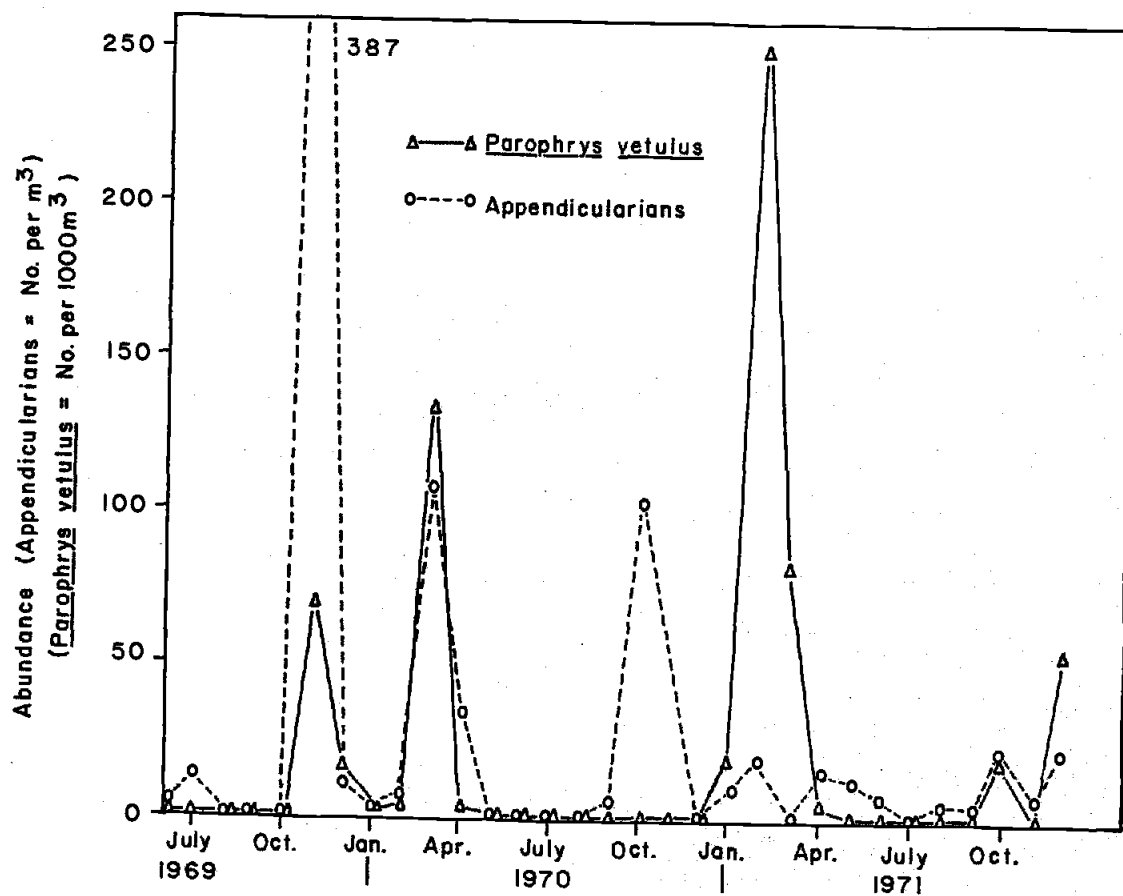


Figure 15. *Parophrys vetulus* larvae and appendicularian mean abundances at NH5 from June 1969 through December 1971 (*Parophrys* information from Mundy 1984, appendicularian information from Peterson and Miller 1976).

all three years of the study conducted by Peterson and Miller (1976). In 1971, the peak occurred in mid-February and was composed of high numbers of mature and immature Pseudocalanus sp. and Calanus spp., indicating an actively reproducing population. Net mesh size was too large to retain the smallest nauplii and life stages of Pseudocalanus, but larger Calanus nauplii were sampled. Zooplankton abundances decreased in March and April. Oikopleura abundance followed the same trend, but Oikopleura abundance was low during the entire year of 1971 (Figure 15), particularly in comparison to much higher copepod abundances.

There is no information on zooplankton abundances during the major year of this study, 1973. The winter of 1973, however, had light winds and reduced cloud cover (Laroche and Richardson 1979), prerequisites for higher plankton abundances. Thus, 1973 may have been a year of high larval food availability. This speculation is further supported by the high degree of feeding incidence displayed by both Parophrys and Isopsetta larvae during 1973 (Figure 4). In contrast, Parophrys larvae were less robust and had more empty guts in 1971 (Figures 4 and 13), a year of known poor Parophrys feeding conditions due to low appendicularian abundances.

Relation to Isopsetta Feeding. On 28 June 1971, Isopsetta

larvae ingested a large percentage of Acartia longiremis, in contrast to 1973, when Pseudocalanus sp. was almost exclusively ingested (Tables 1 and 2). However, on 28 June 1971 at NH3 and NH5, A. longiremis were nearly twice as abundant as Pseudocalanus (mean abundances of 80.0 and 42.8 per cubic meter, respectively; Peterson and Miller 1976). Other unusual prey ingested in 1971, Microsetella rosea, lamellibranch larvae, and pteropods, were not taken or were of very low densities in the plankton on 28 June at NH3 and NH5. On 11 June 1972, the three major copepod species consumed, Acartia longiremis, Pseudocalanus sp., and Oithona, were all abundant in the plankton, with mean densities of 87.2, 196.9, and 29.1 per cubic meter, respectively. A. longiremis is more abundant in summer than in winter, and both 1971 and 1972 samples are from June, as compared to 1973 samples from March and April. In addition, the month of June in both 1971 and 1972 was a period of high plankton abundance, as evidenced by the high percentage of guts with food in 1971 and 1972 Isopsetta larvae, and the high numbers of food items per larvae (a mean of 12.9 and 25.5, respectively; Table 2). In contrast, Isopsetta from 1973 had lower numbers of food items in their guts (a total mean of 7.43; Table 1), and larvae were from winter months with commonly lower zooplankton numbers.

In 1973 Isopsetta ingested prey items common in previous plankton surveys, including invertebrate eggs, nauplii, the

copepod Pseudocalanus sp., and appendicularians. Thus, it appears that Isopsetta larvae are opportunistic, feeding upon available prey, instead of being as selective as Parophrys larvae.

Relation to Parophrys Feeding. Although 1971 was a year of low appendicularian abundances, Parophrys larvae still displayed a high degree of selectivity for appendicularian prey (66.3% of the total number of prey items). However, more tintinnids, invertebrate eggs, and nauplii were ingested in 1971 than in 1973 (a year of hypothesized high larval food availability), when appendicularians were ingested almost exclusively (Figures 7 and 8, Table 3).

Perhaps one important mechanism in concentrating appendicularians to densities adequate for successful larval Parophrys feeding are windrows, previously discussed in the section on appendicularians. Windrows have been observed off Oregon on days of light winds, but windrow plankton samples have not been analyzed. Since Parophrys larvae are not primarily neustonic, however, they are not relying totally on windrows. In a 48 hour sampling series conducted by Laroche and Richardson (1979) in March 1975, Parophrys larvae were 4079 times more abundant in the water column (mean sampling depth of 43 meters) than in the neuston (the upper 17.5 centimeters of water). From

both day and night samples, however, most Parophrys larvae taken in the neuston were larger than 10 mm SL, while most from the plankton were less than 10 mm SL. Perhaps older Parophrys larvae aggregate at the surface to take advantage of high densities of appendicularians, in windrows formed during stable periods. Larvae in the laboratory have shown an ability to stay within patches. Larval Engraulis mordax have an increased probability of turning in denser patches (Hunter and Thomas 1974), and larval Pleuronectes platessa decrease their time spent swimming when in higher food densities (Wyatt 1972). Thus, periods of light winds and increased sunlight which often occur in February and March off Oregon may produce concentrations of appendicularians and hence aid feeding of Parophrys larvae.

#### Selective Feeding

Parophrys larvae are highly selective for appendicularians. Larvae of other fish species, most notably the plaice, Pleuronectes platessa, also have this preference based upon gut content analysis of field caught larvae (Shelbourne 1953; Ryland 1964), but laboratory studies have not been conducted. Selective feeding on the basis of prey type as well as size has been displayed by other larval fish species. In the laboratory, Atlantic herring (Clupea harengus) larvae preferred Pseudocalanus

sp. and Oithona sp. copepods to Acartia sp., perhaps due to the greater burst speed exhibited by Acartia (Checkley 1982). In addition, mollusc veligers of a size similar to accepted food items were rejected by older C. harengus larvae, even though they were a major food item of younger larvae. Also in the laboratory, scaled sardine (Harengula pensacolatae), and bay anchovy (Anchoa mitchilli) preferred copepod nauplii, copepodites and copepods to barnacle or Artemia nauplii and invertebrate eggs (Detwyler and Houde 1970). First feeding northern anchovy (Engraulis mordax) fed on four species of dinoflagellates but rejected diatoms and small flagellates (Scura and Jerde 1977). Not all the ingested dinoflagellate species, however, were nutritionally adequate; small E. mordax did not survive on a diet of Gonyaulax polyedra.

Checkley (1982) suggests that food preferences are based upon nutritional value, and that "...recognition of different prey types may depend on prey shape, contrast, and movement, in addition to size." Young larvae may be less selective than older larvae due to inexperience, weaker prey capturing abilities, and a narrower spectrum of available prey. Thus, the diets of small larvae may have a greater diversity of prey items, perhaps even including nutritionally inadequate foods such as mollusc veligers.

The nutritional value of copepods has been proven by their universality as a larval fish food source. Checkley (1982), however, concluded that copepod lipids are undigestible to some larval species with straight guts, such as Clupea harengus. Copepod exoskeletons also hinder complete digestion. In contrast, soft appendicularians are quickly and almost completely digested, which adds to their nutritional value. Appendicularians are also slower moving than copepods, and hence probably easier to capture. Thus, appendicularians may be a better food source than copepods for larval fish in terms of nutritional value and ease of capture, but inadequate due to much lower abundance and seasonality. Larval fish species, such as Parophrys, which depend on appendicularians as a food source, may at times risk starvation-related mortality more than if they were adapted to consume the more abundant copepods. During periods of appendicularian abundance, however, they may be one of the few larval species capable of taking advantage of this food source.

#### Larval Fish and Food Source Co-occurrence

The co-occurrence of larval fish and their food sources is essential for larval survival since starvation may occur after just a few days of food deprivation (May 1974). Starvation is one of the major causes of mortality during the first few months of



planktonic larval existence (Hunter 1976). This stage in the life history, termed the "critical period," is very important because it is the time in which year-class strength may be determined (Hjort 1914; 1926; May 1974).

Timing of spawning is important in the synchronization of larval fish and food source abundances (Cushing 1975). The "match/mismatch" hypothesis developed by Cushing (1978) states that the degree of overlap between peaks of production of larvae and their food might be positively related to the magnitude of the subsequent year-class. Temperature, which influences larval development rate, is also important in the synchronization of larval and food source production peaks. Peak spawning of Atlantic mackerel, Scomber scombrus, in the Gulf of St. Lawrence coincides with maximum summer zooplankton abundances (Ware 1977). Similar relationships occur for other species, among them, anchovy (Engraulis) and sardine (Sardinops) (Vucetic 1975), herring (Clupea harengus) (Bainbridge et al. 1974), cod (Gadus morhua) (Sysoeva and Degtereva 1965), and plaice (Pleuronectes platessa) (Cushing 1969).

Two principal physical factors important in the reproductive timing of many marine fish are temperature and photoperiod. Kruse and Tyler (1983) have found that the timing of Parophrys vetulus spawning off Oregon is primarily linked to

upwelling-influenced changes in bottom temperatures and not photoperiod. They produced a model based upon three hypotheses: (1) summer bottom temperature and gonadal development rate are inversely related; (2) spawning is inhibited by temperatures below about 7.8°C; and (3) spawning is delayed by increases in bottom temperature greater than about 1°C per month. Off Oregon, bottom temperatures and upwelling are inversely related (Kruse and Huyer 1983), and hence Parophrys spawning is inhibited during upwelling. This coincides with abundance information (Laroche and Richardson 1979; Mundy 1984); Parophrys larvae are most abundant during fall and winter months (Figure 15).

Factors other than food availability also influence marine fish reproductive timing; a major consideration is the effect of transport on planktonic eggs and larvae. Currents or upwelling-induced offshore transport may carry eggs and larvae away from spawning grounds. Transport to areas unfavorable to larval survival, in particular away from coastal nursery grounds, could be disastrous to larval survival and subsequent year-class strength (Bishai 1960; Parrish et al. 1981). Spawning time may be coordinated to avoid unfavorable larval transport. Nelson et al. (1977) determined that year-class strength of Atlantic menhaden (Brevoortia tyrannus) is positively correlated to coincidence of spawning time with onshore transport. Pacific hake, (Merluccius productus) spawn mostly in January and February

off California, thus avoiding summer upwelling and associated offshore Ekman transport (Bailey 1981). Offshore transport at the time of spawning and the resultant year-class strength of M. productus are negatively correlated.

#### Parophrys Year-Class Strength

Two studies have been conducted relating environmental parameters to Parophrys year-class strength. Ketchen (1956) found a strong inverse correlation between year-class strength and surface water temperature when planktonic larvae were abundant in Hecate Strait, British Columbia. He proposed that by influencing growth rates, low temperatures prolonged the pelagic stage. Thus, larvae were carried northward by local currents for a longer period, resulting in increased successful settlement in northern nursery grounds.

Hayman and Tyler (1980) investigated factors affecting Parophrys cohort strength off the Oregon coast. In the year of greatest cohort strength, 1961, there was downwelling in March (causing onshore larval transport), less cloud cover in June (resulting in enhanced plankton growth), and, most importantly, high storm frequency intermittent with low wind speeds throughout the winter. The importance of these last two conditions has been

discussed previously in terms of ocean stability. High storm frequency causes mixing of nutrients to surface waters, but between storms, low wind speeds resulting in water column stability allow the accumulation of zooplankton into high densities necessary for successful larval feeding. In addition, low to moderate winds cause windrows, in which appendicularians have been observed to aggregate. In other years, cohort strength was related to factors affecting time of spawning, sea surface temperature, upwelling, and barometric pressure. If upwelling was prolonged, resulting in low bottom temperatures, spawning was delayed. Delayed spawning and strong cohorts were positively correlated, perhaps due to fish weight gain resulting in better quality eggs. The results of their model, however, are not conclusive.

### Conclusions

Off Oregon, transport is northward and onshore in winter, and southward and offshore during the summer upwelling season. Although the strength of alongshore flow in respect to onshore-offshore transport varies, alongshore currents often predominate, and thus larvae are usually retained in zones parallel to the coast (Richardson and Pearcy 1977). Hence, factors other than offshore transport, such as food availability,

may be more critical to larval survival in Oregon coastal waters. Larval fish abundant in summer months occur during periods of maximum zooplankton concentrations, although risking transport away from favorable coastal nursery grounds (Parrish et al. 1981). During winter months, food concentrations may be at times inadequate, but transport is onshore.

Although larval Parophrys and Isopsetta co-occur during part of the year, peak Isopsetta larval abundances (February through May) are nearer to the time of upwelling and maximum zooplankton abundances (Figure 16). In contrast to other winter spawning fish species with narrow spawning periods (Mundy 1984), Parophrys has protracted spawning, from September through March (Figure 16). The potential for competition between these two similar species is further avoided by their different diets. Isopsetta larvae are generalized feeders, while Parophrys larvae are very specific, apparently relying upon appendicularians (also most abundant in fall and winter, Figure 15), as a food source when total zooplankton concentrations are lowest. A mismatch of Parophrys and appendicularian abundance peaks, such as that which occurred in 1971 (Figure 15), could result in increased starvation and a poor year-class strength.

More Parophrys larvae appeared to be in a starved condition in 1971 than in 1973. In 1971: (1) more larvae had empty guts

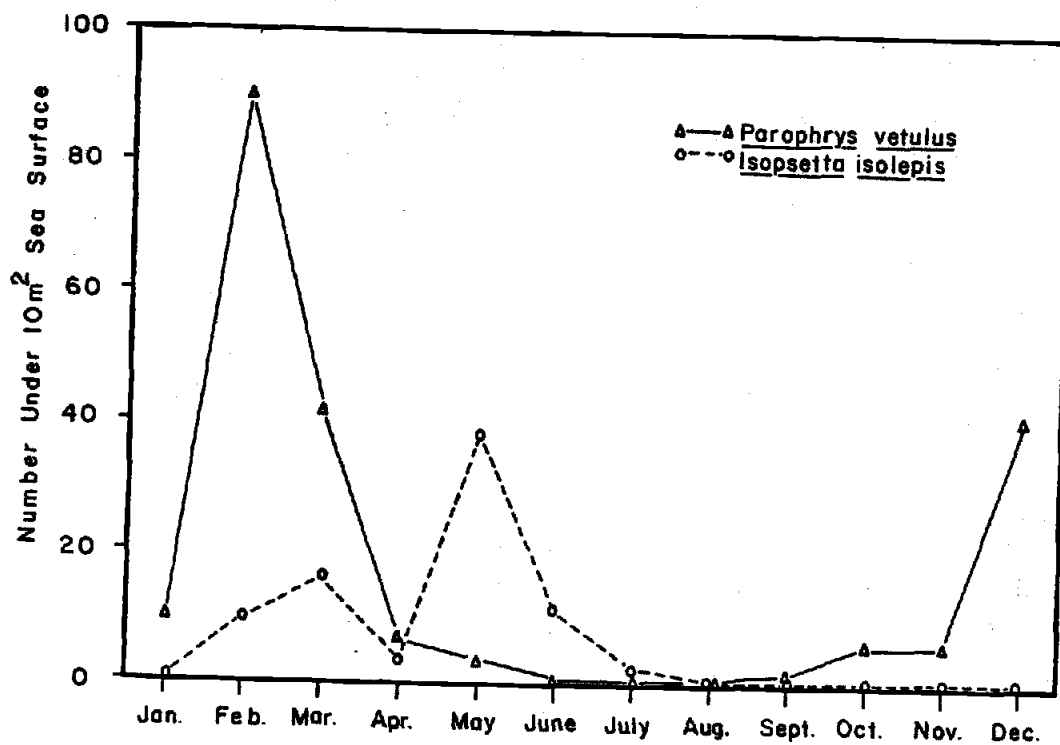


Figure 16. *Parophrys vetulus* and *Isopsetta isolepis* mean larval abundances at NH1, NH3, NH5, and NH10 in 1971 (from Richardson 1977).

than in 1973; (2) more "non-preferred" food items were ingested; (3) larvae were less robust; and (4) a much larger percentage of small Parophrys larvae were collected in 1971 compared to 1973, perhaps indicating decreased survival to larger sizes (Richardson and Percy 1977; Laroche and Richardson 1979). In addition, although larval Parophrys abundances were high in 1971, year-class strength was low, as estimated from commercial catch records (Mundy 1984), indicating low larval survival.

Hence, factors important in determining Parophrys year-class strength are those related to the timing of larvae and appendicularian abundance peaks. A major factor off Oregon is upwelling and resultant temperature differences. Parophrys spawning is suppressed during and after upwelling, due to decreased bottom temperatures (Kruse and Tyler 1983); both Parophrys larvae and appendicularians have abundance peaks during fall and winter when upwelling does not occur (Peterson and Miller 1976; Mundy 1984; Figure 15).

In addition, zooplankton, including appendicularian, abundances may be enhanced in winter months due to higher light levels and increased water column stability resulting from reduced cloud cover and wind speeds, phenomena which often occur off Oregon in February and March (Peterson and Miller 1976). The coincidence in timing of this winter lull with larval abundance

may increase cohort strength. The most beneficial winter weather conditions, however, may be a combination of low wind speeds with high storm frequency (Hayman and Tyler 1980). Storms mix the water column and replenish nutrients, while subsequent stable periods allow accumulation of high densities of zooplankton.

The duration of spawning period lengths of Isopsetta and Parophrys are different, possibly indicative of their different requirements. Isopsetta larvae predominantly feed on the most common and abundant zooplankters, copepods, and thus have a greater chance that an appropriate food source will be available during their more limited pelagic larval stage. The more protracted spawning period of Parophrys, often with multiple abundance peaks, enhances the probability that some larvae are present during high appendicularian abundances, since coincidence of larval and prey abundance peaks is critical in the production of a strong year-class.



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