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Feeding ecology of pelagic larvae of English sole *Parophrys vetulus* and butter sole *Isopsetta isolepis* off the Oregon coast

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ABSTRACT: The food habits of the 2 dominant larval pleuronectids off the Oregon coast – English sole *Parophrys vetulus* and butter sole *Isopsetta isolepis* – were analysed. Most specimens were collected during January–April 1971 and March–April 1973. As is typical of larval fishes, *I. isolepis* larvae ingested a variety of prey which changed with increasing fish size. Small larvae fed predominantly on tintinnids, invertebrate eggs, and nauplii, whereas large larvae consumed more copepodite and adult copepods. In contrast, the diet of *P. vetulus* larvae is very specific; appendicularians (*Oikopleura* spp.) comprised 97 % of the total number of food items consumed in 1973. Both *P. vetulus* larvae and appendicularians are most abundant during fall and winter when total zooplankton concentrations off Oregon are low. *I. isolepis* larvae are most abundant during spring when upwelling stimulates productivity. In 1971, seasonal abundance peaks of *P. vetulus* 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 other food sources such as tintinnids, invertebrate eggs, and nauplii. In 1971 more *P. vetulus* larvae had empty guts than in 1973; this observation suggests increased starvation. In addition, fewer large larvae were present in 1971, perhaps due to higher mortality rates. Hence, in contrast to *I. isolepis* larvae, *P. vetulus* larvae are dependent upon a specific prey; a mismatch of *P. vetulus* and appendicularian abundance peaks may result in significant food-related mortality.

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); factors causing interannual variability in this mortality may thus affect year-class strength. 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. High concentrations of an appropriate food must 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 and are also less efficient at catching prey due to impaired swimming abilities (Laurence, 1972; Blaxter and Ehrlich, 1974; Bailey and Yen, 1983).

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 factor important to larval survival; water currents 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, offshore larval drift may not be an important factor in year-class strength because coastal and offshore larval assemblages remain dis-

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tinct from year to year under differing conditions of upwelling (Richardson and Pearcy, 1977; Laroche and Richardson, 1979).

Parophrys vetulus and *Isopsetta isolepis* are the second and third most abundant species in the Oregon nearshore (2 to 28 km from the coast) larval fish assemblage, following osmerids (Richardson and Pearcy, 1977). *P. vetulus* has an extended spawning season, with peak spawning typically from January to March, though spawning peaks may also occur as early as September (Kruse and Tyler, 1983; Mundy, 1984). *I. isolepis* spawns from February through May (Richardson et al., 1980); thus the larvae of these 2 species co-occur during only part of their pelagic phases.

The development of *Parophrys vetulus* and *Isopsetta isolepis* from egg to benthic juvenile is similar. Larval *P. vetulus* hatch from pelagic eggs in 4 to 12 d, depending upon temperature (Alderdice and Forrester, 1968), at 2.7 to 2.9 mm notochord length. Metamorphosis to the benthic form occurs between 50 and 120 d, at 18 to 22 mm standard length (Laroche et al., 1982; Rosenberg and Laroche, 1982). *I. isolepis* larvae hatch about 6 d after fertilization, at 2.7 to 2.9 mm notochord length (Richardson et al., 1980). Transformation to the benthic juvenile is complete at about 21 mm standard length.

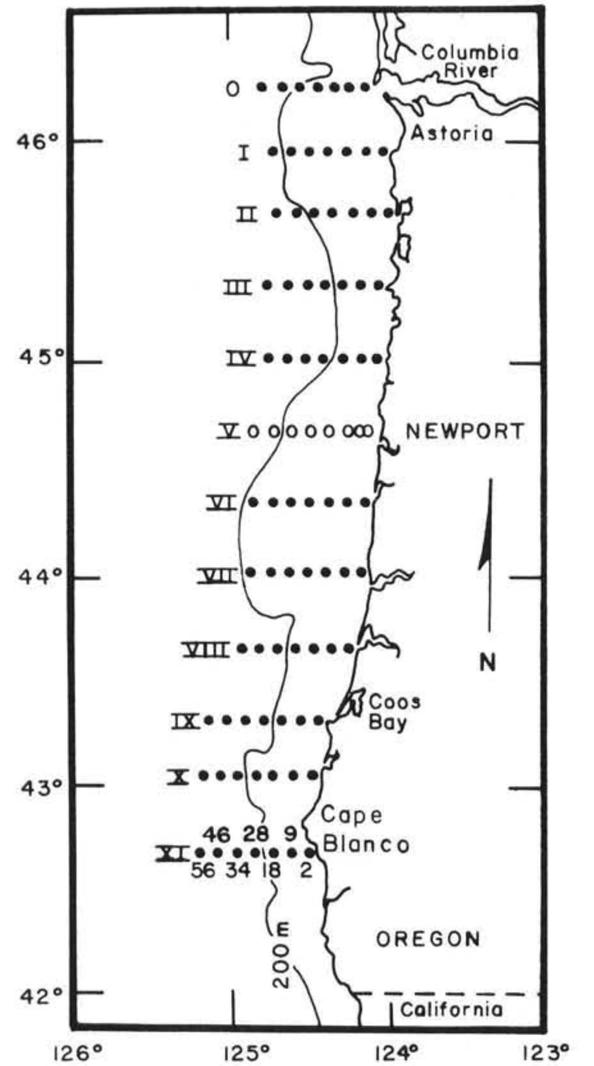

Fig. 1. Sampling stations off Oregon, USA. Numbers along Transect XI: km from shore. Open circles at Transect V: Newport Hydroline (NH; from Laroche and Richardson, 1977)

Laroche and Richardson (1979) observed year-to-year temporal and spatial variations in Oregon coastal larval fish abundances which may reflect ultimate year-class strengths of the cohorts (Hayman and Tyler, 1980). These variations are due to changes in peak spawning times and durations, as well as biotic and environmental factors influencing larval survival. During winter off the Oregon coast, one of the most important factors may be food availability. In this region, summer upwelling results in increased primary production and greater summer larval food abundances (Small et al., 1972; Peterson and Miller, 1977). Because *Parophrys vetulus* spawns during fall and winter, larval food availability may be the most critical factor affecting subsequent year-class strength. In addition, when the morphologically similar larvae of *P. vetulus* and *Isopsetta isolepis* co-occur during winter, competition for the same limited food sources may further affect survival. This has been shown for larval cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* in laboratory experiments (Laurence et al., 1981). In the present study we describe the feeding ecology of the pelagic larval stages of *P. vetulus* and *I. isolepis* in order to improve understanding of 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 from 1971 to 1975 (Richardson and Pearcy, 1977; Laroche and Richardson, 1979). From January 1971 through August 1972, collections were made along the Newport Hydrographic (NH) line (on 44°40′ N, 2–111 km off Newport, Oregon (Fig. 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 (Fig. 1; Laroche and Richardson, 1979). On all cruises, plankton was collected in 70 cm bongo nets with 0.571 mm mesh. Tows were stepped or straight oblique from the bottom or from 150 m to the surface when depth exceeded 150 m. Samples were preserved in 5 % formalin buffered with sodium borate.

Initially, 380 *Parophrys vetulus* larvae and 361 *Isopsetta isolepis* larvae 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. These larvae provided the major source of data. For comparison, however, 183 *P. vetulus* larvae from January through April 1971, 52 *I. isolepis* from June 1971, and 25 *I. isolepis* from June 1972 were also examined. This increased the number of large *I. isolepis* and small *P. vetulus* since these 2 size categories were limited in the 1973 samples. No *P. vetulus* larvae greater than 15.9 mm SL were examined from 1971 because few larger larvae were collected that year.

A sample was selected for examination if it contained at least 10 specimens of either species. Usually, about 10 *Parophrys vetulus* and/or 10 *Isopsetta isolepis* larvae from each selected sample were examined. Fewer than 10 were examined from some samples, however, because of deterioration or more than 10 were examined if they were available. When sorting a sample, the first 10 larvae encountered with intact guts were removed. Where a broad size range was present, however, larvae were selected to obtain the widest possible size spectrum from each sample.

Parophrys vetulus larvae examined from 1973 were from 38 samples collected on 13 d (17 Mar to 20 Apr). *Isopsetta isolepis* larvae from 1973 were from 30 samples from 13 d (17 Mar to 26 Apr). *I. isolepis* and *P. vetulus* larvae co-occurred in 19 of these samples. All samples (except 1) 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. Larvae examined from other years were chosen from day collections (0800 to 1800) to maximize feeding incidence. *P. vetulus* larvae from 1971 were from 13 samples on 7 d (6 Jan to 22 Apr). *I. isolepis* larvae from 1971 and 1972 were selected from single dates because these were the only days that large larvae were taken during daylight hours; larvae from 1971 were from 5 samples taken 28 June; those from 1972 were from 3 samples taken 11 June.

Laboratory techniques

Larval dissection techniques followed Arthur (1976). Briefly, specimens were placed in glycerin, soaked overnight, and examined on a microscope slide. Standard length (snout tip to notochord tip until full notochord flexion, then to the posterior edge of the hypurals) and mouth width (horizontal distance from a frontal view) were measured to the nearest hundredth of a millimeter. Small *Parophrys vetulus* and *Isopsetta isolepis* larvae have a straight gut, which begins to coil at about 4 mm standard length (SL) at which time the gut can be roughly divided into fore, mid, and hindgut areas. The entire gut was removed, placed in glycerin, teased open, and the contents removed; the location of major food items was noted. 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 classified as unidentified but of a certain size range (cephalothorax length about 0.25, 0.50, 0.75, or 1.00 mm). Since in many cases, an animal was dorsoventrally 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 subjectively recorded as follows: (A) stomach fullness: 0: empty, 1: ¼ full, 2: ½ full, 3: ¾ full, and 4: full; (B) digestive stage: 1: food present in undigested condition, 2: food somewhat digested, and 3: food very digested; (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. The % 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 were common prey items and were studied in more detail. They are usually found in the gut digested except for characteristic spheroid fecal pellets. 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, and used to determine the number of appendicularians ingested based on the number of fecal pellets found in a larval fish gut, after Shelbourne (1962). In addition, fecal pellet length to appendicularian trunk length and width were regressed, and confidence limits were determined. Fecal pellets from larval fish guts were measured and classified into eight 0.05 mm length groups with median lengths of 0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, and 0.40 mm, and the results were used to calculate ingested appendicularian size, following Shelbourne (1962).

RESULTS

Variations in feeding

More *Isopsetta isolepis* and *Parophrys vetulus* larvae from daytime samples had food in their guts than did those from nighttime samples (Fig. 2 and 3). After midnight, the percentage of larvae with empty guts increased rapidly, particularly for *P. vetulus*. In addition, food found in *P. vetulus* and *I. isolepis* guts during early morning 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 increased rapidly and remained over 80 % throughout the day.

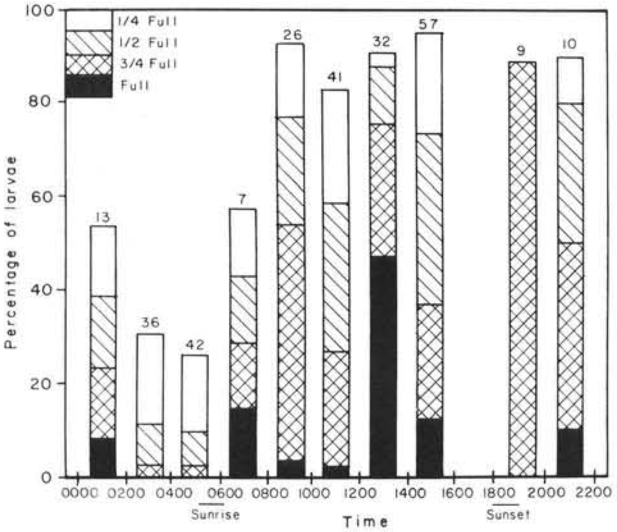

Fig. 2. *Isopsetta isolepis*. Diel variations in gut fullness of larvae from March and April, 1973. From the top of a bar to 100 % represents the percentage of empty guts. Numbers above bars: numbers of larvae examined from that time period. Only larvae 6.0 to 17.9 mm SL are considered because smaller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

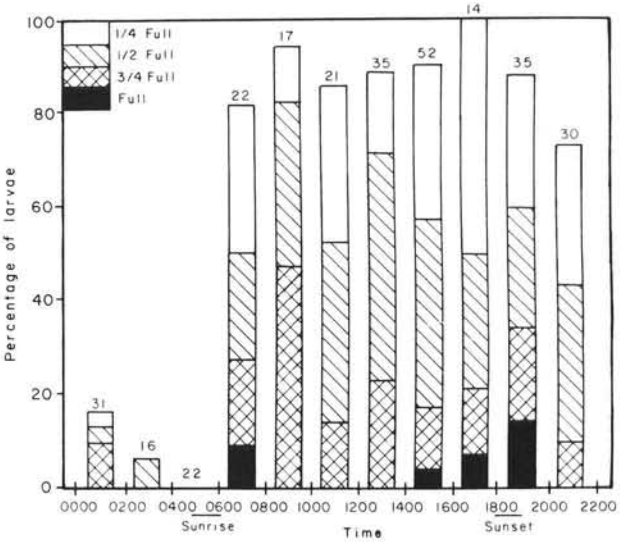

Fig. 3. *Parophrys vetulus*. Diel variations in gut fullness of larvae from March and April, 1973. From the top of a bar to 100 % represents the percentage of empty guts. Numbers above bars: numbers of larvae examined from that time period. Only larvae 6.0 to 17.9 mm SL are considered because smaller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

In both years, there were ontogenetic variations in gut fullness; smaller larvae had higher incidences of empty guts than larger larvae (Fig. 4; Tables 1, 2, and 3). For clarity, only larvae from daytime samples (0800 to 1800) were considered in Fig. 4 since larvae of all sizes from nighttime samples have more empty guts than from daytime samples. More *Parophrys vetulus* larvae collected during 1971 had empty guts than in 1973; all *P. vetulus* larvae below 5 mm SL examined from 1971 had empty guts. All *Isopsetta isolepis* 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 *I. isolepis* from 1973 (Table 1). In all years, *I. isolepis* larvae have a higher maximum and mean number of items in their guts than do *P. vetulus* larvae (Tables 1, 2, and 3).

Diet composition

Isopsetta isolepis. Food items in the guts of larvae were usually in good condition. Crustaceans generally had exoskeletons intact, but tissues digested. Only rarely did prey appear to have been just eaten. In addition, prey were rarely extremely digested and crushed, except in early morning hours (about 0200 to 0600). Food was typically found mainly throughout the midgut and hindgut regions. Food in the hindgut did not generally appear to be more digested than in the midgut. Although there were differences in diet

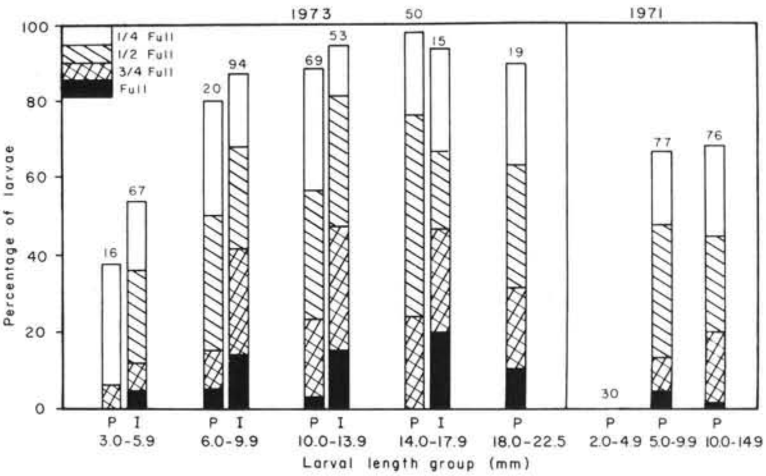

Fig. 4. *Parophrys vetulus* (P) and *Isopsetta isolepis* (I). Ontogenetic variations in gut fullness of larvae from 1973 and 1971. From the top of a bar to 100 % represents the percentage of empty guts. Numbers above bars: numbers of larvae examined from each length group. Only larvae from daytime samples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

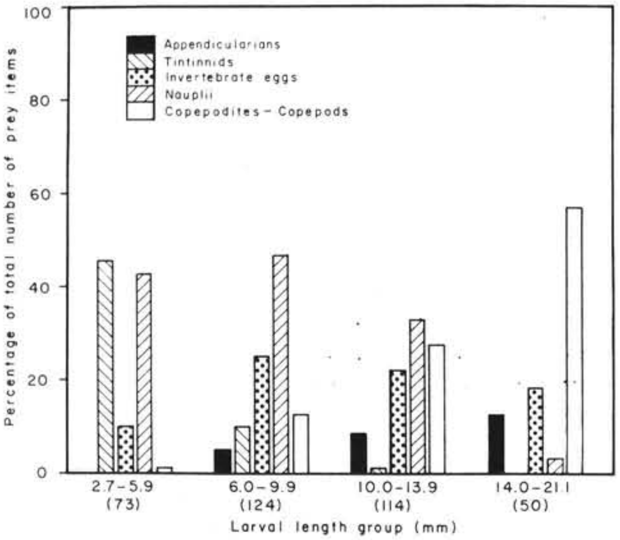

Fig. 5. *Isopsetta isolepis*. Diet composition of major prey items of larvae from 1973. Numbers in parentheses: numbers of larvae examined from each length group

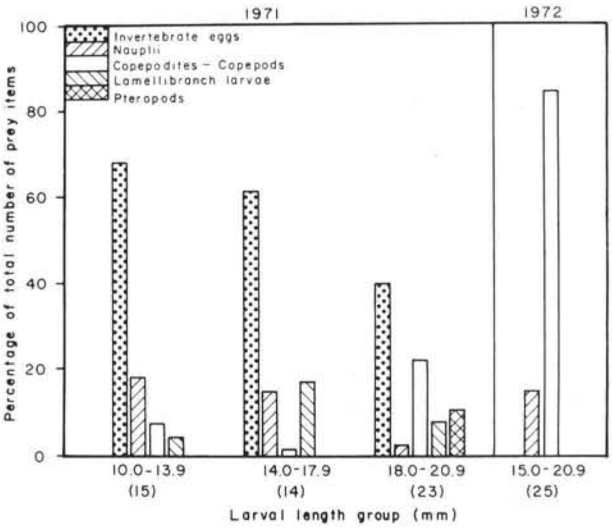

Fig. 6. *Isopsetta isolepis*. Diet composition of major prey items of larvae from 1971 and 1972. Numbers in parentheses: numbers of larvae examined from each length group

between years, no consistent differences were detected between stations within a year. Most guts contained a variety of prey types.

Larvae had a varied diet in 1973 (Fig. 5). Small larvae ingested primarily tintinnids (0.05 mm) and nauplii (0.10 to 0.35 mm, mainly of copepods). With increasing larval size, tintinnids were replaced by larger prey such as copepodite and adult copepods (0.25 to 1.20 mm cephalothorax length); also, nauplii lost importance in the diet above 14 mm SL. The major copepods ingested were *Pseudocalanus* spp. (Table 1). Invertebrate eggs (0.05 to 0.30 mm), many of them *Calanus marshallae* (0.20 mm), were frequently consumed throughout ontogeny. Appendicularians are also a significant prey item, particularly at larger sizes.

Since only 5 larvae greater than 18 mm SL with stomach contents were available for examination from 1973 (Table 1), larger larvae were examined from 2 other years, 1971 and 1972 (Fig. 6, 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 copepodite and adult copepods gained importance with increasing larval size. The 2 species of copepod ingested in 1971, however, were *Acartia longiremis* and the harpacticoid *Microsetella rosea*. Also in contrast to 1973, lamellibranch larvae and pteropods were important diet items in 1971. During 1972 larvae greater than 15 mm SL had a less varied diet than in the other years, ingesting almost exclusively nauplii, copepodites and adult copepods (mainly *Acartia longiremis, Pseudocalanus* sp. and *Oithona* spp.).

Table 1. *Isopsetta isolepis*. Diet composition of larvae from 1973. Numbers in parentheses: percentages by number of a prey species in the previous major category. % N = percentage of the total number of prey items; % F = percent frequency of occurrence

Prey items	Larval length groups (mm)								
	2.7–5.9		6.0–9.9		10.0–13.9		14.0–17.9		18.0–21.1
	% 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)		
Calanus marshallae	(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									
Pseudocalanus spp.			(6.5)		(32.1)		(56.8)		(55.2)
Paracalanus spp.			(3.2)		(2.2)		(1.8)		(3.4)
Ctenocalanus spp.					(.7)		(1.8)		
Cyclopoid									
Oithona 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

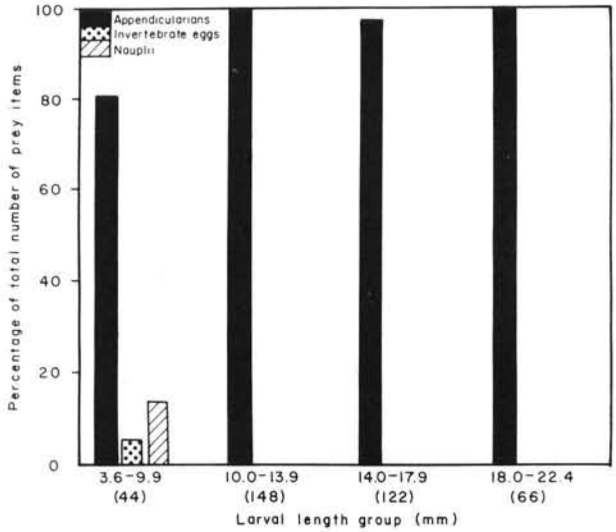

Fig. 7. *Parophrys vetulus*. Diet composition of major prey items of larvae from 1973. Numbers in parentheses: numbers of larvae examined from each length group

Parophrys vetulus. The diet of larvae in 1973 was very different from that of *Isopsetta isolepis* larvae (Fig. 7; Table 3). Appendicularians (*Oikopleura* spp.) were consumed almost exclusively. Only larvae smaller 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 trail. 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 (Fig. 8; Table 3), appendicularians still dominated the diet of larvae greater than 5 mm SL. Tintinnids, invertebrate eggs, and nauplii, however, were ingested to a greater extent than in 1973. No differences in diet in relation to station were apparent for larvae collected from either year.

Larval-prey size relation

Mean prey width increased with larval fish size for both *Isopsetta isolepis* (Fig. 9) and *Parophrys vetulus* (Fig. 10). The minimum width of food ingested remained relatively constant for *P. vetulus* und *I. isolepis*, as did the maximum width of 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 differ-

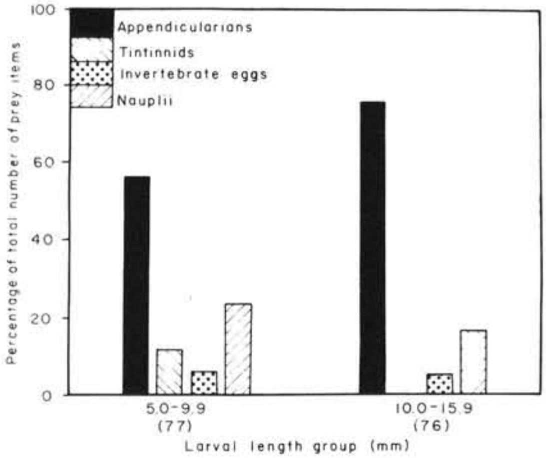

Fig. 8. *Parophrys vetulus.* Diet composition of major prey items of larvae from 1971. Numbers in parentheses: numbers of larvae examined from each length group

ence between fish mouth width and maximum prey width.

For *Isopsetta isolepis,* however, mean prey size increased more than mean prey width indicates, since with ontogeny prey items change from sphere-like forms (tintinnids, invertebrate eggs, nauplii) to more elongated spheroids (copepodites-copepods). Thus, mean prey volume increased more with larval length increase than did mean prey width (Fig. 9).

Appendicularian size relation

The 202 appendicularians (*Oikopleura* spp.) examined from plankton-net collections had a mean of 2.67 fecal pellets with a maximum of 5. This was similar to Shelbourne's (1962) value of 2.65. Only 5 of the 202 appendicularians did not contain fecal pellets, and 78 % had 2 or 3. A relation was established between size of *Oikopleura* spp. and size of their fecal pellets; generally, the larger the appendicularian, the larger the fecal pellets (appendicularian trunk length = 0.23 mm + 2.98 [fecal pellet length], $r^2 = 0.78$; appendicularian trunk width = 0.12 mm + 1.79 [fecal pellet length], $r^2 = 0.70$).

The guts of small *Parophrys vetulus,* from 1973 contained a greater percentage of small fecal pellets; thus, ingested appendicularian size increased with larval

Table 2. *Isopsetta isolepis.* Diet composition of larvae from 1971 and 1972. Numbers in parentheses: percentages by number of a prey species in the previous major category. % 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								
Acartia longerimis	(100)		(75.0)		(58.6)		(15.7)	
Pseudocalanus spp.							(6.2)	
Paracalanus spp.							(.3)	
Cyclopoid								
Oithona spp.							(18.8)	
Harpacticoid								
Microsetella rosea			(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. *Parophrys vetulus.* Diet composition of larvae from 1971 and 1973. Numbers in parentheses: percentages by number of a prey species in the previous major category. % N = percentage of the total number of prey items; % F = percent frequency of occurrence

	Larval length groups (mm)												
	1971					1973							
Prey items	2.7–4.9	5.0–9.9		10.0–15.9		3.6–9.9		10.0–13.9		14.0–17.9		18.0–22.4	
	% N	% N	% F	% N	% F	% N	% F	% N	% F	% N	% F	% 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)			
Calanus marshallae		(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	

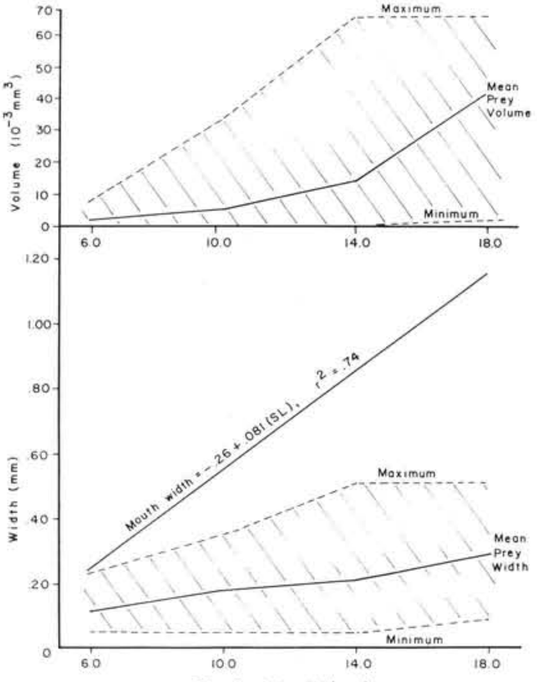

Fig. 9. *Isopsetta isolepis.* Relation between 1973 larval size (n = 361) and mean, minimum and maximum widths and volumes of their prey items as a function of larval standard length. Mouth width indicates maximum size of potential prey

size (Fig. 10). Larvae larger than 14 mm SL, however, contained a range of fecal pellets from the smallest (0.05 mm) to the largest (0.40 mm).

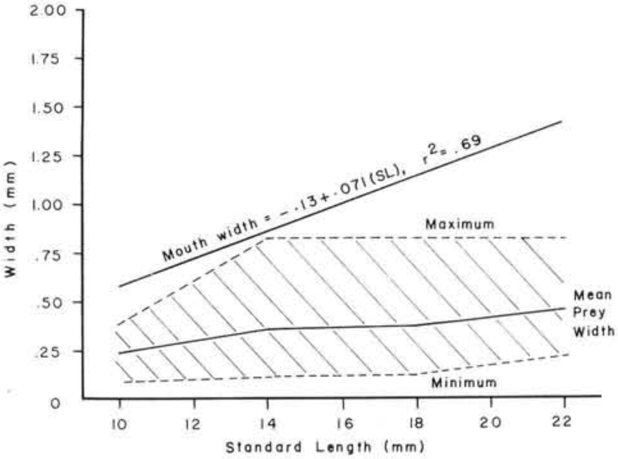

Fig. 10. *Parophrys vetulus.* Relation between 1973 larval size (n = 380) and mean, minimum and maximum widths of their prey items as a function of larval standard length. Mouth width indicates maximum size of potential prey

DISCUSSION

Both *Parophrys vetulus* and *Isopsetta isolepis* larvae displayed a pattern of diurnal feeding typical of larval fishes (Fig. 2 and 3), which generally are visual feeders (Bainbridge and Forsyth, 1971; Arthur, 1976; Last, 1978a, b, 1980; Cohen and Lough, 1983). More *P. vetulus* than *I. isolepis* guts were empty during late night (0200 to 0600), apparently because of the higher digestibility of appendicularians, which lack the hard exoskeletons of copepods.

Ontogenetic variations in feeding incidence were also observed for both *Parophrys vetulus* and *Isopsetta isolepis;* more small larvae had empty guts during daylight hours. Upon capture and fixation regurgitation may be more common at small sizes of larval flatfishes due to the straight gut. The more complex coiled gut at larger sizes could hinder regurgitation (Sherman et al., 1981). Another possibility is an ontogenetic change in feeding success. Small larvae, particularly first feeding larvae, require higher prey concentrations of a more limited size range (0.04 to 0.10 mm) than larger larvae (Hunter, 1981). Small larvae have a shorter perceptive distance, which, combined with slower swimming speeds, results in low searching rates (Hunter, 1972; Houde and Schekter, 1981).

Isopsetta isolepis larvae had a varied diet (Fig. 5 and 6; Tables 1 and 2). The major food sources of *I. isolepsis* are various copepod life stages, which is also true for larval clupeids, engraulids, carangids, gadids, merluciids, sciaenids, and others (Bainbridge and Forsyth, 1971; Arthur, 1976; Last, 1980; Sumida and Moser, 1980; Govoni et al., 1983). 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 *I. isolepis* 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 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 because fish larvae usually engulf oblong prey (such as copepods) head first (Hunter, 1981). Thus, the maximum size of prey ingested by *Isopsetta isolepis* larvae in this study is well below the maximum possible size (Fig. 9). This is a trend commonly observed in other species of larval fish (de Mendiola, 1974; Arthur, 1976; Last, 1978a, b; Sumida and Moser, 1980). Carapace width of copepods may not be a good functional measurement because appendages are not considered. 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).

Prey abundances in the plankton also influence larval diet. The 2 major copepod species ingested by *Isopsetta isolepis* differed between years (Tables 1 and 2), but were of similar sizes, about 1 mm cephalothorax length. In 1973, the primary species was *Pseudocalanus* sp., whereas in 1971, *Acartia longiremis* was dominant. Off the Oregon coast, copepods are the most abundant component of the zooplankton at all times (Peterson and Miller, 1975, 1976, 1977). The most common coastal species in both winter and summer is *Pseudocalanus* sp., and in summer *Acartia longiremis* ranks second in abundance. Thus, *I. isolepis* larvae are ingesting common zooplankton types, although it is not possible to speculate about feeding selectivity without coincident sampling of larvae and their food sources.

In contrast to *Isopsetta isolepis, Parophrys vetulus* larvae have a very specific diet, composed of 97 % appendicularians in 1973 (Fig. 7; Table 3). Thus, competition between the larvae of both species for the same food resources during their pelagic phase is largely avoided. Appendicularians are a major diet component of a number of other pleuronectiform species also, including *Glyptocephalus cynoglossus, Arnoglossus laterna, Microstomus kitt* (Last, 1980), and *Pleuronichthys cornutus* (Kuwahara and Suzuki, 1983). The larval flatfish species best known for ingesting appendicularians (notably *Oikopleura dioica*) is the plaice *Pleuronectes platessa* (Shelbourne, 1953, 1957, 1962; Ryland, 1964; Wyatt, 1974; Last, 1978a). 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 relation between larval predator and appendicularian prey.

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). Given the rapid digestion and difficulty in identifying remains, however, appendicularians may be an even more important component of larval fish diets than gut content analysis indicates.

Smaller *Parophrys vetulus* larvae in this study consumed more non-appendicularian food items than larger larvae, perhaps due to the feeding limitations of small larvae. There also may not be adequate concentrations of very small appendicularians to support small larvae; the size composition of appendicularians off the Oregon coast is unknown. The upper size limit of appendicularians ingested by *P. vetulus* larvae, however, is within the upper size range of appendicularians common off Oregon, as determined by the appendicularians from plankton samples examined in the current work.

In the Oregon coastal region, appendicularians (mainly *Oikopleura* spp.) are most abundant in fall and winter. In surveys conducted by Peterson and Miller (1976) off Oregon from June 1969 through July 1972, appendicularians represented a mean of 5.7 % of the total winter zooplankton catch. *Oikopleura* showed clear peaks of abundance, howev with 60 % or greater of the total yearly density taken in a single month and zero catches during the majority of the year. Appendicularians were rarely observed in areas of active upwelling. Although zooplankton surveys were not conducted off Oregon in 1973, winter zooplankton abundance peaks (approximately an order of magnitude less than abundance peaks during the productive summer season) are common, and occurred in all 3 y of the study by Peterson and Miller (1976). The winter of 1973 was mild with low amounts of cloud cover and light winds (Laroche and Richardson, 1979). These conditions are the prerequisites for higher plankton densities resulting from increased sunlight and water column stability (Lasker, 1975, 1978). Thus, the winter of 1973 was potentially a period of high appendicularian abundances.

Water-column stability may be a major factor in increasing zooplankton 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). Indeed, Hayman and Tyler (1980) have suggested that larval feeding conditions in 1961, the strongest year-class of *Parophrys vetulus* on record off Oregon, may have been promoted by high storm frequency but low average wind speed. Laboratory work on some species suggests that the densities found in the field are rarely sufficient to support high survival (Hunter, 1972; Lasker, 1978); small scale patchiness has been cited as a potential mechanism to account for this discrepancy (Hunter, 1981; Owen, 1981). Appendicularians are known to be patchily distributed. They have been observed to aggregate in parallel slicks, referred to as windrows, which may be formed during periods of mild winds due to wind-wave interaction resulting in Langmuir vortices (Owen, 1966; Allredge, 1982). On days of more intense winds, Alldredge (1982) found appendicularians to be more dispersed due to wind induced chop; thus water column stability may be an important factor in maintaining this system.

In 1971, the appendicularian abundance peak preceded that of *Parophrys vetulus* larvae by several months (Fig. 11; Peterson and Miller, 1976; Mundy, 1984). The diet of *P. vetulus* larvae from 1971 was still dominated by appendicularians (Fig. 8; Table 3), indicating that these larvae are highly selective for appendicularian prey; more *P. vetulus* larvae in 1971 than in 1973 had empty guts (Fig. 4), however, and a much larger percentage of small *P. vetulus* larvae were collected in 1971 during both day and night hours, perhaps indicating decreased survival to larger sizes due to starvation (Richardson and Pearcy, 1977; Laroche and Richardson, 1979).

Given the specific prey requirements for *Parophrys vetulus* larvae, the potential exists for a match-mismatch situation where the peak of spawning may not coincide with the peak productivity of its prey, resulting in significant food-related mortality. 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. A major factor in the synchronization of larval fish and food source abundances is spawning time (Cushing, 1975). Kruse and Tyler (1983) have found that the timing of *P. vetulus* spawning off Oregon is primarily linked to upwelling-influenced changes in bottom

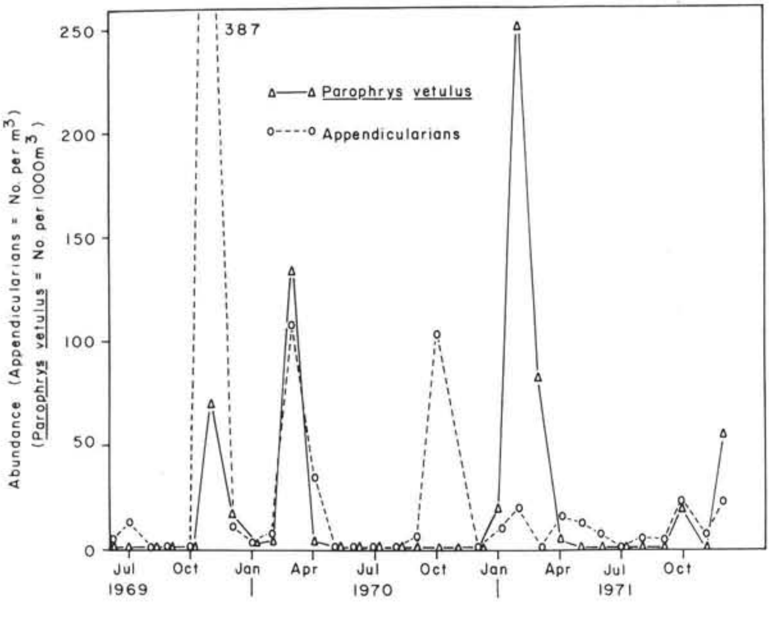

Fig. 11. *Parophrys vetulus* larvae (information from Mundy, 1984) and appendicularian mean abundances (information from Peterson and Miller, 1976) at NH5 from June 1969 through December 1971

temperatures; spawning is inhibited during upwelling. Unlike that of most temperate marine fishes, spawning of *P. vetulus* is characterized by an extended season, with spawning peaks occurring from September to March (Laroche and Richardson, 1979; Mundy, 1984). Since appendicularian abundance may also be affected by upwelling (Peterson and Miller, 1976), the same physical factors may control abundances of both larvae and their prey.

The different spawning period lengths and timings of *Isopsetta isolepis* and *Parophrys vetulus* are adapted to their feeding strategies. *I. isolepis* larvae predominantly feed on the most common and abundant zooplankters, and therefore 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 *P. vetulus*, often with multiple abundance peaks, enhances the probability that some larvae are present during high appendicularian abundances. Hence, factors important in determining *P. vetulus* year-class strength are those related to the timing of larvae and appendicularian abundance peaks.

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