TROPHIC PATTERNS AMONG LARVAE OF FIVE SPECIES OF SCULPINS (FAMILY: COTTIDAE) IN A MAINE ESTUARY

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ABSTRACT

The food habits and trophic relationships of larvae of five species of marine cottids—*Myoxocephalus aenaeus*, *M. octodecemspinosus*, *M. scorpius*, *Triglops murrayi*, and *Hemitripterus americanus*—were examined and compared during winter and early spring when they cooccur at peak abundance in the Damariscotta River estuary, Maine. Overall feeding incidence was high with <14% of the larvae in any species having empty guts. Larvae of all five species began to feed before yolk absorption was complete.

Among the five species, *M. aenaeus* and *M. octodecemspinosus* were most similar in mouth size, prey size, and dominant prey—adult *Microsetella norvegica* in January and February (winter) and *Balanus* nauplii in March (early spring). Mouth size, prey size, and dominant prey in early spring (*Balanus* nauplii) of *Myoxocephalus scorpius* were similar to the other species of *Myoxocephalus*, but the most frequently ingested prey in winter was the centric diatom, *Coscinodiscus* sp. *Triglops murrayi* larvae had relatively larger mouths and ingested somewhat larger prey than similar-sized *Myoxocephalus* larvae, feeding primarily on adult *Pseudocalanus minutus* in both winter and early spring. Although mouth sizes of *H. americanus* and *T. murrayi* larvae were similar, the diet of *H. americanus* was composed almost exclusively of fish larvae, primarily other cottids.

The high incidence of ingestion of *Balanus* nauplii by *Myoxocephalus* and *T. murrayi* in early spring may indicate some degree of density-dependent food utilization by those larvae. Yet other prey, adult *Temora longicornis* and epibenthic harpacticoid copepods, appeared to be preferred over other presumably more abundant zooplankton.

Percent diet overlap was greatest among the three species of *Myoxocephalus* and, except between *M. aenaeus* and *M. octodecemspinosus*, was lower in winter when mean plankton volume (an approximate measure of food supply) was low. Observed differences in vertical distribution resulting in partial spatial segregation of *M. aenaeus* and *M. octodecemspinosus* larvae may reduce competition for food between the two species, thus allowing the consistently high degree of dietary overlap between them.

Prey size (maximum carapace width) at first feeding ranged from 100 to 375 μm among the three species of *Myoxocephalus* and >800 μm for *H. americanus*. There was no dramatic change in prey types or sizes with increasing larval size. Larvae of the five species of cottids were found to most closely resemble hake (genus *Merluccius*) in prey size relationships.

There have been relatively few detailed descriptions of the food habits of marine fish larvae despite the reputed importance of starvation as a primary cause of mortality in the sea (Hunter 1976). Our generalized concept of early feeding ecology in marine fishes is based mostly on highly fecund species whose larvae hatch from small planktonic eggs at 2-3 mm in length with undeveloped eyes and mouths (Arthur 1976; Last 1978a, b; Sumida and Moser 1980). Little is known of trophic relations among larvae of fishes such as the cottids which deposit relatively few, large, demersal eggs and whose planktonic larvae hatch at sizes ≧5 mm, in a relatively advanced stage of development with pigmented eyes and functional mouths (Laroche 1980). Fishes with widely divergent ontogenies would be expected to also have different early trophic relations, whose comparisons may yield further insights into processes controlling survival in the sea.

The kinds of food used in most laboratory studies of foraging behavior, feeding efficiencies, and growth of fish larvae are usually organisms which are easily cultured in quantity but are not natural larval fish prey, or which are known size fractions of wild plankton whose species composition is only approximately known. Laboratory results, based solely on unnatural and/or single prey, or prey described by size only, may have little relevance to the real situation in the sea. It is not unreasonable to suspect that different kinds (and sizes) of prey may sig-

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nificantly affect the feeding and growth of fish larvae. For these reasons, there is a need for additional detailed descriptions of natural prey so that laboratory studies can be designed to investigate the effects of these prey organisms on larval fish behavior, metabolism, and growth.

This study was undertaken to examine and compare the food habits and trophic relationships of the larvae of five species of marine cottids—*Myoxocephalus aenaeus, M. octodecemspinosus, M. scorpius, Triglops murrayi*, and *Hemitripterus americanus*—during winter and early spring when they cooccur at peak abundance in the Damariscotta River estuary, Maine. Data are presented on feeding incidence, diet composition, diet overlap, larval mouth size, and prey size. Trophic patterns are examined with respect to possible interspecific competition and the influence of relative prey abundance and morphology on foraging. Aspects of the feeding ecology of these larvae are compared with the early feeding ecology of other marine fishes.

MATERIALS AND METHODS

Larvae used in diet analyses were collected in surface and bottom tows of a 1 m, 360 μm mesh conical plankton net which was mounted atop a 1.3 m wide × 45.7 cm high Blake trawl (a type of beam trawl). Although larvae were collected throughout the Damariscotta River, a drowned river valley opening into the Gulf of Maine and located on the central Maine coast, most specimens were captured in the middle basin of the estuary (Laroche 1980). *Myoxocephalus* (*M. aenaeus, M. octodecemspinosus*, and *M. scorpius*) and *T. murrayi* larvae were collected, for the most part, on these dates in 1973: 22 January; 6, 20, 21 February; and 5, 6, 19, 20 March. From 26 to 30% of larvae of the four species used in diet analyses were taken in surface tows and 70 to 74% were taken in bottom tows. Larvae of *H. americanus* were rare in collections; therefore, all specimens collected during the period January-April 1972-74 were used in diet analyses.

Prior to preservation in 10% Formalin[2] in the field, an unquantified amount of MS-222 (tricaine methanesulfonate) was added to each sample. The sample was gently swirled as the anesthetic dissolved larvae became inactive. This procedure eliminated defecation and/or regurgitation subsequent to capture.

Before removal of the gut, standard length (SL, to nearest 0.1 mm) and upper jaw length (i.e., distance from symphysis to posterior margin of maxillary along the ventral aspect, to nearest 0.01 mm) were measured using an ocular micrometer in a stereomicroscope. Jaw length rather than gape was used as a measure of potential size of the mouth opening because jaw length was not affected by whether the mouth was opened or closed at the time of preservation and could, therefore, be measured more consistently and precisely. Larvae were placed in a cavity of a double-depression glass slide, and the entire gastrointestinal tract from esophageal sphincter to anus was gently pulled intact from the abdominal cavity. At this time the presence or absence of yolk was noted, and an estimate was made of the quantity of yolk present: one-fourth, one-half, three-fourths of abdominal cavity full or only a remnant remaining. The gut was placed in the other, water-filled cavity of the slide, and the gastric and pyloric regions were teased apart separately using two fine probes. The presence or absence of food items in each of these regions was noted.

Food items were identified to the lowest taxon possible and counted except for undigestable prey remains, such as setae, and unrecognizable debris. *Pseudocalanus* eggs, which were probably ingested with the brooding females, and small diatoms (in March samples only) were likewise not counted. Maximum body width or diameter of most food items was measured.

Larvae were grouped into arbitrarily chosen size intervals, based on overall size distributions, to facilitate intra- and interspecific diet comparisons. Percent frequency of occurrence (%*FO*) and percent of total number (%*N*) of prey ingested by larvae in each size group were calculated for each food category. An estimate of the relative importance of each food category was obtained by multiplying %*FO* by %*N*. Diet overlap was measured using the Schoener index (1970):

$$\alpha = 100 \left[1 - 0.5 \sum_{i=1}^{n} /p_{xi} - p_{yi}/\right],$$

where p_{xi} = proportion (percent by number) of food category i in the diet of species x; p_{yi} = proportion (percent by number) of food category i in the diet of species y; and n = the number of food

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

categories. Percent by volume or weight is, in most cases, more useful than %*N* or %*FO* in measuring diet overlap. However, for predators like larval *Myoxocephalus* and *T. murrayi* whose prey are similar in size (Fig. 1), calculation of the Schoener index using %*N* and %*FO* produces a relatively unbiased estimate of diet overlap (Wallace 1981).

Settled volumes of the ichthyoplankton samples were measured by displacement method in either a 100 or 250 ml graduated cylinder after large jellyfish and macrophytic algae or other large plant debris were removed.

RESULTS

Feeding Incidence

The percentage of cottid larvae with empty guts ranged from 0 to 13 depending on the species, with *T. murrayi* having the lowest overall incidence of empty guts and *H. americanus* the highest (Table 1). Only *M. aenaeus* and *M. scorpius* had equal or higher percentages of empty guts in January and February than in March. In addition to this high incidence of feeding, many larvae examined had begun to feed before yolk absorption was complete (Table 1). A remnant of yolk (often sizeable) was found attached to or closely associated with the liver in feeding larvae over a wide size range: 5.3-9.5 mm SL in *M. aenaeus*; 7.2-11.5 mm SL in *M. octodecemspinosus*; 7.5-10.4 mm SL in *M. scorpius*; 8.5-12.0 mm SL in *T. murrayi*; and 12.0-15.9 mm SL in *H. americanus*.

Among the three species of *Myoxocephalus* larvae with three-fourths of the abdominal cavity filled with yolk ($N = 33$), about 80% had food in their guts. The number of food items found in these larvae ranged from 1 to 4 in *M. aenaeus*, 2 to 12 in *M. octodecemspinosus*, and 1 to 21 in *M. scorpius*. No yolk-sac larvae of *T. murrayi* were collected. Of the seven *H. americanus* larvae with prominent yolk sacs, only two had empty guts. Each of the other larvae contained one food item.

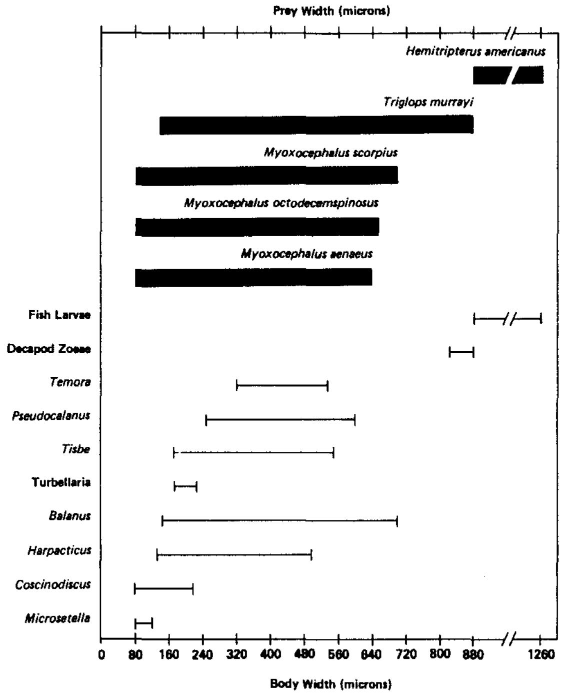

FIGURE 1.—Range in maximum body width (microns) of the major prey ingested by larvae of five species of cottids in the Damariscotta River estuary, Maine.

Diet Composition

Gut contents were examined of 147 *M. aenaeus*, 5.3-9.5 mm SL; 106 *M. octodecemspinosus*, 7.2-12.4 mm SL; 87 *M. scorpius*, 7.5-13.4 mm SL; 58 *T. murrayi*, 8.5-18.1 mm SL; and 24 *H. americanus*, 12.0-16.2 mm SL (Tables 2-10). Percent number of *Coscinodiscus* sp. was calculated only

TABLE 1.—Incidence of *Myoxocephalus*, *Triglops*, and *Hemitripterus* larvae with empty guts, and those with both food and a remnant of yolk present. (N = number of larvae examined.)

	January-February			March		
Species	*N*	% empty	% with yolk + food	*N*	% empty	% with yolk + food
Myoxocephalus aenaeus	18	6	94	129	6	75
M. octodecemspinosus	31	0	100	75	5	66
M. scorpius	18	11	89	69	0	91
Triglops murrayi	22	0	73	36	3	6
	January-April					
Hemitripterus americanus	24	13	83			

TABLE 2.—Summary of food habits of 18 *Myoxocephalus aenaeus* larvae captured on 22 January and 6 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)							
	5.3-6.4				6.5-7.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					1	7.1	1	0.8
Calanoid copepods:								
Temora longicornis					1	7.1	3	2.5
Harpacticoid copepods:								
Microsetella norvegica	3	75.0	9	81.8	14	100.0	104	85.2
Tisbe spp.					2	14.3	2	1.6
Unidentified:								
Adults and copepodites					1	7.1	1	0.8
Coscinodiscus sp.	1	25.0	2	18.2	7	50.0	11	9.0
Total no. food items			11				122	
Number larvae examined	4				14			
Number larvae empty	1				0			

TABLE 3.—Summary of the food habits of 129 *Myoxocephalus aenaeus* larvae captured on 5, 6, 19, and 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)															
	5.5-6.4				6.5-7.4				7.5-8.4				8.5-9.5			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii	12	100.0	34	61.8	43	93.5	158	57.5	37	88.1	115	42.6	20	95.2	90	54.9
Calanoid copepods:																
Temora longicornis					3	6.5	4	1.5	9	21.4	16	5.9	4	19.0	5	3.0
Harpacticoid copepods:																
Microsetella norvegica	4	33.3	9	16.4	24	52.2	47	17.1	23	54.8	51	18.9	13	61.9	12	7.3
Tisbe spp.					10	21.7	13	4.7	10	23.8	20	7.4	5	23.8	9	5.5
Harpacticus spp.					2	4.3	2	0.7	13	31.0	17	6.3	6	28.6	9	5.5
Zaus sp.					2	4.3	2	0.7	3	7.1	4	1.5				
Unidentified:																
Adults and copepodites					5	10.9	6	2.2	3	7.1	4	1.5	1	4.8	2	1.2
Unidentified copepod nauplii					1	2.2	1	0.4					1	4.8	25	15.2
Turbellaria	3	25.0	4	7.3	13	28.3	19	6.9	12	28.6	23	8.5	4	19.0	7	4.3
Ostracoda					2	4.3	2	0.7								
Unidentified invertebrate eggs:																
Single	1	8.3	7	12.7	7	15.2	21	7.6	2	4.8	13	4.8				
Sacs	1	8.3	1	1.8					6	14.3	7	2.6	4	19.0	5	3.0
Coscinodiscus sp.	3	25.0	—		10	21.7	—		10	23.8	—		7	33.3	—	
Setae	2	16.7	—		5	10.9	—		11	26.2	—		3	14.3	—	
Unrecognizable debris	5	41.7	—		13	28.3	—		20	47.6	—		12	57.1	—	
Total no. food items			55				275				270				164	
Number larvae examined	17				49				42				21			
Number larvae empty	5				3				0				0			

in January-February and not in March when barnacle nauplii were the principal prey of larvae, because it is likely that some proportion of these diatom cells were released from the guts of *Balanus* nauplii during digestion. Cells $\leqq 25$ μm in diameter were found inside undigested *Balanus* nauplii taken from the guts of cottid larvae. Flatworms (Turbellaria) ingest diatoms whole (Jennings 1957) and these may also have contributed *Coscinodiscus* cells. Most of the calanoid and harpacticoid copepods ingested by cottid larvae were adults and, for *Temora longicornis,* mostly females. Bundles of setae of undetermined origin seemed to accumulate in the guts of cottid larvae. The most likely sources of these are the appendages of *Microsetella* and *Balanus* nauplii.

Diet Comparisons

Relative importance of each prey taxon was estimated from the product of %*FO* and %*N*. Major prey (%*FO* × %*N*>100) of only similar-sized larvae were ranked according to this value and compared for seasonal as well as inter- and intraspecific differences (Tables 11, 12). In general, the same trophic patterns were present among larvae in size groups not included in these comparisons (Tables 2-10).

In January and February the dominant prey of

TABLE 4.—Summary of the food habits of 31 *Myoxocephalus octodecemspinosus* larvae captured on 22 January and 6 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)							
	7.2-8.4				8.5-9.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					2	28.6	2	1.7
Calanoid copepods:								
Temora longicornis	7	29.2	8	2.5	7	100.0	28	23.3
Harpacticoid copepods:								
Microsetella norvegica	24	100.0	284	89.3	7	100.0	65	54.2
Tisbe spp.	2	8.3	2	0.6				
Harpacticus spp.	2	8.3	2	0.6				
Unidentified:								
Adults and copepodites	3	12.5	3	0.9	2	28.6	3	2.5
Unidentified copepod nauplii	2	8.3	3	0.9	1	14.3	2	1.7
Ostracoda	1	4.2	1	0.3				
Unidentified invertebrate eggs:								
Single					2	28.6	20	16.7
Coscinodiscus sp.	3	12.5	15	4.7				
Setae	1	4.2	—					
Total no. food items			318				120	
Number larvae examined	24				7			
Number larvae empty	0				0			

both *M. aenaeus* and *M. octodecemspinosus* was *Microsetella norvegica*, while *Coscinodiscus* sp. dominated the diet of *Myoxocephalus scorpius* larvae. *Coscinodiscus* sp. cells are bright green in color and the digestive tracts of *M. scorpius* larvae observed in the field before preservation appeared to be this same color. Unlike similar-sized *M. octodecemspinosus* and *M. scorpius*, *Triglops murrayi* larvae fed primarily on adult *Pseudocalanus minutus* and calanoid copepodites, which were largely digested but most resembled, and probably were, immature *Pseudocalanus*. There appeared to be no distinct change in dominant prey types as larvae grew within the size ranges examined. The largest *M. octodecemspinosus* and *M. scorpius* larvae ingested more kinds of prey than smaller larvae, but the reverse was true for *T. murrayi*.

In March, the overwhelmingly dominant prey of all three species of *Myoxocephalus* were *Balanus* nauplii. *Microsetella* ranked second in importance among 7.5-9.5 (9.4) mm SL *Myoxocephalus aenaeus* and *M. octodecemspinosus* larvae, but was replaced by adult *Temora longicornis* in 9.5-12.4 mm SL *M. octodecemspinosus*. No other prey of *M. scorpius* larvae at any size approached the importance of *Balanus* nauplii which were nearly the exclusive prey of this species in March. Mean number of nauplii per *M. scorpius* larva ranged from 12 to 16 depending on larval size, whereas the range in mean number for the other two species of *Myoxocephalus* was only 3-8 nauplii/larva. As in January and February, *Pseudocalanus* dominated the diet of *T. murrayi* larvae in four of six size groups. *Balanus* nauplii ranked second in importance in four size groups, and ranked first in the largest size group. Other fish larvae, primarily *M. aenaeus*, were nearly the exclusive prey of all *H. americanus* larvae examined. Up to four prey larvae were found in the gut of a single *H. americanus* larva, and a 13 mm SL rockgunnel, *Pholis gunnellus*, larva was found coiled up inside the gut of a 13 mm SL specimen. There was no dramatic change in prey types ingested among the five species with increasing larval size. Only the change in the second-ranked prey of *M. octodecemspinosus* larvae from *Microsetella* to *Temora* may have been related to increased size.

The most important seasonal change in diet among cottid larvae was replacement of *Coscinodiscus* sp. and, to a lesser extent, *Microsetella* by *Balanus* nauplii. Barnacle nauplii also became a relatively important component of the diet of *T. murrayi* larvae in March but *Pseudocalanus* continued to dominate the diet of larvae in most size groups.

Diet Overlap

Diet overlap was measured among larvae of four species of cottids (*H. americanus* excluded because of its obviously unique diet), using the Schoener index (1970) which describes the relative amount of dietary overlap between species pairs on a scale of 0 = no overlap to 100 = com-

TABLE 5.—Summary of the food habits of 75 *Myoxocephalus octodecemspinosus* larvae captured on 5, 6, 19, 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)																			
	7.5-8.4				8.5-9.4				9.5-10.4				10.5-11.4				11.5-12.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii	4	80.0	17	39.5	23	95.8	117	45.3	21	87.5	126	61.8	11	84.6	76	76.8	3	60.0	42	77.8
Calanoid copepods:																				
Temora longicornis	1	20.0	2	4.7	8	33.3	14	5.4	13	54.2	36	17.6	9	69.2	17	17.2	4	80.0	11	20.4
Harpacticoid copepods:																				
Microsetella norvegica	3	60.0	19	44.2	16	66.7	51	19.8	11	45.8	26	12.7	1	7.7	2	2.0				
Tisbe spp.					3	12.5	3	1.2	2	8.3	3	1.5	1	7.7	1	1.0				
Harpacticus spp.	1	20.0	2	4.7									1	7.7	1	1.0				
Unidentified:																				
Adults and copepodites	1	20.0	1	2.3	1	4.2	1	0.4	2	8.3	2	1.0	1	7.7	1	1.0				
Unidentified invertebrate eggs:																				
Single	1	20.0	1	2.3	6	25.0	69	26.7	1	4.2	9	4.4	1	7.7	1	1.0	1	20.0	1	1.9
Sacs	1	20.0	1	2.3	3	12.5	3	1.2	1	4.2	2	1.0								
Coscinodiscus sp.	2	40.0	—		2	8.3	—		3	12.5	—		2	1.5			2	40.0	—	
Setae	2	40.0	—		5	20.8	—		6	25.0	—		3	2.3	—					
Unrecognizable debris	2	40.0	—		7	29.2	—		9	37.5	—		7	5.4	—		2	40.0	—	
Total no. food items			43				258				204				99				54	
Number larvae examined	7				25				25				13				5			
Number larvae empty	2				1				1				0				0			

TABLE 6.—Summary of the food habits of 18 *Myoxocephalus scorpius* larvae captured on 22 January and 6 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)											
	7.5-8.4				8.5-9.4				9.5-10.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					1	11.1	2	0.9	3	100.0	3	3.1
Calanoid copepods:												
Temora longicornis					1	11.1	1	0.5	2	66.7	3	3.1
Pseudocalanus minutus					1	11.1	1	0.5				
Unidentified									1	33.3	1	1.0
Harpacticoid copepods:												
Microsetella norvegica	2	50.0	2	6.1	3	33.3	7	3.2	1	33.3	2	2.0
Tisbe spp.									1	33.3	1	1.0
Harpacticus spp.					2	22.2	2	0.9	1	33.3	1	1.0
Zaus sp.					2	22.2	3	2.8				
Unidentified:												
Adults and copepodites					3	33.3	3	1.4	3	100.0	10	10.2
Nauplii					1	11.1	27	12.5	1	33.3	30	30.6
Unidentified invertebrate eggs:												
Single					3	33.3	62	28.7	1	33.3	25	25.5
Coscinodiscus sp.	3	75.0	31	93.9	8	88.9	108	50.0	3	100.0	22	22.4
Unrecognizable debris	1	25.0	—		2	22.2	—		1	33.3	—	
Total no. food items			33				216				98	
Number larvae examined	6				9				3			
Number larvae empty	2				0				0			

TABLE 7.—Summary of food habits of 69 *Myoxocephalus scorpius* larvae captured on 5, 6, 19, 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)																				
	8.5-9.4				9.5-10.4				10.5-11.4				11.5-12.4				12.5-13.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii	14	100.0	165	94.3	28	96.6	426	77.3	12	100.0	182	90.1	8	100.0	120	91.6	6	100.0	95	93.1
Calanoid copepods:																				
Temora longicornis					8	27.6	12	2.2	2	16.7	8	4.0	2	25.0	4	3.1	1	16.7	1	1.0
Unidentified:																				
Adults and copepodites					5	17.2	5	0.9	1	8.3	2	1.0	2	25.0	2	1.5				
Harpacticoid copepods:																				
Tisbe spp.					9	31.0	11	2.0	3	25.0	3	1.5	2	25.0	2	1.5	3	50.0	3	2.9
Harpacticus spp.					7	24.1	9	1.6	3	25.0	3	1.5	1	12.5	1	0.8				
Zaus sp.	1	7.1	1	0.6	3	10.3	3	5.4					1	12.5	2	1.5	1	16.7	1	1.0
Unidentified:																				
Adults and copepodites	1	7.1	1	0.6	2	6.9	8	1.5	1	8.3	2	1.0					1	16.7	1	1.0
Unidentified invertebrate eggs:																				
Single	2	14.3	8	4.6	5	17.2	77	14.0	2	16.7	2	1.0								
Sacs																	1	16.7	1	1.0
Coscinodiscus sp.	2	14.3	—		5	17.2	—		3	25.0	—		3	37.5	—		1	16.7	—	
Setae					3	10.3	—		1	8.3	—		2	25.0	—		1	16.7	—	
Unrecognizable debris	5	35.7	—		10	34.5	—		5	41.7	—		4	50.0	—		2	33.3	—	
Total no. food items			175				551				202				131				102	
Number larvae examined	14				29				12				8				6			
Number larvae empty	0				0				0				0				0			

TABLE 8.—Summary of the food habits of 22 *Triglops murrayi* larvae captured on 22 January and 6, 20, 21 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)																				
	8.5-8.9				9.0-10.4				10.5-11.4				11.5-12.4				12.5-14.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii																	1	33.3	1	2.2
Calanoid copepods:																				
Temora longicornis	1	20.0	2	10.0	1	20.0	1	2.9					2	50.0	8	18.6	2	66.7	7	15.6
Pseudocalanus minutus	5	100.0	9	45.0	5	100.0	20	57.1	5	100.0	17	77.3	4	100.0	31	72.1	3	100.0	24	53.3
Unidentified:																				
Adults					1	20.0	1	2.9					1	25.0	1	2.3				
Copepodites	4	80.0	8	40.0	5	100.0	13	37.0	3	40.0	5	22.7	3	75.0	3	7.0	2	66.7	12	26.7
Nauplii																	1	33.3	1	2.2
Pseudocalanus eggs					1	20.0	—		3	40.0	—		1	25.0	—					
Harpacticoid copepods:																				
Tisbe sp.	1	20.0	1	5.0																
Unrecognizable debris					2	40.0	—													
Total no. food items			20				35				22				43				45	
Number larvae examined	5				5				5				4				3			
Number larvae empty	0				0				0				0				0			

TABLE 9.—Summary of the food habits of 36 *Triglops murrayi* larvae captured on 5, 6, 19, 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)																											
	9.0-10.4				10.5-11.4				11.5-12.4				12.5-13.4				13.5-14.4				14.5-15.4				15.5-18.1			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					1	33.3	7	43.8	2	40.0	21	33.3	2	50.0	15	45.5	4	66.7	33	42.9	5	100.0	31	62.0	9	100.0	59	64.8
Calanoid copepods:																												
Temora longicornis																	2	33.3	2	2.6	3	60.0	8	16.0	2	10.3	9	9.9
Pseudocalanus minutus	2	100.0	6	85.7	2	66.7	7	43.8	3	60.0	6	9.5	4	100.0	16	48.5	6	100.0	29	37.7	3	60.0	8	16.0	7	77.8	14	15.4
Unidentified:																												
Adults					1	33.3	1	6.3	1	20.0	1	1.6													1	11.1	4	4.4
Copepodites	1	50.0	1	14.3					1	20.0	1	1.6	2	50.0	2	6.1	2	33.3	2	2.6	1	20.0	1	2.0	1	11.1	1	1.1
Pseudocalanus eggs					2	66.7	—						1	25.0	—		2	33.3	—		1	20.0	—		3	33.3	—	
Unidentified:																												
Harpacticoid copepods									1	20.0	1	1.6																
Cyclopoid copepods					1	33.3	1	6.3																				
Decapod zoea																	1	16.7	1	1.3	1	20.0	1	2.0	4	44.4	4	4.4
Unidentified invertebrate eggs									2	40.0	33	52.4					1	16.7	10	13.0	1	20.0	1	2.0				
Unrecognizable debris									1	20.0	—						2	33.3	—		3	60.0	—		8	88.9	—	
Total no. food items			7				16				63				33				77				50				91	
Number larvae examined	4				3				5				4				6				5				9			
Number larvae empty	1				0				0				0				0				0				0			

TABLE 10.—Summary of the food habits of 24 *Hemitripterus americanus* larvae captured on 22 January 1974; 16 February 1972; 7 March 1972; 5, 6, 20 March 1973; 6 March 1974; and 12 April 1972. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)															
	12.0-13.4				13.5-14.4				14.5-15.4				15.5-16.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Decapod zoea					1	20.0	1	20.0								
Fish larvae[1]	8	100.0	9	100.0	4	80.0	4	80.0	4	100.0	6	100.0	4	100.0	8	100.0
Total no. food items			9				5				6				8	
Number larvae examined	10				6				4				4			
Number larvae empty	2				1				0				0			

[1]Includes:
1 - *Pholis gunnellus* (~13 mm SL)
1 - *Lumpenus lampretaeformis*
12 - *Myoxocephalus aenaeus* (~5-6 mm SL)
1 - *M. octodecemspinosus* (~7-8 mm SL)
1 - *Triglops murrayi*
6 - Unidentified cottid larvae
5 - Unidentified fish larvae.

TABLE 11.—Comparison of the major prey of similar-sized cottid larvae from January and February 1973. Food items are listed in order of decreasing rank by the value (in parentheses) of the product, % frequency of occurrence × % of total number; only items with a value >100 are presented. Food item abbreviations are: BN = *Balanus* nauplii; Cosc = *Coscinodiscus* sp.; $E_{(si)}$ = Invertebrate eggs (single); Mn = *Microsetella norvegica*; Ps = *Pseudocalanus minutus*; Tem = *Temora longicornis*; Ts = *Tisbe* spp.; UCalc = Unidentified calanoid copepodites; UHa or n = Unidentified harpacticoid adults or nauplii.

Myoxocephalus aenaeus			
Size range (mm)	6.5-7.4		
Ranked food items	Mn (8,500) Cosc (450)		
Myoxocephalus octodecemspinosus			
Size range (mm)	7.2-8.4	8.5-9.4	
Ranked food items	Mn (8,900)	Mn (5,420) Tem (2,330) $E_{(si)}$ (478)	
Myoxocephalus scorpius			
Size range (mm)	7.5-8.4	8.5-9.4	9.5-10.4
Ranked food items	Cosc (7,043) Mn (305)	Cosc (4,445) $E_{(si)}$ (956) UHn (139) Mn (106)	Cosc (2,240) UHn (1,029) UHa (1,000) $E_{(si)}$ (849) BN (300) Tem (200)
Triglops murrayi			
Size range (mm)		8.5-8.9	9.0-10.4
Ranked food items		Ps (4,500) UCalc (3,200) Tem (200) Ts (100)	Ps (5,700) UCalc (3,700)

plete overlap (Fig. 2). Except for the consistently high degree of overlap between the diets of *Myoxocephalus aenaeus* and *M. octodecemspinosus*, overlap among cottid larvae in general

Species	*M. aenaeus*	*M. octodecemspinosus*	*M. scorpius*	*T. murrayi*
M. aenaeus		78.7	64.0	58.2
M. octodecemspinosus	87.3		69.5	67.5
M. scorpius	15.9	16.0		59.6
T. murrayi	3.5	9.1	2.6	

(Upper right: Spring; lower left: Winter)

FIGURE 2.—Matrix of Schoener (1970) index values measuring percent diet overlap among species pairs of cottid larvae from winter (January-February) and early spring (March) collections in the Damariscotta River estuary, Maine.

TABLE 12.—Comparison of the major prey of similar-sized cottid larvae from March 1973 (*Myoxocephalus* spp. and *T. murrayi*) and January-April 1972-74 (*H. americanus*). Food items are listed in order of decreasing rank by the value (in parentheses) of the product, % frequency of occurrence × % of total number; only items with a value >100 are presented. Food item abbreviations are: BN = *Balanus* nauplii; DZ = decapod zoea; $E_{(si)}$ = Invertebrate eggs (single); FL = fish larvae; H = *Harpacticus* spp.; Mn = *Microsetella norvegica*; Ps = *Pseudocalanus minutus*; Tem = *Temora longicornis*; Ts = *Tisbe* spp.; Tur = Turbellaria; UCala or c = Unidentified calanoid adults or copepodites; UCyc = Unidentified cyclopoids. (* = tied rank.)

Myoxocephalus aenaeus								
Size range (mm)	7.5-8.4	8.5-9.5						
Ranked food items	BN (3,753) Mn (1,036) Tur (243) H (195) Ts (176) Tem (126)	BN (5,226) Mn (452) H (157) Ts (131)						
Myoxocephalus octodecemspinosus								
Size range (mm)	7.5-8.4	8.5-9.4	9.5-10.4	10.5-11.4	11.5-12.4			
Ranked food items	BN (3,160) Mn (2,652)	BN (4,340) Mn (1,321) $E_{(si)}$ (668) Tem (180)	BN (5,408) Tem (954) Mn (582)	BN (6,497) Tem (1,190)	BN (4,668) Tem (1,632)			
Myoxocephalus scorpius								
Size range (mm)		8.5-9.4	9.5-10.4	10.5-11.4	11.5-12.4	12.5-13.4		
Ranked food items		BN (9,430)	BN (7,467) $E_{(si)}$ (241)	BN (9,000)	BN (9,160)	BN (9,310) Ts (145)		
Triglops murrayi								
Size range (mm)			9.0-10.4	10.5-11.4	11.5-12.4	12.5-13.4	13.5-14.4	14.5-15.4
Ranked food items			Ps (8,570) UCalc (715)	Ps (2,921) BN (1,459) *UCala (210) *UCyc (210)	$E_{(si)}$ (2,096) BN (1,459) Ps (570)	Ps (4,850) BN (1,332) UCalc (305)	Ps (3,770) BN (2,275) $E_{(si)}$ (217)	BN (6,200) *Ps (960) *Tem (960)
Hemitripterus americanus								
Size range (mm)						12.0-13.4	13.5-14.4	14.5-15.4
Ranked food items						FL (10,000)	FL (6,400) DZ (400)	FL (10,000)

was greater in early spring (March) than in winter (January and February). Diets of the three species of *Myoxocephalus* usually overlapped more with each other than did any with the diet of *T. murrayi*. This difference was more pronounced in winter than in early spring.

Larval Mouth Size and Prey Width

Because mouth size or gape determines maximum size of prey ingested, the ratio of upper jaw length (mm) to standard length (mm) was used to compare relative mouth sizes among cottid larvae (Blaxter and Hempel 1963; Shirota 1970). Jaw length to standard length ratios were most similar at all stages of development among the three species of *Myoxocephalus* (Table 13). Larvae of *T. murrayi* and *H. americanus*, regardless of stage of development, had larger mouths than *Myoxocephalus* larvae. Only *H. americanus* larvae had jaw teeth within the size range observed.

All food items found in cottid larvae had been swallowed whole. Since fish larvae have been observed to swallow their prey head-first with appendages and setae folded back, the critical dimension of a potential food item is maximum body width (Blaxter 1965; Arthur 1976). Maximum widths of the major prey of larval cottids ranged from 80 to 1,260 μm (Fig. 1). Among individual prey items, *Balanus* nauplii exhibited the widest size range and *Microsetella* the narrowest. The harpacticoid and calanoid copepods were somewhat similar in size, while the largest prey overall were decapod zoea and fish larvae.

Prey size at first feeding was estimated for larvae of *Myoxocephalus* and *H. americanus* from the width of prey found in guts of larvae with three-fourths or more of their abdomens full of yolk. No yolk-bearing larvae of *T. murrayi* were found with this condition. *Myoxocephalus aenaeus* ($N = 14$) ingested *Microsetella* and stage 2 or 3 *Balanus* nauplii ranging in size from 100 to 360 μm. *Myoxocephalus octodecemspinosus* ($N = 5$) ingested only 100 μm wide *Microsetella*. *Myoxocephalus scorpius* ($N = 9$) ingested primarily *Coscinodiscus* and *Microsetella* which ranged from 80 to 220 μm; however, a single *Balanus* nauplius and unidentified harpacticoid copepod were found measuring 375 and 260 μm, respectively. First-feeding *H. americanus* larvae were also primarily piscivorous. Maximum width of most prey larvae (dorsally across the eyes) could not be measured because of advanced state of digestion, but one intact larva measured 950 μm. The only other prey found in yolk-sac *H. americanus* larvae was an 880 μm wide decapod zoea.

No consistent pattern of increased prey size with increased larval size or advanced stage of development was apparent over the size range of cottid larvae observed in these analyses. Overall size range of prey ingested by *Myoxocephalus* and *T. murrayi* larvae overlapped extensively (Fig. 1). Among *Myoxocephalus* larvae, *M. scorpius* ingested slightly larger prey than did the other two species which reflects the greater frequency of *Balanus* nauplii and low incidence of *Microsetella* in its diet. *Triglops murrayi* larvae ate food items over the widest size range and *H. americanus* over the narrowest size range.

DISCUSSION

The incidence of yolk retention in feeding cottid larvae was high over a wide size range, presumably representing a long period of time. Initiation of feeding before complete yolk absorption has been previously observed among larval flatfishes, gadoids, and herring (Blaxter 1965; Last 1978a, b; Sumida and Moser 1980). Arthur (1976), however, never found both yolk and ingested food in larvae of northern anchovy, *Engraulis mordax*; Pacific sardine, *Sardinops sagax*; or jack mackerel, *Trachurus symmetricus*. Food ingestion prior to complete yolk absorption may be advantageous to fish larvae by allowing time for trial-and-error learning, which has been

TABLE 13.—Comparison of relative mouth size among larval cottids using the ratio of upper jaw length (mm) to standard length (SL). N = number of larvae measured.

	Larvae used in diet analysis				Smallest larvae with yolk sac			
			Upper jaw length/SL				Upper jaw length/SL	
Species	*N*	Mean SL (mm)	Mean	Range	*N*	Mean SL (mm)	Mean	Range
Myoxocephalus aenaeus	84	7.4	0.11	0.10-0.13	12	6.3	0.10	0.09-0.10
M. octodecemspinosus	72	9.7	0.11	0.09-0.13	15	7.7	0.10	0.09-0.11
M. scorpius	61	10.3	0.12	0.09-0.13	10	8.4	0.11	0.09-0.12
Triglops murrayi	35	13.8	0.13	0.12-0.15	1	7.1	(0.13)	—
Hemitripterus americanus	20	13.9	0.15	0.13-0.17	1	13.0	(0.15)	—

shown to increase feeding success in early larvae (Blaxter 1965; Hunter 1980), as well as by prolonging the time before larvae become totally dependent on an exogenous food supply which is limited in abundance and distribution (Laurence and Rogers 1976). Potential or actual energy deficits prior to or coincident with the initiation of feeding were found to occur in the tautog, *Tautoga onitis* (Laurence 1973), and Pacific sardine, *Sardinops sagax* (Lasker 1962), both relatively fecund species having planktonic eggs and larvae. Yet, deficits based on the amount of yolk absorbed did not occur until after feeding had begun in rainbow trout, *Salmo gairdneri*; brown trout, *Salmo trutta*; bluegill, *Lepomis macrochirus*; and largemouth bass, *Micropterus salmoides*, all of which have relatively low fecundity, and demersal eggs and larvae (Laurence 1973). Although energy budgets have not been described for them, it is likely that cottids have yolk-utilization characteristics similar to this latter group of fishes.

The relatively higher incidence of empty guts among the almost exclusively piscivorous larvae of *H. americanus* may also be related to trophic energetics. Since fish larvae probably supply more energy per unit effort as prey than do crustaceans because of larger size and lack of indigestible exoskeletons, ingestion of single, large, highly digestible prey would reduce the need for continuous foraging. Larvae of *H. villosus* in the Japan Sea, like those of its congener in the Gulf of Maine, also feed on other fish larvae (Okiyama and Sando 1976). Most reports of piscivorous larvae have come from observations of laboratory-reared larvae, particularly scombroid fishes (Beyer 1980; Hunter 1980).

The larval diets of four of five species of cottids in the Damariscotta River estuary were distinctly different, despite similarities in mouth size and morphology and the absence of obvious specialized morphological adaptations for feeding. Last (1978a) also observed differences in larval diets among pleuronectiform fishes in the North Sea and concluded that this represented a mechanism whereby direct competition for food is avoided. There are many theoretical and practical difficulties in assessing the significance of competition as a cause of dietary divergence in fishes (Zaret and Rand 1971; Weatherly 1972), yet existence of competition among tropical stream fishes has been inferred from observed reductions in diet overlap during periods of lowered food supply (Zaret and Rand 1971). Comparisons of dietary overlap and food supply among the larvae of *Myoxocephalus* and *Triglops* species during winter and early spring indicated a similar pattern. The lowest values of percent diet overlap, i.e., occurrence of the most dissimilar diets, among five of six possible pairs of species combinations occurred in January and February, and coincided with lowest prey abundance as indicated by the lower mean plankton volume (an approximate measure of food supply) of the two periods compared, 16.8 ml ($n = 22$) vs. 31.0 ml ($n = 25$) in March.

Percentage diet overlap between *M. aenaeus* and *M. octodecemspinosus*, whose larvae were the most abundant in the estuary (Laroche 1980) and who had the most similar food habits, remained relatively high and constant through winter and early spring. Some mechanism other than dietary shifts, i.e., changes in dominant prey, may act to reduce competition between larvae of these two species. Although both species were more abundant 1.5 m above the bottom than in the upper 1.5 m during winter and spring months, *M. aenaeus* larvae were 5 times more abundant while *M. octodecemspinosus* were only 1.7 times more abundant (Laroche 1980). Such relative differences in vertical distribution resulted in spatial separation of most *M. aenaeus* and *M. octodecemspinosus* larvae. If competition is indeed an important factor in diet determination among cottid larvae, this spatial separation may explain the high degree of dietary overlap between these two species.

Density-independent food exploitation (Hyatt 1979) by fish larvae has not been demonstrated by quantitative comparisons of prey abundance in larval guts to their abundance in the plankton. Blaxter (1965) cited numerous examples, mostly qualitative, of apparent selection among herring larvae for specific taxa of copepod and diatom prey over other prey which were more abundant in the plankton. Qualitative comparisons of the composition and relative abundance of the zooplankton present during winter and spring months of 1972 in the Damariscotta River estuary (Lee 1974) and prey found in larval cottids from winter and spring 1973 yielded indirect evidence of density-independent foraging among these larvae. Although zooplankton species composition and abundance may vary from year to year, relative constancy has been demonstrated in larval diets of at least two of the five species of cottids in the estuary. Townsend (1981) observed that the principal prey of *M. octodecemspinosus*

(*Microsetella*, *Temora*, and *Balanus* nauplii) and *M. scorpius* larvae (*Balanus* nauplii and *Coscinodiscus*) in the Damariscotta River estuary during winter and spring 1979 were the same as reported from 1973.

Copepods which were relatively abundant during winter and spring months in the Damariscotta River estuary were *Eurytemora herdmani*, *Oithona similis*, and *Pseudocalanus minutus* (Lee 1974). Of these species only *Pseudocalanus* was an important prey of cottid larvae (one species, *Triglops*). *Oithona*, a relatively small cyclopoid, was abundant in early spring but was not eaten by cottid larvae. However, two somewhat larger species were eaten: *Temora longicornis*, whose abundance in winter was variable and lower than in summer and fall, and *Pseudocalanus*. Ivlev (1961) noted that when food is plentiful, fish will take the largest available prey present. But this does not explain why larvae preferentially ate *Temora* and not the same-sized but probably more abundant *Eurytemora* or why they apparently "preferred" the smaller species of pelagic, harpacticoid copepod, *Microsetella norvegica*, over the larger, abundant winter species *Parathalestris croni*. It is perhaps significant that four of the five major prey of *Myoxocephalus* and *Triglops* larvae, *Balanus* nauplii, *Temora*, *Pseudocalanus*, and *Microsetella* were also found to be important natural prey of fish larvae in widely different regions (Lebour 1918, 1919; Sherman and Honey 1971; Arthur 1976; Last 1978a, b). Food selection by fish larvae is controlled by factors such as prey size (the most investigated variable), morphology, catchability (as determined by swimming speeds, escape responses, etc.), and availability (temporal and spatial distribution). None of these factors are well understood.

Most studies of the feeding ecology of fish larvae have focused on prey size, but color (Arthur 1976) and body transparency may also be important cues for "selection" of various copepod prey by fish larvae. All of the harpacticoid copepods ingested by cottid larvae were brightly colored: *Tisbe* spp., red and white stripes; *Zaus* sp., blue-green; *Harpacticus* sp., brown; and *Microsetella*, red. Furthermore, except for *Microsetella*, all are epibenthic forms whose abundance in the water column would not be expected to be high (Noodt 1971). Among the calanoid copepods, differences in body transparency and resulting visibility to predators may explain why *Temora* (which has a dense, thick carapace) was ingested by cottid larvae rather than the more abundant but nearly transparent *Oithona*.

Balanus nauplii, which at times during late winter and early spring can be the most abundant zooplankter in the Damariscotta River estuary (Lee 1974), were the most ubiquitous prey of cottid larvae and appeared to be ingested in direct relation to their abundance in the plankton, i.e., in density-dependent fashion. Comparison of frequencies of occurrence of the six naupliar stages of *Balanus* ingested by *Myoxocephalus* and *Triglops murrayi* larvae in early and late March showed that, with one exception, larvae of all four species caught in early March were feeding solely on naupliar stages 1-3 (Table 14). Later in the month when *Balanus* nauplii became the dominant zooplankter in most ichthyoplankton samples, larvae of all four species (i.e., larvae of varying size and, presumably, prey-catching ability and "preference") were feeding on all six naupliar stages. Percent frequency of occurrence of each stage was remarkably similar among the four cottid species, suggesting that these values might actually reflect relative abundance of each stage in the plankton assuming that each stage is equally susceptible to capture and ingestion. The apparent reliance of cottid larvae on *Balanus* nauplii may be explained by the tendency, observed among adult fishes, to ingest more intermediate-sized rather than larger prey when both are present in abundance (Ivlev 1961; Hyatt 1980). Among larval cottid prey, naupliar

TABLE 14.—Percent frequency of occurrence (%*FO*) of six naupliar stages of *Balanus* spp. (Crisp 1962) in the guts of four species of cottids on (1) 5-6 March and (2) 19-20 March 1973.

Species:	*M. aenaeus*		*M. octodecemspinosus*		*M. scorpius*		*T. murrayi*	
Dates:	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
No. larvae:	40	78	35	40	33	37	13	23
	%*FO*	%*FO*	%*FO*	%*FO*	%*FO*	%*FO*	%*FO*	%*FO*
Balanus nauplii								
Stage 1	7	5	12	6	6	1	—	3
Stages 2,3	93	52	87	41	91	45	100	45
Stages 4,5	—	31	—	38	0.6	41	—	48
Stage 6	—	5	—	3	—	6	—	2
Stage unknown	0.6	6	2	11	2	7	—	2

stages of *Balanus*, particularly stages 2-4, are somewhat smaller than adult *Temora* and *Pseudocalanus*.

Among fish larvae whose food habits have been reported, cottid larvae most resemble hake (genus *Merluccius*) in prey size at first feeding and in changes of prey size with growth. The first prey ingested by most marine fish larvae range in width from 50 to 100 μm (Houde 1973; Hunter 1980). First prey of hake and cottid larvae are larger: 50-400 μm for *Merluccius productus*; 500 μm mean prey width for *M. merluccius hubbsi*; 100-375 μm for three species of *Myoxocephalus*; and >800 μm for *H. americanus* (Sumida and Moser 1980; de Ciechomski and Weiss 1974). Among fish larvae that ingest 50-100 μm wide prey at first feeding, there is usually a distinct and often dramatic increase in prey size with development. This is seen typically as a change from a diet of copepod eggs and nauplii to one of advanced copepodites and adults. No dramatic increase in prey size or progression in prey types occurs in cottid and hake larvae.

Hunter (1980) recently attempted to categorize marine fish larvae into distinct ecological roles based on those behavioral and physiological traits primarily associated with feeding. Two distinct groups, engrauliform and scombriform, based on extensive field and laboratory observations of northern anchovy and Pacific mackerel larvae, emerged from his analyses. Cottid larvae share some scombriform traits such as relatively large mouths and prey. Similarities in feeding posture, maneuverability, and swimming speed may be inferred because of features in body shape shared by cottid and Pacific mackerel larvae. These larvae, however, would be expected to differ significantly in rates of metabolism and growth because of the different environmental temperature regimes they inhabit: 14°-21°C for highest abundances of Pacific mackerel (Kramer 1960) and 0°-4°C for cottid larvae (Laroche 1980). In this regard, cottid larvae more closely resemble hake larvae which inhabit deeper, colder oceanic waters than either anchovy or Pacific mackerel. Hunter (1980) suggested that hake larvae may belong to a third trophic group characterized by reliance on large prey, a feature already shown to be shared with cottid larvae, and slow metabolism and growth. Although growth rates have not been estimated for cottid larvae, increases in monthly median lengths of ≦1 mm (Laroche 1980) and relatively stationary modes in length-frequency distributions during winter and spring in the Damariscotta River estuary (Townsend 1981) may be explained, in part, by slow growth rates.

Despite some apparent similarities, there are notable differences in the early life histories of hake and the five species of cottids: for example, egg size, 0.98 vs. 1.5-4 mm; size at hatching, 2.4 vs. 5-12 mm; and stage of eye and mouth development at hatching, partial vs. complete. The significance of differences such as these in further distinguishing ecological roles among fish larvae will be better understood only after the early feeding ecology of more species has been investigated.

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