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The relations between larval fishes and zooplankton in two inshore areas of the Gulf of Maine

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Abstract. Larval fishes and zooplankton were sampled in two hydrographically different areas on the coast of the Gulf of Maine: Sullivan Harbor, an embayment in eastern Maine, and the Damariscotta River estuary in western Maine. Sampling was conducted at weekly intervals from late winter to early summer in each area in 1979 and 1980. Phytoplankton chlorophyll concentrations were determined in each area in 1979. The time of peak catch rates of the dominant larval fish species occurred one to three weeks earlier in the western sample area, the Damariscotta estuary, than in Sullivan Harbor in the east. The phytoplankton and zooplankton blooms also occurred one to three weeks earlier in the Damariscotta estuary than in Sullivan Harbor. These timing trends are believed to result from the differences in the seasonal hydrographic changes of the inshore and coastal source waters. Analyses of the feeding, length-frequencies, and condition factors of the dominant larval fish species, *Pholis gunnellus*, are used to relate the apparent survival of the larvae to the timing of appearance of their forage organisms, the dynamics of which are determined by the local hydrography and resultant phytoplankton dynamics.

Introduction

Studies on the early life history stages of fishes have shown that the year class strength of a fish stock is influenced at least in part by the severity of larval mortality, an ideal first put forward by Hjort (1914, 1926) in the form of the 'critical period' concept. He suggested that catastrophic mortalities of fish larvae occur due to starvation as a result of low planktonic food densities at the time of transition from the yolk sac stage to active feeding. Support for this concept comes from numerous laboratory studies on the feeding of fish larvae which have shown that sufficiently high concentrations of planktonic food are crucial to the successful first feeding, and hence survival of the larvae (O'Connell and Raymond, 1970; Lawrence, 1974, 1977; Houde, 1974, 1977, 1978; Houde and Scheckter, 1978; Lasker and Zweifel, 1978). However, the demonstration of a critical period in the field has been extremely limited (Shelbourne, 1957; Lasker, 1975). Various phenomena have been suggested which could exacerbate the effect of a critical period and result in high mortalities of fish larvae. It has been suggeted that variations in the timing of seasonal plankton blooms might result in the mismatch in time between fish larvae and their food (Cushing, 1969), and May (1974) pointed out that a similar situation would occur if larvae were advected to areas where plankton production was low. These latter ideas stemmed from the assumption that adult breeding cycles are regulated such that the larval progeny hatch at a time propitious for finding food, a strategy for dealing with a critical period (Crisp, 1954). Support for the idea of timed spawnings in fishes was prof-

fered by Cushing (1967) who showed that variations in spawning times of the herring populations in the northeast Atlantic were linked to differences in production cycles between the areas. He also pointed out that if the strategy of spawning were to insure that the larvae began feeding at the height of the production of planktonic food, then the survival of that sock would be vulnerable to variations in the production cycle (Cushing, 1970). The results of a field study investigating the nature of this coupling between the plankton production cycle and the success of larval fishes are presented here.

Study Areas

Two inshore areas of the Gulf of Maine were selected as sample sites (Figure 1). These two areas, the Damariscotta River estuary in western Maine and Sullivan Harbor in eastern Maine, were selected for comparison because a hydrographic front off Penobscot Bay separates the coastline into two different hydrographic regimes. West of Penobscot Bay there is a combination of increased river runoff and reduced tidal mixing, favoring a more rapid development of vertical stratification in spring and summer. East of Penobscot Bay tidal mixing is enhanced and the development of vertical stratification is much reduced throughout the warmer months. It has already been shown that the two inshore areas reflect the hydrography of their immediate source waters (Townsend, 1981), and that the differences in hydrography along the coastal Gulf of Maine influence the timing of the spring phytoplankton and zooplankton blooms (Bigelow, 1926; Fish and Johnson, 1936; Bigelow *et al.*, 1940; Lillick, 1940; Sherman, 1970), with propagation beginning first in the western Gulf. Thus, the Damariscotta estuary and Sullivan Harbor provide appropriate geographic settings to examine how crucial the timing of spring plankton blooms is to the timing of spawning and the survival of larval fishes.

Materials and Methods

Field sampling for larval fishes and zooplankton was conducted at weekly intervals in each of the two study areas from late January to July in 1979 and late January to May in 1980. A 61-cm mouth diameter bongo net frame with 505 μm mesh plankton nets (No. 0) on each side was used for sampling larval fishes (Posgay and Marak, 1981). Below this on the same wire was a 20-cm mouth diameter bongo frame for sampling zooplankton. In 1979, 80 μm mesh nets (No. 20) were used on the small bongo. It became apparent that clogging of the No. 20 mesh nets might be reducing filtration through the meshes and a 165 μm mesh net (No. 10) was placed on one side beginning in April 1979. In 1980, No. 10 nets were used exclusively on the small bongo. A General Oceanics digital flow meter was mounted in each of the four nets.

A single station was occupied in each study area. Replicate surface and deep tows were taken, above and below the level of no net residual tidal motion, giving a total of four tows. The objective, however, was not to determine the depth distributions of ichthyoplankton and zooplankton in the two shallow areas but rather to arrive at a good estimate of the overall relative abundances of the specific organisms in each study area. The nets were towed for 10 min at

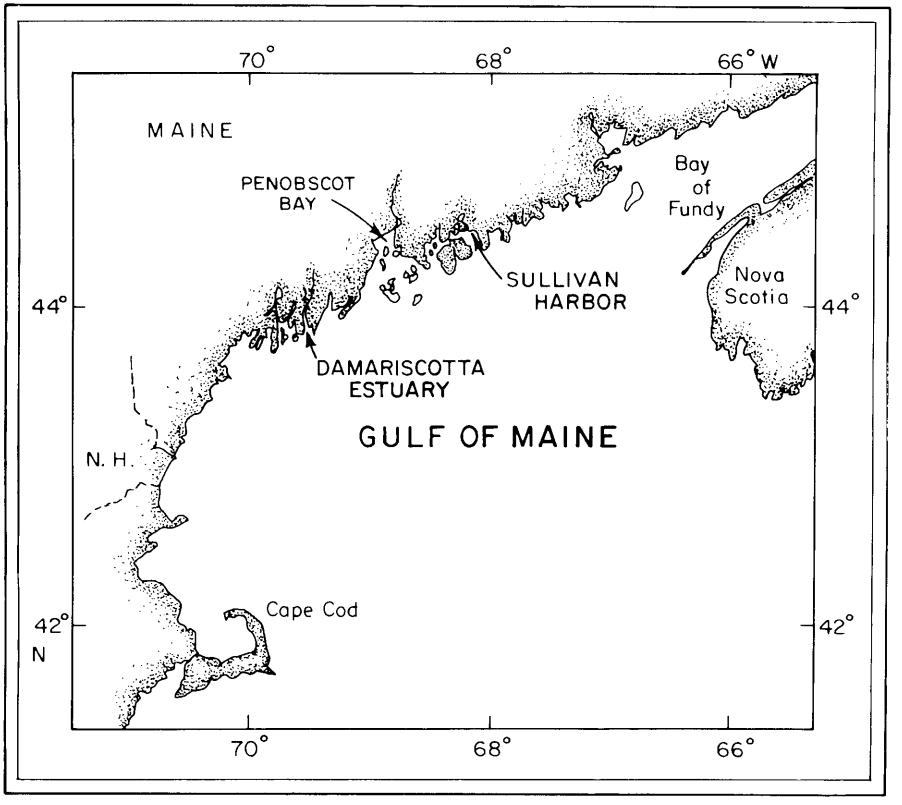

Fig. 1. Map of the Gulf of Maine showing the locations referred to in the text.

~3 knots (1.5 m/s). All samples were collected as close to mid-day as possible since it was necessary to capture fish larvae which had food in their digestive tract. Various studies have shown that larval fishes sampled at night generally do not have food in the gut (Blaxter, 1965; Schumann, 1965; Braum, 1967; June and Carlson, 1971; Kjelson *et al.*, 1975).

One side of the 61-cm bongo samples was preserved in 5% buffered formalin after first relaxing the fish larvae with 1 g of tricaine methanesulfonate (MS-222). Both sides of the small bongo samples were preserved in 5% buffered formalin. Water samples for chlorophyll analysis were collected in 1979 at depths of 2 m (surface) and 15 m (near bottom) in Van Dorn bottles. Ten ml of water were filtered through glass fiber filters and the filters frozen at −18°C. These were later analyzed fluorometrically for chlorophyll *a* concentration by the method of Yentsch and Menzel (1963) using the equations of Lorenzen (1966).

Zooplankton settled volumes were determined for all the 20-cm bongo samples as an approximate index of biomass by allowing each to settle overnight in a graduated cyclinder. Species abundance and composition estimates were made by

pooling the 20-cm bongo samples of the same mesh size for a particular date and area, diluting the pooled sample at 10–20 times the settled volume and subsampling a 1 ml aliquot with a Stempel pipette. All zooplankton in the aliquot were counted and identified to species, when possible, in a Segdwick-Rafter cell.

All fish larvae from the preserved 61-cm bongo samples were identified and counted. When present, at least 40 individuals of each of the dominant larval fish species for each sample date and area were measured to the nearest 0.5 mm total length (T.L.) and length-frequency distributions constructed. If <40 were present, all were measured.

Relative condition factors as modified from LeCren (1951) were determined for the dominant larval fish species. This condition factor incorporated the allometric equation:

$$W = aL^b$$

where; W = dry weight of larva in mg

L = length of larva in mm (T.L.)

and a and b are constants. The relative condition factor, K, for a larva is then:

$$K = \frac{W}{L^b} = a$$

The value of the power, b, was first determined for each species for a particular sample area and year. A subsample of ~30 larvae (or half the number available) for each date was measured to the nearest 0.5 mm T.L., dried overnight in an oven at 38°C (Chenoweth, 1970) and weighed to the nearest 0.01 mg. All the data for that species, year and study area were used to solve the allometric equation for the exponent, b, using a geometric mean functional regression (Ricker, 1973).

Gut contents of the dominant larval fish species were examined for each year and area. When available, 10 larvae per species from each sample date and area were examined. An index of relative importance of each food taxon for each sample was computed. The index was a form of the one presented by George and Hadley (1979) and was computed as follows: the percent frequency of occurrence of each food taxon (the percentage of the 10 or so larvae that had that food item present in the gut), and the percentage of each food taxon of the total number of those taxon items eaten by all 10 or so larvae in the sample, were calculated. The index of relative importance (IRI) was then:

X_a = % frequency of occurrence + % total number for food taxon, a.

$$IRI_a = \frac{100\,X_a}{\sum_{a=1}^{n} X_a}$$

where n = total number of different food taxa found in the larvae from that sample.

Results

A total of 26 species of fish larvae was caught in this study. Emphasis is given

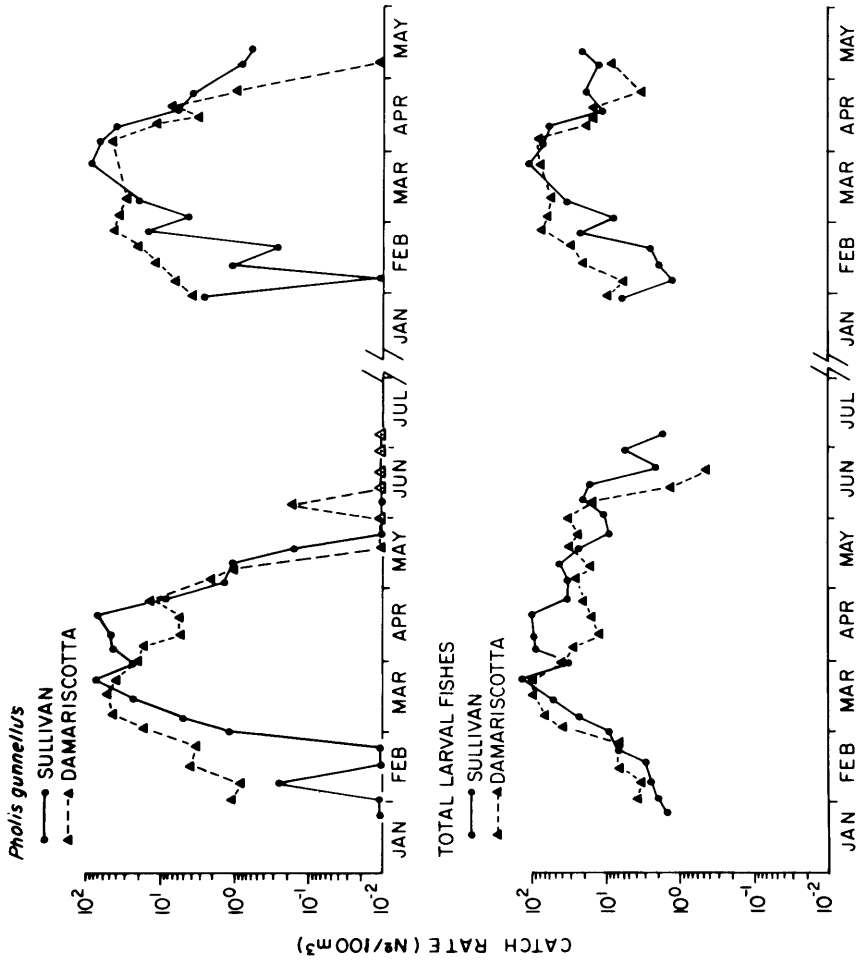

Fig. 2. Catch rates of larval *P. gunnellus* and total larval fish catch rates for the Damariscotta estuary and Sullivan Harbor in 1979 and 1980.

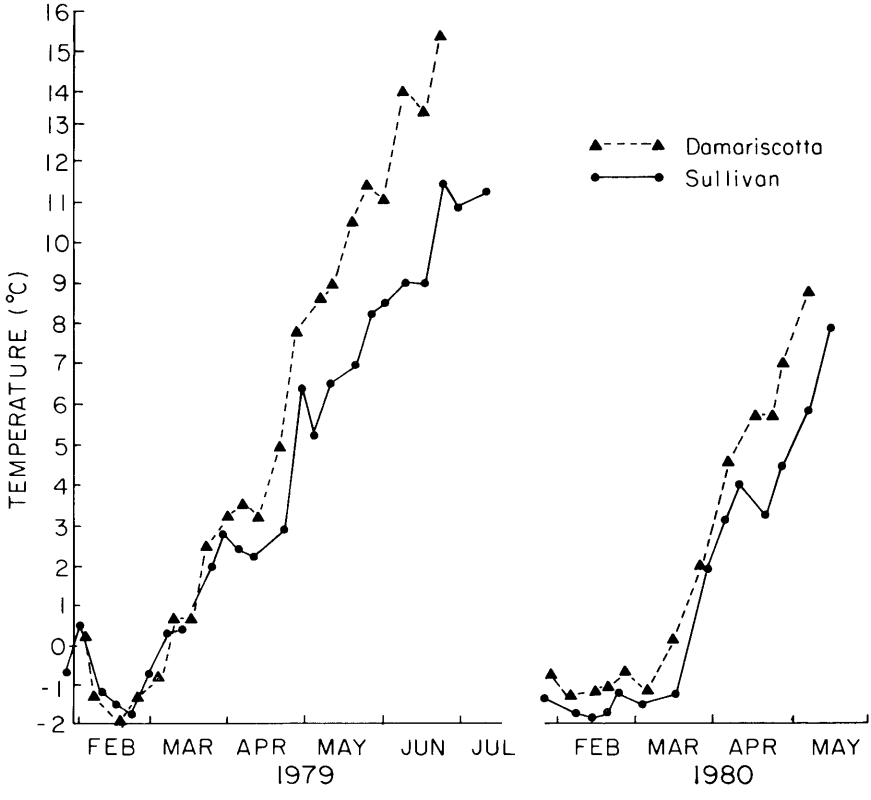

Fig. 3. Average of the surface to bottom water temperature for the Damariscotta estuary and Sullivan Harbor, 1979 and 1980.

to the results pertaining to the numerically dominant species, *Pholis gunnellus* L. Additional details of the analyses for the other, less abundant species are given in Townsend (1981). *P. gunnellus* was the numerically dominant species in both the Damariscotta estuary and Sullivan Harbor, as it is typically dominant during the winter-spring period in other areas of the coastal Gulf of Maine (Graham and Boyar, 1965; Chenoweth, 1973; Hauser, 1973; Laroche, 1980; Shaw, 1981).

In both years of the study, *P. gunnellus* larvae appeared in large numbers first and reached peak catch rates approximately one to two weeks earlier in the Damariscotta estuary than in Sullivan Harbor (Figure 2). The same was true for the other dominant species, including *Myoxocephalus octodecemspinosus, M. scorpius*, and *Lumpenus lumpretaeformis* and was expressed in the total larval fish catch rates (Figure 2). The *P. gunnellus* larvae in the Damariscotta estuary appeared in high numbers earlier in 1980 than in 1979 while there was no apparent variability between years in Sullivan Harbor.

The progression of water temperatures as related to vernal warming differed between Sullivan Harbor and the Damariscotta estuary for both years (Figure 3),

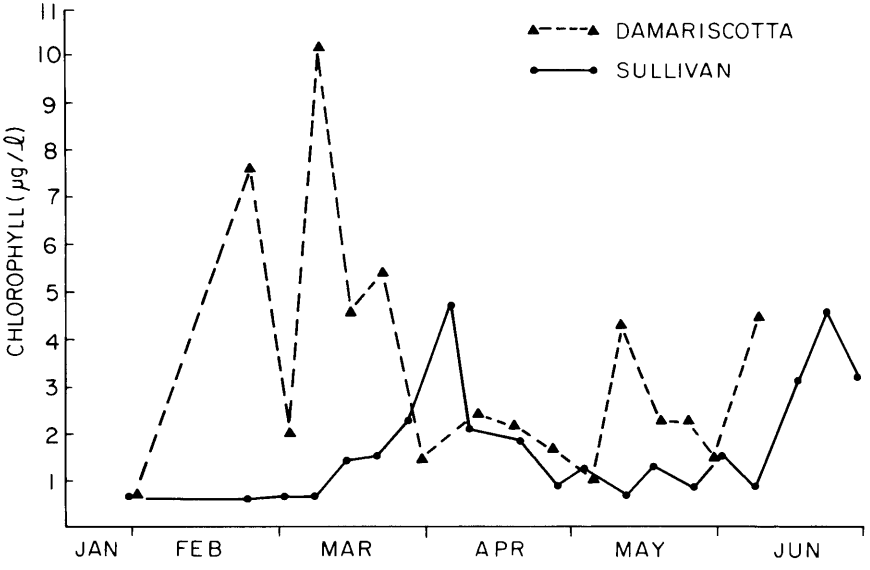

Fig. 4. Chlorophyll α concentrations for the Damariscotta estuary and Sullivan Harbor, 1979. The mean values of either two or four samples are plotted.

and reflected the general trend for the coastal Gulf of Maine (Bigelow, 1927). Sullivan Harbor warmed slower than the Damariscotta. The differences in temperature between the areas, combined with or due to the effects of differences in salinity stratification and tidal mixing, appeared to be related to the timing of the phytoplankton blooms. In 1979 (the only year data are available) the phytoplankton biomass as reflected by chlorophyll concentration indicated late winter – early spring blooms which differed in timing between the two areas (Figure 4). There were two blooms in the Damariscotta, on 23 Feburary and 8 – 22 March, followed by low but fluctuating chlorophyll levels into early summer. There was only a single chlorophyll pulse early in the year in Sullivan Harbor which lasted from 29 March to 19 April. This was followed by post-bloom chlorophyll levels and a later increase in summer.

The biomass peaks of zooplankton in 1979, as roughly represented by settled volumes, are shown in Figure 5. Two early season zooplankton settled volume peaks immediately followed the two chlorophyll peaks in the Damariscotta estuary in 1979, and the early April chlorophyll peak in Sullivan Harbor in 1979 was concurrent with a small zooplankton settled volume pulse. The late winter – early spring zooplankton peaks in 1980 showed a similar timing trend; those in Sullivan Harbor (18 February and late April) lagged behind the Damariscotta estuary (12 February and 11 March) by 1 – 2 weeks. It should be noted that the smaller mesh nets used during 1979 (80 μm) caught diatoms as well as zooplankton and these phytoplankters probably contributed significantly to elevated settled volume estimates. In addition, the extreme volume recorded on

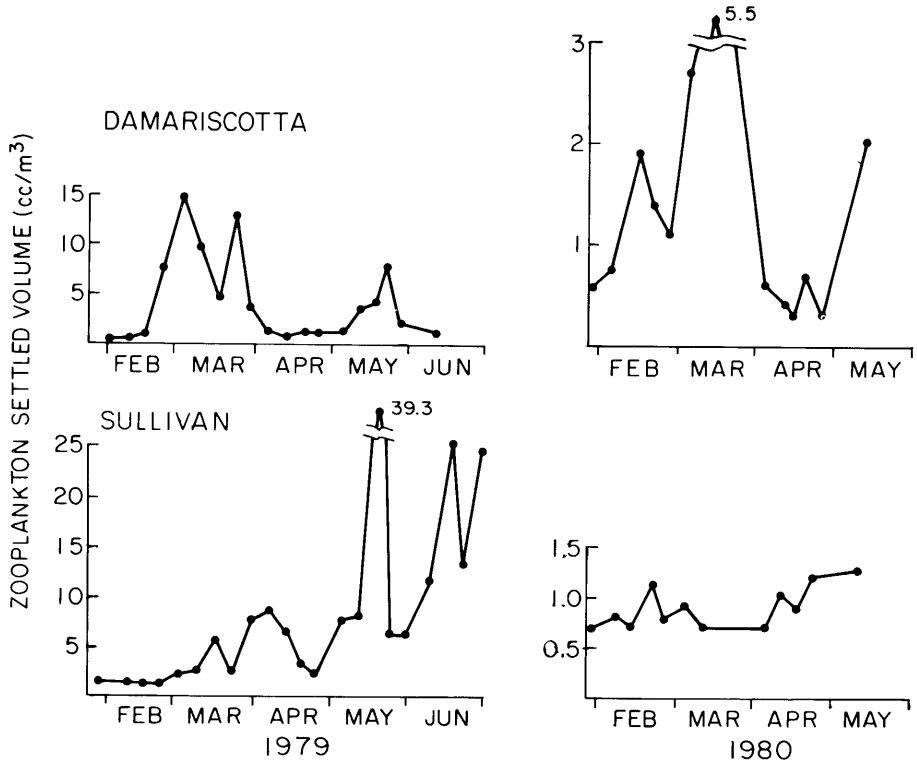

Fig. 5. Settled volume zooplankton biomass estimates for the Damariscotta estuary and Sullivan Harbor, 1979 and 1980. The 1979 samples were collected with No. 20 (80 μm) mesh nets and the 1980 samples with No. 10 (165 μm) mesh nets.

15 March in Sullivan Harbor (Figure 5) was the result of a short bloom of *Phaeocystis* sp. which contributed to net clogging and an anomalously high settled volume estimate.

Determinations of survival and mortality rates of larval fishes in the field are extremely difficult. Changes in catch rates from plankton samples are usually compounded by immigration and emigration of larvae from a sample site and therefore little information on survival and mortality can be gleaned directly from the plots of catch rates in Figure 2. The examination of length-frequency distributions with time, however, helps to establish qualitatively the time at which the survival of a population of recently recruited larvae from the eggs into the plankton exceeds larval mortality. Table I shows such data for *P. gunnellus* larvae. The important features to be noted in Table I are the times at which the populations of *P. gunnellus* larvae begin to show an increase in lengths. These times are between 8 – 30 March and 11 – 25 March for the Damariscotta estuary in 1979 and 1980, and 5 – 10 April and 27 March to 10 April in Sullivan Harbor in 1979 and 1980, again displaying a lag in timing between the two areas. Before such times it is assumed that larvae were hatching from the eggs, entering the

plankton and dying soon thereafter as a result of unfavorable environmental conditions. Therefore, before these times at which survival of newly hatched larvae exceeded mortality, there were no increases in lengths evident for the populations. After these times, conditions appear to have become favorable for survival and this was reflected by growth in length for the population as a whole. The time at which the larval lengths begin to increase appear to occur after the initial rise in the relative condition of the larvae (Figure 6). The trend is not as clear for the Sullivan Harbor, 1980, data which show high condition factor values early in the season.

The results of the feeding analyses show that smaller copepod nauplii became important food items in the diet of *P. gunnellus* at about this time in the Damariscotta estuary for both years (Table II). In particular, *Acartia* sp. and *Eurytemora herdmani* nauplii first appeared in the diet on 22 March, about the time at which the catch rates of the smaller developmental stages of copepods in the plankton tows increased (Figure 7), perhaps beyond some threshold density. It appears that the diet of the larvae of *P. gunnellus* reflected the availability of food organisms in the zooplankton. It could be assumed that since the larvae were not growing they did not derive nutritional benefit, and hence increased survival, until the smaller copepod nauplii appeared in the plankton and were in turn preyed upon. The major zooplankton species before this time included the larger adult and copepodid stages of copepods and *Balanus* sp. nauplii.

The situation in Sullivan Harbor in 1979 was somewhat different from the Damariscotta estuary in that the smaller copepod nauplii did not enter into importance in the diet of the larvae, nor did they become abundant in the zooplankton as compared with the Damariscotta. With the exception of *Microsetella norvegica*, which was the dominant zooplankter in Sullivan Harbor, the relative abundance of copepods in general was lower than in the Damariscotta by one to two orders of magnitude. Rather, the important food items coincident with the inferred survival times of the *P. gunnellus* larvae were unidentified invertebrate eggs and barnacle casts (Table III). It was at this time that the unidentified invertebrate eggs showed an increase in catch rate in the zooplankton in Sullivan Harbor (late March – early April). The relative abundance of the adult barnacle casts of cirral setae in the zooplankton net samples was not quantified, but such filaments and fragments of their associated endopodites and exopodites of the thoracic appendages of adult barnacles are very common in the plankton and most likely represent molts. It would appear that the fish larvae were gaining nutritive value from these and/or their associated bacterial flora since it was at the time when these food items became important in the diet that the populations displayed increased length and presumably increased survival. The seasonal occurrence of barnacle casts in the plankton is most likely related to the relative frequency of molting and the abundance of adults in the area. The first barnacle molt of the season occurs immediately after liberation of a brood of nauplii (Stubbings, 1975). In Sullivan Harbor this would be most intense from February through March as indicated by the appearance of barnacle nauplii in the plankton samples. Stubbings reported that the rate of molting gradually increases with increasing tempeature after the first molt to a rate of about one molt per 10 – 15

Table I. Length-frequencies of *P. gunnellus* larvae caught during 1979 and 1980 in Sullivan Harbor and the Damariscotta River Estuary. The numbers of larvae in each mm interval are given as well as the mean and standard deviation for each sample date.

Length (T.L.) mm	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total	$\bar{x}$	S.D.
Damariscotta, 1979																									
Date: 1 II 79			2	7	2	1																	12	12.2	0.84
7 II 79				5	3	1			1														10	13.0	1.56
15 II 79				4	9	12	13	2															40	14.0	1.09
23 II 79			3	3	10	8	1	1															27	13.3	1.29
2 III 79			10	27	26	26	5																94	12.9	1.10
8 III 79		1	13	36	68	39	6	4	1														168	13.0	1.13
16 III 79			1	4	15	24	10	7	2		1												64	14.1	1.38
22 III 79			4	26	53	40	17	12	3														156	13.6	1.29
30 III 79				4	11	16	11	10	6	1		1											60	14.7	1.63
6 IV 79				1	2	7	27	29	29	19	6	1		1									122	16.4	1.53
11 IV 79					1	4	10	9	16	11	7	4	1		1								64	17.0	1.90
18 IV 79				1		2	2	1	9	10	9	11	8	5	1	2							61	19.0	2.38
25 IV 79							1						3	2	2	6	4	2	1				21	23.4	2.56
4 V 79												3	3	4	3	8	5		1				27	23.1	1.83
Sullivan, 1979																									
Date: 8 II 79	1	1																					2	9.5	0.70
1 III 79			1	1	1	1																	4	12.5	1.29
7 III 79		1	2	17	12	7																	39	12.6	0.94
15 III 79		2	4	26	43	32	4	1															112	13.0	1.03
23 III 79	1	1	10	65	84	26	4	3															194	12.7	0.98
29 III 79			5	21	51	30	13	2															122	13.3	1.05
5 IV 79	1		15	41	25	15	2	1															100	12.5	1.11
10 IV 79			3	10	14	25	28	14	2	1													87	14.2	1.42
19 IV 79			1	2	22	31	50	50	27	10	5	3											201	15.4	1.61
26 IV 79					4	3	6	17	11	8	9	6	2	3	1								70	17.3	2.31
3 V 79			1			1		2		2	3	1	3	2	1				1				17	19.2	3.70
10 V 79								1	2			3		1			2		1				10	21.0	3.61

Length (T.L.) mm	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total	$\bar{x}$	S.D.
Damariscotta, 1980																									
Date: 29 I 80			1	16	17	11																	45	12.8	0.82
4 II 80			2	12	13	14	4		1														46	13.2	1.19
12 II 80			2	23	59	20	2																106	13.0	0.75
19 II 80				16	92	65	30	7		1													211	13.6	0.98
26 II 80		1	6	46	85	27	6	5															176	13.0	1.00
4 III 80				6	63	58	14	5	1			1											148	13.7	1.02
11 III 80				10	47	35	19	6															117	13.7	1.01
25 III 80		1		4	24	48	54	23	14	4	1	2			1								176	14.8	1.60
4 IV 80				1	5	4	14	36	44	30	11	7	1	3	1	2	1		1				161	17.2	2.17
11 IV 80					1	3	3	7	13	14	12	8	1	3									65	17.8	1.94
14 IV 80							1	2	13	6	6	11	5	5									50	18.9	1.87
18 IV 80							2	1	3	7	13	14	13	12	6	4		2	7	2	1		87	21.2	3.06
25 IV 80								1			1	2	1		2	4	2	2		2		1	18	23.6	3.50
Sullivan, 1980																									
Date: 28 I 80			3	12	9	5																	29	12.6	0.91
11 II 80			2	4	6																		12	12.3	0.78
18 II 80					1																		1	13.0	–
25 II 80			7	38	48	15																	108	12.7	0.80
3 III 80			1	15	20	8	1																45	12.8	0.82
10 III 80				41	69	23	2																135	12.9	0.73
27 III 80			4	88	81	21	4	1															199	12.7	0.81
3 IV 80			5	19	48	55	22	9	2	2	1												163	13.7	1.34
10 IV 80			1	5	18	53	32	21	6	2	1												139	14.5	1.30
17 IV 80				1	4	12	22	21	18	7	1												86	15.7	1.41
24 IV 80						2	4	8	8	9	5	8	1										45	17.6	1.82
5 V 80						1			1	3	1	2	3	2	1								14	19.6	2.41
11 V 80													1	2	1								4	22.0	0.82

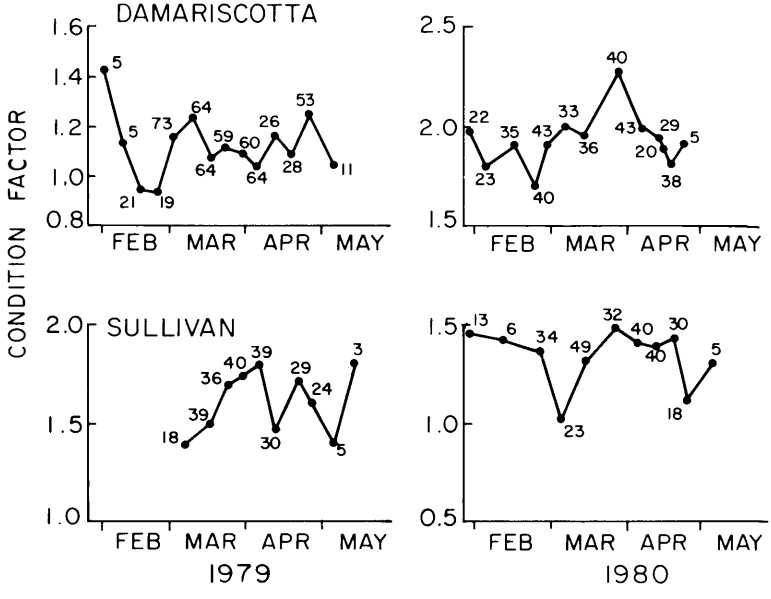

Fig. 6. Relative condition factors for *P. gunnellus* larvae from the Damariscotta estuary and Sullivan Harbor, 1979 and 1980. The sample size for each point is given.

days in summer. This could explain an increase in this food source in late March and early April in Sullivan Harbor. The nutritional nature of this material might be that the casts promote bacterial and protozoan aggregations on them but this remains to be investigated.

The feeding analysis results for 1980 were similar to those for the previous year (Tables IV and V). Again, the important food items in the diet of the *P. grunnellus* larvae during March in the Damariscotta were copepod nauplii and were coincident with rising condition factors (Figure 6), an increase in zooplankton biomass (Figure 5) and increasing lengths in the *P. gunnellus* populations (Table IV). Unfortunately, the abundances of smaller copepod nauplii in the plankton at this time could not be estimated reliably because of the larger mesh nets used to sample the zooplankton that year (165 μm). The major food items for the larvae in Sullivan Harbor in 1980 were again unidentified invertebrate eggs and barnacle casts (Table V), and again it is evident that these food items were important in determining the times of increasing lengths of the larval population.

Discussion

Although the feeding analysis results are in instances sketchy there does appear to emerge a general relationship coupling local hydrographies, the numbers of larval fish food items in the plankton, larval condition factors, and the times at which growth and assumed survival of the *P. gunnellus* larvae began. Although *P. gunnellus* fed on larger copepods early in the season, when copepod nauplii appeared in the plankton in sufficient densities the larvae apparently switched to

Table II. Summary of gut content of *P. gunnellus* larvae, Damariscotta River estuary, 1979.

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
1 Feb	*Pseudocalanus minutus* adults	8	4	12.5Y, 12.5, 13.0, 14.0Y	100.0
		No. larvae examined = 7			
		No. with empty guts = 3, (12.5Y, 12.5Y, 11.0Y)			
15 Feb	*P. minutus* adults	6	5	14.0, 14.0, 14.5, 16.0, 16.5	26.19
	P. minutus copepodites	5	3	13.5, 14.0, 14.5	18.06
	P. minutus nauplii	9	5	14.0, 14.5, 14.5, 15.0, 16.0	31.23
	Balanus sp. nauplii	4	4	14.0, 14.5, 15.5, 16.0	19.61
	Unid. copepodites	1	1	14.0	4.90
		No. larvae examined = 13			
		No. with empty guts = 2, (15.5, 15.5)			
23 Feb	*P. minutus* adults	9	6	12.5, 14.0, 14.0, 14.5, 15.0, 15.5	52.84
	P. minutus copepodites	1	1	12.0	7.39
	P. minutus nauplii	5	4	12.5, 14.0, 14.5, 15.0	7.39
	Microsetella norvegica adults	1	1	15.0	7.39
		No. larvae examined = 10			
		No. with empty guts = 2, (13.0, 14.0)			
2 March	*P. minutus* adults	9	6	12.5, 12.5, 13.0, 13.5, 14.0, 15.0Y	49.56
	P. minutus nauplii	2	2	12.5, 15.0	13.91
	Balanus sp. nauplii	9	3	12.5, 15.0Y, 15.0	36.52
		No. larvae examined = 12			
		No. with empty guts = 4, (12.5, 13.0, 13.0, 14.5)			
8 March	*P. minutus* adults	11	6	14.0Y, 14.0, 14.0, 15.5, 16.0, 16.5	79.93
	P. minutus copepodites	1	1	15.0	9.02
	Balanus sp. nauplii	2	2	14.0, 14.5Y	18.05

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
16 March	*P. minutus* adults	8	6	13.5, 14.0, 15.0, 15.5, 16.0, 17.0	30.82
	Balanus sp. nauplii	8	3	14.5, 15.0, 15.5	21.15
	Acartia longiremis adults	2	2	14.5, 15.0, 15.5	9.32
	Eurytemora herdmani nauplii	1	1	14.5, 14.0	4.66
	Tisbe sp. adults and copepodites	4	3	14.0, 14.5, 15.5	15.41
	Parathalestris sp. adults	1	1	15.5	4.66
	M. norvegica adults	1	1	14.0	4.66
	Unid. Harpacticoid adults	1	1	17.0	4.66
	Unid. Harpacticoid nauplii	1	1	14.5	4.66
		No. larvae examined = 12			
		No. with empty guts = 1, (14.0)			
22 March	*P. minutus* copepodites	5	3	16.0, 16.0, 17.0	14.17
	P. minutus nauplii	2	2	16.0, 16.0	8.33
	Balanus sp. nauplii	11	5	14.5, 15.5, 16.0, 16.0, 16.0	25.83
	Acartia sp. nauplii	16	6	14.0, 14.5, 14.5, 16.0, 16.0, 16.5	33.33
	E. herdmani nauplii	4	3	14.0, 15.5, 16.0	13.33
	Unid. copepod nauplii	2	1	15.5	5.0
		No. larvae examined = 10			
		No. with empty guts = 1, (14.5Y)			

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
6 April	*P. minutus* adults	2	1	18.0	3.17
	P. minutus copepodites	5	3	15.5, 17.0, 18.5	9.13
	P. minutus nauplii	7	5	15.5, 16.0, 17.0, 17.5, 18.5	14.68
	A. longiremis adults	2	2	18.0, 18.5	5.56
	Acartia sp. copepodites	4	3	17.0, 17.5, 18.5	8.73
	Acartia sp. nauplii	10	5	15.5, 16.0, 17.5, 18.5, 19.5	15.87
	Temora longicornis adults	17	4	15.5, 17.0, 17.5, 20.0	16.27
	T. longicornis copepodites	3	2	15.5, 19.5	5.95
	E. hermandi adults	1	1	19.5	2.78
	E. hermandi nauplii	5	3	15.5, 16.0, 17.0	9.13
	Unid. copepod copepodites	3	2	16.0, 20.0	5.95
	Unid. copepod nauplii	1	1	18.5	2.78
		No. larvae examined = 10			
		No. with empty guts = 0			
11 April	*P. minutus* adults	2	2	17.5, 18.5	34.92
	T. longicornis adults	3	1	18.0	30.16
	T. longicornis copepodites	1	1	18.0	17.46
	Synchaeta sp.	1	1	17.5	17.46
		No. larvae examined = 4			
		No. with empty guts = 0			

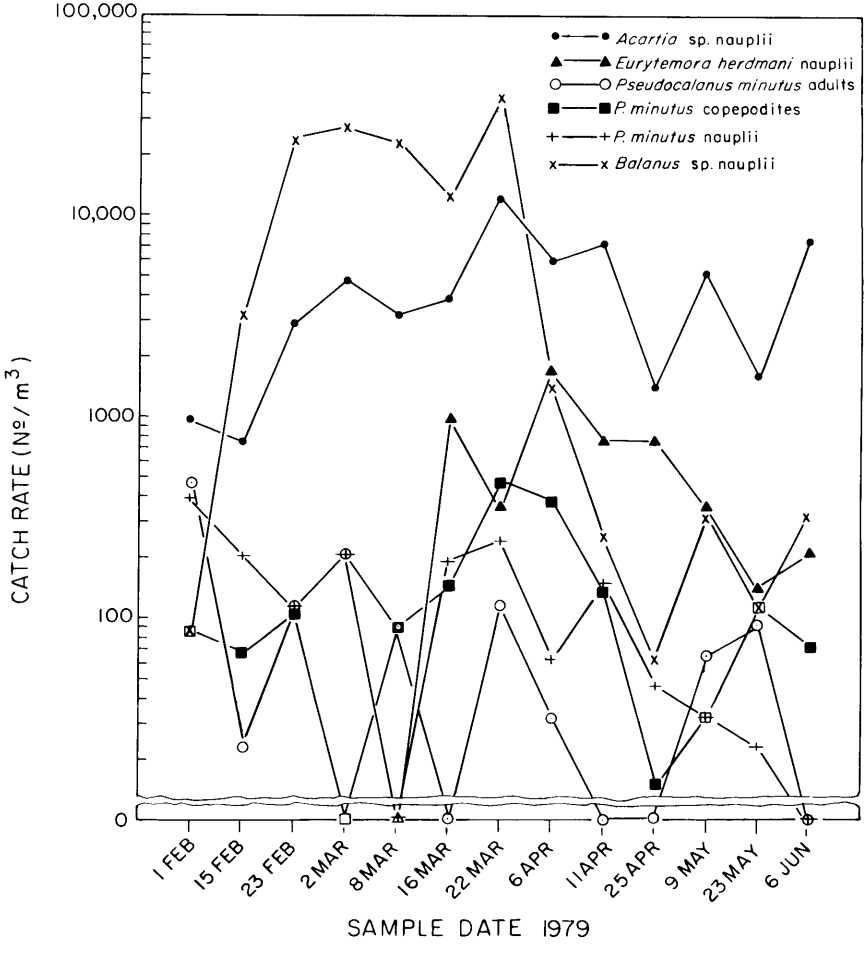

Fig. 7. Catch rates of the major components of the zooplankton in the Damariscotta estuary, 1979. A more complete description of the zooplankton fauna in both sample areas for both years is given in Townsend (1981).

these and derived benefit from doing so. The apparent switch, however, may have been an artifact in that the greater importance of copepod nauplii in the diet may be a function of the chance of encountering these in the plankton rather than a switch in selective predation. Affecting the chance of an encounter would be the swimming speeds of the planktonic organisms in question; i.e., a faster moving zooplankter might be encountered more often by a fish larva in a statistical sense, but not in a feeding sense, where the larva might not be able to capture such a organism. Slower swimming but abundant organisms, above some threshold density, might therefore be more beneficial as it indeed appears they were for *P. gun-*

nellus. Those factors determining the benefit of food items would therefore include their density in the plankton, the amount of energy expended by a larvae to capture (and digest) a food item, and the nutritional quality of the item.

The important food items for *P. gunnellus* in the Damariscotta estuary, then, would be small copepods and copepod nauplii. The importance of copepod nauplii to first feeding larval fishes has been reported by many workers (May, 1970; Kjelson *et al.*, 1975; Last, 1978a, 1978b; Keast, 1980). Copepod nauplii did not become important food items, however, until there were sufficient numbers in the plankton. The importance of high concentrations of food items to the successful first feeding of fish larvae has been emphasized in the past (O'Connell and Raymond, 1970; Laurence, 1974; Houde, 1975, 1977, 1978; Houde and Schekter, 1980) and some workers have suggested that the timing of a plankton bloom in relation to the timing of larval fish production may be critical to the success of a year class (Cushing, 1969; Wyatt, 1972; May, 1974). An alternative model, the continual recruitment of recently hatched fish larvae into the water column over a period of time sufficient to overlap the variation in the timing of the seasonal bloom, would obviate such a critical timing theory. The progression of length-frequency distributions presented in this study show that there appears to be an extended input of recently hatched *P. gunnellus* larvae and that when the bloom of important food items occurs, apparent survival and growth of those larvae present surpass mortality.

Although continual hatching of larvae would be expected to dominate such length-frequency distributions resulting in smaller average sizes, there is no apparent skewing of these distributions with time to represent those larvae which survived and grew. For instance, Townsend (1981) showed that, based on otolith analyses, *P. gunnellus* larvae grow on the average 1.5 – 2.0 mm per week. If there were significant survival of those larvae which hatched early in the year, then one would expect that this would be reflected in the length-frequency distributions being skewed and giving larger standard deviations. This did not happen until after the forage organisms of the larvae appeared in high densities (Table I).

It is quite possible, as Fish and Johnson (1937) have suggested, that local populations of fishes have adapted their spawning times to match the hydrographic trend along the coastal Gulf of Maine and thus spawn later toward the east. Such a reproductive strategy has been proposed for fishes in general – that spawning is timed to match the production cycle of a particular geographic area (Cushing, 1967, 1970). This relationship appears to hold for many temperate latitude species (Crisp, 1954; Qasim, 1956; Bagenal, 1971). It would seem likely that superimposed on this must be a mechanism to cope with the variabilty in timing of the plankton production cycle. Although there appears to be a consistent relative pattern in the timing of plankton blooms along the coast of the northern Gulf of Maine, the absolute time at which the blooms begin varies from year to year. Bigelow (1926), Bigelow *et al.* (1940) and Lillick (1940) have shown that initiation of the winter-spring phytoplankton bloom can occur anytime between January and April. Once this bloom begins it proceeds eastward along the coast in relation to the development of vertical stratification of the water column. Precisely timed spawning of fishes could not account for this yearly variability

Table III. Summary of gut content analyses of *P. gunnellus* larvae, Sullivan Harbor, 1979.

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
1 March	*Tisbe* sp. adults	1	1	14.5	24.44
	Coscinodiscus sp.	2	1	13.5	37.78
	Unid. copepod nauplii	2	1	14.0Y	37.78
		No. larvae examined = 6			
		No. with empty guts = 3, (13.0Y, 13.0, 14.5Y)			
15 March	*Pseudocalanus minutus* adults	2	2	14.5, 14.5	12.59
	P. minutus nauplii	2	1	14.0	8.04
	Balanus sp. nauplii	5	2	14.0, 15.0	17.83
	Coscinodiscus sp.	1	1	13.0	6.29
	Unid. invertebrate eggs[a]	16	6	12.5, 13.0, 14.0, 14.0, 14.5, 14.5	55.24
		No. larvae examined = 10			
		No. with empty guts = 3, (13.5Y, 14.5, 14.5)			
29 March	*P. minutus* adults	1	1	15.5	5.33
	Tisbe sp. adults	1	1	14.5	5.33
	Unid. seteger	1	1	15.0	5.33
	Unid. invertebrate eggs[a]	148	7	13.5, 14.0, 14.0, 14.5, 15.0Y, 15.0, 15.5	84.01
		No. larvae examined = 10			
		No. with empty guts = 2, (14.0Y, 14.5)			
5 April	*P. minutus* adults	2	2	14.0, 14.5	33.33
	Tisbe sp. adults	1	1	14.5	16.67
	Temora longicornis copepodites	1	1	14.0	16.67
	Unid. copepod nauplii	1	1	15.5	16.67

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
	Thalassiosira sp. chains	1	1	15.5	16.67
		No. larvae examined = 10			
		No. with empty guts = 5, (12.0Y, 13.5, 14.0, 16.0)			
10 April	*Balanus* sp. nauplii	1	1	14.5	12.5
	Tisbe sp. adult	1	1	14.5	12.5
	P. minutus nauplii	1	1	14.5	12.5
	Balanus casts[c]	5	5	14.5, 14.5, 15.0, 15.0, 16.0	62.5
		No. larvae examined = 10			
		No. with empty guts = 5, (12.0Y, 13.5, 14.0, 14.0, 14.5)			
19 April	*P. minutus* adults	1	1	16.0	4.69
	P. minutus copepodites	3	3	16.5, 16.5, 18.5	14.08
	P. minutus nauplii	6	5	16.0, 16.5, 16.5, 17.0, 18.5	24.93
	T. longicornis adults	1	1	16.0	4.69
	T. longicornis copepodites	2	2	16.0, 17.0	9.38
	Unid. invertebrate eggs[b]	1	1	16.5	4.69
	Balanus casts[c]	8	8	16.0, 15.5, 16.0, 16.5, 16.5, 17.0, 17.5, 19.5	37.54
		No. larvae examined = 10			
		No. with empty guts = 0			

[a]Probably *Pseudocalanus minutus* eggs.
[b]Probably *Littorina* sp. eggs.
[c]Adult *Balanus* sp. setae from molts. The presence of any, which were usually clumps of ~100 setae and associated debris, were treated as a single food item.

Table IV. Summary of gut content analyses of *P. gunnellus* larvae, Damariscotta River estuary, 1980.

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
4 Feb	*Pseudocalanus minutus* adults	2	2	14.5, 15.0	16.33
	T. minutus copepodites	1	1	14.5	8.16
	Microsetella norvegica adults	1	1	14.5	8.16
	Belanus sp. nauplii	9	6	12.5Y, 14.5, 14.5, 14.5, 14.5, 15.0	59.18
	Unid. debris	1	1	14.5Y	8.16
		No. larvae examined = 10			
		No. with empty guts = 0			
19 Feb	*P. minutus* nauplii	1	1	14.5	20.0
	Balanus sp. nauplii	2	2	15.5Y, 16.0	40.0
	M. norvegica adults	1	1	14.5	20.0
	Synchaeta sp.	1	1	15.0	20.0
		No. larvae examined = 10			
		No. with empty guts = 6			
4 March	*P. minutus* nauplii	4	3	14.5Y, 14.0, 15.5	47.06
	P. minutus copepodites	*1*	*1*	*14.0*	*13.24*
	Acartia sp. nauplii	3	3	13.5, 14.0, 14.0	39.70
		No. larvae examined = 120			
		No. with empty guts = 5			
11 March	*P. minutus* copepodites	6	4	14.5Y, 14.0, 15.5	15.09
	P. minutus neuplii	20	5	15.0, 14.0Y, 16.5, 15.0, 15.5	25.80

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
	Temora longicornis	2	2	15.0, 15.0	6.99
	Oithona similis adults	2	2	15.0, 14.5	6.99
	Acartia sp. nauplii	18	7	15.0, 15.0, 16.5, 15.5, 14.5, 15.5, 15.0	30.58
	Eurytemora herdmani nauplii	2	2	14.0, 15.0	6.99
	Unid. Harpacticoid adults	1	1	15.0	3.50
	Unid. copepod nauplii	2	1	14.5	4.05
		No. larvae examined = 10 No. with empty guts = 0			
25 March	*P. minutus* copepodites	13	9	16.5, 17.0, 16.0, 14.5, 15.5, 16.0, 14.0, 15.5, 15.0	22.90
	P. minutus nauplii	77	10	16.5, 16.5, 17.0, 16.0, 14.5, 15.5, 16.0, 14.0, 15.5, 15.0	37.19
	T. longicornis copepodites	2	2	17.0, 15.5	4.92
	O. similis nauplii	2	2	16.5, 14.5	4.92
	E. herdmani nauplii	2	2	17.0, 16.0	4.92
	Acartia sp. nauplii	24	8	16.5, 17.0, 16.0, 14.5, 15.5, 16.0, 15.5, 15.0	22.69
	Unid. copepod nauplii	1	1	16.0	2.46
		No. larvae examined = 10 No. with empty guts = 0			

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
4 April	*P. minutus* copepodites	4	4	16.0, 18.0, 16.0, 17.5	17.43
	P. minutus nauplii	2	2	19.0, 16.0	8.71
	T. longicornis copepodites	1	1	18.0	4.36
	E. herdmani nauplii	1	1	16.0	4.36
	Acartia sp. nauplii	25	8	16.0, 18.0, 16.0, 18.0, 16.0, 17.5, 17.5 15.5	50.27
	Balanus sp. nauplii	4	2	18.0, 19.0	10.53
	Unid. copepodites	1	1	17.5	4.36
		No. larvae examined = 10 No. with empty guts = 1, (20.0)			
14 April	*P. minutus* adults	1	1	19.0	4.41
	T. longicornis adults	7	5	20.0, 20.5, 18.5, 21.0, 19.5	23.95
	T. longicornis copepodites	9	2	20.5, 18.5	15.52
	M. norvegica adults	1	1	19.5	4.41
	Acartia sp. copepodites	1	1	21.0	4.41
	Acartia sp. nauplii	12	4	20.5, 18.5, 18.0, 19.5	25.29
	Tisbe sp. adults	1	1	19.5	4.41
	Unid. Harpacticoid adults	3	3	19.5, 21.0, 18.5	13.22
	Unid. copepod nauplii	1	1	18.0	4.41
		No. larvae examined = 10 No. with empty guts = 2, (16.5, 18.5)			

Table V. Summary of gut content analyses of *P. gunnellus* larvae, Sullivan Harbor, 1980.

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
11 Feb	*Pseudocalanus minutus* adults	1	1	13.5	100.0
		No. larvae examined = 6			
		No. with empty guts = 5, (11.5Y, 11.5Y, 12.5Y, 13.0, 13.0)			
25 Feb	Unid. debris[a]	10	10	12.5, 12.5, 13.5, 14.0, 12.5, 13.0, 13.0 13.5, 12.5, 14.0	100.0
		No. larvae examined = 10			
		No. with empty guts = 0			
10 March	*P. minutus* copepodites	1	1	14.0	5.46
	P. minutus nauplii	18	7	14.5, 14.0, 14.0, 12.5, 14.0, 12.5, 13.5	50.50
	Balanus sp. nauplii	1	1	14.5	5.46
	Unid. Harpacticoid copepodites	1	1	14.0	5.46
	Unid. Harpacticoid nauplii	2	1	14.5	6.58
	Unid. invertebrate eggs[b]	16	2	12.5, 12.5	26.53
		No. larvae examined = 10			
		No. with empty guts = 2, (13.0, 13.0)			
26 March	*P. minutus* copepodites	1	1	13.5	11.73
	P. minutus nauplii	3	3	13.0, 13.5, 13.5	35.18
	Balanus sp. nauplii	3	3	12.5, 13.5, 14.0	35.18
	Unid. Harpacticoid copepodites	2	1	13.5	17.90
		No. larvae examined = 10			
		No. with empty guts = 4, (12.5, 12.5, 13.5Y, 13.5)			

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
3 April	*P. minutus* copepodites	6	4	15.0, 15.0, 14.0, 13.5	14.51
	P. minutus nauplii	18	5	16.0, 15.0, 14.0, 15.0, 14.5	22.33
	Acartia sp. copepodites	1	1	16.0	3.43
	Acartia sp. nauplii	1	1	15.0	3.43
	Balanus sp. nauplii	1	1	13.5	3.43
	Unid. copepod copepodites	1	1	13.5	3.43
	Unid. copepod nauplii	1	1	13.5	3.43
	Unid. invertebrate eggs[b]	45	7	16.0, 15.0, 15.0, 13.5, 15.5, 15.0, 15.0, 14.5	39.15
	Unid. debris	2	2	15.0, 14.0	6.86
		No. larvae examined = 10 No. with empty guts = 0			
10 April	*P. minutus* adults	3	3	17.0, 18.0, 16.0	9.54
	P. minutus copepodites	2	2	16.0, 16.5	6.36
	P. minutus nauplii	6	3	15.5, 16.0, 16.5	10.26
	Temora longicornis adults	6	6	16.0, 15.5, 18.0, 15.5, 16.0, 16.5	19.08
	Unid. Harpacticoid adults	2	1	15.5	3.47
	Unid. invertebrate eggs[c]	104	9	16.0, 16.0, 15.5, 17.0, 15.5, 18.0, 15.5, 16.0, 16.5	51.34
		No. larvae examined = 10 No. with empty guts = 1, (14.0)			

Date	Food taxon	Number of food items	Frequency of occurrence	Larval lengths in mm and presence of yolk sacs (Y)	Index of relative importance
17 April	*T. longicornis* adults	1	1	19.5	6.62
	Unid. Harpacticoid adults	1	1	15.0	6.62
	Unid. invertebrate eggs[c]	5	2	15.5, 16.0	20.59
	Coscinodiscus sp.	1	1	17.5	6.62
	Balanus casts[d]	9	9	15.0, 19.5, 17.5, 16.0, 17.0, 15.0, 15.0, 15.5, 16.5	59.56
		No. larvae examined = 10			
		No. with empty guts = 1, (18.0)			
24 April	*P. minutus* adults	4	3	19.5, 16.5, 19.0	20.09
	P. minutus copepodites	2	2	19.0, 17.0	11.97
	T. longicornis adults	5	4	19.5, 18.0, 17.0, 16.0	26.07
	Eurytemora herdmani adults	2	2	16.5, 18.0	11.97
	Acartia longiremis adults	1	1	18.0	5.98
	Unid. Harpacticoid adults	2	2	16.5, 20.0	11.97
	Balanus casts[d]	2	2	16.5, 19.5	11.97
		No. larvae examined = 10			
		No. with empty guts = 1, (18.0)			

[a]Small dark particles, may be phytoplankton remains. Presence of any is treated as a single food item.
[b]Probably *Pseudocalanus minutus* eggs.
[c]Probably *Litorina* sp. eggs.
[d]Adult *Balanus* sp. setae from molts. The presence of any, which were usually clumps of approximately 100 setae and associated debris, are treated as a single food item.

and indeed there was a large between year difference in the abundance cycles of *P. gunnellus* larvae in the Damariscotta estuary (Figure 2, Table I) and in the initiation of the zooplankton blooms there (Figure 5). An extended presence of larvae in the plankton, however, would insure that at least some were present when a bloom of food organisms of sufficient quality and quantity for survival occurred. Such a reproductive pattern is common to certain planktonic copepods which produce eggs and nauplii over a period of several months (Heinrich, 1962; Marshall, 1949; Lee, 1975) during which time developing broods of copepods can be associated with specific phytoplankton pulses (Marshall, 1949).

The larvae of *P. gunnellus* also showed this relationship. The larvae were present in the water column in both the Damariscotta estuary and Sullivan Harbor from February to April and May. Survival of these larvae presumably did not occur until mid- to late March in the Damariscotta estuary and early to mid-April in Sullivan Harbor. Qualitative evidence of the time at which survival exceeded mortality was based on initiation of the progression of length-frequency distributions with time. Before this occurred mortality of the larvae by starvation could be assumed to roughly equal or surpass recruitment of recently hatched larvae into the plankton. It was not until suitable planktonic food organisms appeared in sufficient densities that apparent survival and growth exceeded mortality. Also at this time there was generally an increase in relative condition factors.

This study suggests that missing year classes of fishes might not be the direct result of the larvae missing the plankton bloom. The extended presence of larvae in the water column would insure against this. Such extended durations of fish larvae in the plankton appear to be common in northwest Atlantic fishes (Colton *et al.*, 1979). Probably the best test for this hypothesis would be to examine the age structures of the larvae throughout the time they are in the water column and calculate age specific mortalities. This was not possible in the present study becasue of unexpected problems in preserving the larval otoliths. Assuming that the model is valid, it still lacks the mechanism which results in the continual release of newly hatched larvae over extended periods. This could happen in two ways – by protracted spawning periods (Shackley and King, 1977), or by variable egg hatching times. Each of the dominant fishes in this study lays clumps of demersal and adhesive eggs (Bigelow and Schroeder, 1953). It is possible that an adaptive value of such egg clumps is the prolonged release of larvae, hatching from the periphery of the clump inward, thus assuring a supply of larvae over an extended period. There are probably many such mechanisms and this represents an area for further research.

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