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Comparison of inshore zooplankton and ichthyoplankton populations of the Gulf of Maine*

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ABSTRACT: Zooplankton and ichthyoplankton were sampled in 2 hydrographically different areas on the US Maine coast: Sullivan Harbor in eastern Maine and the Damariscotta estuary in western Maine. Sampling was conducted from late winter to early summer in each area in 1979 and 1980. Phytoplankton chlorophyll concentrations were determined for each area in 1979. Phytoplankton and zooplankton blooms appeared to be coupled and differed in timing between areas in 1979. Timing of peak zooplankton abundances was not appreciably different between areas in 1980, but was earlier in the season than in the previous year. Times of maximum catch rates of dominant larval fish species were closely coupled to plankton dynamics.

INTRODUCTION

Seasonal cycles of zooplankton abundance and species composition in the coastal and offshore waters of the Gulf of Maine have received attention from a number of investigators (Bigelow, 1926; Clarke, 1933, 1934; Redfield, 1939, 1941; Redfield and Beal, 1940; Colton et al., 1962; Sherman, 1965, 1966, 1968, 1970; Sherman and Perkins, 1971). Their findings suggest that the cycle follows that of the phytoplankton with a peak in late spring just after the phytoplankton bloom, although at times the zooplankton reaches maximum biomass during summer (Sherman, 1965, 1966, 1968). The peak in abundance of both phytoplankton and zooplankton occurs earlier in the western Gulf of Maine and spreads gradually to the east with the onset and development of thermal stratification during spring and summer (Bigelow, 1927).

In contrast to coastal and offshore waters, zooplankton of the inshore embayments and estuaries of the Gulf of Maine are known from only a few isolated accounts and the interpretation of differences along the coast is difficult. Willey (1913, 1915) and Legaré and McLellan (1960) reported on the zooplankton of the Passamaquoddy Bay area; Lee (1975) and Lee and McAlice (1979a) studied the Damariscotta River estuary; and McAlice (1973) reported on the Sheepscot River-Montsweag Bay estuarine system (Fig. 1). With the exception of the study by McAlice (1973) the above workers sampled only at monthly or seasonal intervals and used various large mesh nets, hampering intercomparisons between areas.

The ichthyoplankton of the inshore waters of the Gulf of Maine has been documented, but only for estuarine systems and nearby waters in the central area of the Maine coast (Graham and Boyar, 1965; Chenoweth, 1973; Hauser, 1973; Laroche, 1980, 1982; Shaw, 1981; Townsend and Graham, 1981). Studies in

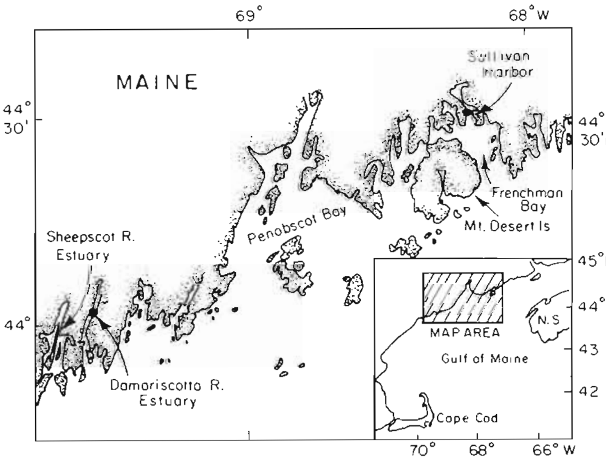

Fig. 1. Map of the 2 sampling stations in the Damariscotta River estuary and Sullivan Harbor, in relation to the US Maine coast and the Gulf of Maine. N. S.: Nova Scotia, Canada

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each of these estuaries showed that in general the highest catch rates of larval fishes occurred in the spring, which is close to the times of the spring phytoplankton and zooplankton blooms in this region.

This paper presents the results of a comparative study of the abundance and species composition of zooplankton and ichthyoplankton as they relate to hydrography and, in Year 1 of the study, phytoplankton biomass, in 2 inshore areas on the coast of Maine sampled from late winter to early summer during 1979 and 1980. The 2 sample areas, the Damariscotta estuary in western Maine and Sullivan Harbor – an embayment in eastern Maine (Fig. 1) – were chosen to represent the hydrographic variation along the Maine coast from west to east (Townsend, 1981, 1983).

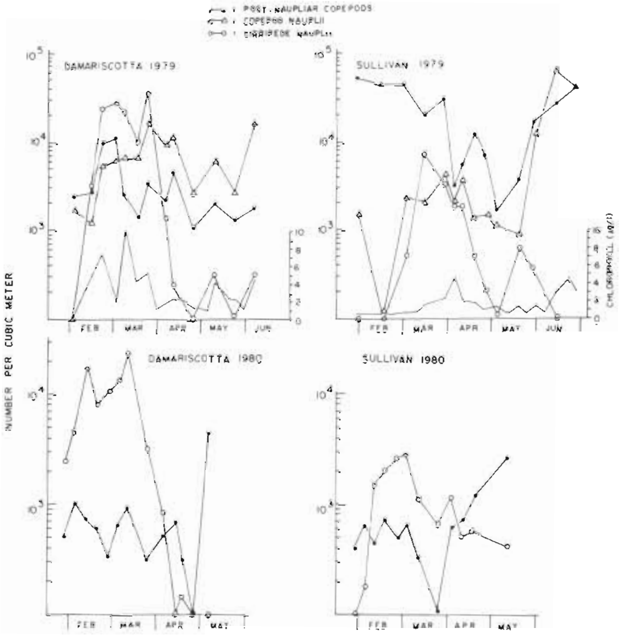

Fig. 3. Abundances of the major zooplankton groups comparable between areas for 1979 and 1980 and chlorophyll *a* for both areas in 1979. Mean values of either 2 or 4 chlorophyll samples are plotted. The 1979 zooplankton samples were collected with 80 µm mesh nets, the 1980 samples with 165 µm mesh nets

MATERIALS AND METHODS

Field procedures

Weekly ichthyoplankton samples and biweekly, with some weekly, zooplankton samples were collected from January to July in 1979 and January to May in 1980 in both the Damariscotta estuary and Sullivan Harbor. Details of the study areas and sampling methods are given elsewhere (Townsend, 1981, 1983) and are summarized here. A 61 cm diameter bongo net frame was used to sample the larval fishes and a 20 cm diameter bongo was used on the same wire to sample the zooplankton (Posgay and Marak, 1981). The large bongo was fitted with 505 µm mesh nets on each side. In 1979, 80 µm mesh nets were used on the small bongo initially but due to problems with net clogging a 165 µm mesh net was placed on one side of the paired bongo after the first 3 mo of sampling. Only 165 µm mesh nets were used on the small bongo in 1980. A single station was sampled in each area with replicate surface and deep tows taken during midday. Temperatures and salinities were measured with a Beckman RS5-3 field salinometer-thermometer. Chlorophyll samples were taken in 1979 only.

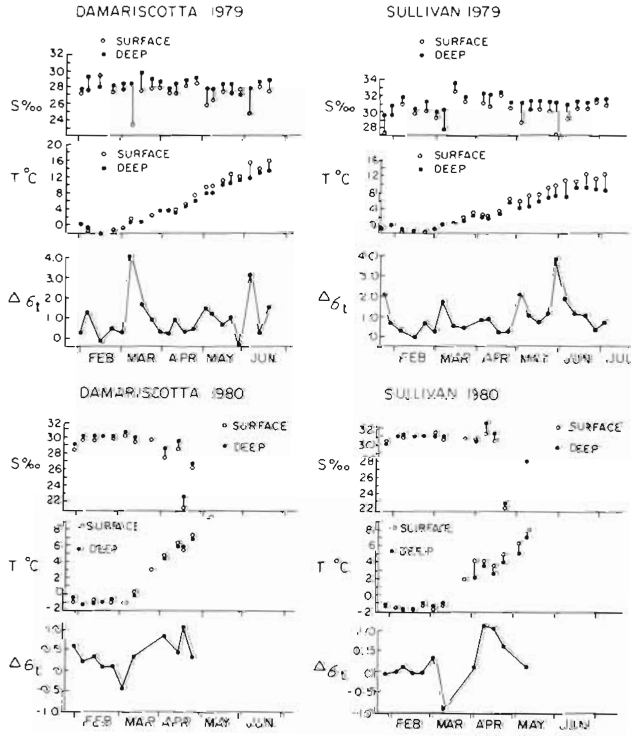

Fig. 2. Surface and deep (deep is 15 m in Sullivan Harbor and 25 m in the Damariscotta estuary) temperatures and salinities, and surface to deep differences in sigma-t for the Damariscotta estuary and Sullivan Harbor, 1979 and 1980

Laboratory procedures

Zooplankton settled volumes were determined for all 20 cm bongo samples by allowing each to settle overnight in a graduated cylinder. Because the main sources of plankton sampling variability are generally between net tows, both between and within stations, and the least variability is caused by subsampling in the laboratory (Platt et al., 1970; Lee and McAlice, 1979b), the zooplankton species composition and abundance determinations were made by pooling the replicate samples. The 20 cm bongo samples of the same net mesh size for a particular date and area were combined and the pooled sample was diluted to 10 to 20 times the settled volume. All zooplankton in a 1 ml aliquot were counted and identified to species, when possible, in a Sedgwick-Rafter cell. All fish larvae from one side of the preserved 61 cm bongo were identified and counted. The chlorophyll *a* determinations were made fluorometrically by the method of Yentsch and Menzel (1963) using the equations of Lorenzen (1966).

RESULTS

Hydrography

The vertical stability of the water column in each area in 1979 was apparently controlled more by salinity stratification than by temperature (Fig. 2). There were marked pulses in increased stability (top to bottom sigma-t differences) in the Damariscotta estuary in early March and early June, and several smaller pulses in Sullivan Harbor in late January, early March, early May, and a large peak in early June of that year. In

Table 1. Estimated numbers of zooplankton organisms per cubic meter, Damariscotta River estuary, 1979. Samples were collected with 80 µm mesh (No. 20) plankton nets

Taxa	Sample date												
	1 Feb	15 Feb	23 Feb	2 Mar	8 Mar	16 Mar	22 Mar	6 Apr	11 Apr	25 Apr	9 May	23 May	6 Jun
Phylum Protozoa													
Class Rhizopoda													
Unidentified foraminiferans	67			208		49	235	31					
Class Ciliata													
Tintinnopsis sp.				5208	12522	12097	62832	3047	1700				
Unidentified tintinnids				208									
Phylum Aschelminthes													
Class Nematoda													
Unidentified nematodes	67	45		416	180	49			34			70	2124
Class Rotifera													
Synchaeta sp.	89	23		416	361	12487	33529	1269	1350	1953	3868	94	432
Trichocerca sp.						49		31					
Keratella sp.						117			33	31	33		
Phylum Mollusca													
Class Gastropoda													
Littorina sp. eggs									17				
Unidentified gastropod larvae	45	23		208				31	67		66	23	72
Class Bivalvia													
Unidentified straight-hinge larvae	22											47	4968
Phylum Annelida													
Class Polychaeta													
Unidentified trochophore larvae				625	630	49	235	285	1650	6449	4229	2894	468
Unidentified seteger larvae				208					17	31	196	1458	432
Phylum Arthropoda													
Class Crustacea													
Subclass Cirripedia													
Cirripede nauplii	89	3307	24342	27500	22972	10292	39529	1492	250	62	327	117	324
Cirripede cyprids								984	233				
Subclass Copepoda													
Acartia longiremis (Lilljeborg) adults	291	638	800	869	360	341	235	158	2000	62	295	367	432
Acartia sp. copepodites	45	91				146	470	857	966	620	786	705	1152
Acartia sp. nauplii	985	729	2971	4791	3243	3853	12588	6000	7250	1426	5081	1647	7668
Calanus finmarchicus (Gunnerus) adults	22												
Centropages hamatus (Lilljeborg) nauplii									516	124	229	23	288
Eurytemora herdmani Thompson and Scott adults	45								17			47	36
E. herdmani copepodites									216	62	327	47	
E. herdmani nauplii						975	352	1777	783	775	360	141	216
Microsetella norvegica (Boeck) adults and copepodites	1432	1573	8800	10000	1982	878	2235	253	933	341	163		
M. norvegica nauplii	22					98	117	190	200		32	47	288
Oithona similis Claus adults and copepodites	22	182	457	208		49	117	31	50		33		
O. similis nauplii	156	45	114		270		117		67			70	
Pseudocalanus minutus (Krover) adults	470	23	114	208	90		117	31			66	94	
P. minutus copepodites	89	68	114		90	146	470	380	133	15	33	117	72
P. minutus nauplii	380	205	114	208		195	235	63	150	46	33	23	
Temora longicornis (Muller) adults	22	136		208	90			94	67		98	70	36
T. longicornis copepodites								539	400	62	327		180
T. longicornis nauplii	134	228	1828	1250	2702	1414	3647	1333	1083	434	426	494	360
Unid. Harpacticoid adults and copepodites	156	23			90				34	31	33	23	72
Unid. Harpacticoid nauplii						149	117		34	31	66	329	1836
Unid. copepod nauplii	45				361	243	352	127	133	31			72
Unid. copepod eggs	67	68	114			146	588	31	366	124	33		
Phylum Chordata													
Class Larvacea													
Oikopleura sp.												47	
Other –													
Unid. invertebrate eggs	268	114	800	1250	270	946	235	158	167	31	262		936
Hansen's nauplii				208									

each instance, the peaks in stability were the result of influxes of low salinity surface water. These events were synchronous between areas and most likely represented maxima in freshwater runoff from land into the systems. The average salinities in 1979 were persistently lower in the Damariscotta than in Sullivan. The water temperatures were similar between areas until early March when warming proceeded more rapidly in the Damariscotta; the difference in water temperature was about 1 to 1.5 °C in March.

In 1980, there was very little vertical stability in either area until March (Fig. 2). It was late March when the water column began to stabilize in the Damariscotta estuary and early April in Sullivan. The differences between surface and deep salinities were very slight in each area, with no significant fresh water additions until late April. However, these salinity differences were still more important than temperature in stabilizing the water column. The water temperatures in the Damariscotta estuary were persistently higher than those in Sullivan Harbor throughout the sampling period.

Table 2. Estimated numbers of zooplankton organisms per m^3, Sullivan Harbor, 1979. Samples were collected with 80 μm mesh (No. 20) plankton nets

Taxa	Sample date													
	31 Jan	16 Feb	1 Mar	15 Mar	29 Mar	5 Apr	10 Apr	19 Apr	26 Apr	3 May	17 May	31 May	14 Jun	28 Jun
Phylum Protozoa														
Class Rhizopoda														
Unidentified foraminiferans	26													
Class Ciliata														
Unidentified tintinnids				72				28			2113			3384
Phylum Aschelminthes														
Class Nematoda														
Unidentified nematodes			120						215	274			2526	
Class Rotifera														
Synchaeta sp.	26			72	436	156	345	169	86	55	905	952	2526	12615
Trichocerca sp.													421	
Phylum Mollusca														
Class Gastropoda														
Littorina sp. eggs						156	86	56	258	274	302		210	307
Unidentified gastropod larvae		24	80	214	436				215	55	603	666	421	
Class Bivalvia														
Unidentified straight-hinge larvae									86	55		4571	18315	7692
Phylum Annelida														
Class Polychaeta														
Unidentified trochophore larvae			40	286	727		259	84	129	164	302	381	1052	923
Unidentified seteger larvae						312	345	56	86		302	571	1894	923
Phylum Arthropoda														
Class Crustacea														
Subclass Branchiopoda														
Evadne nordmani Loven												95	1263	1538
Subclass Cirripedia														
Cirripede nauplii	52	24	520	7450	3345	1875	1898	507	215	109	603	381		
Cirripede cyprids													210	
Subclass Copepoda														
Acartia longiremis (Lilljeborg) adults		24	80	72			86			164		666	1052	
Acartia sp. copepodites								56	129	109		95	421	923
Acartia sp. nauplii	234		320	931	1309	625	1121	591	387	383	1509	1142	3368	1538
Calanus finmarchicus (Gunnerus) nauplii	104	24						28				190		
Eurytemora herdmani Thompson and Scott nauplii							259	84		55				
Microsetella norvegica (Boeck) adults and copepodites	51588	45425	45360	20274	32581	3281	4831	8535	4258	657	3018	11142	20842	35692
M. norvegica nauplii	26		40				86	56	559	109	905	9238	57052	30153
M. norvegica eggs	156	121	120	143	145		259	3690	2236	218	905	5238	4421	4923
Oithona similis Claus adults and copepodites	807	340	360	358			86	140	86			95		923
O. similis nauplii	859		1240	788	1891	781	1380	338	344	438		1047	1894	4307
Pseudocalanus minutus (Kroyer) adults	52	73		72				84	43	55				
P. minutus copepodites		48	40	72						219		285	631	615
P. minutus nauplii	234	97	320					84	43	55		95	842	1538
Temora longicornis (Muller) adults										55			842	
T. longicornis copepodites		24						140		55				307
T longicornis nauplii	234	24	520	358	827	625	776	309	129	109		1238	1473	3384
Unid. Harpacticoid adults and copepodites				72			690	56	473	218		95	631	307
Unid. Harpacticoid nauplii				72			172		43					
Unid Copepod nauplii									43					
Subclass Decapoda														
Hyas sp. zoea								28						
Phylum Chordata														
Class Larvacea														
Fritillaria borealis Lohmann									43		603	952	210	
Other –														
Unid. invertebrate eggs					3927	781	345		903	109	3924	1047	421	

Chlorophyll

Chlorophyll *a* concentrations in 1979 reached peaks in the Damariscotta estuary in late February and early to mid-March followed by lower values and a third peak in May (Fig. 3). There were 2 peaks in chlorophyll in Sullivan Harbor, in early April and June. The chlorophyll levels in Sullivan Harbor were generally lower than the Damariscotta.

Zooplankton

The estimated abundances and species composition of zooplankton are summarized in Tables 1 to 4. The tintinnid, *Tintinnopsis* sp. had the highest peak abundance in the Damariscotta estuary in 1979, reaching its peak abundance on 22 March, as did the other 2 abundant taxa, the rotifer *Synchaeta* sp. and cirripede nauplii. The species composition in Sullivan Harbor

Table 3. Estimated numbers of zooplankton organisms per m^3. Damariscotta River estuary, 1980. Samples were collected with 165 µm mesh plankton nets

Taxa	Sample date												
	29 Jan	4 Feb	12 Feb	19 Feb	26 Feb	4 Mar	11 Mar	25 Mar	4 Apr	14 Apr	18 Apr	25 Apr	6 May
Phylum Protozoa													
Class Rhizopoda													
Unidentified foraminiferans						27					6		20
Class Ciliata													
Paratavella sp									21				
Unid. tintinnids										7	6		
Phylum Aschelminthes													
Class Nematoda													
Unid. nematodes											30		
Class Rotifera													
Synchaeta sp.				14			33		7			15	62
Phylum Mollusca													
Class Gastropoda													
Littorina sp. eggs					30				102	66	105	5	41
Unid. gastropod larvae		16	38						7				62
Phylum Annelida													
Class Polychaeta													
Unid. trochophore larvae													
Unid. seteger larvae					15				21		6		167
Phylum Arthropoda													
Class Crustacea													
Subclass Cirrepedia													
Cirripede nauplii	2506	4789	17574	8344	11363	13713	24117	3285	856	22	154		
Cirripede cyprids							33	1916	600	37	49		
Subclass Copepoda													
Acartia clausi Giesbrecht adults													20
Acartia sp longiremis (Lilljeborg) adults	223	356	321	229	61	138	131	45	23	102	43		833
Acartia sp copepodites	140	348	302	158	122	385	262	274	358	249	136		2187
Acartia sp. nauplii		8	38	43		55	65	23	7	29	12		1145
Calanus finmarchicus (Gunnerus) adults				14		55							
C. finmarchicus nauplii								45			6		
Centropages hamatus (Lilljeborg) adults													62
C. hamatus nauplii													62
Eurytemora herdmani Thompson and Scott adults	25	25			46		65		7	22	37		146
E. herdmani copepodites			19										333
E. herdmani nauplii						55	65						83
Oithona similis Claus adults and copepodites	16	124			46		164		29	22			20
Paratholistris croni (Kroyer) adults and copepodites				28									
Pseudocalanus minutus (Kroyer) adults	58	49	19		15	55	164						41
P. minutus copepodites	24	17	19		15	27	98			7			
P. minutus nauplii		8	38		30		131	91	29	7	18		
Temora longicornis (Muller) adults	66	66	75	72	15		65		7	22	12		167
T. longicornis copepodites									88	161	49		875
T. longicornis nauplii				14				46	7		6		312
Tortanus discaudaths (Thompson and Scott) adults		17		14		27			7				
Unid. Harpacticoid adults and copepodites			19	57						117	42	5	41
Unid. Harpacticoid nauplii				43	30						18	10	20
Unid. copepod nauplii		8											41
Subclass Decapoda													
Hyas sp. zoea*										14		5	
Phylum Chaetognatha													
Sagitta elegans Verrill*	8												
Other –													
Hansen's nauplii									14		6		
Unid. invertebrate eggs	8			14									

* Larger organisms such as decapod larvae and chaetognaths were visually present in the raw samples but were not adequately subsampled by the Stempel pipette

in 1979 was different from the Damariscotta (Tables 1 and 2). The dominant species in Sullivan was the harpacticoid copepod *Microsetella norvegica* which was at peak abundance on the first sample date, 31 January.

Comparisons of the 1979 and 1980 zooplankton results are complicated by the fact that most of the smaller organisms were undersampled by the 165 µm nets used in 1980. A comparison of the 165 µm and 80 µm mesh nets is given in Table 5. In particular, *Tintinnopsis* sp., *Synchaeta* sp., polychaete trochophore larvae, adult and copepodid *M. norvegica*, and all copepod nauplii were undersampled in 1980, whereas the adult and copepodid stages of most copepods and cirripede nauplii were sampled more representatively. The dominant zooplankters in each area in 1980 were cirripede nauplii (Tables 3 and 4) which reached peak abundances earlier than the previous year.

Table 4. Estimated numbers of zooplankton organisms per m^3. Sullivan Harbor, 1980. Samples were collected with 165 µm mesh plankton nets

Taxa	Sample date 28 Jan	5 Feb	11 Feb	18 Feb	25 Feb	3 Mar	10 Mar	26 Mar	3 Apr	10 Apr	17 Apr	11 May
Phylum Protozoa												
Class Ciliata												
Unid. tintinnids	8											
Class Rhizopoda												
Unid. foraminiferans	8			110	48	28	8	25	17	17	48	16
Phylum Aschelminthes												
Class Nematoda												
Unid. nematodes	8		10	24	8	9	23	8		17		32
Class Rotifera												
Synchaeta sp.	8			86			8			9		275
Phylum Mollusca												
Class Gastropoda												
Littorina sp. eggs										388	95	210
Unid. gastropod larvae	16		20	37	56	104	31	8		9		97
Class Bivalvia												
Unid. straight-hinge larvae					8	8				35		161
Phylum Annelida												
Class Polychaeta												
Unid. trochophore larvae						19	31	8	26	17	35	
Unid. seteger larvae						19			8			
Phylum Arthropoda												
Class Crustacea												
Subclass Branchiopoda												
Evadne nordmani Loven												32
Subclass Cirripedia												
Cirripede nauplii		187	1500	2006	2862	2880	1138	666	1164	502	584	420
Cirripede cyprids						9		77	191	405	48	16
Subclass Copepoda												
Acartia clausi Giesbrecht adults											12	
Acartia longiremis (Lilljeborg) adults	66	8	30	12			31	8	147	141	346	1116
Acartia sp. copepodites	8	24	20			9	17	25	226	326	358	647
Acartia sp. nauplii					8	19		8	34	26	83	178
Calanus finmarchicus (Gunnerus) adults	8			12							24	
Eurytemora herdmani Thompson and Scott adults	16	8						8		35		
E. herdmani copepodites								8		26	12	
E. herdmani nauplii									8			
Microsetella norvegica (Boeck) adults and copepodites	8	33	30	98	40	38				88	36	81
Oithona similis Claus adults and copepodites	223	464	230	344	233	390	147		113	44	24	194
O. similis nauplii				37			8			9		
Pseudocalanus minutus (Kroyer) adults	33	81	70	123	104	85	46		26	9	48	291
P. minutus copepodites	8	16	40	110	112	152	70	42	43	44	203	194
P. minutus nauplii	8	57		172	88	152	70	42	43	26	36	
Temora longicornis (Muller) adults									17	35	60	178
T. longicornis copepodites			10	12					26	9	108	81
T. longicornis nauplii						9					24	
Tortanus discaudatus (Thompson and Scott) adults	8											48
T. discaudatus copepodites	8											
Unid. Harpacticoid adults and copepodites	16	8		24	16		23	17		26	24	16
Unid. Harpacticoid nauplii								17				
Unid. copepod adults	8	16	10									
Unid. copepod eggs										26		
Phylum Echinodermata												
Unid. pluteus larvae												97
Phylum Chordata												
Class Larvacea												
Fritillaria borealis Lohmann									8	9		954
Other –												
Unid. invertebrate eggs				184	24		8	8	8			

Ichthyoplankton

A total of 24 species of larval fishes were caught during this study. The catch rates and seasonalities for all species caught in both sample areas are given in Tables 6 to 9. The dominant species for both the Damariscotta estuary and Sullivan Harbor was *Pholis gunnellus*. Other dominant species occurring in each area included 3 cottid congeners, *Myoxocephalus scorpius, M. aenaeus* and *M. octodecempspinosus*, and the stichaeid *Lumpenus lumpretaeformis*. These results, for the Damariscotta, are similar to those reported previously for this area (Graham and Boyar, 1965; Chenoweth, 1973; Hauser, 1973; Laroche, 1980, 1982; Shaw, 1981). A complete discussion of the ecology of the cottid larvae is given by Laroche (1982).

Although differing somewhat in relative abundances, the late winter larval fish faunas in Sullivan Harbor and the Damariscotta estuary were quite similar. However, they differed considerably in species composition later in the season. In particular, *Liparis atlanticus* and *Ammodytes* sp. larvae were abundant in Sullivan Harbor, but were only poorly represented in the Damariscotta. Conversely, *Osmerus mordax* and fall-spawned *Clupea harengus* larvae were abundant in the Damariscotta and rare in Sullivan Harbor. There are no previously published accounts of the fish larvae from Sullivan Harbor or waters nearby with which to

Table 5. Comparison of counts and abundance estimates of zooplankton sampled in the Damariscotta River estuary, 11 April 1979, with a 20 cm Bongo net equipped with an 80 µm mesh net on the port side and a 165 µm mesh net on the starboard side. Two surface and deep 10 min tows were taken and the samples pooled. The No. 20 net sample was diluted to 2000 ml and the No. 10 net sample was diluted to 1000 ml. A 1 ml aliquot from each was counted. Organisms were divided into rough size categories

Taxon	No. 20 Net		No. 10 Net	
	Raw count	No. m^{-3}	Raw count	No. m^{-3}
Smaller organisms				
Keratella sp.	8	133	–	–
Tintinnopsis sp.	102	1700	2	14
Synchaeta sp.	81	1350	1	7
Unid. gastropod larvae	4	67	–	–
Unid. polychaete trochopores	99	1650	13	96
Acartia sp. nauplii	435	7250	14	103
Eurytemora herdmani nauplii	47	783	1	7
Centropages hamatus nauplii	31	516	–	–
Microsetella norvegica nauplii	12	200	–	–
M. norvegica adults and copepodites	56	933	1	7
Oithona similis nauplii	4	67	–	–
Pseudocalanus minutus nauplii	9	150	2	14
Temora longicornis nauplii	65	1083	–	–
Unid. harpacticoid nauplii	2	34	–	–
Unid. copepod nauplii	8	133	–	–
Unid. copepod eggs	22	366	–	–
Hansen's nauplii	–	–	3	22
Unid. invertebrate eggs	10	167	–	–
Larger organisms				
Unid. polychaete setegers	1	17	4	29
Unid. nematodes	2	34	1	7
Littorina sp. eggs	1	17	6	44
Acartia longiremis adults	12	200	32	235
Acartia sp. copepodites	58	966	102	750
E. herdmani adults	1	17	3	22
E. herdmani copepodites	13	216	37	272
O. similis adults and copepodites	3	50	15	110
P. minutus copepodites	8	133	1	7
T. longicornis adults	4	67	8	59
T. longicornis copepodites	24	400	36	264
Unid. Harpacticoid adults and copepodites	2	34	3	22
Cirripede nauplii	15	250	38	279
Cirripede cyprids	14	233	38	279
Volume filtered	119.8 m^3		135.9 m^3	
Settled volume	113 cm		82 cm	

Table 6. Abundances and species composition of fish larvae (expressed as number of larvae per 100 m^3), Damariscotta River estuary, 1979

Sample date	Species *Ammodytes* sp.	*Anguilla rostrata*	*Aspidophoroides monopterygius*	*Clupea harengus*	*Cryptacanthodes maculatus*	*Hemitripterus americanus*	*Liopsetta putnami*	*Liparis atlanticus*	*L. coheni*	*Lumpenus lumpretaeformis*	*Menidia menidia*	*Microgadus tomcod*	*Myoxocephalus aenaeus*	*M. octodecemspinosus*	*M. scorpius*	*Osmerus mordax*	*Pholis gunnellus*	*Pollachius virens*	*Pseudopleuronectes americanus*	*Syngnathus fuscus*	*Triglops murrayi*	*Ulvaria subbifurcata*	Total
1 Feb				0.17					0.43	1.45				0.26			1.12	0.09					3.52
7 Feb				0.10						0.82			0.27	0.92	0.19		0.91						3.21
15 Feb				0.17					0.09	0.81			0.47	0.62	0.90		3.88						6.93
23 Feb					0.09					0.05			0.28	0.69	2.22		3.35	0.09					6.76
2 Mar				0.47	0.18				0.10	2.94			1.33	3.70	12.43		17.65	0.18			0.10		39.07
8 Mar	0.16			0.78	0.08				0.26	2.30		0.09	5.96	4.10	13.83		44.37	0.08					72.01
16 Mar	0.08			1.69	2.95	0.25	0.33		1.92	3.69			6.33	6.07	25.66		54.64	1.52			0.08		105.22
22 Mar	0.16			8.55	0.73				0.30	2.83		0.08	12.83	6.56	17.39		46.24	4.04					100.13
30 Mar	0.50			2.91	1.24	0.34	0.36		0.09	0.78		0.19	5.16	0.68	0.67		22.32	3.36					38.59
6 Apr	0.65			2.59	0.08	0.08	0.73			0.08			6.40	0.09		0.08	18.38	0.17					29.34
11 Apr	0.51	0.17		4.28	0.08								0.33	0.09	0.08		5.68	2.19					13.41
18 Apr	1.01	0.10	0.56	4.58				0.10		0.19			0.75				6.00	3.71					16.70
25 Apr	1.00	0.09	0.16	1.75			0.59			0.09			1.54				14.80	0.34	1.38			0.18	21.92
4 May	0.07			1.73	0.08		0.16						0.37			1.40	2.32	0.07	1.28			20.52	28.00
9 May				1.43												6.77	1.14	0.07	0.94			7.07	17.42
18 May																19.25			4.62			10.11	33.99
23 May								0.09								21.96			2.96			0.67	25.69
30 May								0.17								29.72			5.42			1.40	36.72
6 Jun											0.18					13.42	0.18		1.97			0.54	16.28
13 Jun																1.08			0.10			0.18	1.35
20 Jun																0.16			0.16	0.16			0.48

Table 7. Abundances and species composition of fish larvae (expressed as number of larvae per 100 m^3), Sullivan Harbor, 1979

Sample date	Species *Ammodytes* sp.	*Anguilla rostrata*	*Aspidophoroides monopterygius*	*Clupea harengus*	*Cryptacanthodes maculatus*	*Hemitripterus americanus*	*Hippoglossoides platessoides*	*Liopsetta putnami*	*Liparis atlanticus*	*L. coheni*	*Lumpenus lumpretaeformis*	*Cyclopterus lumpus*	*Microgadus tomcod*	*Myoxocephalus aenaeus*	*M. octodecemspinosus*	*M. scorpius*	*Osmerus mordax*	*Pholis gunnellus*	*Pseudopleuronectes americanus*	*Triglops murrayi*	*Ulvaria subbifurcata*	Total
24 Jan											0.96				0.14	0.43						1.52
31 Jan					0.09						1.68				0.26							2.03
8 Feb					0.18					0.08	1.37				0.50	0.08		0.26				2.48
16 Feb					0.19						2.06				0.75							3.00
22 Feb					0.09					0.10	4.82				1.52	0.10						6.62
1 Mar					0.08						4.72				0.84	2.31		1.22		0.10		9.27
7 Mar	0.08				0.33	0.08				0.85	4.40			0.19	6.70	4.68		5.36				22.68
15 Mar	.46			0.19	0.94					0.44	12.05			0.26	9.78	5.13		24.10				53.35
23 Mar	35.38				2.79	0.70				1.61	1.03		0.61	9.83	4.02	9.83		77.49		0.08		143.38
29 Mar	1.13			0.49	4.05	0.33				0.32	3.12			1.15	0.65			22.79				34.68
5 Apr	19.02				1.03	0.18		0.18		1.95	2.08			23.66	0.89	0.87		45.81				95.66
10 Apr	19.08			0.63	0.57	0.43		0.09	0.34	1.47	2.05		0.09	20.64	0.76	1.51		48.73		0.09		96.45
19 Apr	19.60		0.09	1.83					1.94	0.71	2.63			0.71	0.31	3.96		77.46				109.23
26 Apr	13.04			0.84		0.56		0.19	3.73	0.18				7.04	0.09	0.54		9.47			0.10	35.77
3 May	9.98			1.62		0.19			19.46		0.09			0.97		0.10		1.53	0.30		0.09	34.34
10 May	2.19	0.08		2.24		0.53			35.13					0.55			1.15	1.10	0.87			43.83
17 May	2.74		0.09						24.45					0.11			0.27	0.17	2.51		0.36	27.69
24 May						0.09	0.10		7.36			0.09					0.48		1.69		0.47	10.29
31 May	0.08						0.09		8.35								0.18		1.43		1.07	11.20
7 Jun									19.06			0.09					0.09		2.12		0.98	22.35
14 Jun									9.35								0.17		7.80		1.71	19.23
21 Jun									0.77										0.69		0.78	2.23
28 Jun									1.08										1.45		3.64	6.17
5 Jul									0.20			0.09							1.36		0.20	1.85

compare my results. The overall abundances of the dominant late winter species increased earlier in the Damariscotta than in Sullivan Harbor by 1 to 3 weeks. The peak abundances of these species, like the zooplankton, occurred earlier in 1980 than 1979 in each area.

DISCUSSION

The timing of the late winter–early spring phytoplankton bloom in 1979 in the Damariscotta estuary was similar to that reported by Cura (1981) for 1978. He reported that the chlorophyll levels were generally low

Table 8. Abundances and species composition of fish larvae (expressed as number of larvae per 100 m^3), Damariscotta River estuary, 1980

	Species																	
Sample date	*Ammodytes* sp.	*Anguilla rostrata*	*Aspidophoroides monopterygius*	*Clupea harengus*	*Cryptacanthodes maculatus*	*Hemitripterus americanus*	*Liopsetta putnami*	*Liparis coheni*	*Lumpenus lumpretaeformis*	*Myoxocephalus aenaeus*	*M. octodecemspinosus*	*M. scorpius*	*Osmerus mordax*	*Pholis gunnellus*	*Pollachius virens*	*Pseudopleuronectes americanus*	*Ulvaria subbifurcata*	Total
29 Jan				0.18				0.18	0.88	2.36	1.57			3.95				9.12
4 Feb				0.18					0.53	1.24	1.41			6.50				6.21
12 Feb				0.11		0.19		0.09	0.88	2.51	3.07	1.31		12.03				21.16
19 Feb				0.29	0.86				1.39	3.10	2.66	2.79	0.10	20.66	0.08			31.92
26 Feb				0.33	0.99	0.16		0.50	1.81	11.14	4.40	12.46		42.44				74.22
4 Mar				0.17	0.26			0.18	0.43	6.35	0.69	16.87		37.57	0.08			62.51
11 Mar		0.19		0.19	1.03					8.65	2.57	14.96		29.78				57.37
25 Mar	1.06	0.35		16.25				0.87	0.17	19.00	2.28	13.91		34.88	1.75			90.52
4 Apr	1.16			34.22		0.59			0.14	1.44	0.14	1.31		49.31	0.29			88.60
11 Apr	0.33	0.17		6.31		0.18				0.74		0.17		12.13	1.01			21.04
14 Apr				12.51		0.16	0.32		0.08	0.74				3.31	0.08			17.21
18 Apr	0.26		0.17	8.73			0.09			0.94	0.08			7.77	0.08			18.13
25 Apr	0.08		0.09	2.28			0.09			0.18				1.02			0.16	3.89
6 May				0.17									1.20			2.58	5.51	9.47

Table 9. Abundances and species composition of fish larvae (expressed as number of larvae per 100 m^3), Sullivan Harbor, 1980

	Species																		
Sample date	*Ammodytes* sp.	*Anguilla rostrata*	*Aspidophoroides monopterygius*	*Clupea harengus*	*Cryptacanthodes maculatus*	*Hemitripterus americanus*	*Liopsetta putnami*	*Liparis atlanticus*	*L. coheni*	*Lumpenus lumpretaeformis*	*Microgadus tomcod*	*Myoxocephalus aenaeus*	*M. octodecemspinosus*	*M. scorpius*	*Pholis gunnellus*	*Pollachius virens*	*Pseudopleuronectes americanus*	*Ulvaria subbifurcata*	Total
28 Jan									0.09	2.93		0.09	0.56		2.66				6.33
5 Feb					0.18					0.63			0.35	0.09					1.25
11 Feb					0.10				0.10	0.48		0.10	0.10		1.19				2.06
18 Feb					0.17				0.09	0.62			1.32		0.27				2.47
25 Feb					0.94				0.08	1.29		0.10	4.46	0.53	15.70				23.09
3 Mar					0.41				0.24	0.35		0.26	1.89	1.05	4.45				8.74
10 Mar	0.09				1.50				0.88	0.52	0.09	0.97	6.48	5.81	20.51				36.84
26 Mar	10.66				0.55	1.06			1.10			1.81	4.05	1.96	91.90				113.09
3 Apr	3.85	0.09		0.19	1.76	0.46			1.40	1.09	0.09	1.55	3.54	2.75	67.71				84.48
10 Apr	12.07			0.33	0.23	0.84	0.61	0.17	0.57	0.09	0.33	10.71	0.25	2.44	41.16	0.09			70.05
17 Apr	3.35			0.95					0.24			0.71		0.08	6.68				12.02
24 Apr	11.23		0.27	1.40		0.10	0.10	1.31	0.38			2.49	0.10		3.82				21.21
5 May	11.29		0.09	0.08		0.08	0.15	1.99							0.83	0.15	0.30		14.96
11 May	6.79							15.12				0.62			0.62		1.54	0.31	24.99

in February (0.7 to 1.0 $\mu g l^{-1}$) and reached a peak on 20 March (3.6 $\mu g l^{-1}$). He noted that the bloom that year occurred within 7 d after the average in situ light intensity exceeded 40 $ly\,d^{-1}$, and that it was not triggered by a sudden influx of nutrients. Hitchcock and Smayda (1977) reported a similar response in Narragansett Bay to this apparently critical light intensity. This phenomenon may explain the difference in timing of the early phytoplankton blooms between areas in my study. The late February–early March bloom in the Damariscotta in 1979 occurred before any marked influx of freshwater or increase in vertical stability and began as the water temperature was climbing above about 1 °C. In Sullivan Harbor, the late March–early April bloom also occurred as the water temperature increased above 1 °C and did not correspond to any marked increase in vertical stability. It is quite possible that if the 1 to 1.5 C° change in temperature were of only minor importance, that differences in in situ light intensities may have controlled the timing of these blooms. Although not measured in this study, extinction coefficients might have been greater in Sullivan Harbor where, in addition to being shallower than the Damariscotta, the mean tidal range is about 0.5 m greater in Sullivan (3.2 m vs 2.8 m). It could be argued that tidal mixing resulted in a higher suspended particulate load in Sullivan Harbor, and that a greater solar elevation later in the spring was required to give a critical in situ light intensity for a phytoplankton bloom. Bigelow et al. (1940) also reported that the peak in phytoplankton in 'the coastal waters near Mt. Desert Island', which is at the mouth of Frenchman Bay and Sullivan Harbor, generally lags behind the western Gulf of Maine.

The times of peak abundances of the major groups of zooplankton common to both sample areas, i.e. post-naupliar copepods, copepod nauplii and cirripede nauplii, are shown in Fig. 3. It appears that the abundance cycles of these groups in 1979 in the Damariscotta were coupled to that of the phytoplankton. Each group began to increase in numbers in late February, commensurate with rising chlorophyll concentrations. The copepod nauplii and cirripede nauplii, as well as *Synchaeta* sp. and *Tintinnopsis* sp. (Table 1), reached maximal abundances at the end of the phytoplankton bloom while the post-naupliar copepods peaked in early March. The abundance curve of cirripede nauplii in 1980 in the Damariscotta was similar in shape to the previous year but occurred earlier in the season, while the abundances of post-naupliar copepods were lower than in the previous year and fluctuated before rising abruptly on the last sample date. Lee (1975) reported that the copepods in the Damariscotta estuary had 2 abundance peaks in 1972, one in early June and the other in August and September, which more closely resembles my results in 1980 than in 1979. The post-naupliar copepod maximum occurred much earlier in 1979 than in 1980 in the Damariscotta, suggesting that year to year variability is quite significant. The abundances of the major groups of zooplankton in Sullivan Harbor in 1979 were relatively high before the phytoplankton bloom there, and were much lower than in the Damariscotta. It is quite possible, however, that grazing pressure early in the season in Sullivan delayed the time of and suppressed the phytoplankton bloom.

The post-naupliar copepods in Sullivan Harbor in 1979 were dominated by a single species, *Microsetella norvegica*, which was most abundant on the first sample date (Table 2). The abundance of this species reached its lowest value on 3 May, but began to increase again until the last sample date on 28 June. The numbers of *M. norvegica* nauplii began to increase in late April. These results are consistent with those of Fish and Johnson (1937) who reported that this species 'swarmed' in Frenchman Bay in July and August of 1930 and outnumbered all other zooplankton species combined. Fish (1955) noted that spawning of *M. norvegica* in the inner Gulf of Maine began during April in 1932, and that propagation reached its peak in July and early August. He reported that there was a progressive delay in spawning to the eastward and that by September propagation had ceased in the entire Gulf in both 1931 and 1932. It appears from my results that spawning of *M. norvegica* can occur later than September or that the development of the young during summer and fall is sufficiently slow to produce a large population of adults and copepodites in winter. The presence of eggs throughout the 1979 sampling period in my study would suggest that spawning can occur during much of the year. The abundance of this species in 1980 could not be adequately assessed because of the larger mesh nets used that year.

As in Damariscotta estuary, cirripede nauplii in Sullivan Harbor appeared earlier in 1980 than in 1979. The late season increase in post-naupliar copepods also occurred earlier in 1980. Although it is commonly accepted that the seasonal cycles of zooplankton and phytoplankton are strongly linked (Cushing, 1959), it has been demonstrated only rarely (i.e. Toner, 1981). The abundances of zooplankton in my study appeared to be strongly linked to the phytoplankton in 1979 in the Damariscotta estuary but less so in Sullivan Harbor. Rather, the zooplankton preceded the phytoplankton peak in Sullivan that year. In addition, the timing of peak abundances of zooplankton in each area in 1980 was earlier than the previous year. This was most obvious for the abundant cirripede nauplii. The release of these barnacle nauplii in the spring is usually synchronized with the phytoplankton bloom (Barnes, 1962), and indeed this appeared to be the case in the Damariscotta in 1979, but they preceded the bloom in Sullivan Harbor. Thus, the earlier appearance of these nauplii in 1980 does not necessarily indicate that the phytoplankton bloom that year was also earlier.

The times of peak abundances of the dominant larval fish species appeared to be coupled to the spring plankton blooms. In 1979 the rises in abundance of the dominant larval fish species occurred 1 to 3 wk earlier in the Damariscotta estuary than in Sullivan Harbor, as did the zooplankton. Also, like the zooplankton, the rises in abundance of the fish larvae occurred earlier in each sample area in 1980 than the previous year. A causative link between the zooplankton abundances and larval fish abundances seems likely. This was examined closely for *Pholis gunnellus* larvae (Townsend, 1983) whose survival and growth appeared to depend upon the dynamics of its planktonic food. The relation in time between the abundances of the dominant fish larvae and the plankton biomass is shown in Fig. 4 for 1979 (1980 sampling ended early and these results were not plotted). These data show that the late-winter early-summer larval fish assemblages occurred in 2 groups in both Damariscotta estuary and Sullivan Harbor, and each group corresponded to distinct pulses in plankton biomass.

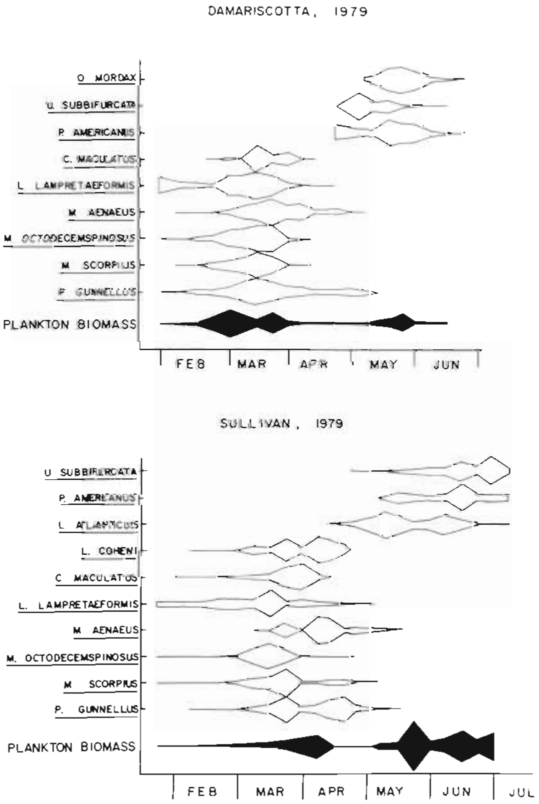

Fig. 4. Graphical representation of relative abundances of the dominant fish larvae in relation to plankton biomass for Damariscotta estuary and Sullivan Harbor, 1979. The widths of each species abundance plot is relative to itself, i.e. the widest portion indicates the time that species reached maximum abundance (Tables 1 to 4). Plankton biomass equals the settled volume biomass estimates from 80 μm mesh 20 cm bongo samples

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