

# Recruitment of copepod nauplii into the plankton: importance of diapause eggs and benthic processes

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**ABSTRACT:** During the last 10 yr it has been shown that the eggs of many zooplankters (e.g. copepods, cladocerans, tintinnids) occur in bottom sediments of coastal regions. Accumulations of these eggs on the sea-bottom may represent an important source for the recruitment of individuals into the plankton. We examined vertical distribution and viability of copepod eggs at several locations in Buzzards Bay, Massachusetts USA. Cylindrical cores were obtained by divers. In the laboratory each core was divided at 1.0 cm intervals to a maximum depth of 10.0 cm. From each layer 2 subcores were taken. One was suspended in seawater and incubated for several days at 19 °C. Hatched nauplii were collected, counted, and reared for identification. Viable eggs (evidenced by appearance of nauplii) were found at all depths in the sediment. The greatest densities ( $10^6$  to  $10^7$  m<sup>-2</sup>) often occurred several cm below the water-sediment interface. Egg abundance was not significantly correlated with sediment grain size. The other subcore was sonified so that the eggs of *Labidocera aestiva* could be removed, counted, and incubated (to determine viability). Laboratory feeding experiments indicate that diapause and subitaneous eggs of *L. aestiva* remain viable after being consumed by either *Capitella* sp. 1 or *Streblospio benedicti* which are common benthic consumers in regions where eggs occur. The relative importance and influence of physical factors (waves, tidal and wind-driven currents) and biological factors (feeding and bioturbating activities of benthic animals) on the distribution, abundance, and viability of eggs on the sea-bottom is discussed.

## INTRODUCTION

During the last 10 yr it has become increasingly apparent that the eggs of many marine planktonic copepods occur in the bottom sediments of coastal regions (reviewed by Grice and Marcus, 1981). It has been suggested that the survival of these eggs, during periods which are not suitable for the existence of stages in the water column, is critical for the perpetuation of such species. A previous study (Kasahara et al., 1975a), documented the seasonal changes in egg abundance in the uppermost 1 cm of the sediments. In several species the peak in egg abundance preceded the disappearance of adults (and other planktonic stages) by ca. 1 mo. Thereafter, the number decreased considerably and it was proposed that the decline reflected mortality due to predation by benthic animals

or decay by microorganisms (Kasahara et al., 1975a; Uye, 1980) However, other evidence in the literature tends to refute this hypothesis. Diapause eggs of both *Labidocera aestiva* and *L. bipinnata* have a tough outer covering that resists being ruptured if poked with a needle (Uye et al., 1979; Marcus, pers. obs.). Similarly the egg of *Tortanus discaudatus* soon after being released from the female develops a tough protective chitinous case, which is resistant to bacterial degradation (Johnson, 1967). These facts suggest that some eggs which reside in the sediments might be resistant to digestion by predators and microbial decay processes.

In this paper I present data derived from laboratory feeding experiments, that demonstrate survival of eggs of *Labidocera aestiva* after passage through the gut of 2 polychaete species. I also report the existence of large quantities ( $10^6$  to  $10^7$  m<sup>-2</sup>) of viable eggs between 1.0 and 10.0 cm depths in sediments from Buzzards Bay, Massachusetts, USA. Results suggest that the temporal decline in egg abundance reported for the uppermost

centimeter of the sediments is due to the translocation of eggs from the sediment surface to deeper strata, and does not necessarily reflect mortality. The redistribution of eggs could be the result of resuspension due to wave action, current flow and tidal mixing, or the feeding and burrowing activities of benthic animals. Accumulations of such large numbers of viable eggs at depth in the sediments may have an important influence on the population dynamics of planktonic communities by providing a potentially large source of nauplii for recruitment.

### MATERIALS AND METHODS

To evaluate the impact of predation on egg mortality we conducted several feeding experiments in the laboratory using diapause and subitaneous eggs of the calanoid copepod *Labidocera aestiva*. Females produce subitaneous eggs during summer and fall in the Woods Hole region, whereas diapause eggs are produced only during fall. Both egg types are ca. 112  $\mu\text{m}$  in diameter, with a smooth outer surface.

Eggs were obtained from *Labidocera aestiva* females collected in the field or reared in the laboratory. For each experiment, 300 to 700 eggs (diapause or subitaneous) were mixed with ca. 2.0 g of prepared sediment and seawater (filtered through a 5  $\mu\text{m}$  mesh bag) in a small dish. The sediment was collected from Buzzards Bay and frozen until needed. It was then thawed and sieved through a 70  $\mu\text{m}$  Nitex mesh screen. The material that passed through the mesh was used in the experiments to ensure that extraneous eggs and predators were not present. Two predator species were tested, *Capitella* sp. 1 (provided by J. Grassle) and *Streblospio benedicti* (provided by L. Levin). Each species is common in the areas where eggs normally occur in the bay. The test animals were kept in filtered seawater for 12 h prior to each experiment, and then 6 to 10 *Capitella* sp. 1 or 3 to 6 *S. benedicti* were added to the dishes with the egg-sediment mixture. The dishes were placed at 19 °C for 12 to 24 h, after which the contents were examined with a dissecting microscope. Fecal pellets were collected from each dish with a pipette. Many of the pellets contained eggs. For each experiment, some pellets were dissected to extract the eggs which were then placed in filtered seawater in screwcapped jars, and incubated at 19 °C. Other pellets that contained eggs were left intact and placed in filtered seawater in a second set of jars. These were also incubated at 19 °C. Eggs that had not been offered to predators, and so were never ingested, were placed in a third set of jars and incubated, to serve as controls. The jars placed at 19 °C were examined within 4 to 5 d and the number of eggs that hatched was recorded.

The conditions under which the eggs or pellets were incubated (i.e. 19 °C) after the feeding period reflected the type and prior history of the eggs used in each experiment. Subitaneous eggs will normally hatch within 2 to 3 d if incubated at 19 °C. Diapause eggs can be induced to hatch by chilling them at 5 °C for 2 to 4 wk, followed by warming to 19 °C. Hatching will then occur in 2 to 3 d. For Experiments 1 and 2 subitaneous eggs were used, so the incubation temperature was 19 °C. For Experiments 3 to 6 diapause eggs had already been chilled for the required minimum period of 4 wk, so that subsequent to feeding these eggs and pellets were placed directly at 19 °C to induce hatching.

On several occasions fecal pellets containing what appeared to be eggs of *Labidocera aestiva* were observed in the sediment samples (see below) collected from Buzzards Bay. These pellets were incubated at 19 °C and the number of eggs that hatched was recorded.

To evaluate the importance of translocation, I investigated the vertical distribution, abundance, and viability of eggs in the bottom sediments at several stations (3, 6, 10, 12, and 14) in Buzzards Bay, MA (Fig. 1). At each station, 2 cores were carefully inserted into the sea bottom by SCUBA divers, then capped at the top and bottom, and transported upright to the surface. In the laboratory, the cores were subdivided at 1.0 cm intervals to a maximum depth of 10.0 cm. Two subcores (A and B) were taken from the central region of each layer. The volume of each subcore was 1.77  $\text{cm}^3$ . Subcore A was suspended in 100.0 ml of filtered seawater in a dish, which was then covered and placed at 19 °C and a 20 h to 4 h light-dark cycle, for 4 to 7 d. Every 2 to 4 d the contents of the dishes were examined. Nauplii were collected by decanting the seawater and filtering the material through a 70  $\mu\text{m}$  Nitex mesh screen. Clean filtered seawater was added to the dishes with sedi-

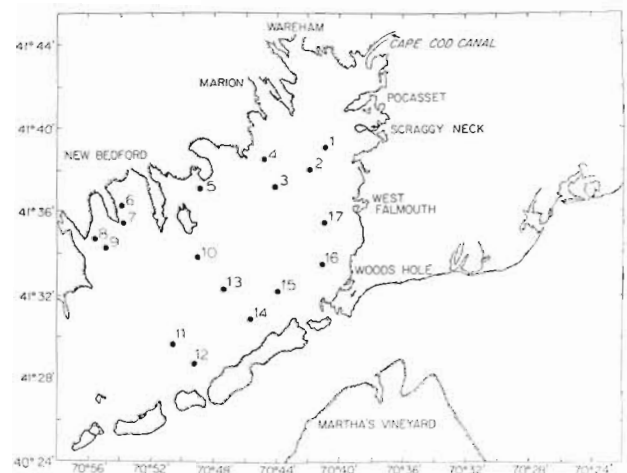


Fig. 1 Sampling sites in Buzzards Bay

ment which were then returned to the incubator. The fraction retained on the mesh was washed into a small chamber and observed with a dissecting microscope to count the number of nauplii present. As time permitted, nauplii were reared to a recognizable stage for identification. The diet consisted of a mixture of *Rhodomonas lens*, *Gymnodinium nelsoni*, *Gonyaulax polyedra*, *Prorocentrum micans*, and *Scrippsiella trochoideum*.

The number of nauplii determined by this method reflects the number of viable eggs that hatch under the specific conditions imposed in the laboratory. Therefore the values do not necessarily reflect the total number of eggs present in the sediment.

By analyzing the B subcores in a variety of ways, I found that the most accurate and efficient method for determining the number of eggs in a sample involved the use of high frequency sound which Wall and Dale (1968) had shown to be effective for the extraction of dinoflagellate cysts from sediments. The sediment sample was suspended in filtered seawater in a 250.0 ml plastic beaker, which was then placed in an ultrasonic water bath for 10 to 15 min. After sonication the material was filtered through a 70 µm Nitex mesh screen and the fraction remaining on the screen was observed with a dissecting microscope. After such treatment, smooth eggs of various sizes were readily visible and could be counted. Spiny eggs however tended to be caught-up in fibrous material and were more difficult to recognize. To achieve an accurate count of their numbers was therefore more time consuming.

This protocol was followed to determine the vertical distribution and viability of eggs of *Labidocera aestiva* in the bottom sediments at Station 14 in Buzzards Bay. The results of the preliminary experiments on sonication indicated that egg viability was not altered by the treatment. Four collections were obtained between October 1982 and February 1983. After the eggs were extracted from the sediments, and counted, they were placed in filtered seawater in dishes and incubated at 19 °C. After 4 to 5 d the number of these eggs that hatched was determined. The eggs that did not hatch were chilled at 5 °C for 4 wk, and then warmed at 19 °C. The number of additional eggs that hatched after this treatment was then recorded.

On 16 November 1982 we conducted a survey in Buzzards Bay to identify appropriate sites for further study. The 17 sites that were visited included the 5 which were previously sampled by the SCUBA divers. At each station sediment was collected with a Van Veen grab. After being hauled to the surface, a plastic vial (4.0 cm diameter) was inserted into the surface of the collected material and then capped. In the laboratory the vial was kept frozen for grain size determina-

tion. At the time of analysis, the upper 2.0 cm of sediment in each vial was removed and treated by standard methods (Folk, 1974). At 9 of the stations (1, 2, 5, 6, 10, 11, 15, 16, and 17) a second vial sample was also taken from the grab material. In the laboratory the entire upper 1.0 cm of sediment was suspended in filtered seawater in a dish and incubated and monitored for nauplii as described for Subcore A.

## RESULTS

In the laboratory predation experiments hatching was observed for both subitaneous and diapause eggs that were dissected from fecal pellets as well as those still contained in pellets (Table 1). The proportion of diapause eggs that hatched after ingestion was comparable (all  $\chi^2_{.05} < 3.84$ ) to the hatch of control eggs, however the hatch for ingested subitaneous eggs was significantly (both  $\chi^2_{.05} > 3.84$ ) lower than controls. The pellets obtained from the field collected samples were all approximately 250 µm in width and 500 µm in length, and morphologically similar. They contained as many as 4 eggs. All together 15 eggs were observed and after incubation at 19 °C, 60 % of these hatched. However, each pellet was surrounded by a membrane which apparently prevented the escape of some nauplii. Eventually these individuals died.

Table 1. *Labidocera aestiva*. Percent hatch of ingested eggs dissected from or inside fecal pellets, and uningested control eggs

Experiment no./ Egg type	Number of eggs	Hatch (%)
<b>Subitaneous</b>		
(1) <i>Streblospio benedicti</i>		
Eggs, dissected	20	50
Control	50	80
(2) <i>Capitella</i> Sp. 1		
Eggs, dissected	12	66
Control	89	92
<b>Diapause, pre-chilled</b>		
(3) <i>Streblospio benedicti</i>		
Eggs, dissected	25	84
Eggs in pellets	18	100
Control	94	90
(4) Eggs, dissected	24	87
Control	100	83
(5) <i>Capitella</i> sp. 1		
Eggs, dissected	25	80
Eggs in pellets	14	86
Control	93	90
(6) Eggs, dissected	21	80
Control	100	83

Table 2. Total number of nauplii hatched from each subsample, after incubation of Subcore A at 19°C for 7 d. Numbers in parentheses: water depth in m; dashes: subsample not analyzed

Station and collection date	Core no.	Depth interval (cm)									
		1	2	3	4	5	6	7	8	9	10
Station 3 (15) 10/8/82	1)	73	33	58	40	13	16	26	-	-	-
	2)	98	184	8	7	-	-	-	-	-	-
Station 6 (8) 7/2/82	1)	390	105	132	99	75	45	2	0	0	0
	2)	425	445	-	-	94	37	10	0	0	0
Station 9 (7) 11/16/82	1)	14	14	-	-	-	-	-	-	-	-
	2)	14	29	-	-	-	-	-	-	-	-
Station 12 (17) 11/16/82	1)	46	27	-	-	-	-	-	-	-	-
	2)	81	-	-	-	-	-	-	-	-	-
Station 14 (16) 6/23/82	1)	60	50	28	24	21	-	-	-	-	-
	2)	63	135	158	111	-	140	43	-	-	-
7/ 6/82	1)	57	34	47	40	6	13	0	5	2	0
	2)	23	20	102	-	22	24	15	6	6	0
7/21/82	1)	29	21	11	161	252	194	90	10	48	30
	2)	97	9	11	14	111	28	35	22	7	7
10/20/82	1)	94	175	51	232	68	-	-	-	-	-
	2)	217	307	506	178	73	-	-	-	-	-
11/16/82	1)	124	400	184	319	43	-	-	-	-	-
	2)	62	519	201	269	146	-	-	-	-	-

For the sediment samples collected by diving, viable eggs (indicated by the presence of nauplii) were found at all depths, although not in every core (Table 2). The greatest number did not necessarily occur in the uppermost centimeter of the sediments but often occurred several centimeters below the water-sediment

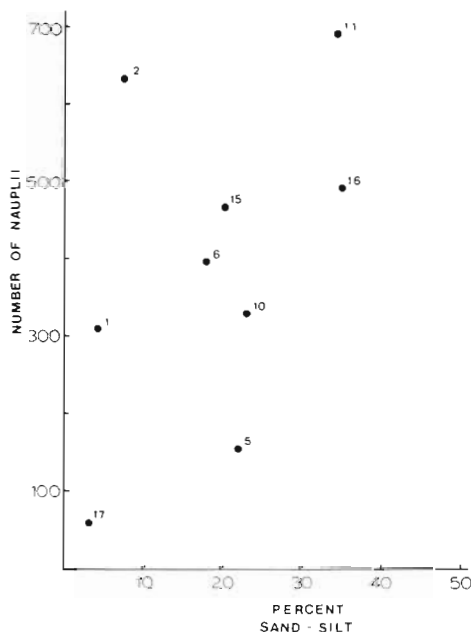


Fig. 2. *Labidocera aestiva*. Scatter diagram of number of nauplii hatched from sediments collected on 16 November 1982 after incubation at 19°C for 1 wk vs percent of total sediment in the 31 > 125 μm size fraction

interface. The number of nauplii that hatched from the incubated sediments varied as much as an order of magnitude for comparable depth strata from different stations and sometimes between cores from the same station. Since these values reflect the laboratory conditions tested in this study, it is probable that incubations at different temperatures and for different periods of time would yield different results. Unfortunately due to time constraints not all subsamples could be analyzed. By rearing nauplii that hatched from some of the subsamples, several species were positively identified, *Labidocera aestiva*, *Centropages hamatus*, *Acartia hudsonica*, *A. tonsa*, and *Eurytemora americana*. For the sediment samples collected with the Van Veen grab on 16 November 1983 a significant correlation between the number of nauplii hatching from incubated sediments and grain size of the sediments was not evident (Fig. 2).

The total number of *Labidocera aestiva* eggs extracted from the sediments collected at Station 14 varied throughout the study period ranging from 58 to 88 (Table 3). The overall mean was  $73.1 \pm 8.9$  and there is no significant difference between the mean values for each collection date (tested by ANOVA,  $F = 0.8$ ). Although a trend towards decreasing numbers for the entire 5.0 cm interval was not evident as time progressed, the proportion of eggs in the uppermost centimeter declined as the season progressed. However, this decrease was complemented by an increased proportion of eggs in the 2.0 cm layer. Little change



Table 3. *Labidocera aestiva*. Proportion of total number of eggs in the B subsample from each 1.0 cm depth interval to 5.0 cm at Station 14

Date	Core no.	Total	Depth layer (cm)				
			1	2	3	4	5
10/20/82	1	81	.66	.17	.11	.06	0
	2*	70	.73	.27	-	-	-
11/16/82	1	58	.59	.19	.14	.07	.01
	2	75	.52	.24	.05	.12	.07
12/22/82	1	88	.44	.32	.11	.11	.01
	2	72	.50	.33	.07	.08	.02
2/ 1/82	1	68	.47	.37	.12	.03	.01
	2	73	.58	.34	.07	0	.01
$\bar{X}$ 73.1 ± 8.9							
* Only based on top 2.0 cm. Subsample from 3 cm was spilled and other subsamples could not be analyzed due to lack of time							

was observed below this level for the period of study. The percent hatch of eggs extracted from the sediments varied (Table 4). For the first 2 collections in October and November, the proportion of eggs that hatched after the initial incubation at 19 °C increased with depth in the sediments. By December and February however, this trend was no longer apparent. Most eggs which did not hatch after the initial incubation at 19 °C did so after being exposed to 5 °C for 4 wk.

### DISCUSSION

Elucidation of factors that influence the temporal and spatial patterns of marine species on both ecological and evolutionary time scales is a fundamental

problem in biological oceanography. For investigators interested in determining the basis of quantitative and qualitative fluctuations in zooplankton communities, it has become increasingly evident that attention must be given not only to features of the pelagic environment, but also the benthic environment. During the last 10 yr it has been shown that the eggs or cysts of many copepods as well as other planktonic organisms (i.e. cladocerans, tintinnids, dinoflagellates) occur in the bottom sediments of coastal regions (Dale and Yentsch, 1978; Onbe, 1978a, b; Paranjape, 1980; Grice and Marcus, 1981; Anderson et al., 1982). Accumulations of these stages on the bottom may represent an important source for the recruitment of individuals into planktonic populations. To evaluate their importance it is necessary to assess the distribution, abundance, and viability of these stages in the sediments and to elucidate the factors which influence these parameters as well as the actual recruitment process of individuals back into the planktonic population.

This paper provides the first evidence that the eggs (especially diapause eggs) of a planktonic marine copepod are resistant to digestion by predators. Such resistance has been demonstrated for diapause eggs of freshwater copepods, cladocerans, and rotifers (Mellors, 1975; Gilbert and Wurdak, 1978; Hairston et al., 1983). Diapause eggs of *Labidocera aestiva* appear to be more resistant to digestion than subitaneous eggs as indicated by the greater mortality of subitaneous eggs after ingestion (Table 1). The capacity to survive after ingestion may be influenced by the feeding and digestive processes of the predator species. The 2 animals tested in this study do not have crushing mouthparts or claws, and thus it is possible that other more powerful predators may be capable of breaking the eggs. Moreover, if material is processed and passes through

Table 4. *Labidocera aestiva*. Number of eggs/subsample for each 1.0 cm depth interval at Station 14. Numbers in parentheses: proportion of these eggs that hatched after initial incubation at 19°C for 4 to 5 d and after chilling at 5 °C and then warmed to 19°C

Date	Core no.	Depth layer (cm)				
		1	2	3	4	5
10/20/82	1	53 (.21/.85)	14 (.62/.77)	9 (.66/.89)	5 (1.00/1.00)	0
	2	51 (.43/.80)	19 (.74/.95)	-	-	-
11/16/82	1	34 (.26/.41)	11 (.10/**)	8 (.62/.88)	4 (.75/1.00)	1 (1.00/1.00)
	2	39 (.23/.92)	18 (.72/**)	4 (1.00/1.00)	9 (.78/.89)	5 (.80/.80)
12/22/82	1	39 (.80/.90)	28 (.68/.93)	10 (.70/.90)	10 (.90/1.00)	1 (1.00/1.00)
	2	36 (.94/.94)	24 (.75/.83)	5 (.80/.80)	6 (.83/.83)	1 (1.00/1.00)
2/ 1/83**	1	32 (.81)	25 (.92)	8 (.75)	2 (1.00)	1 (1.00)
	2	42 (.95)	24 (1.00)	5 (.20)	0	2 (.50)
* Samples evaporated						
** Samples were not chilled						

the gut rapidly the effect of digestive enzymes on the eggs may be minimized.

Under natural conditions in the field, diapause eggs of *Labidocera aestiva* sink to the sea bottom, remain viable, and overwinter in the sediments. Hatching presumably occurs in spring as water temperature rises (Marcus, 1979). Thus diapause eggs may be exposed to benthic predators and microorganisms for several months. The capacity to resist digestion and decay must be highly adaptive and help to ensure the availability of a large pool of eggs for recruitment of nauplii into the planktonic population. Although subitaneous eggs may also sink to the bottom prior to hatching, it is unlikely that they remain viable in the sediments for more than a few days. During this time, resistance to predation would certainly be an adaptive characteristic, but the lack of a hard protective coating for these eggs suggests that certain energetic and developmental constraints of trade-offs may preclude this adaptation. We are currently investigating the resistance of eggs of other species, as well as the effects of other predators to assess the widespread significance of the phenomenon.

In previous studies investigators reported on the distribution and abundance of copepod eggs in the uppermost centimeter of the sediments indicating that this layer contained the greatest numbers of eggs (Kasahara et al., 1974, 1975a; Kasahara and Uye, 1979). These investigators suggested that as the season progressed the decline in the number of eggs occurring in the top layer of the sediment reflected mortality due to predation (Kasahara et al., 1975a; Uye, 1980). Based upon our results I suggest that transport of the eggs to deeper levels in the sediment was the primary mechanism responsible for the decline observed in the uppermost centimeter, and that ingestion by predators actually serves to promote the ultimate recruitment of nauplii from eggs on the sea-bottom.

I contend that the temporal changes in the abundance of eggs of *Labidocera aestiva* observed for the upper 5.0 cm of the sediments (Tables 3 and 4) during winter indicates that the net direction of egg movement is downward. If so, then it follows that eggs occurring deeper in the sediments are older (i.e. were produced earlier in the season) than eggs occurring above them in the sediments. The hatch data (Table 4) support this hypothesis. For the first 2 mo, the proportion of eggs that hatched after the initial incubation at 19 °C increased with depth in the sediments. This pattern reflects the diapause condition of most eggs produced by *L. aestiva* during fall in the Woods Hole region. Diapausing eggs do not hatch immediately, even if conditions are suitable, but rather must first complete a refractory period (Marcus, 1979). The duration of this phase is shortened by exposure to cold

temperatures. Once it is completed, eggs will hatch if conditions are appropriate. I suggest therefore that the eggs which were isolated from the sediments and hatched after the initial incubation at 19 °C had completed their refractory phase. Those that did not were probably produced later in the season and therefore had not yet completed their refractory phase. Eggs that did not hatch initially were still viable however, as evidenced by their subsequent hatching at 19 °C after exposure to 5 °C for 2 to 4 wk in the laboratory. The pattern is not as obvious for the December and February collections since by this time most eggs have completed their refractory phase, regardless of when they were produced. Deviations from the general pattern might also reflect individual differences in the hatching response of eggs, as well as variation in the overall redistribution of the eggs.

The experiments which involved the incubation of sediments collected by divers from several sites in Buzzards Bay (Table 2) demonstrate the existence of very large numbers ( $10^6$  to  $10^7$  m<sup>-2</sup>) of viable copepod eggs throughout the upper 10.0 cm of the sediments, with peak values often occurring below the uppermost centimeter. Similar distribution patterns have been reported for dinoflagellate cysts (Anderson et al., 1982). An important question suggested by these results is whether or not the eggs occurring in the deeper sediment layers still constitute a potential source of individuals for recruitment of nauplii into the planktonic populations. Although our data indicate that the eggs do remain viable, previous studies have reported that eggs do not hatch while buried under sediment (Kasahara et al., 1975b; Landry, 1975; Uye and Fleminger, 1976; Uye et al., 1979; Uye, 1980). If the eggs are an important source of nauplii then presumably they must be deposited at the water-sediment interface or be resuspended into the water column. To gain insight into this problem it is necessary to consider what factors influence the distribution of eggs in the sediments.

The results presented herein and available in the literature suggest the following scenario. After an egg is released into the water column it sinks and may reach the bottom, prior to hatching. Once on the bottom the egg may be resuspended into the water column and transported to a new location. If eggs accumulate in specific regions on the sea bottom then such areas may act as seed beds and provide an important source of nauplii for recruitment into the planktonic population. A similar mechanism has been proposed to account for bloom formation of dinoflagellates (Dale, 1976; Anderson et al., 1982). Dale (1976) reports the occurrence of large numbers of dinoflagellate cysts in muddy sediments and suggests that cysts and fine grain sediment particles accumulate together on the



sea bottom due to similar sedimentary characteristics. Although a significant correlation between the number of nauplii hatching from the incubated sediments and grain size was not evident in this study (Fig. 2), a correlation between the total number of eggs present and grain size may nevertheless exist. The results only represent the number of viable eggs present in the sediments that are induced to hatch by the laboratory incubation. Deviations from a value predicted on the basis of sedimentary characteristics and corresponding grain size might arise if the mortality rate of eggs differs between areas. For example, lower oxygen concentrations are more characteristic of muddy sediments than sandy areas. This difference could lead to a greater mortality of eggs in the fine grained sediments. If such sediments were incubated in the laboratory the number of nauplii that would emerge would be lower than predicted based solely on sedimentary characteristics. Alternatively, since eggs are often sticky (own obs.) they may stick to each other or other particles and accumulate in regions on the sea bottom that reflect the sedimentary characteristics of the aggregated material, and not the individual egg.

Vertical translocation of eggs throughout the sediments may be due to turbulence and particle mixing, resulting from waves, tidal and wind driven currents, and bioturbation. The relative importance of these factors will depend on many parameters such as depth of the water column, composition and binding of the sediments, time of the year, and the presence of benthic animals. Aubrey (1979) reports large (2.0 to 30.0 cm) changes in sand level off the California coast throughout the year for depths less than 10.0 m. On the other hand, in regions such as Long Island Sound or Buzzards Bay at depths less than 10.0 m, only the top 2.0 to 3.0 cm of sediments are typically affected by physical forces (Rhoads, 1974; Aller, 1980). At a depth of 15.0 m only the top 0.5 cm may be affected. Aller (1980) reports that large storms can disturb the sediments at depths greater than 15.0 m, however the effect is reduced if the sediment surface is bound by microbial and algal films (Rhoads, 1974; Rhoads et al., 1977, 1978). Bioturbation may decrease the stability of sediments, making them more susceptible to resuspension (Rhoads and Young, 1970; Yingst and Rhoads, 1978; Rhoads and Boyer, 1982; Grant et al., 1982) and thereby promote the translocation of eggs. In addition, the activities of benthic animals may directly affect the movement of eggs. The upper sediment layers which tend to contain the highest numbers of eggs also contain the greatest densities of potential predators (Mare, 1942; Sanders, 1960; Weiser, 1960; Rhoads, 1974). Many of these animals feed at the water-sediment interface or in the upper few centimeters of the sediment, and deposit their fecal pellets at the sediment

surface. *Capitella* sp. 1 and *Streblospio benedicti* are 2 such species. Since we have shown in this study that eggs remain viable after ingestion by these predators, the deposit of their pellets at the sediment surface places the eggs in an ideal position for subsequent hatching. Eggs transported to deeper strata may be returned to the surface by "conveyor-belt" species (Rhoads and Young, 1970; Rhoads, 1974) which feed at substrate depths as great as 20.0 cm, but deposit their pellets at the surface. Thus, the ingestion of eggs by some benthic animals may actually be critical to the maintenance of planktonic populations since by this process eggs are continually returned to the surface of the sediments where if conditions are appropriate they can hatch and give rise to a new generation.

In shallow coastal waters storm events, current flow, and bioturbation may all interact and influence the translocation and eventual hatching of eggs. Under natural conditions in the field, large bursts of hatching may be the result of widespread resuspension due to major storm events (Landry, 1978). In the absence of such large-scale physical disturbance and in deeper waters bioturbation may be of primary importance. Person-Le Ruyet (1975) reported that bursts of *Acartia clausi* nauplii appeared in laboratory cultures, after the addition of the harpacticoid *Tisbe furcata* to the cultures. Presumably, the harpacticoid stirred up the sediment on the bottom of the culture dishes which promoted hatching of the *A. clausi* eggs. These results demonstrate that turbulence due to bioturbation alone is sufficient to promote hatching. Bioturbation may provide a mechanism for the continuous turnover of sediments and thereby the gradual release of individuals from the sea-bottom as suggested by Dale and Yentsch (1978) and Tyler et al. (1982) to account for the appearance of red tide in coastal areas. Since the erodibility of sediments may differ between sites due to differences in the distribution of deposit-feeders (Rhoads et al., 1978), resuspension events should also be localized thereby providing a mechanism for the differential release of eggs from the sediments.

It is clear that numerous factors may influence the distribution, abundance, and viability of eggs on the sea bottom. Gaining insight into the temporal and spatial hatching patterns of these eggs requires an understanding of such factors and how they interact. Such information will shed light on regulation of recruitment patterns, population dynamics and fluctuations in the composition of planktonic communities.

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#### LITERATURE CITED

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