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How important are starvation periods in early larval development for survival of *Crangon septemspinosa* larvae?

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ABSTRACT: Laboratory experiments on newly hatched larvae of the sand shrimp *Crangon septemspinosa* were conducted to study larval vulnerability to food deprivation. Larvae subjected to 6 different feeding regimes were well adapted to temporary lack of food, dependent on time and duration of starvation periods. Critical periods for larval development were the first 24 h after hatching, stage III and, to a lesser extent, metamorphosis. Food deprivation during the first 7 d resulted in a prolongation of stage I and more so stage II. After this period, larvae in the starvation treatments tended to reduce the duration of subsequent larval stages. Number of molts prior to metamorphosis ranged from 4 to 7 and were fewest in larvae fed every day. A majority (57.9 %) of the larvae reached the juvenile stage after 5 molts. Neither the duration of larval development nor the size of the juveniles obtained from the various treatments showed significant differences. The possible importance of starvation as a recruitment regulatory process for *C. septemspinosa* is discussed in terms of food availability during the major hatching period in Chesapeake Bay and adjacent waters.

INTRODUCTION

Large annual fluctuations in commercial fishery landings have been well documented for many marine species including crustaceans (for recent reviews on marine invertebrate fishery management see e.g. Caddy 1989). Although recruitment regulatory processes are not yet fully understood, variable growth and mortality in the larval phase influences recruitment success for most marine species with planktivorous larvae. Key factors for larval survival are predation, starvation or limited food resources, and oceanographic conditions that may advect larvae into unfavorable environments. However, 2 determinants of early life mortality – starvation and predation – are closely linked by growth and development processes (Bailey & Houde 1989).

Crustacean larvae are highly sensitive to starvation (for review see Olson & Olson 1989), and effects of food deprivation on decapod larvae have been studied in a number of species (for review see McConaugha 1985). In general, lack of suitable food in the early development of planktotrophic decapod larvae increases mortality, prolongs duration of larval development (e.g. Anger & Dawirs 1981, Anger et al. 1981, Dawirs 1984), and reduces the ability of the larvae to successfully capture prey (Paul & Paul 1980). In addition, food deprivation alters the ultrastructure of the hepatopancreas; this may result in an irreversible change of its original structure and consequently in a loss of the capability to absorb and store lipids in the hepatopancreas (Storch & Anger 1983, Anger et al. 1985). The interaction between starvation periods and molt cycle in zoea I larvae has been investigated in a variety of decapod larvae (Anger 1987). Starvation periods also influence morphogenesis (McConaugha 1985), e.g. the thickness of the epidermis (Anger 1984), phototactic responses and swimming behavior (Cronin & Forward 1980, Shirley & Shirley 1988), as well as respiration and biomass of decapod larvae (Dawirs 1983, Anger 1986). However, it should be stressed that the overwhelming majority of the above-mentioned studies were carried out with brachyuran larvae, and little is known about the vulnerability of caridean larvae to food deprivation.

The sand shrimp *Crangon septemspinosa* plays an important role in food energy transfer in tidal marsh-estuarine ecosystems such as the Chesapeake Bay (Price 1962, Haefner 1979, Modlin 1980). Larvae can be found year-round in the plankton of the Chesapeake Bay and adjacent waters, with maximum production

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between January and June (Sandifer 1973, Wehrtmann 1990). The winter hatching period generally coincides with times of reduced total biomass (see Baird & Ulanowicz 1989). Consequently, it is possible that larvae encounter starvation periods shortly after hatching. In contrast to other Crangonidae such as *C. crangon* and *C. allmanni* (Dalley 1980, Gurney 1982, Criales & Anger 1986), larval development in *C. septemspinosa* under controlled conditions in the laboratory is poorly documented (Tesmer & Broad 1964). The purpose of the study was to evaluate the effects and significance of food deprivation on development in the early larval phase of *C. septemspinosa*.

MATERIAL AND METHODS

Ovigerous females of *Crangon septemspinosa* were dredged between January and March 1989 in the lower Chesapeake Bay, USA, in standardized 1 min dredge tows using a commercial crab dredge, 1.83 m at the mouth, with a wire mesh lining of 12.5 mm on the side. The shrimps were brought to the Chesapeake Biological Laboratory in Solomons, Maryland (USA), and kept in a flow-through seawater tank until the embryos were in an advanced developmental stage. Then, females were transferred to an aerated 5 l aquarium (15 to 18° C and ca 20 ‰) and starved until larvae hatched.

Larvae were reared individually in 20 ml glass vials with filtered seawater (1 µm) at constant temperature (18° C), salinity (20 ‰), and a 12:12 L:D photoperiod. Larvae were fed on a mixture of newly hatched *Artemia* sp. (ca 10 nauplii ml^{-1}) and *Brachionus plicatilis* (ca 100 ml^{-1}) cultured on *Chlorella* sp. The experiments were checked every 22 to 24 h for surviving larvae and exuviae; larvae were considered dead when opaque and/or when no movements of any external or internal structure could be detected. Larvae were transferred to a clean vial with filtered seawater and then fed according to the daily feeding schedule. Larvae to be switched from a feeding to a starvation regime were washed in filtered seawater before being placed into a new vial to avoid accidental transfer of food organisms.

Based on the assumption that continuous absence of food (longer than 2 consecutive days) is not likely to occur in an estuarine environment such as the waters adjacent to the Chesapeake Bay (see Baird & Ulanowicz 1989), 6 different feeding regimes were tested (Fig. 1). Larvae in the 'Control' were fed every day while larvae in the 'Starvation Control' were starved during the whole experiment. The number of days of starvation within the other treatments during the initial 7 d (indicated by the number in the treatment label) varied from 2 ('Nofood 2d') to 5 d ('Nofood 5d'). Except for the Starvation Control, all larvae were fed the same after Day 7. Larvae for the Control, Nofood 3d, Nofood 2d and Nofood 5d hatched on 19 January 1989 from a single female, and larvae for the Starvation Control and Nofood 4d originated from one batch each on 22 January and 15 March 1989, respectively. Each treatment originally contained 50 newly hatched larvae, and experiments were terminated when all larvae metamorphosed or died. Juvenile size was measured from the tip of the rostrum to the end of the telson using an ocular micrometer in a stereomicroscope.

Mean values for development time are given as arithmetic means and standard error and 95 % confidence interval. Differences between mean values were tested by means of Student's *t* statistics and considered statistically significant when $p \leq 0.05$.

To compare survival rates within the different feeding conditions and larval stages, 50 larvae in each treatment were randomly split into 5 groups and statistically treated as replicates. After arcsine transformation (Sokal & Rohlf 1987) percent survival in replicate groups was analyzed by ANOVA. Scheffe multiple range tests (Lehmann 1986) on 95 % confidence intervals were applied to analyze the means. Those values were re-transformed to percentages.

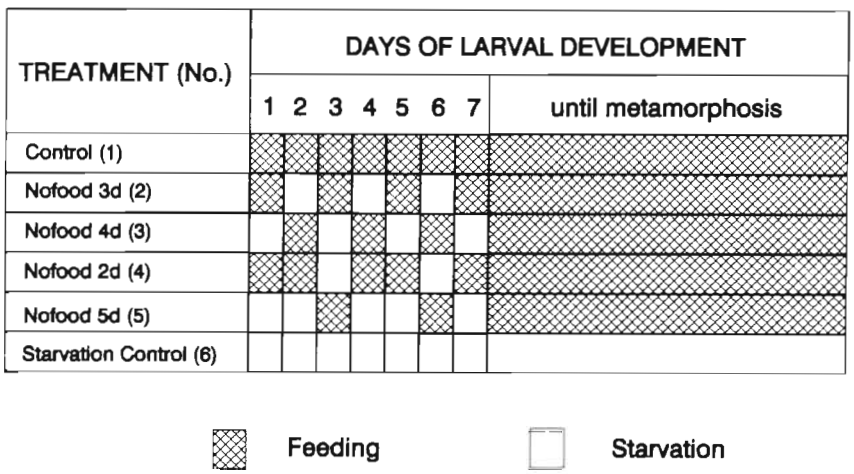

Fig. 1. Feeding regimes for *Crangon septemspinosa* larvae within the 6 different treatments. The number in the treatment labels indicates the number of starvation days; for further explanation see 'Material & Methods'

RESULTS

General survival

Most larvae (85.7 %) survived either stage I (39.7 %) or stage II (60.3 %) by Day 5, and no statistically significant differences ($p > 0.05$) in survival rates for the first 5 d were detected among the treatments (Fig. 2). Thereafter, a sharp decline in survival was observed in Nofood 4d, Nofood 5d, and Starvation Control (Fig. 2). At the end of the experiment, survival rates in Nofood 4d, Nofood 5d and Starvation Control were significantly less (Scheffe grouping B, Table 1) than in the other food level groups (Scheffe grouping A, Table 1).

Complete larval development

Completion of larval development was greatest in the Control (44 %), followed by Nofood 3d (38 %) and Nofood 2d (28 %). In Nofood 5d, 2 larvae molted successfully to the second stage, and 1 larva metamorphosed after 23 d. In the Starvation Control 2 larvae reached stage II; however, all were dead by Day 7.

The number of larval stages prior to metamorphosis varied between 4 and 7 with the feeding regime (Table 2). Most larvae from all treatments (57.9 %) reached the juvenile stage after 5 molts. Larvae fed every day reached metamorphosis in the fewest number of molts.

The mean duration of larval development until metamorphosis in the different feeding regimes is shown in Table 3. Larval development in Nofood 4d (No. 3) was significantly longer compared to the other treatments. Lack of food after 1 or 2 d of initial feeding (Nofood 3d and Nofood 2d, respectively) also resulted in a prolongation of larval development; however, the differences compared to the Control (mean duration = 18.2 d) were not statistically significant ($p > 0.05$).

Table 1. *Crangon septemspinosa*. Summary of survival rate statistics of larvae in 6 different feeding regimes. The same letters in the grouping by the Scheffe multiple range test indicate no significant differences ($p > 0.05$) between feeding regimes (for further details regarding the statistical procedure see 'Material & Methods')

Treatment (No.)	Mean survival (%)	± SE	Scheffe grouping
Control (1)	43.6	0.61	A
Nofood 3d (2)	35.9	0.07	A
Nofood 2d (4)	25.2	0.38	A
Nofood 4d (3)	3.7	0.62	B
Nofood 5d (5)	0.4	0.41	B
Starvation Control (6)	0.0	0.00	B

Table 2. *Crangon septemspinosa*. Frequency distribution of the number of stages required to reach metamorphosis by larvae. Percentages in each treatment add up to 100 % representing the total number of juveniles obtained in the feeding regime; results from the Starvation Control are excluded, because all larvae died before reaching metamorphosis

Treatment (No.)	No. of stages prior to metamorphosis							
	4		5		6		7	
	%	n	%	n	%	n	%	n
Control (1)	31.8	7	63.6	14	4.6	1	00.0	0
Nofood 3d (2)	11.1	2	61.1	11	11.1	2	16.7	3
Nofood 2d (4)	15.4	2	53.8	7	23.1	3	7.7	1
Nofood 4d (3)	00.0	0	00.0	0	33.3	1	66.7	2
Nofood 5d (5)	00.0	0	100.0	1				

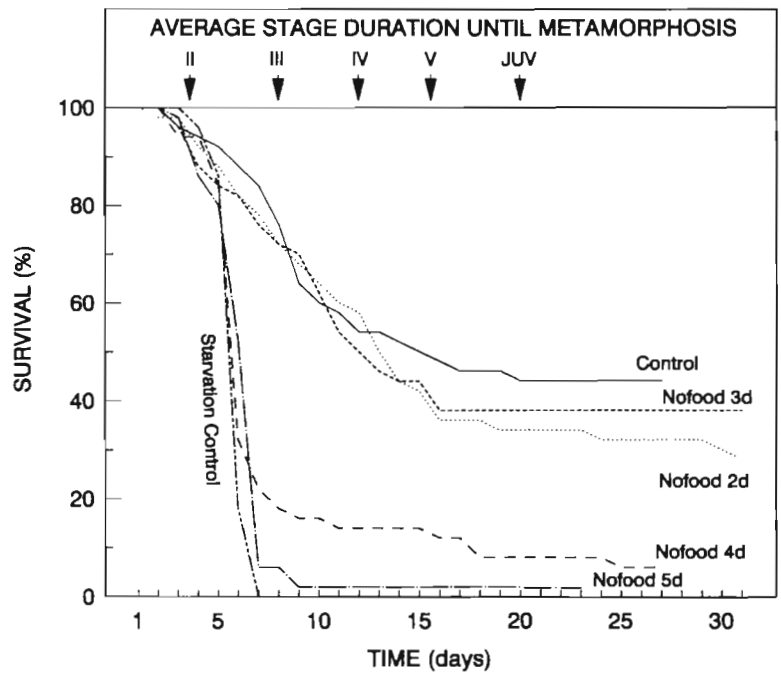

Fig. 2. *Crangon septemspinosa*. Percent survival of larvae within the 6 different feeding regimes during the course of the experiment. Arrows indicate commencing stages; the values base on stage-specific means of developmental time for all larvae regardless of feeding regime. Since the majority of the larvae reached metamorphosis after 5 molts, only these stages are indicated by arrows

Larval stage specific duration and survival

Larval stage duration related to feeding regime is presented in Table 4. Starvation periods during the first 7 d mostly affected the duration of stage I and II. Lack of food during one of the first 2 d after hatching (Nofood 3d and Nofood 4d) caused a statistically significant ($p < 0.05$) prolongation of stage I (3.69 and 4.86 d, respectively) compared to the Control (3.19 d). Any food deprivation resulted in a significant delay in development of stage II. Although not statistically significant ($p > 0.05$), there was a tendency for survivors of stage II that had undergone days of starvation to shorten the duration of the subsequent larval stages compared to the Control (Table 4).

Survival within larval stages generally decreased from stage I to stage III (Table 5). Although lowest survival was observed in Nofood 2d, Nofood 3d and Control during the third larval stage, there were no statistically significant differences in stage-specific survival (ANOVA; $p > 0.05$) among treatments (Table 5).

Size of juveniles

Juveniles from the different feeding regimes did not differ significantly in size ($p > 0.05$). The mean size of juveniles ranged from 4.0 mm (Control and Nofood 5d) to 4.3 mm (Nofood 4d). The largest juvenile measured 5.0 mm (Nofood 3d) while the smallest was 3.3 mm (Control). The size of the juveniles increased with the number of larval stages prior to metamorphosis, although differences were not statistically significant ($p > 0.05$).

DISCUSSION

This study was designed to evaluate the general vulnerability of *Crangon septemspinosa* larvae to starvation and does not allow any conclusions concerning critical prey concentration or food quality. The experimental methods suffer from potentially serious artifacts, e.g. the absence of predators and unnaturally high temporal variation in food. Although the rearing methods that were applied may not have facilitated maximum growth and survival (for discussion of container effects see Swanberg et al. 1990), these culture techniques (food and container size) are commonly used in similar experiments with decapod larvae (Anger & Dawirs 1981, Criales & Anger 1986, Harms & Seeger 1989). Despite the limitations of laboratory rearing experiments (see Olson & Olson 1989), the present results do provide some indications of the potential importance of food limitation for the larval development of *C. septemspinosa*.

Feeding during the first 24 h after hatching is important for further survival and development. Comparing results between Nofood 3d (No. 2) and Nofood 4d (No. 3) emphasizes the importance of the initial first feeding period (Fig. 2), although larvae in these treatments were subjected to different starvation periods (3 versus 4 d). These findings confirm previous observations on brachyuran larvae (e.g. Anger & Dawirs 1981, Anger et al. 1981, Dawirs 1983, 1984, Anger 1987).

Table 3. Mean duration ($\bar{x}$), standard error ($\pm$), extremes and sample size of larval development in days within the different feeding regimes; the results of the Starvation Control are excluded, because all larvae died before completion of larval development

Treatment (No.)	Mean duration		Extremes		Sample size
	$\bar{x}$	$\pm$	Min.	Max	n
Control (1)	18.2	0.64	14	27	22
Nofood 3d (2)	21.1	1.10	16	31	18
Nofood 2d (4)	21.9	1.20	16	31	13
Nofood 5d (5)	23.0	0.00			1
Nofood 4d (3)	26.7	0.33	26	27	3

Table 4. *Crangon septemspinosa*. Larval stages: mean duration ($\bar{x}$), standard error ($\pm$) in days and sample size (n) within feeding regimes

Stage	Treatment (No.)																	
	Control (1)			Nofood 3d (2)			Nofood 4d (3)			Nofood 3d (4)			Nofood 5d (5)			Starvation Control (6)		
	$\bar{x}$	$\pm$	n	$\bar{x}$	$\pm$	n	$\bar{x}$	$\pm$	n	$\bar{x}$	$\pm$	n	$\bar{x}$	$\pm$	n	$\bar{x}$	$\pm$	n
I	3.19	0.06	47	3.69	0.07	42	4.86	0.14	22	3.41	0.07	46	6.50	1.50	2	3.50	0.50	2
II	3.74	0.13	38	4.72	0.16	32	6.71	0.29	7	5.13	0.18	32	4.00		1			
III	3.68	0.17	28	3.82	0.16	22	3.40	0.51	5	4.10	0.27	21	3.00		1			
IV	3.81	0.25	26	3.26	0.18	19	2.75	0.48	4	3.72	0.28	18	3.00		1			
V	3.80	0.20	15	3.56	0.18	16	3.25	0.25	4	4.21	0.28	14	4.00		1			
VI	5.00		1	3.60	0.25	5	3.00	0.41	4	4.50	0.29	4						
VII				3.67	0.33	3	4.00	0.00		4.00		1						

Table 5. *Crangon septemspinosa*. Cumulative survival (mean percent ± standard error) within the first 5 larval stages for the different feeding regimes; n: number of larvae within the treatments that completed stage V

Treatment (No.)	Mean survival within stages (%) ± SE					n
	I	II	III	IV	V	
Control (1)	96.3 (2.45)	84.7 (5.61)	74.2 (3.32)	98.9 (4.32)	92.6 (13.55)	15
Nofood 3d (2)	87.2 (3.97)	77.7 (1.70)	71.8 (3.64)	95.4 (7.05)	98.9 (4.32)	16
Nofood 4d (3)	41.5 (6.61)	24.7 (11.59)	84.6 (20.47)	96.2 (19.49)	100	1
Nofood 2d (4)	96.6 (5.21)	67.1 (0.15)	67.9 (3.32)	89.5 (7.60)	98.2 (7.32)	14
Nofood 5d (5)	1.7 (2.45)	45.0 (45.00)	100	100	100	1
Starvation Control (6)	1.7 (2.45)	00.0				0

The importance of the initial feeding directly after hatching may partly explain the predominance of stage I decapod larvae in surface waters (e.g. Dittel & Epifanio 1982, Lindley 1986, Wehrtmann 1986). It is likely that newly hatched larvae immediately seek food which generally is more abundant in the upper water column than in the bottom area except, perhaps, in shallow areas. Although behavioral responses of larval decapod crustaceans to light are complex and variable (Forward & Buswell 1989), results on phototaxis and swimming behavior of early stage *Rhithropanopeus harrisii* larvae (Cronin & Forward 1980) showed increased positive phototaxis with increased starvation and in some cases reduced negative phototaxis. However, the effects of starvation on phototaxis are likely to be species-specific, and behavioral responses of larval *Crangon septemspinosa* to light are unknown.

Other critical periods in larval development of *Crangon septemspinosa* are stage III and metamorphosis (Table 4). Studies on stomach and mandible development indicate a change in feeding behavior commencing with stage III (Regnault 1972). This critical period coincides also with the onset of considerable morphological variability in larval *Crangon* spp. (Criales & Anger 1986). A similar pattern of reduced survival at these stages has also been documented for other crangonid (Regnault & Costlow 1970, Regnault 1971, Criales & Anger 1986) and palaemonid larvae (Reeve 1969, Wickins 1972a, b). For *C. septemspinosa*, these increased mortalities coincide with drastic changes in amino acid composition probably due to increased metabolic activities (Regnault 1971).

Larvae of *Crangon septemspinosa* showed relatively high survival rates during the first 4 to 6 d regardless of the feeding condition. A similar trend has been observed in different anomuran and brachyuran zoeae (Sulkin 1975, Anger & Dawirs 1981, Harms & Seeger 1989) and megalopae (Farrelly & Sulkin 1988). However, Anger et al. (1981) detected relatively high initial mortality in brachyuran larvae subjected to food deprivation, and they related it to low viability of individual larvae. The energy reserves necessary to maintain larval metabolism are stored in the form of lipids in the hepatopancreas, mainly in the R-cells (Storch & Anger 1983, Anger et al. 1985). Even re-feeding after a starvation period immediately after hatching cannot re-establish the ultrastructure of the R-cells (Storch & Anger 1983). The utilization of energy reserves in the hepatopancreas cells may explain the initial high survival of *C. septemspinosa* under all feeding conditions. However, the depletion of these energy sources and the irreversible change in the ultrastructure of the R-cells may be responsible for the drastic increase in mortality within Nofood 4d, Nofood 5d, and Starvation Control (Fig. 2).

Some newly hatched larvae of *Crangon septemspinosa* were still able to molt despite food deprivation commencing immediately after hatching. Several studies with different species (Anger et al. 1981, Dawirs 1984, Harms & Seeger 1989) confirm the necessity for brachyuran and anomuran larvae to feed immediately after hatching in order to start the molt cycle. The 2 molting larvae in the Starvation Control and the metamorphosis of 1 larva after an initial 2 d starvation period indicate that newly hatched *C. septemspinosa* larvae apparently have the potential to begin molting even without any external energy supply. This finding compares favorably with results reported for starved *Palaemonetes pugio* (Broad 1957) and *Pandalus borealis* (Stickney & Perkins 1981) larvae. However, *C. nigricauda* larvae die within 4 d at stage I if no food is ingested (Villamar & Brusca 1987). Further studies should be carried out to determine if *C. septemspinosa* larvae generally hatch with sufficient internal energy resources to molt to the second stage without an external food supply.

Starvation periods in early development increased the number of molts prior to metamorphosis (Table 2). In contrast to Lebour (1931), who proposed a 5-stage development for crangonid shrimp larvae, variability in both larval forms and pathways of larval development of different *Crangon* species has been well documented (Criales & Anger 1986, Villamar & Brusca 1988). Variations in instar number in larval *Palaemonetes* sp. (Broad 1957, Knowlton 1974), *Palaemon serratus* (Reeve 1969) and *Callinectes sapidus* (Sulkin 1978) have been related to diet. Criales & Anger (1986) stated that malnutrition in *C. crangon* and *C. allmanni* is apparently a condition affecting morphogenesis; the results of the present study strongly support this. However, based on the

present results, it should be noted that an increase in the number of larval stages before metamorphosis does not necessarily lead to a significant prolongation of the larval planktonic period (Table 3) or to a significant size-difference in the resulting juveniles.

Starvation periods in early development resulted in a prolongation of stage I and II (Table 4). The lengthening of these stages can be viewed as an additional period necessary to accumulate enough reserves to molt successfully to the next instar. This interpretation is supported by studies conducted with brachyuran larvae under starvation conditions (Anger & Dawirs 1981, Anger et al. 1981). After reaching the second instar, however, early starved larvae tended to shorten the duration of the subsequent stages (Table 4). Similar results were obtained for 2 species of brachyurans (Anger & Dawirs 1981, McConaugha 1982). The underlying processes of partial compensation in development rate after an early period of unfavorable conditions are not yet understood. Therefore, further studies should focus on possible cues responsible for this ecologically important regulatory mechanism.

The prolongation of the development time of the first 2 larval stages under the effect of starvation (Table 4) may be important to the recruitment process: since the early stages of small individuals tend to be most vulnerable to predation (Bailey 1984, Morgan 1987, 1990), a lengthening of the initial planktonic phase may result in a higher cumulative mortality rate at the end of the larval period. In addition, starvation diminishes the swimming ability of decapod larvae (Cronin & Forward 1980, Shirley & Shirley 1988) and thus reduces the larval ability to escape and survive attacks of planktivorous predators. However, an interpretation of the results presented in Table 4 with regard to possible mortality rates in the field is critical because the larval rearing in the laboratory was conducted in the absence of predators.

Crangon septemspinosa larvae proved to be well adapted to food shortage in a 'patchy' environment produced by the study design. The findings regarding survival and developmental rate in Nofood 3d clearly demonstrate that even a 24 h starvation period after initial feeding does not result in mass mortality. In addition, major hatching activities of *C. septemspinosa* in the Chesapeake Bay and adjacent waters take place from March to June (Sandifer 1973, Butt 1986, Wehrtmann 1990) coinciding with the spring phytoplankton bloom (Marshall 1980, Marshall & Cohn 1983, Marshall & Lacouture 1986) and a general rise in biological activity (Baird & Ulanowicz 1989). Thus, larvae have the opportunity to graze at least on phytoplankton, a suitable food for *Crangon* larvae (Villamar & Brusca 1987). Tidally induced phytoplankton patchiness in the estuarine environment has been documented for the Middle Atlantic Bight (Dustan & Pinckney 1989), and such periodic aggregations may locally improve the larval feeding conditions. Therefore, it is likely that newly hatched *C. septemspinosa* larvae may be able to encounter sufficient food to support further development. However, starvation may have significant impact on survival rates when hatching larvae are transported into offshore areas with unfavorable conditions (e.g. concerning temperature regime and food quantity).

To clarify the importance of starvation for *Crangon septemspinosa* larvae as a recruitment regulatory process, information regarding natural prey, spatio-temporal occurrence of these prey taxa and critical prey concentrations required for daily maintenance of the larvae are needed. Furthermore, knowledge about interactions between sand shrimp larvae and their potential predators, for example bay anchovy *Anchoa mitchilli*, would help to understand recruitment variability.

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