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VERTICAL DISTRIBUTION AND DIEL MIGRATION OF *CRANGON SEPTEMSPINOSA* SAY, 1818 (DECAPODA, CARIDEA) ON GEORGES BANK, NORTHWEST ATLANTIC

BY

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ABSTRACT

We sampled for vertical distribution and possible diel vertical migration (DVM) of *Crangon septemspinosa* Say, 1818 on and around Georges Bank, Northwest Atlantic, between 1995 and 1999. Both juveniles and adults were found to undergo DVM, being distributed within the lower water column (and perhaps on or in the bottom) during the day, and distributed throughout the water column at night, with higher abundances seen in all depth strata at night. Differences in vertical distribution were also found based on location and chlorophyll concentration for juveniles, but no effects were seen of season, salinity, temperature, lunar periodicity, year, or copepod prey for either juveniles or adults. Variation in vertical distribution and DVM were only moderately well explained (50% of the total variance) by the above factors, suggesting that some other factor(s) not measured by us (e.g., predation) were potentially also controlling the vertical distribution and diel migration of *C. septemspinosa* on Georges Bank.

RÉSUMÉ

Nous avons échantillonné *Crangon septemspinosa* Say, 1818 sur et autour de Georges Bank, Atlantique nord-ouest, entre 1995 et 1999 pour sa distribution verticale et ses possibles migrations verticales journalières (DVM). Juvéniles et adultes ont présenté des DVM, étant distribués dans la colonne d'eau basse (et peut être sur ou dans le fond) durant la journée, et distribués à travers toute la colonne la nuit, avec de plus fortes abondances trouvées dans toutes les strates verticales pendant la nuit. Chez les juvéniles des différences de distribution verticale ont aussi été trouvées en relation avec la localisation et la concentration en chlorophylle, mais aucun effet n'a été trouvé pour la saison, la salinité, la température, le cycle lunaire ou les proies de copépodes aussi bien pour les juvéniles que pour les adultes. Les variations de distribution verticale et de DVM ont été seulement modérément expliquées (50% de la variance totale) par les facteurs précités, suggérant que d'autre(s) facteur(s) non mesurés (e.g., prédation) pourraient aussi contrôler la distribution verticale et la migration diurne de *C. septemspinosa* sur Georges Bank.

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INTRODUCTION

Crangon septemspinosa Say, 1818 (sand shrimp) is commonly found in estuaries of the northwestern Atlantic Ocean and is distributed from the Gulf of St. Lawrence, Canada to the east coast of Florida, U.S.A. (Price, 1962). *C. septemspinosa* utilize seagrass beds (Heck et al., 1989), mussel farms and non-vegetated sandy substrates as habitat (Clynick et al., 2008). Whiteley (1948) and Brown et al. (2005) found *C. septemspinosa* in the water column above Georges Bank, but rarely outside the 100 m isobath (although Brown et al. (2005) found adults up to 500 m depth). Thus, while *C. septemspinosa* are often thought of as bottom dwellers, they are not confined to the benthos.

C. septemspinosa is a primarily nocturnal, carnivorous predator, but at times, can be omnivorous. Stomach contents have been found to contain primarily crustaceans (e.g., copepods and amphipods), but also plant material and polychaetes (Wilcox & Jeffries, 1974). *Neomysis americana* (Smith, 1873) has been found to be a large part of their diet (Price, 1962), as have post-larval blue crab (Olmi & Lipcius, 1991), post-settlement winter flounder (*Pseudopleuronectes americanus* (Walbaum, 1792)) (Taylor, 2005), and winter flounder eggs (Taylor & Danila, 2005). Wilcox & Jeffries (1974) found that the majority of *C. septemspinosa* feeding was done at night, with onset initiated by darkness and peaking around midnight and dawn. *C. septemspinosa* are in turn fed on by black crowned night heron (*Nictocorax nictocorax* (Linnaeus, 1758)) (Hall & Kress, 2008), Atlantic tomcod (*Microgadus tomcod* (Walbaum, 1792)), grubby (*Myoxocephalus aenaeus* (Mitchill, 1814)) (Joseph et al., 2006), skates and rays (Rajiformes) (Price, 1962).

C. septemspinosa is able to tolerate a broad range of salinities and temperatures. Adults have been caught at salinities ranging from 2 to 32‰ (Locke et al., 2005), though adults were not able to osmoregulate when the salinity was raised to 45‰ in laboratory testing (Haefner, 1969a). Adults have been caught in temperatures ranging from 0 to 28°C (Price, 1962; Locke et al., 2005). Grabe (2003) found that densities of shrimp were greatest at temperatures above 16°C, though Modlin (1980) stated that they disappear from the Mystic River Estuary (Connecticut, U.S.A.) when temperatures exceeded 20°C and returned when temperatures dropped back below 20°C.

Previous studies have shown the abundance of *C. septemspinosa* in the water column to be greater at night than during the daytime (Heck et al., 1989; Joseph et al., 2006) and that activity was also higher at night, with two peaks — during initial onset of darkness and during dawn (Taylor & Peck, 2004). Several studies have examined the abundance and distribution of *C. septemspinosa* in bays and estuaries (e.g., Price, 1962; Haefner, 1976; Modlin, 1980; Corey, 1981; Grabe, 2003), but few observations have been made of this species offshore (Whiteley, 1948; Brown et al., 2005). Brown et al. (2005) looked at the abundance and broad-scale distribution of *C. septemspinosa* on Georges Bank and found higher abundances on the crest of the Bank than in the deeper, off-bank regions. Whitely (1948) stated that *C. septemspinosa* were more often caught in the deeper water stratum than at the surface.

The pattern of organisms being found near the surface at night, but at depth during the day, is typically referred to as diel vertical migration and is often thought to be a predator avoidance strategy (Bollens & Frost, 1989; Hays, 2003; Bollens et al., 2011), although abiotic factors can also play a role. Lougee et al. (2002) found a changing pattern of vertical distribution and migration in zooplankton with respect to halocline depth. In addition, temperature (Saborowski et al., 2000) and ultraviolet radiation (Speekmann et al., 2000; Williamson et al., 2011) may play a role in vertical distribution and migration patterns of zooplankton. However, no previous studies have explicitly examined the vertical distribution and possible diel migration of *C. septemspinosa* in the water column. Thus the goal of this study is to examine the diel vertical distribution (and possible migration) of *C. septemspinosa* juveniles and adults on Georges Bank in relation to bottom depth, season, temperature, salinity, chlorophyll and copepods (prey species) and lunar periodicity over a period of five years (1995-1999).

MATERIAL AND METHODS

Study area

Georges Bank (40°30′N 66°W-42°N 69°W) is a submarine bank located between Cape Cod, Massachusetts and Cape Sable, Nova Scotia in the northwestern Atlantic Ocean. The Bank is one of the most productive seamount ecosystems in the world (Cohen & Grosslein, 1987) and home to important commercial fisheries (Bigelow, 1926). The Bank is geographically defined by the 200 m isobath and is approximately 150 km wide by 280 km long (fig. 1). Shoals at the peak of the Bank can be as shallow as 30 m. An anti-cyclonic gyre is the dominant circulation pattern around the Bank (Limeburner & Beardsley, 1996). The substrate on the Bank is a mix of sand and gravel of glacial origin (Lough et al., 1989). The Bank can be divided into four physical regions based on hydrodynamics: the northern flank (50-200 m), the Bank crest (⩽60 m), the shallower southern flank (60-150 m), and the deeper southern flank (>150 m) (Butman & Beardsley, 1987). Upper Slope Water/Gulf Stream Water maintains a relatively constant flow through the Northeast Channel below 100 m (Ramp et al., 1985).

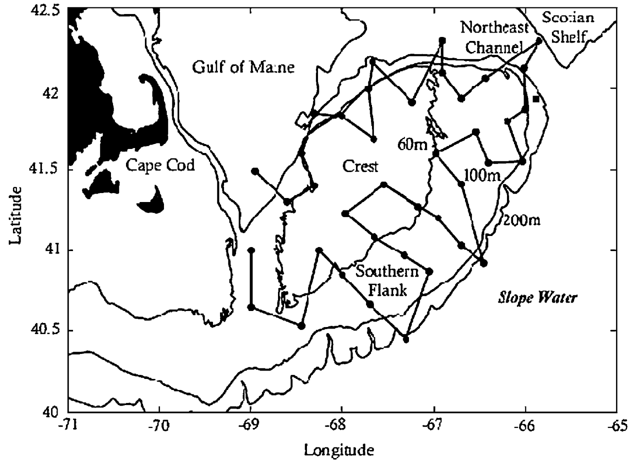

Fig. 1. Bathymetry (60, 100 and 200 m), cruise track, station locations (filled dots) and regions of note for the GLOBEC Georges Bank Broad Scale Survey Cruises (1995-1999).

Sampling methodology

The Georges Bank region was sampled monthly during February-July 1995 and January-June 1996-1999 as part of the GLOBEC Georges Bank broad scale survey cruises. The cruise track consisted of ca. 40 sampling stations (fig. 1). Sampling was undertaken at as many stations as possible on each cruise, allowing for problems with equipment and weather (table I). The Global Ocean Ecosystems Dynamics (GLOBEC) Northwest Atlantic/Georges Bank Study was designed to investigate the biological and physical oceanographic processes that affect four target species, *Calanus finmarchicus* (Gunnerus, 1770), *Pseudocalanus* spp., *Gadus morhua* Linnaeus, 1758 (cod) larvae and *Melanogrammus aeglefinus* (Linnaeus, 1758) (haddock) larvae on the Bank (GLOBEC, 1992). As part of the GLOBEC Georges Bank broad scale survey cruises, macrozooplankton and micronekton were sampled in January-June 1995-1999. This program was designed to target larval/juvenile fishes and the predators of the GLOBEC target species, such that many thousands of *Crangon septemspinosa* were collected in the net samples. These individuals are the focus of this paper.

A 10 m^2 Multiple Opening/Closing Net and Environmental Sampling System (MOC10) (Wiebe et al., 1985) was used to sample macrozooplankton and micronekton. The MOC10 consists of a 10 m^2 frame with five 3 mm mesh nets. The MOC10 allows for sampling discrete depth strata by remotely opening and closing the nets from the ship. The MOC10 was towed in a double oblique manner (1 net down, $\leqslant$4 nets up) with a goal of sampling 5000 m^3 of water per net. The MOC10 was lowered to 700 m depth, or within 10 m of the bottom, whichever was less, and the nets were opened and closed at predetermined depths (nominally 100, 40,

TABLE I
Dates of GLOBEC Broad Scale Survey Cruises with number of stations sampled with the MOC10

Date of cruise	Number of stations sampled
1995	
10-20 February	5
13-24 March	3
11-22 April	6
9-18 May	16
5-15 June	23
10-20 July	27
1996	
10-22 January	2
13-25 February	9
11-22 March	12
8-20 April	5
6-17 May	12
3-13 June	38
1997	
13-20 January	8
11-23 February	8
16-28 March	13
22 April-2 May	14
19-28 May	20
18-28 June	32
1998	
7-19 January	16
7-17 February	13
15-27 March	13
15-27 April	20
11-23 May	21
16-26 June	32
1999	
11-24 January	15
11-23 February	11
10-23 March	1
16-28 April	19
19-27 May	19
14-24 June	32

15 and 0 m) during the ascent of the tow with a winch speed of approx. 5 m/min. The MOC10 was also equipped with conductivity, temperature and depth (CTD) sensors (see http://globec.whoi.edu/globec_program.html). The timing of the tows depended on when the ship arrived on station and the weather conditions. While the overall survey design (e.g., stations, depths and seasons to be sampled) was intended to target larval and juvenile fishes and invertebrate predators (GLOBEC,

1992), many other macrozooplankton and micronekton were also commonly collected.

Once on board the nets were rinsed to move all animals to the cod ends and the contents of the cod ends were preserved in 5-10% formalin. The samples were analyzed in the laboratory and all specimens were identified to lowest possible taxon (Williams, 1984). *Crangon septemspinosa* individuals were identified to species. The total length (TL) of up to 50 individuals in each sample was measured at the time of identification. After analysis all samples were re-preserved in 5-10% formalin.

Analysis

Individual *C. septemspinosa* were divided into juveniles ($\leqslant$19 mm TL) and adults ($>$19 mm TL) based on Corey (1981). The abundance data were converted into a Weighted Mean Depth (WMD) using the following formula (Bollens et al., 1993; Rollwagen-Bollens et al., 2006):

$$\text{WMD} = \sum (A_i D_i) \Big/ \sum A_i,$$

where A_i is the abundance of individuals collected in a given sample and D_i is the depth strata sampled.

The software package Minitab® 16 (Minitab, State College, PA, U.S.A.) was used for all statistical analyses. Comparing the vertical distribution of plankton species is problematic due to the patchy nature of their distributions and traditional parametric statistical methods have been argued to be invalid in these cases (Solow et al., 2000; Beet et al., 2003). The non-parametric Chi-square test was used to test for diel differences in depth strata distribution (Zar, 1996). To compare the WMD and test for vertical migration and the effects that abiotic factors may exert, a Sigma-restricted General Linear Model (GLM) was used to test for combined effects of time (day/night), location (off-bank, crest, or flank), lunar periodicity (gradient of the moon's state with 1 = full moon and 0 = new moon), season, salinity, temperature, year, chlorophyll concentration, and WMD of prey species (copepods). An Anderson-Darling test for normality was conducted on the residuals to ensure that they were normally distributed (Zar, 1996). Nighttime was defined as the period between 30 min after official sunset and 30 min prior to official sunrise, while daytime was defined as the period between 30 min after official sunrise and 30 min prior to official sunset. Official sunrise, sunset and lunar periodicity data were obtained from the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneDay.php). The depth strata used for comparisons were 0-15 m, 15-40 m, 40-100 m and $>$100 m, corresponding to the target depth strata for the ascending net tows. The seasons were defined as:

winter (January and February); spring (March, April and May); and summer (June and July). The locations were defined by bottom depth as Crest ($\leqslant$60 m), Flank (60-150 m) and Off-Bank ($>$150 m).

RESULTS

During 30 cruises from 1995 to 1999, 465 MOC10 tows were made, yielding 1388 discrete samples. Over 1.3 million individuals from 426 distinct taxa were identified and enumerated. The larger dataset will be reported elsewhere. In this paper we report only on *Crangon septemspinosa*, the eighth most abundant species, which comprised 12 784 individuals, almost 1% of all specimens collected over the five-year period. Of these, 12 077 were captured during nighttime tows and 777 were captured during daytime tows. The mean ($\pm$ standard error) abundance (No./1000 m^3) for *C. septemspinosa* was 1.74 $\pm$ 0.27. The maximum abundance (No./1000 m^3) of shrimp estimated from any one sample was 161.3 in January 1997. The majority of individuals collected were adults (61.7%) and they were most abundant during the spring months. Both adults and juveniles were found in higher abundances on the flank than on the crest, and were rarely found in the off-bank regions.

The monthly mean water temperature ranged between 4.64°C (February 1997) and 10.0°C (July 1995 and June 1995), with an overall mean of 7.3°C (fig. 2). The monthly mean salinity ranged between 32.0 (February 1997) and 33.9‰ (May 1995), with an overall mean of 32.6‰ (fig. 2). The monthly mean chlorophyll a concentration ranged between 0.55 (January 1996) and 5.87 μg/l (March 1999), with and overall mean of 1.87 μg/l.

The vertical distribution of *C. septemspinosa* over all samples showed a highly significant difference between day versus night ($X^2 = 100.4$, $P = 0.000$) (fig. 3). Likewise, both adult and juvenile *C. septemspinosa* showed highly significant diel differences in vertical distribution across all samples ($X^2 = 23.3$, $P = 0.000$ and $X^2 = 17.2$, $P = 0.001$, respectively) (fig. 3). Chi-square tests could not be performed to compare seasonal or interannual differences because at least one expected value was less than 1 in each instance. Similarly, the number of individuals caught at the surface (0-15 m) was too low to allow for valid chi-square analysis except for the comparisons noted above involving all samples.

The results of the GLM comparing adult *C. septemspinosa* WMD and our variables did not explain a large percentage of the variability of their vertical distribution (r^2(adj.) $= 0.5064$). Adult *C. septemspinosa* vertical distribution was not significantly related to location, chlorophyll concentration, year, time of day, salinity, temperature, lunar periodicity, season, or prey (copepod) distribution (table II).

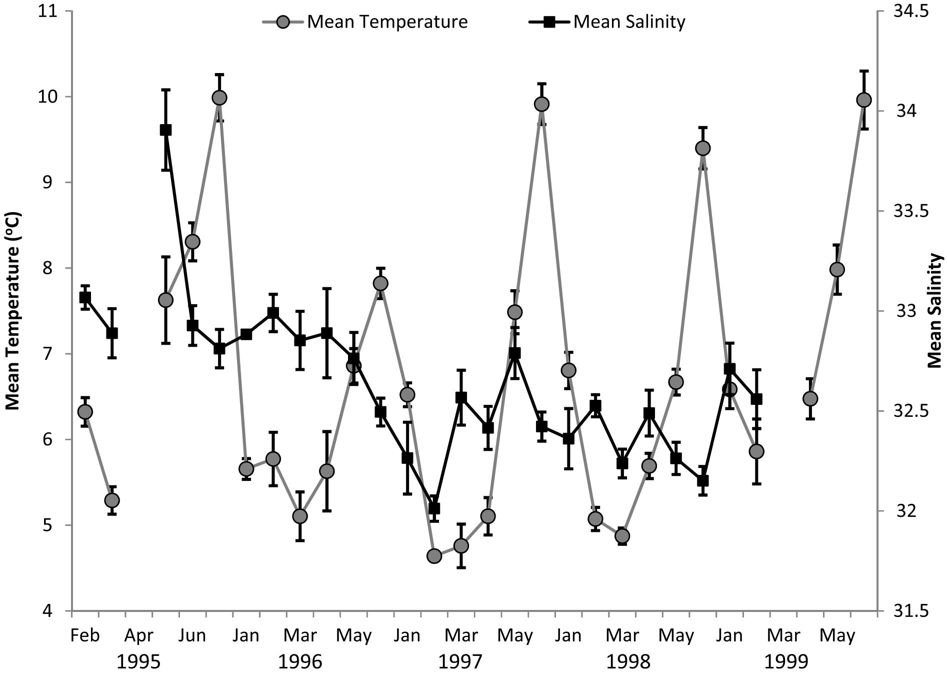

Fig. 2. The monthly mean (± SE) of the temperature (°C) and salinity for all samples collected on the GLOBEC Georges Bank Broad-Scale Survey cruises (1995-1999).

For juvenile *C. septemspinosa*, the results of the GLM analysis comparing WMD and various environmental variables were more significant (r^2(adj.) = 0.7162). Juvenile *C. septemspinosa* vertical distribution was significantly affected by location and chlorophyll concentration (table II). However, we found no signif-

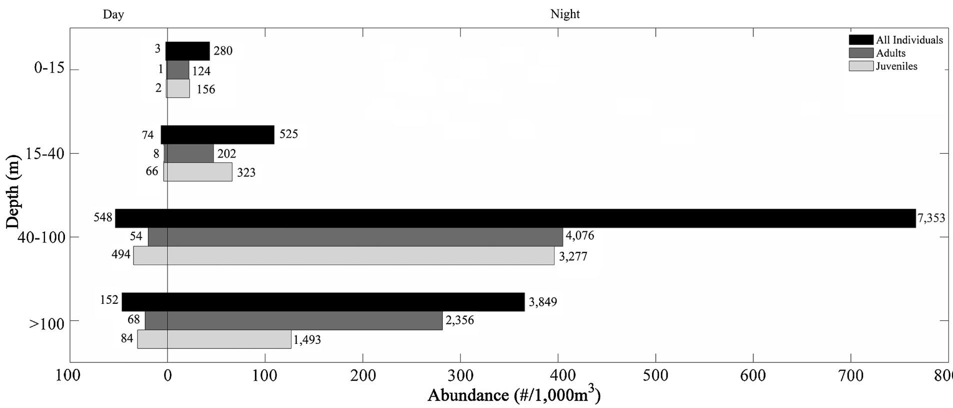

Fig. 3. The vertical distribution of all individual, adult and juvenile *Crangon septemspinosa* Say, 1818 on Georges Bank (1995-1999). The bars indicate the mean abundance of individuals at particular depth strata. Numbers next to bars reflect *n*-values.

TABLE II

Results of the General Linear Model comparing adult and juvenile *Crangon septemspinosa* Say, 1818 and the measured physical parameters and prey distribution

Variable	Adults		Juveniles	
	F-value	*P*-value	*F*-value	*P*-value
Season	0.55	0.586	2.66	0.107
Time of day	1.16	0.295	1.67	0.219
Salinity	0.68	0.421	0.15	0.708
Temperature	1.54	0.229	0.34	0.568
Lunar periodicity	0.64	0.879	1.18	0.390
Year	0.92	0.472	0.51	0.730
Location	1.93	0.173	8.20	0.005
Chlorophyll concentration	0.21	0.653	5.59	0.034
Prey distribution	0.72	0.407	0.15	0.702

icant effect of time of day, year, season, salinity, temperature, lunar periodicity, or prey (copepod) distribution on vertical distribution.

DISCUSSION

Diel vertical migration of zooplankton, where organisms are typically found at depth during the day and near the surface at night, is now commonly thought to be a predator avoidance strategy (Bollens & Frost, 1989; Hays, 2003; Bollens et al., 2011), although abiotic factors can also play a role (e.g., Williamson et al., 2011). This behavior is not confined to zooplankton species, however, as many species of fish have been shown to exhibit diel vertical migration patterns. Auth et al. (2007) found greater densities of ichthyoplankton off the Oregon coast at all but one depth stratum during the night when compared to the daytime, and also noted a diel vertical migration pattern. A reverse diel vertical migration pattern is sometimes seen as well, with organisms at the surface during the day and at depth at night (Frost & Bollens, 1992). Brown et al. (2010) noted that *Caranx crysos* (Mitchill, 1815), a pelagic carangid fish, was typically found in the upper 10 m of the water column during the day, but migrated below 20 m at night.

In our study *Crangon septemspinosa* was found to be far more abundant at night than during the day. This difference in abundance is likely attributable to the majority of individuals being on or near the bottom during the day, and thus inaccessible to our sampling. The significant difference seen by us in the diel vertical distributions of *C. septemspinosa* is indicative of the typical diel vertical migration pattern. While the shrimp were not found at, or near, the surface in large numbers, they were found throughout the water column at much larger numbers at night than during the day. This indicates they were migrating off the bottom and into the water column to a larger degree during the night. This difference in presence during the night and relative absence during the day could be the cause of the contradictory results between the chi-square and general regression with regard to diel vertical distribution. Because adult shrimp were found in much larger numbers during the night, the difference in numbers would show up as a more significant P-value in the chi-square test.

The diel vertical migration pattern of *C. septemspinosa* was seen across all seasons sampled (winter, spring and summer). The migration patterns in winter and spring showed a higher proportion of individuals in the upper 40 m than in summer for both adults and juveniles. Locke et al. (2005) found that the metabolic needs of *C. septemspinosa* increased with temperature. As such it would be expected that the shrimp would be more actively feeding in the spring and summer months than in winter. However, we found no correlation between vertical distribution and water temperature with either the adult or juvenile shrimp.

The moon has been shown to have some influence on vertical distribution of some zooplankton. For instance, Pinot & Jansa (2001) used an Acoustic Doppler Current Profiler to show that when the moon was full the backscatter from zooplankton that would normally be seen in the upper 30 m was found at deeper depths. We also found an effect of lunar periodicity on the vertical distribution of juveniles, with deeper WMDs during periods of increased moonlight. This pattern was not seen for adult shrimp.

We did not find a significant difference in the vertical distribution of adult *C. septemspinosa* when comparing them to the different regions of Georges Bank, as defined by bottom depth, but we did find a difference in juveniles. Neither juvenile nor adult *C. septemspinosa* were found in the upper 100 m of the off-bank regions, and, in fact, only 5 individual juveniles were found during the entire sampling period in the off-bank regions. The retentive circulation pattern of water on and around Georges Bank (Limeburner & Beardsley, 1996) could account for the predominance of the individuals being found in the crest and on-bank regions. In addition, no inter-annual differences in the vertical distribution of juvenile or adult *C. septemspinosa* were seen on Georges Bank.

Experiments have shown that *Crangon septemspinosa* is tolerant of salinities ranging from 3-32‰ and temperatures ranging from −3 to 25°C (Haefner, 1969b), although adults have been caught in temperatures as high as 28°C (Locke et al., 2005). Jeffery & Revill (2002) performed aquarium studies and looked at the distribution of *Crangon crangon* (Linnaeus, 1758) in relation to trawling in the North Sea and found them to be higher in the water column when temperatures exceeded 9.7°C and lower in the water column when temperatures were below 5.7°C. Daewel et al. (2011) used a numerical model to test the hypothesis that juvenile brown shrimp (*C. crangon*) utilized selective tidal stream transport (STST) to time their movement into the upper layers of the water column. The differences in juvenile *C. septemspinosa* vertical distribution on Georges Bank that we observed could not be attributed to either salinity or temperature. However, temperature and salinity can be used to define particular water masses, and as such, Brown et al. (2005) showed that *C. septemspinosa* were found almost exclusively within Georges Bank/Gulf of Maine Water (as defined by Flagg, 1987) and were unaffected by warm water intrusions caused by warm core rings impinging on the Bank. This is in keeping with our results showing no significant difference in the vertical distribution of adult shrimp with respect to salinity and temperature.

The vertical distribution of crangonid shrimp has been little discussed in the literature. Ours is the first long-term study examining the vertical distribution of crangonids in situ. Our data show significant differences in vertical distribution of both juvenile and adult *C. septemspinosa* on Georges Bank, indicative of a normal diel migration pattern (up during the night, down during the day) seen in many other species of invertebrates and fish. This vertical distribution and diel migration pattern showed significant differences between locations, and with respect to chlorophyll concentration in juveniles. The wide range of environmental variables we examined explained a large amount (72%) of the overall variation in vertical distribution patterns of *C. septemspinosa* juveniles, but only 50% in adults, suggesting that other factors not measured by us (e.g., predators) should be considered in future studies.

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