

**Abstract.**—A suction dredge survey was conducted in the Bahamas in a tidal flow field system which contained a nursery ground for the economically significant gastropod *Strombus gigas* (queen conch). Settlement of larval conch within the system was associated with the specific location of the nursery and positively correlated with subsequent recruitment to the juvenile population (<45 mm shell length). Settlement was relatively independent of habitat features including depth, sediment characteristics, and macrophytes. Conversely, densities of micro-predators (small crabs, shrimp, and predaceous gastropods) capable of consuming early postsettlement conch were often correlated with habitat features such as seagrass shoot density, seagrass detritus, and organic content of the sediment. The density of small xanthid crabs (mode=1.5 mm carapace width) was positively correlated with density of live postsettlement conch (mean  $\leq 4/m^2$ ), suggesting that conch settle in predator-prone areas or that the crabs respond numerically to small conch (or both). Densities of xanthids were very high (to  $>200/m^2$ ), and the crabs probably represent an important source of mortality for small conch in the primary nursery ground. Shells of dead conch indicated that molluscan and asteroid predators probably caused most of the predatory mortality on young conch that settled outside the nursery. Because critical settlement and recruitment habitats for queen conch are associated with particular hydrographic conditions, these habitats cannot be identified or predicted simply by mapping obvious features such as seagrass cover, depth, or sediment type. An understanding of dynamic processes, such as larval transport and retention, selective settlement mechanisms, and trophic ecology, will be required to identify critical nursery habitats.

## Settlement and recruitment of queen conch, *Strombus gigas*, in seagrass meadows: associations with habitat and micropredators

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Distribution of marine species with planktonic larvae is a function of both pre- and postsettlement processes. Location of reproductive sources, physical and oceanographic processes, duration and survivorship of larval stages, and larval behavior combine to determine settlement location, whereas predation, suitable habitat, and the behavior of early juveniles affect the number of individuals that survive to represent juvenile recruitment (Keough and Downes, 1982; Luckenbach, 1984; Connell, 1985). Experiments conducted in the laboratory with a large variety of species have shown that settlement in the field is probably a nonrandom process for the majority of marine invertebrates, and settlement behavior is usually assumed to place juveniles in habitats most suitable for growth or survival (or both) (Hadfield and Scheuer, 1985; Butman and Grassle, 1992; Grassle et al., 1992; Davis and Stoner, 1994; Stoner et al., 1996a).

Despite an abundance of data and experiments on settlement, relatively little is known about the relative importance of settlement rate and postsettlement predation in controlling local recruitment of

most species to juvenile stages (Osman and Whitlatch, 1995). Because early postsettlement juveniles of many benthic species, especially those associated with soft sediments, are difficult to survey, quantitative data related to recruitment often depend upon observations of the smallest juveniles that can be detected easily. The result is a relatively poor understanding of the crucial period between settlement and first detection in the benthos (Keough and Downes, 1982; Luckenbach, 1984).

Queen conch (*Strombus gigas*) is a large gastropod that has great economic significance throughout the Caribbean and adjacent regions (Appeldoorn, 1994). Despite the wealth of information now available for conch larvae (Davis, 1994; Stoner and Davis, 1997), juveniles in year class 1 (e.g. Marshall, 1992; Iversen et al., 1987; Appeldoorn, 1994), and adults (Appeldoorn, 1988; Stoner and Sandt, 1992), little is known about larval settlement and the early postsettlement stage. Newly settled queen conch (<10 mm) are cryptic, often buried (Iversen et al., 1989; Sandt and Stoner, 1993), and are readily preyed upon by micropredators such as xanthid

crabs and certain polychaetes (Ray-Culp et al., 1997). Queen conch <50 mm shell length have rarely been encountered in the field (Iversen et al., 1994; Ray and Stoner, 1995; Iversen and Jory, 1997), and the only density data extant for these small conch were collected by Sandt and Stoner (1993) near Lee Stocking Island, Bahamas. However, queen conch settle at a large size (1.2 mm), compared with many other mollusks, and even the smallest juvenile, unless crushed completely, leaves an identifiable shell record of its settlement in the sediment (our study). This record can be used to examine the settlement-recruitment relationship and spatial variation in settlement.

Our study had three primary objectives. First, we conducted an extensive dredge survey for newly settled queen conch in and around a well-studied nursery area in the central Bahamas during the summer recruitment season in 1992. The survey was designed to test the hypothesis that the long-term distribution pattern of year-class 1 and 2 conch was associated with settlement pattern. The sum of live and dead individuals was used as an index of settlement at each sampling station, and the number of surviving (live) conch served as an index of recruitment. Through this survey, we gathered the first quantitative data on the distribution of queen conch <45 mm shell length (1.5–44 mm). Second, we used observations of shell damage sustained by dead individuals to determine the primary predatory forms on newly settled queen conch. We also examined spatial variation in predation type. Third, we examined the effects of environmental characteristics, such as depth, sediments, macrophytes, older conspecifics, and distribution of potential predators, on the observed distribution of newly settled queen conch.

## Study area

The Exuma Cays are an important source of queen conch for a large fishery in the Bahamas; the island chain is 250 km long, bordered to the east by the Exuma Sound, and to the west by the Great Bahama Bank. Water exchange occurs through numerous tidal inlets separating the islands, creating extensive tidal flow fields on the shallow bank. Nurseries of juvenile conch (1- and 2-yr-old, 70–150 mm SL) are located primarily on the bank side of the Exuma Cays near these inlets and are typically associated with seagrass meadows (2–4 m deep) that are flushed with clear, oligotrophic water from the Sound during flood tide (Stoner et al., 1996b).

We elected to survey postlarval conch in a tidal flow field located west of Lee Stocking Island and south of Norman's Pond Cay because the conch nurs-

ery near Shark Rock (Fig. 1) is well studied. Prior to sampling, five years of data had been collected on the distribution and abundance of 1- and 2-year-old juvenile conch, and environmental characteristics such as seagrass biomass, depth, and tidal currents had been mapped (Jones, 1996; Stoner et al., 1996b). Drogue studies have shown that, on flood tide, water from the Sound enters the inlet north of Lee Stocking Island, passes close to Shark Rock, and flows west of the nursery for a distance that is dependent on wind conditions and tidal phase (e.g. spring, neap) (Stoner et al., 1994). Tidal currents, which reach 100 cm/s at midtide, flow between sand bars in an S-shaped pattern following the bank bathymetry (Fig. 1B). The middle of the tidal channel is ~3 m deep and vegetated primarily with the seagrass *Thalassia testudinum*. Depth and seagrass density gradually decrease from midchannel to bare sand on both sides of the channel. Tidal range is ~1 m.

Annual surveys conducted between 1988 and 1992 showed that aggregations of juvenile queen conch always grazed within a 2-km long section of the tidal flow field close to Shark Rock (Fig. 1) and, at any given time, occupied only portions of the suitable habitat available (Stoner et al., 1996b). Stations for this study were established with reference to long-term distribution of conch in this area (Stoner and Waite, 1990; Stoner and Ray, 1993; Ray and Stoner, 1994) and to represent both down-channel and across-channel dimensions of the flow field. One line of stations was established in midchannel down the flow field from Adderly Cay (A) to Cook's Cay (F) with an attempt to locate all of the stations in similar depth and moderate seagrass shoot density. Stations A and F were each located ~4 km from the geographic center of the traditional nursery ground (Fig. 1), and stations B and E were located ~250 m outside the northeastern and southwestern ends of the nursery, respectively. Stations C3 and D3 were each established ~500 m from the geographic center of the nursery (Fig. 1C).

To represent the across-flow field dimension, five more stations were selected along two transects that lay perpendicular to the main axis of the tidal current at stations C3 and D3, as well as across the seagrass gradient. *Thalassia testudinum* density ranged from 4 to 704 shoots/m<sup>2</sup> and from 0.5 to 178 g dry wt/m<sup>2</sup> across this gradient in 1991 (Ray and Stoner, 1994) (Fig. 1C). Three stations were established along the D transect in addition to D3, increasing in macrophyte cover from bare sand at D1 to high seagrass and detrital biomass at D4. Along transect C, two stations were established in addition to C3, ranging from sand to moderate seagrass shoot density and macrophyte biomass. There were no areas of high seagrass biomass present near transect C and,

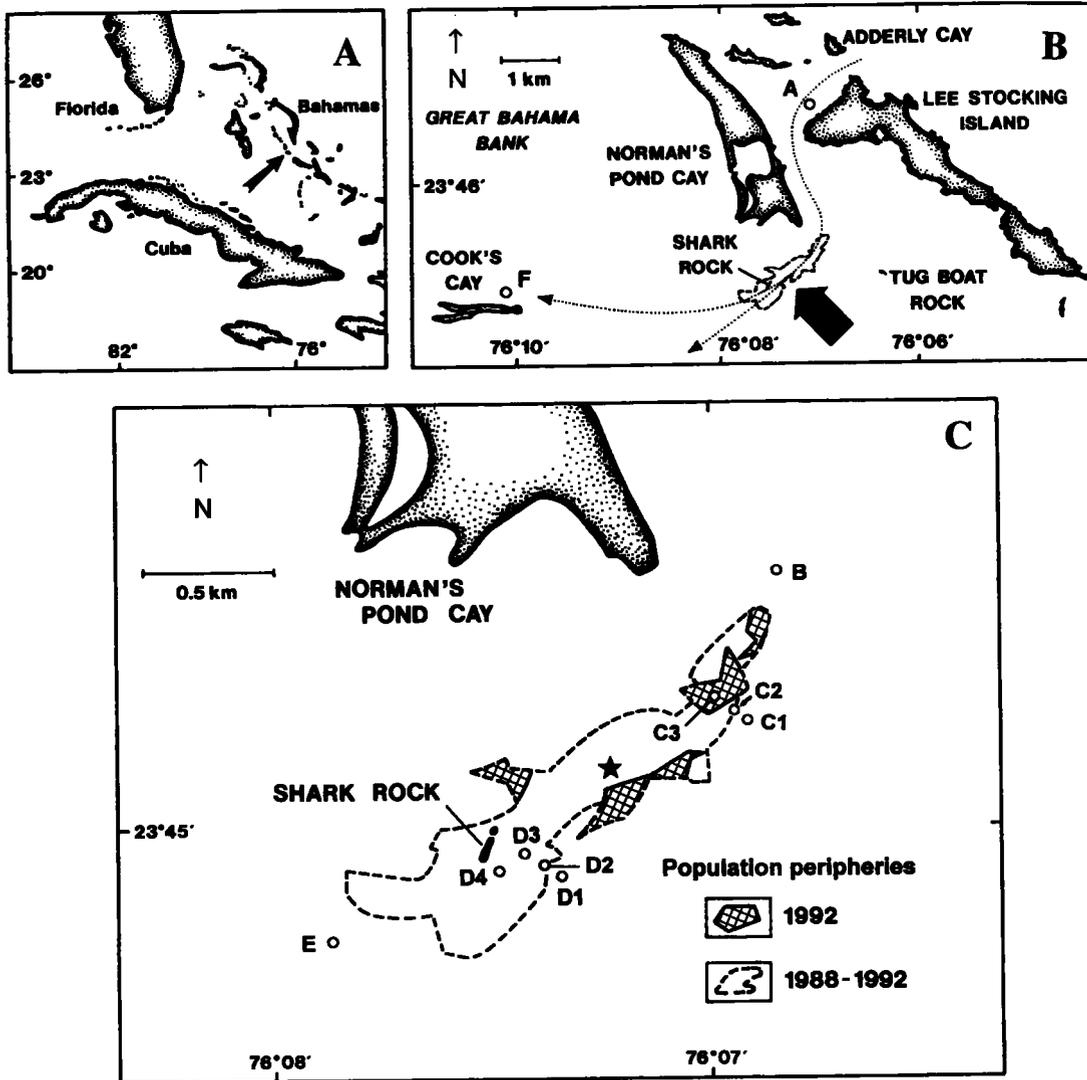


Figure 1

(A) Study area in the southern Exuma Cays, central Bahamas. (B) On the flood tide, water from Exuma Sound passes between Adderly Cay and Lee Stocking Island, flowing in an S-shaped pattern past Shark Rock towards Cook's Cay (dotted arrow). Stations A and F represented ends of the flow field. (C) Nine more stations were selected with respect to the long-term (1988–92) location of the juvenile queen conch aggregation, delineated by dashed line. In July 1992, just before dredge sampling was conducted, the aggregation occupied the areas shown in hatched polygons. Star indicates center of aggregation.

consequently, no station was directly comparable to D4. Other environmental characteristics, such as depth and certain sediment characteristics, also varied across the flow field (see "Results" section, Tables 1 and 2).

## Methods

### Dredge sampling

Given that maximum densities of conch veligers are observed during midsummer (June through August)

and that the larval period lasts 3–4 weeks (Davis et al., 1993), dredge sampling for newly settled conch was conducted at the end of the summer, 24 August to 1 September 1992. Scuba equipment was used for all underwater work. At each of the 11 stations, water depth was measured and corrected to mean low water (MLW), and duplicate sediment samples were collected with a PVC core (diameter=40 mm, depth=5 cm) prior to dredging.

Sediment samples were rinsed with freshwater and dried at 80°C to constant weight. A subsample (~15–20 g) was incinerated at 550°C in a muffle furnace

for 4 h to determine organic content, calculated as the percent difference between dry weight and ash-free dry weight. A second rinsed subsample (~20 g) was analyzed by using standard dry sieve procedures (Folk, 1966), and product moment statistics were used to calculate mean grain size (McBride, 1971). The silt-clay fraction (>4.0  $\phi$ , <62 mm), always < 9% of sediment dry weight, was not fractionated.

Replicate dredge sample plots ( $n=5$  for all stations, except C3, where  $n=6$ ) were delineated by a circular enclosure made of aluminum sheet metal (area=0.5 m<sup>2</sup>, height=0.3 m) that was placed haphazardly at each station. The enclosure was pushed securely into the sediment to prevent escape of motile fauna. In the middle of each sample plot, the number of *Thalassia testudinum* shoots was counted in a quadrat (25 × 25 cm). A gasoline-powered suction dredge (modified from Brook, 1979) was used to collect year-class 0 queen conch, other macrofauna, and associated macrophytes from each plot. The dredge created high-pressure water flow which, as a result of Venturi principle, drew algae, detritus, sediments, and macrofauna through a PVC intake tube (diameter=7.6 cm) into a mesh bag (40 × 70 cm, 1.2 mm mesh). Preliminary sampling in the study area and observations of year-class 0 conch (<45 mm SL) indicated that conch in the nursery ground buried no deeper than 5 cm into the sediment. Therefore, sediments from plots with seagrass were removed to the depth at which *T. testudinum* rhizomes occurred (usually 8–15 cm); in bare sand, dredging was 8–10 cm deep. Unlike the other macrophytes, living seagrass did not detach easily and was not collected with the dredge material. The mesh bags holding the dredged materials were tied securely underwater and later fixed in a 10% formalin-seawater mixture containing rose bengal as a staining agent. After 24 hours, each sample was rinsed onto a sieve (1.2 mm) and preserved in 70% ethanol until sorted.

Macrophytes were sorted into three components: *T. testudinum* detritus (senescent blades and fragments), the green macroalga *Batophora oerstedii*, and the red algae *Laurencia* spp. Occasionally fronds of calcareous green algae (including *Halimeda* spp., *Penicillus capitatus*, *Udotea* spp., and *Rhipocephalus phoenix*) were collected, but they were sparsely distributed and not quantified. Each fraction was rinsed with freshwater to remove salts and dried at 80°C to constant weight (~24 h) so that biomass (g dry wt/m<sup>2</sup>) could be calculated.

For ease in extracting newly settled queen conch and their potential predators, sediments were divided into two fractions, those retained on 1.2- and 2.0-mm sieves. A conch was classified as alive if its soft tissue and operculum were intact. Shortly after

death, the operculum detaches from the foot, and soft tissues decompose quickly. Therefore, dead and living conch were easily distinguished. We do not believe that conch shells were damaged during collection because the dredge apparatus lifted samples off the bottom by suction that could be controlled and the materials collected did not pass through an impeller. Care was also taken so that the fauna were not damaged in sieving. None of the conch classified as alive at collection had damaged shells, and most other taxa, such as polychaetes and crabs, were in good (i.e. whole) condition.

To gain insight into modes of predation, shells of dead conch were classified as 1) whole and undamaged, 2) drilled, 3) peeled back along the spire line, or 4) crushed. Whole shells of dead conch were attributed to predation by mollusks or asteroids (Jory, 1982; Iversen et al., 1986; Ray and Stoner, 1995), drilled shells were probably the result of mollusk kills (Vermeij, 1987), and peeled and crushed shells were attributed to crustaceans (Randall, 1964; Vermeij, 1982, 1987; Davis, 1992). Whole shells can also result from nonpredatory mortality. The proportion of dead individuals was used as an indicator of post-settlement mortality.

Whole shells (from both live and dead conch) were measured for shell length. When only a shell spire or shell aperture was found, total shell length for the dead animal was calculated on the basis of regression formulae derived from measurements of 20 whole shells ranging in size from 3 to 40 mm total length:

$$\text{Length} = (\text{spire length} \times 2.4) - 1.8; \quad [r^2=0.991]$$

$$\text{Length} = (\text{aperture length} \times 1.6) + 0.5. \quad [r^2=0.998]$$

Given that queen conch settle into nursery grounds during a distinct season, it was possible to determine if an individual had indeed settled in 1992 on the basis of its size, color, and the amount of biological encrustation. Settlement of queen conch can occur at the beginning of May, and growth rates during the early postsettlement period may be as great as 0.45 mm/d (Ray and Stoner, 1994); therefore, we considered conch  $\leq 45$  mm in total shell length to be members of year-class 0. Also, conch shells lose their pink interior color within a few weeks after death. Animals that settled in 1992 were easily discerned on the basis of shell size and color.

Xanthid and portunid crabs and alpheid shrimps were extracted from samples because they were abundant and known to be significant predators of postsettlement conch (Ray-Culp et al., 1997). Olivid and marginellid gastropods were also removed and counted as potential predators. Carapace width (includ-

ing lateral spines) of crabs was measured, carapace length for shrimps, and shell length of gastropods.

### Data analysis

To discern station differences, density data from the dredge sampling were log-transformed ( $\log_{10}(n+1)$ ) to improve homogeneity of variance (Cochran's test,  $P>0.05$ ) and analysed by using 1-way ANOVA following the guidelines of Day and Quinn (1989). Tukey's multiple comparison test was performed to determine pairwise relationships. Seven measures of density were examined: live conch, dead conch, total conch, alpheid, portunids, xanthids, and total predators.

Relationships between these seven density measures and eight environmental variables (water depth, distance of the station from the center of juvenile queen conch aggregation, sediment grain size, sediment organics, *Thalassia testudinum* shoot density, weight of *T. testudinum* detritus, and biomass of the macroalgae *Batophora oerstedii* and *Laurencia* spp.) were examined with pairwise correlation. Log-transformation improved the relationships, and Pearson correlation coefficients are reported for the log-transformed variables.

The relationships between conch density (live, dead, and total) and each of the five predator fami-

lies were also examined with correlation. Variables were not transformed in the analysis because transformation did not improve the correlations.

## Results

### Habitat characteristics

Depth down the flow field was relatively uniform, ranging from 2.8 to 3.3 m at MLW, except at E where depth was 2 m (Table 1). Across the flow field at transect D, depth increased from bare sand (1.3 m) to high seagrass density (3.3 m), and, at transect C, greatest depth (3.5 m) occurred in low density seagrass (C2). Sediments were fine to medium sands (1.4–2.6  $\phi$ ), with mean grain size decreasing slightly (increasing  $\phi$ ) with depth over both transects C and D (Table 1). Organic content of the sediments across transect D also increased with depth, ranging from 2.7% (station D1) to 5.2% (station D4). The range of organic content in the down flow-field dimension was 3.0–4.6%.

*Thalassia testudinum* shoot density decreased down the flow field from 784 to 320 shoots/m<sup>2</sup> (Table 2). Across the channel, shoot density increased rapidly from 0 to >500 shoots/m<sup>2</sup> in both transects, as had been in-

**Table 1**

Habitat characteristics for 11 dredge stations in the Shark Rock flow field. Depth was at mean low water and distance was measured from each station to the center of the juvenile queen conch nursery (see Fig. 1). Means and the range of values (parentheses) are given for sediment grain size and organics ( $n=2$  for all stations except C3, where  $n=3$ ). Data for stations C3 and D3 are given twice for ease of comparison in both flow-field dimensions.

Station	Depth (m)	Distance (km)	Sediments	
			Grain size ( $\phi$ )	Organics (% dry wt)
Down flow field, midchannel				
A	2.8	3.60	2.57 (2.56–2.58)	4.08 (3.68–4.50)
B	3.0	1.00	1.81 (1.78–1.84)	4.05 (3.46–4.65)
C3	3.1	0.55	1.84 (1.63–1.95)	3.54 (3.17–3.75)
D3	2.8	0.55	2.07 (2.04–2.10)	4.56 (4.43–4.69)
E	2.0	1.10	1.89 (1.86–1.92)	2.95 (2.95–2.95)
F	3.3	4.50	2.04 (1.97–2.12)	3.99 (3.98–4.00)
Across flow field				
Transect C				
C1	2.0	0.70	1.51 (1.27–1.74)	2.18 (2.16–2.21)
C2	3.5	0.70	1.78 (1.73–1.83)	3.31 (3.09–3.53)
C3	3.1	0.55	1.84 (1.63–1.95)	3.54 (3.17–3.75)
Transect D				
D1	1.3	0.60	1.44 (1.27–1.60)	2.72 (2.60–2.84)
D2	2.1	0.55	1.73 (1.72–1.74)	3.12 (3.06–3.19)
D3	2.8	0.55	2.07 (2.04–2.10)	4.56 (4.43–4.69)
D4	3.3	0.70	1.87 (1.60–2.14)	5.24 (5.12–5.37)

Table 2

Macrophyte characteristics for 11 dredge stations in the Shark Rock flow field (see Fig. 1). Shoot count and detritus values are for *Thalassia testudinum*. All values are mean  $\pm$ SE ( $n=5$  for all stations except C3, where  $n=6$ ). Data for stations C3 and D3 are given twice for ease of comparison in both flow-field dimensions.

Station	Shoot density (no./m <sup>2</sup> )	Biomass (g dry wt/m <sup>2</sup> )		
		Detritus	<i>B. oerstedii</i>	<i>Laurencia</i> spp.
Down flow field, midchannel				
A	784 $\pm$ 36	353 $\pm$ 49	0.02 $\pm$ 0.01	0.20 $\pm$ 0.05
B	640 $\pm$ 65	144 $\pm$ 20	0.80 $\pm$ 0.40	0.04 $\pm$ 0.03
C3	536 $\pm$ 26	30 $\pm$ 11	0.007 $\pm$ 0.004	0.20 $\pm$ 0.18
D3	528 $\pm$ 36	139 $\pm$ 20	24.08 $\pm$ 6.00	0.84 $\pm$ 0.27
E	352 $\pm$ 22	29 $\pm$ 10	44.76 $\pm$ 4.77	0.66 $\pm$ 0.13
F	320 $\pm$ 17	34 $\pm$ 8	2.18 $\pm$ 0.57	0 $\pm$ 0
Across flow field				
Transect C				
C1	0 $\pm$ 0	0.06 $\pm$ 0.04	0.02 $\pm$ 0.03	0 $\pm$ 0
C2	288 $\pm$ 44	37 $\pm$ 14	1.76 $\pm$ 0.45	0.34 $\pm$ 0.18
C3	536 $\pm$ 26	30 $\pm$ 11	0.007 $\pm$ 0.004	0.20 $\pm$ 0.18
Transect D				
D1	0 $\pm$ 0	0.08 $\pm$ 0.04	0.06 $\pm$ 0.04	0 $\pm$ 0
D2	240 $\pm$ 36	14 $\pm$ 4	3.68 $\pm$ 0.32	1.60 $\pm$ 0.04
D3	528 $\pm$ 36	139 $\pm$ 20	24.08 $\pm$ 6.00	0.84 $\pm$ 0.27
D4	544 $\pm$ 22	180 $\pm$ 17	0.22 $\pm$ 0.23	1.58 $\pm$ 0.83

tended in the sampling design. A similar increase occurred with *T. testudinum* detritus, with the exception of a relatively low value at station C3 (Table 2), where the aggregation of year-class 1 and 2 juvenile conch undoubtedly had a grazing effect (Fig. 1). As was intended, shoot density and detritus biomass increased across transect D, and values were highest at station D4. Algal biomass was noticeably high only at stations D3 and E (where standing crops of *Batophora oerstedii* were 24 and 45 g dry wt/m<sup>2</sup>, respectively), and particularly low at station C3 (grazed by conch). Biomass of *Laurencia* spp. was low at all stations ( $\leq 1.6$  g dry wt/m<sup>2</sup>).

### Newly settled conch

Newly settled queen conch were collected in dredge samples at all 11 stations except F (Fig. 2). Down the flow field, mean total density was relatively high (8–12 conch/m<sup>2</sup>) at stations B, C3, and D3, and low (0–2.4 conch/m<sup>2</sup>) at stations A, E, and F, although differences were only significant between C3 and F (Fig. 2). There was a significant negative correlation between total conch and distance from the geographic center of the long-term aggregation (Table 3); both total density and density of dead conch decreased with distance from C3 (Fig. 2). All of the conch collected at stations A and E were dead, as were most (60–86%) from the other down flow field stations. Live

conch were collected at stations B, C3, and D3, with maximum density (4 conch/m<sup>2</sup>) observed at B.

Across the flow field, mean total conch density appeared to increase with seagrass density in transect C (Fig. 2), although differences were not significant. Values were relatively uniform at all of the stations in transect D, ranging from 4.0 to 8.4/m<sup>2</sup>. Live newly settled conch were most abundant at stations C3 (1.7/m<sup>2</sup>) and D3 (1.6/m<sup>2</sup>), where seagrass density was moderate. Significant numbers of live individuals were also collected at the other stations with at least some seagrass (C2, D2, D4). However, all of the conch dredged from the bare sand stations (C1, D1) were dead.

When data for 11 stations were included in the analysis, live conch density (the index of recruitment) had a significant positive correlation with total conch density (the index of settlement) (coefficient of correlation [ $r$ ]=0.703,  $P=0.016$ ). The percentage of the total conch that were dead provides an index of mortality. This index was negatively correlated with settlement ( $r=0.654$ ,  $P=0.04$ ).

Live individuals ranged in size from 3.3 mm to 38.5 mm with the mode at 10–14.9 mm (Fig. 3). Dead individuals ranged in shell length from 1.5 to 44 mm with the mode at 1.0–4.9 mm. The percentage of dead conch with whole, undamaged shells decreased across the flow field along both transects in the direction of increasing seagrass density and increasing density of

**Table 3**

Pearson correlation coefficients ( $n=11$ ) for the pairwise relationship between each of seven dependent variables (i.e. newly settled queen conch and predators) and eight independent variables. Depth was at mean low water; distance was measured from station to center of juvenile queen conch aggregation (see Fig. 1); grain size and organics are for sediments; shoot density and detritus values are for *T. testudinum*. \*  $0.01 < P < 0.05$ ; \*\*  $0.001 < P < 0.01$ ; \*\*\*  $P < 0.001$ . All of the dependent variables were transformed ( $\log_{10}(x+1)$ ) prior to analysis.

	Live conch	Total conch	Xanthids	Alpheids	Portunids	Olivids	Marginellids
Depth	0.474	0.123	0.710*	0.428	-0.081	0.063	0.231
Distance	-0.393	-0.770**	0.141	0.358	-0.158	0.165	-0.346
Grain size	-0.027	-0.312	0.533	0.821**	0.337	-0.254	-0.233
Organics	0.346	0.196	0.868***	0.694*	0.041	-0.398	0.304
Shoots	0.454	0.168	0.812**	0.924***	0.496	-0.460	0.273
Detritus	0.085	0.038	0.537	0.947***	0.515	-0.707*	0.103
<i>B. oerstedii</i>	-0.106	-0.260	0.120	-0.091	-0.013	0.164	-0.020
<i>Laurencia</i> spp.	-0.026	0.182	0.237	0.164	-0.311	-0.205	0.082

year-class 1 and 2 conch (Table 4). The pattern of crushed shells was reverse. In the down flow-field dimension, the percentage of whole empty shells was lowest at stations within the nursery ground and at station F. Crushed shells made up the highest proportion of dead, newly settled conch within the nursery area. Overall, few shells were drilled (2.8%) or peeled (13.5%), and most were crushed (56.7%).

**Conch predators**

Xanthid crabs (mostly *Micropanope* spp.) composed the predator group with the greatest densities and governed the density distribution of total predators in both flow-field dimensions (Fig. 4). Xanthids were most abundant (102–286 per  $m^2$ ) at stations B, D3, and D4, and were  $\leq 36/m^2$  at all other stations. Alpheid density decreased down the flow field (Fig. 3), increased with seagrass density across the flow field (Figs. 3 and 4), and had a high positive correlation with detritus ( $r=0.947$ , Table 3). Xanthid and alpheid densities also had high positive correlations with *Thalassia testudinum* shoot density and sediment organics (Table 3). Portunid crab densities were relatively low, compared with the two other crustacean families. They decreased down the flow field from a maximum at A ( $7.6/m^2$ ) to 0 at F (Fig. 4).

Of the two predaceous mollusc families observed, the Olividae were most abundant at stations C2 ( $18/m^2$ )

**Table 4**

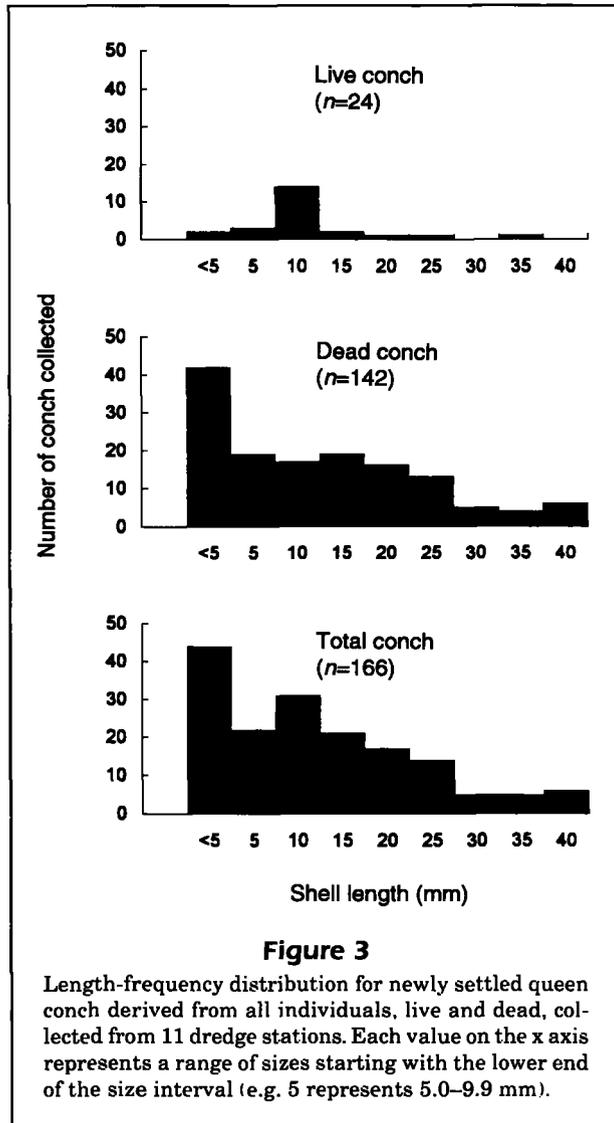
Number of dead newly settled queen conch dredged from 11 stations for each of four shell conditions (see text for definitions). Values are station percentages followed by (n). Data for stations C3 and D3 are given twice for ease of comparison in both flow field dimensions.

Station	Whole	Drilled	Peeled	Crushed	Total
Down flow field, midchannel					
A	33.3 (2)	16.7 (1)	0 (0)	50.0 (3)	(6)
B	6.7 (1)	0 (0)	13.3 (2)	80.0 (12)	(15)
C3	9.7 (3)	0 (0)	25.8 (8)	64.5 (20)	(31)
D3	18.7 (3)	0 (0)	12.5 (2)	68.8 (11)	(16)
E	33.3 (1)	0 (0)	33.3 (1)	33.3 (1)	(3)
F	0 (0)	0 (0)	0 (0)	0 (0)	(0)
Total	14.1 (10)	1.4 (1)	18.3 (13)	66.2 (47)	(71)
Across flow field					
Transect C					
C1	57.1 (4)	0 (0)	28.6 (2)	14.3 (1)	(7)
C2	17.6 (3)	0 (0)	5.9 (1)	76.5 (13)	(17)
C3	9.7 (3)	0 (0)	25.8 (8)	64.5 (20)	(31)
Total	18.2 (10)	0 (0)	20 (11)	61.8 (34)	(55)
Transect D					
D1	64.7 (11)	0 (0)	5.9 (1)	29.4 (5)	(17)
D2	55.6 (5)	11.1 (1)	22.2 (2)	11.1 (1)	(9)
D3	18.7 (3)	0 (0)	12.5 (2)	68.8 (11)	(16)
D4	25.0 (5)	10.0 (2)	0 (0)	65.0 (13)	(20)
Total	38.7 (24)	4.8 (3)	8.1 (5)	48.4 (30)	(62)
Grand total <sup>1</sup>	27.0 (38)	2.8 (4)	13.5 (19)	56.7 (80)	(141)

<sup>1</sup> Stations C3 and D3 are included only once in grand total.

and F ( $25/m^2$ ) (ANOVA,  $F_{10,45}=5.69$ ,  $P<0.001$ ). Values were  $\leq 7.2/m^2$  at all other stations and the data were not plotted. Olivids were negatively correlated with detritus (Table 3). The Marginellidae were most abundant at B ( $9.2/m^2$ ) and D4 ( $6.8/m^2$ ) and densities were  $\leq 2/m^2$  at all other stations, but the differences





Live conch density had a high positive correlation with xanthid density ( $r=0.825$ ,  $P=0.002$ ), marginellid density ( $r=0.695$ ,  $P=0.02$ ), and total predator density ( $r=0.794$ ,  $P=0.004$ ), whereas relationships with densities of alpheids, portunids, and olivids were not significant ( $P \geq 0.38$ ). There were no significant relationships with any of the predator families ( $P \geq 0.15$ ) for dead or total conch densities.

## Discussion

### Age of postlarvae and settlement dates

The shell lengths of dredged newly settled conch provide insight into when settlement occurred. Using the middle of the week-long sampling period as the

**Table 5**

Size range and mode for three crustacean and two molluscan families of potential predators of newly settled conch collected at 11 dredge stations.

Family	Measurement	Range (mm)	Mode (mm)
Xanthidae	carapace width	1.0–14.5	1.5
Alpheidae	carapace length	1.0–7.8	4.2
Portunidae	carapace width	1.5–36.1	3.4
Marginellidae	shell length	1.7–6.1	3.2
Olividae	shell length	2.0–11.6	3.2

endpoint (28 August 1992), we estimated a summer average growth rate of 0.39 mm/day (Ray and Stoner, 1995), and considering settlement at 1.2 mm shell length (Davis, 1994), we determined that animals in the 10–15 mm modal size class would have settled 3–4 weeks earlier, between 24 July and 5 August. The largest live individual (38.5 mm) would have settled on about 24 May, and the smallest (3.3 mm) would have settled on 23 August. Dead conch ranged from 1.5 to 44 mm SL. According to the same assumptions, they would have been in the benthos for 1–110 days at the time of death. Therefore, settlement recorded in our samples began in early May and continued through at least late August. It should be pointed out that our intent was to collect young conch as close to the peak settlement period as possible, near the end of August. However, it is known that larvae are present in the water column near Lee Stocking Island until at least late September (Stoner and Davis, 1997), and our collections probably do not represent total settlement at Shark Rock in 1992.

There are three possible explanations for the fact that dredging yielded relatively few live conch outside the 10–14.9 mm modal class. First, there could have been a major settlement event between late July and early August. Queen conch larvae were collected at the Shark Rock nursery ground on 13 dates between late May and mid-September 1992 (Stoner and Davis, 1997); however, relatively few late-stage larvae were found in these collections, and it is impossible with the available data to determine if the modal size of survivors resulted from a period of high settlement rate. Nevertheless, this is the most parsimonious explanation. Second, the high number of year-class 0 conch in the 10–14.9 mm range may also be related to high survivorship in conch settling between late July and early August, compared to conch settling at other times. However, the steep decline in numbers of individuals with size could be a reflection of the natural, high mortality of small conch (dis-



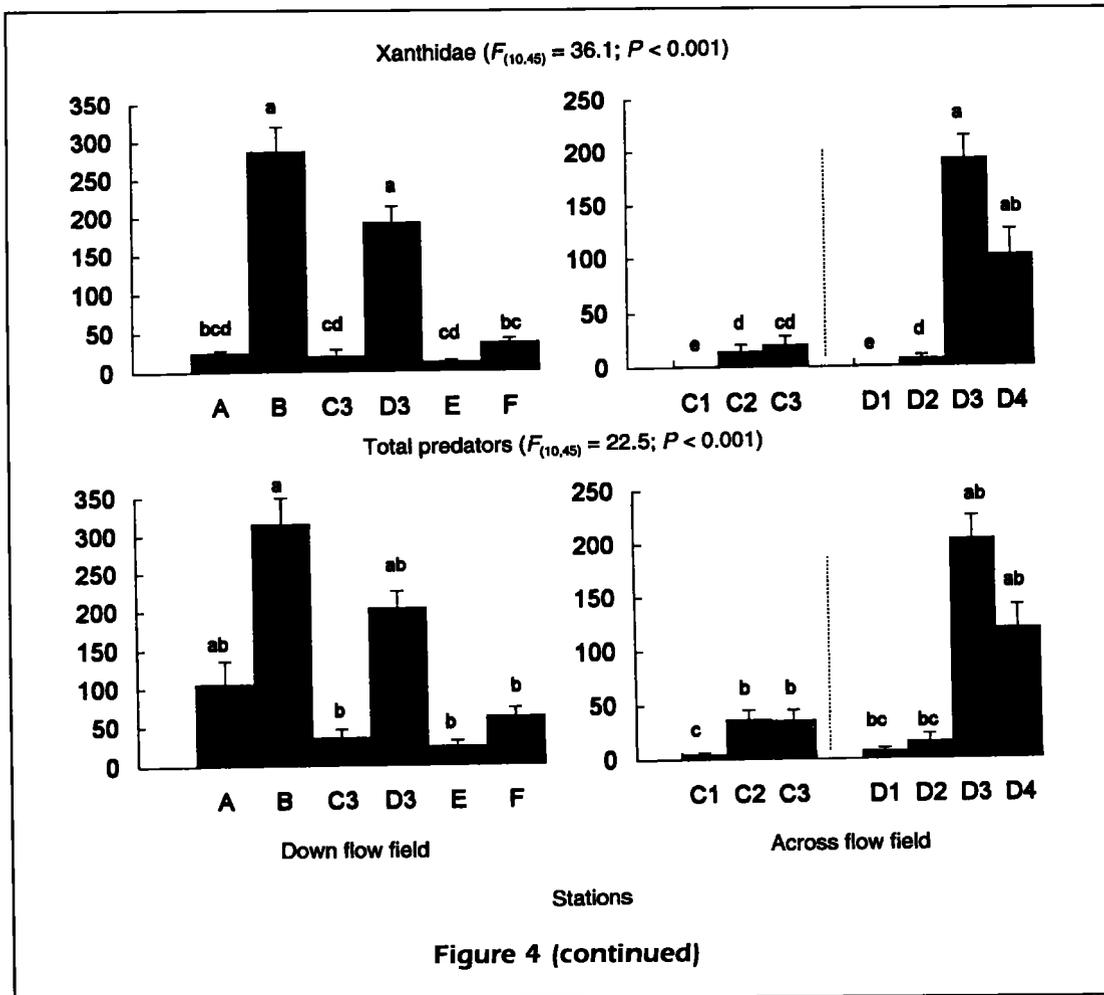


Figure 4 (continued)

benthic invertebrates when settlement occurs in low density

After an extensive review of the literature, Butman (1987) concluded that settlement patterns in invertebrates associated with soft sediments are a function of passive accumulation and deposition of larvae over spatial scales of kilometers and that active habitat selection occurs primarily over smaller scales (centimeters to meters). Data on the abundance of queen conch veligers over the Shark Rock tidal flow field (Stoner and Davis, 1997) may support this conclusion. Although newly hatched larvae (300–500  $\mu\text{m}$ ) were collected well beyond the Shark Rock nursery, at station F on 12 of 13 sampling dates in 1992, neither midstage larvae (500–900  $\mu\text{m}$ ), competent larvae (>900  $\mu\text{m}$ ), nor newly settled conch were ever collected there, suggesting that late-stage larvae are somehow concentrated at the nursery location. At maximum flood-tide current, velocity near the surface decreases by approximately 75% between station A, north of Lee Stocking Island, and Shark Rock. Near the bottom, the decrease in velocity is more than

95% (Stoner and Ray-Culp<sup>1</sup>). We also know that maximum flood tidal excursion in this flow field occurs near the Shark Rock nursery area on neap tide; therefore, the nursery is bathed in oligotrophic water (and perhaps larvae) from the Exuma Sound on every tide, whereas areas farther out on the bank are not (Jones, 1996; Stoner et al., 1996b). These hydrographic characteristics may result in the deposition of larvae in the long-term nursery area, or the lower bottom-water velocities may allow them to settle.

Density of newly settled conch had a strong negative correlation with distance from the center of the traditional nursery ground but was relatively independent from all other environmental characteristics tested (i.e. depth and various qualities of sediments, seagrass, and macroalgae). This finding indicates that conch settlement cannot be explained

<sup>1</sup> Stoner, A. W., and M. Ray-Culp. 1997. Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 74 Magruder Road, Highlands, NJ 07732. Unpubl. data.

simply by fine-scale hydrodynamic relationships associated with seagrasses and macroalgae, as observed for certain other invertebrates including mollusks (Eckman, 1987; Harvey et al., 1993, 1995). In fact, conch larvae settled in approximately equal densities across the seagrass gradient at transect D which spanned only 250 m. Therefore, the structure provided by macrophytes appears not to influence settlement of conch larvae even though older juveniles prefer seagrass habitats and are associated with an optimal shoot density (Stoner and Waite, 1990).

Although accumulation of competent larvae near the Shark Rock nursery is the most parsimonious explanation for the observed settlement and recruitment patterns, earlier experiments indicate that seemingly similar seagrass beds offer different qualities that have significant effects on larval and juvenile conch. Laboratory experiments have shown that macrophytes collected from stations within the Shark Rock nursery (B, C3, D3, D4) induced significantly higher metamorphosis than the same types of substrata collected outside the general nursery area (stations A, F) (Davis and Stoner, 1994). Growth rates of newly settled conch (1.2 mm) fed seagrass detritus from the different sources reflected metamorphic responses on the same substrata (Stoner et al., 1996a), and when 1-yr-old juvenile conch were transplanted to stations A and F, growth rates were low in comparison with those in the Shark Rock nursery (Stoner et al., 1994). It is clear, therefore, that the nursery area is trophically unique, despite visual similarity to surrounding areas.

Micro-organism films that coat the sediment in soft-bottom communities are known to be important inducers of metamorphosis in conch and other invertebrates, most likely because they are associated with favorable nutritional requirements for postlarvae (Scheltema, 1961; Gray, 1974; Davis and Stoner, 1994; Stoner et al., 1996a). Characteristics that make the Shark Rock nursery an attractive location for settling larvae and an ecologically suitable habitat for juveniles probably stem from hydrodynamic properties of the location that affect nutrient cycling and productivity patterns in certain algal foods for conch (Stoner et al., 1994, 1996b). Field manipulations will be needed to distinguish direct effects of hydrodynamics (i.e. larval transport and retention) from indirect effects such as hydrographic mediation of biological productivity, habitat choices, and postsettlement processes.

Postlarval conch recruited to the same habitats traditionally occupied by 1- and 2-yr-old animals. This association is probably not the result of conspecific attraction because settlement was equally high at stations with and without older conspecifics. This

result corroborates an earlier laboratory study showing that cues associated with previously settled juveniles (slime trails, feces, and the older conch themselves) did not elicit larval metamorphosis (Davis and Stoner, 1994).

### The role of micropredators on conch recruitment

Although settlement of queen conch was relatively independent of habitat features other than location, predator distributions were highly correlated with seagrass shoot density, detrital abundance, and sediment organics and grain size. Numerous studies have shown that animal abundances in seagrass beds are correlated with certain measures of habitat complexity such as seagrass blade density or biomass, detrital biomass, leaf characteristics, or rhizome structure (Orth et al., 1984; Stoner and Lewis, 1985). The association between benthic macrofauna and physical structure may be related to food abundance or predation, or both. There is abundant experimental evidence that the physical structure provided in seagrass beds reduces predation rates on invertebrates (Heck and Wilson, 1987; Heck and Crowder, 1991). Potential conch predators dredged in this study were prey species themselves, and they undoubtedly derived some measure of protection or nutrition from the habitat, or both.

Predation on early postsettlement stages can be an important process affecting the number of invertebrate settlers that survive to recruit into a population (Thorson, 1966; Keough and Downes, 1982; Osman and Whitlatch, 1995). Heavy losses to micropredators during the first days or weeks after settlement can severely diminish or eliminate a prey species, and even regulate community composition (Osman et al., 1992; Osman and Whitlatch, 1995). It is apparent from the length frequency of dead conch collected in this study that very high mortality occurs immediately after settlement, when conch are <5-mm shell length. Queen conch have many predators at this size (Ray-Culp et al., 1997), and one of the most important is probably the xanthid crab *Micropanope* sp., which was the most abundant invertebrate counted in dredge samples. The crab is capable of killing conch that are up to 0.5 times its own carapace width (Ray-Culp et al.<sup>2</sup>). Although a large proportion of the xanthids collected were too small (mode=1.5 mm) to kill even newly settled conch

<sup>2</sup> Ray-Culp, M., M. Davis, and A. W. Stoner. 1998. Escaping the xanthid crab gauntlet—the role of size, density and habitat for newly-settled queen conch. Caribbean Marine Research Center, 805 E. 46th Place, Vero Beach, FL 32963. Unpubl. manusc.

(1.2 mm), xanthids up to 10 mm were far more abundant than conch, and they undoubtedly play a major role in conch mortality. The high positive correlation between live conch and xanthids suggests that conch settle in areas prone to high predator abundance. However, with typical summer growth rates, mentioned earlier, conch would escape predation by xanthids in about 10 days when they reach 5 mm shell length. Consequently, predator-prey relationships associated with the early postsettlement stages may be highly dynamic, with suites of predators shifting rapidly over time.

There was an increase in conch survivorship from bare sand to moderate density seagrass over both cross-channel transects. A similar trend was obtained experimentally when year-class 0 and 1 juveniles were tethered over an analogous seagrass gradient near transect D (Ray and Stoner, 1994, 1995). Highest mortality occurred on bare sand and in highest seagrass biomass whereas lowest mortality occurred in moderate biomass. It appears that a certain amount of seagrass structure provides protection, but too much is detrimental. However, in the down flow field dimension, survivorship was highest within the traditional nursery ground, and distribution is clearly related to both settlement and survivorship in this dimension.

### Identifying critical habitats

Our findings have important management implications for queen conch and other species associated with seagrass beds. First, it may not be possible to determine the value of a particular site for a species on the basis of simple habitat maps. Even descriptions of the beds that include seagrass species composition, biomass, and shoot density do not provide adequate information to identify critical habitats for conch. Value of specific seagrass bed locations also depends upon hydrography, larval retention, larval settlement, predator abundance, and the related survivorship. Persistence in the locations of queen conch nurseries near Lee Stocking Island (Stoner et al., 1996b; Jones, 1996) indicates that these factors are relatively constant over periods of several years, and that the specific locations may be as "critical" as habitat type. Only certain seagrass beds are suitable for queen conch; these must be identified and protected. Furthermore, in many areas of the Caribbean, conch populations have been devastated by overfishing, and there is an intense interest in rehabilitating them through releases of hatchery-reared juveniles. Transplant experiments have shown that juvenile conch will survive and grow only in very specific locations, and releases must be made in loca-

tions that ensure economically acceptable survivorship (Stoner, 1994). Clearly, thorough knowledge of distributional mechanisms is necessary to make predictions on the habitat requirements of queen conch and other managed species.

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