

Winter mass migration of juvenile queen conch *Strombus gigas* and their influence on the benthic environment

Allan W. Stoner

Caribbean Marine Research Center, 100 E. 17th Street, Riviera Beach, Florida 33404, USA*
and Lee Stocking Island Exuma Cays, Bahamas

ABSTRACT: From February through March 1988, mass migration of juvenile queen conch *Strombus gigas* was observed in the Exuma Cays, Bahamas. This represents the second documentation of mass migration in the species but unlike the first aggregation of 1-yr old conch, this migration was comprised primarily of individuals 2 yr old. Like the earlier mass migration, advance of the aggregation was in the direction of the ebb tide. Progression of the aggregation started and stopped 3 times during the 1 mo observation period. Non-moving clusters of randomly oriented individuals were formed as a response to increasing wave action associated with the passage of cold fronts. Grazing by conchs in the aggregation had a significant influence on the biomass of seagrass macrodetritus and epiphytes, but not on living seagrass blades. A tagging experiment showed that the aggregation dispersed at $4.1\% \text{ d}^{-1}$. Rapid increase in conch density with the passage of the migration provides further support for the hypothesis that such migrations serve as a dispersal mechanism for juvenile conchs from centers of recruitment.

INTRODUCTION

The queen conch, *Strombus gigas*, is a large commercially significant gastropod common in the Caribbean Sea and Bahama Islands (Brownell & Stevely 1981), and the general life history is relatively well known for the period after the first year of life (see Randall 1964). After being buried in the sediments of shallow sand habitats for the first year, juvenile queen conchs emerge and move to seagrass meadows where plant detritus and algal foods are abundant. The juvenile conchs continue to be associated primarily with seagrass beds for the next 2 yr. At ca 3.5 to 4.0 yr, the conchs reach sexual maturity and have a size of at least 180 mm total shell length. Adults are found in seagrass meadows and offshore sand and algal plains, usually deeper and distinct from the juvenile habitats. Thus over the life history of the species, individuals tend to move from shallow inshore sands to deeper, offshore sites.

Mechanisms related to migration and orientation in

Strombus gigas are unknown; however, inshore/off-shore migrations are known to occur seasonally in relation to reproductive behavior (Robertson 1959, Randall 1964, Weil & Laughlin 1984) and ontogenetic migration to deeper water with increasing age has been documented (Randall 1964, Hesse 1979, Weil & Laughlin 1984). Ontogenetic migration may also take the form of migration en masse in the offshore direction. In the spring of 1987, Stoner et al. (1988) discovered mass migrations of newly emerged 1-yr old *S. gigas* in the Exuma Cays, Bahamas. One migrating aggregation had over 100 000 individuals with density as high as $319 \text{ conchs m}^{-2}$. The aggregation was observed for a period of 14 wk, during which time it advanced in the direction of the ebb tidal flow. Mass migration was hypothesized to represent dispersal of juveniles from centers of larval recruitment, and to be initiated by density-dependent behavior.

New observations and experimentation with a winter mass migration of ca 2-yr old *Strombus gigas* are reported here. Orientation, progression rate, dispersion rates, responses to weather conditions, and effects of the migrating aggregation on the benthic community are discussed.

* Address for correspondence

MATERIALS AND METHODS

The new aggregation of *Strombus gigas* juveniles was observed first on 12 February 1988, in the vicinity of previously sighted migrations, near Children's Bay Cay in the Exuma Cays, central Bahama Islands. The aggregation was located in 1.5 m depth (MLW), in an area characterized by strong, reversing tidal flows, and 1.0 m of tidal range. The firm carbonate sand bottom is vegetated with a sparse stand of the seagrass *Thalassia testudinum*.

Dimensions of the aggregation were measured with a long tape, and densities of conchs within the aggregation were determined by counting all individuals within either 1.0 or 0.5 m² frames which were placed at various positions along the band of conchs. Densities in advance of and behind the aggregation were determined by counting all conchs within circles of 2.5 m radius (19.6 m²), evenly spaced and replicated 3 times on each side of the aggregation. Density measures in front of and behind the aggregation were made before and after the passage of the migration at Positions B, C, D, and E (Fig. 1). Each circle was positioned with its circumference 1.0 m from the aggregation. Length-frequency data were collected by measuring all conchs within the above described areas with large calipers. Individuals with flared lip of the shell were classified as adults; all others were considered to be juveniles.

As the aggregation progressed over the seagrass meadow in the direction of the ebb tidal flow, between 5 and 9 stakes were placed at the forward edge of the aggregation, the number of stakes decreasing as the aggregation dispersed at the ends over time. New stakes were placed at intervals of between 1 and 2 d and the rate of progression of the aggregation was determined by measuring the distance between stakes placed on the different dates.

Orientation was determined for conchs in actively migrating segments of the aggregation, in segments of the aggregation which were clustered and not migrating (see below), and in front of the aggregation. This was accomplished by placing a compass directly over an individual and noting the compass direction of the anterior end of the shell.

Rates and directions of dispersion from the aggregation were determined by tagging 190 individuals in the aggregation with short pieces of highly visible vinyl cord on 23 February 1988. The spaghetti tags (Floy Tag and Manufacturing, Inc.) were tied around the spire and spines of the shells and tag loss is assumed to be zero. The tagged conchs were then tracked as they either remained with or dispersed from the aggregation over subsequent days. Six counts were made between 24 February and 11 March 1988.

Macrophyte collections were made at 3 locations

before and after passage of the conch aggregation (Positions B, C, and D, Fig. 1). All macrophytes within 0.25 m square quadrats were collected from locations in line with Stakes 1 through 5, 1 quadrat per stake. In the laboratory, these macrophytes were separated by species (including a category for macrodetritus comprised mostly of senescent seagrass blades), dried at 80 °C, and weighed.

Individual seagrass blades were collected at Positions C and D (Fig. 1) for determination of epiphyte loads before and after passage of the aggregation. In each of the 5 locations described above for macrophyte samples, 10 to 12 green seagrass blades were cut at the sediment, placed in plastic bags, and preserved with 5 % formalin-seawater mixture. In the laboratory, the leaves were placed in 10 % phosphoric acid to remove the calcareous shells of various epizoans. Epiphytes were scraped from the leaves with a sharp blade, taking care not to remove seagrass tissue. Epiphytes and seagrass blades were dried separately at 80 °C and weighed. Epiphyte biomass was quantified on the basis of grams epiphytes per gram seagrass blade, where the 10 to 12 blades were combined.

For determination of conch feeding activity, 115 to 140 mm conchs were collected in front of the aggregation, from within the migrating aggregation, and from non-moving clusters. The conchs were frozen immediately after collection. Later, they were thawed, extracted from their shells, and stomach fullness was coded from 0 (empty) to 5 (distended with food).

During the investigation, weather observations were recorded daily, as well as wave conditions at the study site. Water temperature was also measured daily or near so.

RESULTS

Dynamics of mass migration

The queen conch aggregation was first discovered on 12 February 1988, as a long band of juveniles arranged along an east-west orientation. On 18 February, the aggregation was measured and 9 stakes were placed at approximately equal intervals along its south edge. At this time, the aggregation was 51 m long and arranged in a nearly straight line. Stakes were placed along the aggregation on several subsequent dates to provide a scale drawing of its movement and dimensions (Fig. 1). By 23 February, the aggregation had moved an average of 14.6 m to the southeast, in the direction of the ebb tide. Over the next 2 wk observation, migration continued in the same direction with the west end of the aggregation dispersing most rapidly. By 25 February, the consolidated segment of the aggregation was 25 m long with an extension of ca 20 m of high density

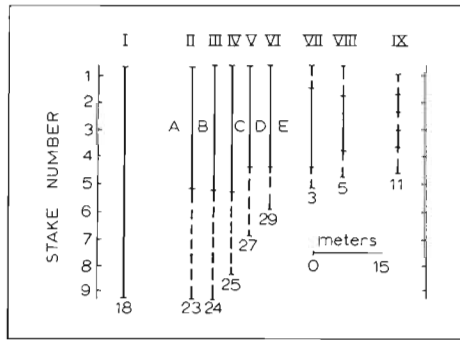


Fig. 1. Scale drawing of progression of mass migration of juvenile conchs in Exuma Cays, Bahamas, between 18 Feb and 11 Mar 1988. Continuous lines: discrete, band-like formation of high density conchs with date shown at bottom of each vertical line; dashed lines: sections of aggregation which were dispersed. Roman numerals refer to location of the aggregation, and capital letters show positions on the bottom where biological measurements were made before and after passage of the aggregation. Distance moved by the aggregation between 3 and 11 Mar was estimated. Direction of ebb tide was from left to right, perpendicular to the axis of the aggregation

conch, but where shells were not touching each other. Both ends of the aggregation were dispersing by 3 March, and on 11 March only 2 short segments (5 m each) of the aggregation remained in the consolidated form. At this point, observations were terminated.

Progression of the front was highly variable and dependent upon weather conditions (Fig. 2). The aggregation stopped forward movement, and broke into very high density clusters on several occasions (e.g. on 3 March, there were nearly 200 conch m^{-2} in non-moving clusters). Partial clustering occurred on 18 February concurrent with low water temperature for the period (24 °C) and high velocity southerly winds which set up strong wave surge in the study site. The aggregation remained clustered and relatively stationary through 19 February with continuing strong south wind. Clustering occurred again on 27 February concurrent with a second drop of water temperature and strong wind from the north and west. The third major clustering event was observed on 3 March, when winds from the east southeast again set up strong wave action at the study site, although a temperature minimum did not occur at that time.

Conch density within the aggregation (Fig. 2) was highest, at 200 m^{-2} , on 3 March during clustering periods (Fig. 2), and lowest, at 40 m^{-2} , between 23 and 25 February when water temperature was high, wind was slow, and the aggregation was moving across the seagrass meadow at highest velocity (to 4.7 $m d^{-1}$). After passage of the aggregation, conch density in the seagrass meadow increased from an average of 0.08 to 1.06 conchs m^{-2} . At the 4 positions where density changes were observed before and after passage of the

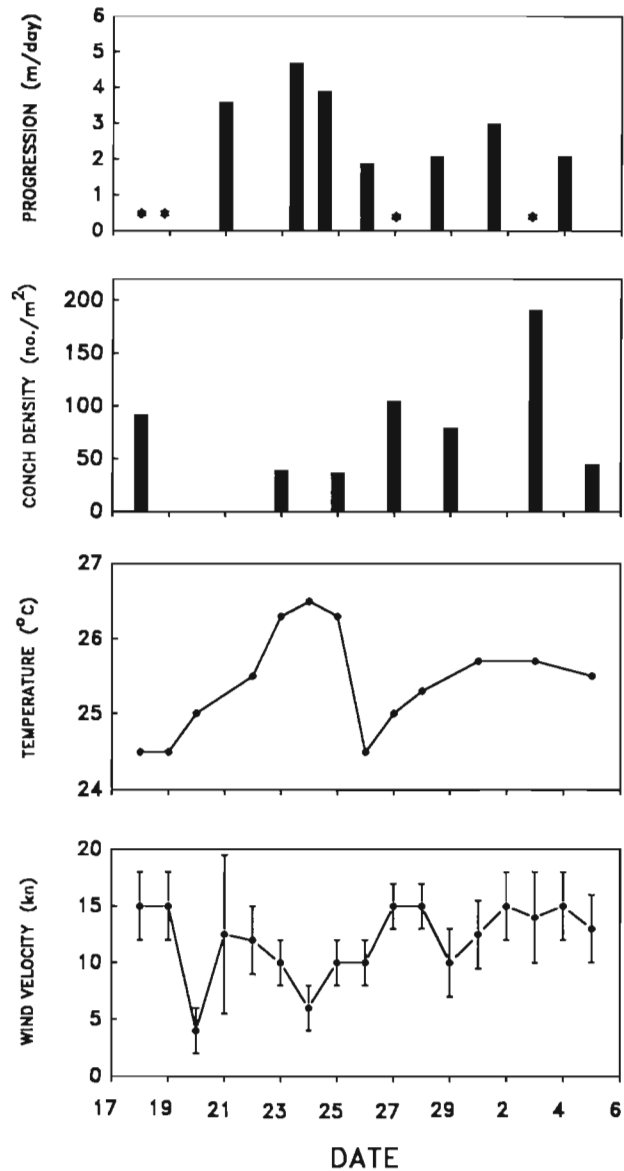


Fig. 2. *Strombus gigas*. Progression of the conch aggregation and density of conchs in the aggregation as they relate to water temperature and wind velocity between 17 Feb and 6 Mar 1988. *Indicate dates during which there was no forward progression of the aggregation

aggregations, the increase ranged from 4 times at Position D to 36 times at Position C (Fig. 3). Wilcoxon's signed-ranks test for paired comparison showed that the density of conchs after each passage of the aggregation was significantly greater than that before passage ($T_s = 0$, $n = 12$, $p = 0.002$).

Length-frequency data were collected on 18 February for conchs in the aggregation and behind the aggregation with no significant difference in mean size (Kolmogorov-Smirnov test, $p > 0.05$). Those in the aggregation had a mean total shell length of 135 mm

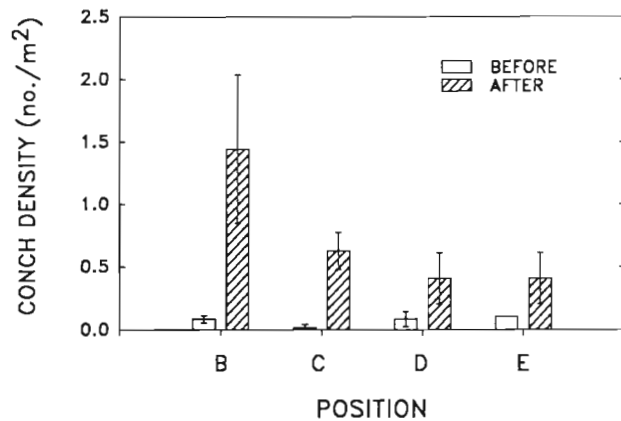


Fig. 3. *Strombus gigas*. Density of conchs at 4 different positions in seagrass meadow before and after passage of the conch aggregation

(SD = 11, n = 128) with a range of 106 to 181 mm. Behind the migration the mean size was 131 mm (SD = 11, n = 87) with a range of 104 to 163 mm. Only 3 of the total number measured were adults; 2 were in the aggregation.

Orientation was measured on 29 February for 3 sets of conchs: (1) individuals in front of the aggregation, (2) individuals within actively moving portions of the aggregation, and (3) individuals within clumped segments of the aggregation (Fig. 4). Of the conchs in front of the aggregation, 59 % were oriented within 45° of the ebb flow, and the orientation was significantly different from random ($\chi^2 = 20.25$, $p < 0.001$). Of the conchs within the migrating aggregation, 83 % were oriented within 45° of the ebb flow, a highly significant orientation ($\chi^2 = 68.0$, $p < 0.001$), and less than 1.0 % of the animals had their lips buried. Conchs in clustered segments showed a high degree of partial burial (80 %) and random orientation ($\chi^2 = 2.576$, $p > 0.05$). It appears, therefore, that actively moving conchs showed orientation with the ebb tidal current and that this tendency was strongest in individuals within a mass migration.

Dispersion of the aggregation was observed over a period of 18 d, from 23 February to 11 March (Fig. 5). One day following initial tagging, 146 tagged individuals were found in the mass migration. On the second day 169 tags were in the aggregation, with a steady decrease thereafter. The simple linear regression of numbers of tagged individuals found in the aggregation over days of observation was significant ($F = 70.38$, $p < 0.001$, $R^2 = 0.934$), and the negative slope of the regression showed that the aggregation was dispersing at a rate of 4.18 % d^{-1} during the study period. The initial decline in the number of tags in the aggregation may have been related to disturbance of the tagged individuals.

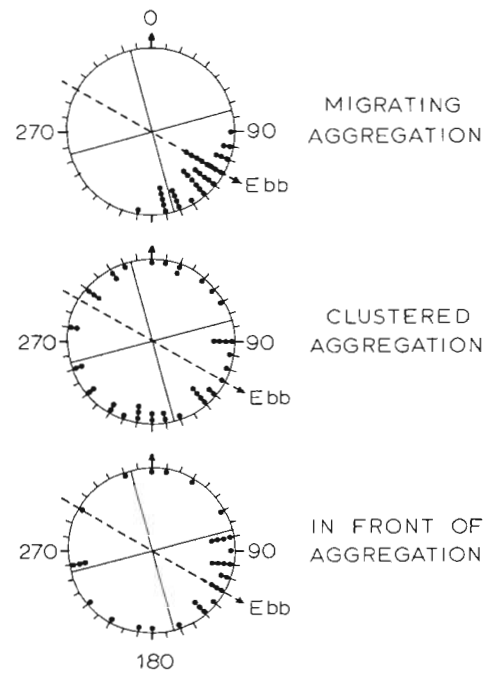


Fig. 4. *Strombus gigas*. Orientation of conchs within actively moving and non-moving (clustered) segments of the aggregation, and in front of the aggregation. (●): Number of conchs with siphonal ends of shell oriented in specified compass directions. Ebb tidal flow averaged 120° magnetic

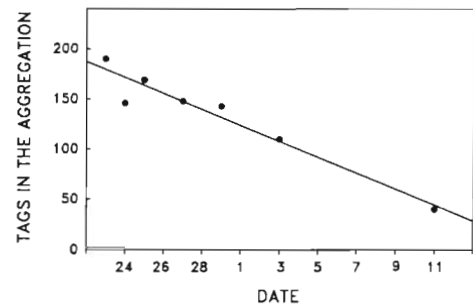


Fig. 5. *Strombus gigas*. Number of tagged conchs found within the aggregation after initial placement of 190 individuals on 23 Feb 1989

Effects on the benthos

Wilcoxon's signed-ranks test for paired comparison showed that seagrass biomass values before and after the passage of the conch aggregation were not significantly different ($T_s = 21$, $n = 12$, $p = 0.158$) (Fig. 6). The standing crop of macrodetritus showed a dramatic decrease after passage of the conch migration at Positions B and C in the seagrass meadow, but little change at Position D (Fig. 6). The effect of conchs on detrital biomass, however, was highly significant ($T_s = 10$, $n = 12$, $p = 0.011$) because detritus decreased in abun-

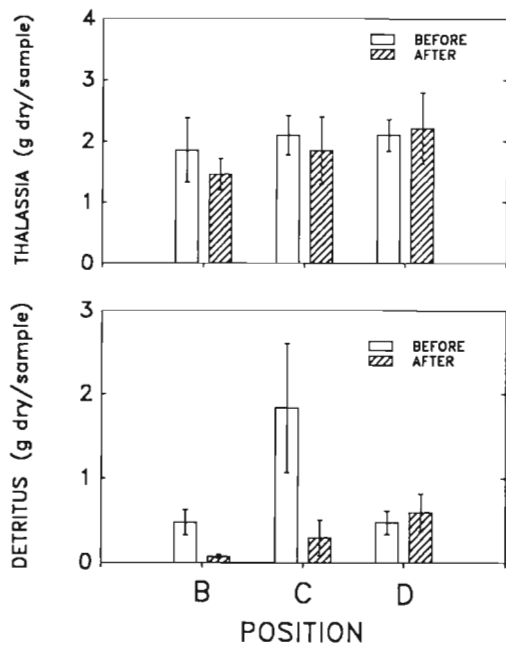


Fig. 6. Biomass of living seagrass and macrodetritus at different positions in the seagrass meadow before and after passage of the conch aggregation

dance at all but 2 of the locations examined before and after passage of the aggregation.

Epiphytes living on the blades of *Thalassia testudinum* were also reduced significantly in biomass with the passage of the aggregation (Wilcoxon's signed-ranks test, $T_s = 0$, $n = 8$, $p = 0.012$) (Fig. 7). Epiphyte biomass was just over 0.06 g dry wt of epiphytes per g dry wt of seagrass before the passage of the conch aggregation over both Positions C and D, but reductions of 56 and 62 % of epiphyte biomass were observed at the 2 positions. Certain unidentified epiphytes were not grazed, but there was also a noticeable decrease in the abundance of bottom-dwelling

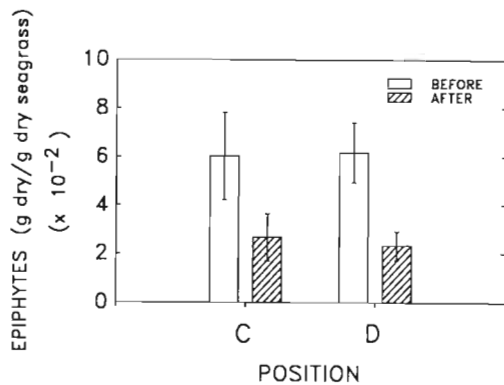


Fig. 7. Biomass of seagrass epiphytes at 2 different positions in the seagrass meadow before and after passage of the conch aggregation

algae, including *Batophora oerstedii*, with passage of the aggregation.

Other notable, but unquantified, effects of the aggregation were a general 'cleaning' of the sediment surface. The surface of the carbonate sediment behind the aggregation was white, as opposed to the light brown color of the sediment in front of the aggregation. After passage of the aggregation the sediment appeared to be free of filamentous algae and small detrital particles. Conch fecal pellets were abundant on the surface of the sediment after passage of the aggregation.

Feeding activity of the conchs varied with location relative to the aggregation. Individuals in front of the aggregation were actively feeding and had full stomachs (fullness index = 4.5 ± 0.5 , mean \pm SD). In the migrating aggregation the index was 3.0 ± 0.8 , and in clustered segments of the aggregation, stomachs were relatively empty (1.3 ± 0.8).

DISCUSSION

This report represents the second analysis of mass migration in juvenile queen conch. Unlike the first report of mass movement in 1-yr old conch in April through July 1987 (Stoner et al. 1988), the new observation was made during the coldest time of year and was comprised primarily of conchs 2 yr old. Stoner et al. (1988) hypothesized that mass migration was a result of synchronous emergence of conchs from the sediment at ca 1 yr of age and an ontogenetic shift in habitat from sandy shoals to adjacent seagrass meadows. The observation of 2 yr old conch in mass migration suggests 2 alternative hypotheses: either the mass migration was a remnant of an aggregation formed in the spring of 1987, or that aggregations may form independent of emergence phenomena. Two observations indicate that the latter case may be true. First, it is known that movement in the direction of ebb flow is promoted by high densities of juvenile queen conch (Stoner et al. 1988). Second, during the fall and winter of 1988 to 1989, newly metamorphosed juveniles (< 20 mm shell length) and juveniles less than 1 yr old (35 to 50 mm) were observed in seagrass habitats near the location of the mass migration and not in sandy shoals as has been predicted*. Shift of habitat, therefore, may not be necessary for the formation of a band-like aggregation, but mechanisms remain unknown at this time.

Two kinds of behavior were witnessed in the new observations – the mass migration of a conch aggregate, and clustering of conchs as a response to weather

* Mass migration of 1 yr old conchs did not occur at the study site in 1988

conditions. The 2 behavioral patterns may be independent as the winter clustering of conchs was discussed by Hesse (1976, 1979). She found as many as 22 conchs in what were called 'clumps' formed primarily during winter. Although the clumps were considerably smaller than those found in this study, the mechanisms are probably the same. Hesse suggested that burial and clumping, apparently triggered by rough weather and declining temperature, was a means of stabilization during periods of wave surge. Given that clustering occurred with rough weather in the absence of declining temperature on one occasion, wave action alone probably initiates clustering behavior.

Just as conchs held in enclosures may deplete most of the usable food from seagrass beds (Stoner 1989) and show significant density-dependent growth rates (Appeldoorn & Sanders 1984, Siddall 1984) the movement of a conch aggregation may be related to depletion of foods. Measurements made in this study show that the movement of a high density conch aggregation over a seagrass meadow resulted in dramatic effects on the benthic environment. Conchs in the aggregation were feeding actively as indicated by stomach fullness, and preferred foods such as epiphytes and detritus (Robertson 1961, Randall 1964, Hesse 1976, Woon 1983, Stoner unpubl.) were significantly reduced with the passage of the aggregation. Rate of progression may be determined by the amount of food available; although unquantified, progression was noticeably slower where patches of the alga *Batophora oerstedii* were present. Mass migration in queen conch, therefore, may have properties similar to those of other herbivores such as sea urchins (Lawrence 1975, Chapman 1981). Additionally, grazing of epiphytes and detritus must have a major influence on other components of the benthic community such as epifaunal Crustacea and the smaller Mollusca, and removal of epiphytes may influence the production of the seagrasses.

The February 1988 aggregation was small, relative to that observed in April 1987, it moved more slowly, and it dispersed almost entirely over a 4 wk period. It is impossible, however, to compare duration of the migrations because the times of formation are unknown. Given the fact that abundance of conchs in front of the moving aggregation was nearly zero and many times greater behind, there seems little doubt about the role of mass migration in dispersing conchs across nursery habitats. As in the earlier migration, progression was in the direction of the ebb tidal flow which would take animals to deeper water over the long term. Stoner et al. (1988) hypothesized that such migrations may re-

present dispersion from centers of larval recruitment. Whether or not the aggregations begin as concentrated centers of early post-metamorphic conch has yet to be determined, but the implications of mass migration for fisheries management may be great.

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