WINTER MASS MIGRATION OF JUVENILE QUEEN CONCH, *Strombus gigas*, AND THEIR INFLUENCE ON THE BENTHIC ENVIRONMENT

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ABSTRACT

In February 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 one year old conch, this migration was comprised of individuals approximately two years 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 three times during the month long observation period, with the band-like aggregation forming many tight clusters of randomly oriented individuals as a response to declining water temperature or increasing wave action associated with the passage of cold fronts. The passage of the aggregation had a significant influence on the biomass of macrodetritus and epiphytes, but not living seagrass. A tagging experiment showed that the aggregation dispersed at 4.1% per day. The rapid increase in conch densities with the passage of the migration provides further support for the hypothesis that such migrations serve as dispersal mechanism for juvenile conch from centers of recruitment.

INTRODUCTION

The queen conch, Strombus gigas, is a large commercially significant gastropod common to the Caribbean Sea and Bahama Islands (Brownell & Stevely 1981). The general life history is relatively well known for the period after the first year (see Randall 1964). It is believed that after being buried in the sediment for the first year, juvenile queen conch emerge and move to seagrass meadows where detrital and algal foods are abundant, and where they spend most of the next two years. At approximately 3.5 to 4.0 years, the animal reaches sexual maturity and has a size of 180 mm in total shell length or more. These large individuals are found in seagrass meadows and offshore sand and algal plains, usually 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 of the species are unknown; however, inshore/offshore 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). In the spring of 1987, Stoner et al. (1988) discovered mass migrations of newly emerged one-year old Strombus gigas in the Exuma Cays, Bahamas. One migrating aggregation had over 100,000 individuals in densities as high as 319 animals/m^2, and was observed for a period of 14 weeks, advancing 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 approximately two year old *Strombus gigas* are reported here. Orientation, progression rate, dispersion rates, responses to weather conditions, and the effects of the migrating aggregation on the benthic community are discussed.

METHODS AND MATERIALS

An 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. Dimensions of the aggregation were measured with a 30 m long tape. Densities of animals within the aggregation were determined by counting all animals in either 1.0 by 1.0 m or 0.5 by 1.0 m areas which were replicated at various positions along the band of animals. Densities on both sides of the aggregation were determined by counting all animals within circles of 2.5 m radius, replicated three times on each side. Length-frequency data were collected by measuring all animals within the above described areas with large calipers. Density measures outside the aggregation were made before and after the passage of the aggregation at positions B, C, D, and E (Fig. 1).

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 days and the rate of progression of the aggregation was determined by measuring the distance between paired stakes placed perpendicular to the direction of movement.

Animal orientation was determined for animals 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 animal noting the compass direction of the siphon.

Rates and directions of dispersion from the aggregation were determined in an experiment where 190 individuals within the aggregation were tagged with short pieces of highly visible vinyl cord on 23 February. These animals were then tracked as they either remained with or dispersed from the aggregation over the subsequent days. Six counts were made between 24 February and 11 March, 1988.

Macrophyte collections were made at three locations before and after passage of the conch aggregation (positions B, C, and D, Fig. 1). All macrophtes within 0.25 m square quadrats were collected from locations in line with stakes 1 through 5, one 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 five 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. Then epiphytes were carefully scraped from the leaves with a sharp blade, taking care not to remove seagrass tissue. Epiphytes and seagrass blades were then dried separately at 80°C and weighed. Epiphyte biomass was quantified on the basis of grams epiphytes per gram seagrass blade, where the 10-12 blades were combined.

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 Febraury 1988, as a long band of juveniles arranged along an east-west orientation. On 18 February, the aggregation was measured and nine 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 two weeks of observation, the 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 approximately 20 m of high density conch, but where shells were not touching each other. Both ends of the aggregation were dispersing by 3 March, and on 11 March only two short segments (5 m each) of the aggregation remained in the consolidated form. At this point, observations were terminated.

Progression of the wave was highly variable and dependent upon weather conditions (Fig. 2). During certain periods, the migration stopped forward movement, and the aggregation broke into very high density clusters (e.g., on 3 March, there were nearly 200 conch/m^2 in non-moving clusters). At least partial clustering occurred on 18 February concurrent with low water temperature for the period (24 °C) and high velocity southerly winds which set up a strong wave surge in the study site. The aggregation remained relatively stationary and clustered 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 was observed on 3 March, when winds from the east southeast again set up strong wave action at the study site, although there was no temperature low at that time.

Animal densities were highest during clustering periods (Fig. 2), ranging from 200/m^2 on 3 March to approximately 40/m^2 between 23 and 25 February, when water temperature was high, wind was low, and the aggregation was moving across the seagrass meadow at highest velocity (to 4.7 m/day).

Length-frequency data were collected on 18 February for conch in the aggregation and behind the aggregation. Those in the aggregation had a mean total shell length of 135 mm (S.D. = 11; n = 128) with a range of 106 to 181 mm. Behind the migration the mean size was 131 mm (S.D. = 11; n = 87) with a range of 104 to 163 mm. Only three of the total numbers measured were adults; two were in the aggregation.

Orientation was measured on 29 February for three sets of animals: 1) conch in front of the aggregation, 2) conch within actively moving portions of the aggregation, and 3) conch within clumped segments of the aggregation (Fig. 3). Six percent of all animals in front of the migration had their lips buried in the sediment and thus were inactive; however, these conch showed a tendancy to be oriented in the direction of the ebb current. Fifty-nine percent of the animals were oriented within 45° of the ebb flow, and the orientation was significantly different from random ($X^2 = 20.25$, $p < 0.001$). Eightly-three percent of the conch within the migrating aggregation were oriented within 45° of the ebb flow, a highly significant orientation ($X^2 = 68.0$, $p < 0.001$), and less than 1.0% of the animals were buried. Animals in clumped segments showed a high degree of burial (80%) and random orientation ($X^2 = 2.576$, $p > 0.05$). It appears, therefore, that actively moving conch showed orientation with the ebb tidal current and that this tendancy was strongest in individuals within a mass migration.

Dispersion of the aggregation was observed over a period of 18 days, from 23 February to 11 March (Fig. 4). In the first day after initial tagging of 190 individuals in the aggregation, the number of tags found remaining with the mass migration dropped sharply to 146 individuals. The number increased to 169 in the second day, and decreased steadily for the rest of the period. It is likely therefore, that the initial decline was related to disturbance of the tagged individuals. The simple linear regression of numbers of tagged individuals remaining in the aggregation over days of observation was significant ($F = 70.38$, $p < 0.001$, $R^2 = 0.934$), and the slope of the regression showed that the aggregation was dispersing at a rate of 4.18% per day during the study period.

Mass migration of queen conch served to disperse the animals across the seagrass bed. After passage of the aggregation, conch densities in the seagrass meadow increased from an average of 0.08 animals/m^2 to 1.06 animals/m^2. At the four positions where density changes were observed before and after the passage of the aggregation, the increase ranged from 4 times at position D to 36 times at position C. Analysis of variance (Table 1) showed interaction effects of position and the aggregation because density behind the aggregation deceased with position from B to E. The effects of wave passage on the density of animals in the seagrass bed, however, were dramatic (Fig. 5).

Effects on the Benthos

Conch had no significant effect on the standing crop of living Thalassia testudinum (Fig. 6; Table 2) at any of the three positions were macrophytes were collected before and after the aggregation passed. The standing crop of macrodetritus, however, showed variable response to the passage of the conch migration. Two-way ANOVA (Table 2) indicated that there were significant interaction effects of position and time. This is explained by the fact that detritus was very abundant at position C before the passage of the aggregation and by the lack of effect of the conch at position D. At positions B and C, however, there was a dramatic decline in detrital abundance with the passage of the conch migration.

Epiphytes living on the blades of Thalassia testudinum were reduced significantly in biomass with the passage of the aggregation over two different positions in the seagrass meadow (Fig. 7, Table 3). Epiphyte biomass was just over 6.0 g dry weight of epiphytes per g dry weight of seagrass before the passage of the conch aggregation over both positions C and D. This biomass was not reduced to zero by the passage, but by 56 and 62% of the original standing stock. It appeared that certain unidentified species were not grazed. There was also a noticeable decrease in the abundance of bottom-dwelling algae with passage of the aggregation; these included Batophora sp.

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. ~~.pa~~

DISCUSSION

This report represents the second analysis of mass migration in juvenile queen conch. Unlike the first report (Stoner et al., 1988) of mass movement in one-year old conch in April through July, 1987, the new observation was made during the coldest time of year and was comprised of animals approximately two years old. Stoner et al. (1988) hypothesized that mass migration was a result of synchronous emergence of conch from the sediment at approximately one year of age and an ontogenetic shift in habitat from sandy shoals to adjacent seagrass meadows. The observation of two-year old conch in mass migration suggests two alternative hypotheses: either the mass migration was a remnant of an aggregation forming the previous spring, 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 of 1988, newly metamorphosed juveniles (<20 mm shell length) 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.

It is likely that two kinds of behavior were witnessed in the new observations - the mass migration of a conch aggregate, and clustering of conch as a response to weather conditions. The two behavioral patterns may be independent as the winter clustering of conch was discussed by Hesse (1976, 1979). She found as many as 22 conch in what were called "clumps" formed primarily during winter months. 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.

Just as conch held in enclosures may deplete most of the usable food from seagrass beds (Stoner, in review) 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. Preferred foods such as epiphytes and detritus (Robertson 1961, Randall 1964, Hesse 1976, Woon 1983, Stoner, unpubl. data) were significantly reduced with the passage of the aggregation and rate of progression may be determined by the amount of food available. Although unquantified, the rate of progression was noticably slower where patches of the alga Batophora oerstedi 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). 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 may influence the production of the seagrasses.

The February aggregation was small, relative to that observed in April, it moved more slowly, and it dispersed almost entirely over a four week period; but it is impossible to compare duration of the migrations because the times of formation are unknown. It is clear, however, from the new experimentation, that such migrations are responsible for dispersing animals across nursery habitats. Stoner et al. (1988) hypothesized that such migrations may represent dispersion from centers of larval recruitment. Given the fact that abundance of conch in front of the new aggregation was nearly zero, there seems little doubt about the role of mass migration in dispersal. Whether or not the aggregations begin as concentrated centers of early post-metamorphic conch has yet to be determined, but the implications for fisheries management could be great.

ACKNOWLEDGEMENTS

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Table 1: Results of analysis of variance for density of conch on the seagrass meadow before and after the passage of the conch aggregation over four different positions.

Source	df	MS	F	P
Position	3	0.366	6.317	0.005
Aggregation	1	2.528	43.616	< 0.0001
Position X Aggregation	3	0.365	6.300	0.005
Error	16	0.058		

Table 2: Results of analysis of variance for macrophyte abundance before and after the passage of the queen conch aggregation, at three different positions in the seagrass meadow.

Source	df	MS	F	P
		Living *Thalassia*		
Position	2	0.546	3.068	NS
Aggregation	1	0.189	1.064	NS
Postion X Aggregation	2	0.132	0.741	NS
Error	20	0.178		
		Macrodetritus		
Position	2	1.500	10.993	< 0.001
Aggregation	1	2.320	17.006	< 0.001
Position X Aggregation	2	1.485	10.881	< 0.001
Error	20	0.136		

Table 3: Results of analysis of variance for epiphyte abundance before and after the passage of the queen conch aggregation, at two different positions in the seagrass meadow.

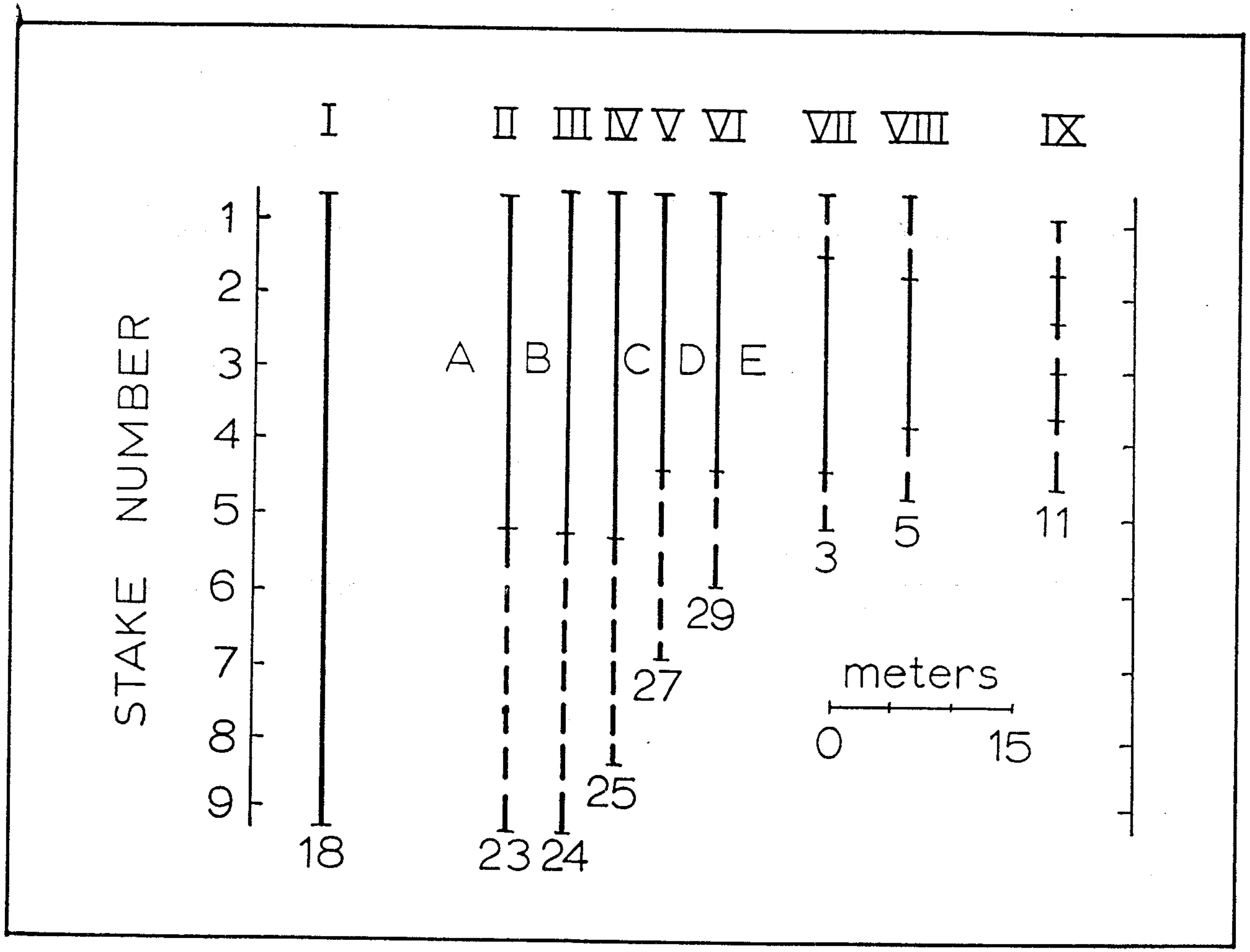
Source	df	MS	F	P
Position	1	0.040	0.018	NS
Aggregation	1	54.629	25.380	< 0.001
Position X Aggregation	1	0.254	0.118	NS
Error	13	2.152		

LIST OF FIGURES

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

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

Fig. 1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VII
VIII
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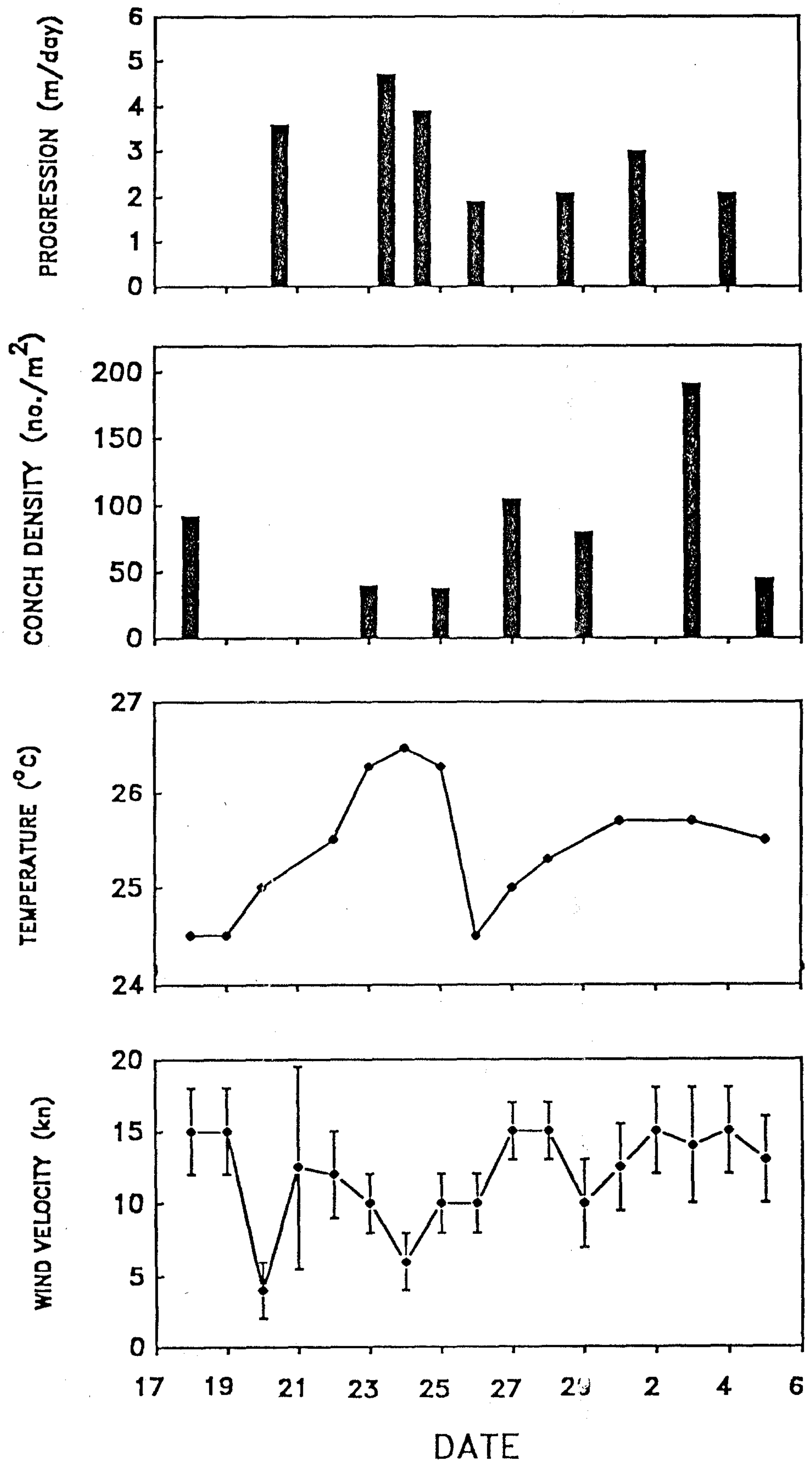
Fig. 2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4
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25
26
27
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DATE

Fig. 3

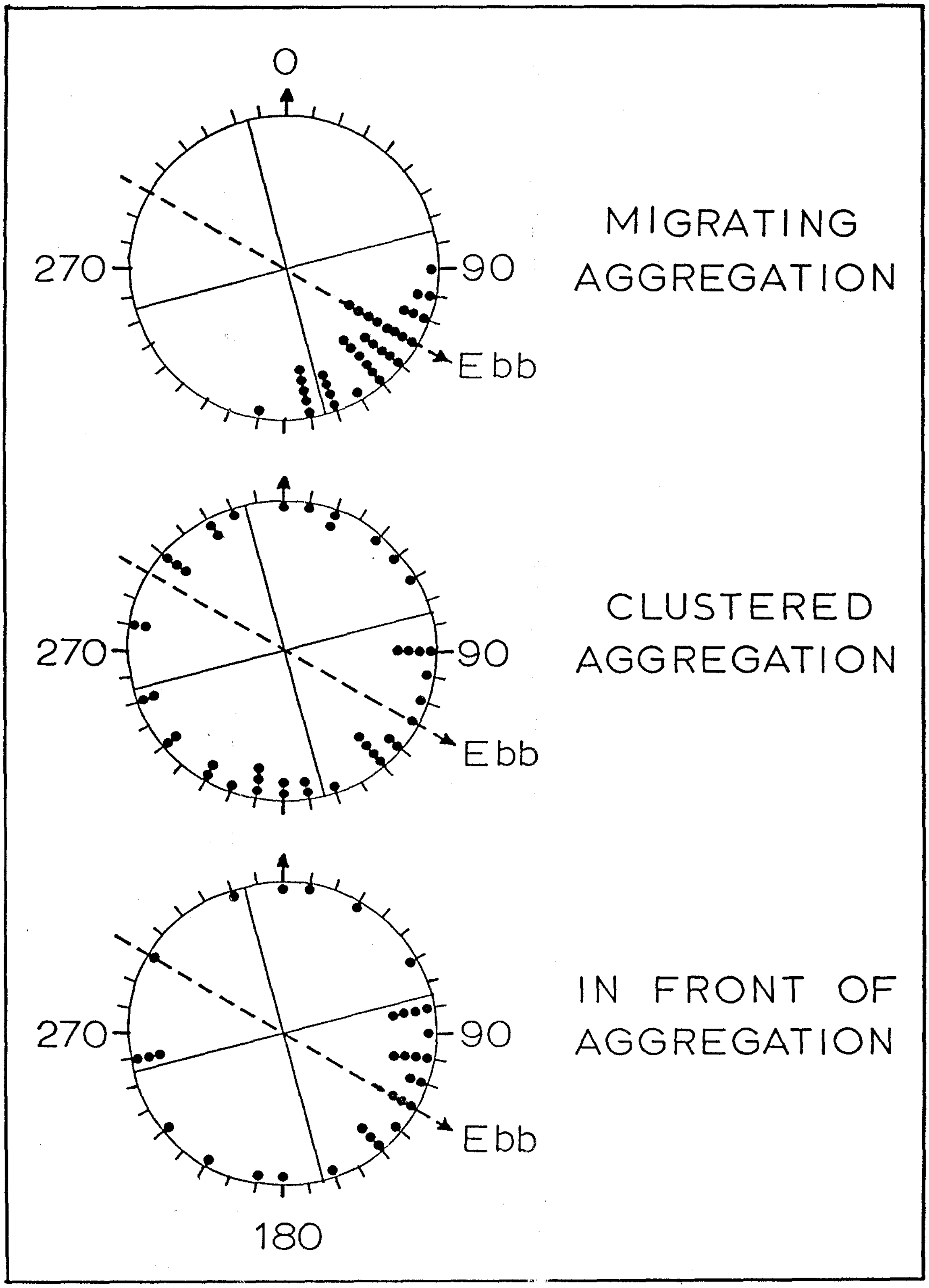
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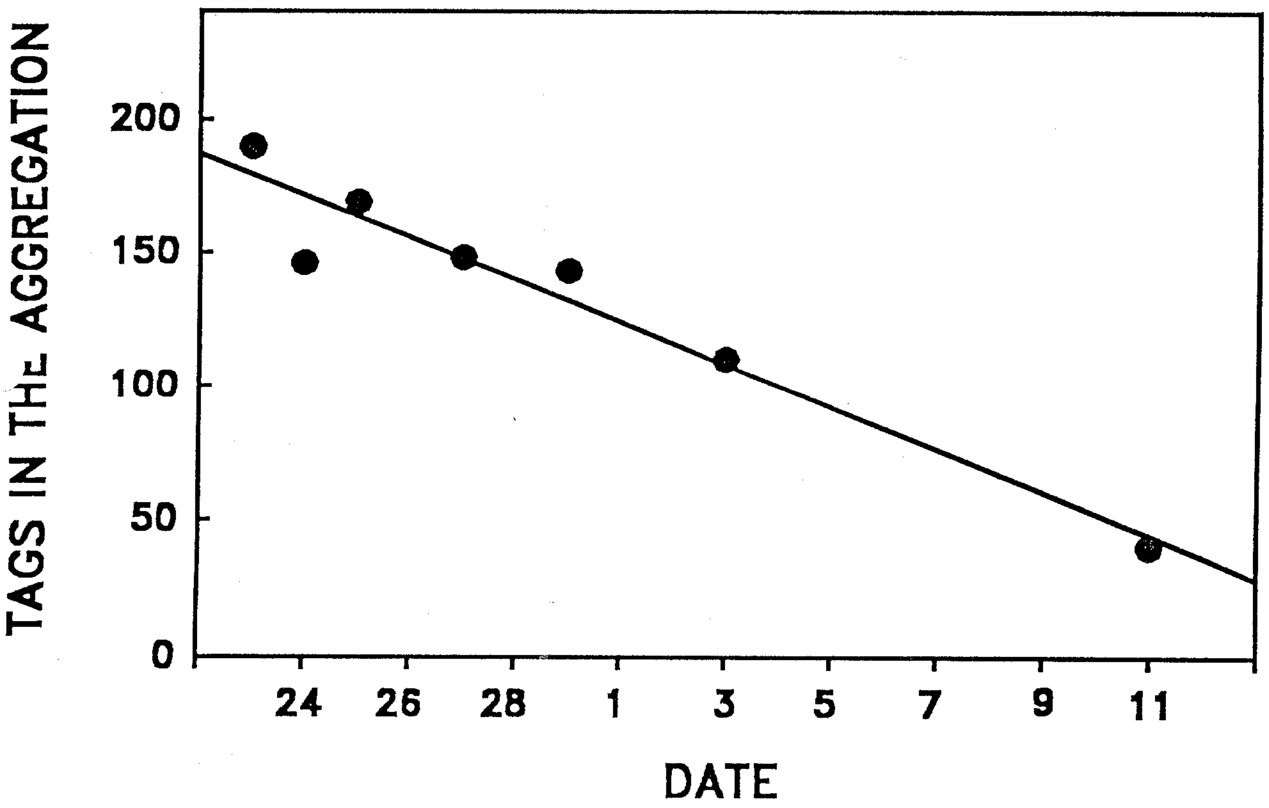
Fig. 4



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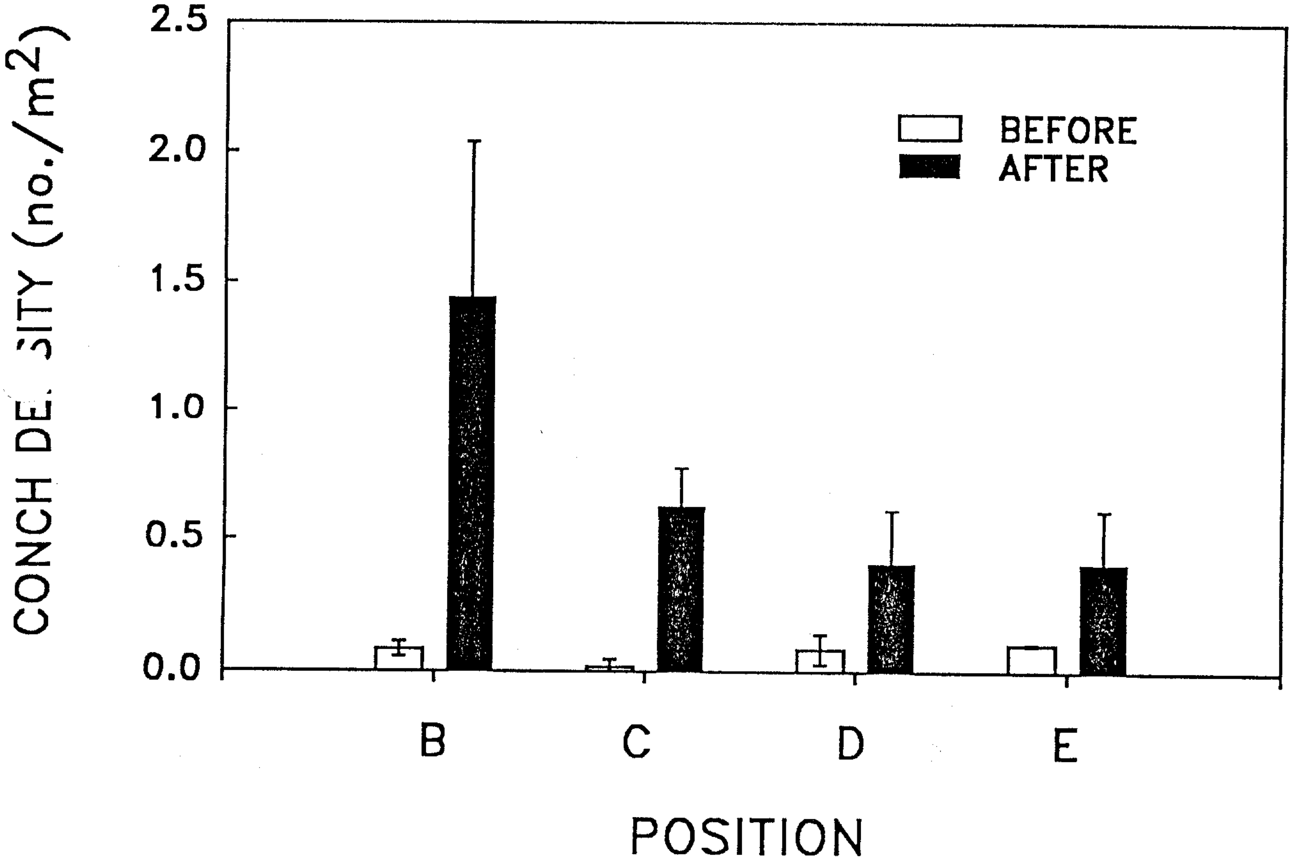

CONCH DE. SITY (no./m2)
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1.5
1.0
0.5
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BEFORE
AFTER
B
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D
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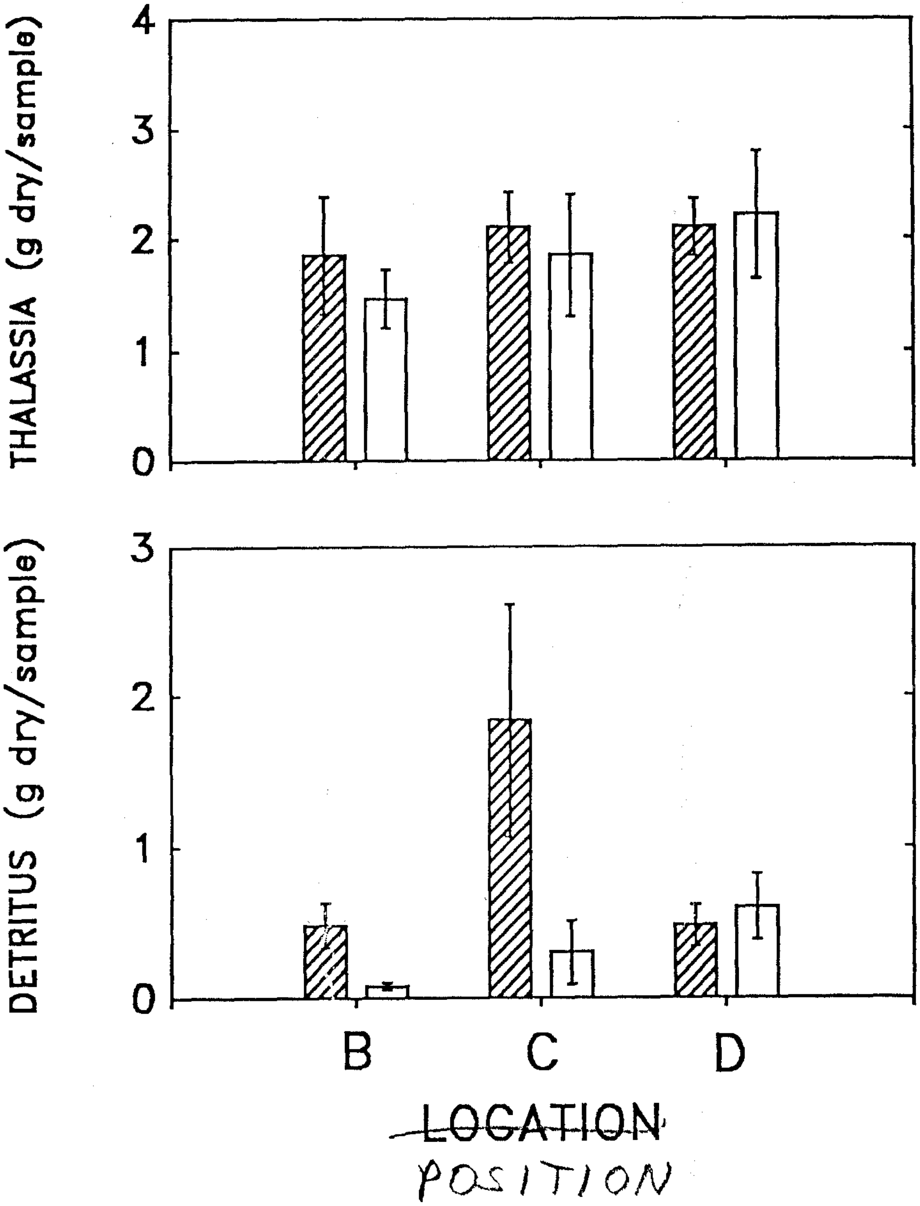
POSITION

Fig. 6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3
2
1
0
DETRITUS (g dry/sample)
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2
1
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POSITION

Fig. 1