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Bivalves (Tellinacea: Donacidae) on a North Carolina Beach: Contrasting Population Size Structures and Tidal Migrations

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ABSTRACT: Populations of the beach clams *Donax parvula* and *Donax variabilis* overlap spatially in North Carolina (USA). However, previous studies may have lumped these species. Hence differential patterns of growth and potential differences in tidal migrations may have been obscured. Intertidal populations of *Donax* spp. were sampled monthly during 1976 and 1977 with a core tube and a hand dredge along transects perpendicular to shore. Juveniles of 2 *Donax* species colonized the beach in late winter. *D. variabilis* individuals grew more rapidly than *D. parvula*, and these 2 populations were easily distinguished during summer by size differences. Tidal migrations of both species ceased in late summer. *D. parvula* moved offshore, but *D. variabilis* remained on the beach, stranded during low tides. These populations appear to undergo seasonal migrations between beach and subtidal habitats. Emigrations from the beach may be related to temperature declines and reproductive requirements. Summer stranding of *D. variabilis* might be an adaptation to fish and crab predation, or an avoidance reaction to crowding stress.

INTRODUCTION

Bivalves of the genus *Donax*, which frequent sandy beach intertidal zones, often rank high among dominant beach macrofauna components along the western Atlantic coast (Pearse et al., 1942; Edgren, 1959; Wade, 1967; Leber, 1977; Matta, 1977; Reilly and Bellis, 1978). Although population studies have been reported for many western Atlantic *Donax* species (Morrison, 1971), others have been neglected, especially *Donax parvula* Philippi, which frequents southeast USA beaches.

Whereas *Donax parvula* is easily distinguished from *D. variabilis* Say by the lack of distinct radial sculpture over most of the shell, it has often been misidentified as *D. variabilis*. Some studies of North Carolina *Donax* south of Cape Hatteras (Pearse et al., 1942; Turner and Belding, 1957; Dexter, 1969) have not distinguished between *D. variabilis* and the smaller *D. parvula* (Morrison, 1971; Hugh Porter, pers. comm). Thus, possible differences in growth or tidal migrations may have been obscured. Seasonal changes in population size structure and tidal migrations are described here for *D. variabilis* and *D. parvula* from a North Carolina high-wave-energy beach.

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MATERIALS AND METHODS

Donax spp. were sampled monthly from January 1976 through April 1977 during a 15 month comparison of beach macrofauna (Leber, 1977) at Bogue Banks, a North Carolina barrier island (Fig. 1). The study site is about 30 km West of Morehead City (Carteret Co., NC), 1.5 km East of Bogue Pier, and encompasses 1 km of shore on this south facing, high-energy beach. Waves at the study site were typically 0.5 to 1.3 m from crest to trough during the study. Width of the beach from the base of the fore dune to spring tide high water mark averaged 15 m. Beach slope ratio averaged 11:1. The low tide terrace added an additional 40 m to beach width during low spring tides. Semidiurnal tidal fluctuations varied in amplitude from 0.7 to 1.25 m. The beach was composed of quartz sand with a median grain size of 250 μm (Leber, 1977). I discriminated 4 zones: spray, damp, wash and surf (Fig. 2) after Wade's (1967) scheme in which there was no damp zone.

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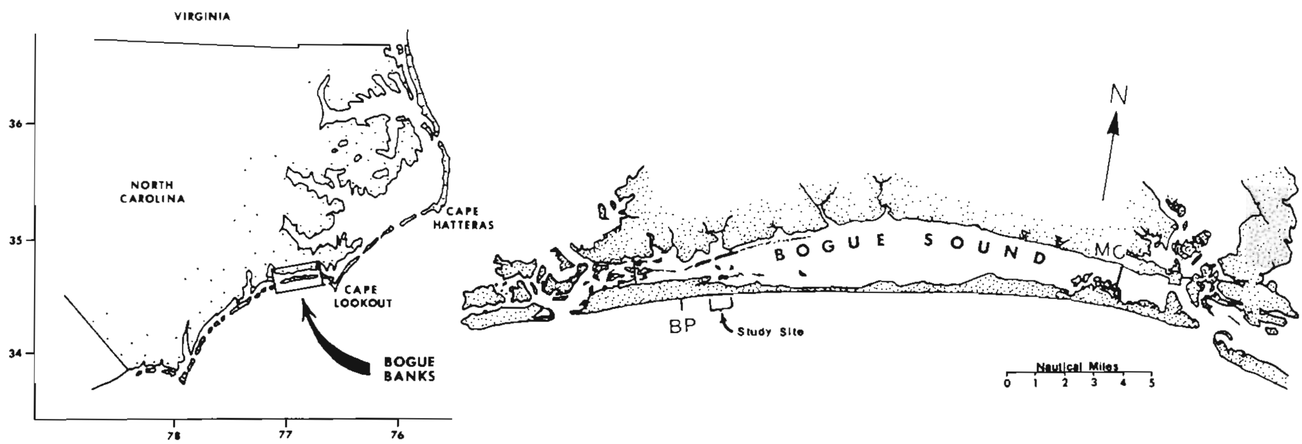

Fig. 1. Study site on Bogue Banks, North Carolina, USA. BP: Bogue Pier; MC: Morehead City

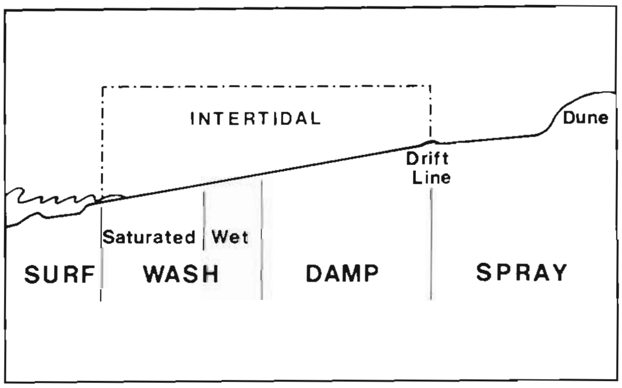

Fig. 2. Profile of study area indicating beach zonation during ebb tide (modified after Wade, 1967). Wash zone: covered intermittently by each incoming wave; its movement up and down the beach slope is governed by tidal flow. Damp zone: area of intertidal zone left exposed on ebbing tide; at its uppermost boundary lies the drift line that is deposited at high tide and consists of accumulated plant and animal debris

Monthly collections were made during mid to low tides along transects perpendicular to shore with 5 cm diameter cores, sieved through 1 mm mesh screen, and by a 1 mm mesh lined hand dredge that was pulled through the wash zone. Five replicate cores spaced 1 m apart, and perpendicular to the transect axis, were taken at 2 m intervals along a transect. Core sampling was supplemented by hand dredge sampling to collect large numbers of individuals for population size distribution analyses. Replicate dredge hauls were obtained from low, mid, and upper wash zone levels. Specimens were preserved in 70 % ethanol and identified and measured (shell length) at the laboratory.

RESULTS

Juvenile recruitment to the wash zone occurred in 1976 during both February and November for *Donax variabilis*, and in February for *D. parvula* (Fig. 3). Recruitment individuals of both species were partially missed by samples owing to the large mesh size of sieves. The smallest individuals fell through the 1 mm mesh; however, damped recruitment pulses are obvious in the size frequency histograms (Fig. 3). Second-year *D. variabilis* recolonized the wash zone in March, presumably after overwintering in subtidal areas. *D. variabilis* exhibited rapid growth during early summer, and by July modal size of the population was

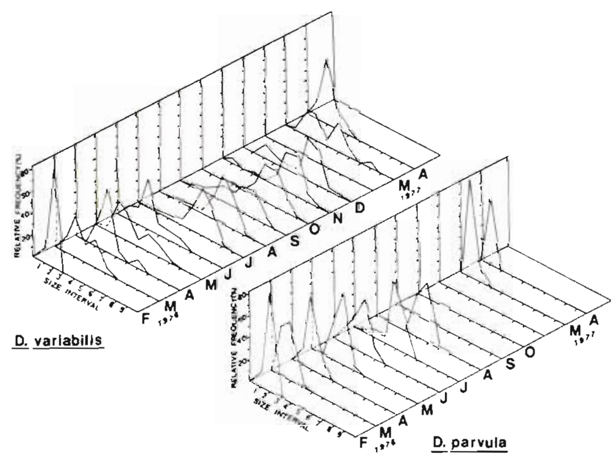

Fig. 3. *Donax* size-frequency diagrams for individuals collected during study. Shell length indicated in 2.5 mm intervals; first interval is 3.5–6.0 mm. January 1976 and 1977, and February 1977 are not included as fewer than 10 individuals were collected in those months

considerably larger than that for the *D. parvula* population (Fig. 3). *Donax* were most abundant during spring and summer; tidal migrations of both species varied seasonally (Leber, in press) and are summarized below.

Donax variabilis and *D. parvula* migrated together in the wash zone through July 1976, their position on the beach fixed by tidal patterns. But in August, *D. parvula* disappeared from intertidal zone samples. There was no indication of mortality, but rather, a seaward migration of *D. parvula* from the wash zone on the beach to a subtidal habitat. *D. parvula* individuals were collected with cores in 1 m deep water in the surf zone following their disappearance. Tidal migrations of *D. variabilis* also ceased in August, however, the population remained high on the beach in damp sand, only briefly submerged during high tides (Fig. 4).

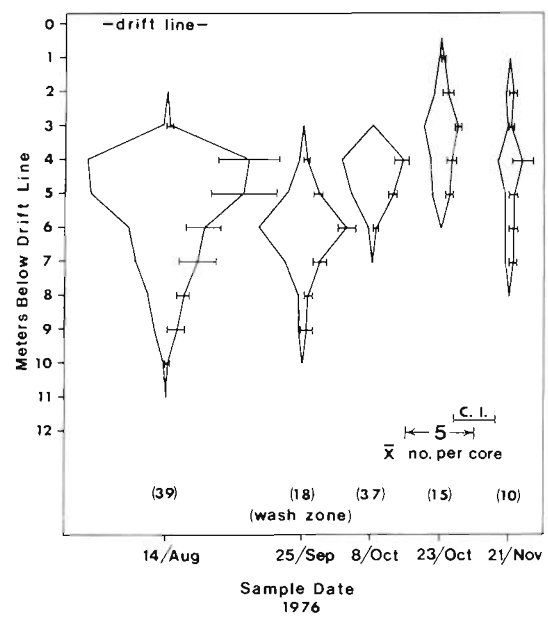

Fig. 4. *Donax variabilis.* Mean number per core and 95 % confidence intervals for individuals stranded on beach during ebb tides in late summer and fall 1976. Individuals were not found stranded during other months, but migrated up and down the beach with the tide. Distances (m) of top of wash zone from drift line at start of collections is given in brackets. Confidence intervals are symmetrical, but indicated here only for right margins of kite diagrams

During low-tide collections in late summer and fall, the *Donax variabilis* population remained concentrated in a narrow (3 to 7 m) band high in the intertidal zone (Fig. 4). By late November, densities had declined, and individuals were buried 10 cm deep in the sand. *D. variabilis* disappeared from collections in December, and few individuals (< 10) were found during January or February 1977 despite intensified sampling efforts. Juvenile *D. parvula* and *D. variabilis* recolonized the beach in March 1977.

Water temperatures during this study ranged from 5° to 28 °C, air temperatures from 2° to 38 °C (Leber, in press). Fall temperatures were characterized by a steep decline.

DISCUSSION

Pearse et al. (1942) and Turner and Belding (1957) describe *Donax variabilis* as a daily tidal migrant that maintains its position in the wash zone throughout tidal cycles. Edgren (1959) and Marsh (1962) report stranding of this species at low tide. Both patterns were evident for *D. variabilis* at Bogue Banks until December when the clams disappeared from the intertidal zone. Stranding was not observed for *D. parvula*, which moved to a subtidal habitat in mid summer. Summer habitats of these 2 congeners parallel those reported for *D. variabilis* and *D. texasianus* Philippi in Texas by Loesch (1957), those for *D. striatus* Linné and *D. denticulatus* Linné in the West Indies by Wade (1967), and those for *D. variabilis (D. roemeri protracta)* and *D. fossor* Say in North Carolina by Morrison (1971).

The disappearance of *Donax variabilis* from the beach in December was likely a consequence of emigration. Matta (1977) has noted *D. variabilis* movements into offshore regions in fall in North Carolina. The most parsimonius explanations for emigrations of *Donax* spp. from beach to subtidal habitats are that these movements are physically controlled, and/or a consequence of spawning requirements. The late fall exodus of *D. variabilis* from the beach coincided with a sharp decrease in water temperature from October (27 °C) to November (13 °C) (Leber, in press). Both *D. parvula* and *D. variabilis* appear to spawn during winter, as the beach was repopulated by juveniles in the spring. Thus, reproduction could be contingent upon temperature regulated emigration from the beach to a subtidal habitat.

Alternatively, the gradual decrease in *Donax variabilis* abundance may have been a consequence of predation by fish (*Menidia menidia, Menticirrhus americanus, Paralichthys* sp., *Trachinotus carolinus*) and crabs *(Ocypode quadrata, Arenaeus cribrarius)* that feed at night in the wash zone on *Donax*, and are abundant in late summer (Leber, in press). Also, low-tide stranding of *D. variabilis* high in the intertidal zone during late summer and fall may be an adaptation to predation pressure. A population remaining high on the beach throughout tidal exchanges would be exposed to these wash zone predators only at night during high tides.

Behavioral mechanisms involved in tidal migrations of *Donax* were discussed by Mori (1938, 1950), Turner and Belding (1957), Wade (1967), Ansell (1969), Trueman (1971), and McLachlan et al. (1979). When temporarily stranded in damp sand on a falling tide, reduced intensity of stimulation from acoustic wave shock and drying sand induce both *D. denticulatus* and *D. variabilis* to respond to the backwash of a wave by pushing upward with the foot and emerging from the substrate, whereupon they are carried down the beach by wave drag (Turner and Belding, 1957; Trueman, 1971). Emergence from the sand during flood tide is apparently related to both a behavioral response to some threshold level of acoustic shock, as waves pound closer to the clams, and erosion of sand by the churning motion of waves (Trueman, 1971). Clams are then transported up the beach after emergence by the momentum of advancing waves.

The basis for low-tide stranding of *Donax variabilis*, which clearly underwent tidal migrations for several months prior, is another matter. Stranding high in the intertidal is a consequence of interrupted tidal migration, owing to a lack of response to environmental cues that stimulate emergence on an ebb tide. This behavior reversal might be explained as a sequential step in a metabolic shutdown in order to avoid excessive energy use owing to some physical condition, or to low food availability. But what is the adaptive significance of becoming inactive in a hostile habitat, the upper intertidal, that is subjected to long periods of exposure? Rather, a stress-induced shutdown would likely occur in a more optimal location such as mean tide level, or closer to low tide level on the beach.

Alternatively, this behavior reversal, which initiates stranding of the entire population, might be an antipredatory adaptation. The origin of emergence behavior in several bivalves can be traced partly to a chemosensory response to certain predators (Ansell, 1969; Ansell and Trevallion, 1969). During the evolution of tidal migratory behavior, *Donax variabilis* movements up the beach on flood tides may have been reinforced by an escape response to crab and fish predators. Were predation on *Donax* intense, down slope migrations on the ebb tide would have been selected against. Selection would favor individuals that discontinued migrations. Following this hypothesis, stranding should be advantageous only during periods of high predation intensity. The environmental cue for stranding behavior in extant *D. variabilis* populations might be increased frequency of harrassment by predators. Any demonstration that stranding in *D. variabilis* is initiated during periods of low wash zone predation intensity (winter and spring months at Bogue Banks) would falsify this hypothesis.

Finally, late summer stranding of *Donax variabilis*, concurrent with the movement of *D. parvula* into subtidal regions, may have been a response to spatial limitations imposed by the vast numbers of mole crabs, *Emerita talpoida* Say, and *Donax* migrating together in the wash zone at that time. As combined *Donax* and *Emerita* densities in the wash zone approached 5,000 ind. m^{-2} in August (Leber, in press), filter feeding by *Donax* might have been impaired. During a later study at the same site (Reilly and Bellis, 1978), densities of *Donax* and *Emerita* were considerably lower, and any crowding effects correspondingly reduced. Neither stranding of *D. variabilis*, nor a summer exodus of *D. parvula* were evident in that study.

The present study shows that 2 *Donax* species present on Bogue Banks in 1976 and 1977 differed in population size structures and occupied vastly different summer habitats. Whereas *D. parvula* moved to deeper water in late summer, *D. variabilis* clearly remained aggregated during late summer and fall in a high-density narrow band located in the upper intertidal zone. The basis for low-tide stranding of *D. variabilis* is still far from clearly established, and hypotheses posed here that account for stranding need critical evaluation. Lab and field experiments are needed to assess any predation or crowding effects on *Donax* migrations.

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