Long-term structure, disturbance, and recolonization of macroinfauna in a New Hampshire sand beach[1]

EDUARDO JARAMILLO
Instituto de Zoología, Universidad Austral de Chile, Valdivia, Chile
ROBERT A. CROKER
Department of Zoology and Jackson Estuarine Laboratory, University of New Hampshire, Durham, NH, U.S.A. 03824
AND
EDWARD B. HATFIELD
Maple Street, Freedom, NH, U.S.A. 03836

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The southern portion of Foss Beach, New Hampshire, was totally eroded of sand during the second quarter of 1977. Long-term community data from the beach since 1971 served as background for studying recolonization by burrowing invertebrates after redeposition of sand. About 2 years were required for the beach to regain much of its sand, and another year passed before a complete coverage of sand was long lasting. Twenty-five species of macroinfauna were recorded from the beach during a 13-year period, seven of these only from the postdisturbance beach. The polychaetes *Scolelepis squamata* and *Paraonis fulgens*, and the amphipods *Acanthohaustorius millsi* and *Amphiporeia virginiana*, were the most abundant species. The numbers of species and abundances of polychaetes were the primary influences on the pattern of variation of the total macroinfauna before disturbance. Polychaetes also dominated during early recolonization, 1.5–2 years after sand erosion, particularly species with planktonic larval stages. During this time, *Capitella* sp. exhibited abundances up to 10 times mean values for the predisturbance period. Four years after sand erosion, the macroinfauna had largely recovered.

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L'érosion a complètement enlevé le sable de la partie sud de la plage de Foss Beach, New Hampshire, au second trimestre de 1977. Des données accumulées depuis 1971 ont servi de données de base à l'étude de la recolonisation, par les invertébrés fouisseurs, du sable redéposé. Il a fallu environ 2 ans pour que la plage ne se refasse et 1 année supplémentaire avant que la couverture ne soit installée à demeure. Vingt-cinq espèces fouisseuses ont été recensées sur la plage en 13 ans, dont sept après l'érosion. Les polychètes *Scolelepis squamata* et *Paraonis fulgens* et les amphipodes *Acanthohaustorius millsi* et *Amphiporeia virginiana* étaient les espèces les plus abondantes. Le nombre d'espèces et la densité des polychètes constituaient les paramètres majeurs de variation de la faune totale avant l'érosion. Les polychètes, en particulier les espèces à larves planctoniques, ont aussi dominé le début de la recolonisation pendant 1,5 à 2 ans. À ce moment, la densité de *Capitella* sp. a pu atteindre jusqu'à 10 fois les densités témoins. Quatre ans après l'érosion, la faune des invertébrés fouisseurs s'était refaite en grande partie.

[Traduit par la revue]

Introduction

A disturbance can be defined as a biotic or abiotic event producing alteration or destruction of food and space resources, affecting one organism or an entire community (McCall 1978; Dethier 1984). After disturbance, recolonization in the marine environment proceeds over days to months (Thistle 1981), with opportunistic species (sensu MacArthur and Wilson 1967) initially occupying the defaunated habitat (see Dauer and Simon 1976; Grassle and Grassle 1974; McCall 1978; Sanders et al. 1980; Santos and Simon 1980). Disturbances are known to represent an important causative factor for spatial heterogeneity, and consequently for the structure and dynamics of natural communities (Johnson 1972; Sousa 1984).

Intertidal soft-bottom assemblages are subject to relatively predictable and common disturbances, such as seasonal sand movements (Daly and Mathieson 1977; Littler et al. 1983), feeding by epibenthic crabs and horseshoe crabs (Botton 1984; Woodin 1978, 1981) and wading birds (Howard and Lowe 1984; Kent and Day 1983), bait digging by humans (McLusky et al. 1983), outbreak of red tides (Dauer and Simon 1976; Santos and Simon 1980), and biogenic reworking activity of the macroinfauna (see reviews by Gray 1981; Rhoads 1974; Rhoads and Boyer 1982). Soft-bottom assemblages are also subject to other aperiodic and less predictable disturbances such as oil spills, dredging, or sudden storms.

During the second quarter of 1977, all sand was eroded from the southern end of Foss Beach, New Hampshire. This event provided us with the opportunity to follow the recolonization of the intertidal macroinfauna in a North American boreal habitat, where no previous information was available for this type of disturbance. Long-term data gathered since 1971 concerning seasonal community structure and population fluctuations at Foss Beach served as a convenient baseline for examining recolonization after redeposition of sand.

Methods

Foss Beach, New Hampshire, faces easterly (Fig. 1) and is partially protected from wave action by an adjacent boulder shore and extensive rock outcrops to the south (Croker 1977). The habitat studied is at the southern end of Foss Beach, and is attenuated landward by the presence of a steel and rock faced seawall; consequently, the highest levels of available sand for burrowing animals are slightly below mean high-water neap (MHWN) level. This southern portion of Foss Beach

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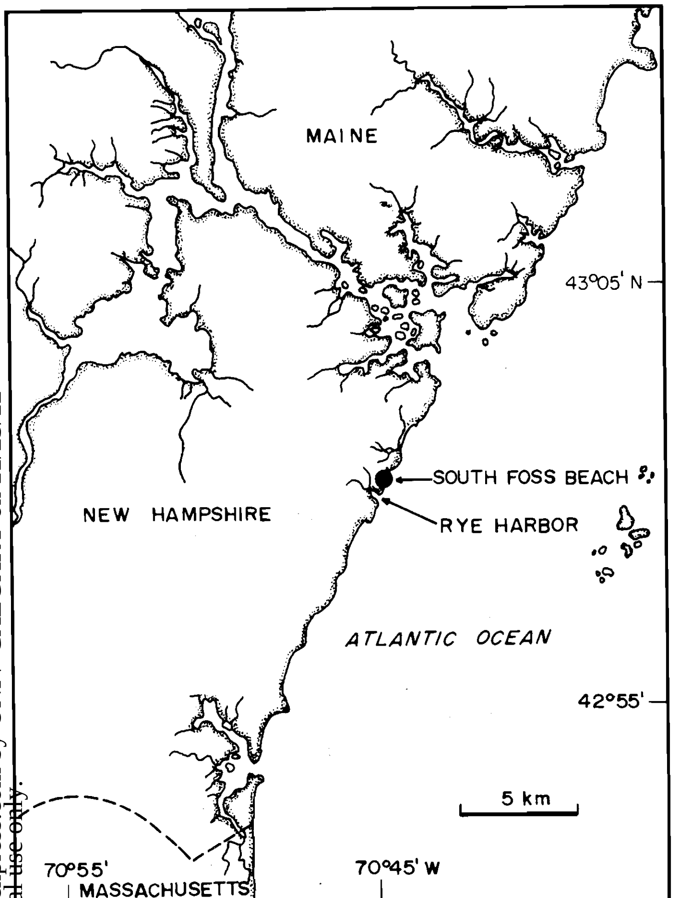

FIG. 1. The New Hampshire coast showing the location of South Foss Beach.

(hereafter called SFB) was seasonally sampled (March and July) from March 1971 to March 1977. There was no sand on SFB on July 20, 1977; complete erosion of sand from the habitat must have occurred between late March and July 1977. Erosion of sand to this extent had never been observed here since our studies began in 1971. On July 20, 1977, a full transect was carried out on the sand beach some 200 m north of the sand-eroded habitat. Thus, community and population data appearing in subsequent figures for July 1977 are for this transect only. These data are presented for comparative purposes, and as an indication of the species potentially available for recolonization of the eroded habitat nearby. After the beach had regained sufficient sand in December 1978, macroinfaunal sampling was carried out every 2 months until November 1979, and thereafter seasonally until July 1984. Triplicate 0.04-m^2 samples, 10 cm deep, were collected at each of four or five beach levels on a transect extending from the highest levels of the beach to the level of predicted low tides. Sand samples were washed through a 0.5 mm mesh sieve, and the coarse residue, including animals, was brought back to the laboratory. Diversity (Shannon–Wiener index) and evenness indices for the fauna were analyzed after Brower and Zar (1977). Samples of the upper 5 cm of beach sand were taken at irregular intervals from 1971 to 1984 for sediment analyses with an Emery settling tube. The sedimentary parameters were calculated according to Folk (1980).

Results

The habitat

Between July 1972 and March 1977, the values of the sediment graphic mean (M_z) varied between 2.02 and 2.27 ϕ. The overall mean for this time period was 2.18 ϕ (±0.08 SD), corresponding to fine sand (Folk 1980). Particle sorting ranged between 0.30 and 0.34 0 ϕ, with an overall mean of 0.32 ϕ (±0.02 SD), signifying very well sorted sand (Folk 1980).

The beach was essentially free of sand from July 20, 1977 until early winter 1977–1978. A small amount of sand then came and went, and the beach subsequently remained without sand again from February to September 1978. During the next 21 months, varying amounts of sand were periodically deposited and then lost. Relatively good coverage was present by June 1980, and by November 1980, sand coverage was essentially complete. By July 1981, a portion of the beach as far as several hundred metres north of SFB was now relatively free of sand. Our general observations during this period indicated that sand was being supplied to SFB both from the north and from a subtidal sandbar located nearby. By late November 1981, the northern portion of Foss Beach again had excellent sand coverage. This sand coverage then persisted throughout the entire Foss Beach for the duration of the study period.

Between mid-1979 (when the beach began to significantly recover sand) and July 1984, the sediment graphic mean ranged between 2.04 and 2.23 ϕ. The overall mean for this period was 2.11 ϕ (±0.07 SD). Particle sorting values varied between 0.10 and 0.43 ϕ with an overall mean of 0.31 ϕ (±0.11 SD). Thus, like the pre-erosion beach, SFB during sand recovery can be characterized as having fine, very well sorted sand, but with a wider sorting range.

The macroinfauna

Twenty-five species were collected and identified from SFB (Table 1). Of these, 11 species occurred sporadically (in less than 5 out of 26 seasonal collections during 1971–1984). These were nine polychaete species, the bivalve *Tellina agilis*, and the enteropneust *Saccoglossus kowalewskii*. On the other hand, the polychaetes *Scolelepis squamata*, *Paraonis fulgens*, and *Capitella* sp. occurred in all, or almost all, of the seasonal collections, as did the amphipods *Acanthohaustorius millsi* and *Amphiporeia virginiana*.

Long-term population fluctuations, 1971–1977

Seasonality of the SFB macroinfauna before complete sand erosion was expressed in the overall pattern of total macroinfaunal abundance and number of species (Fig. 2). With the exception of 1975 and 1977 for total abundance, and the period 1975–1977 for the number of species, the higher values for both community parameters typically occurred in summer (July). The values of the Shannon–Wiener Index ranged from 1.18 to 2.01 (Fig. 2), with an overall mean of 1.59 for the period 1971–1977. Evenness was highest in July 1971 (0.85) and March 1972 (0.81), and lowest in July 1973 (0.51) (Fig. 2). The overall mean for the 7-year period was 0.68.

Abundances of amphipods and polychaetes were typically higher for summer collections (Fig. 3). The polychaetes peaked in 1973 and 1974, bringing the total macroinfaunal abundances to their highest values for the period 1971–1977 (Fig. 2). The number of amphipod species showed little variation, while the number of polychaete species showed a steady increase to 1973, and then a steady decline through 1977, paralleling a similar response of polychaete abundances during the 1970's.

Temporal variations in the number of polychaete species and in polychaete abundances were largely responsible for the pattern of variation of similar parameters for the total macroinfaunal community (Figs. 2 and 3). *Acanthohaustorius millsi* and *Amphiporeia virginiana* were the numerically dominant amphipod species (Fig. 4). As usual in northern New England, *Acanthohaustorius millsi* was generally more abundant in July

TABLE 1. South Foss Beach macroinfauna: occurrence of taxa at each sampling month, 1971–1981 and 1984

		1971		1972		1973		1974		1975		1976		1977		1978	1979						1980		1981	1984	
	Reproduction	Mr	Jl	Mr	Jl	Mr	Jl	Mr	Jl	Mr	Jl	Mr	Jl	Mr	Jl	D	Ja	Mr	My	Jl	S	N	Ap	Je	Jl	Ap	Jl
Nemertinea																											
Micrura albida Verrill	pel		x		x	x	x		x	x	x	x		x		x					x	x	x	x	x		
Oligochaeta				x		x		x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x		
Polychaeta																											
Scolelepis squamata (Muller)	pel	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x
Paraonis fulgens (Levinsen)	pel			x	x	x	x	x	x	x	x	x	x	x	x					x	x	x	x	x	x	x	x
Capitella sp.	pel–br			x	x	x	x	x	x	x	x	x	x			x	x	x		x	x	x	x	x	x		
Spiophanes bombyx (Claparede)	pel				x	x	x		x																		
Spio setosa Verrill	pel							x												x	x	x					
Nephtys caeca (Fabricius)	co					x	x		x													x		x			
Nephtys bucera Ehlers	co						x				x	x	x	x						x		x				x	
Nephtys sp.	co						x	x											x			x					
Nephtys longosetosa Oersted	co	x								x		x															
Nereis succinea (Frey & Leukart)	pel															x		x	x	x							
Nereis virens Sars	pel																							x			
Scololepides viridis (Verrill)	pel															x	x	x									
Eteone longa (Fabricius)	pel															x	x	x									
Pygospio elegans Claparede	pel																			x	x	x					
Amphipoda																											
Acanthohaustorius millsi Bousfield	br	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x	x	x	x	x	x	x	x	x
Haustorius canadensis Bousfield	br	x	x	x	x	x	x	x	x	x	x				x						x	x	x	x	x	x	x
Amphiporeia virginiana Shoemaker	br	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x		x	x	x	x	x	x	x
Bathyporeia quoddyensis Shoemaker	br	x	x	x	x		x	x	x	x	x		x		x						x	x			x		
Psammonyx nobilis (Stimpson)	br	x	x	x	x	x	x	x	x	x	x	x	x	x		x			x					x	x		
Isopoda																											
Chiridotea tuftsi (Stimpson)	br					x	x			x											x	x					
Cumacea																											
Mancocuma stellifera Zimmer	br	x	x		x	x	x		x		x	x	x		x						x	x			x		
Bivalvia																											
Tellina agilis Stimpson	pel															x	x					x					
Hemichordata																											
Saccoglossus kowalewskii (Agassiz)	pel															x											

NOTE: Mr, March; Jl, July; D, December; Ja, January; My, May; S, September; N, November; Ap, April; Je, June; pel, pelagic larvae; br, brooding; co, cocoons.

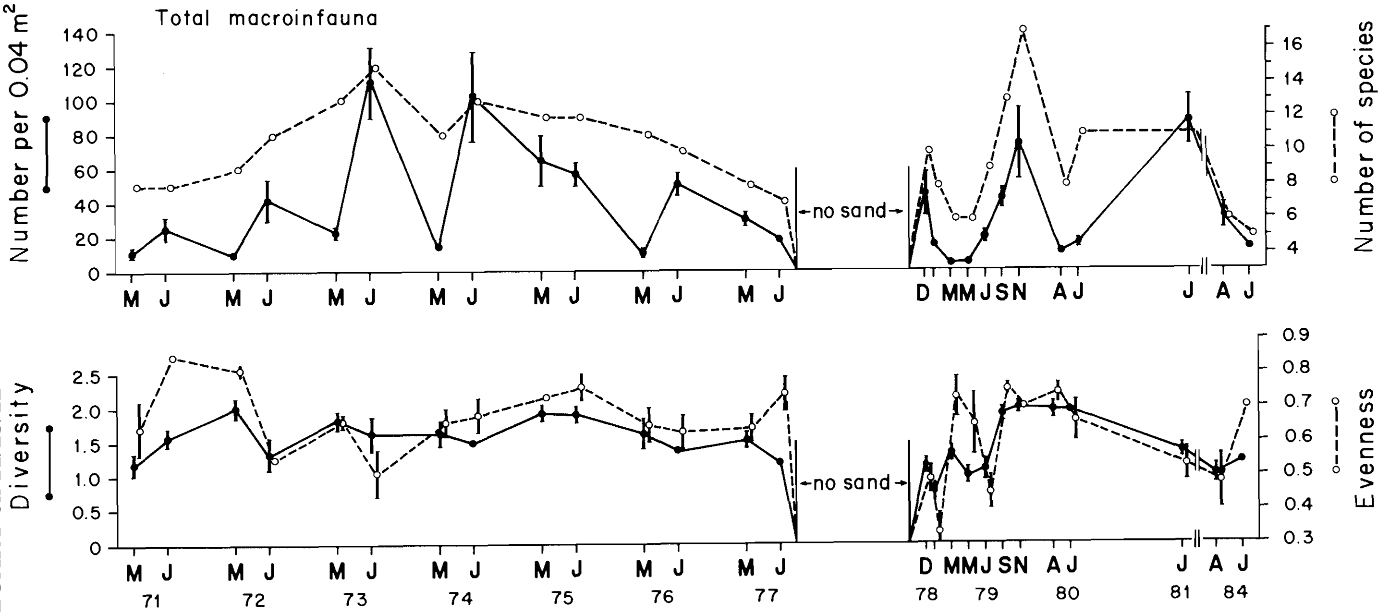

FIG. 2. Long-term fluctuations in abundance and numbers of species (upper) and diversity and evenness (lower) of the total macroinfauna. Vertical bars are one standard error.

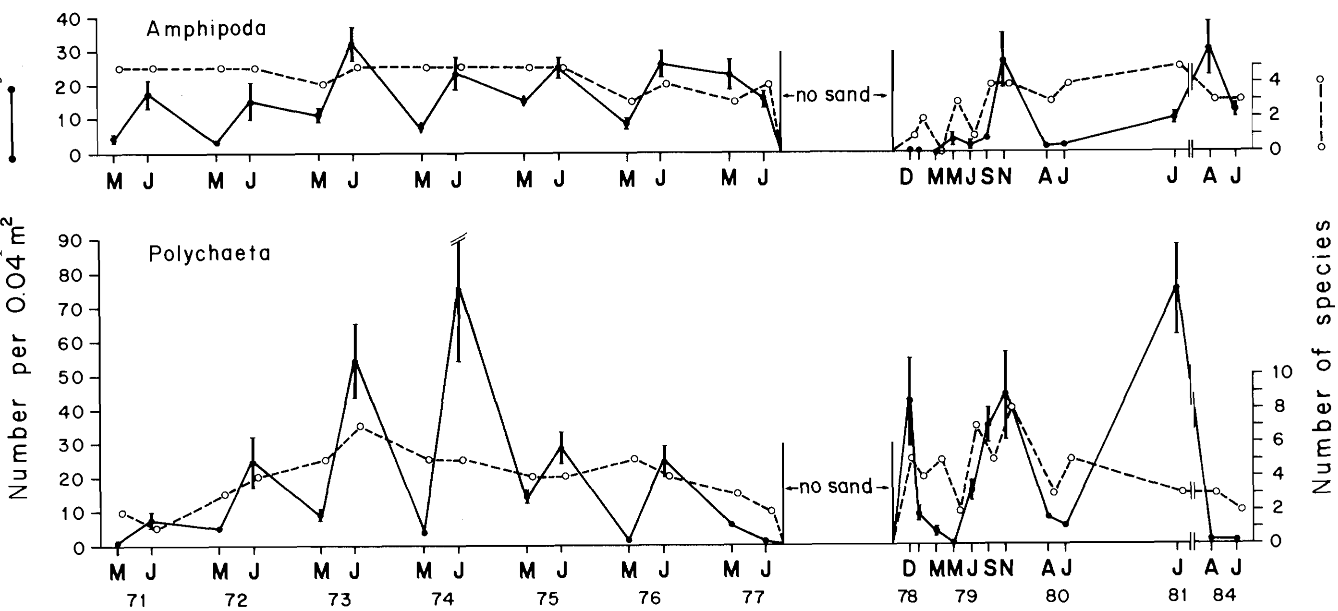

FIG. 3. Long-term fluctuations in the abundance and total numbers of species of Amphipoda and Polychaeta.

(Croker and Hatfield 1980), while *Amphiporeia virginiana*, a very mobile species that is active in the surf zone (Hager and Croker 1980), showed a more irregular pattern of abundance (Fig. 4). The remaining amphipods, *Haustorius canadensis*, *Bathyporeia quoddyensis*, and *Psammonyx nobilis*, were very rare or sporadic (Fig. 4). *Scolelepis squamata*, *Paraonis fulgens*, and *Capitella* sp. were the numerically dominant polychaete species, and typically also had their highest abundances in July (Fig. 5).

Intertidal distribution

The intertidal distribution of the most abundant amphipod and polychaete species for each sampling date is presented in Figs. 6 and 7. The vast majority of *Acanthohaustorius millsi* occurred below the 80-cm level, i.e., between mean tide level (MTL) and mean low-water neap (MLWN) levels (Fig. 6). This species exhibited either seaward movements during summer 1972–1976 or landward movement during one summer (1977) (Fig. 6). On more exposed, wider beaches, *A. millsi* moves landward during summer as does the co-occurring amphipod *Haustorius canadensis*, a rare species at SFB (Croker and Hatfield 1980). The mobile *Amphiporeia virginiana* exhibited a shifting intertidal distribution (Fig. 6).

The large majority of the populations of the polychaetes *Scolelepis squamata* and *Paraonis fulgens* also occurred below the 80-cm level. *Capitella* sp. exhibited a relatively narrow

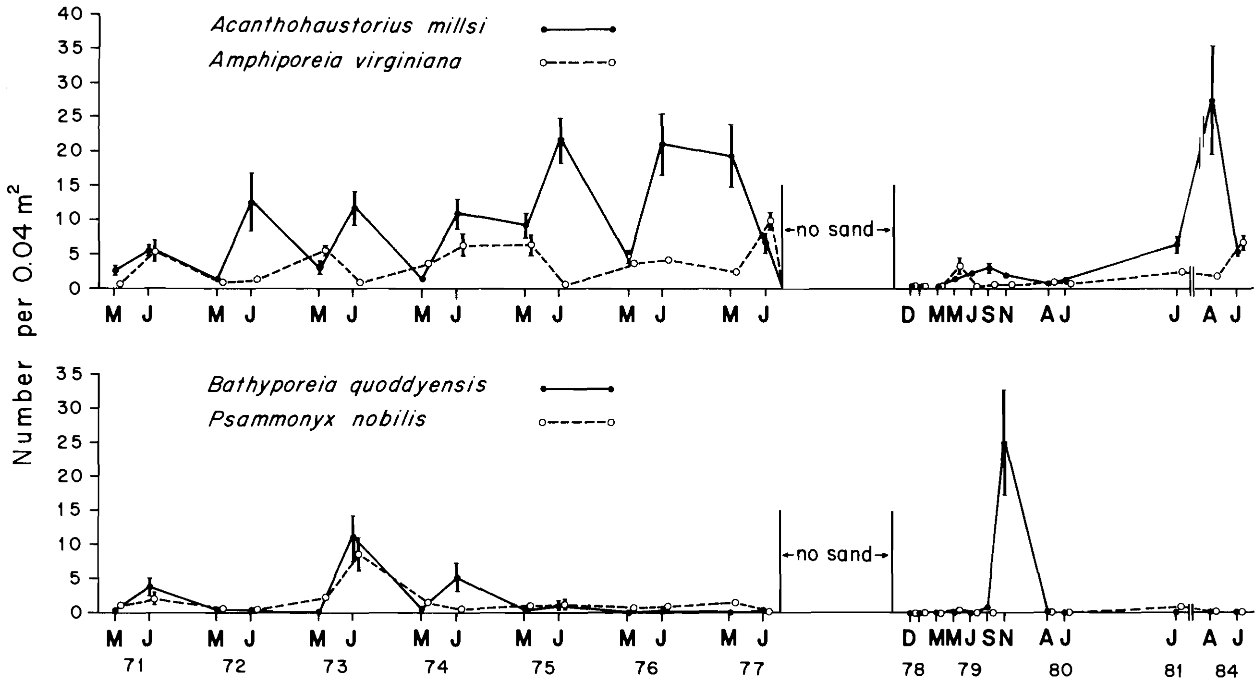

FIG. 4. Long-term fluctuations in the abundance of amphipod species.

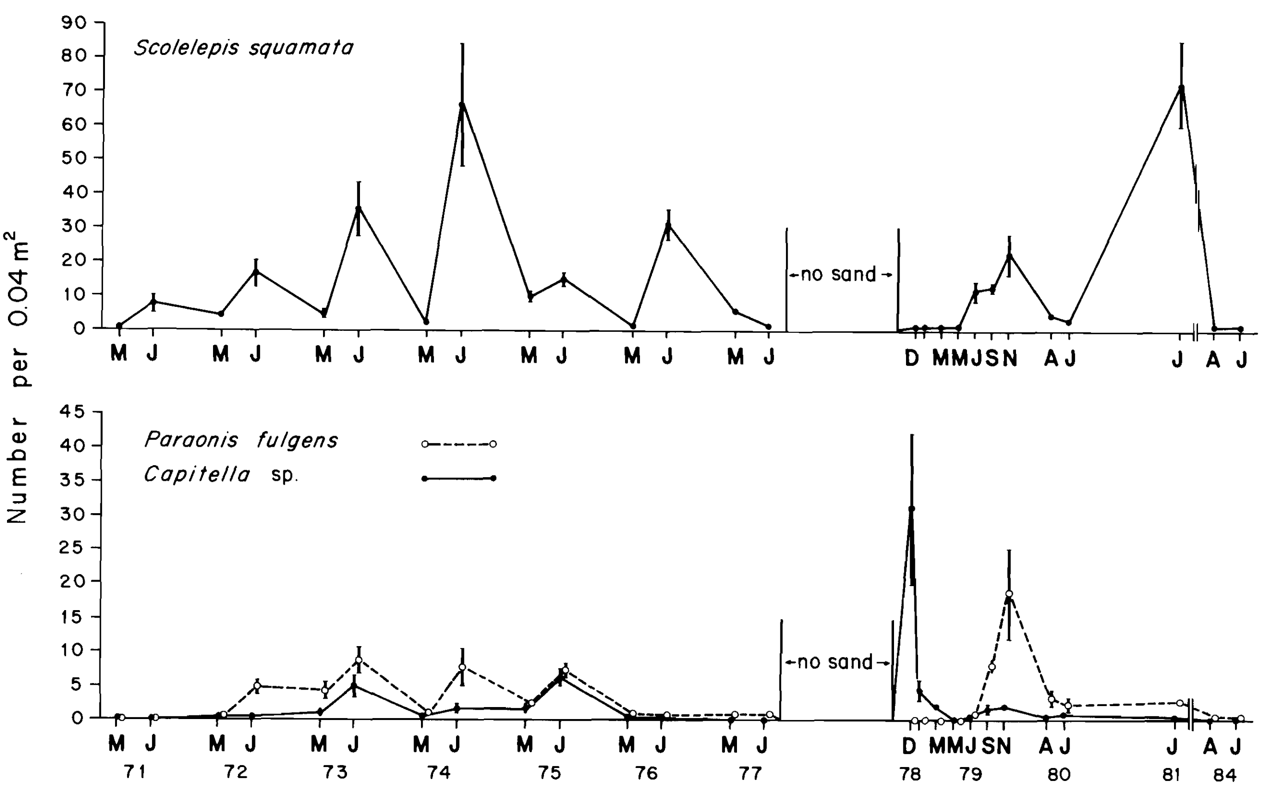

FIG. 5. Long-term fluctuations in the abundance of the most common polychaete species.

distribution, from slightly above to slightly below MLWN level. A seaward movement in summer was common for these three polychaete species (Fig. 7).

Recolonization pattern: the first 10 months

In December 1978, when a moderate amount of redeposited sand was first observed, polychaetes dominated the fauna both in abundance and in number of species. Amphipod abundances remained very low for the first 9–10 months, although the number of amphipod species reached predisturbance values during this time. Polychaete abundances dropped off after the initial high peaks in December 1978, and then increased strongly (as did the number of polychaete species) over the ensuing year (Fig. 3). The polychaete peak in December 1978

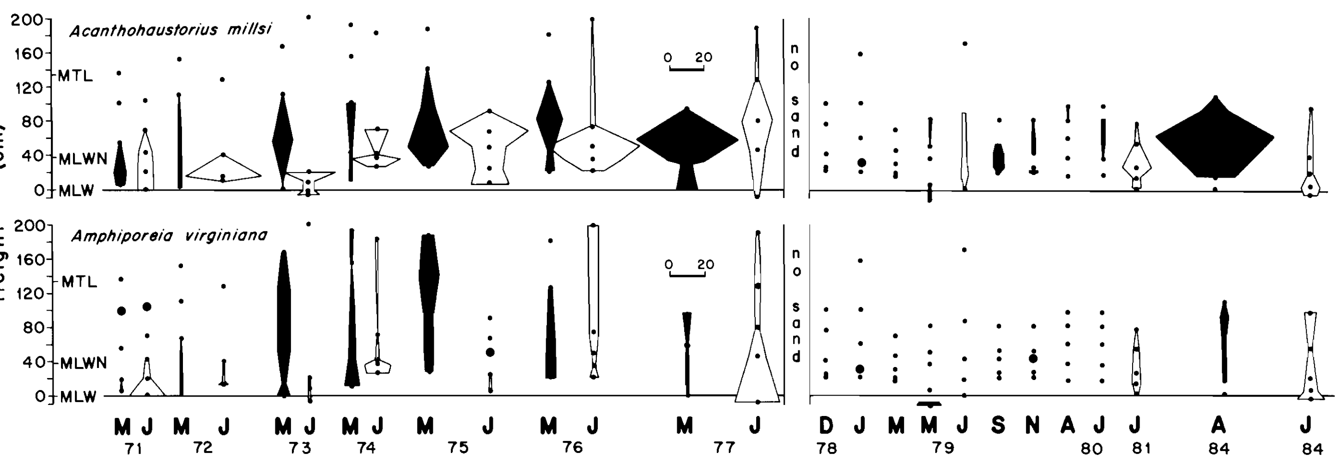

FIG. 6. Intertidal distribution of the most common amphipod species. Winter–early spring and summer distributions are represented by black and white kites, respectively. Small circles represent stations on the transect; large circles indicate mean abundances <1 individual. MTL, mean tide level; MLWN, mean low-water neap; MLW, mean low water.

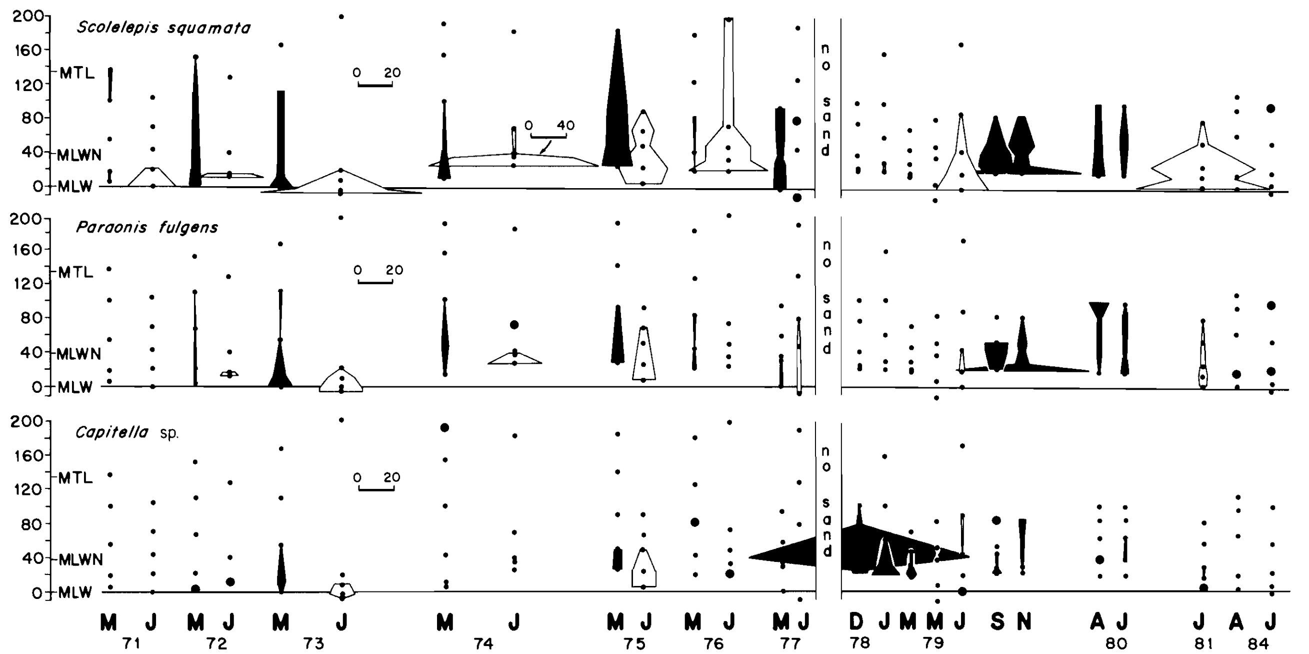

FIG. 7. Intertidal distribution of the most common polychaete species; for details see Fig. 6.

was caused chiefly by a rapid increase in *Capitella* sp. (Figs. 5 and 7), which reached an abundance of 31.3 animals per 0.04 m^2, nearly 5 times higher than the highest abundance reported before disturbance (July 1975, Fig. 5) and nearly 10 times higher than the mean abundance for the period 1971–1977. By early 1979, *Capitella* sp. abundance had declined to low levels. Other polychaete species contributing to the peak in early December 1978, *Nereis succinea*, *Scololepides viridis*, and *Eteone longa*, were not seen again after early to mid 1979 (Table 1).

Before- and after-disturbance comparison

Before the disturbance, 18 species were encountered at SFB during 1971–1977 (Table 1). Following sand erosion, seven additional taxa, all with pelagic larvae, appeared in collections for the first time, and most at low abundances (<1/0.04 m^2). These were the polychaetes *Nereis succinea*, *N. virens*, *Scololepides viridis*, *Eteone longa*, and *Pygospio elegans*, the bivalve *Tellina agilis*, and the hemichordate *Saccoglossus kowalewskii* (Table 1).

After the ephemeral *Capitella* sp. pulse of December 1978, total macroinfaunal abundances comparable to those of the predisturbance period were not observed again until late 1979 (Fig. 2), more than 2 years after the complete erosion of sand from SFB. In general, the lowest diversity and evenness values were found during the first months of recolonization (i.e., December 1978 – July 1979) (Fig. 2).

The polychaetes were the first to recover from disturbance, regaining numbers of species similar to predisturbance values as soon as macroinfaunal recolonization began in December 1978, and regaining substantial abundances during 1979. The most common polychaetes, *Scolelepis squamata* and *Paraonis fulgens*, recovered during this latter period. On the other hand, amphipod recovery was slower, with the amphipods not reaching predisturbance numbers of species or abundances until September–November of 1979 (Fig. 3). However, the amphipod pulse for November 1979 consisted primarily of one species, *Bathyporeia quoddyensis*, a more subtidal species occasionally turning up as scattered aggregations in low intertidal sands. *Acanthohaustorius millsi*, the most abundant amphipod species, did not recover to predisturbance abundance levels until the summer of 1981, 4 years after complete sand erosion.

Discussion

Haustoriid amphipods and polychaete worms are the two prominent components of the sand beach communities of northern New England, where species composition and relative abundances depend in large part on the degree of wave exposure. Both numbers and relative abundances of polychaete species are inversely related to the intensity of wave exposure (Croker 1977; Croker et al. 1975). At SFB, a partially protected habitat, for example, the polychaetes were the dominant contributors to macroinfaunal abundances in half of the predisturbance seasonal collections over a period of 7 years (Fig. 3), and the number of polychaete species was higher than that of more exposed beaches nearby, e.g., Long Sands, Maine (Croker 1977). Seasonal fluctuations of the macroinfauna during the predisturbance period were predictable, with higher abundances and seaward movements of the two most abundant species, the polychaete *Scolelepis squamata* and the amphipod *Acanthohaustorius millsi*, during summer.

Polychaetes also clearly dominated the macroinfauna numerically during the early recolonization of the beach in late 1978 to March 1979. At this time, polychaetes were primarily represented by species with pelagic larval stages, which had either intermediate predisturbance abundances, e.g., *Capitella* sp., or were not collected previously at Foss Beach, e.g., *Nereis succinea*, *Scololepides viridis*, and *Eteone longa*. These pioneering species were not seen later, or showed very low abundances, coinciding with the reappearance of the dominant predisturbance polychaetes, *Scolelepis squamata* and *Paraonis fulgens*, during the latter half of 1979. Life history characteristics such as planktonic larval stages and longer reproductive periods, as well as dispersal via adult stages, together confer on polychaetes greater pioneering opportunities compared with brooding amphipods, and have been implicated in the response to other disturbance events where polychaetes were pioneer species (Rosenberg 1972; Grassle and Grassle 1974; Simon and Dauer 1977).

The number of amphipod species at SFB increased steadily as increasing amounts of sand were redeposited during 1979; these species presumably were recruited from the adjacent sand beach to the north as well as from subtidal sands located nearby. Nevertheless, with few exceptions, amphipod abundances remained quite low during the first 2 years of recolonization, despite reproductive pulses of sand-burrowing amphipod species during spring and summer months. In addition to the volume of sand available, the kinds and amounts of food resources in these sands could materially affect the composition and size of amphipod populations.

SFB is characterized by a superficial layer of fine sand on and around a gravel and cobble substratum. The partial protection from wave action afforded the beach by seaward rock outcrops and the adjacent boulder shore was reflected by the presence of a reduction layer at sand depths of 5–15 cm, and carbon : nitrogen ratios of sand averaging 26.3 : 1 during the years before sand erosion (Croker et al. 1975). Consequently, the complete removal of sand from the beach in 1977 came as a surprise, particularly because no severe storm event could be identified from either local or regional weather data.

For years we have considered SFB a good example of an intertidal sand habitat with low faunal abundance but relatively high diversity via evenness. Several crustacean and polychaete species that are typically more abundant in the subtidal zone have also occasionally turned up in scattered aggregations on the lower beach. Until 1977 the most obvious physical change in the beach was the modest seasonal transition from summer sand deposition to winter sand erosion. Complete sand erosion in 1977 changed this pattern and provided us with an opportunity to observe the resilience of the intertidal sand community after a severe disturbance. The macroinfauna at SFB had largely recovered in 1981, 4 years after sand erosion in 1977. This recovery time was longer than those recorded after natural or simulated disturbances in other areas of the east coast of North America. For example, Santos and Simon (1980) reported that the time for macroinfaunal recovery was 7–9 months in intertidal sands annually defaunated by outbreak of red tides in Hillsborough Bay, Florida. McCall (1977) observed that the abundance of macroinfauna colonizing azoic sediments placed in subtidal silty sands (14 m) of Long Island Sound exceeded the abundances of natural sediments after only 10 days. Zajac and Whitlatch (1982) observed that for defaunated sediments placed in shallow areas of Alewife Cove, Connecticut, the macroinfauna reached a community structure similar to that of control sediments in 14–30 days. Lastly, Van Blaricom (1982) showed that macroinfaunal abundances of subtidal sands (17 m) in Southern California, exposed to simulated ray digging, reached abundances of control areas hours to days after disturbance.

Once again, *Capitella* sp. turns up as a prominent pioneer species, although in numbers far lower than those reported in more organically rich intertidal (West Falmouth, Massachusetts, Grassle and Grassle 1974) and subtidal (Long Island Sound, McCall 1977) Atlantic coast soft-bottom habitats that were experimentally manipulated. The availability of organic matter in the sediments has been suggested as a significant factor in the appearance and abundance of opportunistic deposit feeders such as *Capitella* (e.g., Thistle 1981; Zajac and Whitlatch 1982). The amount of organic matter present in littoral sediments is largely controlled by habitat characteristics such as wave exposure and grain size (e.g., Gray 1981; Sanders 1958). Thus, differences in these habitat characteristics between SFB and the sites studied at West Falmouth and Long Island Sound are probable causes of the differences in the abundances of *Capitella*. In addition, differences in the availability of *Capitella* larvae during the initial recolonization phase may be important in this regard.

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