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The comparison of macrobenthic recolonization patterns near and away from crab burrows on a sublittoral sand flat[1]

by Simon F. Thrush[2,3]

ABSTRACT

This study assessed the influence of crab burrows (*Macrophthalmus hirtipes*) on localized patterns of macrobenthic colonization on a sand flat at 6 m depth in Otago Harbor, New Zealand. 150 m^2 of surface sediments were artifically disturbed to simulate a storm and core samples were collected 2, 4, and 30 days later. At each time, samples were randomly collected near and away from crab burrows.

A general pattern of high abundances away from burrows was apparent for most common taxa, number of taxa, number of individuals, and dominant polychaete feeding guilds. The differences in abundance near and away from burrows were evident over the three sampling occasions.

On the basis of their potential for suspension and transport in the water column during a storm, individuals were allotted to two groups: movable and stationary. Significant trends of increasing abundance over time were found for the movable group, stationary group, and the total number of individuals in samples collected away from burrows. Samples collected near burrows showed a slight but nonsignificant decrease in abundance over time. Changes in the number of taxa over time were not significant, although a similar visual trend as observed for the total number of individuals was apparent. The same taxa were common near and away from burrows, but differences in abundance produced different patterns of colonization. The low abundances around burrows were attributed to the disturbance generated by crabs walking in and out of burrows. Generally the results reported in this study are similar to those which report the influence of ghost shrimps (*Callianassa* spp.) on macrofauna. This study also demonstrated that patterns of abundance near and away from burrows were maintained during recolonization after a simulated storm disturbance.

1. Introduction

A variety of biotic and abiotic factors have been demonstrated to influence the structure and function of communities. Two such factors, biogenic structures and disturbance, are known or inferred to play important roles in determining the structure of communities in marine soft sediments. Generally most studies have only considered the influences of one factor at a time. Yet the various influences on community

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structure may interact or become increasingly important under certain environmental conditions. Biogenic structures within sediments (tubes, burrows, fecal mounds and pellets) affect many geophysical and geochemical properties such as topography, shear strength, porosity, particle size, nutrient concentrations, redox potential, pH, and gas diffusion (Rhoads and Boyer, 1982; Aller, 1982). These factors together with increased heterogeneity may influence the distribution of microbes and meiofauna, which are often abundant around biogenic structures (Reise, 1984; Meadows and Tait, 1985). Furthermore, the distribution and abundance of individual macrofaunal populations are often influenced by biogenic structures. For example, polychaete tubes may physically influence the patterns of larval settlement (Eckman, 1983). Tubes of the polychaete *Diopatra* have been shown to adversely influence the foraging behavior of large epibenthic predators and thus provide refuges for potential prey (Woodin, 1978). Ban and Nelson (1987) have demonstrated that tube structures of *Diopatra* do not provide refuge from predators under all circumstances and have indicated that a critical density of tubes was necessary to interfere with the activities of predators. Luchenbach (1987) has extended the studies on *Diopatra* tubes of Woodin (1978, 1981) and demonstrated that the recruitment of certain benthic species was inhibited by the dense assemblage of resident macrofauna around tubes.

The role of disturbance in natural communities has been extensively reviewed (Thistle, 1981; Dayton, 1984; Probert, 1984; Sousa, 1984; Picket and White, 1985; Diamond and Case, 1986; Begon *et al.*, 1986). The spatial and temporal scales of disturbance are important and may range from rare, acute, unpredictable catastrophes affecting large areas to localized chronic events which occur predictably during the lifetime of an organism. The nature of the patchiness created by disturbance affects the level of resource availability, the survival of residual organisms in the patch, and rate of invasion and the success of establishment of new organisms (Sousa, 1984). In marine soft sediment communities this can result in a mosaic pattern to community structure with different patches containing assemblages at different successional stages.

Storms disturb coastal benthic communities by resuspending surface sediments and scouring the seafloor, resulting in the death or removal of benthic organisms (Yeo and Risk, 1979; Dobbs and Vozarik, 1983). A number of surveys of coastal benthic communities have inferred the importance of storms in affecting the distribution and abundance of benthic fauna, generating patchiness, and downgrading successional status (Rees *et al.*, 1977; Rachor and Gerlach, 1978; Glemarec and Menesguen, 1980). In Long Island Sound (U.S.A.), McCall (1977) noted differences in macrobenthic community structure down to a depth of about 30 m which, on the basis of experimental studies, he attributed to the effects of storms.

Except in the severest cases, disturbance to the seafloor during a storm is unlikely to remove or kill all organisms. Large, deep burrowing, or heavy organisms are less likely to be removed from the sea bed and these residual organisms may influence the recolonization of the disturbed area. This may be especially important if the residual organisms construct structures in the sediment. One such resident organism is the burrowing ocpodid crab *Macrophthalmus hirtipes* which create relatively large burrows (about 1–3 cm diameter) and which may influence patterns of recolonization. An experimental test was conducted to determine the distribution and abundance of macrofauna around crab burrows after a disturbance designed to simulate a storm. It was expected that the crab burrows would reduce the abundance of common species and might generate a disparity in trophic structure near and away from burrows. Rates of colonization were expected to be lower, with different species or functional groups possibly showing an increased predominance around burrows.

2. Methods

This experiment was conducted on a small sublittoral sandbank at about 6 m depth in Otago Harbor (48S, 171E), South Island, New Zealand. The sandbank was situated on the edge of a channel and exposed to tidal currents of about 50–100 cm s^{-1} (Rainer, 1981). Burrows of the mud crab *Macrophthalmus hirtipes* were the only large biogenic structures in this sediment. Observation based on seven 20 m^2 transects indicated that the density of burrows was 1.1 m^{-2}. The burrows of this species are shallow (down to 6 cm) and generally have a single entrance (Nye, 1974).

To simulate the effects of surface sediment resuspension which would occur during a storm, 150 m^2 of sediment was vigorously raked to a depth of about 2 cm and the dislodged sediments were resuspended and dispersed into a strong tidal current (about 100 cm s^{-1}) with jets of compressed air.

Storms disturb relatively large areas of the seafloor (<100 m^2). The spatial scale of disturbance is likely to be a major factor influencing recolonization. Consequently, artificial disturbances which attempt to mimic storms should be conducted over as large an area as practical. It is often not possible to replicate artificial disturbances in large homogeneous areas of sandflat. This study was conducted on one apparently homogeneous area. No sampling was conducted prior to the start of the experiment to prevent any initial sampling from possibly influencing the macrobenthic community prior to the artificial storm disturbance.

Sediment samples were collected 2, 4 and 30 days after the disturbance using a 78.5 $cm^2 \times 10$ cm corer. On each sampling occasion 15 samples were collected from random positions at least 1 m away from burrow entrances and a further 15 samples were collected at burrow entrances which were adjacent to randomly defined points. Samples were not collected from the same position on subsequent sampling occasions. Samples were sieved (0.5 mm mesh size) and the residue fixed in 4% formalin in seawater with 1% Rose Bengal. Fauna in 10 of the 15 replicate samples from each of the sampling occasions and positions were sorted, identified to the lowest possible taxonomic level and counted. This provided a good estimate of differences in population and community structure.

Maldanid polychaetes could not be identified to species owing to the large numbers of individuals which were damaged during collection and taxonomic difficulties (whole specimens of *Maldane* sp. and *Axiothella* sp. were collected). Similarly, species of the spionid polychaete genus *Boccardia* could not be separated (whole individuals of *B. acus*, *B. syritis* and *B. lamellata* were collected). Polychaetes of the genus *Capitella* are described as *Capitella* spp., as representatives of a supraspecies complex. The oligochaetes consisted of two undescribed species of *Limnodriloides* sp. and one species of *Grania* sp. (Dr. C. Erseus, pers. comm.).

To assess the influence of crab burrows on trophic structure, polychaetes were allotted to the general feeding guilds described by Fauchald and Jumars (1979), see Table 1. Polychaetes were the commonest macro-organisms collected and were represented by the highest number of taxa. Other organisms were not allocated to feeding guilds owing to the lack of information on local species and feeding behavior.

The Freidman's test (Conover, 1980) was used to assess the significance of differences in the abundances of common taxa, number of taxa, number of individuals, and polychaete feeding guilds near and away from burrows over the three sampling occasions. Where the Freidman's test proved significant, the Mann-Whitney *U* test was used to assess the significance of differences in abundance near and away from burrows for each sampling occasion (Conover, 1980). The significance level at which the Mann-Whitney *U* tests were conducted was adjusted to overcome the problem of increasing type one error with multiple comparisons of each variable over the three sampling occasions. The equation: $0.05 = 1 - (1 - \alpha)^n$ (Zar, 1984) demonstrated that for the three comparisons an α level of 0.017 was appropriate. Sample medians and approximate 90% nonparametric confidence intervals (Iman and Conover, 1984) are used for graphic comparisons of abundances from the two sample positions on the three sampling occasions in Figures 1, 2, 3, and 4. The significance of trends of changing abundance over time were tested using Kendall's rank correlation coefficient (Conover, 1980). Statistical significance is presented at the level achieved by each analysis conducted using SAS (1987) software.

3. Results

The results of the Freidman's analysis demonstrated that the abundance of *Capitella* spp, maldanids, *Boccardia* spp., number of taxa, and number of individuals near and away from burrows was significantly different over the three sampling occasions. For the variables which demonstrated an overall significance more individuals were collected away from burrows, except for maldanids collected on day 2 (Figs. 1 and 2). *Boccardia* spp. recorded a significant difference in abundance near and away from burrows on every sampling occasion. The number of taxa and number of individuals recorded significant differences on the 4 and 30 day sampling occasions respectively. Even for taxa which did not show significant differences in abundance

Table 1. The feeding guilds to which polychaete families were allocated and the categories of potentially movable and stationary to which benthic fauna were allocated prior to analysis for trends of changing abundance over time.

Organism	Polychaete feeding guild	Potentially	
		Movable	Stationary
Orbiniidae	B.M.X.	+	
Paraonidae	S.M.X.	+	
Spionidae	S.D.T.		+
Capitellidae	B.M.X.	+	
Maldanidae	B.S.X.		+
Nephthyidae	C.M.J.		+
Sphaerodoridae	B.M.X.		+
Syllidae (sphaerosyllids)	C.M.J.	+	
Nereidae	C.M.J.		+
Glyceridae	C.D.J.		+
Eunicidae	C.D.J.		+
Lumbrineridae	C.M.J.	+	
Oweniidae	S.D.T.		+
Pectinariidae	B.M.X.		+
Terebellidae	S.S.T.		+
Sabellidae	F.S.T.	+	
OLIGOCHAETES	—	+	
AMPHIPODS (Phoxocephalidae)	—	+	
(Corophiidae)	—		+
ISOPODS	—	+	
BIVALVES	—		+
GASTROPODS	—		+
OPHIUROIDS	—	+	
HOLOTHUROIDS	—		+
PHORONIDS	—		+

B.M.X. = Subsurface deposit—Motile—Other structure (usually eversible pharynx)
S.M.X. = Surface deposit—Motile—Other structure (usually eversible pharynx)
S.D.T. = Surface deposit—discreetly motile—Tentaculate
B.S.X. = Subsurface deposit—Stationary—Other structure (usually eversible pharynx)
F.S.T. = Filterfeeder—Sessile—Tentaculate
C.M.J. = Carnivore—Motile—Jawed
C.D.J. = Carnivore—Discreetly motile—Jawed
S.S.T. = Surface deposit—Sessile—Tentaculate After Fauchald & Jumars (1979)

over the three sampling occasions similar patterns are apparent with generally higher abundances away from burrows.

The abundance of polychaete feeding guilds near and away from burrows on the 3 sampling occasions (Fig. 3) showed the same pattern as observed for individual taxa. The two feeding guilds surface deposit-sessile-tentaculate and carnivore-discreetly

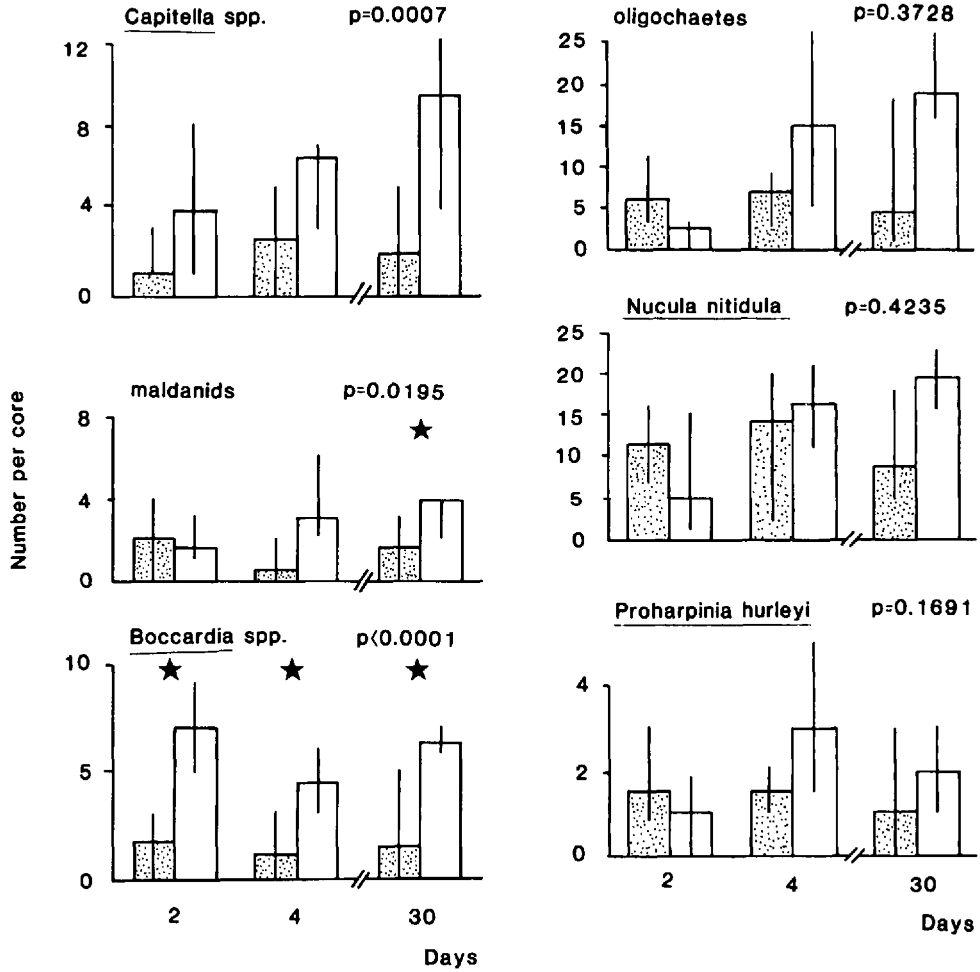

Figure 1. Variation in the abundance of common taxa collected on the three sampling occasions. Each block represents the median abundance. Error bars represent the ~90% nonparametric confidence interval. Stippled blocks represent abundances near burrows and clear blocks represent abundances away from burrows. The probability value for each graph is the result of the Freidman's test. Stars indicate significant differences in abundance between the two sampling conditions on each sampling occasion (Mann-Whitney *U* test).

motile-jawed which were present in this habitat were not presented in Figure 3 owing to their low total abundance (1 and 6 individuals respectively). The polychaete assemblage was strongly dominated by deposit feeders, and motile worms were more abundant than discreetly motile or sessile worms. Apart from the poorly represented guilds of filterfeeder-sessile-tentaculate and carnivore-motile-jawed, Freidman's tests of differences in the abundances of each feeding guild near and away from burrows over time were significant. The guild surface deposit-discreetly motile-tentaculate

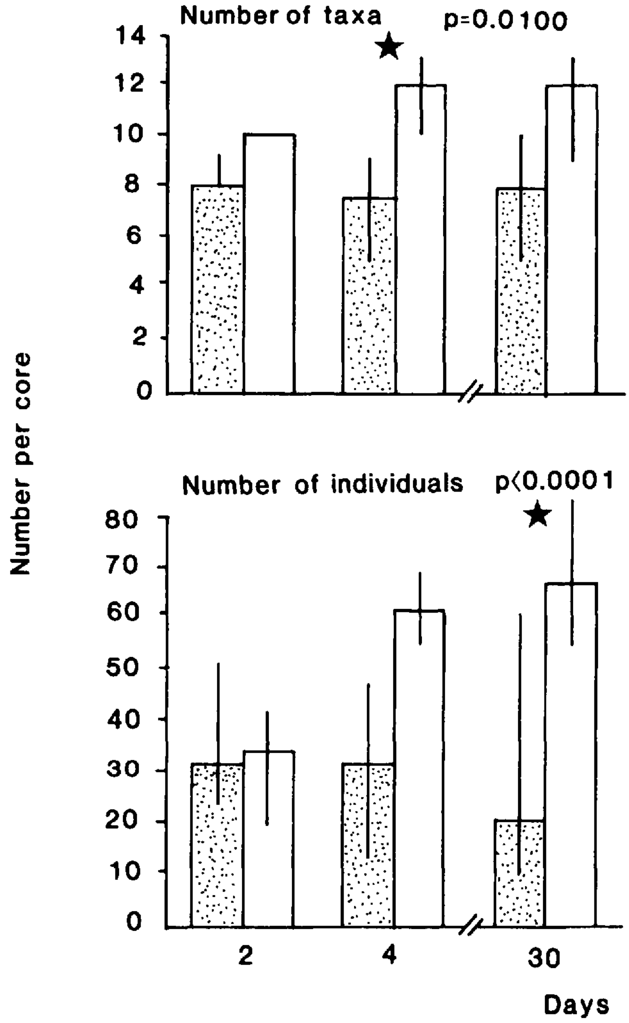

Figure 2. Variation in the number of taxa and number of individuals recorded in the two sampling conditions over the three sampling occasions. (See Fig. 1. legend).

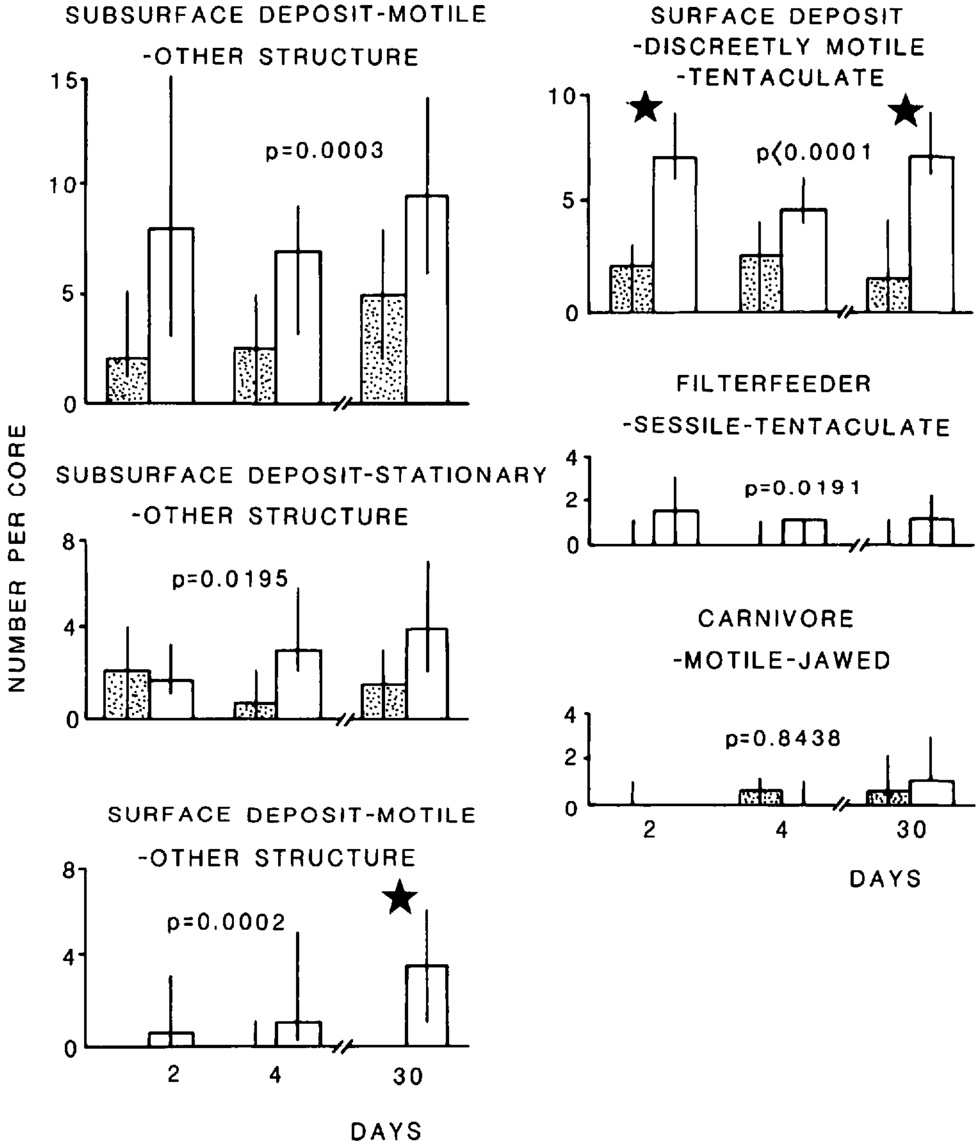

Figure 3. Variation in the abundance of polychaete feeding guilds recorded in the two sampling conditions over the three sampling occasions. (See Fig. 1. legend.)

recorded significantly higher abundances away from burrows on the 2 day and and 30 day sampling occasions. Surface deposit-motile-other structure (usually eversible pharynx) polychaetes also recorded a significant difference on the 30-day sampling. Numbers were generally higher in samples collected away from burrows and none of the feeding guilds were more abundant near crab burrows.

The storm simulation was only expected to affect some of the macrobenthos. Species

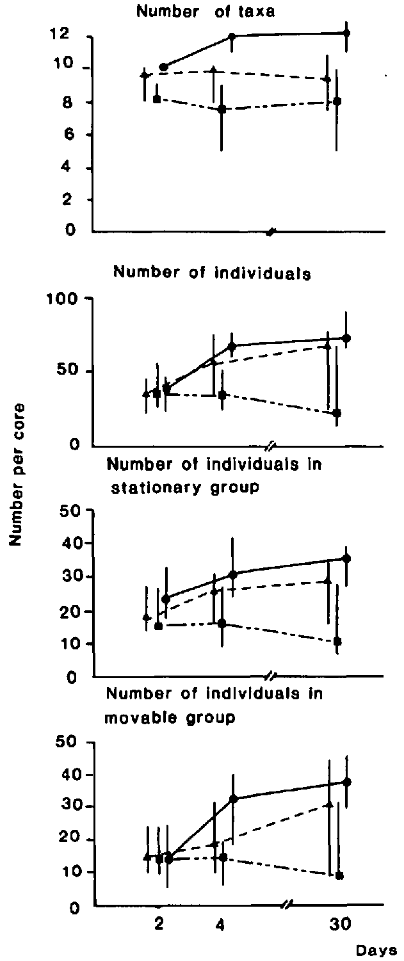

Figure 4. Changes in abundance over time for number of taxa, total number of individuals, number of individuals in the stationary grouping and number of individuals in the movable grouping (See Table 1 and text for details). Circles connected with full lines represent samples collected away from burrows ($n = 10$). Squares connected with dot-dashed lines represent samples collected near burrows ($n = 10$). Triangles connected by dashed lines represent the total sample ($n = 20$). Each point is the median abundance and the error bars represent the ~90% nonparametric confidence interval.

which burrow deep into the sediment, construct large heavy tubes, or have heavy shells were expected to be affected to a lesser extent than the small surface living organisms. Consequently, taxa were grouped into two categories prior to analysis: those expected to be movable and those expected to remain stationary. The two groups were formed on the basis of morphology, depth within the sediment, and tube construction. The classification did not take into account the potential behavioral characteristics of the

Table 2. The significance (p) of Kendall's correlation (t) of potentially movable and stationary organisms, number of individuals and number of taxa with time after storm simulation.

		Near burrows	Away from burrows	Overall
Movable	$t =$	−0.0923	0.4005	0.1552
	$p =$	0.5299	0.0062	0.1284
Stationary	$t =$	−0.0814	0.3968	0.1280
	$p =$	0.5807	0.0069	0.2093
Number of Individuals	$t =$	−0.1419	0.4678	0.1743
	$p =$	0.3320	0.0014	0.0861
Number of Taxa	$t =$	−0.1047	0.2428	0.0792
	$p =$	0.4895	0.1158	0.2093

species during storms, such as deeper burrowing or swimming in the water column. The two groups, as well as the total number of individuals and number of taxa, for samples collected near and away from burrows and in total are shown in Figure 4. The movable group shows a significant increase in abundance over time for samples collected away from burrows (Table 2). In samples collected near burrows a slight decrease in abundance over time was apparent but this was not significant. Similar patterns were apparent for the stationary group and number of individuals. The total number of taxa did not significantly change over time. For number of individuals, number of taxa, movable and stationary groupings the total abundances for each sampling occasion, irrespective of where the samples were collected, did not show a significant increase over time. Except for the number of taxa, a visual trend of increasing abundance was apparent.

4. Discussion

This study has demonstrated that following a disturbance designed to simulate a storm, patterns of macrobenthic recolonization were different near and away from crab burrows. The same taxa were present near and away from burrows but some common taxa (*Capitella* spp., maldanids and *Boccardia* spp.), the total number of taxa, and number of individuals were significantly more abundant away from burrows over the three sampling occasions. The disturbance reduced the abundance of some common taxa and the total number of individuals, but it did not result in a complete defaunation. Although a visual trend of increasing number of taxa with time was apparent, it was not significant. Examination of the abundances of the individual taxa did not indicate the replacement of specific taxa over time. Increases in abundance after the disturbance was rapid and little difference in the abundances was apparent 4 days after the disturbance in comparison to 26 days later.

Biogenic structures have been shown or inferred to play a major role in determining soft sediment community structure, yet little information is available on the way in which biogenic structures influence patterns of recolonization. Resident organisms which modify their habitat are likely to influence localized patterns of recolonization. The pattern of macrofaunal distribution recorded in this study was most likely the result of disturbance caused by the crabs walking in and out of burrows. This disruption may be especially important in influencing sediment stability and limiting the establishment of larvae and adults after disturbance. Similarly, at least part of the decrease in macrofaunal abundance recorded during some predator enclosure experiments has been attributed to the movement of crabs in cages (Virnstein, 1977; Thrush, 1986). This highlights the importance of not generalizing on the role of biogenic structures in soft sediments without considering the activities of the resident animals. Burrows which contain large mobile crustaceans are expected to have a very different influence on community structure than burrows which contain sedentary organisms. This study indicates that crab burrows play a similar role to the burrows of ghost shrimps (*Callianassa* spp.) which exclude macrobenthic organisms from tidal flats (Aller and Dodge, 1974; Peterson, 1977; Suchanek, 1983; Murphy, 1985; Posey, 1986).

The movement of sediment and localized changes to grain size associated with crab burrows may result in resources being available to surface sediment living organisms which are not found away from burrows. This study has not indicated that the areas around burrows are preferentially exploited by any common taxa or particular polychaete feeding guild. Furthermore, the analysis of polychaete feeding guilds indicates that the crab, *Macrophthalmus hirtipes* a deposit feeder, is causing reductions to all polychaetes including deposit feeders. As discussed by Posey (1986), considering the effect of *Callianassa calaforniensis* on intertidal sandflats, this indicates the difficulties of extending the predictions of the trophic group amenalism hypothesis (Rhoads and Young, 1970) beyond the habitat and conditions for which it was originally described.

Increases in the size, density, and variety of biogenic structures are expected along gradients of successional change in soft sediments (Rhoads *et al.*, 1977; Pearson and Rosenberg, 1978), with end-point communities often containing large, mobile, burrowing animals. The presence of organisms which lower the abundance of macrofauna directly adjacent to their burrows may contribute to the decrease in diversity reported from end-point communities (Valiela, 1984). When such organisms remain after a disturbance, they are likely to reduce the abundance of macrofauna in the immediate vicinity of their burrows and influence patterns of recolonization. This study demonstrated that the pattern of macrofaunal abundance created by *Macrophthalmus hirtipes* was reasonably consistent during recolonization after a disturbance designed to simulate a storm.

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REFERENCES

Aller, R. C. 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water, *in* Animal-Sediment Relations, P. L. McCall and M. J. S. Tevesz, eds., Plenum Press, NY, 366 pp.

Aller, R. C. and R. E. Dodge. 1974. Animal-sediment relations in a tropical lagoon, Discovery Bay, Jamaica. J. Mar. Res., *32*, 209–232.

Ban, S. M. and W. G. Nelson. 1987. Role of *Diopatra cuprea* Bosc (Polychaeta: Onuphidae) tubes in structuring a subtropical infaunal community. Bull. Mar. Sci., *40*, 11–21.

Begon, M., J. Harper and C. R. Townsend. 1986. Ecology: Individuals, Populations and Communities, Blackwells Scientific Publications, Oxford, U.K., 876 pp.

Dayton, P. K. 1984. Processes structuring some marine communities: are they general?, *in* Ecological Communities: Conceptual Issues and the Evidence, D. R. Strong Jr., D. Simberloff, L. G. Abele and A. B. Thistle, eds., Princeton University Press, NJ, 613 pp.

Diamond, J. and T. J. Case. 1986. Community Ecology, Harper and Row Publishers, NY, 641 pp.

Dobbs, F. C. and J. M. Vozarik. 1983. Immediate effects of a storm on coastal infauna. Mar. Ecol. Prog. Ser., *11*, 273–279.

Conover, W. J. 1980. Practical Nonparametric Statistics, 2 ed., J. Wiley and Sons, NY, 493 pp.

Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment. Limnol. Oceanogr., *28*, 241–257.

Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev., *17*, 193–284.

Glemarec, M. and A. Menesguen. 1980. Functioning of a muddy sand ecosystem: seasonal fluctuations of different trophic levels and difficulties in estimating production of the dominant macrofaunal species, *in* Marine Benthic Dynamics, K. R. Tenore and B. C. Coull, eds., University of South Carolina Press, Columbia, SC, 451 pp.

Iman, R. L. and W. J. Conover. 1983. A Modern Approach to Statistics, J. Wiley and Sons, NY, 497 pp.

Luckenbach, M. W. 1987. Effects of adult infauna on new recruits: implications for the role of biogenic refuges. J. Exp. Mar. Biol. Ecol., *105*, 197–206.

McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res., *35*, 221–266.

Meadows, P. S. and J. Tait. 1982. Bioturbation, geotechnics and microbiology at the sediment water interface in deep-sea sediments, *in* Proceedings of the Nineteenth European Marine Biological Symposium, P. E. Gibb, ed., Cambridge University Press, Cambridge, U.K., 541 pp.

Murphy, R. C. 1985. Factors affecting the distribution of the introduced bivalve, *Mercenaria mercenaria*, in a California lagoon—The importance of bioturbation. J. Mar. Res., *43*, 673–692.

Nye, P. A. 1974. Burrowing and burying by the crab *Macrophthalmus hirtipes*. N.Z. J. Mar. Freshwat. Res., *8*, 243–254.

Pearson, T. H. and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanog. Mar. Biol. Ann. Rev., *16*, 229–311.

Peterson, C. H. 1977. Competitive organisation of the soft-bottom macrobenthic communities of Southern California lagoons. Mar. Biol., *43*, 343–359.

Picket, S. T. A. and P. S. White. 1985. The Ecology of Patch Disturbance and Patch Dynamics, Academic Press Inc., Orlando, FL, 455 pp.

Posey, M. H. 1986. Changes in the benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis.*, Mar. Ecol. Prog. Ser., *31,* 15–22.

Probert, P. K. 1984. Disturbance, sediment stability, and trophic structure of soft-bottom communities. J. Mar. Res., *42,* 893–921.

Rachor, E. and S. A. Gerlach. 1978. Changes of macrobenthos in a sublittoral sand area of the German Bight, 1967 to 1975. Rapp. -v. Reun. Cons. int. Explor. Mer, *172,* 418–431.

Rainer, S. F. 1981. Soft-bottom benthic communities in Otago Harbour and Blueskin Bay, New Zealand, N.Z. Oceanographic Instit. Mem., *80,* 37 pp.

Rees, E. I. S., A. Nicholaidou and P. Laskaridou. 1977. The effects of storms on the dynamics of shallow water benthic associations, *in* Biology of Benthic Organisms, B. F. Keegan, P. O'Ceidigh and P. J. S. Boaden, eds., Pergamon Press, Oxford, 630 pp.

Reise, K. 1984. Tidal Flat Ecology, Springer-Verlag, Berlin, 191 pp.

Rhoads, D. C., R. C. Aller and M. Goldhaber. 1977. The influence of colonizing benthos on physical properties and chemical diagenesis of the estuarine seafloor, *in* Ecology of Marine Benthos, B. C. Coull, ed., University of South Carolina Press, SC, 467 pp.

Rhoads, D. C. and L. F. Boyer. 1982. The effects of marine benthos on physical properties of sediments, A successional perspective, *in* Animal-sediment relations, P. L. McCall and M. J. S. Tevesz, eds, Plenum Press, NY, 366 pp.

Rhoads, D. C. and D. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res., *28,* 150–178.

SAS, 1987. Statistical analysis software, Version 5.16, SAS Inc., Cary, NC, U.S.A.

Sousa, W. P. 1984. The role of disturbance in natural communities. Ann. Rev. Ecol. Syst., *15,* 353–391.

Suchanek, J. H. 1983. Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidae) bioturbation., J. Mar. Res., *41,* 281–298.

Thistle, D. 1981. Natural physical disturbances and communities of marine soft bottoms. Mar. Ecol. Prog. Ser., *6,* 223–228.

Thrush, S. F. 1986. Community structure on the floor of a sea lough: are large epibenthic predators important? J. Exp. Mar. Biol. Ecol., *104,* 171–183.

Valiela, I. 1984. Marine Ecological Processes, Springer-Verlag, NY, 546 pp.

Virstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology, *58,* 1199–1217.

Woodin, S. A. 1978. Refuges, disturbance, and community structure: A marine soft-bottom example. Ecology, *59,* 274–284.

—— 1981. Disturbance and community structure in a shallow water sand flat. Ecology, *62,* 1052–1066.

Yeo, R. K. and M. J. Risk. 1979. Intertidal catastrophies: effect of storms and hurricanes on intertidal benthos of the Minas Basin, Bay of Fundy. J. Fish. Res. Bd Can., *36,* 667–669.

Zar, J. H., 1984. Biostatistical Analysis, Prentice-Hall, NJ, 718 pp.

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