LONG-TERM CHANGES IN THE STRUCTURE OF A POLYCHAETE COMMUNITY ON ARTIFICIAL HABITATS

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ABSTRACT

A mediterranean polychaete community was studied for 10 years since the first settlement to examine community dynamics and to compare it with the model proposed by Hughes (1984) for benthic invertebrates. Cluster analysis (Q-mode) pointed out the presence of four main periods during the colonization process in agreement with edaphic changes produced by the colonization and disappearance of mussels. During this time the pattern of species abundance changed from a log series distribution (with few dominant species) towards a truncated log normal distribution (with many rare species) characteristic of a more complex community structure.

Natural communities are composed of a variable number of rare, abundant, and dominant species which contribute to determining the pattern of species abundance. This pattern results from historical and present interactions between biotic and abiotic components and may reveal something fundamental about the basic principles and constraints which have driven the evolution of the community (Putman, 1994).

Generally, colonization of a new substratum lead to an increase in community complexity, as far as the number of species, number of individuals and their interactions are concerned. Disturbance events can control the level of diversity and the final community structure (Connell, 1978; Huston, 1979).

According to resource-apportioning theories, the partition of available resources affects the potential number of species present, while biotic interactions control relative population size (May, 1975; Putman, 1994). In this view, a community primarily ordered in respect to one dominating ecological factor, as is the case in the early successional stages, conforms to a logarithmic or broken stick distribution resulting from the presence of few highly dominant species and the almost total absence of rare species (May, 1975). In this type of distribution if the decreasing frequency of species is plotted against number of species the curve thus obtained could be approximated rather well by a logarithmic series (Legendre and Legendre, 1983). Nevertheless, complex communities, ordered by a multiplicity of interactions, such as those during the late stages of succession, fit a log-normal distribution, due to the presence of few dominant and rare species and the abundance of quite common species (May, 1975). This distribution is the Gaussian, or normal curve, based on a variable increasing geometrically, which in this case is the number of individuals in each species (Legendre and Legendre, 1983).

Disagreement with the concept that marine benthic communities generally display log-normal or log-series distributions have been pointed out by many Authors (Lambshead et al., 1983; Hughes, 1984; 1985; Lambshead and Platt, 1985) who have verified a broader diffusion of the truncated log-normal distribution. In that case dominant species are generally more abundant than indicated by a log-series, while rare species are more important than indicated by a log-normal distribution. Consequently, the curve of abundance of species where the numbers of specimens are grouped into geometrically increasing classes is truncated by the ordinate.

Hughes (1984) proposed a model concerning the structure and dynamics of

benthic marine invertebrate communities, starting that space availability and disturbance rather than food, are the most important controlling factors. In this view, community structure depends on population dynamics and is controlled by species recruitment, behavior, mortality, and competition (Hughes, 1985).

A study of the long-term development of a benthic community starting from a new substratum could be helpful in understanding the most important changes in the structure of the community during and after the colonization process. To this end, the Fregene Artificial Reef (Mediterranean Sea) was studied for 10 years and four main phases were identified: "Pioneer settlement period;" "Mussels (*Mytilus galloprovincialis*) dominance phase;" "Regressive period;" "Climax type steady state" (Ardizzone et al., 1989; 1994). Mussels appeared, dominated the community by altering the structure of the substratum, and finally started to decrease until they disappeared. Thus, a study of the temporal trend of the polychaete community, which turned out to be the most important zoobenthic taxon associated with mussels (Gravina et al., 1989), may be useful to verify the model proposed by Hughes (1984), and to evaluate the effects of edaphic changes (mussel disappearance) as a type of disturbance.

MATERIALS AND METHODS

Study Area.—The artificial reef is located in the Tyrrhenian Sea 8 km north of the outlet of the Tiber River and 2.4 km offshore (Fig. 1). The bottom is silty sand and the depth ranges from 12–14 m. Organic materials from the effluents of Rome and carried by the Tiber River make the waters eutrophic (Ardizzone and Giardini, 1982). A total of 56 groups of five-cube blocks having rough surface (each cube 8 m^3) were placed covering a benthic surface of 60,000 m^2 in March 1981 (Ardizzone et al., 1989).

Sampling Technique.—Epibenthic samples were collected by SCUBA divers at various intervals from May 1981 to October 1985 and from January 1991 to September 1992. According to the minimal sampling area proposed by Bellan Santini (1969), two replicates of 400 cm^2 were scraped from vertical walls of a block. The collected material was fixed in 10% buffered formalin and polychaetes were sorted, identified and counted.

Data Analysis.—Normal cluster analysis (Q-mode) was performed to identify the main steps during the temporal evolution of the community. Spearman rank correlation index (Daget, 1979) was used to measure similarity, while hierarchical grouping was performed by means of the Lance and Williams (1967) aggregation algorithm (average-linkage method). To analyse the temporal trend of the polychaete community and to compare it with the Hughes' model, time series of total number of species, frequency of rare species (ratio between number of species with less than four individuals and total number of species), and Shannon Wiener Diversity Index (H') (Shannon and Weaver, 1949) were computed. Changes in the polychaete community structure were also detected using dominance-diversity curves (plotting the logarithmic abundance of each species in descending rank sequence) and species abundance distributions (with the number of individuals in a log scale).

RESULTS

The first settlement of pioneer species was observed in June 1981 with hydroids, barnacles, and the serpulids *Pomatoceros triqueter* and *Hydroides elegans*; this was followed by the dominance of mussels (*M. galloprovincialis*) during the next 3 years (August 1981 to November 1983). The presence of mussels altered the substratum so that sediments were gradually deposited. Progressive edaphic changes led to the disappearance of mussels and other hard bottom species (winter 1983 to winter 1985). After 10 years, community composition was different due to the absence of mussels and the presence of particulate matter and fine sediment trapped among dead barnacles. Bryozoa were the only sessile species extensively distributed on the artificial substratum at this time (Ardizzone et al., 1989; 1994).
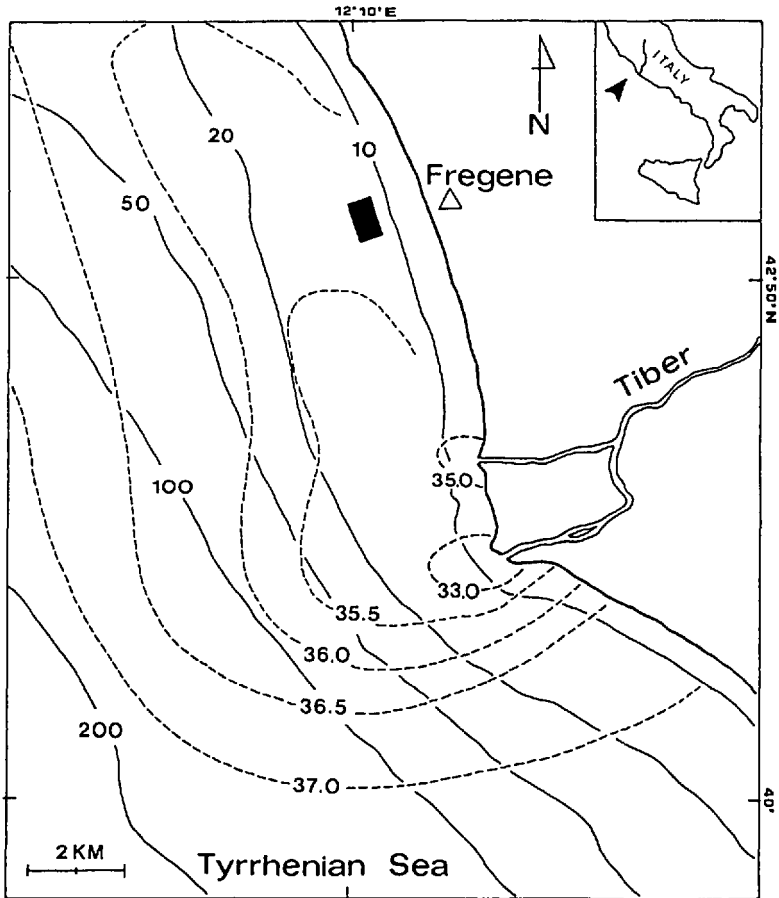
Figure 1.   Map showing the study area and location of the artificial reef (dark rectangle). Solid lines are isobaths in meters and dashed lines indicate mean surface salinity in parts per thousand.

A total of 81 species and 5,970 individual polychaetes were collected. The most abundant species were: *Pomatoceros triqueter* (25.7%), *Hydroides pseudoncinata* (12.4%), *P. lamarckii* (10.4%), *Serpula concharum* (8.6%) and the spionid *Polydora ciliata* (9,4%) only recorded after 1991.

A chronological cluster was performed on 22 samples to identify the main steps in the evolution of the polychaete community (Fig. 2). Four groups of sampling months stand out for a similarity level of 60%. Group A includes samples collected during the first year; Group B includes samples of the second year and one sample from July 1983. Group C includes samples of third and fourth year, and samples of the year 10 belong to Group D and were the most diverse.

Temporal changes in the community structure are shown by trends in the total number of species and individuals, the frequency of rare species and the value of diversity (H') (Fig. 3). Five main consistent changes in the orientation of trends are evident. During the first period, which corresponds to cluster group A, the number of species increased more than the number of individuals. Diversity increased as a result of more rare species. Community structure, as detected by the dominance-diversity plot, showed a linear trend characteristic of log-series distributions (Fig. 4–5). During the second period, which nearly corresponds to the cluster group B, the number of species was steady with an increase in the number of individuals. The percentage of rare species decreased as well as diversity. At
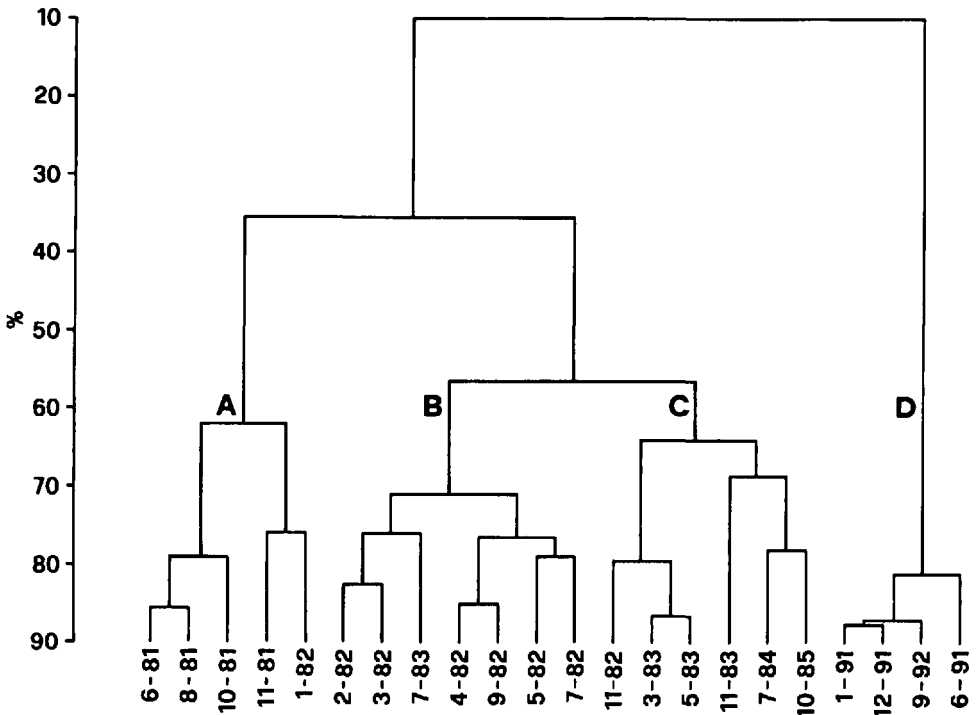
Figure 2.   Cluster resulting from normal classification analysis (Q-mode) using the Spearman rank correlation index and the Lance and Williams aggregation algorithm.

this time some species, such as *Ceratonereis costae, Nereis falsa* and *Harmothoe extenuata,* became dominant whereas others were lost. The slope of the dominance-diversity curve was less marked, indicating a more complex community structure resulting from a truncated log normal distribution (Figs. 4–5). In the third period, corresponding to the cluster group C, increases occurred in polychaete species and diversity. A reduction in polychaete species, individuals and diversity was apparent in the last sample collected in October 1985. Trends in the dominance-diversity plot emphasized a progressive change in the structure of the community. During the fourth period, which overlaped with cluster group
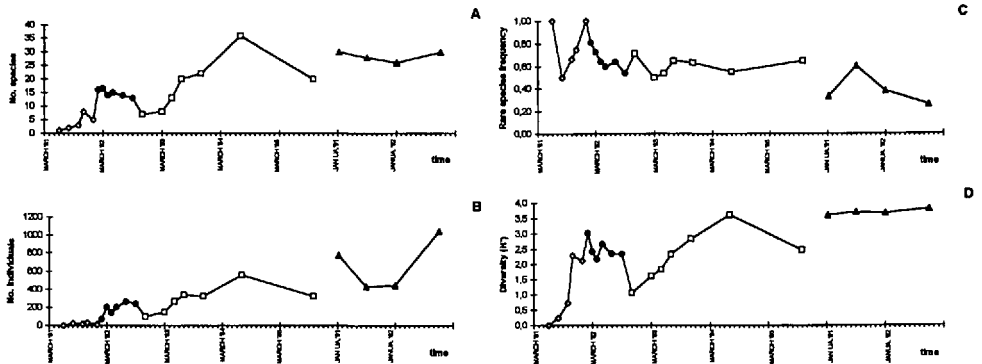

Figure 3.   Temporal trend in the number of polychaete species (A), individuals (B), frequency of rare species (C), and diversity (D). The four main temporal changes are identified by different symbols. ◇: First period (June 1981 to January 1982); ●: Second period (February 1982 to September 1982); □: Third period (November 1982 to October 1985); ▲: Fourth period (January 1991 to September 1992).

CLUSTER GROUP A

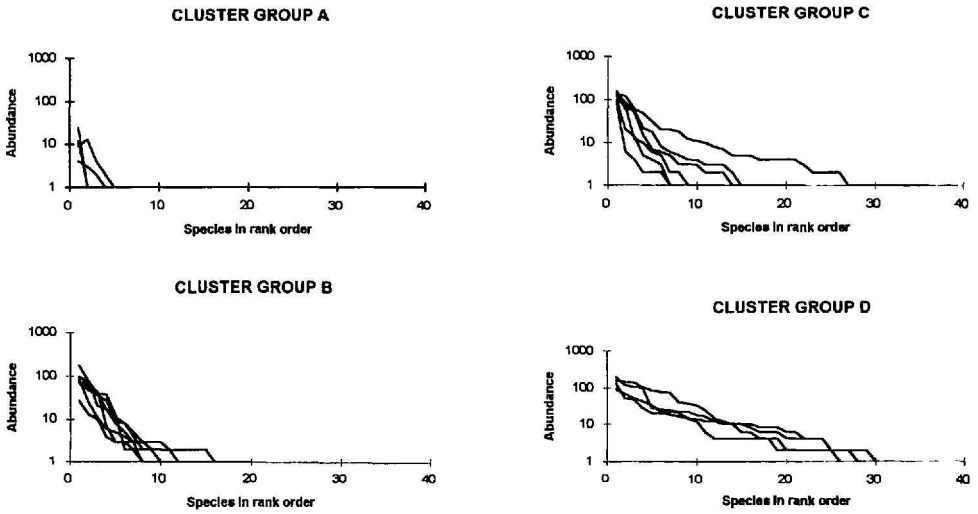CLUSTER GROUP C

CLUSTER GROUP B

CLUSTER GROUP D

Figure 4. Dominance-diversity curve for the four periods identified by cluster analysis.

D, the polychaete community changed in composition and was characterized by the highest number of previously unrecorded species. Although a change in polychaete abundance and in the percentage of rare species occurred, community structure was quite stable during the last two years as indicated by stability in the number of species and diversity. The dominance diversity plot also showed less steep curves approximating the truncated log-normal distribution.

DISCUSSION

The 10-year study of the polychaete community on an artificial substratum in the Mediterranean Sea showed a series of changes both in its structure and its composition in agreement with the model proposed by Hughes (1984). He defined two main stages, respectively "non interactive" and "interactive," during the process of colonization of a new substratum. Obviously; the time required for the development of the community is not numerically quantified as dependent on the
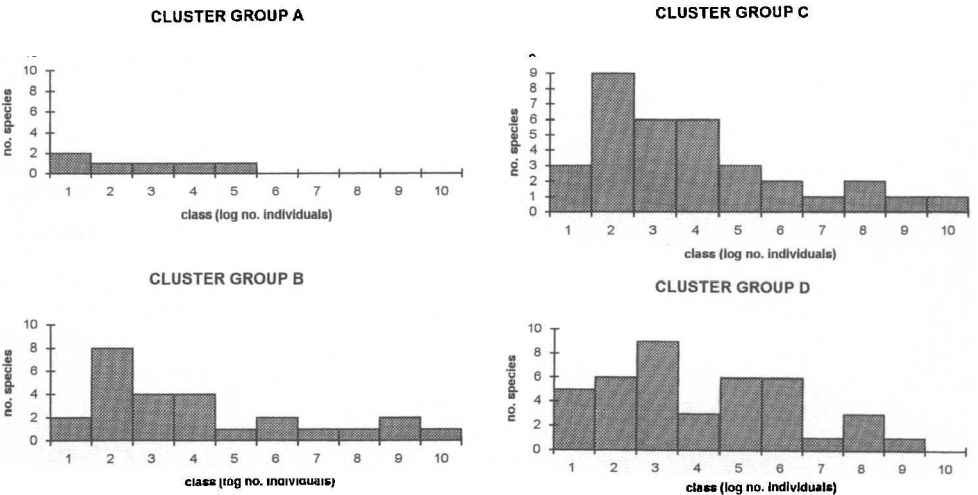
CLUSTER GROUP A

CLUSTER GROUP C

CLUSTER GROUP B

CLUSTER GROUP D

Figure 5. Species abundance distributions for the four periods identified by cluster analysis.

conditions of the environment. The first stage conincided with our phase of colonization during which many species settled on the substratum and were present with a low number of individuals. Competitive interactions were minor. Community structure conformed quite well with the log series distribution. During this phase, the growth of the polychaete community was consistent with that of the mussel (*M. galloprovincialis*). The highest density values of their mussel population coincided with low biomass because of the presence of only young specimens (Ardizzone et al., in press). The second stage was reached only when the density of the polychaete community increased through the growth of some species. Competitive interactions became more important so that less competitive species were gradually displaced by a few species which became abundant. The model forecasts a decrease in species richness at this time (Hughes, 1984) but, in contrast, a rather stable value of this parameter was observed in this study. This could be due mainly to a progressive change in the edaphic conditions resulting from the implementation of substratum heterogeneity. The progressive growth in density and size of mussels led to high values of biomass, and new recruitments contributed to a more complex population structure (Ardizzone et al., in press). The role of habitat complexity, both in terms of spatial heterogeneity and architectural complexity in implementing species richness, was reviewed by Sebens (1991). He used mussel beds as an example of the most complex substrata of subtidal areas. Subsequently, the evolutionary trend of the community provided by Hughes' model (1984) depends on the rate of disturbance. Given reasonable stability, dominance increases, diversity decreases. However, perturbation events tend to reduce those populations of dominant species increasing available space for new colonizers as stated by Connell's "Intermediate Disturbance Hypothesis" (1987). Disturbance events in our third phase, consisted of edaphic changes due to the progressive increase in "mussel mud" trapped among shells. This was later responsible for the decline of the mussel bed (Ardizzone et al., in press) which led to a temporary increase in species richness and diversity in the polychaete community. At the same time the polychaete community changed its structure according to the temporal and spatial patchiness created by the progressive decrease in mussel density. Gravina et al. (1989) also detected a progressive change in the composition of the polychaete community by means of analysis of both newly arrived and lost species. Changes in edaphic conditions in 1985 due to the disappearance of mussels resulted in a disturbing event which led to a decrease in the number of species, individuals and diversity. Nevertheless, a new equilibrium was reached in 1991–92 as shown by stable trends in the number of species present and diversity. The steady state of the community has also been confirmed by the study of colonization and decolonization rates (Ardizzone et al., 1994).

Hughes' model predicts that in the late stages of colonization only a small proportion of species achieve the rapid geometric growth rate that would give a typical log normal distribution. This kind of growth is prevented by an increase in mortality and reduction of recruitment. The progressive decline of geometric growth among species produces a concave dominance-diversity curve with a small number of dominant species and many rare species and truncated log normal distribution.

CONCLUSIONS

The settlement and temporal evolution of the polychaete community on a new artificial substratum in the Mediterranean Sea can be described by the model proposed by Hughes (1984) concerning the structure and dynamics of benthic com-

munities. During the first 2 years of colonization, the trend of the polychaete community largely conformed to the model. Thereafter, disturbance identified as edaphic changes in the mussel bed were confirmed as the driving force in the change of the polychaete community. Disturbance led to temporary implementation and subsequent reduction of community diversity. Five years after the disappearance of mussels the polychaete community seem to reach an equilibrium. Finally, temporal trends in dominance-diversity curves and in species abundance distribution proved to be a good means for pointing out the progressive changes in the community structure.

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