

MRCDOC
89-2037

**TECHNICAL REPORT
TO THE
CALIFORNIA COASTAL COMMISSION**

I. Soft Bottom Benthos

MARINE REVIEW COMMITTEE, INC.

**William W. Murdoch, Chairman
University of California**

**Byron J. Mechalas
Southern California Edison Company**

**Rimmon C. Fay
Pacific Bio-Marine Labs, Inc.**

**Prepared by:
Jon Kastendiek
Keith Parker
Art Carpenter**

**Project Principal Investigator:
Arthur M. Barnett**

**Chief Scientists:
Laurence Lovell
Thomas D. Johnson
Karen D. Green**

July 1989

This report analyses and presents the results of studies of MEC Ecological Consultants, which were done on behalf of the MRC over the period 1980-1988, under the direction of Dr Arthur M. Barnett. Their Final Report to the MRC "MEC Biological Project San Onofre Generating Station Monitoring Studies on Mysids and Soft Bottom Benthos" (30 November 1987, MEC03287056) provided the starting point for the analyses in the present report.

TABLE OF CONTENTS

Summary	iii
1.0 Introduction.....	1
2.0 Methods	5
2.1 Field sampling.....	5
2.2 Laboratory Analysis	6
2.2.1 Analysis of BIO cores	6
2.2.2 Analysis of P/C cores	7
2.3 The study periods	9
2.4 Analytical methodology.....	9
2.4.1 Individual taxa	10
2.4.2 Pooled taxa and trophic motility groups.....	11
2.4.3 Biomass	13
2.4.4 Test for changes in abundance.....	13
2.4.5 Trends in deltas with time - Analysis of covariance	17
2.4.6 Correlations between biological and physical/chemical variables	18
3.0 Results	19
3.1 General description of the fauna.....	19
3.2 Changes and trends in abundance.....	21
3.2.1 Eight meter depth	22
3.2.1.1 Individual taxa	22
3.2.1.2 TM groups	24
3.2.1.3 Biomass.....	27
3.2.1.4 Number of taxa per sample	27
3.2.2 18 meter depth.....	28
3.2.2.1 Individual taxa	28
3.2.2.2 TM groups	31
3.2.2.3 Biomass.....	35
3.2.2.4 Number of taxa per sample	36
3.2.3 Effects at 6700 meters from the plant.....	36
3.3 Relationships with physical/chemical characteristics	37
3.4 Changes in frequency of occurrence	39
3.4.1 Eight meter depth	40
3.4.2 Eighteen meter depth.....	41
4.0 Discussion.....	44
5.0 References.....	53
6.0 Tables	57
7.0 Figures	83

APPENDICES

Appendix A. Survey dates	A-1
Appendix B. The frequency of zero abundance values of individual taxa, trophic-motility (TM) groups, and biomass at the sampling locations	B-1
Appendix C. The trophic-motility (TM) groups and their component taxa.....	C-1
Appendix D. The mean (and standard error) densities (per core) of individual taxa, trophic-motility (TM) groups, and biomass (gms wet weight) at the sampling locations in both sampling periods	D-1
Appendix E. Conversion of percent relative change into factors of change	E-1
Appendix F. Summary of the results of the multivariate BACIP test for change in abundance.....	F-1
Appendix G. Summary of the results of the tests for trends with time of the Impact-Control deltas in abundance	G-1
Appendix H. Plots of the Impact-Control deltas against time for those individual taxa, trophic motility groups, and biomass measures which displayed a significant change in abundance or a significant trend in deltas in the after period	H-1
Appendix I. The mean (and standard error) densities (per sample) and frequency of zero abundance values of all trophic motility groups at sampling locations in both sampling periods.	I-1
Appendix J. The mean (and standard error) densities (per sample) and frequency of zero abundance values of all taxa at all sampling locations in both sampling periods.	J-1
Appendix K. The mean (and standard error) number of taxa (per sample) at all sampling locations in both sampling periods.	K-1
Appendix L. Rankings of the twenty most abundant taxa found at each sampling location at both 8 and 18 meter depths in both Before (=preop) and After (=op) periods.	L-1
Appendix M. Comments on differences between contractor's and MRC's soft benthos reports.....	M-1

SUMMARY

Unconsolidated, or soft, sediment covers the sea floor in a large area around the San Onofre Nuclear Generating Station (SONGS). This bottom habitat supports a large and varied assemblage of species of invertebrates which live in and on the substrate. In 1980 the MRC predicted that the operation of the circulating water system of SONGS Units 2 and 3 might increase the numbers of soft sediment invertebrates by converting planktonic organisms withdrawn into the plant into detrital material. This material would be discharged by the diffusers and eventually fall to the sea floor where the bottom fauna would feed upon it. The major goal of the MRC soft benthos study was to test this prediction, and to determine whether, by contrast, the operation of SONGS reduced the abundance of organisms within this assemblage.

During this study benthic samples were taken at two depths, eight and 18 meters, at six locations downcoast from SONGS. The locations were 700, 1100, 1900, 3350 (at eight meters and 3200 m at the 18 meter depth), 6700 and 9400 meters downcoast from the generating station. Collecting samples at these sites allowed us to determine how far downcoast SONGS affected the biota; sampling at the two depths allowed comparison of effects on the benthos at the depth of the intake structures and of a depth equivalent to that just seaward of the end of the diffuser lines.

The biological variables measured were the numbers of organisms found in cores of sediment taken from the bottom. Since there was a noticeable change in the benthos throughout the study area between the Before period and the After period (probably due, in part, to the El Nino of 1982-1984) we focused our attention

on those species which were frequently encountered during both periods. Furthermore, since the great majority of species in this speciose assemblage (over 600 taxa were identified during the study) are of low abundance and infrequently sampled, we combined taxa into larger taxonomic groups, and into trophic-motility (TM) groups in which taxa with similar feeding behavior and motility characteristic were combined. These groups and those abundant and commonly occurring individual taxa were tested for abundance changes with a multivariate analysis of variance comparing the changes in the Impact area (defined as the four stations closest to SONGS within approximately four km downcoast of the plant) to those in the control area (the two most distant sampling locations). We estimated the distance from SONGS over effects occurred by comparing separately the changes in abundance at each of the Impact stations to those at Control.

We tested for temporal trends in the After Impact-Control differences in density. These trends would indicate if differences between Impact and Control changed over time and might give insight into whether effects will continue, or might change, beyond the period the samples were taken.

We tested for patterns of disappearance (or appearance) close to SONGS relative to Control among a large group of species at both depths by comparing the frequency of occurrence at an Impact and a Control site, first in the Before period and, again, in the After period. Forty-six taxa were tested for these changes at the eight meter depth and 85 at the eighteen meter depth. These species, collectively, accounted for over 95% of the total benthos at both depths.

We also measured various physical and chemical characteristics of the sediment at each of the sampling locations. These data were then correlated with

the abundance measures. This was done in an attempt to gain insight into any potential mechanism that might be responsible for the observed changes.

In general, the results of the study support the MRC's predictions. This is especially true for the benthos at the 18 meter depth. Among the aggregate measures of the benthos, the pooled taxa and TM groups, there was remarkable consistency of results. The benthos, combined, increased in the Impact area at various distances from SONGS. Increases were also detected in all of the combined taxonomic groups (polychaetes, molluscs, and crustaceans) and the major groupings based on the depth in the sediment the animals fed (surface and subsurface). When the TM groups were subdivided further, significant changes were almost universally increases. Among the individual taxa which showed significant changes in abundance five increased in relative abundances near SONGS relative to Control, one decreased, and the seventh increased at one Impact site and decreased at another.

Positive trends in the After deltas, indicating that abundances at Impact stations increased over time relative to Control, were detected in many TM groups. Again, they far outnumbered the number of negative trends detected (found in only one TM and one individual species).

A positive response on the part of the benthos at this depth is also indicated by the patterns in changes of frequency of occurrence among individual taxa. Eighteen species were sampled more frequently near SONGS relative to Control in the After period while only two became less frequently sampled. Finally, the total number of taxa found in samples also increased significantly near the plant in the After period.

At the eight meter depth, the pattern in the results was more variable. Among the seven individual taxa tested the only two that showed significant abundance changes increased in the Impact area relative to SONGS; *i.e.*, the same type of change as in deeper water. However, while three taxa showed positive trends in the After deltas, two showed negative trends, indicating that density at Impact stations was decreasing relative to that at Control over time. The major difference between 8 and 18 meters occurred among the TM groups. When all taxa are combined, a significant decrease in relative abundance was detected. Combined polychaetes declined, but combined crustaceans increased at several Impact locations. All surface feeding animals combined increased, while no change in the subsurface feeders was detected. As expected from the behavior of these large groupings, several of the smaller TM groups increased and several decreased. However, even though there was a mixture of increases and decreases in relative abundance among these TM groups, the number of TM groups (and individual species) that showed positive trends in the After deltas outnumbered those with negative trends.

The results regarding changes in frequency of occurrence also corroborate the mixture of increases and decreases in mean abundance. Seven species increased in the frequency of occurrence near SONGS relative to Control while three decreased. A change in the number of species found per sample was not detected at this depth.

Thus, it appears that the benthos at 18 meters in the Impact area has steadily increased over time relative to Control. In many cases the trend has been sufficiently strong that when averaged over the entire After period a change in abundance is observed. However, at eight meters during the early part of the After

period, the densities in the Impact area were less than at control. And while these Impact densities steadily increased relative to control through the After period, when averaged over the period a decrease in mean abundances was detected. Some of the reductions in the early part of the After period coincide with the release into the sea of the unconsolidated sand material in the construction laydown pad of Units 2 and 3.

There were discernible patterns in the distance over which effects were detected. At eight meters, declines in abundance were generally restricted to distances of 1100 meters downcoast and, conversely, increases were generally found from 1900 to 3350 meters downcoast. This spatial pattern is also consistent with the potential effects of the release of the sand laydown pad whose effects are likely to be localized to the region nearer SONGS.

At the 18 meter depth the pattern in effects with distance involves groups feeding at different depths in the sediment. The combined subsurface feeders increased only to 1100 meters downcoast, while various surface feeding TM groups increased in abundance throughout the Impact area to 3350 meters downcoast of the plant.

While there is strong evidence that plant affects the benthos to a distance of approximately 3 km, the evidence for effects at greater distance is not as strong. The strongest pattern in effects occurring from the vicinity of the plant to 6700 meters from the plant is found in the increases observed in two small TM groups found at the 18 meter depth.

While the exact mechanisms responsible for the observed increases in the benthos are unknown, increased detrital material remains a likely contributor. Correlations between physical/chemical (p/c) variables and densities were numerous but not very strong and did not explain much of the variability in the density measures. However, the p/c variables that were most often correlated with densities were measures associated with detrital material, organic carbon and phaeopigment content of the sediments. And while the measured relationships were not strong they were more common and stronger at the 18 meter depth, the depth where the discharge plume is more prevalent.

The effects of the operation of SONGS on the soft benthos, a general increase in abundance, suggest that they may relate to the results of MRC studies of other groups of organisms. Increases in mysid shrimps in the same general area may also result from the addition of particulate food on or near the bottom. The increases in the soft benthos may also be related to the observed increases in benthic fishes, many of which feed on the benthic invertebrates under study.

1.0 INTRODUCTION

A large portion of the sea floor in the vicinity of SONGS is unconsolidated, or soft, sediments. Except for the area approximately 0.5 to 2.0 km downcoast of the diffusers of Units 2 and 3 and between the depths of 11 and 16 meters, where rocky substrate supports the San Onofre kelp forest, the areas around SONGS are soft sediments. Particularly, the areas around the intakes of SONGS and the areas seaward of the diffusers are exclusively soft sediment. The average grain size of these sediments varies from coarse to fine (from sands to muds) as depth varies from shallow to deep (but see Technical Report B: Cohesive Sediments for a discussion of an anomaly in this grain size-depth relationship which appeared in the Impact area in the After period).

These sediments harbor a large number of invertebrate species representing many phyla. These species represent the largest faunal group (in number of species) potentially affected by SONGS. This group is not only diverse taxonomically but contains organisms exhibiting a large array of different feeding habits and patterns of habitat utilization. It is the extent of the habitat and the complex, diverse nature of the community within it that makes the effects of SONGS of interest. Furthermore, this species assemblage is a principal food source for benthic fishes and an impact of the operation of SONGS on this assemblage could, therefore, also result in changes in those species that feed upon it.

This report assesses the impact of the operation of San Onofre Nuclear Generating Station (SONGS) on the invertebrates living in and on soft sediments in the vicinity of the generating station. The MRC studies of these animals started in 1977 and ended in 1987. They were conducted by Marine Ecological Consultants,

Inc. (MEC). The earlier studies (1977-1979) estimated the effects of Unit 1. The results of these studies were used to predict the effects of Units 2 and 3 and to establish appropriate sampling designs to test for effects of Units 2 and 3.

The predicted effects of SONGS Units 2 and 3 on the soft benthos were that close to the diffusers (within one kilometer), sediments would be coarsened in grain size, but further away the sediments would become finer (Murdoch *et al.*, 1980). At all distances the sediment would be enriched with detrital material. The general result of these changes would be an increase in the abundance, number of species, and, perhaps, an increase in annual production of biomass. However, the predicted enrichment of the soft benthos was not expected to influence the production of sport and commercial fish.

The present report presents the results of the studies on the impact of Units 2 and 3. Data used to address this question were gathered from November, 1979 to December, 1986. The principal aim of the study was to determine if the abundance of infaunal and epifaunal invertebrates changed in the vicinity of SONGS' as a result of plant operation. As in other MRC reports the principal method of study was to compare the change in abundance that occurred in an Impact area from the preoperational (Before) period to the operational (After) period to the change that occurred at a distant Control location over the same time period. The relative difference in the changes observed between the two locations is a measure of the effect of the generating station.

The effects on both the soft sediments and the organisms in it were expected both to change gradually with distance from the generating station and to persist at a location. Furthermore, unlike local hard substrate, soft sediments are a

continuous and extensive habitat. The MRC, therefore, decided to sample the benthos at a number of stations at various distances along a gradient downcoast from SONGS. This gradient permits an estimate of the spatial extent of SONGS' influence.

A third line of investigation was to examine the relationships between various physical and chemical characteristics of the sediment and the abundance of the fauna. Previous studies (e.g. Biernbaum 1979, Bloom *et al.* 1972, Flint 1981, Gray 1974, Rhoads 1974, Young and Rhoads 1974) have shown that the soft benthos is often sensitive to the physical and chemical nature of the sediments in which they live. It was hoped, therefore, that examining these relationships in the area around SONGS would give insight into the possible mechanisms by which the generating station caused any observed changes.

While, the results presented in this report deal primarily with the effects of SONGS on the density (numbers per unit volume of sediment) of individual species and species groups, effect on changes in the species composition of the assemblage are also addressed. Changes in species composition were addressed at length in MEC's Final Report, which presents the results of a cluster analysis designed to group, by similarity of species composition, the species assemblages found at each sampling location in both Before and After sampling periods (Barnett, *et al.*, 1987). The results of the analysis indicated that the assemblages at all sampling locations in the Before period formed a group (cluster) distinct from the cluster formed by the assemblages found at all locations in the After period. These results indicated that a striking change in species composition occurred between the Before and After periods (probably in response to the El Nino of 1982-1984), but that, in general, the change occurred throughout the entire study area, including both Impact and

Control locations. In the present report a different analytical procedure is used to determine SONGS' effect on species composition. Many individual species are tested for Before-After differences in their frequency of occurrence at Impact and Control locations.

2.0 METHODS

2.1 Field Sampling

Benthic samples were collected, at depths of 8 m and 18 m, at six distances downcoast from SONGS Unit 1: 700m, 1100m, 1900m, 3200m (18m depth) or 3350m (8m depth), 6700m, and 9400m (Figure 1). Note that to obtain the distances in reference to the midpoint of Units 2 and 3 approximately 300 meters should be subtracted as the Units 2 and 3 diffusers are located downcoast from Unit 1.

The 8m depth was selected because it corresponded to the depth of water in which the SONGS intakes are located. The 18m depth corresponds to the depth at the seaward end of the Unit 2 diffuser, the diffuser which extends farthest offshore. It was predicted that the discharge plume of the diffusers would generally be directed offshore and that the plume would be pushed either upcoast or downcoast depending on ambient longshore current conditions. Longshore currents move in the downcoast direction approximately 60% of the time (Marine Review Committee Final Technical Report L: Physical and Chemical Oceanography) and the sampling stations were placed at six distances in this direction to provide an estimate of the distance over which the effects of SONGS would extend.

Each longshore station was permanently marked by a spar buoy attached to a steel plate on the bottom. On each survey, divers collected at least three sediment cores for physical/chemical (P/C cores) analysis and at least four cores for analysis of the benthos (BIO cores) at each station. The cores were taken at randomly chosen locations within a circle 20 m in diameter centered on the bottom plate (see Appendix B, Subsection B.2.1, of Barnett *et al.*, 1987, for a complete description of

the field program protocol).

The P/C core was 5.1 cm in diameter, had a surface area of 20.6 cm² and was inserted 8 cm into the sediment. The core was removed from the sediment and capped from beneath. The BIO core was 7.6 cm in diameter, had a surface area of 45.6 cm², and was inserted 10 cm into the sediment, dug out, and capped from beneath. Cores were placed in labeled bags and transported back to the laboratory for processing.

2.2 Laboratory Analysis

2.2.1 Analysis of BIO cores

Sediment from the BIO cores was washed through a 0.5 mm screen and the retained material fixed with 5-10% buffered Formalin-freshwater. After 48-72 hours, the Formalin was replaced with 70% isopropyl alcohol for long-term preservation of the sample.

Three of the four BIO cores taken at each station were analyzed and one was stored for possible future reference (see Appendix B, Subsection B.2.2, of Barnett, *et al.*, 1987, for a complete description of the laboratory analysis protocol). The fourth core collected at the station was usually the one stored. Samples designated for analysis were first sorted for animals under a dissecting microscope at 10-12X magnification. Animals were placed in labeled alcohol-filled vials according to four taxonomic categories: crustaceans, molluscs, polychaetes, and "others" (other phyla). Nematodes were counted but not removed from the sorted samples. Animals within each taxonomic category were identified to the lowest taxon possible.

After the animals were identified, animals from each of the replicate cores were combined according to taxonomic category, excess alcohol was removed by vacuum pump for 10 seconds, and wet weights of each of the four groups were measured to the nearest 0.01 gm.

After the animals were removed, the remaining material from each of the three replicates from a station were combined, and the average macrodetritus content of the samples was determined. The composite sample was swirled and the macrodetritus was poured off onto a preweighed filter. Macrodetritus was identified to categories of old (anoxic) and new terrestrial particles, marine macrophytic particles, animal tubes, organic particles, and inorganic particles. The percent composition (to the nearest 5%) of each category was visually estimated. The filter was then dried at 80° C for 10-12 hours and weighed (to nearest 0.01 gm). The dry weight of the composite macrodetritus samples was divided by three to yield an estimated macrodetritus dry weight per core. During the preoperational and interim period, the types of macrodetritus were not identified.

Counts for the identified taxa were reported as number per core. Composite wet weight biomass measurements were reported for each station as total wet weight. The estimated macrodetritus dry weight and percent composition were reported for each sample.

2.2.2 Analysis of P/C cores

In the laboratory, P/C samples were split longitudinally (Appendix B, Subsection B.2.1, of Barnett, *et al.*, 1987, contains a complete description of the protocol for sample processing in the laboratory). Two composite samples were

made from the halves of the three replicate cores. Each composite sample was then homogenized. One sample was analyzed for grain size and total organic carbon (TOC). The other was analyzed for chlorophyll-a, phaeopigments, and organic nitrogen. (Organic nitrogen analysis was discontinued in 1984 after no variation with distance longshore or time was observed.)

Sediment cores to be analyzed for grain size were stored at 0°C. For the analysis, a 20-50 ml subsample was transferred to a 240 ml bottle, mixed with 150 ml of deflocculent (sodium hexametaphosphate), and allowed to stand overnight. The sand fraction was shaken through and collected on eleven U.S.A. Standard Testing Sieves, which ranged in 0.5 phi intervals from 4.0 to -1.0 phi (see Appendix B, Subsection B.2.3.1 of Barnett, *et al.*, 1987, for a complete grain size analysis protocol). When combined with the silt-clay weight, the weights of the fraction retained on each sieve and on the bottom catch plate gave the grain size distribution for each sample.

During the preoperational period, the fraction of particles smaller than 4 phi was reported as "percent silt/clay". Beginning with the March 1982 survey, pipette analysis of the silt/clay fraction (5 phi to 8 phi) in whole phi intervals was added to the sieve analysis of the sand fraction.

Total organic carbon (TOC) in sediment samples was measured with an Oceanography International model 524-B analyzer (Appendix B, Subsection B.2.3.2, of Barnett, *et al.*, 1987, provides the protocol for TOC analysis). Subsamples (20-50 g) were dried at 70° C for 12 hours, ground to powder, placed in preweighed and precombusted ampules, and reweighed. Phosphoric acid and potassium persulfate were added, then oxygen was introduced to oxidize and purge the inorganic carbon.

The ampules were next sealed, heated in an autoclave, and the CO₂ measured with a non-dispersive infrared analyzer. A standard curve was generated by measuring the CO₂ evolved from known concentrations of potassium biphthalate.

2.3 The Study Periods

Sixteen Before surveys were made at both depths. Fifteen were made on a triweekly basis from November 1979 to November 1980, and an additional survey was conducted in June, 1981. During the After period 31 surveys at both 8 m and 18 m depths were conducted from June 1984 to December 1986. The sampling dates are presented in Appendix A.

The first After survey was made in June, 1984, approximately twelve months after Units 2 and 3 obtained operating levels characteristic of the After period. This delay was intended to allow any cumulative SONGS-induced changes in the benthic environment to be reflected in the benthic community.

2.4 Analytical Methodology

Numbers and biomass of particular taxa and in pooled groups of taxa ("trophic-motility", or TM, groups, see Section 2.4.2, below) were the basic variables used in the analytical procedures. The test variables were the total numbers of organisms per taxon or group in all cores combined from each location at a given depth.

Also basic to the analytical procedures was that data from the 8 m and 18 m depth contours were analyzed separately. In most of the analyses the 700, 1100,

1900 and 3200/3350 meter stations were treated as separate Impact locations and the values from the 6700 and 9400 meter locations were averaged and treated as the Control. The mean of the two far locations was used as a single Control for three reasons. First, SONGS' effects were not expected to extend as far as the 6700 meter location (see Final Technical Report L: Physical/Chemical Effects of SONGS) and our analyses indicate that this is true (Section 2.4.4). Second, the mean of the 6700 and 9400 meter locations makes for a more statistically stable and representative Control. Finally, combining the two distant stations gives a more straightforward and easily interpreted statistical analysis than would a set of analyses using each of these stations separately as a Control.

Previous experience with MRC data cautioned us to the effect of many zero abundance values on the results of the test for changes in abundance. Many zero values allow the constants added to the log transformation to overly influence the test results. Consequently, prior to statistical analysis, the taxa (both individual and pooled) and TM groups were screened for the occurrence of zeros; taxa or TM groups with over 50% zeros at any sampling location during either Before or After periods were eliminated from the analytical procedures.

2.4.1 Individual taxa

Over 600 taxa were identified in the laboratory. However, most occurred infrequently and at low abundance. From the 8 meter depth we tested seven individual taxa for abundance changes: the polychaete worms *Acesta catherinae*, *Amastigos acutus*, and *Prionospio pygmaea*; the amphipods *Jassa falcata* and *Rhepoxynius menziense*; the cumacean *Diastylopsis tenuis*, and unidentified nematode worms. The record of their frequency of occurrence is presented in Appendix B.

Sixteen taxa from the 18 meter depth were tested for abundance changes. They include five polychaetes (*Acesta catherinae*, *Aricidea wassai*, *Mediomastus californiensis/ambiseta*, *Paraprionospio pinnuata*, *Prionospio pygmaea*, and *Tauberia gracilis*), four amphipods (*Jassa falcata*, *Rhepoxynius* sp. juveniles, *Rhepoxynius stenodes*, and *Sychelidium shoemakeri*), three ostracods (*Euphilomedes carcharodonta*, *Parasterope hulingsi*, and *Rutiderma rostrata*), a tanaid (*Leptochelia dubia*), a bivalve (*Tellina modesta*), and unidentified nematodes. The record of their frequency of occurrence is presented in Appendix B.

2.4.2 Pooled taxa and Trophic Motility groups

Two approaches have been used to reduce and simplify the complex information yielded by species assemblages. One approach is purely mathematical and uses multivariate techniques to classify sampling locations into pooled groups based on their species composition or to group species based upon their distribution (e.g., Boesch, 1973; Smith, 1976; Dorsey *et al.*, 1983; Stull *et al.*, 1986). Because the classification method is largely descriptive, tests of significance are of doubtful validity. In addition, this approach does not address the underlying factors that affect the organization of the community.

A second approach, followed here (and described in detail in Barnett *et al.*, 1987), entails analyzing taxa falling into groups defined on the basis of ecological information about life cycles, distribution, or trophic relationships (e.g., Fauchald and Jones, 1978; Pearson and Rosenberg, 1978; Whitlatch, 1980; Dorsey *et al.*, 1983). The use of trophic groups provides numbers that are amenable to hypothesis testing, although it is sometimes difficult to assign unambiguously some species to a well-defined group, often because the feeding behavior is either variable or poorly