Recurrent Groups of Megabenthic Invertebrates on the Mainland Shelf of Southern California in 1994

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ABSTRACT

Several hundred species of megabenthic invertebrates inhabit the soft-bottom environs of the mainland shelf of southern California. This study identifies and describes recurrent groups of megabenthic invertebrates based on a region-wide survey of the Southern California Bight (SCB). During July and August 1994, trawl samples were collected at 114 randomly selected stations from Point Conception, California, to the United States-Mexico international border at depths of 10 to 200 m. Recurrent groups (i.e., groups of frequently co-occurring species) were identified and described using Fager's recurrent group analysis. Of the 204 species of invertebrates collected, only 31 formed recurrent groups or associates. Seven recurrent groups of invertebrates with two to six species per group were described. Each group was characteristic of a different bathymetric zone but some also represented specific habitats within a depth zone (e.g., shelf-break, submarine canyons). The Middle/Outer Shelf Group was comprised of the most frequently occurring species. Most of the recurrent group species were dominant species in earlier descriptions of megabenthic assemblages based on ordination and classification analysis. Although recurrent groups have not previously been described, it is anticipated that megabenthic invertebrate core groups are likely to be found primarily in the Middle/Outer Shelf and Outer Shelf Groups.

INTRODUCTION

The megabenthic (i.e., large epibenthic, trawl-caught) invertebrate fauna occupying the mainland shelf of southern California is diverse, consisting of several hundred species (Moore and Mearns 1978). Understanding whether these species are organized — and if so, how they are organized — is useful for determining community functional organization. Knowledge of species organization is a prerequisite for assessing whether fish communities are affected by anthropogenic activities since fish use benthic invertebrates as food. One methodology that has been used to assess the consistency of assemblages is recurrent group analysis (Fager 1957, 1963).

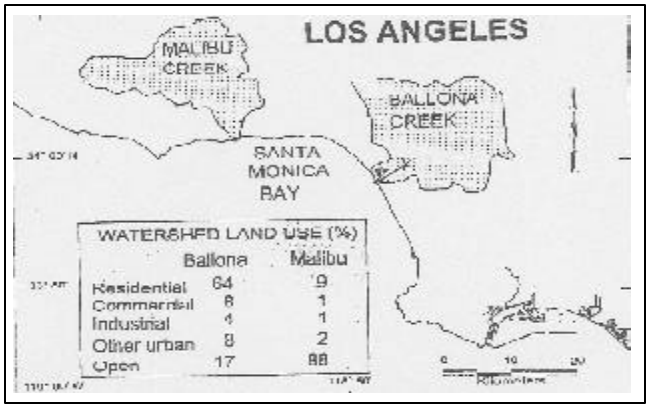
Megabenthic invertebrate assemblages occurring from 1971 to 1985 have been described for the shelf and slope of southern California using ordination and classification methods (Thompson *et al.* 1993). However, recurrent groups of megabenthic invertebrates have not been described for the soft-bottom habitat of the mainland shelf of southern California. Recurrent group analysis is based on presence/absence data and describes groups of species that frequently occur together. Ordination and classification analyses are based on the similarity of species composition and abundance patterns among the stations. A trawl survey of the mainland shelf of the SCB in 1994 (Allen and Moore 1996) provided the opportunity to identify, describe, and refine communities of megabenthic invertebrates throughout the region.

The objectives of this study are (1) to identify recurrent groups of megabenthic invertebrates on the soft-bottom habitat of the mainland shelf of southern California; (2) to describe their bathymetric and geographic distributions within the SCB; and (3) to refine the understanding of megabenthic invertebrate assemblages in the region by comparing the groups with assemblages previously described using ordination and classification analyses.

MATERIALS AND METHODS

Trawl samples were collected at 114 randomly selected stations from Point Conception, California, to the United States-Mexico international border at depths of 10 to 200 m (Figure 1). A stratified random design was used with strata of the following depths: (1) inner shelf —10 to 25 m; (2) middle shelf — 25 to 100 m; and (3) outer shelf —100 to 200 m (Bergen 1996).

FIGURE 1. Stations sampled by trawl on the mainland shelf of southern California at depths of 10 to 200 m, July to August 1994.



Samples were collected from July 12 to August 22, 1994, with 7.6-m head-rope semiballoon otter trawls with 1.25-cm cod-end mesh. Trawls were towed for 10 min at 1 m/sec (2 kt) along isobaths. Megabenthic invertebrates were identified to species, counted, examined for anomalies, and weighed by species to the nearest 0.1 kg. Megabenthic invertebrates were considered to be epibenthic species with a minimum dimension of 1 cm; hence, this classification did not include pelagic, infaunal, or small species that are more effectively sampled by other methods.

Recurrent groups were defined by calculating the index of affinity (IA) of Fager (1963) and Fager and McGowan (1963) for all species pairs. The index is based on the occurrence of each species and co-occurrence of the two species being compared, and is defined by the following equation:

$$IA = \frac{c}{\sqrt{ab}} - \frac{1}{2\sqrt{b}}$$

IA is the index of affinity, **a** is the number of samples in which species A occurred, **b** is the number of samples in which species B occurred, and **c** is the number of joint occurrences of species A and B. In this equation, **b** is always greater than or equal to **a**. The first term is the ratio of joint occurrences of both species to the geometric mean of their individual occurrences. The second term is a correction factor to give weight to values of the first term based upon high occurrences of the more frequently occurring species.

The index was calculated for all pairs of species. Pairs of species with a predetermined level of affinity (e.g., IA = 0.50) were grouped following rules described in Fager (1957). A recurrent group must satisfy the following criteria: (1) All species in the group must have positive affinities with all other members of the group; (2) The group must contain the greatest possible number of species; (3) If several groups containing the same number of species can be formed, those are selected which give the largest number of groups without members in common; and (4) If two or more groups with the same number of species and with members in common can be formed, the group that occurs most frequently must be chosen.

Species were grouped at indices of affinity from 0.50 (a value that is commonly used in recurrent group analysis) to 0.80 at intervals of 0.05. Associates were defined as species that had positive affinities with one or more members of a recurrent group but not with all members of the group. The level of relationship of the groups to each other and to associate species is defined by a connex value. This number is the proportion of possible positive affinities (e.g., IA = 0.50 or greater) between members of two groups or between a group and an associate. The distribution of the 0.50-level groups in the SCB were mapped.

RESULTS

The 204 species of invertebrates collected in this survey represented 116 families, 19 classes, and 8 phyla. The catches were dominated by echinoderm species. Thirteen species occurred at 20% or more of the stations on the mainland shelf (Table 1). The most frequently occurring species were California sand star (*Astropecten verrilli*), ridgeback rock shrimp (*Sicyonia ingentis*), and white sea urchin (*Lytechinus pictus*), which occurred in 70, 59, and 48% of the stations, respectively.

Recurrent group analysis identified seven recurrent groups with two to six species per group and six associate species at the 0.50 level of affinity (Figure 2). The groups and associates included 31 (14%) of the 204 species. The groups generally differed in depth distribution, with each group occurring in one or two of the three shelf depth zones (Figure 3). Only Group 6 was widely distributed along the mainland shelf from the Santa Barbara Channel to San Diego; the remaining groups were found in one or two regions in the SCB (Figure 4).

TABLE 1. Megabenthic invertebrate species occuring in 20% or more of the stations on the mainland shelf of Southern California at depths of 10 to 200 m, July to August, 1994.

Scientific Name	Common Name	Number of Stations	% Stations (n=114)
Astropecten verrilli	California sand star	80	70
Sicyonia ingentis	ridgeback rock shrimp	67	59
Lytechinus pictus	white sea urchin	55	48
Luidia foliolata	gray sand star	54	47
Parastichopus californicus	California sea cucumber	53	47
Ophiura luetkeni	brokenspine brittlestar	44	39
Pleurobranchaea californica	California sea slug	44	39
Ophiothrix spiculata	Pacific spiny brittlestar	33	29
Allocentrotus fragilis	fragile sea urchin	31	27
Loligo opalescens	California market squid	28	25
Acanthoptilum sp	trailtip sea pen, unid.	25	22
Neocrangon zacae	shortkeel bay shrimp	23	20
Rossia pacifica	eastern Pacific bobtail	23	20

Group 1 (Inner/Middle Shelf Group) consisted of three species: purple sea pansy (*Renilla koellikeri*; a colonial hydrozoan); Hemphill kelp crab (*Phodochela hemphillii*); and ringed doris (*Dialula sandiegensis*; a nudibranch) (Figure 2). Group 1 occurred at two stations (2% of the total) on the inner and middle shelf zones at 18 to 43 m (Figure 3). The group occurred only in the south near the United States-Mexico international border (Figure 4A) and had no affinities with other groups (Figure 2).

Group 2 (Middle Shelf Group) consisted of two species: shortneck pear crab (*Erileptus spinosus*) and tubicolous hermit (*Orthopagurus minimus*) (Figure 2). Group 2 occurred at three stations (3% of the total) on the middle shelf at depths of 43 to 113 m (Figure 3). Group 2 was found in the central region in Santa Monica and San Pedro Bays and in the south near the United States-Mexico international border (Figure 4B). Oldroyd coralsnail (*Babelomurex oldroydii*) was an associate of this group (Figure 2). The group had no affinities with other groups.

Group 3 (Middle/Outer Shelf Group) consisted of six species: white sea urchin; ridgeback rock shrimp; California sand star; California sea cucumber (*Parastichopus californicus*); gray sand star (*Luidia foliolata*); and California sea slug (*Pleurobranchaea californica*) (Figure 2). Group 3 was found at 11 stations (10% of the total) on the middle and outer shelf zones at depths of 53 to 150 m (Figure 3). The group was found in the northern and central regions from the Santa Barbara Channel to San Pedro Bay (Figure 4C). California market squid (*Loligo opalescens*), Pacific spiny brittlestar (*Ophiothrix spiculata*), and brokenspine brittlestar (*Ophiura luetkeni*) were associates of this group (Figure 2). The group had affinities with Groups 4 and 6. Group 3 was most strongly associated with brokenspine brittlestar, followed by California market squid, Pacific spiny brittlestar, and then Groups 4 and 6.

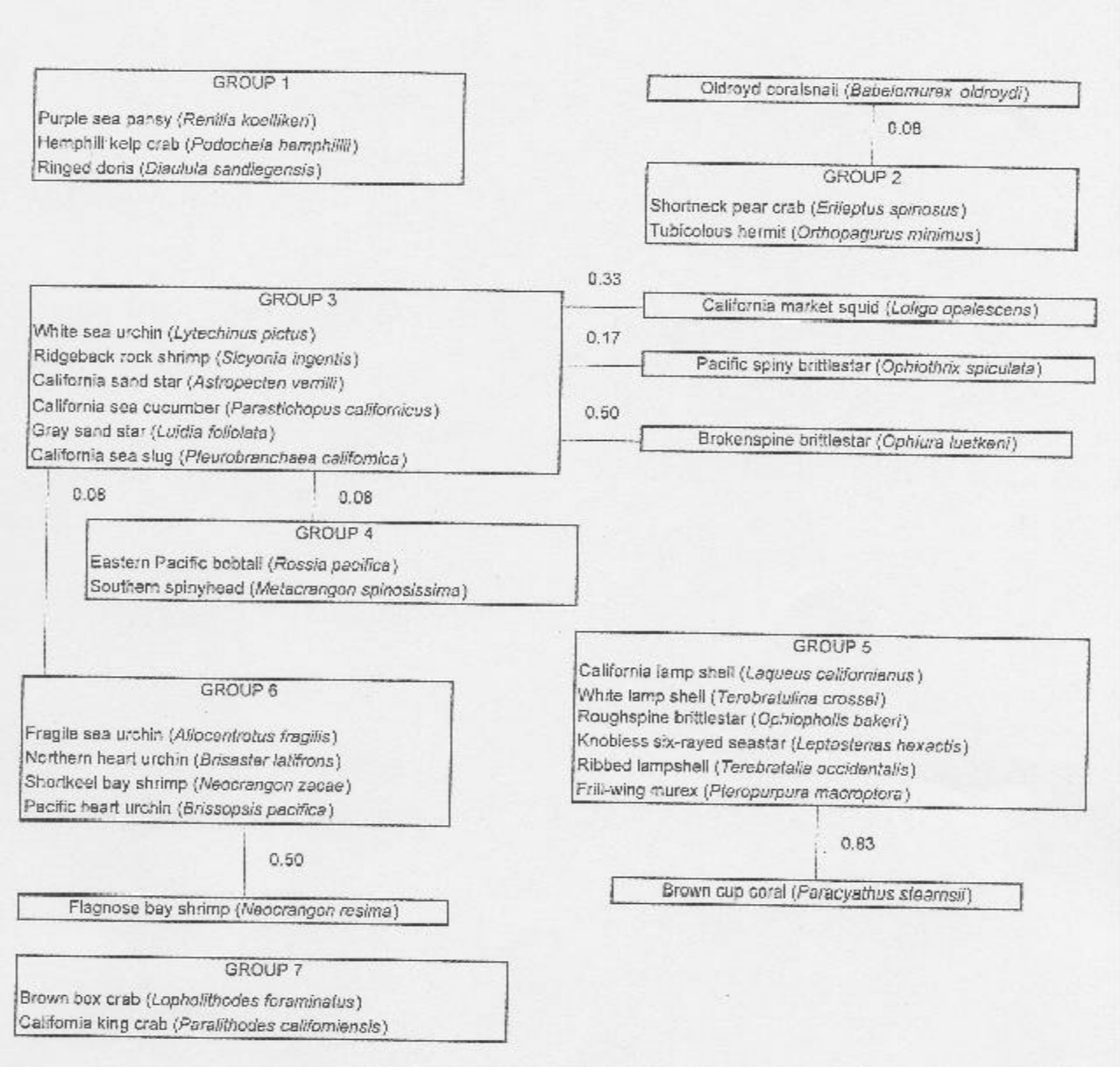
Group 4 (Submarine Canyon Group) had two species: eastern Pacific bobtail (*Rossia pacifica*; a squid) and southern spinyhead (*Metacrangon spinosissima*; a shrimp) (Figure 2). Group 4 occurred at 10 stations (9% of the total) on the middle and outer shelf zones at depths of 75 to 215 m (Figure 3). The group was found in the central region in Santa Monica, Redondo, and San Gabriel Submarine Canyons, and in the southern region in Oceanside Submarine Canyon (Figure 4D). The group had affinities with Group 3 (Figure 2).

Group 5 (Shelf Break Group) consisted of six species: California lamp shell (*Laqueus californianus*); white lamp shell (*Terebratulina crossei*); roughspine brittlestar (*Ophiopholis bakeri*); knobless six-rayed seastar (*Leptasterias hexactis*); ribbed lamp shell (*Terebratalia occidentalis*); frill-wing murex (*Pteropurpura macroptera*; a snail) (Figure 2). Group 5 occurred at two stations (2% of the total) at the shelf break area of the outer shelf at 104 to 113 m (Figure 3). The group was found in the central region in San Pedro Bay and southern region off La Jolla (Figure 4E). Brown cup coral (*Paracyathus stearnsii*) was an associate of this group (Figure 2). The group had no affinities with other groups.

Group 6 (Outer Shelf Group) comprised four species: fragile sea urchin (*Allocentrotus fragilis*); northern heart urchin (*Brisaster latifrons*); shortkeel bay shrimp (*Neocrangon zacae*); and Pacific heart urchin (*Brissopsis pacifica*) (Figure 2). This group occurred in 11 stations (10% of the total) on the outer shelf at depths of 150 to 208 m (Figure 3) throughout the SCB from the Santa Barbara Channel to Oceanside (Figure 4F). Flagnose bay shrimp (*Neocrangon resima*) was an associate of Group 5. Although Group 6 had affinities with Group 3 (Figure 2), it was much more strongly associated with flagnose bay shrimp.

Group 7 (Upper Slope Group) had two species: brown box crab (*Lopholithodes foraminata*) and California king crab (*Paralithodes californiensis*) (Figure 2). Group 7 was found at three stations (3% of the total) on the upper

FIGURE 2. Recurrent groups of megabenthic invertebrates on the mainland shelf of southern California depths of 10 to 200 m, July to August 1994. Index of affinity (IA) = 0.50. Species within a group are listed in order of abundance. Lines show relationships between groups and associates, with values indicating the proportion of possible pairs with IA = 0.50.



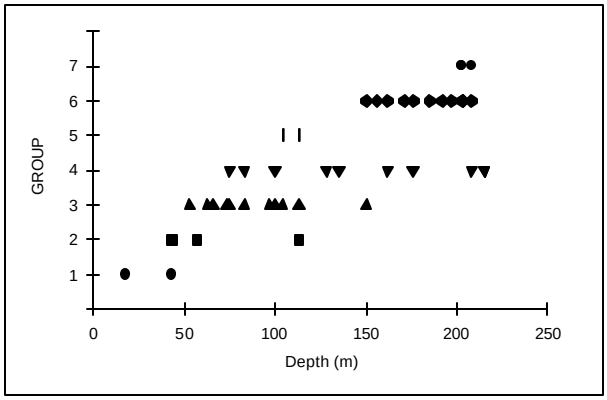
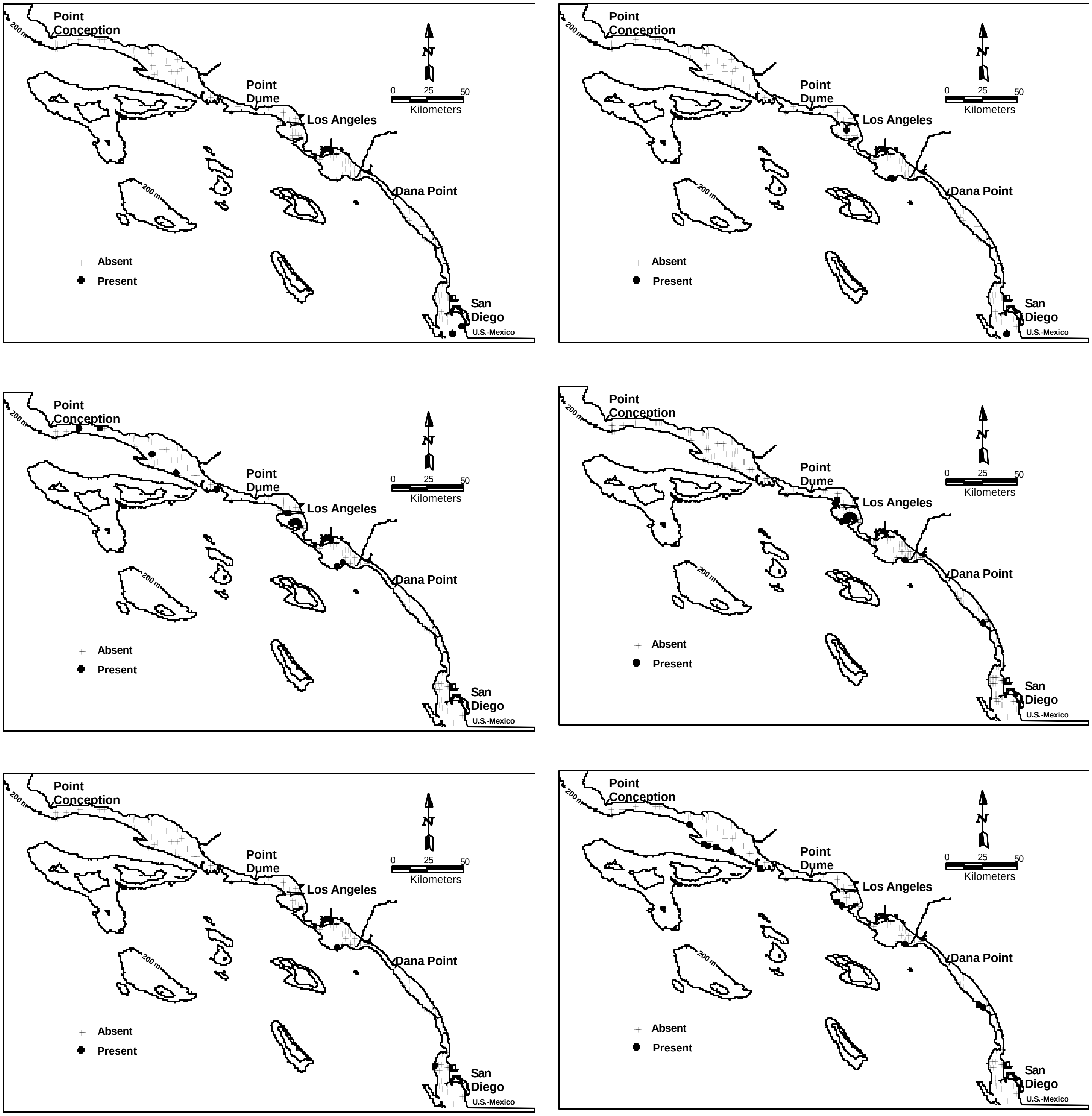
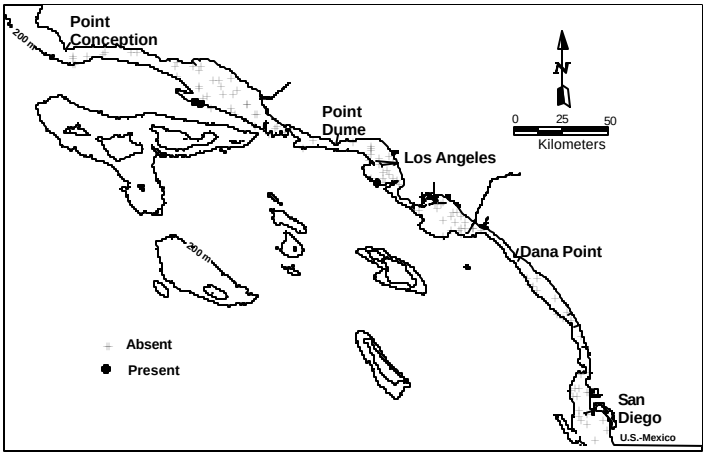


FIGURE 3. Bathymetric distribution of megabenthic invertebrate recurrent groups on the mainland shelf of southern California, July to August 1994.

FIGURE 4. Spatial distribution of major megabenthic invertebrate recurrent groups on the mainland shelf of southern California at depths of 10 to 200 m, July to August 1994: (A) Group 1 — Inner/Middle Shelf Group; (B) Group 2 — Middle Shelf Group; (C) Group 3 — Middle/Outer Shelf Group; (D) Group 4 — Submarine Canyon Group; (E) Group 5 — Shelf Break Group; (F) Group 6 — Outer Shelf Group; and (G) Group 7 — Upper Shelf Group.





slope at depths of 203 to 208 m (Figure 3) in the Santa Barbara Channel (the northern region) and Redondo Canyon (the central region) (Figure 4G). The group had no affinities with other groups (Figure 2).

DISCUSSION

Recurrent groups of megabenthic invertebrates have not been described in previous studies. Seven groups were identified and described in this study. These were mostly associated with specific bathymetric zones. Some of these groups also appeared to occupy distinctive habitats within bathymetric zones. The Middle/Outer Shelf Group (Group 3) and Outer Shelf Group (Group 6) consisted of large, wide-ranging species with obvious differences in ecology (Table 1). The Middle/Outer Shelf Group consisted of the six most frequently occurring species (Table 1).

Some depth segregation of potential ecological counterparts is apparent. For example, among regular urchins, the white sea urchin occurs in the Middle/Outer Shelf Group and the fragile sea urchin occurs in the Outer Shelf Group. However, among heart urchins, the northern heart urchin and Pacific heart urchin (two presumably ecologically similar species) occur together in the Outer Shelf Group. Both species differ geographically, with the former being a boreal/temperate species and the latter a warm-temperate/tropical species (Blake *et al.* 1996). The northern heart urchin is more abundant in the northern SCB, prefers fine or muddy sediments, and is most abundant at 380 m. The Pacific heart urchin is more abundant in the southern SCB, occurs on fine to coarse sediments, and is most abundant at 480 m (Thompson *et al.* 1987).

The Shelf Break Group, which occurred at only two stations, consisted of six species, three of which are brachiopods (lamp shells). Because of the unusually high number of species found in this two-station group, it is assumed that the group represents a brachiopod clump with associated species (possibly on a patch of hard substrate) (Blake *et al.* 1996). The Submarine Canyon Group (Group 7) appeared to be associated with the rugose bottom often found in conjunction with edges, cliffs, and debris of submarine canyons. Certainly, the spiny body morphology of the southern spinyhead suggests that this species does not typically occupy a soft-bottom habitat as do the more common crangonid shrimps represented in the survey. The infrequent occurrence of an Inner/Middle Shelf Group may reflect the low numbers of invertebrate species and low invertebrate abundance on the inner shelf in 1994 (Allen and Moore 1996). It is also possible that the formation of this group and the Upper Slope Group could be due to chance, as both only occurred at two stations,.

Assemblages of megabenthic invertebrates on the shelf and slope of southern California have been described using ordination and classification analysis to define site groups with similar species composition and abundance (Thompson *et al.* 1993). The study defined a number of shelf, slope, and basin assemblages based on data collected from 1971 to 1985. Two major assemblages were identified in the depth range of the mainland shelf: (1) a pre-1980 Palos Verdes Shelf Group; and (2) a post-1981 Storm/El Niño Group. Because the focus of that analysis was on site rather than species groups, the same species can be found in different groups. Nevertheless, the Normal Mainland Shelf and Outer Shelf/Upper Slope site groups of that study correspond to the Middle/Outer Shelf recurrent species group of the 1994 survey. The Middle Slope (300 to 490 m) Group of that study corresponds to the Outer Shelf Group of 1994. The most frequently occurring species in the Normal Mainland Shelf site group were California sand star, ridgeback rock shrimp, and white sea urchin. The most frequently occurring species in the Outer Shelf/Upper Slope site group were ridgeback rock shrimp, California sea slug, and armed box crab (*Platymera* (= *Mursia*) *gaudichaudii*). All of these except armed box crab, were primary members of the Middle/Outer Shelf recurrent species group of the 1994 survey. The most common species in the Middle Slope site group were northern heart urchin, Pacific heart urchin, and fragile sea urchin — all of which were important members of the Outer Shelf recurrent species group. Thus the two analyses, although focusing on different aspects of the assemblage, identified communities with similar species composition. The deeper bathymetric range for the Middle Slope site group suggests that the Outer Shelf recurrent group is probably more representative of a deeper, mesobenthal fauna.

Of the 204 species identified in the 1994 survey, only 14% formed recurrent groups. This finding suggests that a high proportion of the species were either incidental to the habitat or region, or were inadequately sampled by trawl.

Allen (1982) found that of 126 species of fish collected from the same habitat, 26% formed recurrent groups, 68% were incidental (more commonly found in other habitats or biogeographic zones), and 6% were characteristic of the area but ineffectively sampled by trawl. It is probable that a similar distribution applies to the megabenthic invertebrate population, although the percentage of species ineffectively sampled by trawl may be higher because of the smaller size of many invertebrate species.

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