Biodiversity of Macrocrustaceans in the Gulf of California, Mexico

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ABSTRACT.- The Gulf of California, a semi-enclosed sea on the Pacific coast of Mexico, is one of the most biologically diverse regions in the world with approximately 6000 reported macrofaunal (animals larger than 0.5 mm in length) species. About 80% (4800) of the fauna are invertebrates. With 1032 species, macrocrustacea, and in particular Peracarida and Decapoda, comprise an important component of the benthic and pelagic marine fauna of this region. Brachyura (301 species) and Amphipoda (229 species) are by far the most diverse taxa, followed by Caridea (132 species) and Anomura (126 species). Together, these four groups (788 species) represent 76.6% of all macrocrustacean species in the Gulf. Isopoda comprise 80 species, Cirripedia 42 species, Dendrobranchiata 31 species, Stomatopoda 28 species, Thalassinidea 19 species, and Euphausiacea 14 species. The remaining crustacean higher taxa include fewer than ten species each (Copepoda and Ostracoda were not considered). A list of all families, with number of species, in the Gulf is presented, including 9 families of Stomatopoda, 68 families of Peracarida, and 68 families of Decapoda. Euphausiaceans are represented by a single family. For Peracarida, Euphausiacea, Cirripedia, Stomatopoda and Decapoda, there is a clear biodiversity gradient from the Northern Gulf (175, 4, 14, 8, 287 species respectively) to the Central (206, 8, 22, 17, 406 species) and Southern Gulf (221, 14, 30, 22, 490 species. Two databases were created, one based on natural major habitats encountered within the Gulf of California and one based on habitats described for species. In the first, environmental data (depth and substrate) were linked to a map of the Gulf of California divided with a grid of 2 by 2 nautical-mile squares, thus producing a digital matrix of geographic location vs. paired values of environmental conditions. Depth ranges were selected according to availability of data on maps, from 0-20 m (intertidal and shallow water) to > 2500 m. Recorded substrates were sand, mud, coral, rock, rubble and mangrove, including combinations of two or more substrates within a coordinate square. A second database contains depth range (e.g., 35-200 m) and substrates (e.g., mud) reported for individual species. In this database, georeferenced distribution polygons were created for each species, consisting of a maximum of four localities defined by a set of latitude and longitude. A total of 889 crustacean species were included in the second data base, reflecting the fact that precise distributional or environmental data were not available for all species. The two databases were compared to determine numbers of species sharing depth ranges and substrate types within each square of the georeferenced grid, thus allowing calculation of species biodiversity. The presence of a large community of pelagic Amphipods (Hyperiidea and Cyamidae) is reflected by the large number of species in the "water column" habitat (117 species). The remaining Peracarida are generally associated with rocky (83 species) and sandy (67 species) habitats. The majority of decapods and stomatopods are associated with sandy (357 species) and muddy (271 species) substrates, with most of the remainder found on rock (212) or coral (140) substrates or among rubble (102). Twenty-one species of decapod crustaceans are known to occur in the water column, including bentho-pelagic species (e.g., shrimps). Cirripedia are mostly associated with rocky shores and submerged reefs, although a significant number of species is found on magrove prop roots. All Euphausiacea are pelagic. Considering all species of crustaceans for which bathymetric distribution could be established (955 species), occurrence as a function of depth varies considerably. Benthic (871) and pelagic (158)

species were analyzed separately. The highest biodiversity for benthic species occurs in the 0-20 m depth range (687 species; 85% of all benthic crustacean) and the least diversity (12 species) in depths below 2501 m. There is a marked reduction in biodiversity with increasing depth for all groups, particularly from 101 m downward. Vertical distribution of pelagic macrocrustaceans is much more homogeneous than with benthic species (based on 871 species, or 86% of total macrocrustacean fauna). The geographic distribution of benthic crustaceans biodiversity was based on five biodiversity ranges using the percentile method (20%). As expected, the higher biodiversity values for benthic species are in the coastal fringe and around islands, closely following the shallow-water bathymetric contours. Lowest biodiversity (0, 1 or 2 species recorded) occurs in deep water, particularly in the basins. A similar analysis also based on 5 biodiversity ranges (20%) was done for pelagic species. Very high pelagic diversity occurs in the central-southern Gulf, with a strong decrease of biodiversity north of the Midriff Islands.

Keywords: Gulf of California, biodiversity, Crustacea.

Palabras clave: golfo de California, biodiversidad, crustáceos.

Introduction

Large-scale biodiversity studies are rare in marine tropical areas. This is due to a basic lack of infrastructure and expertise in most tropical countries, tied to a lack of adequate funding in third-world countries (see Hatcher et al. 1989, McNeely et al. 1990). The study of healthy tropical ecosystems requires priority attention before irreversible damage occurs. The rapid increase in coastal human population, accompanied by development along subtropical and tropical coasts of the world and growing seashore tourism, are having disastrous effects on endemic flora and fauna (Thorpe et al. 1995, May 1992, Ibarra Obando 1998) and genetic resources. The need to assess the present status of natural marine communities has long been stressed. In the tropics, natural communities are composed of thousands of species which all play strategic roles in ecological processes (Solow 1995, Poore & Wilson 1993). Further, sustainable use of marine and coastal living resources cannot be properly established without an adequate knowledge of biodiversity. In the broad sense, biodiversity not only addresses the variety (or number) of species, but also the variety of body plans (i.e., phylogenetic diversity), the diversity of niches occupied by the flora and fauna, the complexity of food webs, and the genetic diversity of species' populations. Ultimately, cataloging or monitoring the biodiversity of a large ecosystem allows a proper evaluation of the effects of natural (e.g., hurricanes, ENSO events) and anthropogenic factors (e.g., pollution, introduction of alien species, destruction of microhabitats, fishing practices) on the balance and distribution of species.

Success in measuring biodiversity depends upon the sampling effort combined with the systematic knowledge of local fauna (see Madin & Madin 1995, Hatcher et al. 1989). A long sampling effort does not automatically guarantee a successful analysis. A short, extensive sampling effort can lead to a high biodiversity if qualified experts perform analysis of the collected fauna. On the other hand, long-scale sampling program might not be successful if taxonomic expertise is lacking. The Gulf of California has probably enjoyed the largest sustained sampling effort of any region in the Tropical Eastern pacific. Numerous international expeditions and sampling efforts by U.S. scientists and institutions contributed the first scientific collecting/cataloging in this region, and more recently local (Mexican) institutions have contributed greatly to our knowledge of this region. Today there are hundreds of papers available addressing the flora and fauna of the Gulf of California (see Brusca 1980, Schwartzlose & Hendrickson 1983, Brusca et al. 2002, Hendrickx & Brusca 2002).

Compilation and synthesis of primary information available in the published literature is a long-term effort that few scientists or institutions can afford to sustain. Since 1993, however, the "Ma-

crofauna Golfo" project has enjoyed a series of grants that allowed six senior scientists (and many technicians) to compile a complete database for all known macrofauna in the Gulf of California. The main purpose of this study is to propose a georeferenced model of the biodiversity of benthic and pelagic macrocrustaceans in the Gulf of California. Compilation and synthesis of primary information available in the published literature is a long-term effort that few scientists or institutions can afford to sustain.

Material and Methods

Study area.- The study area considered herein corresponds to the Gulf of California as defined by Hendrickx (1992); specifically, the northern boundary is at the mouth of the Colorado River and the southern limits are the tip of the Baja Peninsula (Cabo San Lucas) and Cabo Corrientes, the southern extremity of Bahía Banderas, on the mainland (Fig. 1). This definition of the Gulf of California includes the entire mouth area of this otherwise semi-enclosed sea. These limits differ somewhat with several previous definitions of the Gulf's southern boundary. However, it finds its justification in several factors. First, the area extending south of Topolobampo-Mazatlán, two localities often considered as the southernmost limit of the Gulf of California continental edge, presents a geomorphology similar to the coastal stretch extending north to Guaymas (i.e., long stretches of sandy beaches, few rocky points, ample areas of coastal lagoons, estuaries and esteros, regularly sloping shelf). Second, recent studies on stomatopod and decapod crustacean distribution (see Hendrickx & Salgado Barragan 1991, Hendrickx 1992) have demonstrated that most species found in the southern half of the Gulf of California are tropical species ranging all the way to Central America, Colombia, or even further south to northern Peru. Furthermore, water temperatures in this part of the Gulf follow a similar seasonal pattern, with onshore and shallow water temperatures varying by less than 5 degrees centigrade for any given season of the year and subtidal epibenthic temperatures being almost constant below 90 m depth (Hendrickx 1992).

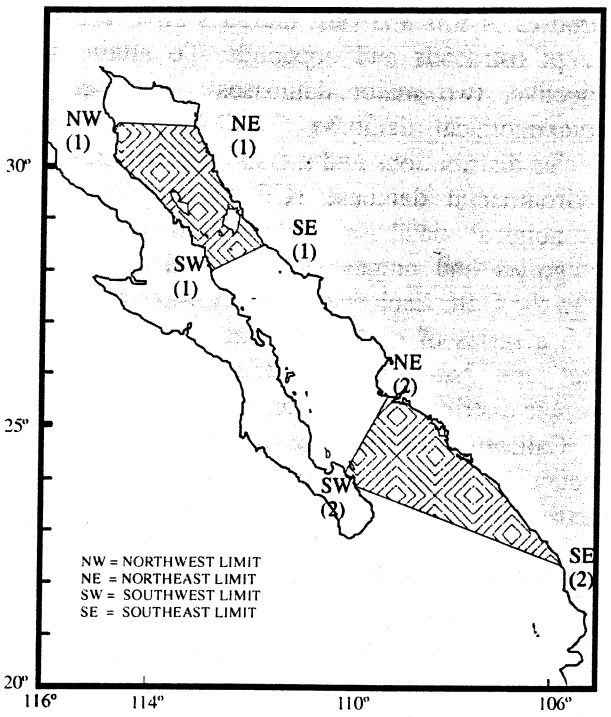

Fig. 1. Distribution polygones using four extreme localities (species 1) and three extreme localities (species 2) within the Gulf of California.

The Gulf of California area, as defined herein, does not necessarily match the Cortez Zoogeographic Province of some authors. Indeed, the exact position of the southern boundary of this subtropical province has been debated in many previously published papers (see Briggs 1974, Brusca & Wallerstein 1979, Thompson et al. 1987, Correa Sandoval & Carvacho 1992, Hendrickx 1992).

As such, the Gulf of California is a large body of water, extending roughly over 258593 km^2, 400 km across in its widest part (measured along parallels) and reaching abyssal depths in its southern section (> 2000 m) and in basins (> 3500 m). The coastal length is estimated at 3260 km (using a 1:250000 map), of which about half is sandy shoreline predominately along the east and northern coasts, while rocky shores and cliffs are characteristic of the Baja Peninsula coast. Regular fresh water supply is almost exclusively restricted to the SE extremity of the Gulf where coastal lagoons connected to perennial rivers and estuaries dissect the coastal plain.

Treatment of data.- Macrocrustacea, for

purposes of this analysis, includes all Crustacea except ostracods and copepods. To attain this objective, two major databases were used: a biotaxonomical database (BIOTAX) including species distributions and a distinct georeferenced environmental database (GEOREN). The biotaxonomical database includes all taxonomic categories and names for all species reported from the Gulf. Each species entry was associated with a series of ecological data (i.e., major habitat and bathymetric distribution) and geographic distribution data (i.e., the area in the Gulf of California where the species is known to occur). Habitats (e.g., rock and corals), bathymetric range, and geographical distribution data were based on both published and unpublished information. Specific ecological data associated with species descriptions or collection records are often scarce; however, it is generally possible to associate a species with a general habitat. Eight major habitats were selected: sandy shore, rocky shore, pebbles, mangrove forest, coral reef, muddy bottom, marine vegetation (benthic species) and "water column" (pelagic species). Intertidal species were species known to occur from supralittoral to infralittoral horizons, without distinction. Geographic distribution for each species was transformed into a distribution polygon defined by a maximum of 4 localities within the Gulf of California; these four localities (NW distribution limit; SW distribution limit; NE distribution limit; and SE distribution limit) are identified in the BIOTAX database by their respective latitude and longitude (Fig. 1). Obviously, species with few known localities (three, two or one) within the Gulf feature a distinctly shaped distribution pattern represented by the number of latitude-longitude combinations in the database. For computational purposes, for species occurring along the mainland Gulf coast and at any given point south of Cabo Corrientes (say, Golfo Dulce, Costa Rica) the SE distribution limit was automatically calculated as Cabo Corrientes, the southernmost locality in the study region.

The GEOREN database was built using published and unpublished data on depth and substrate type in the Gulf of California. Most data were obtained from Brusca (1980), van der Heiden & Hendrickx (1982), Parker (1964), the authors' field notes, and various maps and charts, including those of the INEGI (the Mexican national cartographic office). The entire Gulf was divided into a grid series of squares 2 nautical miles (2 nm) on a side, equivalent to a square of 2 minutes by 2 minutes (Fig. 2). Each square was identified by its latitude and longitude using its central point. In addition, each square had assigned to it a depth range and a benthic substrate type. In coastal areas, it was often necessary to include more than one substrate within a square due to frequent habitat changes over short distances. In all cases the data associated with each square were adjusted according to available data. For instance, bathymetric maps available for the Gulf typically show successive isobaths for 100 m, 200 m, 500 m, 1000 m, 1500 m, 1800 m, 2000 m, 2500 m etc, thus providing ample depth range data for each square of the grid. Because coastal habitats are often highly variable and could not be defined accurately using a 2 nm by 2 nm grid, all squares or fraction of squares adjacent to the coast (either peninsular, insular or continental) were arbitrarily given a depth range of 0-20 m, thus including all strictly intertidal species, intertidal species extending to 20 m, or species featuring a minimum depth distribution range <21 m. Our knowledge of sediment distribution within the Gulf is very incomplete, and in coastal areas specific data are lacking for many localities. Still, the resulting GEOREN database is consistent with our present knowledge of existing habitats, and it allows a preliminary biodiversity distribution model to be established for the region.

A comparative computer program (BIODIX-1) was designed in order to compare the two databases. Each species distributional and ecological (i.e., depth and substrate) data included in the BIOTAX data base were compared with data associated with each square of the GEOREN data base. For any species data set matching the square characteristics, the square was assigned one "biodiversity unit" count (i.e., one species present in the square). The final number of species that matched any given square was considered a "biodiversity" value for that square. Biodiversity ranges were defined and color-coded using a percentage accumulative system with 20% classes. In this system, a color (or symbol) is used to mark all squares with highest biodiversity until the accumulated number of squares represents at least

20% of the total number of squares in the grid. The next biodiversity range is then obtained when a second set of squares accumulating at least 40% of all squares, is defined. Resulting data were used to define biodiversity patterns for 1) pelagic macrocrustaceans, 2) benthic Decapoda and Stomatopoda, and 3) benthic Peracarida and Cirripedia within the study area.

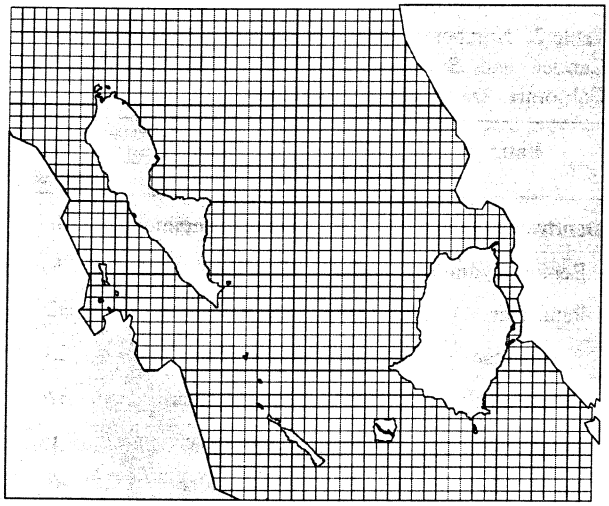

Fig. 2. Definition of the 2 nm x 2 nm grid. Area represented correspond to the Central Gulf of California between Angel de la Guarda and Tiburon Islands.

Results

Biodiversity and species occurrence in major habitats.- The macrocrustacean fauna of the Gulf of California comprises 1029 species. With 301 and 229 species respectively, Brachyura and Amphipoda are by far the most numerous groups, followed by Caridea (132 species) and Anomura (126 species). Together, these four groups (788 species) represent 76.1% of the entire macrocrustacean fauna. Isopoda include 80 species, Cirripedia 42 species, Dendrobranchiata 31 species, Stomatopoda 28 species, Thalassinidea 19 species and Euphausiacea 14 species. The rest of the groups include fewer than ten species each (Tables 1-6).

As in other tropical/subtropical seas, in the Gulf of California Peracarida are a diverse and important taxon, encompassing a wide variety of forms and life styles, including pelagic and parasitic species. Altogether, they represent 325 species (Table 1) belonging to 68 families.

Table 1. Number of species of Peracarida, (Amphipoda, Cumacea, Isopoda, Mysida, Lophogastrida and Tanaidacea) known from the Gulf of California. Data presented by family.

Family	No. Species	Family	No. Species
AMPHIPODA		Lycaeopsidae	2
Gammaridea		Lycaeidae	8
Ampeliscidae	15	Oxycephalidae	14
Amphilochidae	5	Parascelidae	4
Ampithoidae	4	Platyscelidae	10
Anamixidae	2	Pronoidae	9
Argissidae	1	**CUMACEA**	
Bateidae	5	Bodotriidae	4
Corophiidae	20	Diastylidae	3
Dexaminidae	1	Nannastacidae	1
Eusiridae	6	**ISOPODA**	
Gammaridae	11	Anthuridae	4
Hyalidae	4	Paranthuridae	5
Ischyroceridae	3	Aegidae	5
Leucothoidae	2	Cirolanidae	11
Liljeborgiidae	2	Corallanidae	6
Lysianassidae	7	Cymothoidae	11
Melitidae	1	Limnoridae	1
Oedicerotidae	4	Serolidae	1
Phliantidae	1	Sphaeromatidae	7
Phoxocephalidae	10	Jaeropsidae	1
Platyischnopidae	2	Janididae	1
Pleustidae	1	Munnidae	1
Podoceridae	3	Gnathostenetroididae	1
Synopiidae	1	Arcturidae	1
Caprellidea		Hognathidae	1
Caprellidae	2	Idoteidae	13
Cyamidae	7	Bopyridae	6
Hyperiidea		Tylidae	1
Mimonectеidae	1	Ligiidae	3
Scinidae	17	**MYSIDA**	
Lanceolidae	5	Mysidae	2
Cystisomatidae	1	Petalophthalmidae	1
Paraphronimidae	2	**LOPHOGASTRIDA**	
Vibiliidae	8	Eucopiidae	1
Dairellidae	2	Lophogastridae	2
Hyperiidae	15	**TANAIDACEA**	
Phronimidae	8	Apseudidae	2
Phrosinidae	3	**TOTAL**	**325**

The number of species in each family ranges

from 1 to 20 (19 families contain a single species). The most diverse families belong to the Amphipoda: Corophiidae (20 species), Scinidae (17), Ampeliscidae and Hyperiidae (15 each); 54 families contain fewer than 10 species. Contrary to the Stomatopoda and Decapoda which generally contain greater numbers of species and have been much better studied over the past two decades, the Peracarida of the Gulf of California are still not well known, with the exception of the Isopoda for which more taxonomic and ecological information is available than for the other orders. A great deal of information on the taxonomy and distribution of the hyperiidean amphipods is available only in an unpublished doctoral thesis (Siegel-Causey 1982). There is no doubt that many undescribed species of Tanaidacea, Mysidacea, Amphipoda and Cumacea are yet to be discovered in the area. Substrate preference data are available for 286 peracarid species (Table 8). The presence of a large community of pelagic amphipods (Hyperiidea and Cyamidae) is reflected by the large number of species in the "water column" habitat (117 species). The remaining Peracarida are generally associated with rocky (84 species) and sandy (67 species) habitats. Surprisingly, only 8 species have a published record of association with corals, and 2 with mangroves, but these figures are almost certainly an underestimate and reflects, on the one hand, the paucity of research on corals in the Gulf of California, and on the other hand the absence of detailed study of the small macrofauna associated with mangrove forest, in particular with mangrove prop roots.

Decapod crustaceans represent 620 species in 68 families (Tables 2-4). The number of species per family varies considerably (from 1 to 70). The Majidae (sensu Garth 1958) are here subdivided into several families (see Hendrickx 1999). Fifteen families (22%) contain one species, a similar figure as in Peracarida (19 out of 68 families, or 28%), while eight families contain 20 or more species. The most diverse family is Xanthidae (70 species), although it should be noted that several subfamilies of Xanthidae sensu Balss (1957) have recently been given the category of families (see Guinot 1978, Serène 1984). They are maintained here in a single family because of the difficulty in assigning some poorly defined genera (see Guinot, op cit., Martin & Abele 1986). Other families with high numbers of species include the Alpheidae (53 species), Porcellanidae (49 species), Palaemonidae (32) and Pinnotheridae (31) (Tables 3-4). Stomatopods, which share several habitats with decapod crustaceans and are similar in size, are a comparatively much smaller group (28 species), with nine families and a dominance of species in the family Squillidae (13 species) (Table 5).

Table 2. Number of species of shrimps (Dendrobranchiata, Caridea and Stenopodidea) known from the Gulf of California. Data presented by family.

Family	No. Species	Family	No. Species
Dendrobranchiata		Nematocarcinidae	1
Benthesicymidae	2	Gnathophyllidae	1
Penaeidae	10	Palaemonidae	32
Sicyoniidae	11	Alpheidae	53
Solenoceridae	3	Hippolytidae	15
Sergestidae	4	Ogyrididae	1
Luciferidae	1	Processidae	6
Stenopodidea		Pandalidae	9
Stenopodidae	2	Crangonidae	5
Caridea		Glyphocrangonidae	1
Pasiphaeidae	5		
Oplophoridae	3	**TOTAL**	**165**

Data related to substrate are available for 616 of the 648 species of decapods-stomatopods (Table 7). A majority of these species is associated with sandy (357 species) and muddy (271 species) substrates. Fewer species are found on rocky substrates (212), associated with coral (140), or among pebbles (102 species). A surprisingly low number of species are associated with non-mangrove marine vegetation (37 species). This low number might be due, in part, to lack of adequate sampling. Marine algae are diverse in the Gulf of California (Norris 1976, estimated 470 species in the region), but large subtidal growths (e.g., *Sargassum*, *Padina* and *Colpomenia*) are rare. Two species of marine phanerogams have been reported from the Gulf of California (*Zostera marina* and *Halodule wrightii*) (Ibarra Obando & Rios 1993) but these are very rare. Mangrove habitats (proper roots, trunks, mud flats under mangrove cover) host only 28 species of

macrocrustaceans, the vast majority decapods. Twenty-one species of decapod crustaceans occur in the water column (Table 7), including pelagic shrimps and other bentho-pelagic species (i.e., *Pleuroncodes planipes*, *Portunus xantusi*, *Euphylax dovii*).

Table 3. Number of species of Astacidea, Thalassinidea, Palinura and Anomura known from the Gulf of California. Data presented by family.

Family	No. Species	Family	No. Species
Astacidea		Scyllaridae	2
Nephropidae	1	**Anomura**	
Thalassinidea		Coenobitidae	1
Callianassidae	3	Diogenidae	21
Callianideidae	1	Lithodidae	4
Ctenochelidae	1	Paguridae	25
Laomediidae	1	Parapaguridae	2
Upogebiidae	9	Galatheidae	13
Axiidae	3	Porcellanidae	49
Strahlaxiidae	1	Albuneidae	7
Palinura		Hippidae	4
Polychelidae	2		
Palinuridae	4	**TOTAL**	**154**

Other, less diverse taxa that occur in the Gulf of California include: Cirripedia, with 42 species (including two unidentified species of *Heterolepas*); Euphausiacea, with 14 species. There are no published records of Rhizocephala although at least two species have been recognized in the area (pers. obs.). Cirripedia are mostly associated with rocky shores and submerged reefs, with five species recorded from mangrove habitats (Table 8), on prop roots of red mangrove (*Rhizophora mangle)* (Salgado Barragán & Hendrickx, this volume). All Euphausiacea are pelagic.

Biodiversity distribution according to depth.- Considering all species of crustaceans for which bathymetric distributions could be clearly established on the basis of available data (955 of a total of 1029 species), occurrence as a function of depth varies considerably (Fig. 3 and Table 9). For obvious reasons, benthic (871 species) and pelagic (158 species) organisms must be analyzed separately, as depth range for the later corresponds to their vertical position into the water column without consideration of oceanic depth at the locality where the species were captured. As expected, the highest biodiversity for benthic species is found in the 0-20 m strata: 687 species, 85% of all benthic species for which depth ranges are known (810 spp.) (see table 9); and the lowest (12 species) is found in depths below 2501 m. There is a marked reduction in biodiversity below 101 m for all groups. Biodiversity tends to stabilize below 200 m and relatively similar numbers of species are found from 500 m to 2500 m (Fig. 3). Diversity below 500 m is low and represents 7.1 to 1.5% of the total macrocrustacean fauna. When considered separately, a similar trend is observed for the 2 major groups of benthic crustaceans: Decapoda and Peracarida (Table 9).

Table 4. Number of species of Brachyura known from the Gulf of California. Data presented by family.

Family	No. Species	Family	No. Species
Dromiidae	4	Daldorfiidae	2
Dynomenidae	1	Dairididae	1
Cyclodorippidae	3	Parthenopidae	12
Raninidae	5	Atelecyclidae	2
Dorippidae	6	Cancridae	3
Calappidae	10	Portunidae	15
Leucosiidae	16	Goneplacidae	17
Epialtidae	7	Xanthidae	70
Inachidae	12	Pinnotheridae	31
Inachoididae	8	Cryptocheridae	2
Majidae	1	Ocypodidae	11
Mithracidae	20	Palicidae	4
Pisidae	13	Gecarcinidae	3
Tychidae	3	Grapsidae	18
Aethridae	1	**TOTAL**	**301**

Pelagic species are primarily represented by shrimps, euphausiaceans, and hyperiid and cyamid amphipods (whale lice). Pelagic cirripeds consist of species associated with sea-turtles and marine mammals, and two species of *Lepas* that attach to floating objects such as wood, Styrofoam, fishing floats, etc. Contrary to the pattern encountered

with benthic species, the vertical distribution of pelagic macrocrustaceans appears much more consistent, with little variation of species occurrence as a function of depth (Table 9). Maximum biodiversity of pelagic species is found in subsuperficial waters and to 1000 m (63-95 species, depending on depth fringe); below this depth, the number of recorded species drops to a maximum of 51 (1001-1500 m) and a minimum of 18 (> 2501 m) (see table 9). Most pelagic species, in particular crustaceans, have day-night vertical migrations; data related to the Gulf of California vertical migrations of micro and mesonekton, however, are scarce (see Hendrickx & Estrada Navarrete 1996).

Table 5. Number of species of Stomatopoda known from the Gulf of California. Data presented by family.

Family	No. Species	Family	No. Species
Eurysquillidae	2	Lysiosquillidae	1
Gonodactylidae	3	Nannosquillidae	4
Hemisquillidae	1	Tetrasquillidae	1
Parasquillidae	1	Squillidae	13
Pseudosquillidae	2	**TOTAL**	**28**

Biodiversity in the Northern, Central and Southern Gulf.- The Gulf of California invertebrate fauna generally presents a pattern of decreasing species diversity from south to North.

A regular reduction of species number along a south-to-north latitudinal gradient has been previously shown for stomatopods and decapods (Hendrickx & Salgado Barragán 1991, Hendrickx 1992). Our analysis of macrocrustacean species diversity in the major regions of the Gulf (Northern, Central and Southern Gulf, as defined by Findley et al. 2002) shows a clear diversity decrease from south to north (Fig. 4). Indeed, all species included, crustaceans of the Northern Gulf number 498 species (48% of the total Gulf crustacean fauna), while the Central Gulf is inhabited by 659 species (64% of the total), and the Southern Gulf hosts 777 species (75% of the total). A similar trend is observed with the higher taxa.

Table 6. Number of species of Cirripedia and Euphausiacea known from the Gulf of California. Data presented by family

Family	No. Species	Family	No. Species
Cirripedia		Chelonibiidae	4
Cryptophialidae	1	Coronulidae	2
Lithoglyptidae	1	Tetraclitidae	2
Heteralepadidae	2	Archaeobalanidae	4
Oxynaspididae	1	Balanidae	15
Poecilasmatidae	1	Pyrgomatidae	1
Lepadidae	3	**Euphausiacea**	
Pollicipedidae	3	Euphausiidae	14
Chthamalidae	2	**TOTAL**	**56**

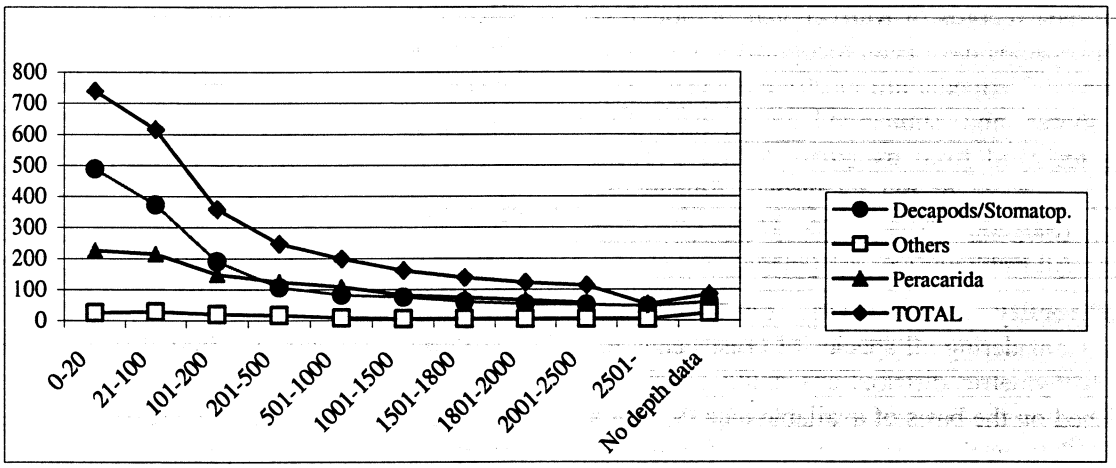

Fig. 3. Biodiversity by depth range for two major groups of macrocrustaceans (Decapods/Stomatopods and Peracarida) and for the rest.

Table 7. Distribution and environmental (depth and substrate) data in biological database. Numbers represent numbers of species for which a given data is available.

Crustacea	Localization	Depth	Substrate	On maps	Not on maps	Total
Brachyura	296	280	280	273	28	301
Shrimps	164	164	163	160	5	165
Lobsters/Anomura	150	151	147	142	12	154
Stomatopoda	28	28	26	26	2	28
Cirripedia	42	24	26	22	21	42
Euphausiacea	13	14	14	13	1	14
Amphipoda (1)	111	110	92	92	19	111
Amphipoda (2)	109	102	120	90	28	118
Cumacea	8	6	7	6	2	8
Isopoda	79	71	63	61	18	80
Mysida	3	2	2	2	1	3
Lophogastrida	1	2	3	1	2	3
Tanaidacea	2	1	2	1	1	2
Peracarida	313	294	292	253	71	325
Decapods/Stomatop.	638	623	616	601	45	648
Others	56	38	40	35	22	56
TOTAL	**1007**	**955**	**948**	**889**	**138**	**1029**

(1) Gammaridea (2) Hyperiidea and Cyamidea.

Table 8. Major habitats occupied by species of crustaceans known to the Gulf of California. Numbers indicate number of species reported for a substrate category. Total of records for each group may be greater than species number due to presence of some species in several habitats.

Group	No. Species	Rock	Sand	Pebbles	Mud	Coral	Mangrove	Marine Vegetation	Water Column	Wood	No data
Brachyura	301	101	175	52	130	53	18	20	2	2	19
Shrimps	165	74	85	10	69	50	1	13	18	0	3
Lobsters	28	13	9	1	16	4	0	0	0	0	4
Anomura	126	15	67	38	43	30	2	2	1	0	5
Stomatopoda	28	9	21	1	13	3	0	2	0	0	2
Isopoda	80	31	29	3	14	4	2	29	0	0	17
Amphipoda (1)	111	52	33	22	18	1	0	12	0	0	19
Amphipoda (2)	118	0	0	0	0	1	0	0	117	0	1
Mysida	3	0	0	0	0	0	0	0	2	0	1
Lophogastrida	3	0	0	0	0	0	0	0	3	0	0
Tanaidacea	2	0	0	0	0	2	0	0	0	0	0
Cumacea	8	0	5	0	3	0	0	0	0	0	1
Cirripedia	42	17	4	9	0	5	5	0	7	12	11
Euphausiacea	14	0	0	0	0	0	0	0	14	0	0

(1) Gammaridea (2) Hyperiidea and Cyamidea

Table 9. Presence of crustaceans known to the Gulf of California at different depth ranges (in meters). Peracarida and Decapoda are divided into benthic and pelagic species. Totals of records for each group may be greater than species number due to the occurrence of species at different depth ranges.

GROUP	Total	0-20	21-100	101-200	201-500	501-1000	1001-1500	1501-1800	1801-2000	2001-2500	>2501	No depth data
Benthic												
Decapods	**600**	470	323	151	70	48	41	26	18	16	12	27
Stomatopods	**28**	21	24	8	2	1	0	0	0	0	0	0
Cirripedia	**36**	18	12	4	2	0	0	0	0	0	0	19
Peracarida												
Amphipoda	**111**	106	71	31	14	4	3	2	0	0	0	1
Isopoda	**80**	65	36	16	7	5	5	4	2	0	0	9
Cumacea	**8**	6	2	1	0	0	0	0	0	0	0	2
Tanaidacea	**2**	1	0	0	0	0	0	0	0	0	0	1
Lophogastrida	**3**	0	0	0	1	2	1	1	1	1	2	1
Mysida	**3**	0	0	0	1	2	2	2	2	2	1	1
Total Benthic	**871**	**687**	**468**	**211**	**95**	**58**	**49**	**32**	**20**	**16**	**12**	**61**
Pelagic												
Cirripedia	**6**	1	1	1	0	0	0	0	0	0	0	6
Decapods	**20**	7	5	10	13	15	11	9	6	6	4	2
Euphausiacea	**14**	7	12	11	12	3	0	0	0	0	0	0
Peracarida	**118**	48	75	68	70	65	40	33	28	22	14	18
Total Pelagic	**158**	**63**	**93**	**90**	**95**	**83**	**51**	**42**	**34**	**28**	**18**	**26**
TOTAL	**1029**	**750**	**561**	**301**	**190**	**141**	**100**	**74**	**54**	**44**	**30**	**81**

Georeferenced Biodiversity Model.- The process of data comparison performed by the BIODIX-1 program requires the availability of specific data on distribution, substrate and depth range for each species. If any of these data are missing, the species is eliminated during the comparison and, consequently, also from the mapping process. On this basis, the total number of species available for mapping is 889 (out of 1029), or 86.4 percent of the total macrocrustacean fauna (Table 7).

For all species, as well as for the major higher taxa, the BIODIX-1 program generated sets of color-coded maps representing biodiversity distribution patterns. It is, however, not possible to reproduce maps for all these groups. The three maps presented herein were selected because of their broad geographic coverage and overall representation of the region.

Twenty percent accumulative classes (five classes in total) were used in the case of benthic decapods and stomatopods because they allow a clear visualization of biodiversity patterns. The five biodiversity ranges were defined automatically by the analysis and provide areas where 0 species have been reported, areas with 1-2 species, areas with 3-5 species, areas with 6-30 species, and areas with 31 to 293 species (Fig. 5). The 293-species value obviously corresponds to the highest macrocrustaceans biodiversity observed in any given 2 nm x 2 nm square within the Gulf of California. It represents 28% of all known species (293 out of 1029) and 33% of all species mapped (i.e., those with complete data). As would be expected, the highest biodiversity values are located in the coastal fringe and around islands. Lowest biodiversity (0, 1 or 2 species recorded) occurs in deep waters, particularly in the basins (e.g., Guaymas, Carmen, Farallon and Pescadero Basins) and at the mouth of the Gulf, which can be clearly identified on the biodiversity map as clear areas (Fig. 5). The deeper central and southwestern sections of the

Northern Gulf (>200 m depth) are also indicated by clear areas, also occurring in the vicinity of Isla Angel de la Guarda and off Guaymas. In the latter cases, it is highly likely that this is artificial and reflects insufficient sampling. The coastal fringes with high biodiversity values (6-30 and 31-293 species ranges) obtained through the BIODIX-1 analysis closely follow the outer margin of the continental platform, wide along the continental and Northern Gulf shores, and narrow along the central and southern Baja Peninsula south of Bahía San Luis Gonzaga (ca. 29°50' N). There is, however, one stretch of the lower platform/ upper slope which features a higher biodiversity than anywhere else in the Gulf; this stretch, located roughly from the southern limit of Bahía Banderas north to the Topolobampo area (ca. 25°30'N), has been recently explored at depths of up to 1300 meters (Hendrickx 1996) and 16 species of macrocrustaceans have been collected below the 750 m depth contour, thus significantly increasing values of biodiversity in this area. More recent data, not included in our analysis, indicate that the biodiversity below 750 m is actually higher (Hendrickx 2001).

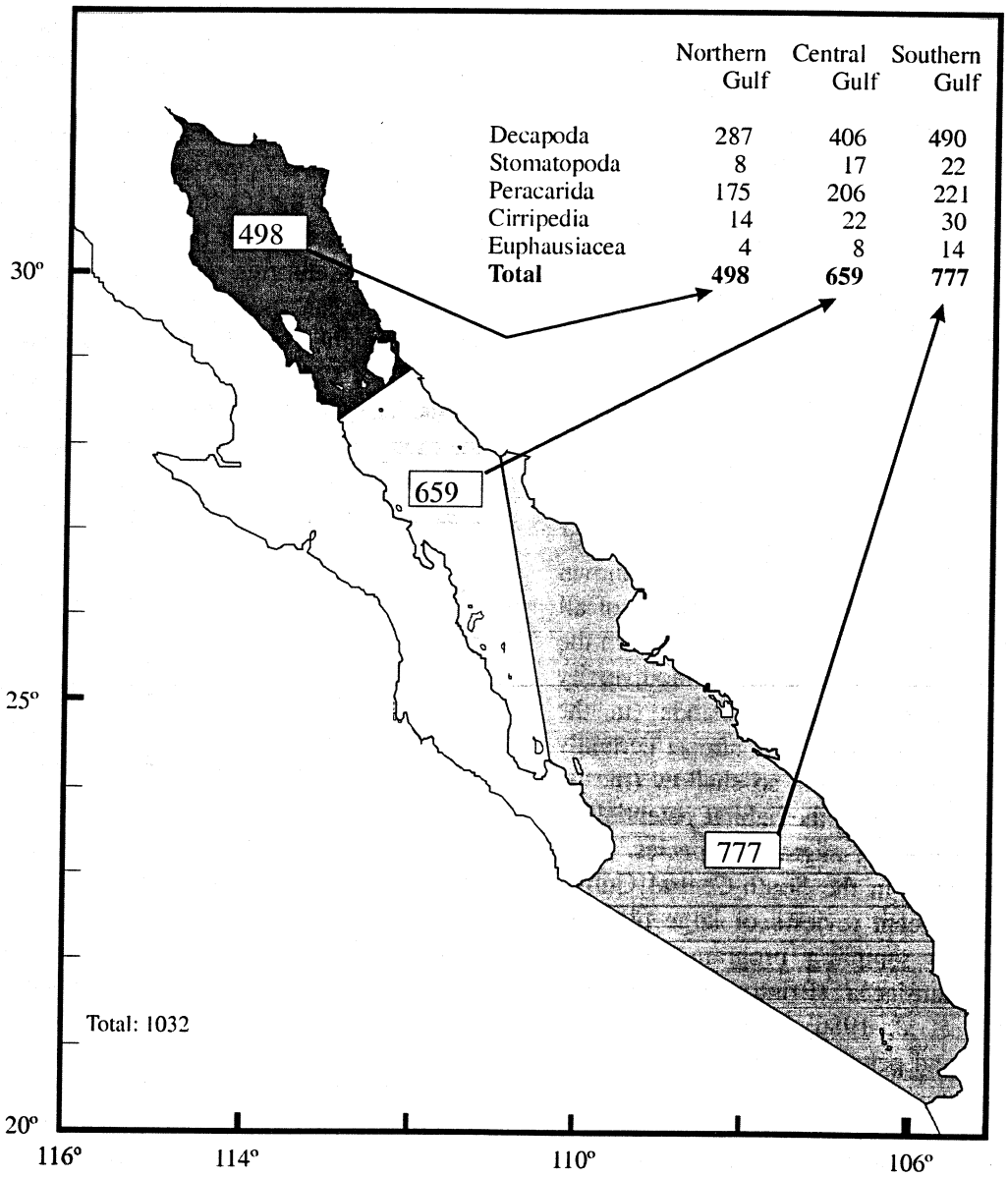

Fig. 4. Distribution of Crustaceans in the Northern, Central and Southern Gulf of California.

A separate analysis of the benthic Peracarida and Cirripedia with 20% classes also provides five biodiversity ranges (0, 1, 2, 3, and 4-80 species). It indicates that benthic cirripeds, isopods, amphipods, cumaceans, tanaids and mysids are mostly found on the continental shelf, around the islands, and in coastal waters (bays and lagoons) (Fig. 6). A very large proportion of the Gulf area considered in this study hosts 1-3 species only, thus suggesting a remarkable lack of information for these taxa, particularly for deeper waters. The highest biodiversity value, 80 species, represents 32.3% of all known species (80 out of 247 species) and 43.2% of all species mapped (185).

Pelagic macrocrustaceans of the Gulf of California number 158 species (Table 9). As for the other two groups, 20% accumulative classes were used, thus defining five biodiversity clusters. Due to little specificty of their habitat – the water column – pelagic species tend to be more widely and homogeneously distributed than benthic species. Most pelagic species recorded during this project are generally distributed off the coastal fringe and none occur in coastal systems. Defined areas are as follows: Areas with 0-19, 20-41, 42-56, 57-79 and 80-105 species (Fig. 7). The 105 species value corresponds to the highest pelagic macrocrustacean biodiversity observed in any given 2 nm x 2 nm square within the Gulf of California. It represents 66.5% of all known species (105 out of 158 species) and 100% of all species on map. Highest biodiversity occurs in the Central-Southern Gulf, with a strong biodiversity decrease north of the Midriff Islands (in the Northern Gulf). This decrease is almost certainly because the Northern Gulf is so shallow (mostly <200 m), thus minimizing the habitat potential for deepwater or vertically-migrating species. High pelagic biodiversity in the South-Central Gulf is not surprising. Recent reviews of large plankton and micronekton sampling programs from the Gulf, for Euphausiacea (Brinton & Townsend 1980, Brinton et al. 1986), Hyperiidea (Siegel-Causey 1982), and pelagic shrimps (Hendrickx & Estrada Navarrete 1996) indicate that most species are widely distributed in the central/southern portion of this region. Pelagic biodiversity also appears to decrease progressively south of 23° of latitude, where fewer studies have been done. In fact, pelagic macrocrustaceans are almost not known at all in tropical waters south of the Gulf of California (Hendrickx & Estrada Navarrete 1989).

Discussion

With a total of 1029 reported species of marine macrocrustaceans, the Gulf of California is probably the most diverse body of water (for this group) that extends into warm temperate latitudes. There are few comparative studies available for other tropical or subtropical areas. Markham et al. (1990) reported 309 species of Crustacea from the Mexican Caribbean coast. Boschi (2000) reported 570 species of decapods (Crustacea: Decapoda) for the Brazilian Province, and 1049 species for the larger Caribbean Province. The first figure is similar to what we have recorded from the Gulf of California (i.e., 621 species), while the latter figure is nearly the same as the Gulf of California value (1029 species) for all macrocrustacean species. The Caribbean province, however, is fully tropical, covers far more area than the Gulf of California, and is particularly rich in corals. The Carolinean Province, which is perhaps the most comparable (subtropical) region, contains 387 species of decapods (Boschi, op cit.) vs. the 620 inhabiting the Gulf of California.

Forty-two Cirripedia have been recorded from the Gulf of California, compared to an estimated 50 species for the entire Pacific coast of Mexico (Young & Ross 2000). Of the 42 Gulf species, two are acrothoracicans (boring barnacles), 10 are pedunculate barnacles, and 30 are acorn barnacles. Only 12 species of Cirripedia have been reported for the entire Atlantic coast of Mexico.

Benthic Peracarida are an important component of the Gulf macrocrustacean fauna. All major groups are certainly underestimated and many undescribed species remain to be discovered. Isopods are probably the best studied peracarid group in the Gulf, but with 80 known species isopod biodiversity is probably still underestimated. Austin (1985) reported 185 species of Isopoda for the cold-temperate region of the Northeast Pacific, whereas Kensley & Schotte (1989) included 280 species for the Caribbean Sea (intertidal to 200 m). The entire

Eastern Tropical Pacific region is inhabited by 124 isopod species (Espinosa Pérez & Hendrickx 2001) of which 120 species are found along the Pacific coast of Mexico (Espinosa Pérez & Hendrickx 2002). Other Peracarida groups are less well known than isopods for there are no comprehensive reports available for anywhere in the Eastern Pacific. For the non-isopod peracarid taxa, it is likely that less than 10 percent of the fauna has been described for the Gulf or for the Tropical Eastern Pacific.

Stomatopods (28 species in the Gulf) and Euphausiaceans (14 species in the Gulf) are probably among the better known groups in the region and, except for some cryptic species of Stomatopoda, the numbers reported here will probably increase very little in future years. The Gulf of California stomatopod fauna includes 70% of the known Tropical Eastern Pacific fauna (Hendrickx & Salgado Barragan 1991, Salgado Barragan & Hendrickx, 1998).

Although a decrease in faunal diversity in deeper waters is a general (global) trend, our analysis (like most analyses) has probably underestimated the Gulf of California macrocrustacean fauna. Lack of adequate taxonomic sampling in areas below 60 m depth, in shallow waters along the central Baja California Peninsula, and in areas where coastal access is difficult, have certainly biased in the data.

Resumen

El golfo de California, un mar semi-cerrado en la costa Pacífico de México, es una de las regiones biológicas más diversificada en el mundo con aproximadamente 6000 especies de macrofauna reportadas (animales más grandes que 0.5 mm de longitud). Casi el 80% (4800) de esta fauna son invertebrados. Con 1029 especies, los macrocrustáceos, en particular los Peracarida y los Decapoda, representan un componente muy importante de la fauna marina bentónica y pelágica de esta región. Brachyura (301 especies) y Amphipoda (229 especies) son los taxones mas diversificados, seguido por los Caridea (132 especies) y por los Anomura (126 especies). En conjunto, estos cuatro grupos (788 especies) representan el 76.5% de todos los macrocrustáceos del Golfo. Los Isopoda contienen unas 80 especies, los Cirripedia 42, los Dendrobranchiata 31, los Stomatopoda 28, los Thalassinidea 19 y los Euphausiacea 14 especies. Los demás taxones de las categorías superiores contienen menos de 10 especies (Copepoda y Ostracoda no fueron considerados). Se presenta una lista de las familias, con el número de especies presentes en el Golfo: nueve familias de Stomatopoda, 68 familias de Peracarida, y 68 familias de Decapoda. Los eufasiaceos tienen una sola familia. En el caso de los Peracarida, Cirripedia, Stomatopoda y Decapoda, existe un claro gradiente de biodiversidad del golfo de California norte (29 a 54%, según la familia, de todas las especies del Golfo) al Golfo central (51 a 65%) y sur (68 a 100%). Dos bases de datos fueron generadas. La primera considera los principales hábitats naturales en el golfo de California y la segunda se refiere a los hábitats descritos para las especies. En el primero, las características ambientales (profundidad y sustrato) fueron ligadas a un mapa del golfo de California dividido en cuadrantes de 2 por 2 millas náuticas, creando así una matriz digital de localización geográfica vs. pares de valores de condiciones ambientales. La selección de las profundidades fue acorde con la información disponible en mapas, desde 0-20 m (intermareal y aguas someras) hasta > 2500 m. Los sustratos considerados fueron: arena, lodo, corales, rocas o piedras (sueltas) y manglar, o bien cualquier combinación de dos o más sustratos. La segunda base de datos incluye el intervalo batimétrico conocido para cada especie (e.g., 35-200 m) y el o los sustratos reportados para esta misma especie. En esta base de datos, se generaron polígonos de distribución georeferenciados para cada una de las especies, con un máximo de cuatro localidades definidas por sus coordenadas. En total, 889 especies de crustáceos fueron incorporadas en la segunda base de datos; las demás especies no contaron con los datos de distribución o de hábitats. Las dos bases de datos fueron comparadas con el fin de determinar el número de especies compartiendo las características de profundidad-hábitats en cada cuadrante; consecuentemente, se obtuvieron valores de biodiversidad para cada cuadrante. La presencia de una amplia comunidad de Amphipoda

pelágicos (Hyperiidea y Cyamidae) se traduce por un elevado número de especies en la columna de agua (117 especies). Los demás Peracarida se asocian generalmente con el ambiente rocoso (84 especies) y arenoso (67 especies). La mayoría de los decápodos y estomatópodos están asociados con fondos arenosos (357 especies) y lodosos (271 especies); las demás especies se encuentran esencialmente en zonas rocosas (212), en corales (140) o entre piedras sueltas (102). Veintiún especies de crustáceos decápodos han sido recolectadas en la columna de agua, incluyendo especies bento-pelágicas (e.g., camarones). Los Cirripedia son, en general, asociados con áreas rocosas y arrecifes sumergidos, aunque un número significativo de especies viven sobre raíces aéreas del mangle. Todos los Euphasiacea son pelágicos. Considerando todas las especies de crustáceos para las que pudo establecerse la distribución batimétrica (948 especies), su presencia en los diversos estratos de profundidades varia mucho. Especies bentónicas (871) y pelágicas (158) fueron analizadas por separado. La biodiversidad mas alta en el caso de las especies bentónicas se presentó en el intervalo de profundidad de 0-20 m (687 especies; 67% de todos los crustaceos bentonicos) y la mas baja (12 especies) por debajo de 2501 m. Hay una reducción marcada de la biodiversidad conforme aumenta la profundidad para todos los grupos, en particular a partir de 101 m. La distribución vertical de los macrocrustaceos pelágicos es mucho más homogénea que en el caso de las especies bentónicas (estimada en base a un total de 871 especies, o 86% del total de macrocrustáceaos). La distribución geográfica de la biodiversidad de los crustáceos bentónicos se analizó en base a cinco intervalos de biodiversidad calculados con el método de los percentiles (20%). Como era de esperarse, la mayor biodiversidad en las especies bentónicas se observa en la franja costera y alrededor de las islas y la menor en aguas profundas, en particular en las cuencas. Un análisis similar, también basado en 5 intervalos (20%) se realizó en el caso del conjunto de especies pelágicas. Una diversidad más alta se encontró en las partes central y sur del Golfo, y una fuerte disminución de la diversidad se observó hacia la región de la barrera de las grandes islas.

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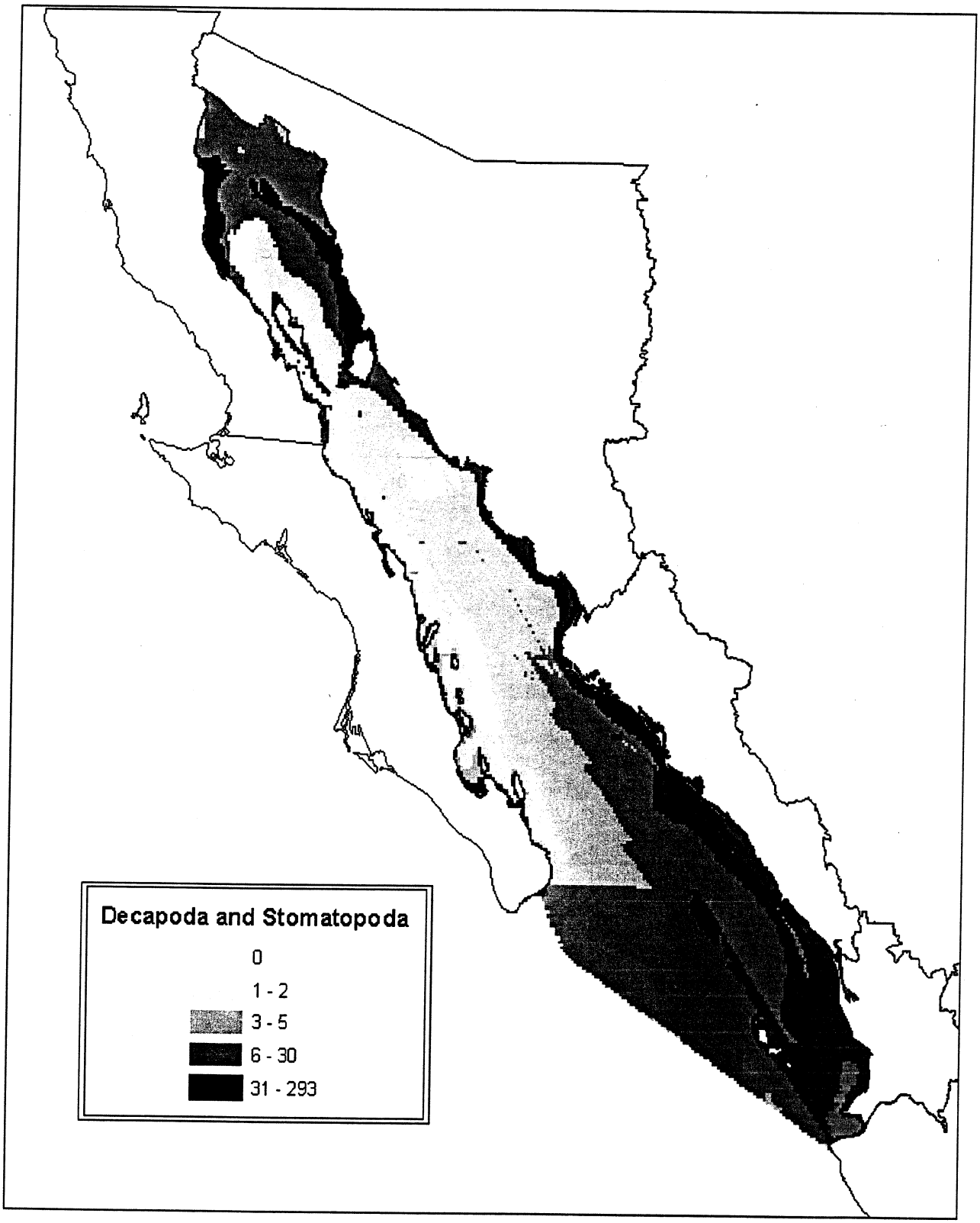

Fig. 5. Decapoda and Stomatopoda. Number of species in different areas of the Gulf of California based on the 2 mn x 2 mn squares.

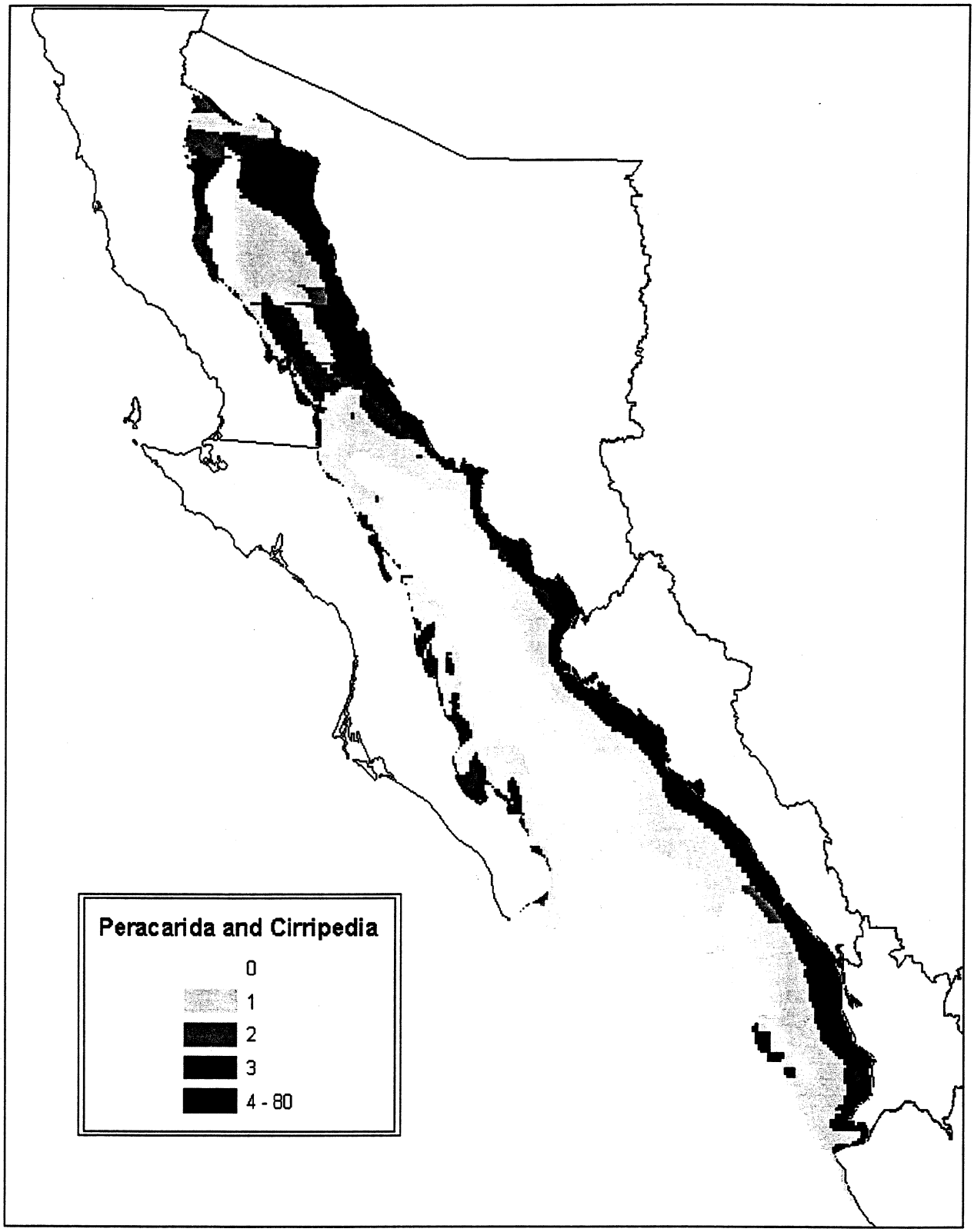

Fig. 6. Benthic Peracarida. Number of species in different areas of the Gulf of California based on the 2 mn x 2 mn squares.

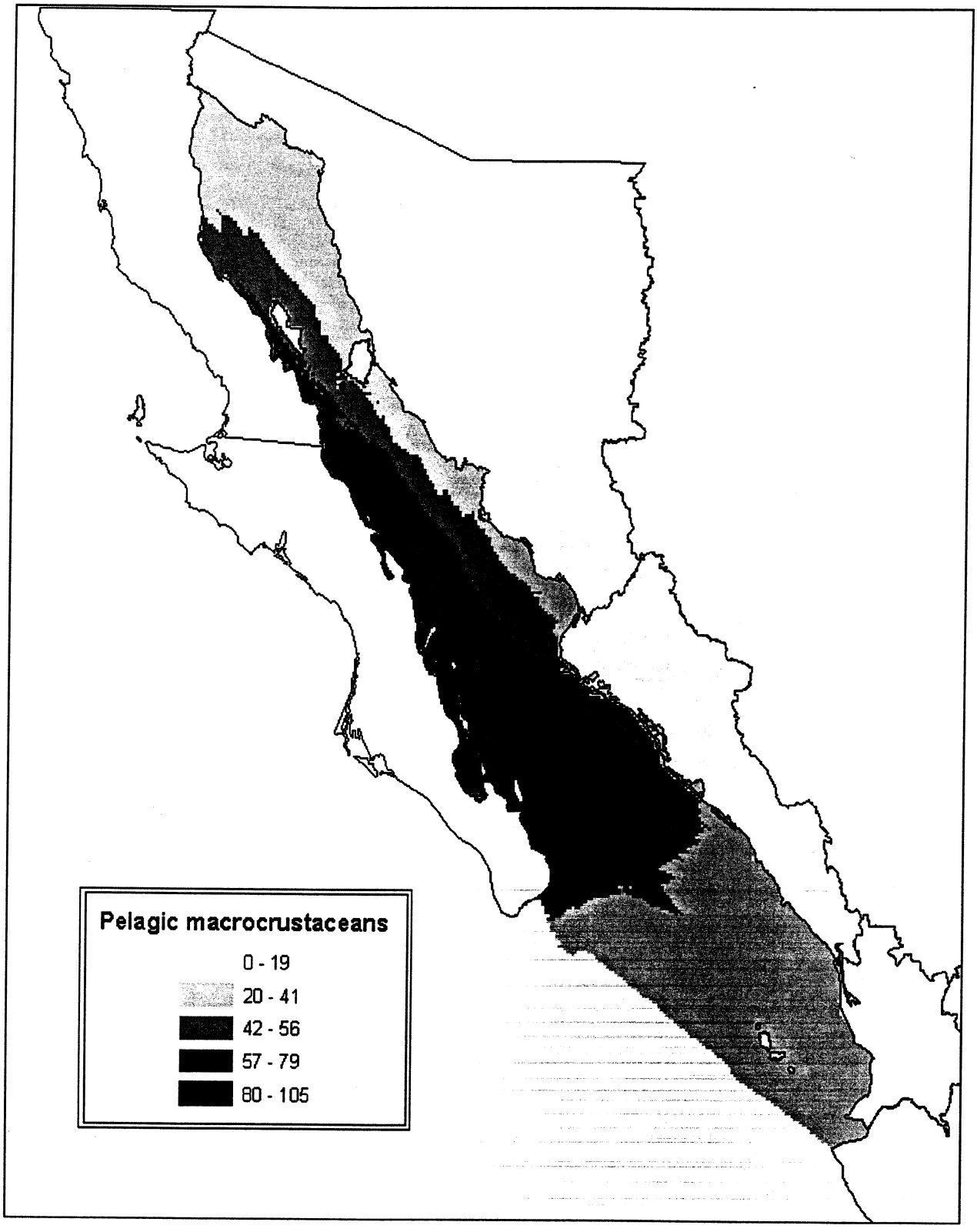

Fig. 7. Pelagic macrocrustaceans. Number of species in different areas based on the 2 mn x 2 mn squares.