CHAPTER 4

Invertebrate Biodiversity and Conservation in the Gulf of California

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Summary

An analysis of the Macrofauna Golfo invertebrate database indicates that the Gulf is home to over 4,900 species of named and described invertebrates. This is estimated to be about 70 percent of the actual invertebrate fauna of the Gulf of California. The most poorly known regions for invertebrates are the open sea and the deeper (below the continental shelf) benthic environment. In the intertidal region of the Gulf 2,158 species occur, although only 45 of these are strictly intertidal in distribution. Thirty-six hundred species occur at or above the 30 m isobath, and 4,078 species occur on or over the continental shelf (200 m and above). Most invertebrates recorded from the Gulf, 4,350 species, inhabit benthic habitats. There have been 329 species recorded from coastal lagoons in the Gulf, 260 of these from mangrove lagoons.

In general, invertebrate diversity increases from north to south in the Gulf. The unique oceanographic attributes and broad seasonal water temperature range of the Northern Gulf create tropical marine conditions in the summer but warm-temperate conditions in the winter. This provides a refuge for many disjunct warm-temperate (i.e., Californian) species in the upper Gulf that are not found in the Central or Southern Gulf. It perhaps also explains the high invertebrate endemicity seen in the Northern Gulf (128 species). Most of the Gulf's invertebrate fauna, however, is tropical and derived from the Tropical Eastern Pacific, and dozens of these species have a transisthmian distribution with populations in the Caribbean. Relative species diversity of invertebrates can be predicted based on substrate and habitat type, although (aside from a few dozen very common species)

the actual presence or absence of a species is difficult to predict and largely stochastic in nature. Overall, the most diverse phyla in the Gulf are Mollusca (2,198 species), Arthropoda (1,062 species), Annelida (722 species), Echinodermata (263 species), and Cnidaria (262 species).

The greatest threats to invertebrates in the Gulf are bottom trawling, hand-collecting by humans during low tides, coastal development, and pollution. In addition, artisanal harvesting of molluscs and swimming crabs (*Callinectes*) is a growing threat. On mainland shores, most large-bodied species at most localities are now gone from the intertidal region. Diversity on islands and on some largely inaccessible stretches of shore (especially on the eastern coast of the Baja California peninsula) are critically important refuges for littoral species now largely extirpated from mainland coasts. Industrial shrimp trawling is probably the most destructive form of fishery in the Gulf to invertebrates and also to the ecological integrity of the seafloor. Estero-based aquaculture is also harmful to invertebrate habitats, and the relocation of shrimp farms inland may ultimately be the only way to protect the fragile coastal lagoons of the Gulf and at the same time find a use for old agricultural land that had been ruined by salinization.

Introduction

Much of the information presented in this chapter was mined from the Macrofauna Golfo Project database, the product of a 10-year effort by many scientists in Mexico and the United States. The database catalogs every macrofaunal species (i.e., animals larger than 5 mm; thus ostracods and copepods are excluded) known to occur in the Gulf of California (*Mar de Cortés,* Sea of Cortez). The project was funded by grants from several organizations, including Conservation International, CONABIO (Comisión Nacional para el Uso y Conocimiento de la Biodiversidad), CIAD (Centro de Investigación en Alimentación y Desarrollo), Pronatura-México, and the Arizona-Sonora Desert Museum. Lead investigators for the *Macrofauna Golfo Project* were: Richard C. Brusca, Lloyd T. Findley, Philip A. Hastings, Michel E. Hendrickx, Jorge Torre, and Albert van der Heiden. The database provides information on taxonomy/classification, geographic distribution (in the Gulf and worldwide), depth, and habitat for about 6,000 species (4,916 invertebrates). An abridged version of the invertebrate data was published by Hendrickx et al. (2005). The complete invertebrate database is available at www.desertmuseum.org/center/seaofcortez/database.php. See Hastings et al. (chapter 5 in this volume) for more information on the Macrofauna Golfo Project, including descriptions of the four recognized biogeographic regions (Northern Gulf, Central Gulf, Southern Gulf, and Southwestern Baja California Sur). For a historical review of invertebrate research in the Gulf of California, see Brusca (2004a,b), Brusca and Bryner (2004), or Brusca et al. (2005). For a review of invertebrate diversity and conservation issues in the Northern Gulf of California, see Brusca (2007c). In this and the following chapter (on fishes), the terms Northern Gulf, Central Gulf, and Southern Gulf refer specifically to those biogeographic regions designated by the Macrofauna Golfo Project and database.

Macroinvertebrate Biodiversity in the Gulf of California

Origins of the Invertebrate Fauna

The invertebrate fauna of the Gulf of California is derived from four sources. Most species are tropical eastern Pacific in origin, whereas others had their origin in the Caribbean Sea or the Transisthmian (Panamanian) fauna (before the uplift of the Panama Isthmus), the temperate shores of California (during the 15–20 glacial periods that pushed cold waters southward and into the Gulf during the past 2 million years), and even across the vast stretch of the Pacific Ocean from the tropical Indo-west Pacific (Walker 1960; Brusca and Wallerstein 1979a; Thomson et al. 1979, 2000; Brusca 1980, 2004a, 2007c; Brusca and Findley 2005). These diverse biotic sources have enriched the diversity of the Gulf of California since its opening 5–6 million years ago.

Among the dozens of contemporary transisthmian species identified to date in the Gulf are: *Nereis riisi, Chloeia viridis, Eurythoe complanata,* and *Spirobranchus giganteus* (Polychaeta); *Phascolosoma perlucens* (Sipuncula); *Conopea galeata* (a gorgonian-commensal barnacle); *Rocinela signata, Cirolana parva,* and *Excirolana mayana* (Isopoda); *Ambidexter symmetricus* (a caridean shrimp); *Sicyonia laevigata* (a penaeoid shrimp); *Acanthonyx petiveri, Cycloes bairdii, Pilumnus reticulatus, Aratus pisonii, Geograpsus lividus,* and *Percnon gibbesi* (brachyuran crabs); *Aplysia parvula* and *Pleurobranchus areolatum* (Opisthobranchia); *Encope grandis* (Echinoidea); and *Molgula occidentalis* (Ascidiacea).

During past glacial events, a number of temperate-water "Californian species" were able to extend their ranges into the Gulf when cold isotherms pushed around the tip of the Baja California peninsula. When water temperatures warmed during subsequent interglacial periods, populations of these coldwater-adapted species became trapped in the Northern Gulf. Most of these cold-water species disappeared from the Gulf during the warmer periods (as today), but a few were adaptable enough to survive. The published literature suggests there are several dozen of these California–Northern Gulf disjunct temperate species. However, some of these records probably represent species whose Southern Gulf and/or southern peninsular distribution has simply not yet been documented (i.e., they probably range throughout coastal waters of the Baja California peninsula). Some others probably represent incorrect identifications (e.g., the crabs *Hemigrapsus oregonensis* and *Hemigrapsus nudus* as well as a number of nudibranchs and chitons). However, probably valid California–Northern Gulf disjunct species include: the long-fingered tidepool shrimp, *Betaeus longidactylus;* the hydroids *Plumularia reversa, Campanularia castellata,* and *Antennularia septata;* the cerianthid anemone *Pachycerianthus aestuari;* the actiniarian anemone *Diadumene leucolena;* the flatworm *Pseudostylochus burchami;* the nemerteans *Baseodiscus punnetti* and *Cerebratulus lineolatus;* the polychaete *Polydora nuchalis;* the echiuran *Urechis caupo;* the amphipod *Corophium uenoi;* the muricid snail, *Pteropurpura macroptera;* the opisthobranch, *Aplysia vaccaria* (the world's largest gastropod); the scaphopods, *Dentalium pretiosum* and *Dentalium vallicolens;* the sea stars, *Henricia aspera* and *Odontaster crassus;* the brittle star, *Ophiopholis longispina;* and the bryozoan, *Microporella cribosa.*

It is tempting to speculate that some California–Northern Gulf species have evolved to the point of separation and now represent California–Gulf sister-species pairs. However, no phylogenetic studies on regional invertebrates have shown this.

Some temperate (Californian) species maintain continuous distributions around the Baja California peninsula and throughout the Gulf, including the following free-living coastal species: *Ophiodromus pugetten-*

sis, Syllis elongata, Gycera tesselata, Diopatra ornata, Diopatra splendidissima (Polychaeta); *Sipunculus nudus* (Sipuncula); *Califanthura squamosissima* and *Paranthura elegans* (Isopoda).

Patterns of Invertebrate Diversity in the Gulf of California

The accumulation of species diversity since the Gulf of California opened has produced one of the most biologically rich marine regions on earth. The diverse benthic habitats and the productive pelagic waters of the Gulf are famous for supporting high numbers of species and large population sizes among many marine taxa: invertebrates, fishes, marine mammals, sea turtles, and marine birds (Brusca et al. 2005; various chapters in this volume). Nearly half of Mexico's fisheries production comes from the Gulf of California (Cisneros-Mata, chapter 6 in this volume).

Invertebrate community composition at any given locality in the Gulf comprises a mix of predictable species combined with a much larger and unpredictable suite of species, where the unpredictability is driven by complex networks of interacting physical and biological factors (e.g., short-term oceanographic and weather events, spawning and recruitment success of local species, variable current regimes). However, *relative* species diversity in the Gulf is quite predictable and largely a function of habitat and substrate type. Benthic invertebrate species diversity (i.e., species richness) is highest in the rocky littoral (intertidal) region, on relatively stable shores, and on intertidal or offshore bottoms composed of softer sedimentary rocks such as sandstone and beachrock ("coquina") or eroded volcanic tuffs and rhyolites. Benthic invertebrate diversity is lowest on beaches composed of smooth hard rocks such as granites and basalts and on unstable beaches of coarse sand or cobble, the latter having perhaps the lowest (benthic) diversity of any coastal habitat. Areas that have a variety of substrate types harbor more species than do more homogeneous ones. Today, diversity on islands in the Gulf far exceeds that on mainland shores, but this is due largely to human impacts and the decline of biodiversity on accessible coastlines during the past few decades. Today, the islands of the Gulf are critically important refugia for species that have been extirpated from the mainland coast.

In the Northern Gulf, species diversity and composition are strongly markedly through the year, creating extreme seasonal variations in seawater temperatures (Alvarez-Borrego 1983; Maluf 1983; Bray and Robles 1991; Lavín et al. 1998; Brusca 2007c).[1] As a result, Northern Gulf waters are essentially a warm-temperate marine environment during the winter but a tropical marine environment during the summer. The distinct seasonal species turnover in invertebrates and algae in this region is striking, as tropical species (e.g., *Gnathophyllum panamense, Ocypode occidentalis, Pentaceraster cumingi, Nidorellia armata, Callinectes bellicosus* and other portunid crabs) disappear during the cold winters and temperate species (e.g., *Pachygrapsus crassipes, Aplysia californica, Betaeus longidactylus*) vanish during the warm summers. The Central Gulf shows far less seasonality in water temperatures, and the Southern Gulf shows hardly any seasonality in environmental conditions or species diversity.

Overall, marine macroinvertebrate diversity in the Gulf of California is exceptionally high: 4,916 named species, with ~30–40 new species being described annually (tables 4.1–4.3). Because of the presence of many undescribed invertebrate species, including many members of the planktonic and offshore communities, this total is estimated to be approximately 70 percent of the actual macroinvertebrate diversity of the Gulf (table 4.3). The most poorly known invertebrate faunas are those of the open sea and of the deeper (>300 m) benthic environments. Faunal diversity decreases gradually from the south to the north.

Overall macroinvertebrate endemicity in the Gulf is 16 percent (782 species). At the phylum level, highest endemism occurs in Brachiopoda (80 percent), Ctenophora (50 percent), Platyhelminthes (41 percent),

TABLE 4.1. Macroinvertebrate species known from faunal regions of the Gulf of California.

Faunal Region	Total	Percentage of Total Gulf Species
Northern Gulf	2,275	46.2
Central Gulf	3,324	67.6
Southern Gulf	3,173	64.6
Upper Gulf of California and Colorado River Delta Biosphere Reserve (subregion of Northern Gulf)	1,048	21.3
Southwestern Baja California Sur	676	13.8

TABLE 4.2 Ecological distribution of macroinvertebrate species in the Gulf of California.

Habitat	Number of Species	Percentage of Total Gulf Species
Sandy bottoms (all depths)	2,026	41.2
Sandy intertidal habitats	1,928	19.9
Rocky bottoms (all depths)	1,644	33.4
Rocky intertidal habitats	1,075	21.9
Mud bottoms (all depths)	1,313	26.7
Coastal lagoons (esteros and estuaries)	329	6.7
Mangrove lagoons	260	5.3
Associated directly with mangrove plants	41	0.8
Coral reefs	172	3.5
Benthic species (all depths)	4,350	88.5
Pelagic species (all depths)	262	5.3
Occurring in the intertidal zone	2,258	43.9
Occurring *only* in the intertidal zone	45	0.9
Occurring above the 30 m isobath	3,600	73.2
Occurring *only* above the 30 m isobath	918	18.7
Occurring above the 100 m isobath	4,019	81.8
Occurring *only* above the 100 m isobath	2,402	48.9
Occurring on and over continental shelf (above 200 m isobath)	4,078	83.0
Benthic species on continental shelf (above 200 m isobath)	4,044	82.3
Pelagic species over continental shelf (above 200 m isobath)	32	0.7
Species occurring *only* on continental shelf (above 200 m isobath)	3,016	61.4

Note: Some species have been recorded from more than one habitat.

Echiura (25 percent), and Mollusca (21 percent). At lower taxonomic levels, highest endemism occurs among Anthozoa (34 percent), Polyplacophora (26 percent), Gastropoda (26 percent), Porifera (25 percent), and Cumacea (25 percent). However, these figures should be viewed with caution because many taxa (e.g., Porifera, Brachiopoda, Cnidaria, Ctenophora, Platyhelminthes, Echiura, Cumacea, Tanaidacea, micromolluscs, Urochordata, Hemichordata) are poorly studied in the Gulf and the Tropical Eastern Pacific in general.

In the Northern Gulf, notably high biodiversity occurs on the very limited intertidal beachrock ("coquina") formations that occur at just four

TABLE 4.3. Known and predicted species diversity in major macroinvertebrate groups in the (entire) Gulf of California.

Phyla and Major Subgroups	Number of Species Recorded	Number of Species Predicted
Porifera	*115*	575
Cnidaria	*262*	526
Hydrozoa	147	292
Anthozoa	108	204
Scyphozoa	7	50
Ctenophora	*4*	20
Platyhelminthes	*22*	110
Nemertea	*17*	30
Sipuncula	*11*	22
Echiura	*4*	7
Annelida	*722*	820
Oligochaeta	1	3
Polychaeta	720	816
Pogonophora	1	1
Arthropoda	*1,062*	1,522
Pycnogonida	15	45
Cirripedia	48	47
Copepoda	?	25
Ostracoda	?	25
Stomatopoda	28	33
Mysida	3	10
Amphipoda	232	464
Isopoda	82	110
Tanaidacea	2	20
Cumacea	8	20
Euphausiacea	14	20
Dendrobranchiata	26	42
Stenopodidea	2	4
Caridea	130	145
Astacidea	1	1
Thalassinidea	20	24
Palinura	8	9
Anomura	131	192
Brachyura	301	336
Mollusca	*2,198*	2,590
Monoplacophora	1	2
Polyplacophora	57	62
Gastropoda	1,534	1,630
Bivalvia	566	848
Scaphopoda	20	25

TABLE 4.3. *(continued)*

Phyla and Major Subgroups	Number of Species Recorded	Number of Species Predicted
Cephalopoda	20	23
Bryozoa (Ectoprocta)	*169*	*338*
Brachiopoda	*5*	*7*
Echinodermata	*263*	*300*
Chaetognatha	*20*	*25*
Hemichordata	*3*	*5*
Chordata	*39*	*292*
Ascidiacea	17	170
Appendicularia	21	40
Cephalochordata	1	2
TOTALS	4,916	7,189

Note: Phylum-level data in *italics.*

Coloradito (Baja California). These small, rare, eroding beachrock habitats harbor disproportionately high species diversity, giving them a priority need for protection. High diversity is also found at Isla San Jorge and Rocas Consag and also on offshore (subtidal) rock outcroppings of the northern Sonora coastal shelf. Exceptionally high biodiversity, including rich pelagic diversity (and abundance) driven by year-round upwelling, distinguishes the Midriff Islands. All of these high-diversity sites serve as important invertebrate refugia and recruitment sources for mainland shores.

The entire benthic region of the Northern Gulf formerly maintained a high species diversity and biomass. However, in subtidal areas susceptible to bottom trawling for commercial shrimps (i.e., shallower than 100 m), much diversity has been lost over the past 50 years as a result of excessive anthropogenic disturbance (see below). Unfortunately, we have almost no knowledge regarding community composition and food web structure for the Northern Gulf's offshore benthic or pelagic communities. One of the most pressing research needs is to achieve an understanding of benthic community structure in this region and an enhanced sense of how profound the effects of bottom trawling have been on this system.

Forty-six percent of the Gulf's macroinvertebrate species occur in the Northern Gulf (2,275 species), and 1,048 (21 percent of the Gulf species) are known from the Upper Gulf of California/Colorado River Delta pods (514 species), and polychaete annelids (285 species) are the most diverse phyla. Within the Mollusca, gastropods and bivalves stand out with 660 and 287 species, respectively. Among Arthropoda, brachyuran crabs, amphipods, and isopods are notably diverse with 167, 126, and 41 species, respectively. Of the macroinvertebrate species known from the Northern Gulf, 128 (5.7 percent) are unique to that area.

Among the species endemic to only the Northern Gulf are two elegant and giant aphroditid polychaetes (*Aphrodita mexicana, A. sonorae*), sometimes called "sea mice," both of which are now greatly reduced in numbers and threatened as a result of excessive bottom (shrimp) trawling. The beautiful coral *Astrangia sanfelipensis,* today known only from the spatially restricted San Felipe/Coloradito "coquina reefs," is also threatened by habitat degradation at those two upper Gulf sites.

A total of 3,324 macroinvertebrate species has been recorded from the Central Gulf (68 percent of the Gulf species), and 3,173 occur in the Southern Gulf (65 percent of the Gulf species). In addition, 676 species (14 percent of the Gulf's invertebrate species) extend their ranges around Baja California's southern tip and up the Pacific coast, between Cabo San Lucas and the northernmost limit of the Bahía Magdalena lagoon complex—a region that extends the Gulf fauna outside the physical boundaries of the Gulf of California.

Examination of tables 4.1 through 4.3 reveals further interesting patterns of invertebrate biodiversity in the Gulf. Although only a single true coral reef occurs in the Gulf (at Bahía Pulmo, south of La Paz: Brusca and Thomson 1977; Robinson and Thomson 1992), 40 species of corals (order Scleractinia) occur in the Gulf (17 in the Northern Gulf, 30 in the Central Gulf, 26 in the Southern Gulf); this makes the coral diversity richer than that of, say, sea anemones (order Actiniaria; 22 species in the Gulf). Corals are most commonly seen on the Gulf's islands, where they are more protected than on mainland shores. Eighteen hermatypic (zooxanthellate) coral species inhabit the Gulf in six genera (*Fungia, Leptoseris, Pavona, Pocillopora, Porites, Psammocora*). Good, seemingly young coral head development can also be seen in Bahía San Gabriel, on Isla Espíritu Santo, where they could be viewed as "patch reefs." The richest area of coral development is in the southwestern part of the Gulf, especially on the islands along that peninsular coastline.

cies), polychaetes (720 species), bivalves (566 species), true (brachyuran) crabs (301 species), echinoderms (263 species), bryozoans (169 species), hydroids (147 species), tidepool (caridean) shrimps (130 species), sponges (115 species), gammaridean amphipods (111 species), hyperiidean amphipods (109 species), isopods (82 species), chitons (57 species), and porcelain crabs (51 species). Also notable is a single species of intertidal marine earthworm (Annelida: Oligochaeta), *Bacescuella parvithecata,* which occurs with rarity in the Northern and Central Gulf.

The 18 species of sea fans (Anthozoa: Gorgonacea) reported from the Gulf (none of which is endemic) are only a small percentage of the actual gorgonian diversity, and we have observed many undescribed species in the region. Similarly, the 7 species of jellyfish reported from the Gulf clearly represent a small fraction—perhaps only 15 percent—of what is actually there. Similarly, the 38 species of tunicates (subphylum Urochordata) reported from the Gulf probably represent only about 15 percent of the actual diversity in this region. The 115 species of sponges (Porifera) recorded from the Gulf probably represent about 20 percent of the region's actual sponge diversity.

Table 4.2 reveals some interesting ecological relationships. As would be expected, most macroinvertebrate species known from the Gulf of California have been reported from shallow waters. There are 2,158 species in the intertidal zone (44 percent of all Gulf species), but of these only 45 (2 percent) are *strictly* intertidal in their distribution. Thirty-six hundred species (73.2 percent) occur at or above the 30 m isobath, and 918 (18.7 percent) occur *only* above the 30 m isobath. There are 4,078 species (83 percent of all Gulf species) occurring on or over the continental shelf (200 m and above), and 3,016 of these (61.4 percent of all Gulf species) occur *only* on or over the continental shelf (i.e., do not occur below the 200 m isobath).

Most macroinvertebrate species known from the Gulf of California—4,350 species (88.5 percent of the Gulf total macroinvertebrate fauna)—are benthic. Only 262 pelagic species (5.3 percent of the total) have been reported, an artificially low number because many undescribed species occur in this region (and because, at the time of this writing, the Macrofauna Golfo Project database excluded ostracods and copepods).

If all depths are considered, then most invertebrates occur on sandy bottoms—2,026 species (41.2 percent of the Gulf's total macroinvertebrate the total fauna). If only the intertidal zone is examined then these percentages reverse, and rocky intertidal regions harbor 1,075 species (21.9 percent of the Gulf's total macroinvertebrate fauna, including three dozen or so species that occur strictly as algal epiphytes in rocky habitats) whereas intertidal sandy beaches harbor 928 species (19.9 percent). Mud bottoms (all depths) harbor 1,313 species (26.7 percent of the Gulf's total macroinvertebrate fauna).

Coastal lagoons and *esteros* (moderately hypersaline coastal, or tidal, lagoons) are notably diverse areas, and these habitats provide extremely important nursery and feeding grounds for the young of many coastal fish and shellfish species, including most commercial finfish and shrimp that are traditionally exploited by the Gulf's fisheries. There have been no published, comprehensive (i.e., all-taxa) surveys of any esteros, or other wetlands, in the Gulf of California. These coastal lagoons (estuaries and esteros) are home to at least 329 species (6.7 percent of the Gulf's total macroinvertebrate diversity); of these, 260 are from mangrove lagoons, where 41 of these species are reported as specifically associated with the mangrove plants themselves (e.g., oysters, sponges, tunicates, and other invertebrates that inhabit mangrove roots and stalks). Whitmore et al. (2005) reported 212 species of invertebrates from mangrove lagoons of Baja California Sur. However, because many undescribed species of sponges and tunicates occur in mangrove lagoons, most living on the mangroves themselves, these numbers underestimate the actual level of diversity in that ecosystem.

Some Comparisons to Other Faunal Regions

So far as we are aware, no other comparable marine region in the world has a database of every known macroinvertebrate species. However, the fauna of the Mediterranean Sea is very well known (far better than the Gulf of California) and shares many historical and oceanographic similarities that make it useful for comparison. Unlike the Gulf, the Mediterranean Sea is largely physically isolated from the tropical waters of the Old World. However, numerous Mediterranean-occurring invertebrate species have emigrated from the Red Sea via the Suez Canal since its opening. At least 558 alien species—most entering through the Suez Channel—have been recorded, including 189 molluscs, 99 arthropods, 85 chordates, 85 macroal-

The current (post-Messinian) Mediterranean Sea is roughly the same age as the Gulf of California: ~5 million years old (earliest Pliocene). Similarly to the Gulf, which has only one true coral reef, the Mediterranean has no true coral reefs. The Mediterranean also has many aquaculture facilities, although they have been in place much longer than those in the Gulf of California. As a result of this history plus heavy shipping traffic, the Mediterranean Sea has many more exotic and introduced species, from around the world, with which to contend.

Overall, about 6,000 species of benthic invertebrates have been reported from the Mediterranean Sea, which could be viewed as a fairly accurate biodiversity estimate given how well known the region is. About 4,350 benthic invertebrate species have been recorded from the Gulf of California. If the known Gulf benthic species count is assumed to represent about 70 percent of the actual invertebrate diversity, than the actual total is close to 6,165, or about the same as in the Mediterranean.

There have been 649 species of sponges (Porifera) recorded from the Mediterranean Sea (597 Demospongiae, 44 Calcarea, 8 Hexactinellida), 48 percent of which are endemic (Pansisni and Longo 2003). In contrast, 115 species of sponges have so far been recorded from the Gulf of California (113 Demospongiae and 2 Calcarea but no Hexactinellida), 29 (resp. 25) percent of which are endemic. The Caribbean–Central American Atlantic sponge fauna is of about the same diversity as that of the Mediterranean, with 640 species. The Sino-Japanese sponge fauna consists of some 589 species and the Indonesian fauna 965 species (Pronzato 2003). These figures suggest that our estimate of only 20 percent of the Gulf's sponge fauna being described so far is "in the ballpark."

The molluscan fauna of the Mediterranean Sea is often said to be the best known in the world, and 2,042 species are listed from the region: 1,482 gastropods, 410 bivalves, 65 cephalopods, and 16 scaphopods (Bello 2003; Oliverio 2003). Molluscs—also one of the best-known invertebrate phyla in the Gulf of California—share a nearly identical diversity, with 2,198 species (1,534 gastropods, 566 bivalves, 20 cephalopods, 20 scaphopods).

The Gulf's bryozoan (Ectoprocta) fauna is still very incompletely described, with 169 named species compared with 476 species of bryozoans reported from the Mediterranean Sea (Rosso 2003). With just 15 named species, the Gulf's pycnogonid fauna is also far from being fully described; note that 56 species have been reported from the Mediterranean (Chimenz Gusso and Lattanzi 2003). The same can be said for the amphipod fauna of the Gulf, which has yielded 232 species to date compared with 466 species reported from the Mediterranean Sea (Bellan-Santini and Ruffo 2003).

A total of 619 species of decapod crustaceans—one of the best-known groups for the area—have been recorded for the Gulf versus only 340 species in the Mediterranean. However, a hefty 27 percent of these Mediterranean species are introduced exotics (D'Udekem d'Acoz 1999). Consequently, the decapod fauna is 2.5 times more diverse in the Gulf than in the Mediterranean. It is interesting that, because of their high market value, the arrival of alien species of shrimps (e.g., *Marsupenaeus japonicus, Metapenaeus monoceros*) and fishes (e.g., *Upeneus moluccensis*) is considered a boon to Mediterranean fisheries (Galil 2007).

Invertebrate Conservation in the Gulf of California

Prior to the 1960s, anthropogenic pressure on the Gulf's environment was minimal, and anyone visiting the region would have witnessed a seemingly endless bounty of sea life that probably did not differ substantially from the diversity encountered by indigenous peoples during past millennia. In the 1960s, a casual walk in the rocky intertidal zone during low tide would reveal dozens of species of large-bodied invertebrates, especially echinoderms, crustaceans, and molluscs. Common in tidepools and at snorkeling depths were large sea stars (*Oreaster occidentalis, Mithrodia bradleyi, Nidorellia armata, Astropecten armatus, Pharia pyramidata, Linckia columbiae, Heliaster kubiniji, Astrometis sertulifera, Luidia columbia* and *L. phragma*), spectacular huge brittlestars (*Ophioderma teres* and *O. panamense, Ophiocoma aethiops* and *O. alexandri*), and large urchins (*Eucidaris thouarsii, Centrostephanus coronatus, Arbacia incisa, Lytechinus pictus, Echinometra vanbrunti*). The dazzling little "barrel shrimp," *Gnathophyllum panamense,* was commonly seen in association with *Eucidaris thouarsii* or on coral heads. Also common were large sea cucumbers, such as *Brandtothuria arenicola* and *B. impatiens, Fossothuria rigida,* and *Isostichopus fuscus.* Large molluscs were also abundant and included many spectacular murexes, cones, olives, and cowries (e.g., *Haustellum elenesis, Phyllonotus erythrostomus, Hexaplex nigritus, Hexaplex princeps, Luria isabellamexicana, Oliva porphyria,* many species of *Conus*). Large beds of sea fans (gorgonians) lived on offshore rocky outcroppings, which were home to rare invertebrates such as basket stars (e.g., *Astrodictyum panamense*). Shallow sandy bottoms were home to enormous beds of sand dollars and heart urchins (e.g., *Encope grandis, Encope micropora,* and *Lovenia cordiformis*), most of which have been decimated by shrimp trawlers (color plate 3).

Except for a few remote stretches of coastline on the Baja California peninsula, there are no longer any sites on the Gulf mainland coast where these large invertebrates exist in abundance in the intertidal zone. Most of these spectacular large-bodied invertebrates have become rare or largely extirpated from the Gulf's mainland shores. Overfishing (for Asian food markets) reduced *Isostichopus fuscus* to so few sites that it is now federally listed in Mexico as a threatened species. A similar fate has befallen offshore trawling grounds. Prior to the 1970s, sorting through a shrimp-trawl haul was a rewarding and exciting experience, and in those days such by-catch provided a living library of the animal kingdom. This is no longer the case, and in areas that have been heavily trawled for decades, life on the seabed is now dominated by scavengers such as skates, rays, and portunid crabs (color plate 4).

Beginning in the 1950s, three factors began to have synergistic negative impacts on the biodiversity of the Gulf. First was the establishment of Mexico's national fisheries program, which led to overgrowth of fishing efforts and subsidized overexploitation of marine resources. Second was the realization that tourism held the potential to generate enormous revenues, which led to national and regional policies that set coastal Sonora, Sinaloa, Nayarit, Jalisco, and the Baja California peninsula on a path toward wholesale destruction of coastal natural resources. The third factor is the disruption of the rivers that once flowed into the Gulf, including all of the once-perennial rivers of Sonora—the mighty Colorado River among them. Exacerbating these impacts has been an explosive and unchecked population growth in southwestern United States and northwestern Mexico (Brusca and Bryner 2004; Stoleson et al. 2005). These environmental challenges are reviewed in some detail in Brusca (2007c), Brusca and Bryner (2004), and Lluch et al. (2007).

Invertebrate Fisheries

Today, every major fishery in the Gulf is probably overfished (Greenberg and Vélez-Ibáñez 1993; Sala et al. 2003, 2004; Brusca et al. 2005; Cisneros-Mata, chapter 6 in this volume). The American Fisheries Society lists the Gulf, especially its northern part, as one of five geographic "hot spots" in North America where numerous fish species are at risk (Musick et al. 2000). Commercially valuable invertebrates are facing the same fates as finfishes, as population sizes of the giant Mexican limpet (*Patella mexicana*), black murex (*Hexaplex nigritus*), pink-mouth murex (*Phyllonotus erythrostomus*), articulate chiton (*Chiton articulatus*), giant sea cucumbers (*Isostichopus fuscus*), octopus (*Octopus bimaculatus* and others), shrimps (Penaeidae), swimming crabs (*Callinectes* spp.), and others have plummeted over the past decade. Even marine algae are overharvested in northwestern Mexico—mainly on the Pacific Baja peninsula, a region that provides about 10 percent of the world production of agarophytes (the most important commercial species being the red alga *Gelidium robustum,* which has been harvested without regulation since 1945).

Industrial shrimp trawling exacts a harsh toll on the Northern Gulf's benthic environment and also along the coasts of southern Sonora and Sinaloa. The ocean bottom in the Northern Gulf was once estimated to be dragged by shrimp nets as frequently as four times per year (Pérez-Mellado and Findley 1985; García-Caudillo 1999; Brusca et al. 2005), although with the recent partial "collapse" of the trawled shrimp fishery in this region that number has fallen. Shrimp trawl nets are indiscriminant killers, raking the seafloor in a clear-cutting fashion, trapping and killing everything in their path (Engel and Kvitek 1998; Watling and Norse 1998; Dayton et al. 2002). The historically high rate of bottom trawling has seriously damaged the Gulf's fragile, soft-bottom, benthic habitats. In addition, trawl nets in the Northern Gulf capture between 10 and 40 kilograms (depending on the location and time of year) of by-catch for each single kilogram of shrimp (Brusca 2004a, 2007c; Brusca et al. 2005). The number of commercial shrimp trawlers in the Gulf grew from 700 in 1970 to a high of 1,700 in 1989 and then decreased to 1,200 in 1999. Until very recently, hundreds of shrimp boats (and artisanal fishers) were still working *within* the upper Gulf's biosphere reserve. "Catch per unit effort" in the shrimp fishery has been declining for decades (documented at least as early as the 1970s; Snyder-Conn and Brusca 1977) while government subsidies artificially sustained the overcapacity of the industrial fishing fleet. Without government subsidies, commercial shrimp trawling would not be economically feasible. In fact, as a result of catch decreases and the advent of shrimp farming in the Gulf (producing cheaper market shrimp), the economics of commercial shrimping shifted so much just after the turn of this century that the number of bottom trawlers working out of the three main fishing ports in the Northern Gulf fell to just 130 boats (115 in Puerto Peñasco, 15 in San Felipe, and none in El Golfo de Santa Clara). Recently, the Mexican government activated a program aimed at reducing the number of industrial shrimpers in the Pacific, paying compensation for any boat willing to cease fishing activity, but the success of that program remains to be seen.

Limited scientific and anecdotal information suggests that sweeping changes in benthic/demersal community structure have taken place over the past 50 years as a result of disturbance from bottom trawling. These changes include an accelerating decrease in the diversity and biomass of the by-catch, possibly heralding a regional benthic/demersal ecosystem collapse (Pérez-Mellado and Findley 1985; Brusca 2007c; Findley, pers. comm.). In the late 1960s, sorting through the by-catch of a shrimp-trawl haul produced hundreds of species of invertebrates (and fishes) in most known phyla. Today, these same bottom trawl nets (in the Northern Gulf) contain only a few dozen species of invertebrates and are dominated by scavenger species (pers. obs.). Invertebrates whose depth range is the same as that dragged by shrimp trawls have suffered enormous destruction, and many are probably on the verge of extinction (e.g., the beautiful giant polychaetes *Aphrodita mexicana* and *A. sonorae;* the sea pen *Ptilosarcus undulatus*), but no empirical studies have been made in this regard. The destruction of the benthic ecosystem has disrupted the food web of the entire Northern Gulf, which has probably altered the pool of available prey for the critically endangered vaquita porpoise, *Phocoena sinus,* and the totoaba, *Totoaba macdonaldi.*

Tourism and Aquaculture

In areas—such as Puerto Peñasco, San Felipe, and San Carlos/Guaymas—of heavy and increasing tourism in the northern and central

Gulf, littoral biodiversity is but a pale shadow of what it was just 25 years ago. Part of the tourism-driven loss is hand-collecting of animals by visitors (and the trampling underfoot of fragile habitats exposed at low tide). But also important is the collection of large molluscs and echinoderms by residents for sale to tourists as curios and of molluscs sold to local restaurants, where they are served in seafood cocktails (e.g., bivalves, gastropods, and octopuses). In the Northern and Central Gulf today, healthy populations of these large-bodied species are found almost exclusively on island refugia or highly inaccessible stretches of the mainland coast, although some still occur in reduced numbers subtidally.

Increasing loss of coastal habitats due to encroaching housing and resort developments, marinas, and aquaculture installations lacking environmental controls are threatening the rich wetlands (estuary and estero habitats) of the Gulf that serve as critical spawning and nursery grounds for shrimp and other invertebrate and fish species. The complex food webs of coastal bays and wetlands also include species not found anywhere else in the Gulf, such as the rare amphioxus (Cephalochordata), *Branchiostoma californiense.*

Much of the coastline of Nayarit, Sinaloa, and Sonora has now been carved up into aquaculture farms (Glenn et al. 2006; Brusca 2007c). Most of these are shrimp farms, and ~95 percent (64 million pounds in 2000) of this farm-raised shrimp makes its way to the United States. About 90 percent of the world's aquaculture facilities are in developing nations, and they are largely "slash and burn" in their approach: bulldozers tear out mangrove forests and other coastal habitats to be replaced with fish or shrimp ponds, many of which cover many square miles. In concept, these coastal ponds are cheap and easy to construct; a pipe at one end of the pond complex pulls clean ocean water in, and a pipe at its other end spits used water out—laden with shrimp (or fish) wastes, excess food, herbicides (used for algal control), antibiotics and other drugs, disease organisms and parasites, and so forth. In recent years, mangroves have not been directly removed during the construction of Gulf shrimp farm operations, but the extent of damage to this ecosystem by proximity to shrimp farming (e.g., changes in estuarine water circulation, siltation and smothering, pollution, eutrophication) has been little examined. Of course, closed and nonpolluting aquaculture systems are possible inland (and required in the United States), but they are more expensive to build and operate.

Coral reefs and coral communities in the Gulf are significantly threatened by divers and boat anchors. Although the Cabo Pulmo Reef has enjoyed various levels of protection for many years and is now a national park, it has also gradually deteriorated over the past two decades because of divers and fishermen as well as several severe El Niño events (and associated sea-surface warming). Although the coral-predating Eastern Pacific crown-of-thorns sea star (*Acanthaster planci*) occurs throughout the Central and Southern Gulf, it apparently does not pose a threat to corals in the region and preys on numerous other invertebrates (as well as on corals). Other coral predators are primarily fishes (e.g., spotted pufferfish, *Arthron meleagris;* parrotfishes, *Scarus* spp.) and a few gastropods, but these also do not appear to be a threat to corals in the Gulf.

Loss of Rivers

All of the rivers that once reached the Gulf of California have been drastically altered or destroyed by overdraft and diversion, and none of the Sonora rivers that once flowed perennially, or semi-perennially, now reaches the sea (these rivers include the ríos Colorado, Magdalena-Altar-Concepción-Asunción, San Ignacio, Sonora, Yaqui, Mayo, and Fuerte). Historically, the Colorado River carried an estimated annual average of 15–18 million acre-feet (maf) of water to its delta (Carriquiry and Sánchez 1999; Cohen et al. 2001; Brusca and Bryner 2004). During the nineteenth century, especially from 1850 to 1880, riverboats steamed from the Gulf of California up the Lower Colorado/Gila River system into Arizona. Until completion of Hoover (Boulder) Dam in 1935, which created Lake Mead, freshwater from the Colorado River flowed into the Northern Gulf throughout the year, with great seasonal floods resulting from spring snowpack melt in the Rocky Mountains. By the time Glen Canyon Dam was completed in 1963, input of Colorado River water to the delta and upper Gulf had completely ceased. For 20 years after completion of that dam, as Lake Powell filled, virtually no water from the river reached the sea. In 1968, flow readings at the southernmost measuring station on the river were discontinued, since there was nothing left to measure.

Today, 20 dams (58 if the Colorado River's tributaries are included) and thousands of kilometers of canals, levies, and dikes have converted the Colorado River into a highly controlled plumbing system in which every drop of water is carefully counted, managed, and litigated. The original water allocation estimates were made in the 1920s and, based on data from an unusually wet time period, assumed an average river flow of about 22 maf per year. However, the river's average annual flow during the last 500 years has actually been about 14 maf/yr. Hence there are now more legal claims to the water than are possible to meet, so it is no wonder that today almost no water reaches the delta. Additionally, most of the delta's wetlands have been converted into farmland or urban sprawl. What was once 2 million acres of wetlands has been reduced to about 150,000 acres (Glenn et al. 1992, 1996, 1999, 2001). As a result of the greatly reduced freshwater flow, the powerful tides of this region now overwhelm the Lower Colorado River channel. During high tides, seawater creates an estuarine basin (estero), for 50–60 km upriver, that averages 2–8 km in width and 16 km wide at its mouth. This marine intrusion has killed most of the freshwater flora and fauna that once lived along the lowermost river corridor.

Prior to construction of Hoover Dam, the annual sediment discharge from the Colorado River into the Gulf was enormous: estimates range from 45 to 455 million metric tons. Accumulated river sediments on the delta are thousands of feet thick. The entire Northern Gulf is considered the "Colorado River Sedimentary Province." However, the reduction of freshwater input and sediment discharge since 1935 has modified the hydrography and oceanography of the Colorado River delta–upper Gulf system, initiating a regime of deltaic erosion. New deltaic deposition no longer takes place, and the entire delta is now exposed to the dynamic forces of extreme tides, currents, and storms, which promote re-suspension and erosion of ancient river sediments as well as the gradual export of sediments out of the delta region. These changes are altering the littoral wetlands and biological equilibrium of the region. They are also destroying habitat for an estimated 340 species of marine macroinvertebrates that inhabit the sand/mud benthic environment of the delta region.

It is likely that the reduction of freshwater input into the upper Gulf, in combination with other anthropogenic factors, has driven some species to (or nearly to) extinction. However, we have so few historical or baseline data for marine organisms of this region that extinctions (or local extirpations) would go unnoticed for commercially unimportant or otherwise little-known species. There has never been a comprehensive dedicated survey of the marine fauna of the upper Gulf and Colorado River delta ecosystem.

The delta clam, *Mulinia coloradoensis,* was probably once one of the most abundant animals of the uppermost Gulf. Windrows of its shells line the beaches of the delta and western shores of the upper Gulf. This species was thought to be extinct until its recent rediscovery in small numbers near the mouth of the river (Kowalewski et al. 2000; Rodríguez et al. 2001a; Cintra-Buenrostro et al. 2004). It has been suggested that the near demise of this species is the result of decreased benthic productivity resulting from upstream diversion of the Colorado River's flow. However, there is no evidence that nutrient levels (and hence productivity) have decreased significantly in the Northern Gulf, and nutrients that have been lost by depletion of riverine input may have been regained in the form of agricultural runoff and deltaic erosion (release of ancient trapped nutrients). Therefore, the near extinction of this clam may be linked to another factor, still unknown, that is related to reduction of freshwater input to the delta.

Freshwater input from the Colorado River is also important to the life history of commercial shrimps of the region. Commercial shrimp catches have been falling since the 1960s, which is due to a combination of overfishing and loss of habitat for young. It has been estimated that an annual influx of just 250,000 acre-feet of Colorado River water could double shrimp production in the Northern Gulf (Galindo-Bect et al. 2000). The young of these shrimp utilize the shallow wetlands and esteros of the region (including the tidelands of the delta) as a nursery, migrating into these areas after their offshore planktonic larval phase. When the shrimp reach a juvenile or subadult stage, they migrate offshore once again.

Rescuing Invertebrate Biodiversity

Since the mid-1980s, a growing conservation movement has emerged in northwestern Mexico led by such nongovernmental organizations as Agrupación Sierra Madre, ALCOSTA, the Arizona-Sonora Desert Museum, CEDO (Centro Intercultural de Estudios de Desiertos y Oceanos), COBI (Comunidad y Biodiversidad), Conservation International-

Mexico, ENDESU (Espacios Naturales y Desarrollo Sustentable), ISLA (Conservación del Territorio Insular Mexicano), Marisla, Naturalia, The Nature Conservancy, Sociedad de Historia Natural Niparajá, Noroeste Sustentable (NOS), The David and Lucile Packard Foundation, Proesteros, Pronatura, ProPeninsula, Wildcoast, World Wildlife Fund–Mexico, and other organizations often associated with local communities. Such organizations have had a powerful influence on natural resource conservation in the Gulf. In addition, the government sector has increasingly stepped up its conservation efforts, especially SEMARNAT (Mexico's ministry of environment and natural resources) and its national commission for protected natural areas (CONANP) and "Islas del Golfo" program. The active participation of these organizations was critical to establishing the Upper Gulf of California and Colorado River Delta Biosphere Reserve, developing conservation priorities for the Gulf and its islands, working with artisanal fishers and indigenous peoples to develop sustainable fisheries, and working with state and federal governmental agencies to push for more protected areas and better protection of the marine and coastal environment. As a result of the efforts of these groups over the past two decades, fisheries laws have tightened up, gillnetting is on the verge of becoming illegal, bottom trawling is becoming better regulated (and, it is hoped, will soon be banned), and high-visibility species such as totoaba and vaquita are attracting the attention of conservationists all over North America (summarized in Brusca and Bryner 2004; Brusca et al. 2005; Brusca 2007c; Lluch-Cota et al. 2007; Carvajal et al., chapter 11 in this volume). Recently, new laws were passed that prohibit use of gill nets with mesh sizes greater than 6 inches and that protect against "destruction of the marine floor" (e.g., shrimp trawling) in all protected areas in the Gulf, including the Upper Gulf of California and Colorado River Delta Biosphere Reserve. These new environmental laws could go a long way toward reducing the incidental take of vaquita and sea turtles and toward protecting the seafloor; however, it will be up to the federal government (PROFEPA, the enforcement arm of SEMARNAT) to enforce them, and many fishers are still protesting or ignoring them.

There remain many fundamental but unanswered questions about the Gulf's ecosystems. What is the nature of the benthic sediment–water column food web in shallow Gulf waters, and how does energy flow through that system? How has that system been affected by bottom (shrimp) trawlers during the past few decades? How are commercial species such as shrimp affected by freshwater input (e.g., from the Colorado River), and how important are annual freshwater pulses from the Colorado River to the marine ecosystems? What are the biological relationships between the Gulf's estuaries/esteros and its open-water (pelagic) ecosystem? How effective are the fully protected marine reserve areas with "no-take zones" for the recovery of marine species (e.g., San Pedro Mártir and Bahía de los Ángeles Biosphere Reserves)?

Despite the considerable damage that has been inflicted by humans on Gulf environments and despite the many lingering threats, there is cause for optimism. If the conservation movement in the Gulf of California continues with its present momentum, then critical new areas will receive protection and better enforcement of currently protected regions should follow. Most urgent is to: (1) ban *all* bottom trawling in the Gulf so that the benthic/demersal ecosystem can, if possible, recover; (2) implement a sustainable management program for fisheries; (3) protect the four "coquina reefs" in the upper Gulf; (4) improve enforcement of existing laws for protected areas; (5) increase public education; (6) ban the take of all marine life from the intertidal zone, except that done through a regulated fishery basis; and (7) better understand the marine ecosystems of the Gulf. Fortunately, one still can find island and isolated coastal refugia, areas not easily accessible by road or large fishing boats, that serve as important shelters for species extirpated elsewhere in the Gulf.

The jointly developed Monterey Bay Aquarium/Arizona–Sonora Desert Museum "Southwest Seafood Watch Cards" have taught and inspired seafood consumers (since 2004) on both sides of the border to restrict their purchases to sustainably harvested seafoods from the Gulf of California and elsewhere. Despite resistance from fishers in Mexico and from U.S. and Mexican seafood purveyors and restaurateurs, evidence suggests that the sustainable seafood programs are having an impact on both sides of the border, though much remains to be done.

NOTE

1. As defined by the Macrofauna Golfo Project, the *Northern Gulf* (GCN) faunal region extends from the marine-influenced Colorado River delta southward to (and in-

cluding) the Midriff Islands (*las Islas del Cinturón*), the largest of which are islas Tiburón and Ángel de la Guarda, and to Bahía San Francisquito (Baja California) and Bahía Kino (Sonora). Within the Northern Gulf is the subregion of the Upper Gulf of California and Colorado River Delta Biosphere Reserve, extending from the delta to a line running from Punta Pelícano (= Roca del Toro; the southern margin of Bahía Cholla and the larger Bahía Adair), Sonora, across the Gulf to Punta Machorro (= Punta San Felipe) at San Felipe, Baja California. The *Central Gulf* (GCC) faunal region ranges from Bahía San Francisquito (Baja California) and Bahía Kino (Sonora) to Punta Coyote (Baja California Sur) and Guaymas (Sonora). The *Southern Gulf* (GCS) faunal region extends southward to Cabo Corrientes, Jalisco, on the mainland and to Cabo San Lucas on the Baja California peninsula. (See fig. 5.4 in the next chapter.)