# THE TEMPERATE AND TROPICAL PLANKTONIC BIOTAS OF THE GULF OF CALIFORNIA

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## ABSTRACT

Studies examining composition and distribution of the planktonic flora and fauna of the Gulf of California have been few. Several are thorough in geographical coverage, though time-change has received little attention. Published species lists and distributional records are now particularly complete for phytoplankton, Foraminifera, Medusae, Siphonophorae, Chaetognatha, and Euphausiacea. New lists of Copepoda and Amphipoda are included in this paper; we also detail biogeographical affinities of these species. All available records of planktonic species are cited (including some not generally available), and faunistic zonation of the gulf is examined in a general way. Studies describing direct (in situ) observations of gulf zooplankton are discussed.

## RESUMEN

El número de publicaciones sobre composición y distribución de la flora y fauna planctónica en el Golfo de California es bajo. Varios estudios son de extenso y detallado alcance geográfico aunque la variabilidad temporal presente en dicha cobertura ha recibido poca atención. Las listas de especies y registros de distribución actualmente publicados están completos, especialmente en el caso de fitoplanction, Foraminifera, Medusae, Siphonophorae, Chaetognatha, y Euphausiacea. Se incluyen nuevas listas para Copepoda y Amphipoda en este trabajo; adémas, se detallan las afinidades biogeográficas de estas especies. Todos los registros disponibles de especies planctónicas son citados y la zonación faunística del golfo es examinada en forma general. Algunos trabajos que describen observaciones directas (in situ) de zooplancton del golfo son revisados.

## INTRODUCTION

The Gulf of California is known to harbor an abundance of plankton (e.g., Osorio-Tafall 1943; Zeitzschel 1969). How productive the gulf is, and the nature of regional and seasonal change in its biological properties, remain largely to be determined. The many hues of the "Vermilion Sea" intrigued navigators for centuries before Streets (1878) found milky-red water

at Bahía Mulege to be thick with the dinoflagellate *Noctiluca mirabilis*, and red-tinged water off Isla Cerralvo to be caused by another "flagellated infusoria."

The gulf extends from 32°N within the zone of the warm-temperate Californian Transition Zone (e.g., Newman 1979) to its mouth in contact with the Panamic Province near the Tropic of Cancer, 23°27'N (Figure 1). Little attention has yet been paid to ways in which the gulf's semienclosed planktonic populations range along its 1,000-km length. On the basis of fish fauna, the gulf encompasses a temperate-tropical transition (Walker 1960). The species of phytoplankton—mainly warm-water cosmopolites—seem now to be reasonably well known (e.g., Round, 1967). Of the zooplankton, lists appear to be most complete for Foraminifera (Bradshaw 1959; Parker 1973), Chaetognatha, Siphonophora, and Scyphomedusae (Alvariño 1969), pontellid Copepoda (Fleminger 1964a, 1967a,b, 1975), and Euphausiacea (Brinton 1979; Brinton and Townsend 1980). Hyperiidean Amphipoda have been studied by Siegel-Causey (1982), whose results presage description of a diverse amphipod fauna.

Interest in examining the biology of gulf plankton in relation to oceanographic processes is increasing. This is due partly to the importance to Mexico of understanding regenerative cycles in these seemingly productive coastal waters, and partly to a developing awareness among oceanographers of the gulf's distinctive topography, including the presence of varved sediments at depths within the oxygen minimum, hydrothermal vents in deep waters, and the substantial containment of biota.

Oceanographic processes expected to be of significance to nutrient renewal and the distribution of organisms in the gulf were outlined by Brinton and Townsend (1980), following Roden and Groves (1959), Griffiths (1968), Alvariño (1969), Roden (1971), and Moser et al. (1974). The climate and circulation of gulf waters are influenced by seasonally reversing winds and changes in solar radiation. The seasonal range in surface temperature is extreme: in the northern part it varies between 14°C in February and 30°C in August, and in the southern part between about 20° and 30°C.
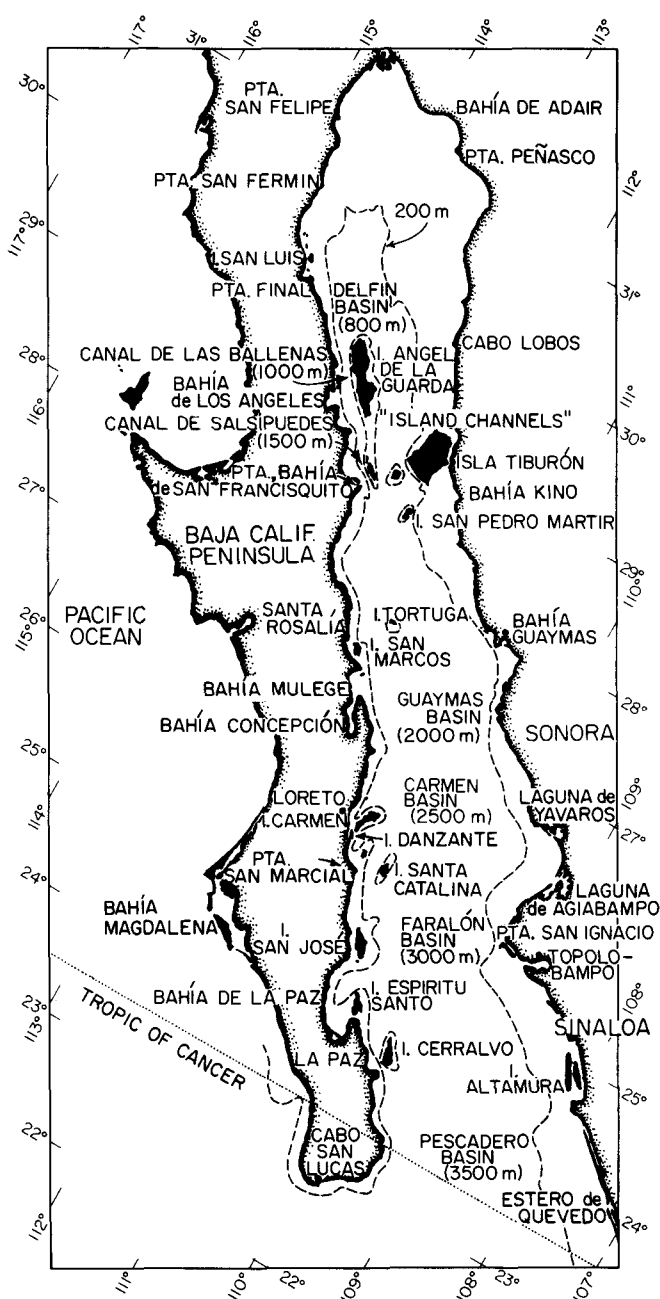
Figure 1. The Gulf of California.

Upwelling, determined by the divergence of the Ekman transport, is strongest along the eastern side of the gulf during the northeasterly winds of winter and spring, as verified by 1980 satellite images of cool plumes extending westward from the eastern coast; upwelling shifts to the western side with the southwesterly winds of summer and early fall, appearing less intense than in the opposite period (Badan-Dangon et al. 1985). During June 1957, the western side was 2° to 3°C cooler than the eastern.

Islands, particularly those along the western gulf, provide coastline that augments the mainland sites for

mixing and upwelling. In channels, notably between Isla Angel de la Guarda and the Baja California peninsula, tidal mixing combines with along-channel current oscillations superimposed on turbulent eddies (Alvarez et al. 1984) to form a persistent cooling system. Island topography may be optimal for persistent upwelling because there is always some coastline parallel to the shifting wind. In the northernmost gulf, the amplitude of the semidiurnal tide and its energy release is 15 times that at the mouth (Filloux 1973). In turn, internal waves are forced by the tides, particularly spring tides (Fu and Holt 1984). Such features reduce the applicability of generalized explanations of nutrient renewal, plankton production, and species distributions in the gulf.

Evaporation exceeds runoff into the gulf, but surface salinity beyond embayments ranges only between 34.4‰ and 35.9‰. (Roden and Groves 1959). This compares with a maximum of about 34.6‰ in the open sea to the west (Love 1973). Therefore, salinity per se probably does not influence the distribution and abundance of plankton in the gulf. Estuaries and lagoons along the southeastern coast nevertheless contribute nutrients, as indicated by primary productivity maxima off that coast during August 1972, associated with lowered surface salinities of 34.4‰ to 34.5‰ (Gilmartin and Revelante 1978).

Diagrams of geostrophic flow during four 1957 cruises (Wyllie 1966) show mean surface flow to have been out of the gulf during February and April. Flow at 200 m—the daytime depths of certain vertically migrating zooplanktons—was much the same. Most winter outflow is along the Baja California coast (Rosas-Cota 1977). By June, surface flow had reversed, entering the gulf across much of the mouth, particularly the central axis and the eastern side (Rosas-Cota 1977), and persisting toward the north as a stream that shifted toward the eastern side by August. Flow at 200 m was opposite to surface flow during the summer (Wyllie 1966). While eastern tropical Pacific water reaches only to the gulf's mouth in winter, it begins to penetrate northward in spring (Alvarez-Borrego and Schwartzlose 1979).

Direct observations supplemented by computations of geostrophic flow have been made of apparent cyclonic cells of circulation extending across the width of the gulf during August 1978 (Emilsson and Alatorre 1980). Such a cell in the 0-50-m layer in the southern gulf provided inflow along the eastern shelf and outflow near the tip of Baja California, not unlike that shown by Wyllie (1966) for August 1957. Another broad eddiform structure seemed to be present farther north in the gulf. Features of this kind are pertinent in examining means of exchange among plankton

populations within the gulf, and between the gulf and the adjacent Pacific. Such cells may relate to the basin topography of the gulf (Figure 1) or may be persistent segments in a long standing-wave in the gulf postulated by Sverdrup (1941), to be discussed in relation to the phytogeographical zonation. Alternatively, the cells may be formed from energy and shear provided by long internal or coastally trapped Kelvin waves that travel northward along the Mexican coast, mainly in summer, and become trapped in the gulf (Christensen et al. 1983). These waves have amplitudes up to 30 cm, periods of up to 10 days, and wavelengths of up to 1,000 km, but provide no appreciable volume transport. Recent evidence (Winant, pers. comm.) indicates that the cells may be not necessarily eddies, but merely zones separating intermittent tongues or jets of offshore flow.

Across the eastern tropical Pacific there is a layer in which oxygen is deficient owing to a combination of vertical stability in the water column and high productivity, with consequent near-deficit oxidative regeneration of nutrients. Between the thermocline and about 700 m, the concentration of oxygen is as low as 0.05 ml/l. According to data in Roden and Groves (1959) and Alvarez-Borrego (1983), the layer becomes diluted inside the gulf. For example, at 23°N, oxygen concentration of 0.1 ml/l was unusual at any season (during 1957) and never occurred in water above 300 m except near the western side in April. Moreover, the lowest oxygen concentration found half-way up the gulf (27°N) was 0.2 ml/l, at 500-m depth.

Oxygen deficiency in the eastern tropical Pacific appears to have much to do with (1) creating an environment for endemism and (2) sharply restricting a number of subtropical species and warm-water cosmopolites from establishing there. Plankton from depths within the oxygen minimum in the gulf was first reported in Sverdrup, Johnson, and Fleming (1946). Although low oxygen concentrations in the gulf appear not to be sufficiently shoal, extreme, or widespread to have played a dominating role in the selection of which species are present, influence upon the pelagic biota remains largely to be determined.

## PHYTOPLANKTON
### Taxonomy and Distribution

For this paper, phytoplankton include only the algae in the water column and surface sediments. Fossil phytoplankton, microalgae of the sedimentary rock, and primary production are not considered. The first four sets of collections (Allen 1923, 1937, 1938; Cupp and Allen 1938), from surface net samples, were analyzed for total cell numbers at each station, without details of the distribution of species. Osorio-Tafall (1943)

described phytoplankton collected from the central and southern littoral during January 1942; in this excellent review article on the Gulf of California, he considered several aspects of natural histories (e.g., geology, hydrography) that might have been pertinent for interpreting species distributions. However, the limited scope of the sampling made it difficult to draw general conclusions.

Gilbert and Allen (1943) attempted a phytogeographical synthesis using phytoplankton collected during cruises of the E.W. Scripps (February-March 1939, October-December 1940) extending from the oceanic entrance of the gulf to the northern deltaic region. This first subsurface sampling to be carried out is significant, for as Round (1967) pointed out, surface productivity in the gulf is at times low because of photoinhibition, but during times of nutrient injection, surface waters may be abnormally rich. Thus, surface samples may be poor indicators of phytoplankton dynamics in the Gulf of California.

The systematic sampling led Gilbert and Allen (1943) to describe four water zones based on species distributions, but with boundaries tending to agree with the antinodes of Sverdrup's (1941) theorized internal wave along the axis of the gulf (Figure 2):

1. Zone A, "southern oceanic"
2. Zone B, "central," characterized by Coscinodiscus wailesii, now recognized as a temperate, coastal diatom (Cupp 1943)
3. Zone C, "northern," characterized by Asterionella japonica, now considered to be a neritic, widespread, warm-temperate diatom
4. Zone D, "inner," characterized by Gonyaulax catanella, now known to occur seasonally in many parts of the gulf as the principal dinoflagellate in toxic red tides.

The distribution of mean diameters of bottom-sediment particles followed a pattern that might have been generated by the wave postulated by Sverdrup (Revelle 1950), and provided support for the idea that such a wave might be a permanent feature of the gulf. Munk (1941) further showed that the theoretical characteristics of this wave were compatible with the gulf's physical topography.

Gilbert and Allen (1943) developed this hypothesis further. The internal wave, having three nodes, would be associated with three circulation cells, or zones, with boundaries at the antinodes. A fourth zone would exist in the northernmost gulf. Horizontal currents, strongest at the nodes, would diminish to zero at the antinodes. Because of the large period of this wave (seven days, or half the lunar fortnightly tide), the Coriolis force would produce circular currents in each zone, the direction in the central zone being opposite to
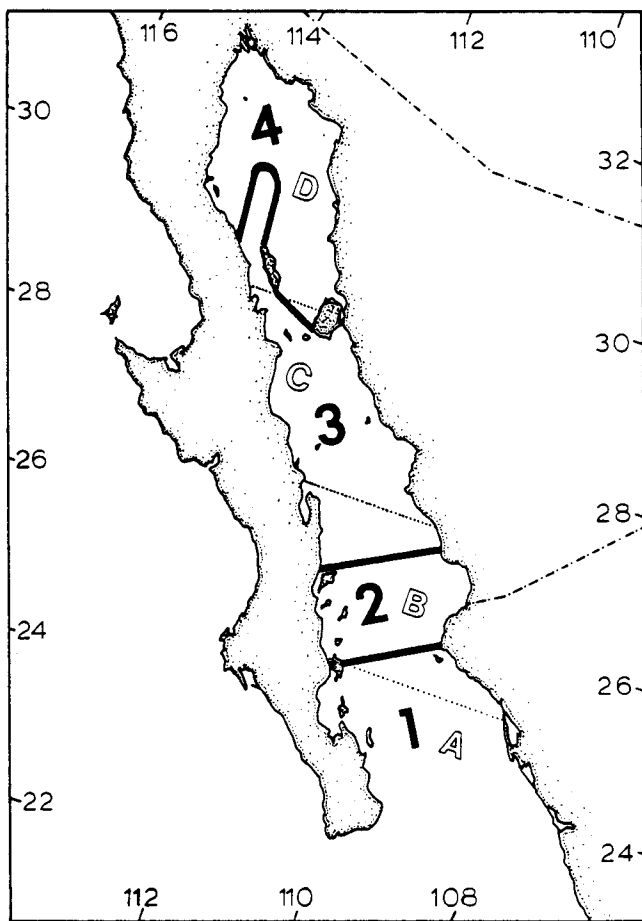
Figure 2. Phytoplankton distribution zones in the Gulf of California. *Dotted lines* indicate zones A-D proposed by Gilbert and Allen (1943); *solid lines* indicate zones 1-4 proposed by Round (1967).

Knowledge of gulf phytoplankton did not improve until Round's (1967) thorough treatment of net samples from March 1959 and 1960, and October-November 1959. He distinguished four zones, which had somewhat different, less artificially constrained boundaries from those of Gilbert and Allen (1943) (Figure 2). He derived a zonation scheme from the deposition of diatoms in surface sediments; however, differences between the two patterns are small and, because of the likelihood that current directions differ with depth, and affect the distribution of phytoplankton onto the bottom, the system of pelagic zonation is expected to be more appropriate in considering the living biota.

Zones 1, 2, and 3 correspond well with the hydrographic regions of Roden and Groves (1959) and support Round's contention that the zones reflect physical processes. Water in southernmost zone 1 is largely eastern tropical Pacific water, relatively depleted of nutrients because of a long residence time in zone 1 (Roden 1958); phytoplankton productivity is usually low, interrupted by seasonal injection of nutrients by upwelling. Griffiths (1968) gave some support for this, while noting that spring upwelling along western Baja California, $23°-24°N$, is more intense than along the western coast of mainland Mexico near Cabo Corrientes. However, because a strong front off Cabo San Lucas prevents nutrient-rich water from the Pacific coast of Baja California from entering the gulf, production of phytoplankton in the southwestern gulf remains less than to the east. Reporting on armored dinoflagellates, Klement (1961) noted that numbers and abundances of *Peridinium* species decreased with distance into the gulf, whereas the *Ceratium* population showed a relative increase; the flora was generally tropical to subtropical, without endemics. In general, the diversity of phytoplankton species decreases in the central region (zone 2) compared to zone 1.

Zone 3 was distinguished by Gilbert and Allen (1943) (their zone C) on the basis of large numbers of *Asterionella japonica*; however, Round (1967) did not record this species at all. *Coscinodiscus lineatus, C. asteromphalus,* and *Stephanopyxis palmeriani* occurred in immense blooms during Round's sampling but were absent in Gilbert and Allen's study. Zones 2 and 3 are characterized by wind-driven upwelling of nutrient-rich water, and tide-driven turbulence near islands (Roden 1958). Conditions responsible for blooms recur year after year, but species dominating the blooms evidently differ (Round 1967).

Zone 3 also includes a tongue of water curving northward between Baja California and Isla Angel de la Guarda, thereby including island channels distinguished by Brinton and Townsend (1980) as a faunistic zone. Blooms of *Chaetoceros radicans* in 1937 and

directions in the northern and southern zones. Since the horizontal currents reverse every half period, the zones would tend to become isolated from each other, but frequent breakdowns of intercellular boundaries should be expected.

Gilbert and Allen (1943) found the northernmost zone to have the greater phytoplankton populations, but lower diversity than zones in the south. Indirect evidence was presented that the seasonal phytoplankton cycle is dependent, in the outer gulf (zones A, B, C), upon upwelling, and in the inner, shallow regions, upon convection processes (see Lepley et al. 1975). The two processes are thought to be initiated in late fall when northwestern winds bring about east-coast upwelling, and when surface cooling lowers the stability of water masses in the basins and shallow regions of the inner gulf. At the onset of summer, when winds reverse and weaken and the surface waters become heated and stratified, the spring phytoplankton growth terminates. Gilbert and Allen (1943) believed this model to be supported by the occurrence of greatest phytoplankton productivity in March.

*Gonyaulax polygramma* in 1959 are recorded from this locality. Such blooms to the west and north of Isla Angel de la Guarda may occur in the mixing of mid-gulf and northern gulf waters as the tidal wave ascending the gulf is deflected by Isla Tiburón into the deep, narrow Canal de Ballenas (Roden and Groves 1959).

The northern gulf (Zone 4) is characterized by a low phytoplankton diversity, with local intense blooms of *Gonyaulax polyedra* and *G. catenella*. Further information about the northern gulf biota is given by Brenner (1962) and Phleger (1964).

Round (1967) concludes that the components of gulf phytoplankton are of tropical origin and that there is little likelihood of endemic species occurring there; it is necessary to look south of 60°S in the South Pacific before the flora changes significantly.

All gulf phytoplankton species reported in the literature have been collated with respect to distributional records (table available from authors). Some patterns may be discerned: many species penetrate the gulf no farther than zone 1 (e.g., *Asterolampra marylandica, Biddulphia mobiliensis, Chaetoceros laevis*, and *Rhizosolenia castracanei*); others are found throughout the gulf (e.g., *Chaetoceros debilis* and *Cyclotella striata*); some species have been found as far north as zone 3, yet not in zone 2 (e.g., *Actinocyclus ehrenbergi, Coscinosira polychorda, Epithemia gibba*); the groups Biddulphioidea and Solenioideae are generally absent from zone 3, but the Discoideae and Actinodiscae are locally dominant there; zone 4 is characterized by low diversity of species, with occasional immense blooms. It may be noted that most collections were obtained during March of different years.

Licea-Duran (1974) examined systematics and distribution of diatoms in Laguna de Agiabampo in Sonora, and Gilmartin and Revelante (1978) sampled the phytoplankton of the lagoons and open waters of the gulf, southward from Isla Tiburón, in fall 1972. Gilmartin and Revelante's results from the open waters agree generally with Gilbert and Allen (1943) and Round (1967), but their southernmost floristic break was drawn at 26°N, north of that reported by Gilbert and Allen or Round (possibly because station positions differed between the studies). This apparent difference was attributed to decreased upwelling and high temperatures, which allowed a northward extension of tropical southern species such as *Trichodesmium hildebrantii, Climacodium biconcavum, Hemiaulus hauckii*, and *Chaetoceros laevis* (see also Gilmartin and Revelante 1978).

In the lagoons the composition and abundance of estaurine phytoplankton differed most from the adjacent open waters when flushing rates of the lagoon were low, and least when flushing rates were high.

Some species were more abundant in the lagoons; for example, *Thalassionema nitzschiodes* in the north was replaced by *Skeletonema costatum* in southern hyposaline lagoons with low flushing rates. The lagoon flora was generally dominated by diatoms, except in two locations: Bahía Guaymas (zone 3) was dominated by the dinoflagellates *Gonyaulax digitale* and *Protoceratium reticulatum*, and Estero de Quevedo (zone 1) was dominated by *Gonyaulax minuta*.

Where dinoflagellates are numerous, phytoplankton maxima may change depth as the motile cells migrate during the 24-hour period. Kiefer and Lasker (1975) described a bloom in Coyote Bay of Bahía Concepción dominated by the dinoflagellate *Gymnodinium splendens* ($1.0 \times 10^5$ cells per liter). The profiles of the concentration of chlorophyll *a* based on fluorescence profiles showed an upper layer at 6-m depth near noon, at 8 m at dusk, and at 15 m near midnight. Upward movement began at 0200, reaching 10 m by daylight. Diatoms contributing to these chlorophyll profiles included *Leptocylindricus danicus, Skeletonema costatum, Cerataulina bergonii*, and *Thalassiothrix frauenfeldii*.

Silicoflagellates were found by Murray and Schrader (1983) to be generally less than 2% of the silicious phytoplankton of the gulf, but up to 5% in blooms. Combining material from surface waters and surface sediments, Murray and Schrader found that the distributions of eight species were related to Round's three biogeographic zones. *Octatis pulchra* was associated with high primary productivity in the central gulf, north of 26°N, especially in the Guaymas and Carmen basins, but was also abundant at the mouth. *Dictyocha messanensis*—cosmopolitan in the North Pacific—tended to dominate where silicoflagellates were rare, as at the gulf's mouth. *D. calida* and two other unnamed tropical *Dictyocha* species were most abundant at the mouth, decreasing northward. *Dictyocha epiodon* and *Distephanus epiodon* are California Current species that sometimes enter the gulf.

## Phytoplankton and Seston Biomass and Chlorophyll

Zeitzschel (1970) examined the roles of the four major phytoplankton taxa in the carbon budget of gulf waters. Dominance by diatoms was evident: they contained 50% of the carbon of living cells, but were only 10% of the number of cells (Figure 3). Naked flagellates, on the other hand, contained only 10% of all carbon, but constituted 70% of numbers. Dinoflagellates contributed 30% of the carbon and 15% of numbers, whereas the much smaller coccolithophores contributed about 10% of carbon and 5% of numbers.

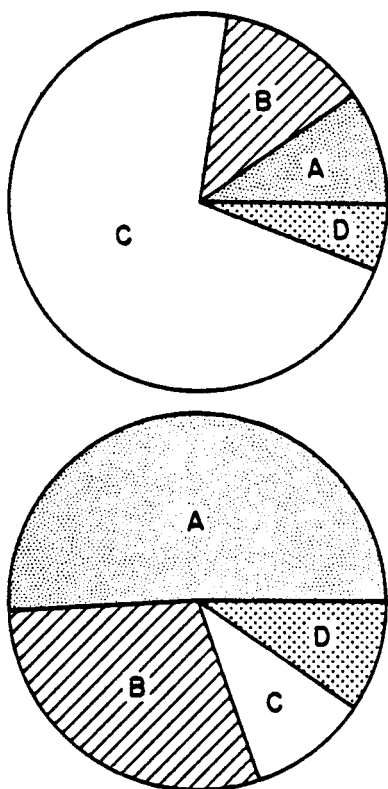Given as average proportions of total weight of seston (living, dead, and inorganic material combined)

Figure 3. Average phytoplankton composition for samples collected at various localities in the Gulf of California, from Zeitzschel (1970). *Top*, percentage composition by number; *bottom*, percentage composition by carbon. *A*, diatoms; *B*, dinoflagellates; *c*, naked flagellates; *d*, coccolithophores.

in the euphotic zone, particulate carbon averaged 34%, chlorophyll *a* 0.09%, particulate nitrogen 5%, and phytoplankton carbon 3.3%. Kiefer and Austin (1974) subsequently examined the effect of phytoplankton concentrations on submarine light transmission in the gulf, and Kiefer and SooHoo (1982) showed that, of the suspended particles in gulf waters, chlorophyll pigments were the dominant light absorbers, with phaeopigments constituting 15%-20% of total chlorophyll pigments in the mixed layer.

Zeitzschel (Figure 4) showed, further, that the number of particles in the seston decreased with increasing particle size, from about $10^3$ per ml for 3$\mu$ particles to 1 per ml for 30$\mu$ particles up to a size of about 100$\mu$, above which numbers (and volumes) dropped sharply, especially in offshore water. The observations held for surface samples as well as for samples at 1% light depth (23-29 m). Detritus was found to average 88.6% of seston in the gulf (see discussion of marine snow under Zooplankton Biomass).

Estimations of phytoplankton concentration have been made over broad sections of the gulf by measuring chlorophyll *a* in water samples. Across the northern gulf during spring, Gendrop-Funes et al. (1978) found values in excess of 20 mg/m$^3$ only at the surface

(Figure 5) and only in the northernmost region (Punta San Fermin across to near Punta Peñasco). Values greater than 10 mg/m$^3$ were observed both at the surface and at 30-m depth in the northernmost gulf and along the eastern side. Lowest values, 2 to 3 mg/m$^3$, were along the axis of the gulf.

The southern end of the gulf is poorer in chlorophyll *a*. Stevenson (1970) found values of 0.5 to 3 mg/m$^3$ during June at the mouth, with one measurement of 9 mg/m$^3$ near the eastern shore (Figure 6); June and August values were in the range of < 0.5 to 2 mg/m$^3$. Griffiths (1965) illustrated the distribution of chlorophyll *a* across an oceanic front at the mouth, noting the highest value, 0.6 mg/m$^3$, at the front.

Studies including the distribution of chlorophyll, zooplankton biomass, and other biological parameters in the eastern tropical Pacific outside of the gulf are in Holmes et al. (1957) and Longhurst (1976).

## ZOOPLANKTON
### Taxonomy and Distribution

Although zooplankton represents one or more trophic levels above the phytoplankton, studies of feeding and gut contents have not been done on zooplankton of the Gulf of California. Most studies have been of distribution and abundance in relation to environmental parameters such as currents, food supply, and water temperature, which undergo extreme seasonal and geographical changes.

The eastern and western sides of the gulf are scarcely 150 km apart, permitting more mixing of neritic and basin waters than is usual along an open coastline. Low concentrations of oxygen within the depth ranges of diurnal or seasonal vertical migrators (to 0.05 ml/l; Brinton 1979) have also been considered in interpreting biogeographical information in the gulf.

The Copepoda, Euphausiacea, and Amphipoda are usually the dominant Crustacea. Cladocera and Mysidacea become relatively conspicuous in the shallower part of the neritic zone. Alldredge and King (1980) emphasized the numerical importance of nearshore organisms, including certain harpacticoid copepods, mysids, and cumaceans, which are benthic in the gulf by day and pelagic at night.

The gulf provides extensive habitats for benthic, neritic decapod crustaceans—conspicuously Brachyura and Penaeidea—because of (1) a long coastline in relation to area, and (2) extensive shoal areas to the north and east. Larvae of these crustaceans are prominent in the zooplankton here, and a few have been described in detail (see Meroplanktonic Decapoda, below). Coastal-neritic and slope-water species of Copepoda also tend to be prominent in the gulf's mixed layer (see Copepoda, below). In this qualitative way,
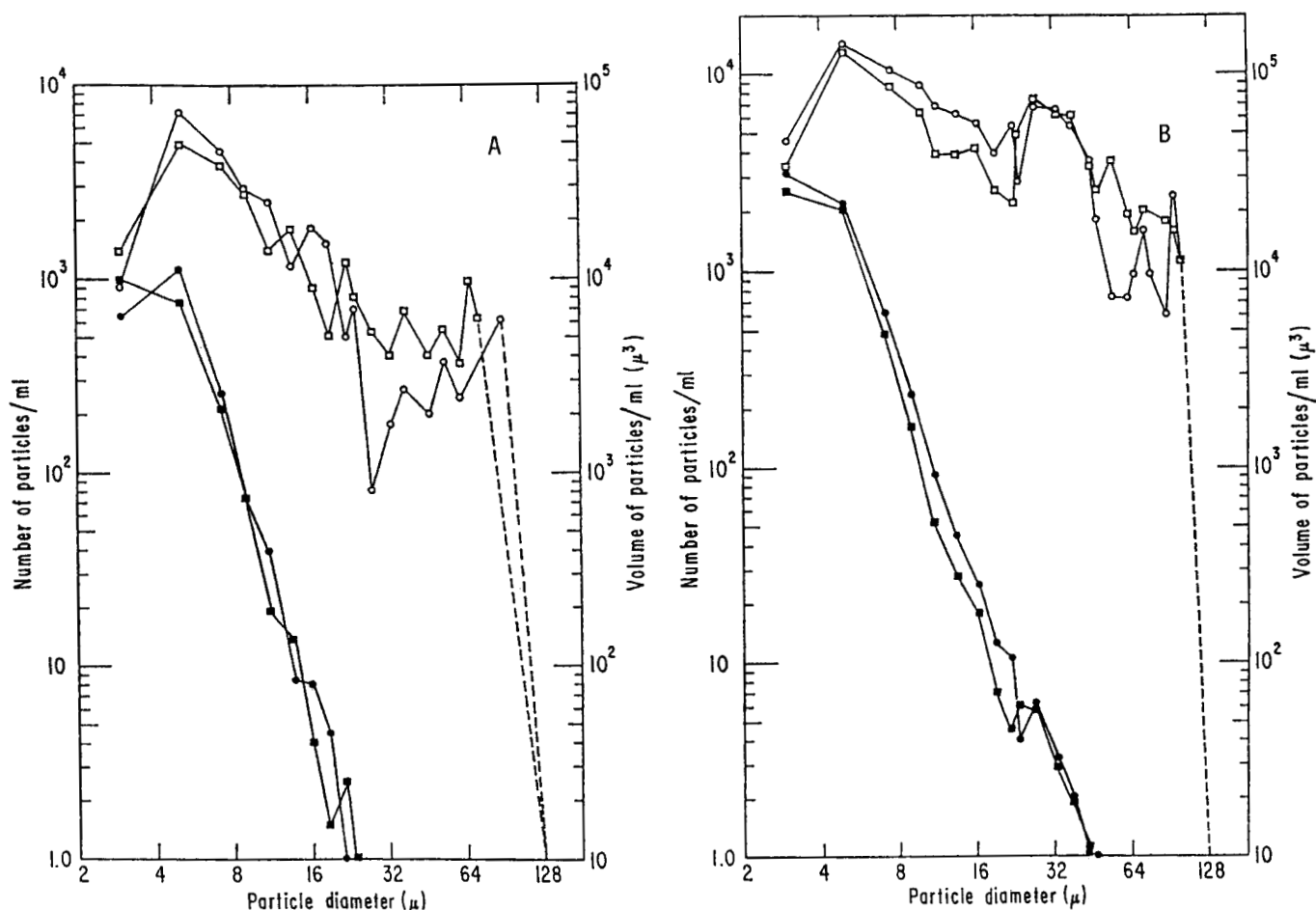
Figure 4. Total number of particles in seston (*solid symbols*) and total particle volume (*open symbols*) plotted against particle diameter. *Circles* indicate surface samples; *squares* represent 1% light depth. *Left*, at an offshore locality mid-Gulf of California (39 m); *right*, at a coastal locality, mid-gulf (23 m) (from Zeitzschel 1970).

the gulf plankton differs from that along the oceanic coast to the west, and from that in the deep sea.

Manrique (1977, 1978) quantified seven major zooplanktonic categories during a year-long study at two localities near Guaymas (Figure 7). He noted the following changes apparently related to the cold- and warm-water regimes of winter-spring and summer-fall:

1. Winter (December-January) plankton, even at this near-tropical latitude (28°N), was dominated by the temperate copepod *Calanus*, now recognized as *Calanus pacificus californicus*, discussed below. *Calanus* then constituted 35%-54% of the organisms caught, and the more coastal *Acartia tonsa* constituted 14%-50%. Sardine eggs appeared in January.

2. In February-March, and May-July, cladocerans (*Penilia, Evadne*) were important. (This was the first record of *Penilia avirostris* Dana in the eastern Pacific [Manrique 1971]).

3. Through May, *Acartia tonsa* dominated the copepods, declining in June with rapid warming from 17°C to 25°C. During October, *Acartia lillje-*

*borgi* replaced *A. tonsa*. *A. lilljeborgi* is listed, below, as tropical.

4. In October, siphonophores increased significantly off Punta Guaymas (sta. 1).

5. At the more open coastal locality (sta. 1), brachyuran larvae peaked in June with summer warming, though they were more evenly present throughout the year at the more sheltered sta. 2.

6. During June-September, the chaetognaths *Sagitta enflata* (warm-water cosmopolite) and *S. euneritica* (coastal) were most evident.

These pioneering observations generate intriguing questions. For example, Cladocera, whose small size indicates a role in using diminutive food particles, appears to have been succeeded by the relatively large and voracious larvae of Brachyura, which were then followed by a bloom or intrusion of Siphonophorae —often versatile carnivores. Extending and broadening such studies are clearly important to our understanding of the composition of zooplankton communities and the food webs functioning within them.
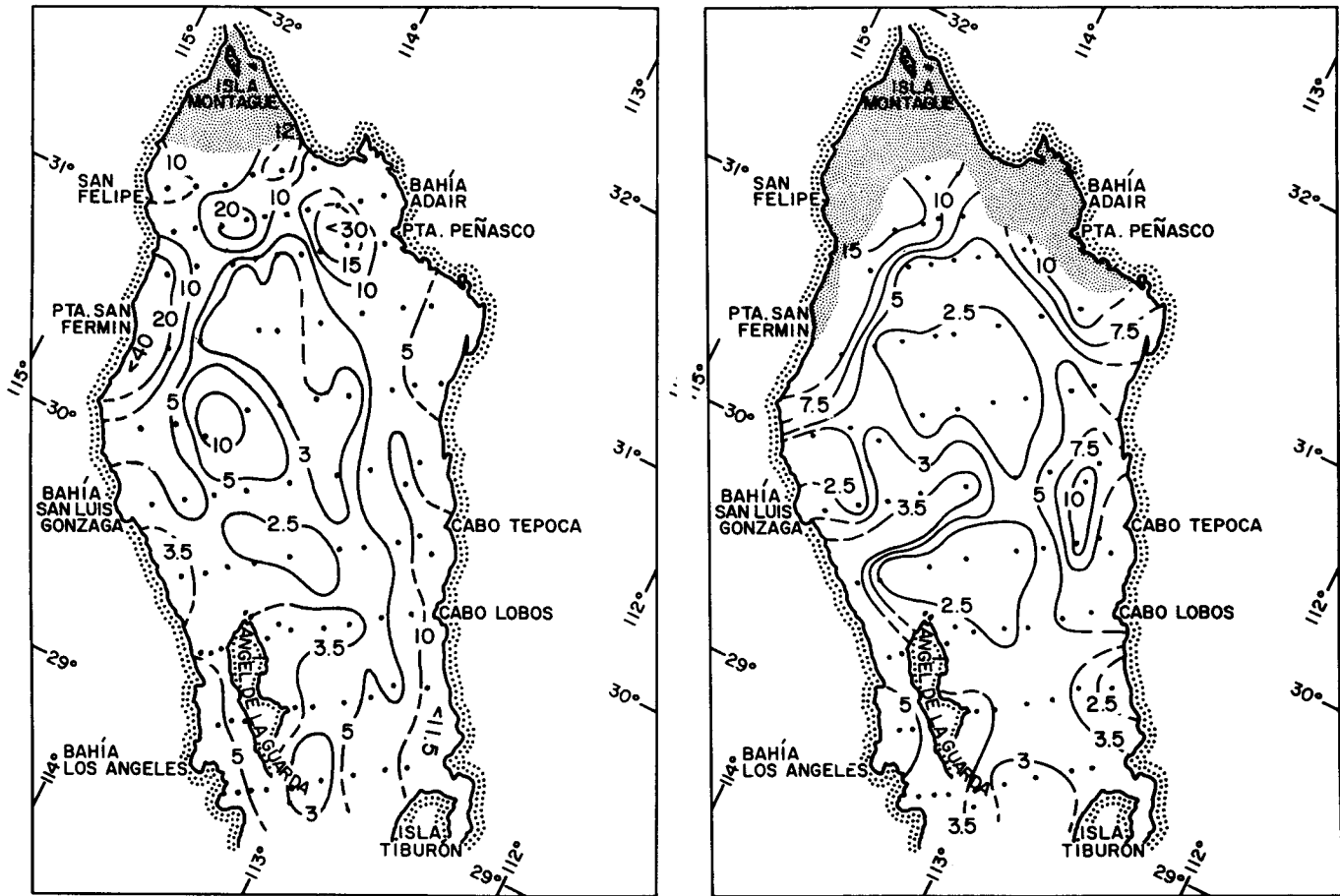
Figure 5. Distribution of chlorophyll a, mg/m³, in the northern Gulf of California in spring. *Left*, at the surface; *right*, at 30-m depth (from Gendrop-Funes, et al. 1978).

## Rhizopoda (Protozoa)

Of the living planktonic Foraminifera and Radiolaria, only the former have been studied in the gulf. Information on Foraminifera in the sediments is given in Natland (1950), Bandy (1961, 1963), Ingle (1973), Lankford and Phleger (1973), and Phleger (1964). Radiolaria in recent sediments are considered by Bandy (1961) and Benson (1964).

Studies of water-column Foraminifera by Bradshaw (1959) and Parker (1973) complement each other. Bradshaw provides pictures of Pacific-wide distributions, including occurrences in the southern part of the Gulf of California during September-October (1952). Parker provides an annotated species list with illustrations of some species, while updating the nomenclature, and gives gulf-wide distributional data for March-April (1959). Whereas Parker's samples were mainly from 50-0-m vertical tows with a 17-cm net of 0.6-mm mesh, Bradshaw's were from a 1-m net of the same mesh, hauled obliquely from 140 m. The species are described in Parker (1962).

Three species associated with the temperate North Pacific are prominent in the Gulf of California:

1. *Globigerina bulloides* was the most abundant foraminiferan in the northern half of the gulf in March-April samples, while at low density at most localities in the southern gulf. During September-October, it became still rarer in the south. Stratified sampling showed maximum numbers of living *G. bulloides* at 10-m depth, and dominance by this species to be below 50 m. (*G. bulloides* occurs throughout the California and Peru currents and occupies the subarctic Pacific and the zone of transition, 35°-45°N; there are scattered records across the subtropical and tropical Pacific.)

2. *Globigerina quinqueloba*, during March-April, was present throughout the gulf excepting the northern shelf region. During September-October, it was not observed in the southern gulf. This species has stronger high-latitude affinities than *G. bulloides*, being predominant in the subarctic Pacific.

3. *Globoquadrina dutertrei* (=*Globigerina eggeri* in Bradshaw [1959]), during March-April, showed highest densities in the northernmost gulf where *Globigerina qinqueloba* was lacking. Records farther south were few from both the spring and late-summer sets of samples. *G. dutertrei's* vertical distribution was
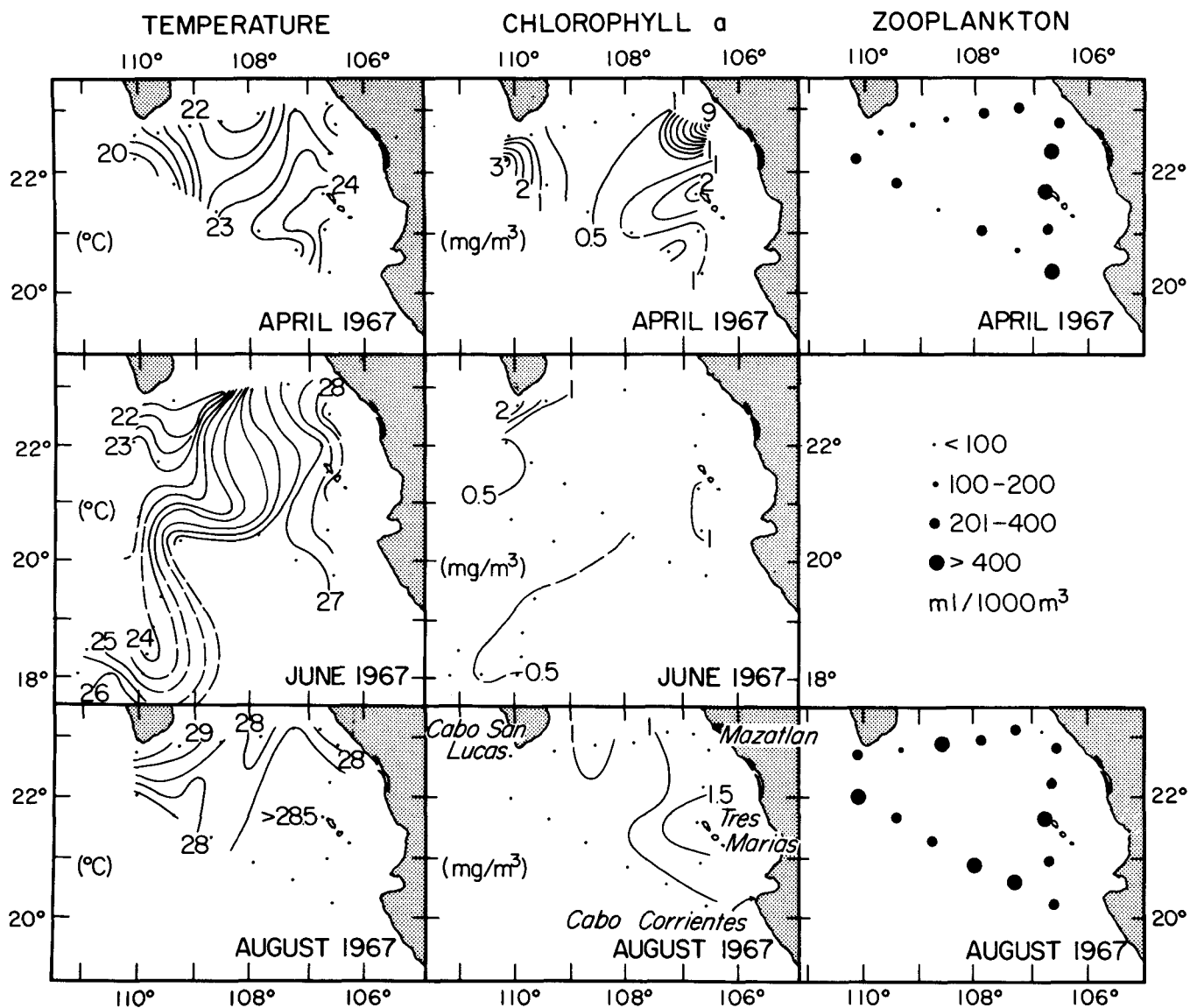
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Figure 6. Distributions of surface temperature, chlorophyll a, and zooplankton, 0-300 m, across the mouth of the Gulf of California during April, June, and August 1967 (after Stevenson 1970).

centered at 50 m. This species occupies the subarctic-subtropical zone of transition, 35°-45°N, in the North Pacific, and extends the length of the California Current as far as the mouth of the gulf.

Four species with warm-water affinities, representing four genera, were frequent in the southern half of the gulf:

1. Most abundant during both March-April and September-October was *Globigerinita glutinata*, a true cosmopolitan species, occurring at all latitudes, though at high density only in the eastern tropical Pacific.

2. *Globigerinella siphonophera*, a warm-water cosmopolite, was also frequent in the southern gulf during both seasons.

3. *Globorotalia enfracta* was common in the southern gulf in March-April, but was not reported in September-October.

4. *Globigerinoides sacculifer* was more frequently recorded in spring than in late summer. Its vertical range was centered at 50 m, or deeper than most species.

Nine additional tropical or tropical-subtropical species occurred sparsely and only in the southern part of the gulf. *Globigerina falconensis* (=*G. bulloides*, part, in Bradshaw); *Globigerina rubescens*; and *Globigerinella adamsi* (=*Globigerinella* sp. in Bradshaw) were observed only in March-April. On the other hand, *Globigerinoides conglobatus*, *Globigerinoides ruber* (=*G. rubra* in Bradshaw), and *Globorotalia cultrata* (=*Globigerina eggeri* in Bradshaw) appeared most frequently during September-October, whereas *Orbulina universa* was observed only in late summer

ZONA DE ESTUDIO
( Manrique,1977)

27°54'N

GUAYMAS

STA.2

STA. 1

III°52'W

[∴∴] COPEPODS

[////] CLADOCERANS

[≡≡≡] CRUSTACEAN LARVAE

[▓▓▓] APPENDICULARIANS

[▒▒▒] FISH EGGS

[▓▓▓] CHAETOGNATHS

[NNN] SIPHONOPHORES

[  ] OTHER GROUPS
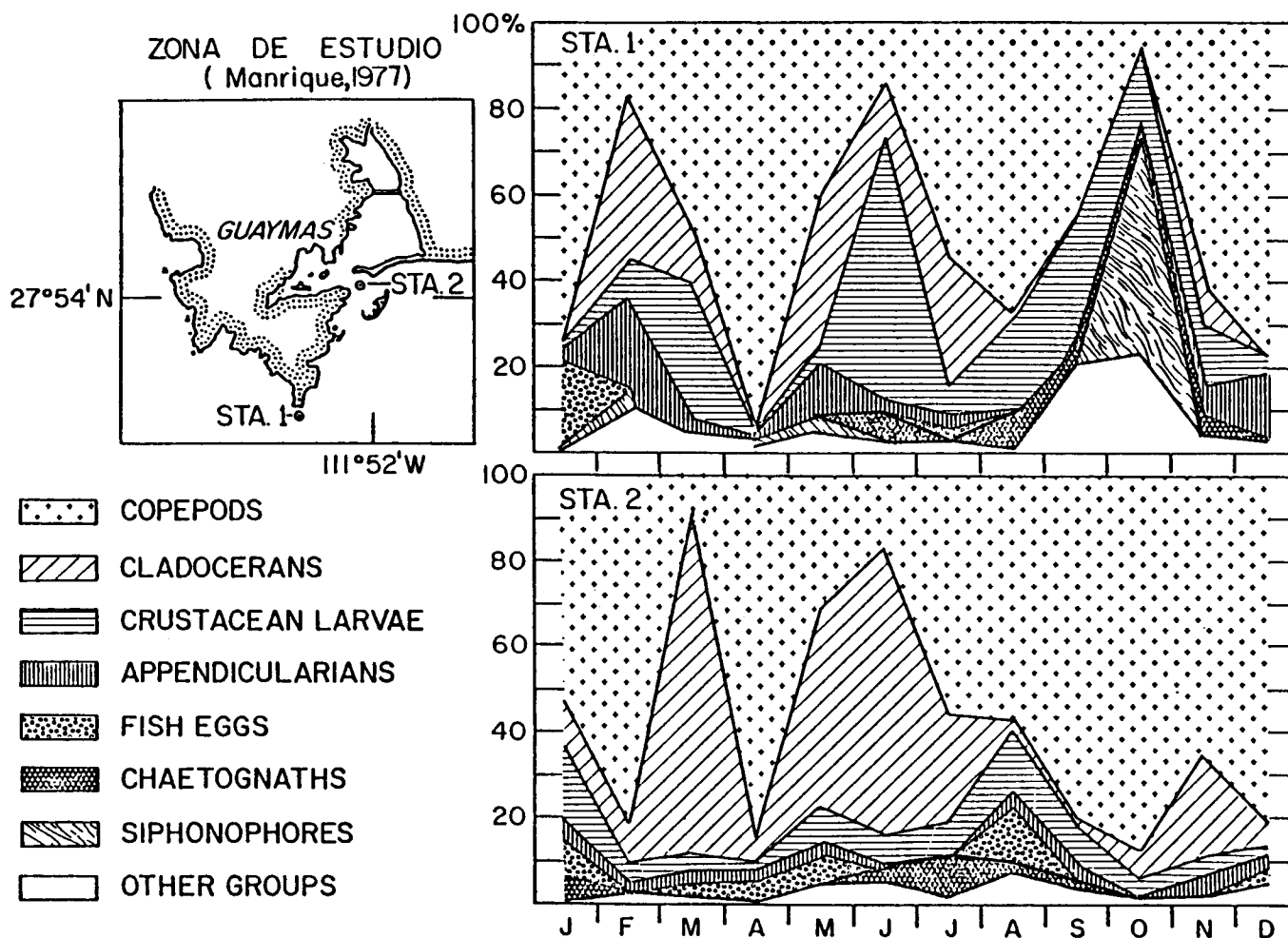
J F M A M J J A S O N D

Figure 7. Proportions of principal groups of zooplankton sampled at two localities through the 12 months of 1971 near Guaymas (from Manrique 1977).

samples. *Hastigerina pelagica* and *Pulleniatina obliquiloculata* were infrequent in the southern gulf during both seasons.

Parker remarked surprise at predominance of the cool-water *Globigerina bulloides* in the northern gulf and at absence of the warm-water cosmopolite *Globigerina calida* during March-April. Bradshaw had found *G. calida* ("*G.*sp.") in the southernmost gulf during September-October. Parker found overall densities of foraminiferans to be greatest in the southern part of the gulf, in association with highest diversity of species. Median abundance values for the two regions were 130/m³ and 14/m³, respectively, with a maximum of 882/m³ at a station near the mouth of the gulf.

### Medusae (Coelenterata)

Maas (1897) described a new medusa from collections in the gulf in 1891 by the U.S. Fish Commission steamer *Albatross*. This was the anthomedusan *Chiarella centripelalis*, which occurred from the mid

to southern gulf. Alvariño (1969) considered this species to be of the gulf's tropico-equatorial fauna. The trachomedusan *Homoeonema typicum* was also described by Maas "from the Gulf of California," but the station (no. 2637) proves to have been in the Gulf of Mexico. Maas also listed the two deep-sea genera of Narcomedusae, *Periphylla* (*P. dodecabostrycha* Brandt + P. *mirabilis* Haeckel?) from mid- and southern gulf, and *Atolla alexandri*, now considered *A. wyvillei*, from mid-gulf.

Bigelow (1909) added eight species, from *Albatross* collections off the mouth of the gulf, 20°-22°N, in 1904-05:

Scyphomedusae: *Nausithoë punctata* Kölliker, *Pelagia panypyra* Perón

Narcomedusae: *Cunina peregrina* Bigelow, *Solmundella bitentaculata* Quoy and Gaimard

Trachomedusae: *Liriope tetraphylla* Chamisso, *Aglaura hemistoma* Perón and Lesueur, *Agalantha digitale* var. intermedia Bigelow, *Rhopalonema velatum* Gegegenbaur.

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Bigelow's paper contains descriptions and illustrations of many more medusae from the eastern tropical Pacific, including a particularly diverse group from Acapulco harbor.

Bigelow (1940) recorded four species obtained by the *Zaca*. In addition to *Chiarella centripelalis* Maas (1897), he listed *Polyorchis penicillate* (Eschscholtz), *Periphylla hyacinthina* Streenstrup, and *Chromatoenema erythrogonum* Bigelow.

Of the species that Bigelow recorded in the gulf, four were among nine species + *Obelia* spp. listed in Alvariño's (1969) analysis of plankton from the February and April 1956 CalCOFI cruises and from deep trawl collections of the Vermilion Sea Expedition.

Alvariño considered *Liriope tetraphylla*—a warm-water cosmopolite, though not characteristic of the eastern tropical Pacific—to be an indicator of California Current water in the gulf. The species was present in the southernmost gulf in both February and April and at a mid-gulf locality in February.

Five medusae were believed by Alvariño to maintain indigenous populations in the gulf: *Rhopalonema velatum* was throughout noncoastal waters from the island channels, 29°N, southward; *Obelia* spp. were at a coastal station in the northern gulf near Punta Peñasco, 31°N; *Philiopsis diegensis* has a tropical range in the Pacific and occurred in mid-gulf; *Leuckartiara octona*, known also from the California Current, occurred in mid-gulf; *Atolla wyvillei*, a bathypelagic, widespread species in Pacific basins, occurred from the Ballenas Channel southward.

Species considered tropical migrants into the southern gulf, and appearing only in the February samples, were *Chiarella centripetalis, Aglaura hemistoma,* and *Solmundella bitentaculata. Colobonema sericeum* occurred at the mouth of the gulf only in April, but was also in deeper Vermilion Sea Expedition samples from the southern gulf.

## Siphonophorae (Coelenterata)

Siphonophores are conspicuous among gelatinous zooplankton of the gulf, particularly in the southern zone. There, diversity of plankton species is greatest, while quantity of "meaty" crustaceans is low.

Distributions of siphonophores in the Pacific are given in Alvariño (1971). Bigelow (1911) described and illustrated numerous species from the eastern Pacific, only one of which, *Porpita pacifica* Lesson, was from the gulf—in oceanic waters at the mouth. Other papers important in identifying siphonophores are those of Sears (1953) and Totten (1954) reporting on material from the Indian Ocean, and Totten and Bargmann (1965).

Occurrences of 18 species during two 1956 cruises in the gulf were reported by Alvariño (1969); 3 were regarded as having permanent populations there:

1. *Muggiaea atlantica* occurred in mid-gulf in February and throughout the gulf in April. This warm-temperate species occupies the subarctic-central transition zone of the North Pacific (40°-45°N) and the California Current southward to the mouth of the gulf (cf. the euphausiid *Nematoscelis difficilis*).

2. *Stephanomia bijuga* has the same range as *Muggiaea atlantica* in the California Current (47°-23°N), but was concentrated in northern and mid-gulf sectors; two records were obtained at the gulf's mouth (23°N).

3. *Stephanomia rubra* was scattered and sparse in the northern and southern gulf. This species occurs in the California Current, 39°-26°N, and widely in the tropics except for the eastern tropical Pacific.

Alvariño regarded three species as indicative of California Current influence: (1) *Lensia challengeri* penetrated to mid-gulf during both February and April, but appeared mainly along the deep-water axis of the gulf; (2) *Eudoxoides spiralis* and (3) *Agalma spiralis* were present in the southern gulf, only during February. These three species are warm-water cosmopolites, 40°N to 40°S in the Pacific. *Eudoxoides spiralis*, however, is conspicuously lacking in the oxygen-deficient part of the eastern tropical Pacific off Mexico and Central America.

Five species were considered tropical-equatorial, though all occur in the southern part of the California Current, and also show scattered records in central Pacific waters. Four of these were recorded at the mouth of the gulf, with a few individuals in mid-gulf: *Lensia campanella, Chelophyes contorta, Diphyopsis mitra,* and *Bassia bassensis. Ennogonum hyalinum* occurred in February, and only in mid-gulf.

Five additional siphonophores were recorded from water over deep basins of the gulf sampled during the Vermilion Sea Expedition: (1) *Bargmannia elongata* and (2) *Chuniphyes moserae* are deep (below ca. 250 m [Alvariño 1967]) inhabitants of mid- and low-latitudes, 45°N to 47°S. (3) *Sulculeoria angusta* is a warm-water cosmopolite, 40°N to 40°S. (4) *Rosacea plicata* is a true cosmopolite, arctic-to-antarctic, which evidently submerges to > 250 m in low latitudes. (5) *Erenna bedoti* is not known from elsewhere in the Pacific.

Observations from a diving saucer off Cabo San Lucas (Barham 1966) showed that siphonophores of the order Physophorae participate in vertical migrations with organisms of the sonic scattering layer. This layer rose near to the surface at the approach of night from a daytime depth of 300-400 m. The Physophorae are characterized by gas-filled flotation zoids

(pneumatophores) at the terminal end of the anterior region (nectosome). Sonic impulses generated by the ship produce an echo reflecting from the pneumatophore. Siphonophores of the genus *Stephanomia* ( = *Nanomia*), or related Physophorae, were believed by Barham to play this role in sound reflection. Genera of Physophorae recorded from the gulf include *Agalma*, *Bargmannia*, and *Erenna*, as well as *Stephanomia*.

Studies of feeding by various species of siphonophores, particularly in the Gulf of California (Purcell 1981a), showed a high order of prey selection among different suborders. Cystonectae, having large gastrozoids, fed primarily on fish larvae. Physonectae, having few large gastrozoids, fed on both large and small copepods and a variety of larger zooplankton. Calycophorae, having many small gastrozoids, fed on small zooplankton, notably copepods. Maximum prey size was correlated with gastrozoid length in all 14 species studied, and number of ingested prey was correlated with their abundance in surrounding waters. A study of feeding energetics in *Rosacea cymbiformis* by Purcell (1981b) showed caloric consumption in a 4-6-hr feeding period after sunrise to be 0.109-0.365 cal/gastrozoid, with daily intake projected to be 2.4-8.2 times that needed to balance metabolism. Large active copepods, crab zoea, pelagic molluscs, mysids, and juvenile shrimp were selected at frequencies above *in situ* abundances.

## The Gelatinous Plankton —Direct Observations

The fragile gelatinous zooplankton have been studied extensively by means of direct observation through use of scuba diving equipment. Hamner and colleagues (1975), particularly Madin (1974) and Alldredge (1976a, b), have attempted to identify adaptive strategies of these forms in several tropical water masses, including the Gulf of California. The gelatinous group includes Hydromedusae, Siphonophora, Scyphomedusae, Ctenophora, Heteropoda, Pteropoda, Thaliacea (salps), and Appendicularia. Many of these groups are poorly sampled by conventional plankton nets, not only because of their delicacy, but also because of swimming or, in the case of pteropods, avoidance-sinking reactions. Hamner et al. (1975) presented a general review of ecological problems being studied by the direct approach. The workers mentioned above emphasize examining the efficacy of filter-feeding mechanisms, including mucous structures, in collecting, concentrating, and transporting particulate organic matter by pteropods, salps, and appendicularians. These animals were found to use mucous sheets, nets, strands, and filters in conjunction with ciliated surfaces to collect a broad size range of organic material.

Complex spherical mucous "houses"—never retained by plankton nets—produced by species of appendicularians in the gulf were studied by Alldredge (1976b). Species varied with respect to frequency and orientation of feeding and pattern of swimming within the house. However, the largest species, *Megalocercus huxleyi*, was generally observed (95% of time) feeding with the tail and body in a horizontal position and the filtering screen anterior to the body. The other species most often fed with the tail downward and the trunk and feeding filter parallel to the surface. These species were *Stegosoma magnum*, *Oikopleura intermedia*, *O. cornutogastra*, *O. rufescens*, *O. longicauda*, and *O. fusiformis*.

Alldredge found that appendicularians could build new houses in 1½ to 5 minutes, but rarely abandoned houses in response to predation by sergeant major fish (*Abudefduf* sp.), medusae, chaetognaths, and ctenophores. Larvae of the euphausiid *Nyctiphanes simplex* and adults of the calanoid copepod *Scolecithrix danae* were observed to rest on the surface of houses or to dart over the plankton-filled filters.

Macroscopic organic aggregates consisting largely of discarded appendicularian houses reached densities of 44 to $1130/m^3$ in the gulf (Alldredge 1976a). Such aggregates were believed to affect the distribution of plankton by introducing spatial heterogeneity and physical structure into an environment often thought to be unstructured.

Alldredge (1981) measured grazing rates of the small appendicularian *Oikopleura dioica* and the larger *Stegasoma magnum* in the gulf by estimating their effect on the concentration of carbon particles in the 2-12 μm size range. The two species filtered seawater equivalent in carbon content to 5.2%-10.7% of natural rate of increase of indigestible-size carbon particles, with the total grazing community capable of depleting the carbon at a rate considerably greater than its replacement. Direct field evidence showed that gulf appendicularians exert significant grazing pressure on natural food assemblages.

Madin (1974) observed feeding behavior of salps (Tunicata:Thaliacea) in the gulf. Data were obtained near Isla Carmen (also from a locality in the Atlantic, near the Bahamas). Ninety-one percent of observed salps were feeding with a continuously renewed mucous net. Food particles ranged from < 1 μm to ca. 1 mm. Digestion was noted as incomplete; because fecal pellets contained much undigested material, they were believed to be a means for transporting significant amounts of carbon out of surface waters.

Madin observed six species (indication was not given as to which were in the Gulf of California and which in the Atlantic study area): *Cyclosalpa affinis*,
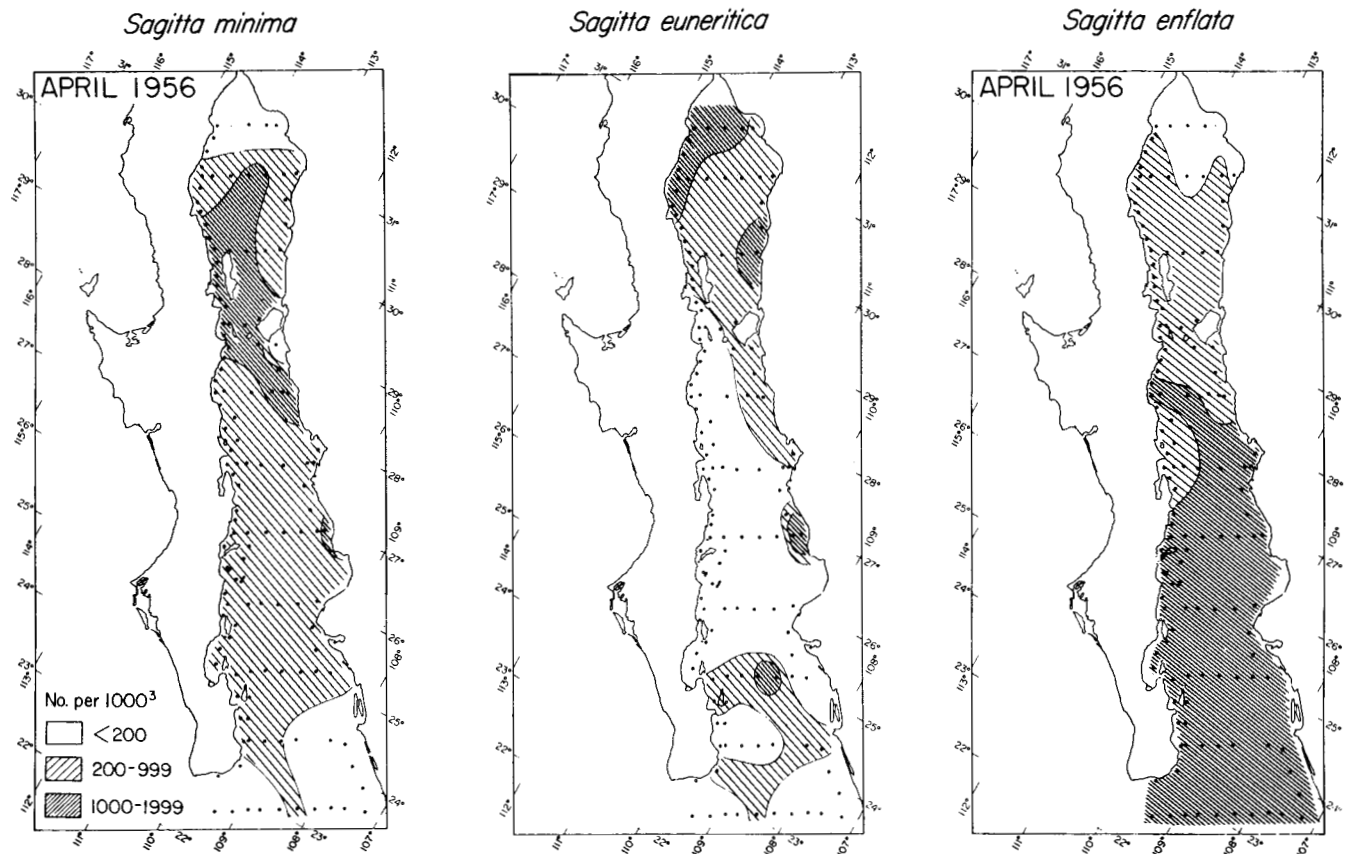
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Figure 8. The three most abundant species of Chaetognatha sampled in the Gulf of California by the April 1956 CalCOFI cruise (after Alvariño 1969).

*C. pinnata*, *Pegea confoederata*, *Salpa maxima*, *Thalia democratica*, and *Weelia cylindrica*. All have been found in the southern part of the California Current (Berner 1967). Salps from plankton samples from the gulf have not been studied; only *Thalia democratica* has been reported (see Plankton Biomass). Associations of Amphipoda Hyperiidea with Salpidae (Harbison and Madin 1977) are now understood to be a regular aspect of the ecology of both groups of animals (see Amphipoda).

Heteropod and pteropod molluscs have not been examined in gulf plankton. Their distributions in the California Current are described in McGowan (1967).

### Chaetognatha

Alvariño (1969) reported 17 species of Chaetognatha in the gulf, compared to 25 in adjacent waters to the west. The species' Pacific biogeography is shown in Bieri (1959) and Alvariño (1964a), and distributions in the California region are in Alvariño (1964a, 1965, 1967). Aspects of bathymetric distribution are in Alvariño (1964b, 1967), and the species are described in Alvariño (1963).

Four species were widely distributed in superficial (0-140-m) layers sampled during February and April

1956, according to Alvariño.

1. The large species *Sagitta enflata* was abundant ($> 2/m^3$) during February, except along the western margin of the gulf, and, during April, in nearly all of the gulf except in island channels (ca. 29°N) and northward (Figure 8). *S. enflata* is a warm-water cosmopolite, which Bieri found to have highest densities in the productive equatorial belt and near coasts of Baja California and Central America.

2. *Sagitta minima*, in February, was abundant in mid-gulf and sparse in the southern gulf. In April, high numbers were on the western side, with maxima in the island channels (Figure 8). This species is strongly associated with northern and eastern boundary regions of the North Pacific Central Water Mass, and Bieri found it lacking in eastern tropical Pacific waters near Central America.

3. *Sagitta euneritica* occurs in marginal waters of the gulf, but its distribution can extend over the basins. Alvariño found highest densities over the northern shelf in April (Figure 8) and the shelf in February. This species in endemic to waters of California, Baja California, and the gulf.

4. *Sagitta decipiens* is a small species considered mesopelagic in most oceanic regions, with a depth dis-
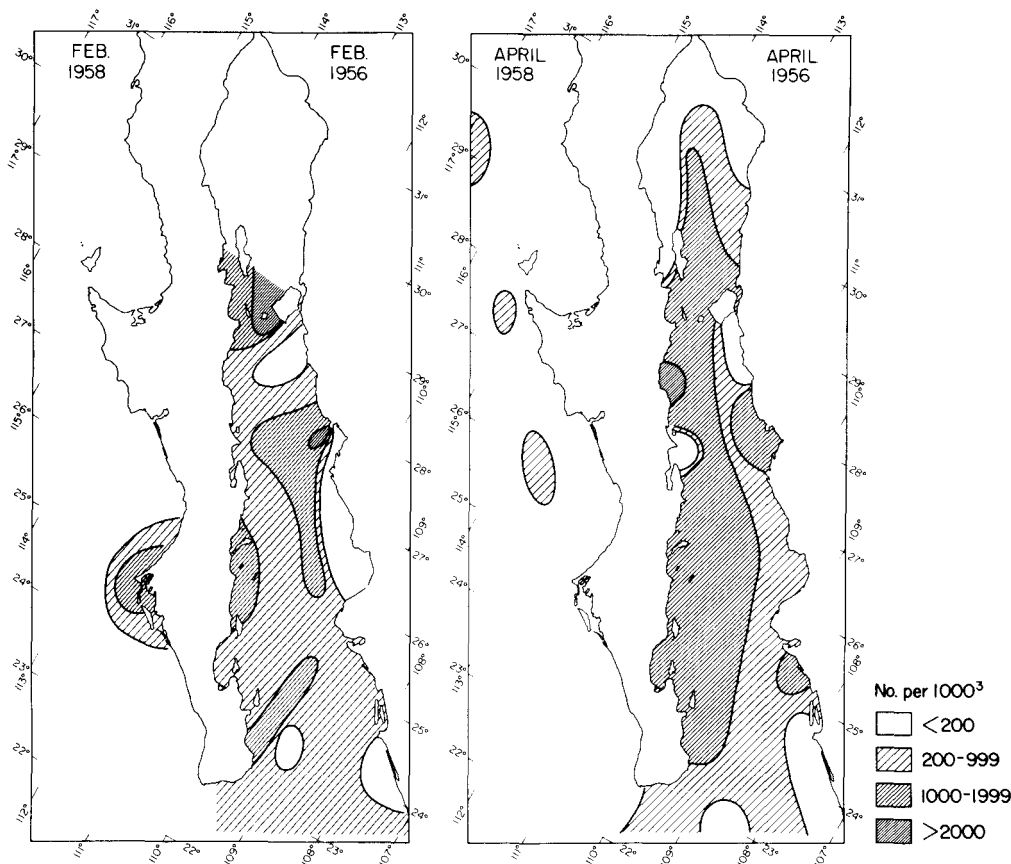
## Sagitta decipiens



Figure 9. Distribution of the chaetognath *Sagitta decipiens* in the gulf during February and April 1956 (after Alvariño, 1969) and to the west of Baja California during February and April 1958 (after Alvariño 1965).

tribution centered near 200 m. During February and April it occurred throughout the gulf in the 0-140-m layer sampled, though at uneven density (Figure 9). It was all but absent over the northern and southwestern shelves. *S. decipiens* occurs widely in the warm-water belt of the Pacific (40°N to 40°S). The species has proven to be patchy and sparse in the upper layer sampled by CalCOFI in the eastern North Pacific — hence the high frequency noted in the upper layers of the gulf was of particular interest to Alvariño, who considered that this distribution could result from the low concentration of oxygen < 2 ml/l) below 200 m, compressing this species to lesser depths.

While *S. decipiens* appears, in the gulf, to "emerge" from its more typical mid-depth habitat, other mesopelagic species — *S. macrocephala* and *S. maxima* — do not, judging by their appearance only in relatively deep samples obtained during the 1969 Vermilion Sea Expedition. The three bathypelagic *Eukrohnia* species — *E. bathypelagica*, *E. fowleri* and *E. hamata* — also were present in collections from deep basins, from mid-gulf southward.

Of several chaetognath species appearing only in the southern half of the gulf, *S. bierii* ranged farthest

north — to mid-gulf, 28°N (Figure 10). This species occurs widely in the eastern tropical Pacific but is commonest at cool northern and southern margins of the region, including much of the California Current (cf. *Euphausia eximia*, Figure 16). Alvariño believed this species' stronger presence in the gulf during February 1956, as compared with April, to indicate relatively strong influence of California Current waters.

*Sagitta hexaptera* was sparse in the 0-140-m layer sampled in the gulf. *S. pacifica* was present only in the southernmost part. These species are warm-water cosmopolites with ranges of 40°N to 40°S in the Pacific, much like *S. enflata*. However, Alvariño notes that *S. hexaptera* lives beneath 100 m, whereas *S. enflata* is above that depth. *S. hexaptera* and *S. pacifica* occur at low density throughout the southern part of the California Current and off the western coast of Mexico, with *S. pacifica* the more offshore (Central Pacific fauna) of the two. On the other hand, *S. enflata* was at high density both in the gulf and in oceanic waters off Mexico.

Other *Sagitta* scarcely penetrating the gulf but present at its mouth during both February and April
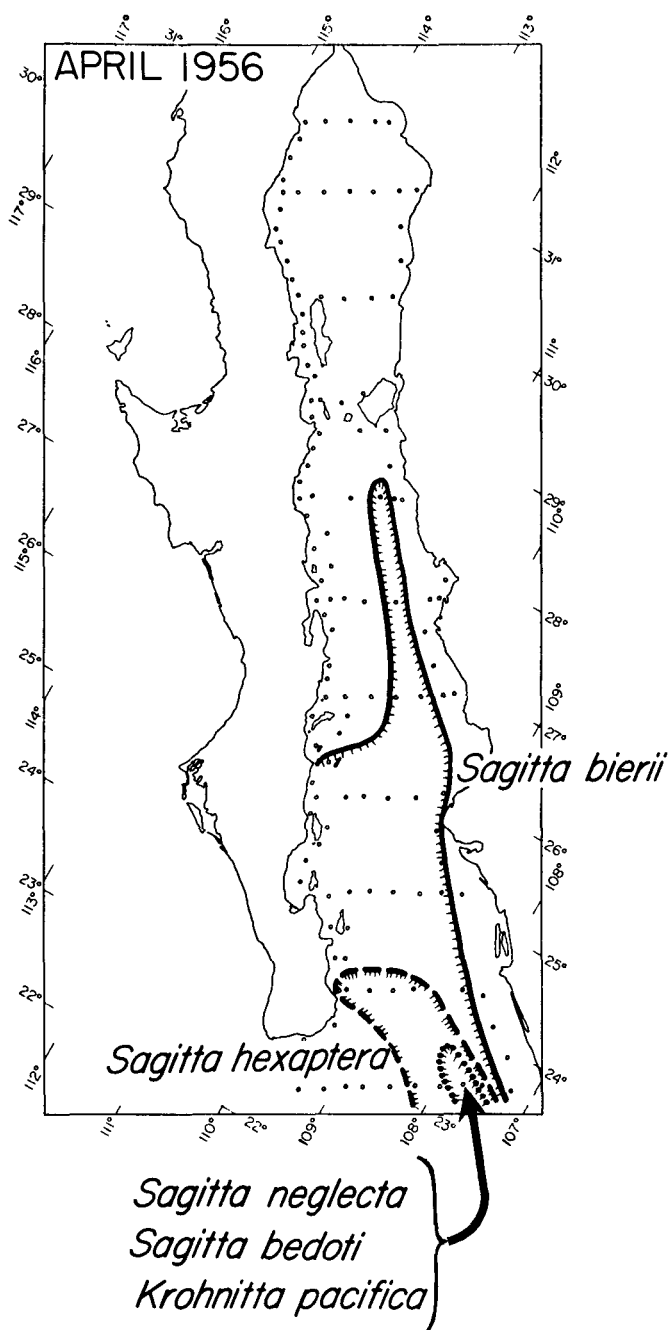
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Figure 10. Distribution of the eastern Pacific chaetognath *Sagitta bierii* in the Gulf of California during April 1956, and of two eastern tropical Pacific species, *S. neglecta* and *S. bedoti*, and of tropical *Krohnitta pacifica* (after Alvariño 1969).

were (1) species with particular affinity for the eastern tropical Pacific, e.g., *Sagitta bedoti* and *S. neglecta* (Figure 10), and (2) the broadly equatorial *S. regularia*.

Two species of *Krohnitta*—*K. pacifica* (Figure 10) and *K. subtilis*—are, respectively, tropical and 40°N-40°S in range. Both are absent from the eastern tropical Pacific off southern Mexico and Central America. In

the gulf they occurred only at the mouth (23°-24°N). These, and the *Sagitta* species present only near the mouth, tended to penetrate farther into the gulf during the cooler regime of February as compared with April.

Notably absent from the gulf were (1) *Sagitta scrippsae*, typical of the cooler part of the California Current; (2) *Sagitta bipunctata* and *S. zetesios*, particularly adapted to oligotrophic Pacific central waters, as opposed to the equatorial zone and the California Current, and (3) species of Bieri's "equatorial west-central" group, e.g., *Pterosagitta draco*, found in the southern and offshore waters of the California Current, and *Sagitta ferox* and *S. robusta,* appearing not to range north of the Tropic of Cancer (23°27'N).

Medina's (1979) data were from two cruises in the southern half of the gulf (28°N, southward) in 1977. Chaetognaths represented up to 18% of the total number of organisms. *Sagitta enflata* was again the dominant species in the gulf, both in relative abundance and in frequency of collection. On occasion, it formed 100% of chaetognaths. *S. minima* followed *S. enflata* in abundance. The presence of *S. euneritica* and *Krohnitta pacifica* along the east coast of the gulf was interpreted, following Alvariño, as indicating penetration of waters from outside the gulf. Medina emphasized problems related to the existing confusion in the taxonomy regarding identification of *S. neglecta, S. regularis,* and *S. bedoti. S. bedoti* was found well within the gulf in 1977, whereas Alvariño had found it only at the mouth in 1956.

## CRUSTACEA
### Copepoda

Published literature on planktonic calanoid copepods does not offer a general taxonomic guide to the species inhabiting the gulf; neither does it provide a species list representative for the region, or information about geographical, seasonal, and vertical distribution of numerically dominant species. Unpublished studies on the gulf's Calanoida, discussed below, indicate that most of the species are also found in the equatorial sector of the Pacific Ocean. Special regional qualities are provided by the small number of species endemic to the eastern tropical Pacific, the few species that are endemic to coastal waters within the gulf, and a number of species typically found in the eastern Pacific off California and Baja California.

Taxonomically useful general introductions to the gulf's offshore species may be found in reports of Grice (1961), Mori (1964), and Park (1968), and generic keys published by Giesbrecht (1892), Rose (1933), Brodskii (1967), Bradford (1972), and Dawson and Knatz (1980). However, in view of many more recent advances in copepod systematics, these refer-

ences should not be used for critical identifications without referring to the most current literature on the taxon under consideration.

Manrique (1977) has already noted the scarcity of published knowledge dealing with the gulf's planktonic copepod fauna. Taxonomic and distributional studies are sparse, and scattered among a handful of papers dealing largely with other regions. Giesbrecht (1895) reported on nine copepod species found at two stations within the gulf sampled by the U.S. Fisheries steamer *Albatross*. Wilson (1950) confirmed three of Giesbrecht's identifications and recorded 32 additional species from four *Albatross* stations. The credibility of Wilson's *Albatross* records is diminished by a frequent lack of agreement between the species listed in his 1950 report and the identity of the voucher specimens deposited by Wilson in the U.S. National Museum (e.g., Fleminger 1965).

Biogeographic appreciation of the copepod fauna in the gulf was brought into perspective only recently. In atlases depicting the distribution of planktonic species in the eastern North Pacific adjacent to California and Baja California, Fleminger (1964a, 1967a) recorded many species collected at stations near the mouth of the gulf. Taxonomic reports characterize a handful of coastal water species that have been collected within the gulf (Johnson 1964; Fleminger 1964b, 1967b; Fleminger and Hulsemann 1973; Manrique 1977). Turcott-Dolores (1972) reported on copepods in the Laguna de Yavaros (ca. 27°N) on the Sonoran coast, while also describing monthly variations in temperature, salinity, and phytoplankton biomass. At the Boca de Yavaros, where waters were most gulflike, the tropical *Acartia lilljeborgi* predominated, followed by *Acartia* sp. (possibly *A. tonsa* or a species close to *A. californiensis*) and *Pseudodiaptomus* sp. (probably *P. wrighti*). Generic studies that report on gulf occurrences of offshore species include one on *Clausocalanus* by Frost and Fleminger (1968), one on *Pontellina* by Fleminger and Hulsemann (1974), and one on *Eucalanus* by Fleminger (1973). Two recent studies provide qualitative and quantitative data on horizontal and vertical distribution of a number of planktonic copepods in the eastern equatorial Pacific south of the gulf's mouth (Arcos and Fleminger 1986; Chen 1986).

Fleminger (1975) considered geographical and morphological relationships among coastal and offshore species of *Labidocera*. Species of this genus provide evidence for a multitude of temperate to tropical planktonic habitats within the gulf (Figure 11). The three species of the "*Labidocera jollae* group" tend to be associated with oligotrophic, "blue-water" environments, and generally occur at low densities. *L. jollae* is a California Current species inhabiting coastal waters

roughly between Cape Mendocino (40°N) and Bahía Magdalena (25°N). Inside the gulf, *L. jollae* is replaced by *L. kolpos*, which extends from the northernmost gulf to 25°N along the eastern coast during winter. The tropical species *L. diandra* appears to be sporadic in the gulf, apparently with considerable seasonal variation. It may reach to mid-gulf on the western side and to about 25°N on the eastern side, at the southern limit of *L. kolpos*. The highest frequency of captures of *L. diandra* occurs between Cabo Corrientes southward to the Gulf of Tehuantepec.

Species of the "*Labidocera trispinosa* group" occur at higher densities. Although their ranges overlap broadly with those of the "*L. jollae* group," species of the two groups do not co-occur; that is, they are not often found in the same net samples. The "*L. trispinosa* group" has relatively "green-water" or eutrophic affinities. *L. trispinosa* is the California Current species. *L. johnsoni* is present in the northern gulf and extends southward along the eastern coast to Mazatlán (22°N) in winter. Tropical *L. lubbocki* has been recorded only along the eastern coast of the gulf—to 26°N; its apparent absence from the southwestern gulf indicates the general lack of green-water habitats there.

Three other more offshore *Labidocera* species, not forming a sibling group, often mix with the coastal water species of the *jollae* and the *trispinosa* groups. Related only at the generic level, the three have been combined in Figure 11 because of their offshore habitat preferences. *L. acuta* is common in the southern California Current and throughout the Gulf of California. Its broadly neritic tendencies are seen in its frequent occurrences in mid-gulf. The broadly tropical *L. acutifrons* is found in the southernmost extension of the California Current and in the gulf along its western side, as far north as Isla San Marcos, 27.5°N. The equatorial species *L. detruncata* also appears in the southernmost California Current and in the southern gulf, from 26°N southward.

A new spinocalanid copepod, *Isaacsicalanus paucicetus*, was discovered just west of the mouth of the gulf on the East Pacific Rise (Fleminger 1983). The new genus and species was collected by the submersible *Alvin* near the seafloor at about 2600-m depth, adjacent to a hydrothermal vent that raises bottom-water temperature from 5° to 15°C. This copepod appears to be of the unique invertebrate fauna associated with such vents.

We anticipate that many of the species inhabiting the California Current (Fleminger 1964a, 1967a) will also be found in the Gulf of California. In fact, unpublished notes on gulf calanoid copepods accumulated by Fleminger while studying the distribution of several copepod genera inhabiting the gulf confirm this. These rec-
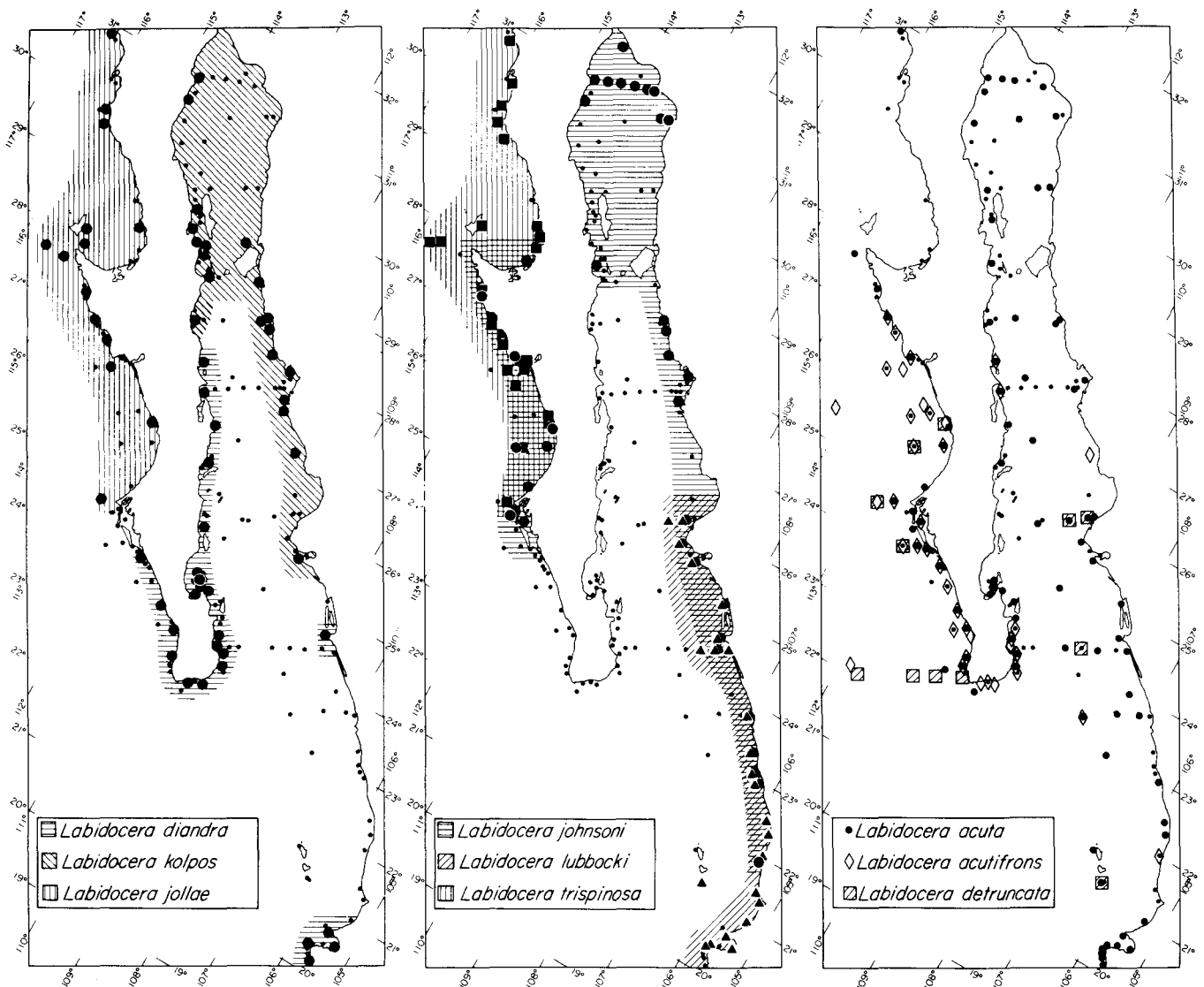
Figure 11. *Labidocera* copepods of the Gulf of California. *Left*, the "*Labidocera jollae* group," illustrating faunistic breaks on both sides of Baja California, and a break on the eastern side of the gulf. *Middle*, overlapping ranges of three species of the "*Labidocera trispinosa* group," an inshore "green-water" group whose members do not usually co-occur in samples with species of the "*L. jollae* group." *Right*, three *Labidocera* species, not closely related, which mix with both of the above groups. All have more offshore habitat preferences: two are oceanic, *L. acutifrons* being broadly tropical, whereas *L. detruncata* is equatorial; *L. acuta* is broadly neritic and equatorial.

ords, added to the published records reviewed above, appear to provide a largely complete list of the calanoid copepod species to be found in the gulf's uppermost 100 m (Table 1). A tentative biogeographical-ecological census of these species is presented in Table 2.

## Ostracoda

Although ostracods are a conspicuous group in the gulf's plankton, there are no reports dealing with them in these waters. Müller (1895) reported only three species in material collected by the *Albatross* inside the gulf. Most notable of these were the type specimens of the large deep-sea species *Gigantocypris pellucida* from the Guaymas and Carmen basins in mid-gulf. Müller also reported two species of Halocypridae from

the gulf: *Chonchoecia armata* Claus and *C. agassizii* Müller.

A few species have been recorded from the California Current to the west of Baja California: *Chonchoecia giesbrechti*, *C. daphanoides*, *C. strilola*, and *Halocypris brevirostris* (Haury 1976).

## Amphipoda

The gulf's amphipod fauna is diverse. Siegel-Causey (1982) recorded 119 species of Hyperiidea (55 considered rare), belonging to 16 families. Distributions were related to water types, based largely upon 1956 and 1957 cruises. In the world oceans, most amphipod species are broadly distributed; although many are warm-water cosmopolites or have extensive

TABLE 1
**Planktonic Copepods That Have Been Found in the Gulf of California**

The following abbreviations signify favored habitat, biogeographic affinities, and relative abundance where available data clearly indicate a trend.

Habitat: e = estuarine waters; c = coastal waters; m = mesopelagic depths of oceanic waters; n = broadly neritic waters; o = oceanic mixed layer.

Biogeographic affinities: temp. = temperate; trop. = broadly subtropical to tropical; equat. = equatorial; end. = endemic to the Gulf of California and contiguous waters to the north or south.

Relative abundance: a = abundant, usually occurring at or near the highest rank in order of numerical dominance; w = abundance or widespread occurrence appears in the cooler months; s = abundance or widespread occurrence appears in the warmer months.

**Calanoida**

*Acartia danae* — o, trop.
*A. lilljeborgii* — c, equat., a-s
*A. negligens* — o, trop.
*A. tonsa, s.l.* — c, temp.-trop., a
*A. sp.** — c
*One or more undescribed forms that appear to be related to *A. californiensis*.

*Acrocalanus andersoni* — n, equat.
*A. gracilis* — n, equat.
*A. inermis, s.l.* — o, equat.
*A. longicornis* — n, trop.
*A. monachus* — n, equat.
*Aetideus armatus, s.l.* — n, trop.
*Augaptilus longicaudatus* — m
*Calanus pacificus, s.l.** — n, temp., a-w
*Appears in Manrique's (1977) list as *C. helgolandicus*, a species *sensu stricto* found only in the N. Atlantic, Mediterranean, and Black Sea.

*C. tenuicornis* — o, temp.
*Calocalanus pavo* — o, trop.
*C. pavoninus, s.l.* — o, trop.
*C. plumulosus, s.l.*
*C. styliremis, s.l.* — o, trop.
*Candacia bipinnata* — n, temp.
*C. catula* — n, equat.
*C. curta* — n, trop.
*C. pachydactyla* — o, equat.
*C. pofi* — n, equat.
*C. truncata* — n, equat.
*Canthocalanus pauper* — c, equat., a
*Centropages furcatus* — n, trop., a
*C. gracilis* — o, trop.
*C. kroyeri**
*This species is well known from neritic waters of the eastern temperate N. Atlantic and Mediterranean. In view of the absence of *kroyeri* from the other studies on gulf copepods and in fact from elsewhere in the Pacific, this record reported by Wilson (1950) is considered unreliable.

*Clausocalanus farrani* — o, trop.
*C. furcatus* — o, trop., a
*C. jobei* — o, temp.
*C. mastigophorus* — o, trop.
*C. parapergens* — o, trop.
*Ctenocalanus vanus, s.l.* — n, temp.
*Euaetideus acutus* — n, trop.
*E. bradyi* — n, trop.

*Eucalanus attenuatus, s.s.* — o, equat.
*E. crassus* — n, trop.
*E. inermis** — m-o, equat., end.
*Includes Wilson's (1950) *E. muticus*, regarded by A.F. to be a junior synonym of *E. inermis*.

*E. pileatus* — c, trop., a
*E. sewelli* — o, trop.
*E. subcrassus* — n, equat.
*E. subtenuis* — o, equat., a
*Euaugaptilus hecticus* — m
*Euchaeta acuta, s.l.* — o, trop.
*E. longicornis* — m, equat.
*E. media* — o, trop.
*E. rimana* — o, trop.
*E. spinosa* — m
*E. wolfendini* — c, equat.
*Euchirella sp.** — m
*An undescribed form inhabiting the eastern tropical Pacific.

*E. venusta* — m
*Haloptilus acutifrons* — m
*H. chierchiae* — m
*H. longicornis, s.l.* — o, trop.
*H. ornatus* — m
*Heterorhabdus papilliger* — o, trop.
*Heterostylites longicornis* — m
*Labidocera acuta* — n, equat., a
*L. acutifrons* — o, trop.
*L. detruncata* — o, equat.
*L. diandra* — c, equat., end.
*L. johnsoni* — c, temp., end.
*L. kolpos* — c, temp., end., w
*L. lubbocki* — c, equat., end.
*Lucicutia clausi* — m
*L. flavicornis* — o, trop.
*L. gaussae* — o
*L. gemina* — o
*L. grandis* — m
*L. ovalis* — o
*Mecynocera clausi* — o, trop.
*Metridia brevicauda* — m
*M. curticauda* — m
*Microcalanus sp.* — m
*Nannocalanus minor* — o, trop.
*Neocalanus gracilis* — o, trop.
*Paracalanus crassirostris, s.l.* — e & c
*P. denudatus* — o, trop.
*P. nanus* — n

TABLE 1 (continued)

| | | | |
|---|---|---|---|
| P. parvus, s.l. | c, trop. & temp., a | Temoropia mayumbaensis, s.l. | m |
| Pareuchaeta californica | m | Undinula darwinii | o, equat. |
| P. grandiremis | m | U. vulgaris | n, trop., a |
| Phaenna spinifera | m | | |
| Pleuromamma abdominalis* | | **Cyclopoida** | |

*Wilson's (1950) Gulf of California records of P. robusta are probably based on misidentification of abdominalis.

| | | | |
|---|---|---|---|
| | | Copilia mirabilis | |
| | | C. quadrata | |
| | | Corycaeus anglicus | |
| P. gracilis | o, trop. | C. brehmi | |
| P. indica? | | C. clausi | |
| Pontella agassizi* | o, equat., end | C. dubius | |

*Wilson's (1950) Gulf of California record of P. atlantica is probably based on misidentification of agassizi.

| | | | |
|---|---|---|---|
| | | C. flaccus | |
| | | C. latus | |
| | | C. lautus | |
| Pontellina plumata, s.l. | o | C. obtusus | |
| P. sobrina | o, equat., end. | C. ovalis | |
| Pontellopsis occidentalis | n, temp., end. | C. speciosus | |
| P. lubbocki | n, equat., end. | Farranula rostrata | |
| P. regalis | o, trop. | Oithona plumifera | |
| Pseudodiaptomus euryhalinus | e & c, end. | O. nana | |
| P. wrighti | e & c, end. | Oncaea media | |
| Rhincalanus nasutus | n, temp., a-w | O. minuta | |
| Scaphocalanus curtus | o, trop. | Sapphirina gemma | |
| S. echinatus | o, trop. | S. nigromaculata | |
| Scolecithricella abyssalis | o | S. opalina | |
| S. ctenopus | o | | |
| S. nicobarica | o | **Harpacticoida** | |
| S. tenuiserrata | o, trop. | Euterpina acutifrons | |
| Scolecithrix bradyi | o, trop. | Macrosetella gracilis | |
| S. danae | o, trop., a | Microsetella rosea | |
| Temora discaudata* | n, trop., a | | |

*Wilson's (1950) records of T. stylifera from the Gulf of California are in error (Fleminger and Hulsemann 1973) and probably represent the misidentification of T. discaudata.

The above information has been collated from papers reviewed in the text and from unpublished notes of A.F. Unpublished data on the gulf's copepod fauna were obtained primarily from examination of 1-m CalCOFI net and ½-m net macroplankton samples collected by oblique and horizontal tows at depths shallower than 150 m and from stations shown in Figure 11.

vertical ranges, highest densities of given species tend to be in either a tropical, subtropical, or warm-temperate zone. Seasonal variation in the gulf was such that in February (1957), 75% of hyperiid species occurring at the mouth, and 25% at 26°N were considered to be tropically derived; in August, 75% at 26°N and 50% at the island channels (29°N) were tropical. North of the islands diversity was low, but abundances were high. Of the gulf's eight "abundant" species, six occurred the full length of the gulf.

Species of the cooler part of the California Current (Bowman 1953)—e.g., Dairella californica, Paraphronima crassipes, Vibilia wolterecki, and Hyperoche medusarum—were rare in the gulf. However, certain abundant and widely distributed species of the California Current—e.g., Vibilia armata, and Primno brevidens—were also abundant throughout the gulf. The most abundant, Lestrigonus bengalensis, was observed in the California Current (Bowman 1953) to

show a bias toward neritic waters, like the gulf's most abundant euphausiid, Nyctiphanes simplex (below).

There were three patterns of distribution, as follows:

1. Present at mouth of gulf in winter-spring, advancing northward in summer: classified as uncommon (unc), common (com), abundant (abd); temperate (temp), subtropical (s-t), tropical (t); epipelagic (epil), mesopelagic-epipelagic (meso-epi)

Hyperiidae

| | |
|---|---|
| Hyperietta stebbingi | unc, temp, epi |
| Lestrigonus schizogeneios | com, temp, epi |
| Phronimopis spinifera | abd, temp, epi |
| Themistella fusca | com, temp, meso-epi |

Phronimidae

| | |
|---|---|
| Phronima stebbingi | unc, temp, epi |
| Phronima bucephala | com, s-t, epi |
| Phronima atlantica | com, s-t, meso-epi |
| Phronimella elongata | unc, cos, epi |

Lycaeopsidae
*Lycaeopsis neglecta*          com, temp, epi
*Lycaeopsis thimistoides*      unc, temp, epi
*Lycaeopsis zamboangae*        com, temp, epi

Phrosinidae
*Phrosina semilunata*          unc, cosmo, meso-epi

Pronoidae
*Eupronoe maculata*            com, cosmo, epi
*Paralycaea hoylei*            unc, s-t, epi

Lycaeidae
*Brachyscelus globiceps*       com, s-t, epi
*Brachyscelus crusculum*       unc, s-t, surf

Oxycephalidae
*Oxycephalus clausi*           com, temp, meso-epi
*Oxycephalus piscator*         unc, s-t, epi
*Rhabdosoma whitei*            com, s-t, epi

Platyscelidae
*Platyscelus serratulus*       com, s-t, epi
*Amphithyrus bispinosus*       com, temp, meso-epi
*Amphithyrus sculpturatus*     unc, temp, epi

2. Found near mouth of gulf only, all seasons

Hyperiidae
*Hyperioides longipes*         com, s-t, epi
*Hyperioides sibagnis*         unc, t, epi

Phronimidae
*Phronima curviceps*           unc, t, epi

Lycaeopsidae
*Lycaeopsis pauli*             unc, s-t, epi

3. Scattered along length of gulf, all seasons

Scinidae
*Scina borealis*               com, cosmo, meso-epi

Vibilidae
*Vibilia armata*               abd, temp, epi

Hyperiidae
*Hyperiietta vosseleri*        com, s-t, epi
*Lestrigonus shoemakeri*       abd, s-t, epi

Phrosinidae
*Primno brevidens*             abd,

Phronoidae
*Eupronoe armata*              com, s-t, epi

Lycaeidae
*Lycaea bovallioides*          com, s-t, epi
*Lycaea serrata*               unc, s-t, epi
*Thamneus platyrrhynchus*      com, s-t, epi

Oxycephalidae
*Simorhynchotus antennaris*    abd, cosmo, meso-epi

Platyscelidae
*Tetrathyrus pulchellus*       abd, temp, meso-epi

Parascelidae
*Thyropus edwardsi*            abd, s-t, epi

Siegel-Causey (1982) discussed the well-known association of hyperiids with gelatinous zooplankton —salps, medusae, siphonophores. The importance of a gelatinous substrate was recognized, pointing to the probability of facultative associations rather than obligate, host-specific parasitism. Consistent co-occurrences (e.g., *Vibilia* spp. and salps), were nevertheless evident.

## Mysidacea

In our examinations of plankton samples from the gulf, it has been evident that the Mysidacean fauna is rich. However, no significant work has yet been done on it. Tattersall's (1951) extensive review of the worldwide distribution of mysids, in which there are many useful keys, descriptions, and illustrations, cites species from both Mexican coasts, but not from the gulf.

TABLE 2
**Biogeographical and Habitat Qualities of Gulf Region Calanoid Copepod Fauna**

| Biogeographical types | No. of species | % of total |
|---|---|---|
| Temperate | | |
| Estuarine-coastal | 4 | 5 |
| Neritic | 5 | 6 |
| Oceanic | 2 | 2 |
| Subtotal | 11 | 13 |
| Tropical-subtropical | | |
| Estuarine-coastal | 2 | 2 |
| Neritic | 8 | 10 |
| Oceanic | 30 | 36 |
| Subtotal | 40 | 48 |
| Equatorial | | |
| Estuarine-coastal | 7 | 8 |
| Neritic | 10 | 12 |
| Oceanic | 9 | 11 |
| Subtotal | 26 | 31 |
| Not placed | 7 | 8 |
| Total | 84 | 100 |
| *Habitat Groups* (biogeographical types combined) | | |
| Estuarine-coastal | 13 | 15.5 |
| Neritic | 23 | 27.5 |
| Oceanic | 48 | 57 |
| Total | 84 | 100 |
| *Endemics* | 11 | 13 |
| *Nonendemics* | 73 | 77 |
| Total | 84 | 100 |

Hansen (1912) recorded *Euchaetomera plebeja* from material collected in 1904-05 by the *Albatross* off Cabo San Lucas. Steinbeck and Ricketts (1941) listed *Archeomysis* sp. (near to *A. maculata*) and *Mysidopsis* sp. at Punta Marcial. Unidentified mysids were among the nearshore "demersal" zooplankton that migrated from a benthic daytime habitat into the water column at night, observed near Isla Danzante, 26°N (Alldredge and King 1980).

The mesopelagic (below ca. 300 m) species are better known. Of the Eucopiidae, *Eucopia australis* was found by Faxon (1893, 1895) in the southern gulf in material from the 1891 cruise of the *Albatross*. Faxon also listed *Gnathophausia willemoesii* from deep water near Islas Tres Marias. Clarke (1962) referred *G. willemoesii* to *G. zoea* in his extensive study of the genus *Gnathophausia*. He recorded two species from the gulf, from trawl collections made during the Vermilion Sea Expedition: *G. zoea*, again near the mouth of the gulf (20°-23°N) and *G. gigas* from the Faralón Basin (25.5°N). Neither the wide-ranging *G. ingens*, which has not been found in the eastern tropical Pacific where oxygen is deficient within the mid-depth habitat of this species, nor the warm-water cosmopolite *G. gracilis* were found in the gulf.

Pequegnat (1965) compiled the world distributions of four species of *Gnathophausia* and gave a key to eight species of the genus. However, there were no records in the gulf.

### Euphausiacea

Euphausiids are prominent in oceanic and offshore-neritic waters of the gulf, but most species avoid the closest coastal zone. First records from the gulf were in Ortmann (1894) from collections obtained by the *Albatross* off Guaymas and about 50 miles farther south. The four species listed were incorrectly identified; they were among the eastern tropical Pacific species later described by Hansen (1911). Hansen (1915) reexamined Ortmann's material and recorded *Nyctiphanes simplex, Euphausia distinguenda, E. eximia*, and *Nematoscelis difficilis* from the gulf. (Ortmann had referred these, respectively, to *Nyctiphanes australis, Euphausia mucronata, E. pellucida*, and *Nematoscelis microps*.) Hansen also recorded *Nematoscelis difficilis* off Isla Santa Catalina (26°N) and "enormous numbers" of *Nyctiphanes simplex* from Bahía San Luis Gonzaga (30°N) in March 1889. Steinbeck and Ricketts (1941) observed water "soupy" with *N. simplex* off Punta San Marcial (25.5°N).

Hansen's 1912 report on euphausiids from the 1904-05 cruises of the *Albatross* included records of four species at the mouth of the gulf during October 1904: *Euphausia lamelligera, E. tenera, E. diomedeae*, and *E. distinguenda* off Cabo Corrientes (20°-21°N) and *E. distinguenda* again, near Cabo San Lucas (22° 45'N). Most of the species inhabiting the eastern tropical Pacific were described and illustrated in this report, including 10 of the 13 now known from the gulf. Further descriptions of euphausiids of this region are in Hansen (1910), Boden et al. (1955), and Brinton (1975). Larval stages of species reported from the gulf have been described: *Nyctiphanes simplex* (Hansen 1910; Boden 1951); *Euphausia eximia* (Knight 1980); *E. gibboides* (Knight 1975); *E. distinguenda* (Hansen 1910); *E. tenera, E. diomedeae, Stylocheiron* spp. (Brinton 1975); *Nematoscelis difficilis*, and *N. gracilis* (Gopalakrishnan 1973).

Brinton (1962) described subspecific forms of *Stylocheiron affine* and *S. longicorne* and showed distributions of euphausiids in the southern part of the gulf during October 1952 (shown in greater detail in Brinton and Townsend 1980). These distributions are of two kinds: (1) species with a population inhabiting the gulf but absent from the southernmost end and thereby appearing to be disjunct from the conspecific population that is widespread in the warm-temperate segment of the California Current (*Nyctiphanes simplex, Nematoscelis difficilis*, and *Euphausia eximia*); and (2) tropical species that were present in the southern gulf (*Nematoscelis gracilis, Euphausia distinguenda, E. lamelligera*, and *E. tenera*).

The RV *Te Vega* subsequently obtained a series of 55 Tucker trawl collections along the deep-water axis of the gulf, from the mouth to north of Isla Angel de la Guarda (30°N) during September-November 1967 as part of an ecological reconnaissance of deep scattering layers (Dunlap 1968). For this material, Vega-R. (1968) worked out the quantitative relationships of the major taxa. The euphausiids, analyzed by Mundhenke (1969), included most of the species previously recorded from the gulf. Of significance were (1) documentation of occurrences of *Nematoscelis difficilis* throughout the gulf, (2) an apparent lack of *Nyctiphanes simplex* south of mid-gulf (27°N), and (3) northward penetration to the Canal de las Ballenas, (29°N) by *Euphausia distinguenda, E. eximia*, and nearly that far by *Nematobrachion flexipes*. Ranges of these species were thus extended well to the north of *Albatross* records. Notably absent from this report were *Euphausia lamelligera* and the genus *Stylocheiron*. However, *Euphausia gibboides*, well known as an offshore species in the California Current, was recorded in substantial numbers northward to the Guaymas Basin; these records need confirmation. Subsequently, *E. gibboides* has not been found in the gulf, though Brinton (1979) reported an isolated instance at the middle of the mouth at 21°N in June 1974,

together with another disjunct southerly occurrence—of *Stylocheiron longicorne* in a patch of low-salinity water from the California Current, evidently from the northwest.

Brinton and Townsend (1980) presented a picture of seasonal development in populations of euphausiids throughout the gulf, based on bimonthly 1957 cruises. Sampling was to a depth of 140m—sufficient for the subadult stages of most gulf species, and for nighttime catches of vertically migrating adults.

Of the nine regular inhabitants of the gulf, those common both to the gulf and the warm-temperate California Current—*Nematoscelis difficilis* and *Nyctiphanes simplex*—consistently had the broadest ranges in the gulf (Figure 12). They were most abundant and reproductive during February-April and February-June, respectively, before August heating (Figure 13). Tropical *Nematoscelis gracilis* showed a range generally complementary to that of *N. difficilis*. *Euphausia eximia*, considered adapted to margins of the oxygen-deficient waters of the eastern tropical Pacific, consistently occupied only the southern half of the gulf. The three tropical *Euphausia* species—*E. distinguenda*, *E. lamelligera*, and *E. tenera*—like *E. eximia*, occupied the southern gulf in February-April, expanding northward during June-August (Figure 14), consistent with Mundhenke's finds. Like the temperate-subtropical species above, the tropical species scarcely reproduced in the gulf during the warm season.

Although most euphausiids have oceanic ranges, there is a species with neritic affinity (Brinton 1962) corresponding to each of ten Pacific littoral provinces. Two of these species occur in the gulf. *Nyctiphanes simplex*'s range corresponds with Ekman's (1953) American Temperate-Tropical Zone, and *Euphausia lamelligera*'s with the Pacific Tropical American. *N. simplex* is abundant in any of the marginal waters of the gulf, and *E. lamelligera* is generally abundant along the broad southeastern shelf (Brinton and Townsend 1980).

In *N. simplex* (Figure 12), maximum production of larvae was in February, when waters were coolest— to 14°C in mid-gulf. In April, high abundances were along both sides of the gulf as far south as the mouth (24°N). There, cool surface temperatures (17°-20°C) persisted, evidently at that time due to upwelling. By August, when temperatures increased to 28°-31°C (Figure 13), numbers of young were reduced (Figure 12), recruitment was at a minimum, and the distributions retracted from both the northernmost shelf region and from the mouth.

*Nematoscelis difficilis* (Figure 12) is the other euphausiid to occupy most of the gulf in 1957, particu-

larly in February, when high densities extended to the mouth, assuring at least seasonal exchange with the California Current population. In April, instances of high density were scattered, and from June to August a reduced population was concentrated toward the west in cooler water (Figure 13). Brinton and Townsend (1980) pointed out that during June and August high temperatures would be expected to limit *N. difficilis* to below 100 m, and shoaling of the 1.5 ml$^{-1}$ oxygen surface to less than 100 m could further narrow the vertical range, thereby restricting this species from much of the southern gulf by August.

There was near-constancy throughout the year in numbers of adults of both *N. simplex* and *N. difficilis*. Numerous *N. difficilis* larvae of February apparently led to an April-June peak in juveniles, and then a stock of young adults in August, expected to reproduce during the ensuing winter.

Euphausiid biomass in the gulf was found to be intermediate between that in the richest and poorest parts of either the California Current or the eastern tropical Pacific, with largest standing stocks corresponding to places and times where *Nyctiphanes simplex* and *Nematoscelis difficilis* were most abundant. Values of 50 to 200 cc/1000 m$^3$ for euphausiids and > 1000 cc for zooplankton were as high as any reported from mid- to low latitudes in the Pacific.

Nine euphausiid species were reported from zooplankton samples obtained in the gulf off the coast of southern Sinaloa in April and August 1981 and January 1982 during the SIPCO cruises of the RV *El Puma* (Sánchez Osuna and Hendrickx 1984). The dominant species was *Euphausia lamelligera*, while *E. distinguenda*, *E. eximia*, and *E. lamelligera* were the most frequently collected. Biovolume measurements indicated that euphausiid shrimps contributed up to 31% of the total biovolume of the catch.

Profiles of vertical distribution of euphausiids west of southern Baja California and across the mouth of the gulf during April-May 1974 illustrate intermingling of California Current and eastern tropical Pacific faunas (Brinton 1979). *Nematoscelis difficilis* (juveniles and adults, Figure 15) remained, day and night, at depths above low oxygen concentrations (ca. 1.0 ml$^{-1}$); *Nematoscelis gracilis* (Figure 15) and other tropical species, on the other hand, migrated down to daytime depths within the oxygen minimum. *Euphausia eximia*, neither strictly tropical nor temperate, tended to avoid low oxygen concentrations tolerated by the tropical species (Figure 16). More coastal *Nyctiphanes simplex* (Figure 17) remained above about 100 m day and night at nearshore localities, but there was a suggestion of vertical migration in mid-gulf.

*Stylocheiron affine* and *S. longicorne* are similar

## Nyctiphanes simplex
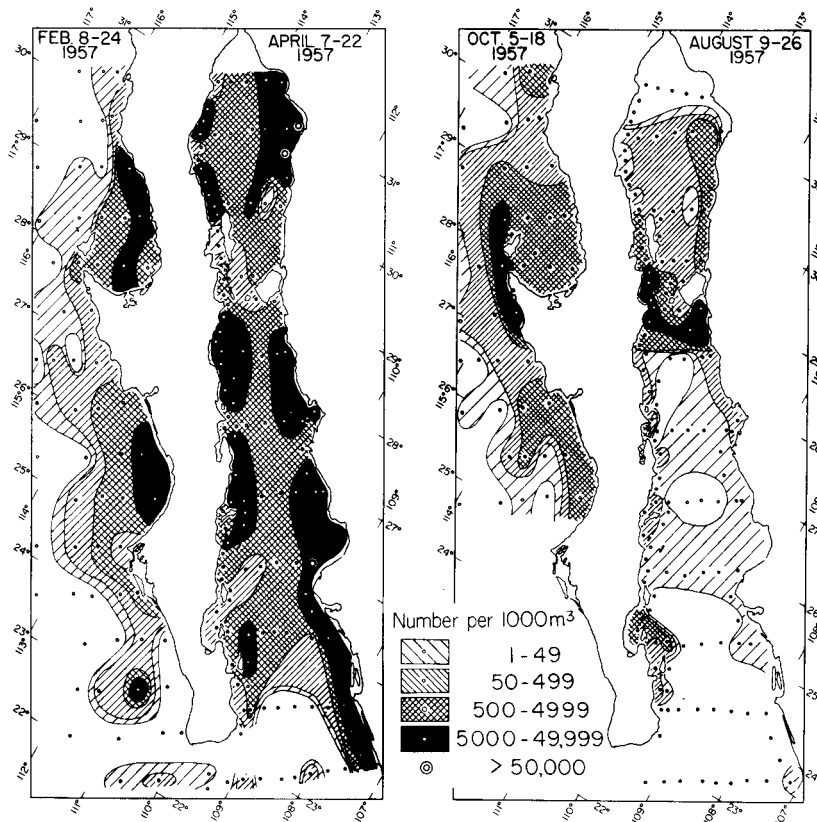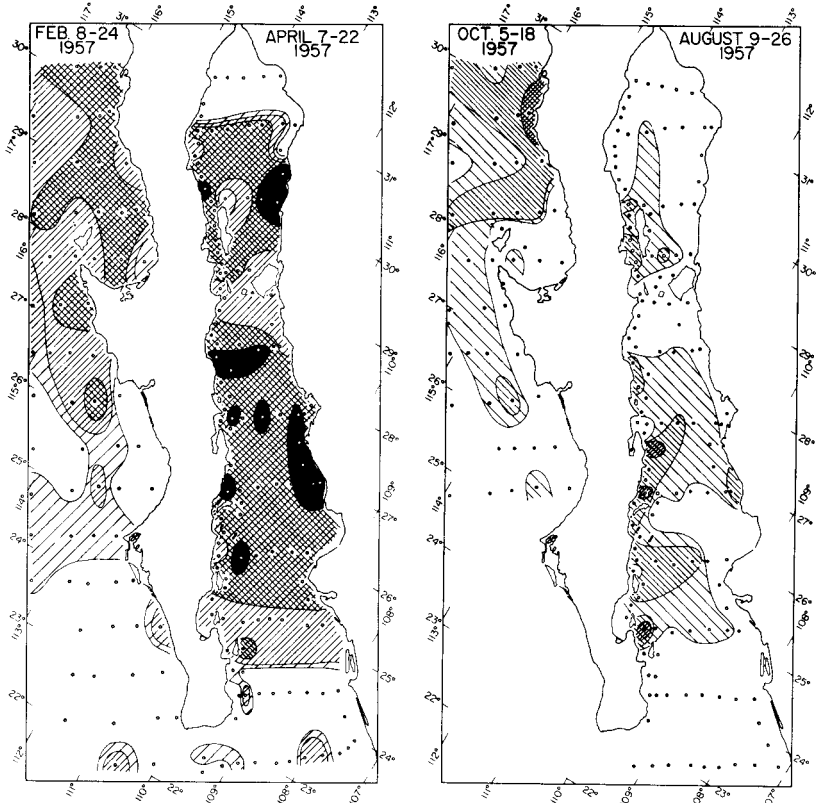


## Nematoscelis difficilis



Figure 12. April and August 1957 distributions of the euphausiids *Nyctiphanes simplex* and *Nematoscelis difficilis* in the Gulf of California (after Brinton and Townsend 1980), and February and October distributions to the west of Baja California (after Brinton 1967).
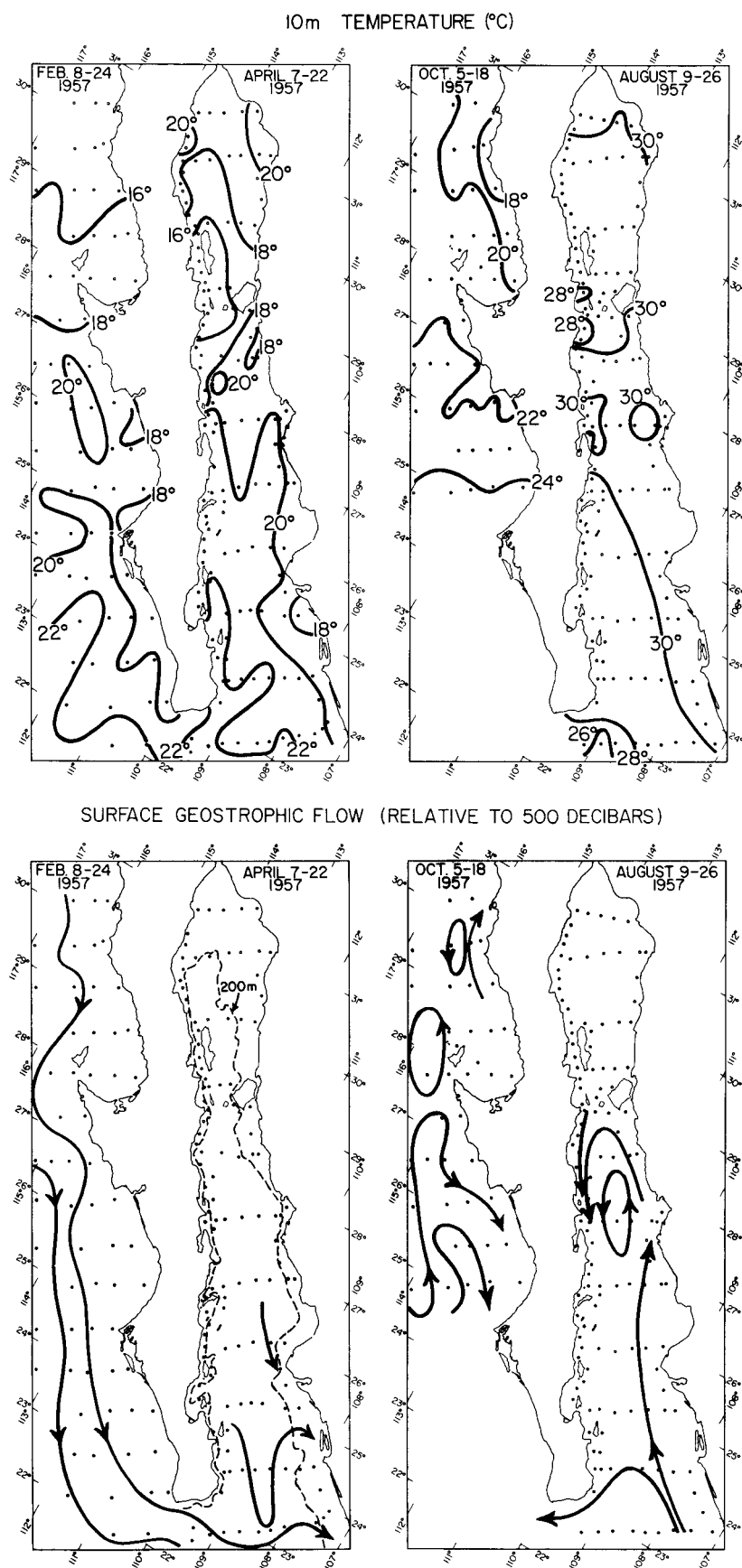
10m TEMPERATURE (°C)

SURFACE GEOSTROPHIC FLOW (RELATIVE TO 500 DECIBARS)

Figure 13. April and August 1957 distribution of 10-m temperature and upper-level geostrophic flow in the Gulf of California, and February and October 1957 distributions to the west of Baja California (after anonymous 1963, and Wyllie 1966).
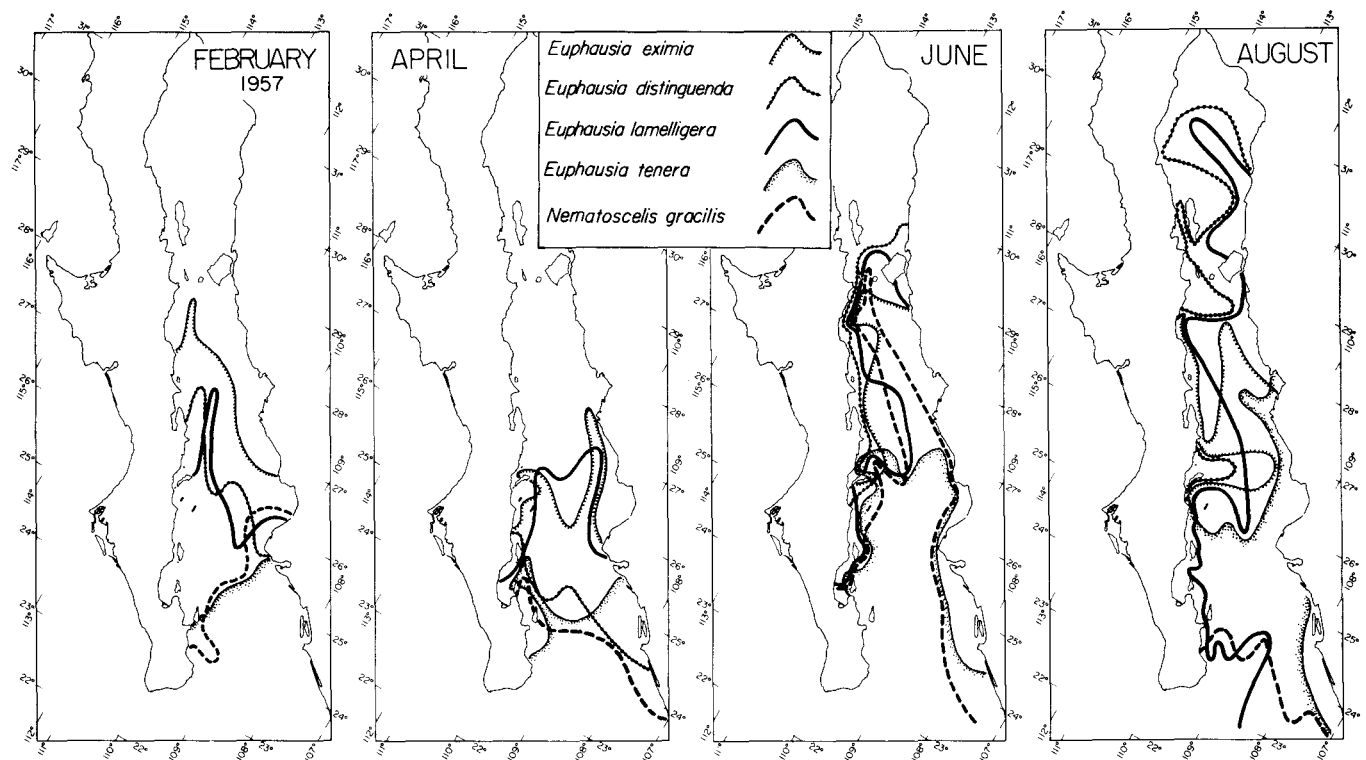
Figure 14. Variation in limits of range in the Gulf of California, during February to August 1957, of the indigenous population of *Euphausia eximia* and of the four tropical euphausiid species (after Brinton and Townsend 1980).

euphausiids that, here, appear not to engage in vertical migration. Both live above the layer having oxygen concentration $< 0.5$ ml$^{-1}$ (Figure 18), but *S. affine*, which inhabits the upper part of the thermocline, ranges north to south across the eastern tropical Pacific, above the oxygen-deficient water, whereas the somewhat deeper-living *S. longicorne* cannot. Why no species of this genus significantly penetrates the gulf is not understood.

## Pelagic Penaeidea (Decapoda)

Of the family Sergestidae, Burkenroad (1937) reported *Sergestes halia* Faxon near Mazatlán and in the mouth of the gulf; *Sergia phorca* (Faxon) in mid-gulf (27° to 28°N); and *Sergestes similis* Hansen, characteristic of cool waters of the California Current, off Isla Tiburón.

Judkins (1972) confirmed that *Sergestes similis* occurs in a seemingly isolated population in the gulf, north of about 25°N. Thus it is a member of the warm-temperate fauna of the North Pacific (cf. *Calanus pacificus californicus*, *Nematoscelis difficilis*) that occupies part of the gulf. Judkins found no other sergestids in Vermilion Sea Expedition trawls from the gulf.

Like many euphausiids, sergestids are strong vertical migrators. Unlike most euphausiids, they tend not to move upward beyond the thermocline. Larval

development in *Sergestes similis* has been described in detail by Knight and Omori (1982).

Judkins (1978) provided keys and descriptions for species of the diverse "*Sergestes edwardsii* group" of *Sergestes*. Although none of this group has been reported from the gulf, four of its species occur in the eastern tropical Pacific and one in the California Current.

Species of the genus *Lucifer* seem to occur in the surface layers of all tropical and subtropical seas. *Lucifer typus* was reported at the mouth of the gulf by Burkenroad (1937).

Of the mesopelagic Penaeidae, only *Benthesicymus tanneri* Faxon is known to occur in the gulf (Faxon 1893, 1895). The widespread genus *Gennadas* seems to be absent.

## Pelagic Caridea (Decapoda)

These large, apparently nonmigrating, mesopelagic carideans are represented in the gulf, according to Faxon (1893, 1895), by *Acanthephyra curtirostris* Wood-Mason, caught by the *Albatross* north of Islas Tres Marias as well as at mid-gulf, and by *Hymenodora glacialis* (Buchholz) from the mid- and southern gulf.

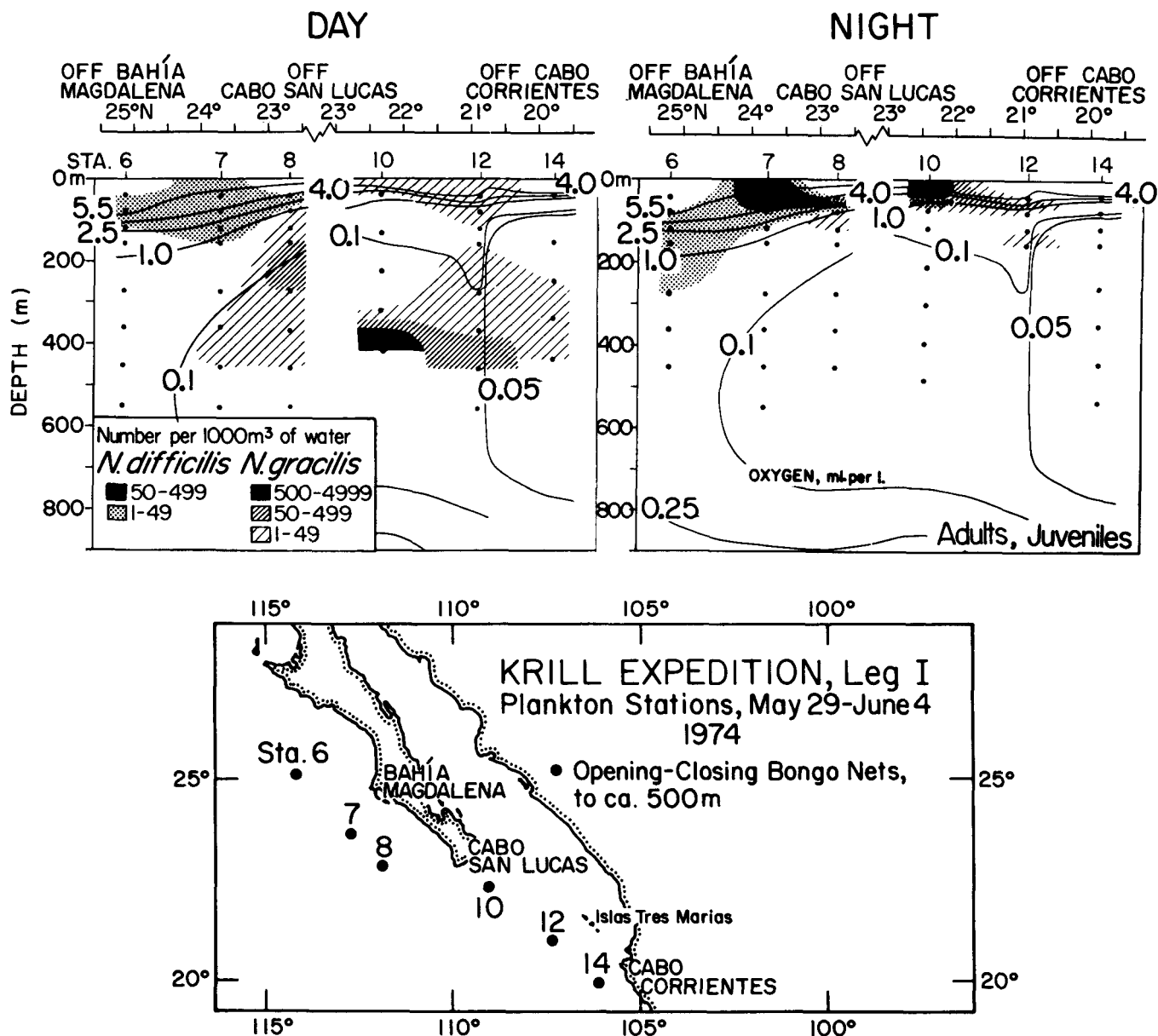The genus *Notostomus* and the family Pasiphaeidae, which commonly occur at depths inhabited by

Figure 15. Vertical distributions of three life phases of the warm-temperate euphausiid *Nematoscelis difficilis* and tropical *N. gracilis*, from Bahia Magdalena to Cabo Corrientes. The line of stations is indicated on map, *below*.

*Acanthephyra* and *Hymenadora*, have not been reported from the gulf.

## Pelagic Larvae of Benthic Decapod Crustaceans

An extensive literature exists dealing with behavior and distribution of *Penaeus* postlarvae in the Caimaanero-Huizache lagoons of the southeastern gulf (22°N). Many of these papers arose from the program on lagoon ecology and shrimp fisheries conducted by the Universidad Nacional Autónoma de México in cooperation with the University of Liverpool. However, little work on the pelagic larvae of these species, appropriate for this review, has been carried out. In

fact, only a few gulf species of decapod meroplanktonic larvae have been examined in any detail.

Planktonic larvae of four species of *Penaeus*, with emphasis upon *P. brevirostris*, were examined from coastal waters off Sinaloa and Sonora (Cabrera-Jiménez 1983). Taxonomic characters for separation of postlarvae were considered.

Johnson (1968, 1971, 1975), studying the phyllosoma larvae of Palinuridae (spiny lobsters) and Scyllaridae (slipper or shovelnose lobsters) in the eastern tropical Pacific, indicated occurrences in the gulf and provided a key for identification (1971). The commonest palinurid in the gulf was the tropical
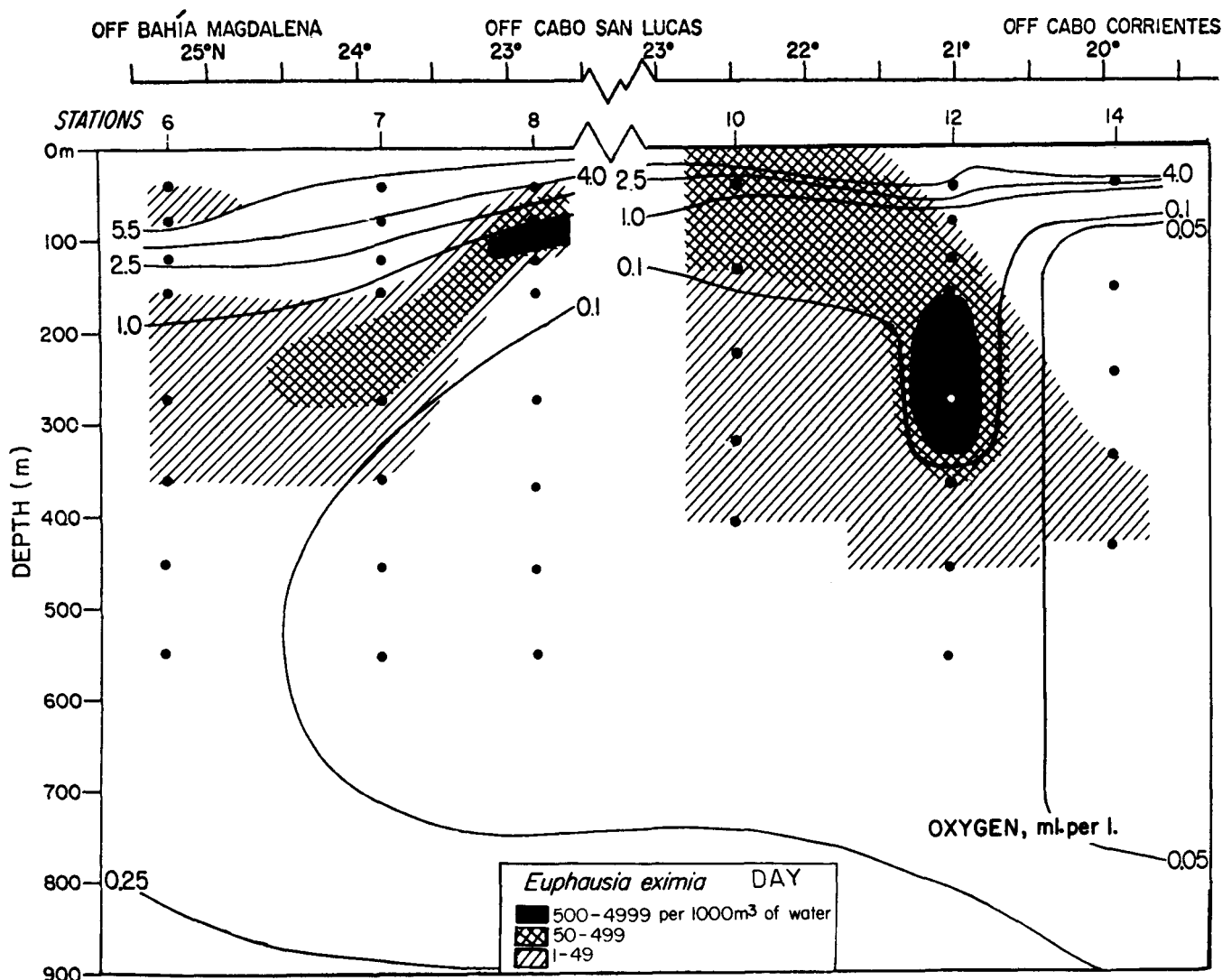
253

Figure 16. Vertical distributions of four life phases of the eastern Pacific euphausiid *Euphausia eximia*, from Bahía Magdalena to Cabo Corrientes (see Figure 15 for map).

*Panulirus inflatus*, which, outside the gulf, ranges from Bahía Magdalena (25°N) to the Gulf of Tehuantepec (16°N). The closely related *P. gracilis* also occurs the length of the gulf, from Kino Bay (31°N) southward (Chapa-Saldaña 1964), but Johnson (1971) found its larvae to be rare in the gulf.

Warm-temperate *Panulirus interruptus* occurs along southern California, southward to Bahía Magdalena. Johnson found larvae only in the northern gulf. Thus California Current and gulf populations appear to be separated.

Only two species of scyllarid lobsters are known from the eastern tropical Pacific, and both occur in the gulf (Johnson 1971). Phyllosoma larvae of *Evibacus princeps* occurred along the entire gulf during the August 1957 CalCOFI cruise but were not present in June samples. Larvae of *Scyllarides astori* appeared in August samples from the southern gulf. A few larvae

of a third gulf species, not yet known, were designated "Phyllosoma x."

Planktonic larvae of primitive burrowing crabs of the family Raninidae are known from the gulf (Knight 1968). Although two species, *Raninoides benedicti* and *R. ecuadoriensis*, have been found as adults in the gulf (Garth 1948, 1960), only the larvae of *R. benedicti* have been recognized. Identification was confirmed by rearing larvae obtained in plankton tows from near Cabo Corrientes. Larval development of this species is described by Knight. Larvae of *R. benedicti* in plankton samples show that it extends into the gulf to about 27°N, near Bahía Concepción. This species and *R. eucadoriensis* are tropical, ranging southward to Ecuador.

Two species of the sand crab *Emerita* (family Hippidae) are known from the gulf. *E. analoga* occurs from at least as far north as British Columbia south-
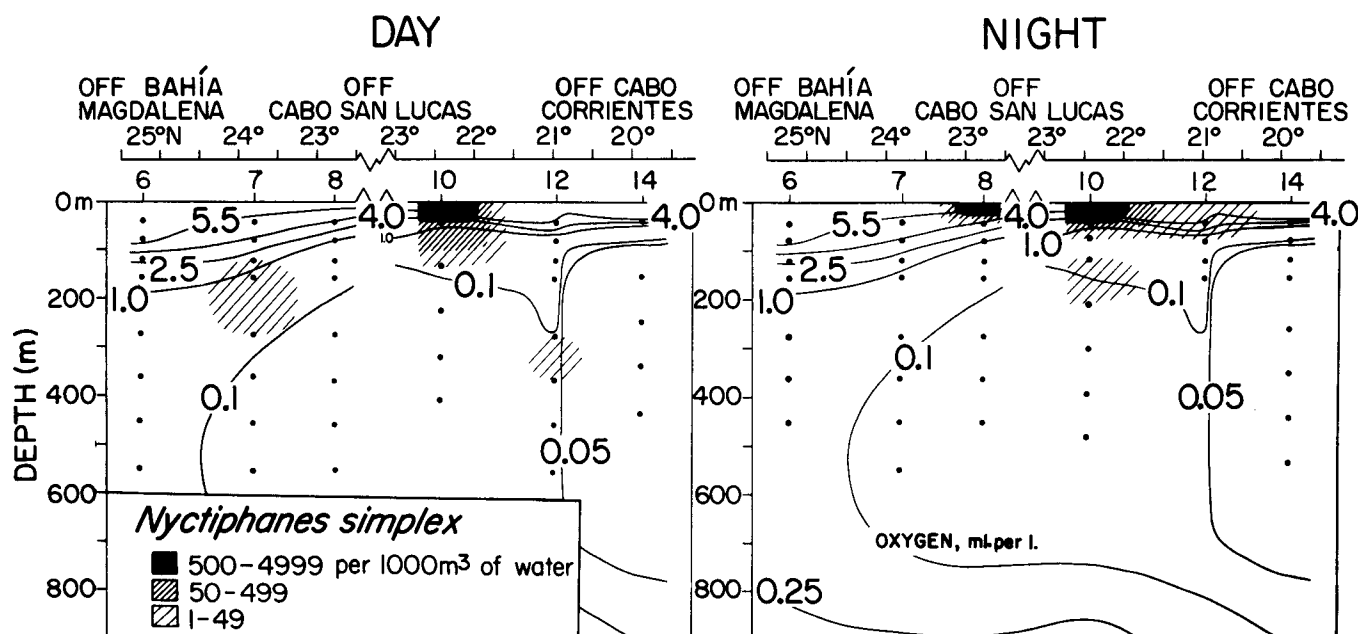
Figure 17. Vertical distribution of the euphausiid *Nyctiphanes simplex*, from Bahía Magdalena to Cabo Corrientes (after Brinton 1979). (see Figure 15 for map).

ward to Bahía Magdalena (records reviewed in Knight 1967). An isolated population has been found in the gulf at Bahía de San Francisquito (28.5°N) in the western gulf (Efford 1969), and *analoga*-like larvae have been recorded in gulf plankton (Knight 1967). *E. analoga* larvae from California waters are described in Johnson and Lewis (1942).

Tropical *Emerita rathbunae* has been also collected from Bahía de San Francisquito (Steinbeck and Ricketts 1941) and southward; Knight (1967) described its larval development, based on larvae hatched from an ovigerous female collected at Mazatlán.

### Demersal Zooplankton

Mobile organisms that periodically emerge from the benthos and swim in the water column were termed "demersal plankton" by Alldredge and King (1980). Distances of such vertical migrations were measured by Alldredge and King (1985) on a subtidal and sand flat in the gulf: (1) small forms—copepods, ostracods, and amphipods—remained within 30 cm of the bottom except at full moon, when many swam upward 1 m or more; (2) syllid polychaetes swam upward at least 2 m; and (3) many large forms, > 2 mm, swam throughout the water column, an activity interpreted as a means of dispersal. In a northern cove of Isla Danzante in the central gulf, demersal copepods were dominated by *Cyclopina schneideri*, with *Pseudocyclops* sp. the predominant calanoid.

### Zooplankton Biomass

Zooplankton biomass is often expressed as wet dis-

placement volume. Such volumes are particularly biased when large amounts of "jelly plankton" are included. In the California Current, and probably also in the gulf, displacement volume of zooplankton of average composition may be converted to either dry weight or carbon using the following factors from Lasker (1966): dry weight = 17.2% of wet weight (or volume); carbon = 42% of dry weight; carbon = 7.2% of wet weight.

The plankton retained by a given type of net depends, in part, upon the mesh size, as well as upon towing procedures. Nevertheless, different methods provide useful information as to rich and poor areas and ranges of variability in the standing stock.

A first description of the distribution of zooplankton biomass in the gulf was that of Farfan (1973), working in the northernmost area. Values were expressed as dry weight for the full water column, < 50 m in the region studied (Figure 19). Amounts of plankton ranged from < 5 mg/m$^3$ to < 150 mg/m over broad areas. Values in excess of 100 mg/m$^3$ were toward the western side in January. March values were generally low, followed by an April-October period when conspicuous maxima fanned out from the northernmost deltaic region.

Cummings (1977) interpreted the distribution of zooplankton biomass in the northern gulf in terms of seasonal upwelling postulated by Roden (1958, 1964), and found correlations between plankton peaks and presumed upwelling maxima.

Griffiths (1968) plotted zooplankton displacement volumes, 0-300 m, across the mouth of the gulf and off southwestern Baja California during spring 1960
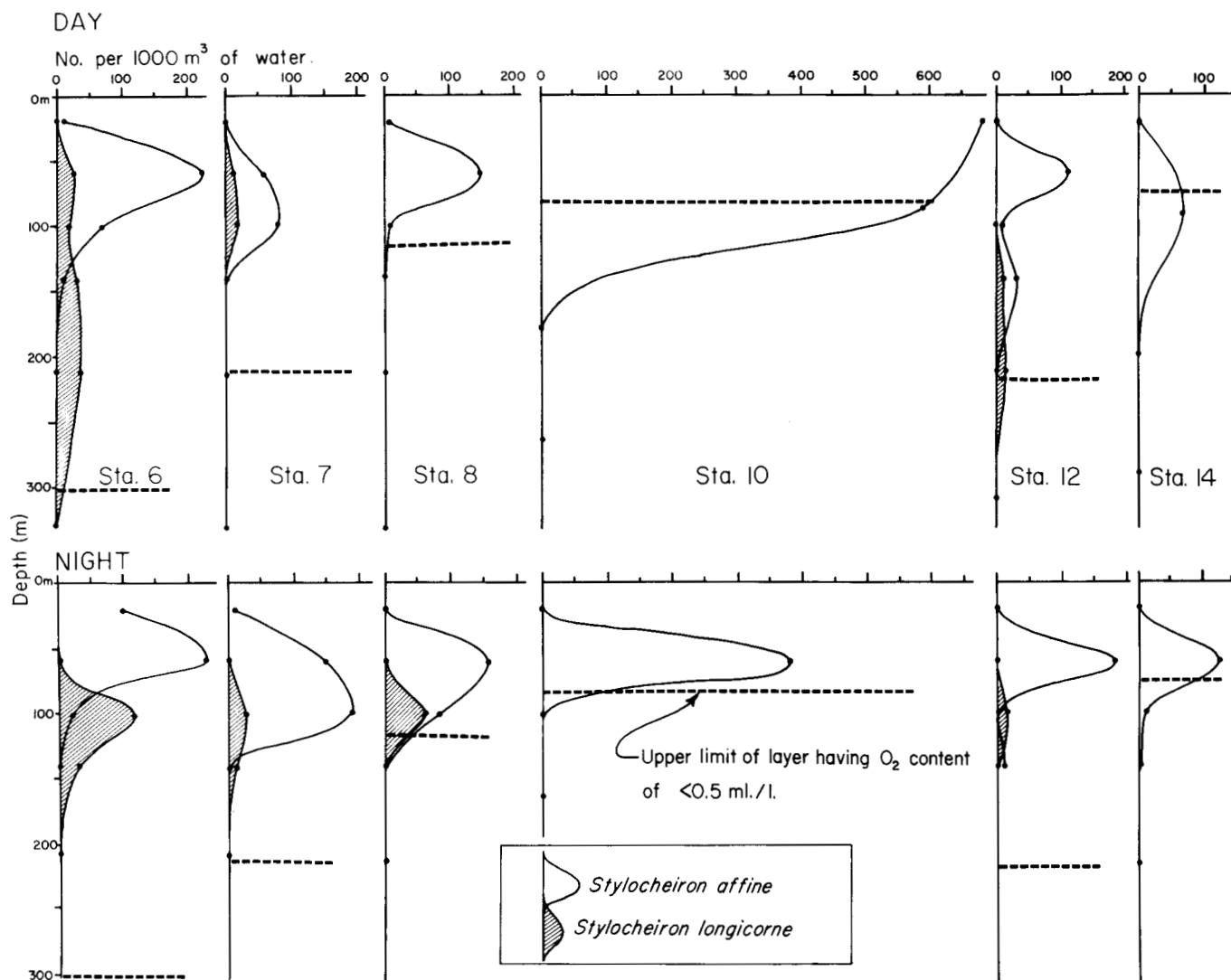
Figure 18. Vertical distributions of the related *Stylocheiron* euphausiids, *S. affine* and the somewhat deeper-living *S. longicorne*, in relation to the upper limit of the layer having oxygen concentration of <0.5 ml/l. Stations extend from off Bahía Magdalena to near Cabo Corrientes (see Figure 15 for map). (after Brinton 1979)

(Figure 20). Values of < 50 to > 200 cc per 1000 m³ were erratically distributed across this region of oceanic fronts. Highest values were to the south of Bahía Magdalena, near Islas Tres Marias, and across the gulf from Cabo San Lucas to near Mazatlán (23°30′ N).

The 1956 and 1957 CalCOFI cruises, which covered much of the gulf, yielded collections for mapping plankton biomass in the 0-140-m layer. These collections were particularly oriented toward sampling the larger zooplankton, especially larval fishes (Moser et al. 1974). The mesh width of 0.6 mm used in these surveys fails to retain any of the material discussed by Zeitzschel, above, and, of the phytoplankton, hardly more than the largest *Coscinodiscus* cells.

The displacement volumes (Figure 21) show dense April peaks in biomass throughout the gulf, consisting largely of the copepod *Calanus pacificus californicus*,

the chaetognath *Sagitta enflata*, and the two euphausiids *Nyctiphanes simplex* and *Nematoscelis difficilis*. High values in April of both years tended to be along the eastern side. However, highest values (> 1000 cc per 1000 m³) were at five localities on the western side of the northern gulf in April 1957, where small salps (*Thalia democratica*) were in bloom. August and February volumes were generally low, with February 1956 being significantly poorer than February 1957 (Table 3). These volumes are of the same order as those found in rich parts of the California Current: coastal and oceanic regions north of Point Conception, and coastal waters of southern California and western Baja California (cf. Isaacs et al. 1969, 1971; Smith 1971, 1974; Fleminger et al. 1974).

Profiles of vertical distribution of zooplankton biomass were obtained by opening-closing bongo nets along the western coast of southern Baja California and
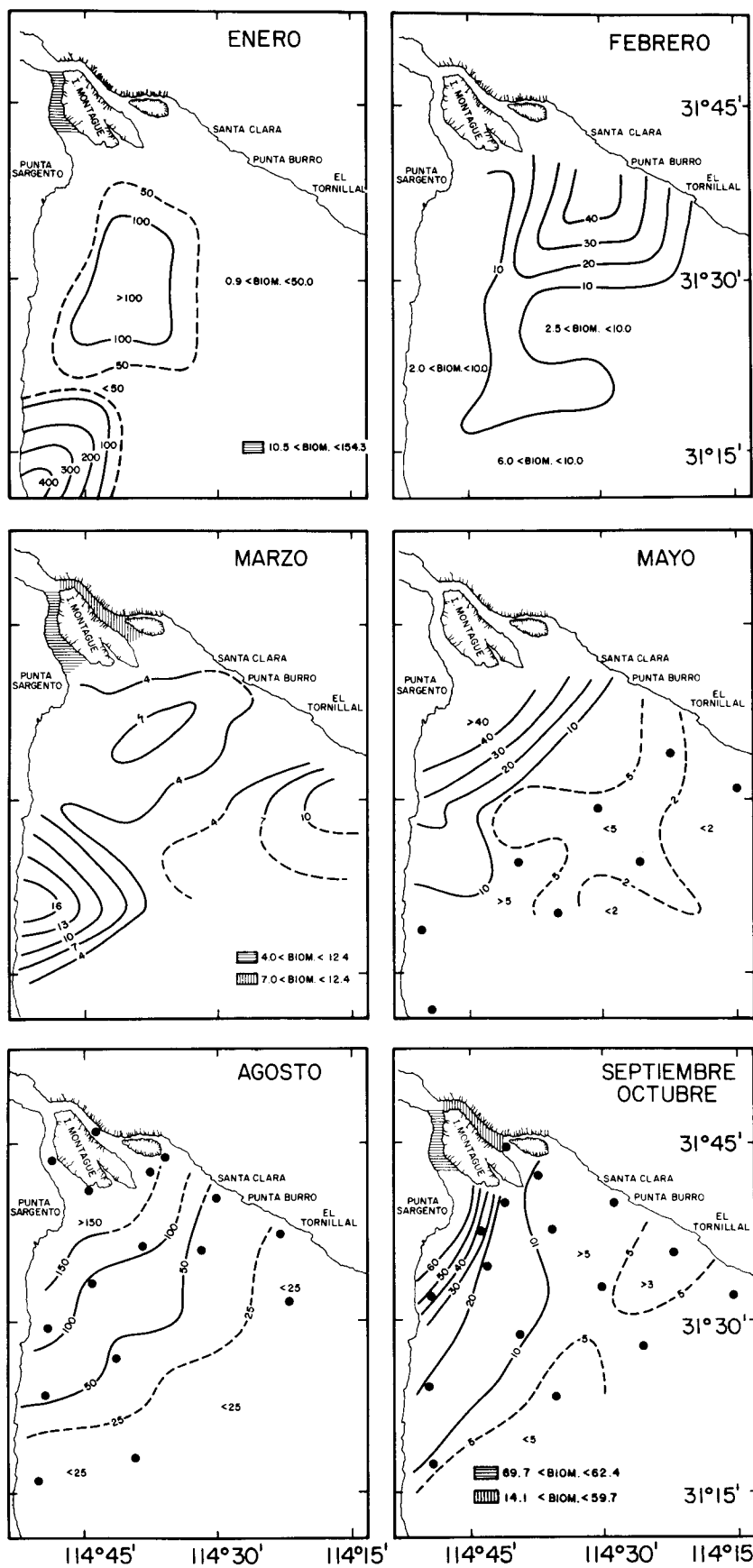
Figure 19. Distribution of zooplankton biomass in the northern Gulf of California during three seasons. Values are expressed as mg dry weight per m³, for the water column (from Farfan 1973).
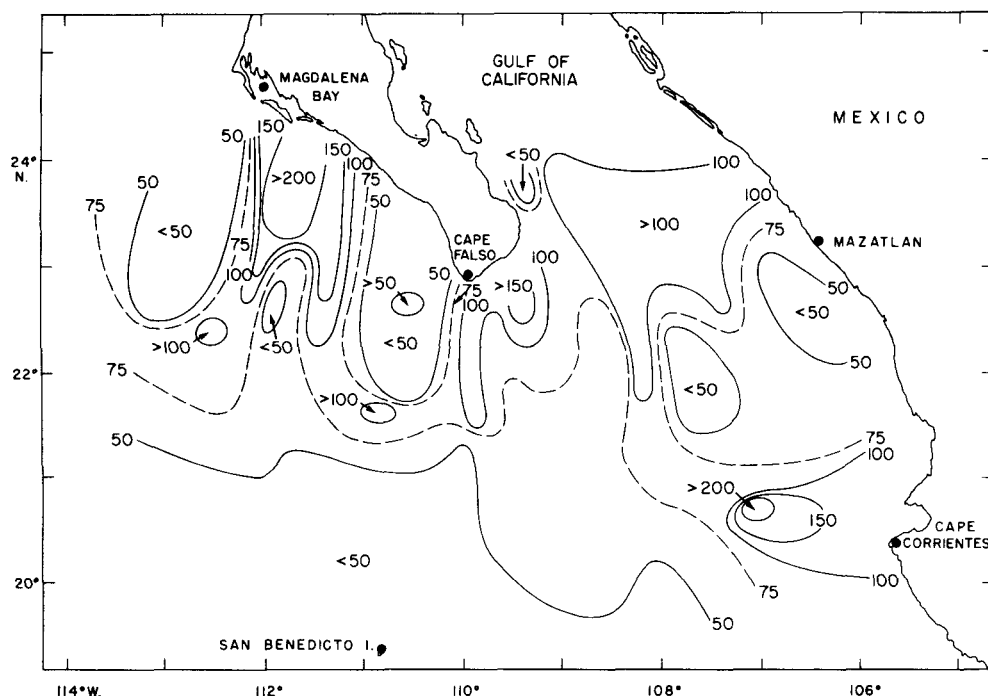
Figure 20. Distribution of standing crop of zooplankton, cc displacement volume per 1000 m³ of water, in layer between the surface and 300 m in the region of the mouth of the Gulf of California, spring 1960 (from Griffiths 1968).

across the mouth of the gulf (Figure 22) during May-June 1974 (Brinton 1979). Highest values were just west and south of Cabo San Lucas, and on the opposite side of the gulf, off Cabo Corrientes. Maxima were at or near the surface. Nighttime maxima exceeded daytime maxima, but values in excess of 25 cc/1000 m³ extended down only to about 100 m at night, compared with 400 m in daytime.

High values to the west of Cabo San Lucas included numerous young stages of the semipelagic red crab, or langostina, Pleuroncodes planipes (Reptantia, Galatheidae) (Figure 22). Only a few individuals were caught across the mouth of the gulf. The nighttime distribution of Pleuroncodes showed dispersal to greater depth than in the daytime, thereby differing from the upward nighttime migration of euphausiids, described above. The pelagic phase of P. planipes in the California Current was analyzed by Boyd (1963) and Longhurst (1967a). Adults occur widely in the gulf south of Isla Tiburón, though the RV Alejandro de Humboldt reported largest catches on the Sonoran coast between Isla San Pedro Martir and Guaymas (Mathews et al. 1974).

An abundance of material appearing to consist of plankton detritus is evident to anyone who has traversed the gulf during calms seas. This material belongs to the approximately 88% of the seston consisting of detritus reported by Zeitzschel (1970). Ephemeral, amorphous aggregates of matter are conspicuous to the naked eye in surface waters but are not

retained by plankton nets. Alldredge (1979) developed techniques to measure and enumerate such aggregates. She found that "marine snow" composed of aggregates of 3 mm or more made up 4% to 8% of total particulate organic carbon, nitrogen, protein, carbohydrate, lipid, and particulate dry weight in surface samples from the gulf: 20% of these aggregates were of recognizable zooplankton origin. The most abundant zooplankton-produced aggregates were found to be the discarded appendicularian houses of Oikopleura sp., Megalocercus huxleyi, and Stegosoma magnum. Agglutination around nuclei of zooplankton-produced mucous appeared to be a common mechanism for compounding small particles into macroscopic marine snow.

TABLE 3
Seasonal Variation in Average Zooplankton Biomass
(Displacement Volume per 1000m³)

| CalCOFI cruise | x | S.D. |
|---|---|---|
| 5602 | 171 | ± 121[a] |
| 5604 | 408 | ± 313 |
| 5702 | 355 | ± 224 |
| 5704 | 490[b] | |
| 5706 | 334 | ± 334 |
| 5708 | 244 | ± 180 |

[a]Isla Tiburón southward, only
[b]Becomes 782 ± 1618 when five samples having numerous small salps, Thalia democratica, are included.
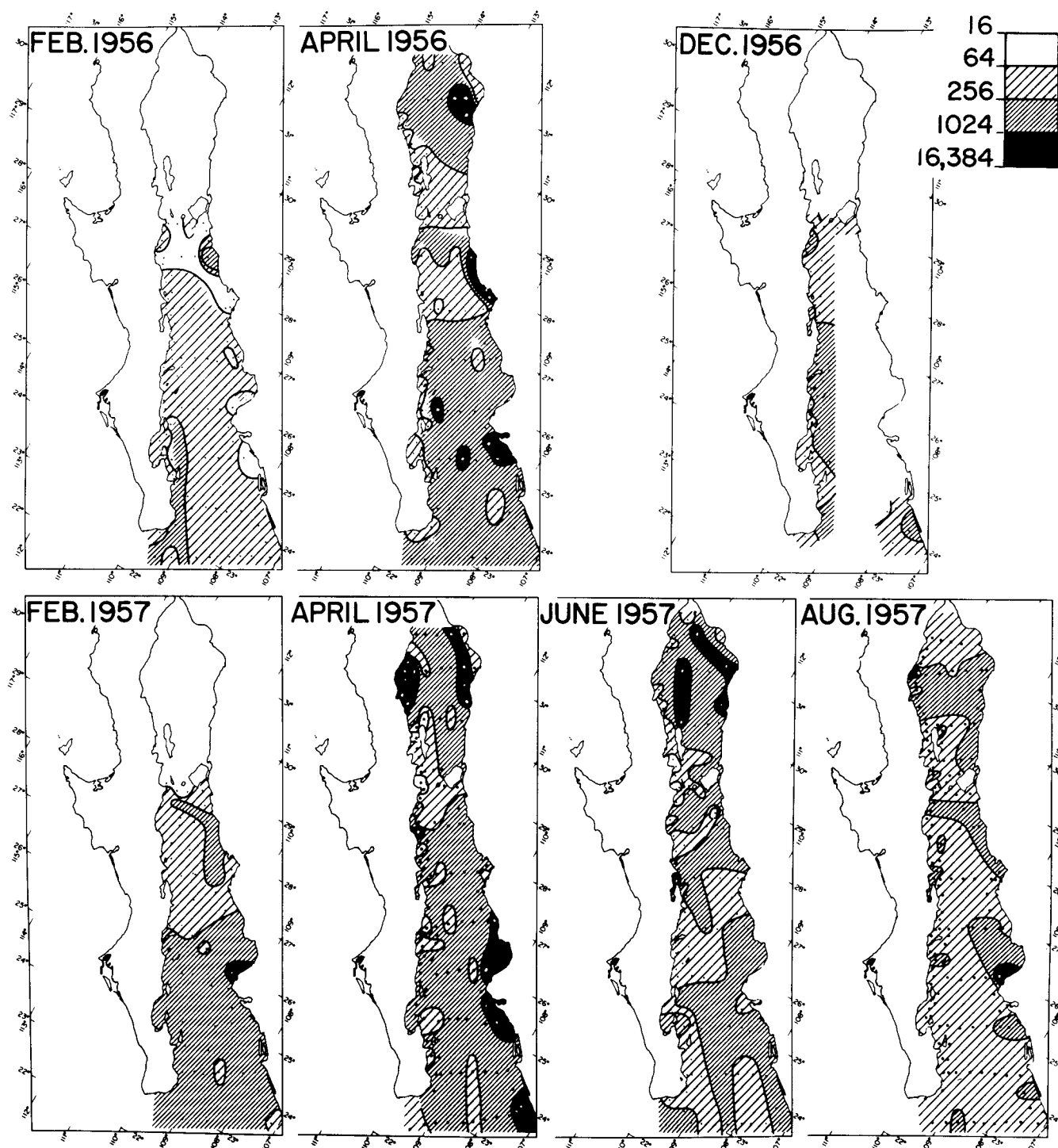
Figure 21. Zooplankton displacement volume, cc per 1000 m³ in the 0-140-m layer sampled by CalCOFI during 1956-57 in the Gulf of California, by means of a 1-m ring net of 0.6-mm mesh width.

## Bioluminescence

During a November-December 1981 cruise to the north end of the Canal de las Ballenas, Lapota and Losee (1984) observed bioluminescing plankton: larvae of the euphausiids *Nyctiphanes simplex* (calyptopis II and furcilia I-III stages and juveniles) and

*Euphausia eximia* (calyptopis I); calanoid copepods *Centropages furcatus*, *Paracalanus indicus*, and *Acrocalanus longicornis*; cyclopoid copepods *Corycaeus speciosus* and *C. latus*; the dinoflagellates *Ceratium breve*, *C. horridum*, and *C. gibberum*. The observations indicated the importance of some of the
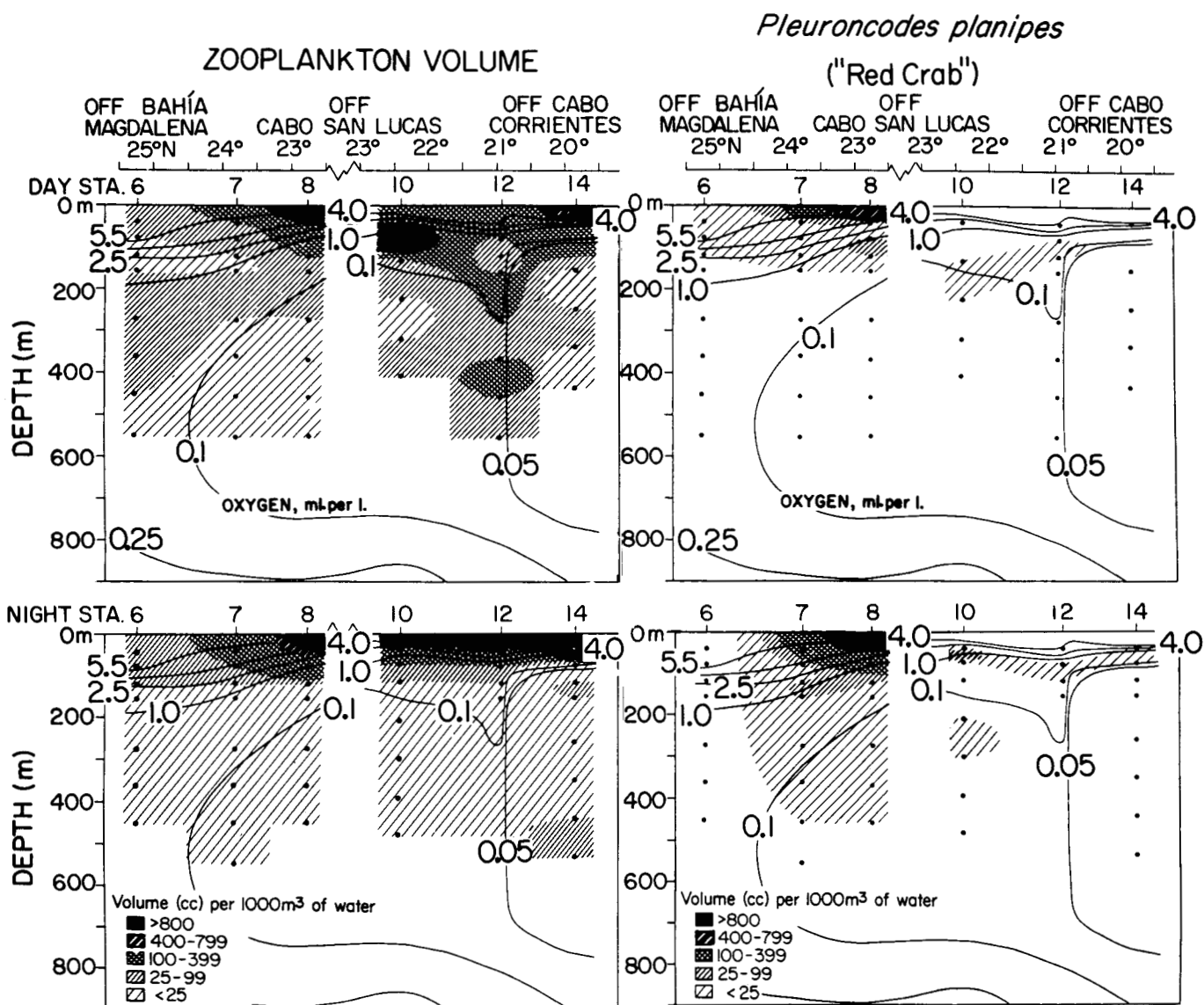
Figure 22.  Day and night vertical profiles of biomass (wet displacement volume) of total zooplankton and the red crab, *Pleuroncodes planipes*, across the terminal part of California Current and the mouth of Gulf of California. Reference isolines are oxygen concentrations. (See Figure 15 for station positions, May-June 1974.)

smaller copepods and euphausiid larvae to surface bioluminescence.

## GENERAL CONCLUSIONS

The plankton analyzed to date has been related to specialties of investigators. Much available material remains to be analyzed. That obtained by CalCOFI or independently by vessels of the Scripps Institution of Oceanography (e.g., the Vermilion Sea Expedition) is catalogued in Snyder and Fleminger (1965, 1972) and Snyder (1979). Examples of lists of material obtained by Mexican vessels are in Granados and Villaseñor (1974) and Departamento de Pesca (1978). What has been caught has been, in part, a function of the kind of net and mesh size used and of the depths sampled; there is no all-purpose sampler.

Differences between schemes of phytogeographical zonation proposed by Gilbert and Allen (1943), based on single dominant species, and by Round (1967), which took into consideration species diversity and amounts of phytoplankton, demonstrate that there may be substantial seasonal and year-to-year changes in species distributions and local productivity in the gulf. On the other hand, the above workers, together with Brinton and Townsend (1980) and Siegel-Causey (1982), working on euphausiid and amphipod crustaceans, respectively, agreed on the existence of (1) a zone north of Islas Tiburón and Angel de la Guarda that is largely neritic and has the greatest (ca. 15°C) seasonal range in temperature, and (2) a southern zone at the mouth, particularly toward the west, in which most groups of plankters are sparse, though not

Foraminifera, and in which tropical species occur regularly. Between these two zones—from the island channels, 29°N, to the Faralón Basin, 25°N—is a region of seasonal flux. Here, in summer, the temperate species either tend to submerge beneath the warming, decreasingly productive surface layer, or become diminished in numbers; i.e., the foraminiferans *Globigerina bulloides* and *G. quinqueloba*, the euphausiid *Nematoscelis difficilis*, and the copepod *Calanus pacificus californicus* are replaced in the upper layers by tropical species.

Moser et al. (1974) emphasized the widespread gulf occurrence of the larvae of two commercially important fishes having cold-water affinities. Larvae of the Pacific mackerel, *Scomber japonicus*, averaged high in abundance among the larvae of all fishes in the gulf, and larvae of the Pacific sardine, *Sardinops sagax caeruleus*, somewhat less, depending on which CalCOFI cruise, 1956 or 1957, is considered. Larvae of five species constituting most of the gulf's depauperate midwater fish fauna were generally the most abundant: the Pacific lightfish *Vinciguerria lucetia*; the small gadoid fish *Bregmaceros bathymaster*; three Myctophidae—*Diogenichtys laternatus*, *Triphoturus mexicanus*, and *Benthosema panamense*; and the deep-sea smelt *Leuroglossus stilbius*. It may be noted here that pelagic crustacean groups having many midwater representatives elsewhere are, like midwater fishes, depauperate in the gulf. There are no midwater euphausiids here, and there appear to be few such mysids and decapods.

One of us (A.F., unpublished data) has found that the enormous gulf population of the copepod *Calanus pacificus californicus* submerges from its winter-spring feeding levels above about 100 m to depths of 200-300 m at which it rests during summer—within layers of relatively low oxygen content. This submergence matches the behavior of *Calanus* to the west of Baja California (Longhurst 1967b; Alldredge et al. 1984). Therefore, the appearance of sparse *Calanus* in the gulf during the summer of 1957 (Figure 23) may have been because only the strongly heated upper 140 m was sampled.

Evidence that such deep submergence may not take place in the euphausiid *Nematoscelis difficilis*, which has the same warm-temperate range as *Calanus pacificus californicus* in the California Current, is the fact that numbers of adult *N. difficilis* in the 0-140-m layer did not decrease significantly in August, as compared with April (Brinton and Townsend 1980). Younger stages were then much reduced, consistent with the pattern in all euphausiid species. *N. difficilis* appears to have a broad vertical range of about 50 m to 200 m, day and night, which may be its means of

accommodating to the seasonal extremes in surface temperatures. The sergestid decapod *Sergestes similis* of the northern gulf and the California Current also avoids surface layers, whatever the temperature or season.

Coastal waters of the gulf may support dense stocks of the more neritic species at any season, but buildups of common forms—temperate or tropical—appear during late winter to spring, when vertical mixing and upwelling seem to be most intense. Certain warm-temperate, neritic and slope-water species of the California Current occur throughout the gulf, though highest densities are usually over the northern shelf or along the gulf's margins. These include the chaetognath *Sagitta euneritica* and the euphausiid *Nyctiphanes simplex*, which range the full length of the gulf but not south of it.

Species groups of coastal copepods in the gulf provided pictures both of mutually exclusive warm-temperate and tropical ranges (the "*Labidocera jollae* group," Figure 11) and of weakly overlapping ranges that could be considered either warm-temperate or tropical (the "*Labidocera trispinosa* group"). The only example of endemic gulf plankton we have found is in this genus, *Labidocera kolpos*; the only nearly endemic example is *L. johnsoni*. Manrique (1977) noted, near Guaymas, the strong winter-spring buildup of *Acartia tonsa* and the almost total replacement of this species in the summer by tropical *A. lilljeborgi*.

In the Copepoda and Euphausiacea, the relatively few temperate species tend to achieve higher densities within the gulf than do warm-water species—notably in winter and spring; but in the Amphipoda, tropically derived species make up the greater numbers. For the overall gulf, including the outer reaches to the south, 60% of foraminiferan species are considered tropical, subtropical, or both, as are 87% of chaetognaths, 86% of calanoid copepods (Table 2), 65% of hyperiid amphipods, and 82% of euphausiids. The North Pacific Central Water Mass euphausiid fauna was conspicuously absent from the gulf. Species that proliferate at the productive margins of the eastern tropical Pacific (called tropical-subtropical in the above percentages) were strongly represented by the chaetognath *Sagitta bierii* and the euphausiid *Euphausia eximia*.

Numbers of tropical-subtropical species of calanoid copepods exceed numbers of tropical and temperate species combined (Table 2). Of these, the majority (75%) were oceanic, the remainder neritic or estuarine-coastal. A similar ratio of oceanic to neritic species prevails in chaetognaths and euphausiids.

The complexities of advection occurring across open tropical and subtropical oceans, together with
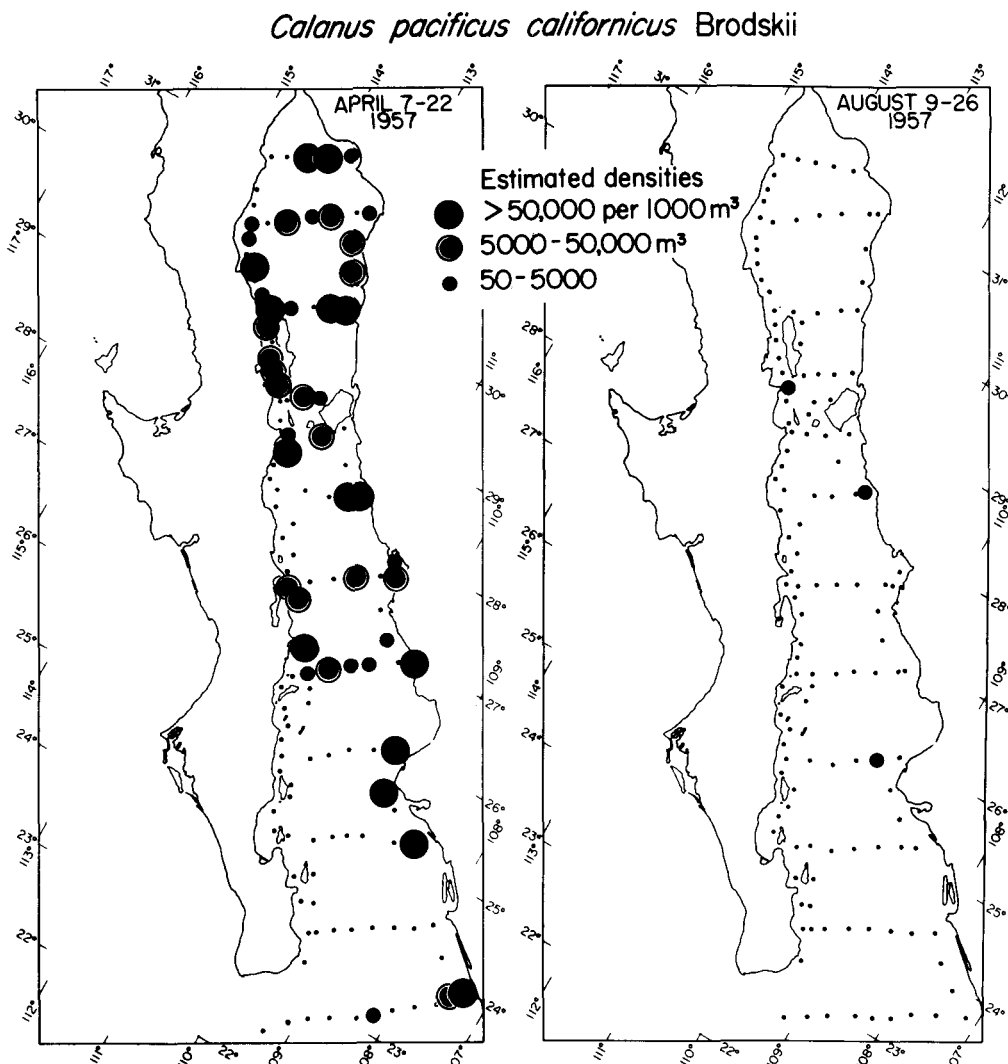
## *Calanus pacificus californicus* Brodskii



Figure 23. Roughly estimated abundance of the copepod *Calanus pacificus californicus* in the 0-140-m layer sampled by CalCOFI during April and August 1957.

weak seasonal change relative to high latitudes, seems to have inhibited study of population developments in most warm-water biotas. However, in the semienclosed gulf, strong seasonality in environmental properties, together with understanding now being obtained of water exchange among zones of the gulf and across the mouth, suggest that unique opportunities exist here for profitable examination of pelagic life processes.

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