

EUPHAUSIIDS IN THE GULF OF CALIFORNIA—THE 1957 CRUISES

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ABSTRACT

Euphausiid crustaceans in the Gulf of California were examined from four bimonthly CalCOFI grid cruises during February through August of 1957. Of the nine species found to regularly inhabit the Gulf, *Nematoscelis difficilis* and *Nyctiphanes simplex* are common to the warm-temperate California Current. These have the broadest ranges in the Gulf, peaking in abundance and reproducing maximally during February–April and February–June respectively, before intense August heating takes place in the Gulf. *Euphausia eximia*, a species having high densities at zones considered marginal to the eastern tropical Pacific, also varies little in range during the year, consistently occupying the southern half of the Gulf. Tropical *Nematoscelis gracilis* shows a range complementary to that of *N. difficilis*; these species overlap in the southern Gulf. Three *Euphausia* species of the tropical Pacific occupy the southern Gulf in February–April, expanding northward during June–August but, like the cool-water species, scarcely reproducing in the Gulf during the warm season. The distributions and abundances of the species and their life stages, particularly the youngest larvae, are described in relation to seasonal variation in flow and temperature in the Gulf.

RESUMEN

Se examinaron crustáceos euphausídeos del Golfo de California tomados durante cuatro cruceros bimensuales de CalCOFI entre febrero y agosto de 1957. De las nueve especies encontradas que regularmente habitan en el Golfo, *Nematoscelis difficilis* y *Nyctiphanes simplex* son comunes en las aguas templada-cálidas de la Corriente de California. Estas especies presentan una distribución amplia en el Golfo, alcanzando una máxima abundancia y reproducción durante febrero-abril y febrero-junio, respectivamente, antes de llegar el calor intenso de agosto. *Euphausia eximia*, una especie de altas densidades en las zonas consideradas marginales al Pacífico tropical oriental, también varía poco en su amplitud de distribución durante el año, ocupando consistentemente la mitad sur del Golfo. *Nematoscelis gracilis*, es tropical y muestra una distribución complementaria con *N. difficilis*; estas especies concurren en el sur del Golfo. Tres especies de *Euphausia* del Pacífico tropical ocupan el sur del Golfo en febrero-abril, extendiéndose hacia el norte durante junio-agosto, pero, como las especies de agua fría, escasamente se reproducen en el Golfo durante la estación cálida. Las distribuciones y abundancias de

las especies y de sus etapas de vida, en particular las de las larvas más juveniles, se describen en relación con las variaciones estacionales en el flujo y las temperaturas de las aguas del Golfo.

INTRODUCTION

The Gulf of California is inhabited by dense stocks of plankton (Osario-Tafall 1946; Zeitzschel 1969). This appendix of the North Pacific Ocean communicates with the eastern boundary circulation at the northern limit of the eastern tropical Pacific, which is characterized by its distinctive oxygen-deficient layer. The 1000-km axis of the Gulf extends from the mouth at the tropic, 23°27'N, to latitude 32°N, which is within the belt of the warm-temperate Californian Transition Zone, discussed most recently by Newman (1979). The Gulf parallels the terminal part of the California Current, which meanders southward on the other side of the Baja California peninsula.

Little attention has been paid to ways in which the Gulf's nearly enclosed planktonic populations range along this stretch of water, which is recognized on the basis of the fish fauna to be one of temperate-tropical transition (Walker 1960). Indeed, only sparse information exists as to the zooplankton species presently occupying the Gulf or to their distribution. Data are best for Foraminifera (Bradshaw 1959; Parker 1973), Chaetognatha, Siphonophora, and Scyphomedusæ (Alvaríño 1969), and pontellid Copepoda (Fleminger 1967, 1975). Hyperiid Amphipoda are presently under study by Siegel-Causey, whose first findings (in press) presage description of a diverse amphipod fauna. Existing knowledge of the plankton of the Gulf of California has been reviewed by Brinton et al. (in press).

Euphausiids sampled across the mouth of the Gulf (Brinton 1979) were grouped as 1) residual from the main stream of the California Current to the north (e.g. *Nematoscelis difficilis*, *Euphausia pacifica*, and *Thysanessa gregaria*), 2) species proliferating at the productive margins of the eastern tropical Pacific (e.g. *Euphausia eximia* and the associated, more coastal *Nyctiphanes simplex*), 3) endemic equatorial vertical migrators adapted to the oxygen-deficient regions (*Nematoscelis gracilis*, *Euphausia diomedeeae*, and indistinctly associated *E. distinguenda* and *E. lamelligera*), and 4) non- or short-distance migrating warm-water cosmopolites that avoid the oxygen deficiency (e.g. *Stylocheiron affine*, *S. carinatum*).

The Gulf deepens into basins with depths up to 1,000 m

in the north and 3,500 m in the south. Hence, there is sufficient vertical space for occupancy by the *Euphausia* and *Nematoscelis* species which undergo vertical migrations of 300 or 400 m. The extent to which euphausiids penetrate the Gulf had been known previously only on the basis of a September-October 1952 CalCOFI cruise along the southernmost part of the western side (Brinton 1962; these 1952 distributions are detailed here along with the 1957 distributions).

Half of the area of the Gulf is neritic, with the broadest shelf in the northern end and along the eastern side (Figure 1). Although most euphausiids have oceanic rather than neritic ranges, nevertheless there is a species with neritic affinities (Brinton 1962; Figures 113, 114) corresponding to each, but one, of the Pacific's ten littoral provinces recognized by Ekman (1953). Two of these occur in the Gulf. *Nyctiphanes simplex*'s range corresponds with Ekman's American Temperate Tropical Zone and *Euphausia lamelligera*'s with the Pacific Tropical American.

Ships of the National Marine Fisheries Service and the Scripps Institution of Oceanography occupied a standardized grid of stations in the Gulf during 1956 (three cruises) and 1957 (four cruises). All employed the CalCOFI techniques regularly used at that time for sampling zooplankton; that is, oblique tows to 140 m, using a 1-m net of 0.55-mm-mesh width, following Ahlstrom (1948). The 1957 cruises provided the most seasonal and geographical coverage and were selected for this study. Net tows generally strained 300 to 400 m³ of water and were standardized to 1,000 m³. Samples were aliquoted and counted using methods described in Brinton (1979).

A biogeographical analysis of fish eggs and larvae in the Gulf (Moser et al. 1974) was based on samples from three of the four cruises discussed here and from three 1956 cruises. Hence, the 1957 fish distributions can be strictly compared with these euphausiid distributions.

Interest in examining biology of Gulf plankton in relation to oceanographic processes has heightened due, in part, to the importance to Mexico of understanding regenerative cycles in these productive coastal waters and also to emerging awareness among oceanographers of the Gulf's distinctive topography, its unique climate, and the substantial containment of its biota. Ayala-Castañares (1979) has characterized it as a natural laboratory.

THE PHYSICAL ENVIRONMENT

Upwelling and Mixing

The climate and circulation of Gulf waters are influenced by seasonally reversing winds and changes in incident heat. Upwelling, determined by the divergence of the Ekman transport, is expected to be strongest along the eastern side of the Gulf during the northeasterly winds

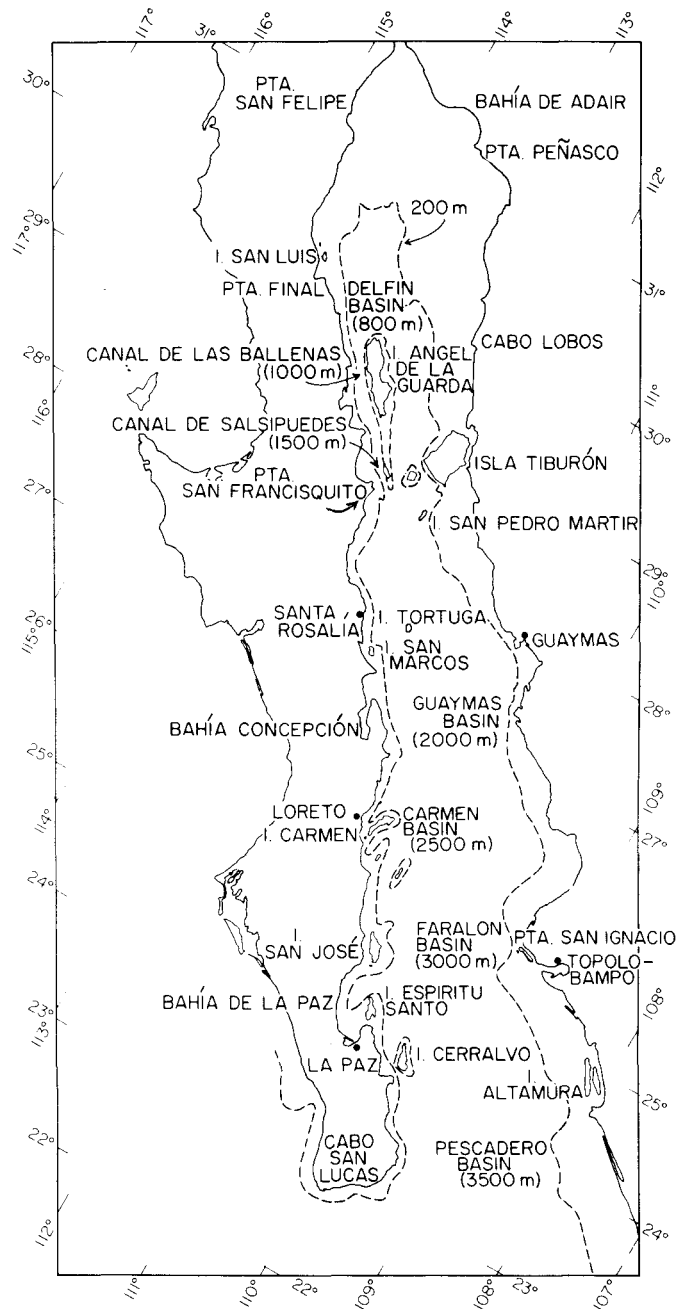


Figure 1. The Gulf of California. Edge of shelf and maximum depths of principal basins are indicated.

of winter and spring and then to shift to the western side during southwesterly winds of summer and early fall (Roden 1971). This is illustrated by the temperature distributions in Roden and Groves (1959) and in Figures 2 and 3 of the present paper; these distributions are based on the 1957 cruise measurements.

The many islands, particularly along the western Gulf, provide much extra coastline which augments the extent of mixing processes and upwelling: 1) in channels between islands or between islands and the coast, tidal mix-

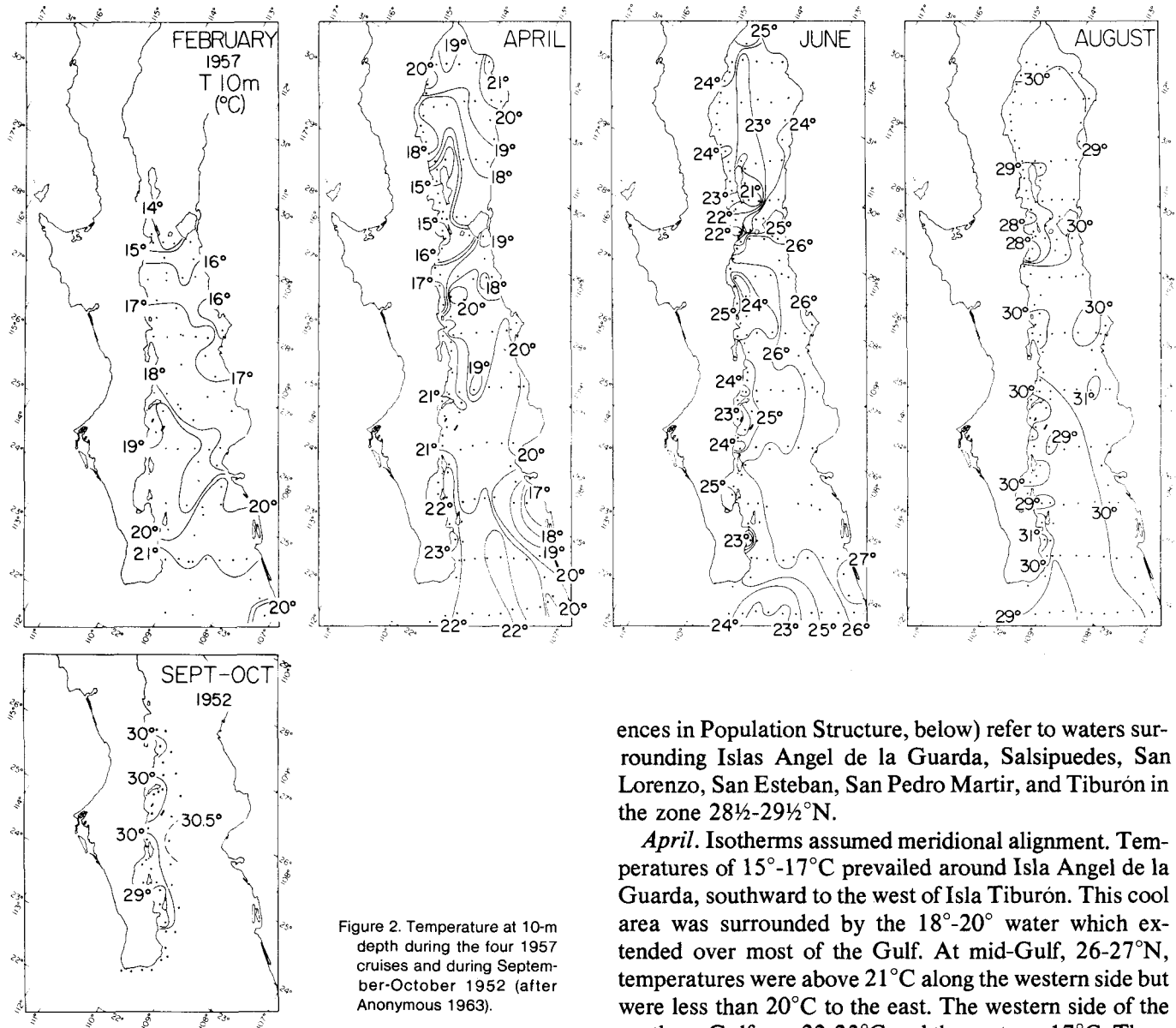


Figure 2. Temperature at 10-m depth during the four 1957 cruises and during September-October 1952 (after Anonymous 1963).

ing can be as intense as it is over the northern shelf and 2) island topography may be optimal for persistent upwelling because there is always some coastline normal to the shifting wind. Such diverse features preclude generalized explanations of nutrient renewal, plankton production, and hence, the distribution of plankton in the Gulf.

Temperature at 10-m Depth (Figure 2)

These temperatures are representative of the mixed layer into which the older life stages of most vertically migrating euphausiid species occurring here usually ascend in the nighttime. Larvae live only in this layer and the upper part of the thermocline (Brinton 1979).

February. Isotherms were roughly zonal, ranging from 14°C in the island channels to 20-21°C at the mouth of the Gulf. The “island channels” (cf. Regional Differ-

ences in Population Structure, below) refer to waters surrounding Islas Angel de la Guarda, Salsipuedes, San Lorenzo, San Esteban, San Pedro Martir, and Tiburón in the zone 28½-29½°N.

April. Isotherms assumed meridional alignment. Temperatures of 15°-17°C prevailed around Isla Angel de la Guarda, southward to the west of Isla Tiburón. This cool area was surrounded by the 18°-20° water which extended over most of the Gulf. At mid-Gulf, 26-27°N, temperatures were above 21°C along the western side but were less than 20°C to the east. The western side of the southern Gulf was 22-23°C and the eastern, 17°C. Thus, the eastern side was cooler in the southern Gulf than farther north.

June. The advance of seasonal warming continued, reaching 23-26°C over most of the Gulf. Only in the mixed waters of the northwestern island channels were temperatures as low as 21-22°C. Along the western side of the mid- and southern Gulf, temperatures responded to effects of the southerly winds and were 2 to 3°C cooler than to the east, thus differing from the condition in April.

August. Temperatures of 29-31°C now prevailed almost throughout the Gulf, with lowest values, to 28°C, again only in the northwestern island channels.

September-October. Temperatures observed in 1952 in the southern Gulf agreed with those of August 1957, indicating that summer conditions may persist into October.

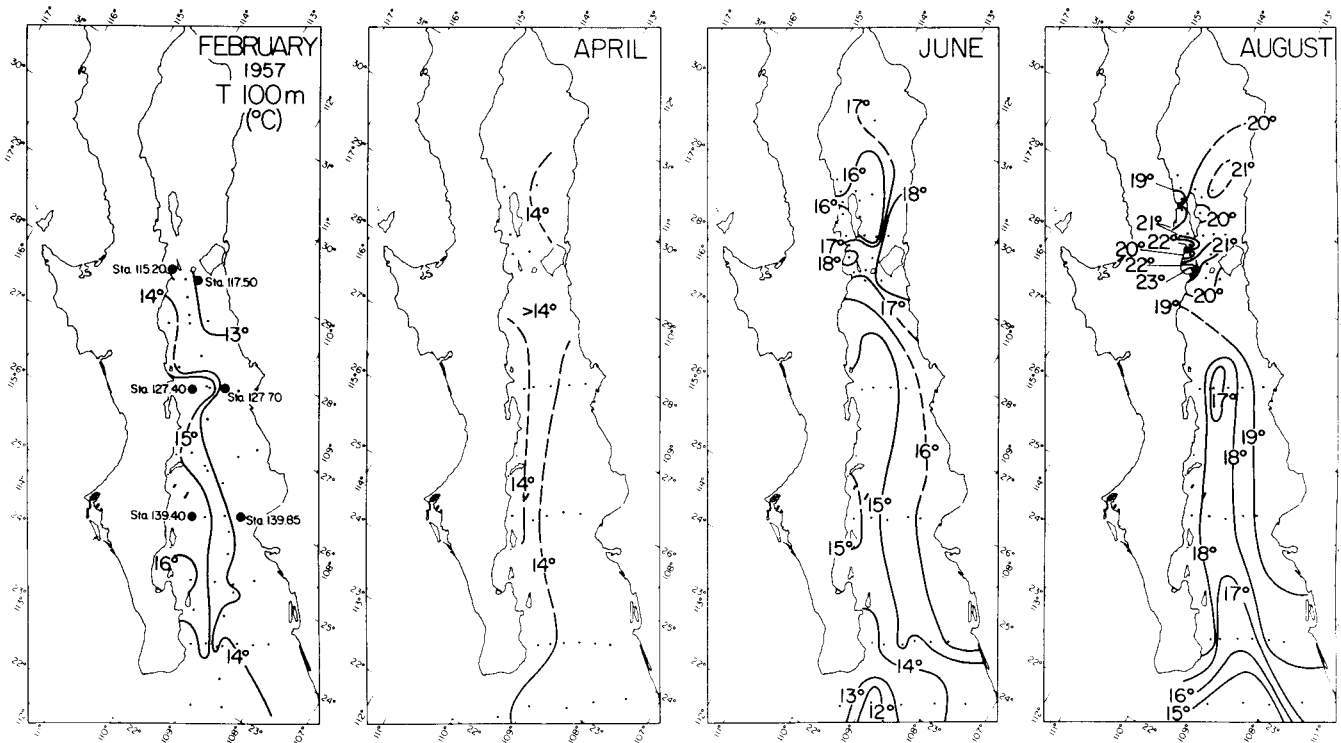


Figure 3. Temperature at 100-m depth (data from Reid et al. 1965). Positions of hydrographic casts are indicated as small dots. Stations for temperature profiles in Figure 4 are indicated by large dots.

Temperature at 100-m Depth (Figure 3)

At 100-m depth, temperature varies seasonally in the Gulf, whereas at 200 m, change is insignificant (Figure 4). At the deep mouth of the Gulf, 100-m temperature remained nearly constant, 14–16°C, throughout the year, whereas in the northern, shallower half of the Gulf, water at this depth warmed from 13–14°C in February–April to 19–23°C in August. In the sector of the island channels (Zone B, Figures 4, 18), this variation reflected the appearance of a summer thermocline following intense winter and spring mixing through the water column. In the mid- and southern Gulf the summer increase was evidently caused both by convection and downward conductive transfer from a surface subjected to progressively intense heating.

Seasonal variation at 100 m was greatest in the eastern Gulf (Figures 3, 4), evidently due to more penetrating June–August warming than took place along the western side where upwelling had become relatively stronger.

One hundred meters approximates the deep limit of the nighttime level of most euphausiids considered here (except the somewhat deeper living adults of *Nematoscelis difficilis*) and is near the upper limit of the levels to which migrating juveniles descend in the daytime, whereas adults of most species go deeper.

February. Upward bending of subsurface isotherms was conspicuous toward the eastern side of the Gulf. This was not evident in the 10-m temperature distribution,

indicating that upwelled water was not reaching the surface layer.

April. At mid-Gulf (26–28°N) there was <14°C water on both sides, but the eastern half was still generally a little cooler than the western.

June. The April situation was now reversed, as also in the surface layer. Isotherms now emerged toward the west.

August. The progression of summer warming was conspicuous, particularly over the broad shelf of the northern Gulf and along the eastern side. Ridging of subsurface isotherms along the Gulf's axis was evident toward the south.

Oxygen

The oxygen-deficient layer in the eastern tropical Pacific lies between the thermocline and about 700 m. The [O₂] in this layer may be as low as 0.05 ml/liter, which is near the limit of measurability. Water having this extreme minimum extended from 21°N off Cabo Corrientes at the mouth of the Gulf, southward to 11°N during June of 1974 (Brinton 1979). During 1957 this layer was diluted when it entered the Gulf. For example, at 23°N [O₂] of 0.1 ml/liter was unusual at any season and never occurred in water above 300 m except near the western side in April (Roden and Groves 1959). Moreover, the lowest [O₂] found half-way up the Gulf, at 27°N, was 0.2 ml/liter at 500-m depth.

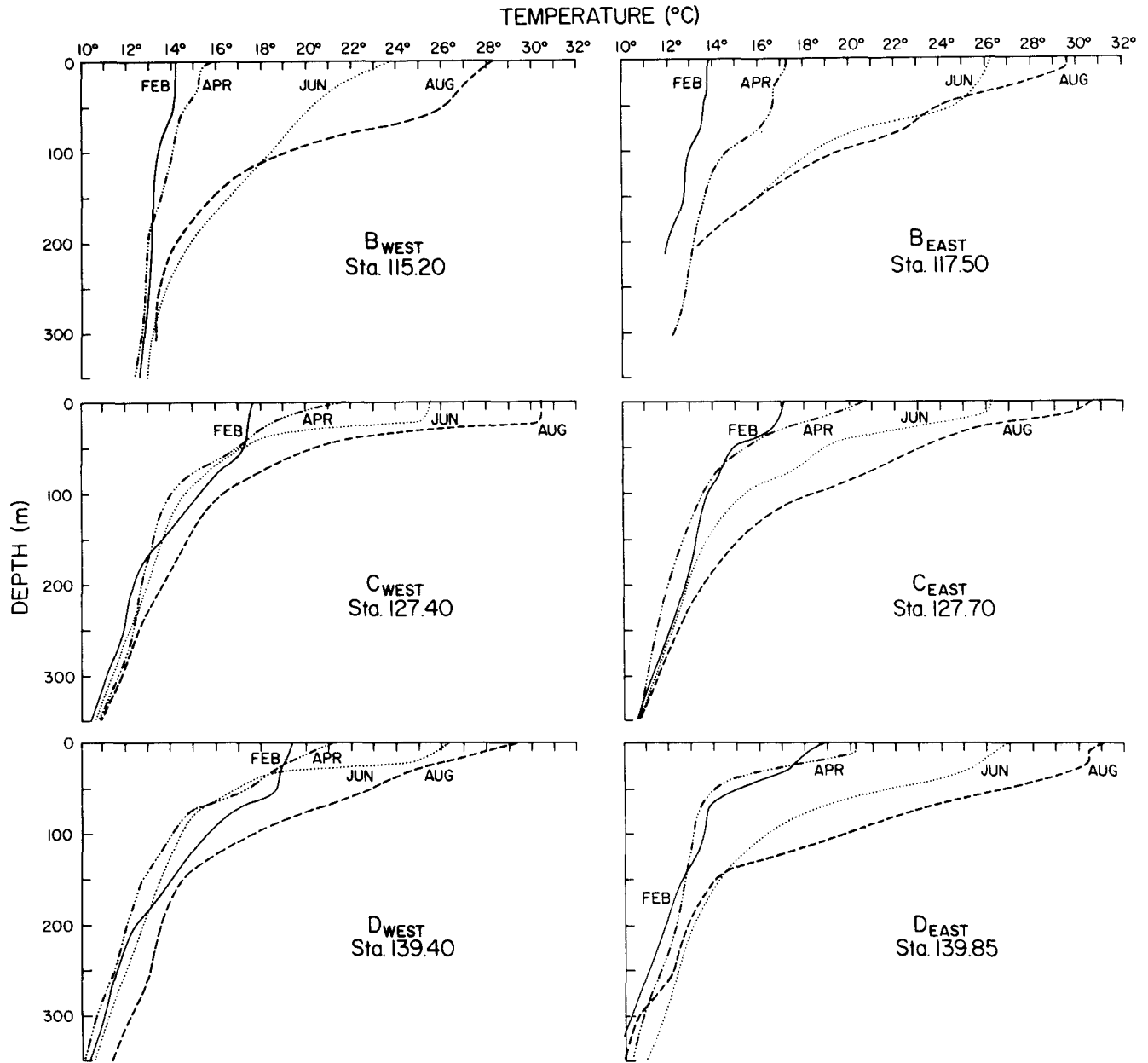


Figure 4. Temperature profiles for February, April, June, and August of 1957 at localities on eastern and western sides of Gulf of California. Zones (B, C and D) and localities are shown in Figure 18 (data from Reid et al. 1965).

Oxygen deficiency has much to do 1) with creating an environment for endemism among euphausiids in the eastern tropical Pacific and 2) with sharply restricting subtropical species and warm-water cosmopolites there. However, it appears not to be sufficiently shoal, extreme, or widespread in the Gulf to have had the same dominating role in the selection of which species are present.

Nevertheless, the depth of a given low-[O₂] surface may be used to show the spread within the Gulf of this salient property of eastern equatorial water as it relates to the 0-300-m range of depth in which most euphausiids are

expected to live. In the basins of the northern Gulf, the 1.5 ml/liter [O₂] surface is below 200-300 m during all seasons (Figure 5). It is deepest during April-June in the strongly mixed waters of the western island channels. By mid-Gulf it shoals to 100-200 m, and at the mouth, to 70-100 m. This surface tilts upward toward the east during the northeasterly winds of February-April, then upward toward the west in June.

Least [O₂] within the 0-300 m layer is at localities where the 1.5 ml/liter surface shoals to 70 m or less. Roden and Groves showed that low values of 0.1-0.5

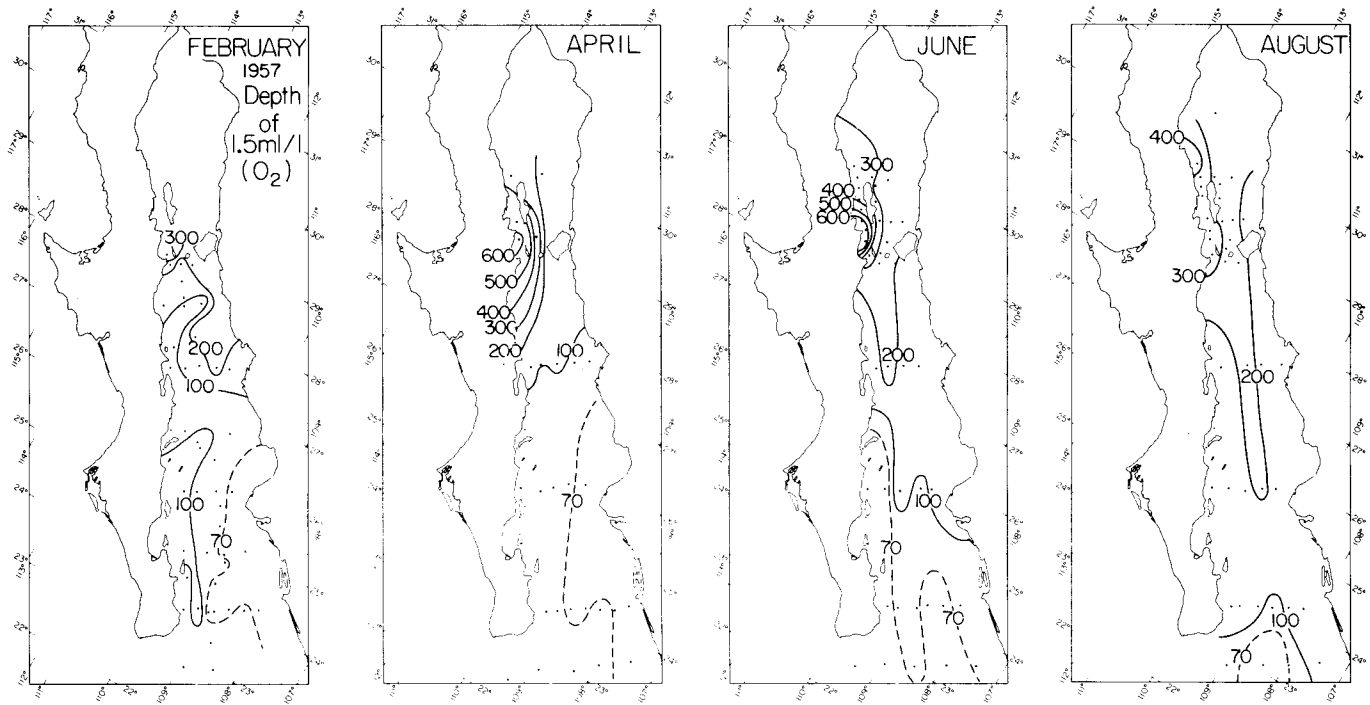


Figure 5. Depth of 1.5 ml/liter concentration of oxygen (data from Reid et al. 1965).

ml/liter are at 100-300 m in the southern Gulf, with the upper limit of the 0.5-ml/liter layer shoalest in February (40-80 m) and deepest in August (150-250 m).

Salinity

Seawater evaporation exceeds freshwater runoff into the Gulf (Roden and Groves 1959), but surface salinity beyond embayments ranges between 34.4 and 35.9 ‰. This compares with a maximum salinity of about 34.0 ‰ in the open sea to the west (Love 1973). Therefore salinity per se is not expected to influence the distribution and abundance of plankton in the Gulf. Estuaries and lagoons along the southeastern coast may nevertheless contribute nutrients to the Gulf, as indicated by the primary productivity maxima, which were observed seaward of that coast during August of 1972, associated with relatively low surface salinities of 34.4-34.5 ‰ (Gilmartin and Revelante 1978).

Currents

The geostrophic flow diagrammed in Figure 6 (after Wyllie 1966) shows mean surface flow to have been out

of the Gulf during February and April. Flow at 200 m—the daytime depths of many migrating euphausiids—was then generally consistent in direction with surface flow. According to Roden and Groves this upper level outflow is compensated by inflow at greater depths.

By June, surface flow had reversed, entering the Gulf across most of the mouth and persisting toward the north as a stream which shifted toward the eastern side by August. Flow at 200 m was opposite to surface flow during the summer.

Direct observations supplemented by computations of geostrophic flow have been made of cyclonic cells of circulation extending across the width of the Gulf during August 1978 (Emilsson and Alatorre in press). 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 described for August 1957. A similar eddy farther inside the Gulf was also indicated. This is pertinent in discussing exchange between the Gulf and the adjacent Pacific and how planktonic stocks may be maintained in the Gulf.

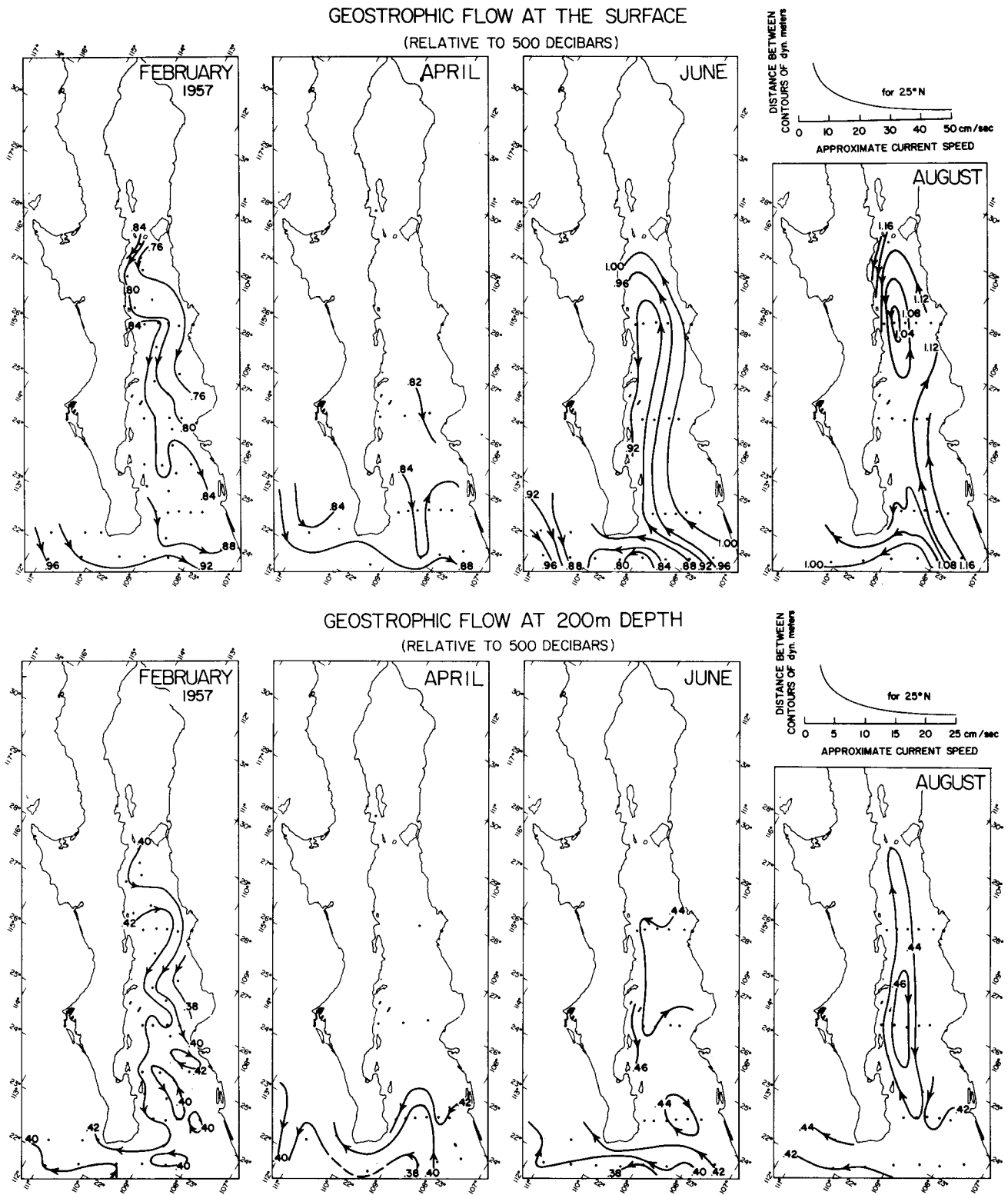


Figure 6. Geostrophic flow at surface and 200 m, relative to 500 decibar surface, inferred from casts at indicated localities (after Wyllie 1966).

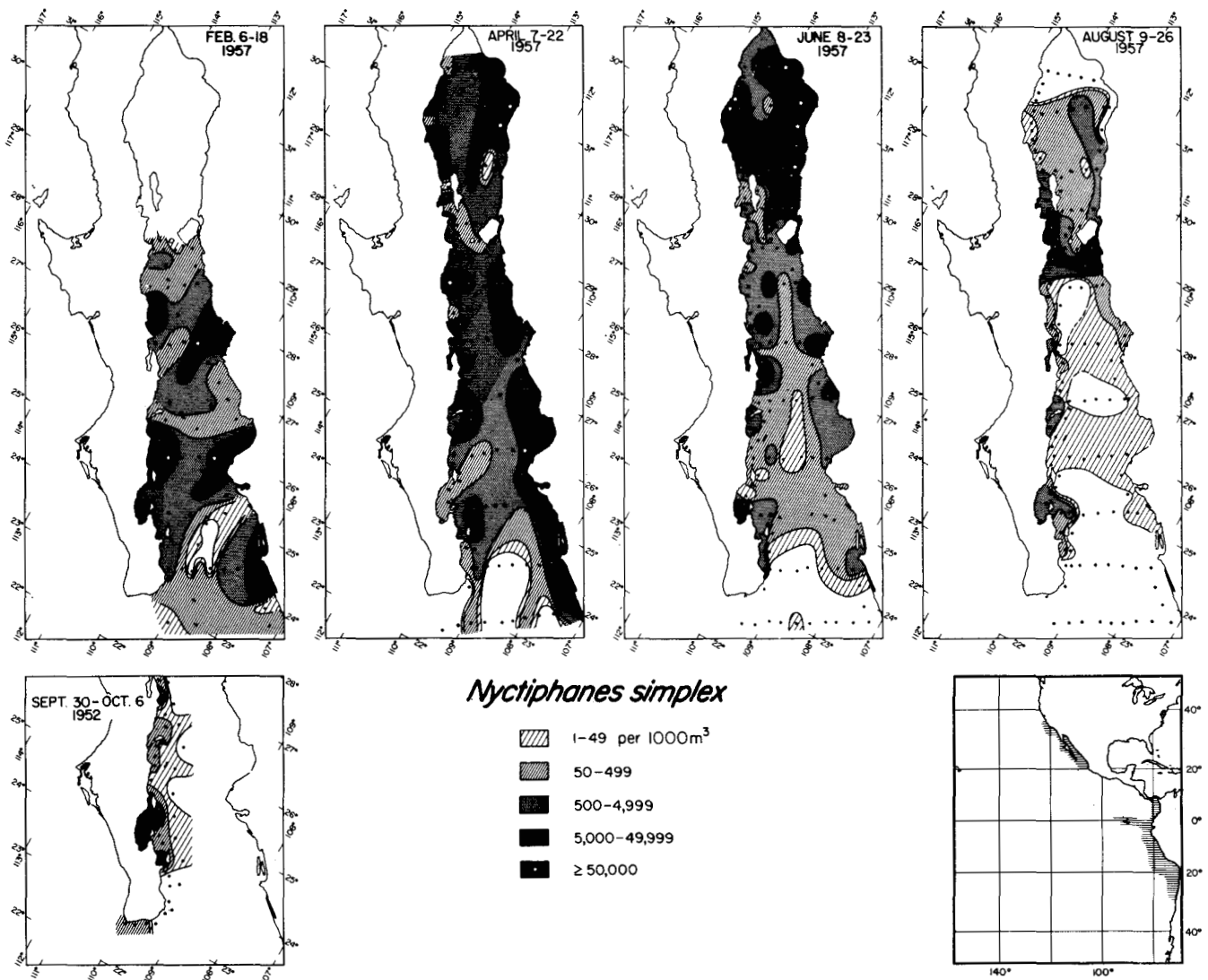


Figure 7. The coastal neritic species, *Nyctiphanes simplex*.

THE SPECIES DISTRIBUTIONS

Nyctiphanes simplex (Figure 7)

This euphausiid has the strongest neritic ties of those inhabiting the subtropical Californian region. Its range typically extends along Baja California northward to southern California, 34°N. During the warm year 1958, it reached 40°N off northern California.¹ *N. simplex* is the most abundant and widespread euphausiid in the Gulf of California during all seasons and has been observed in dense swarms by day (Steinbeck and Ricketts 1941) and in fields of luminescence at night (authors' personal observation), as "*Nyctiphanes*" (night shining) implies.

The vertical range of *N. simplex* seems to vary with

locality (Brinton 1967a, 1979). Clearest evidence of diurnal migration has been found seaward of the shelf. Species of *Nyctiphanes* in other oceans have been described as descending close to the shelf in the daytime where they may feed in the superficial sediments (Mauchline and Fisher 1969; Gros and Cochard 1978). High densities (>5,000/1,000 m³) in the Gulf were found in both day and night samplings.

During 1957, maximum numbers were generally near-shore or over the shelf. In February, when surface isotherms were oriented in an east-west direction (Figure 2), there were three zones with high densities, 27-28°N, 25-26°N, and 24-24½°N on the eastern side. These were located alternately with zones in which densities were moderate, generally <500/1,000 m³. The February distribution extended to the southernmost part of the Gulf, associated with southerly flow in the upper levels (Figure 6).

¹Published reports on the distributions of the Gulf species outside of the area of this study will not be cited repeatedly in the text to follow. These references are, for the California Current, Brinton (1967a, b, 1973); for the eastern tropical Pacific and its transition with the California Current at the mouth of the Gulf, Brinton (1979); for the overall Pacific, Brinton (1962); and for the global picture, Mauchline and Fisher (1969) and Brinton (1975).

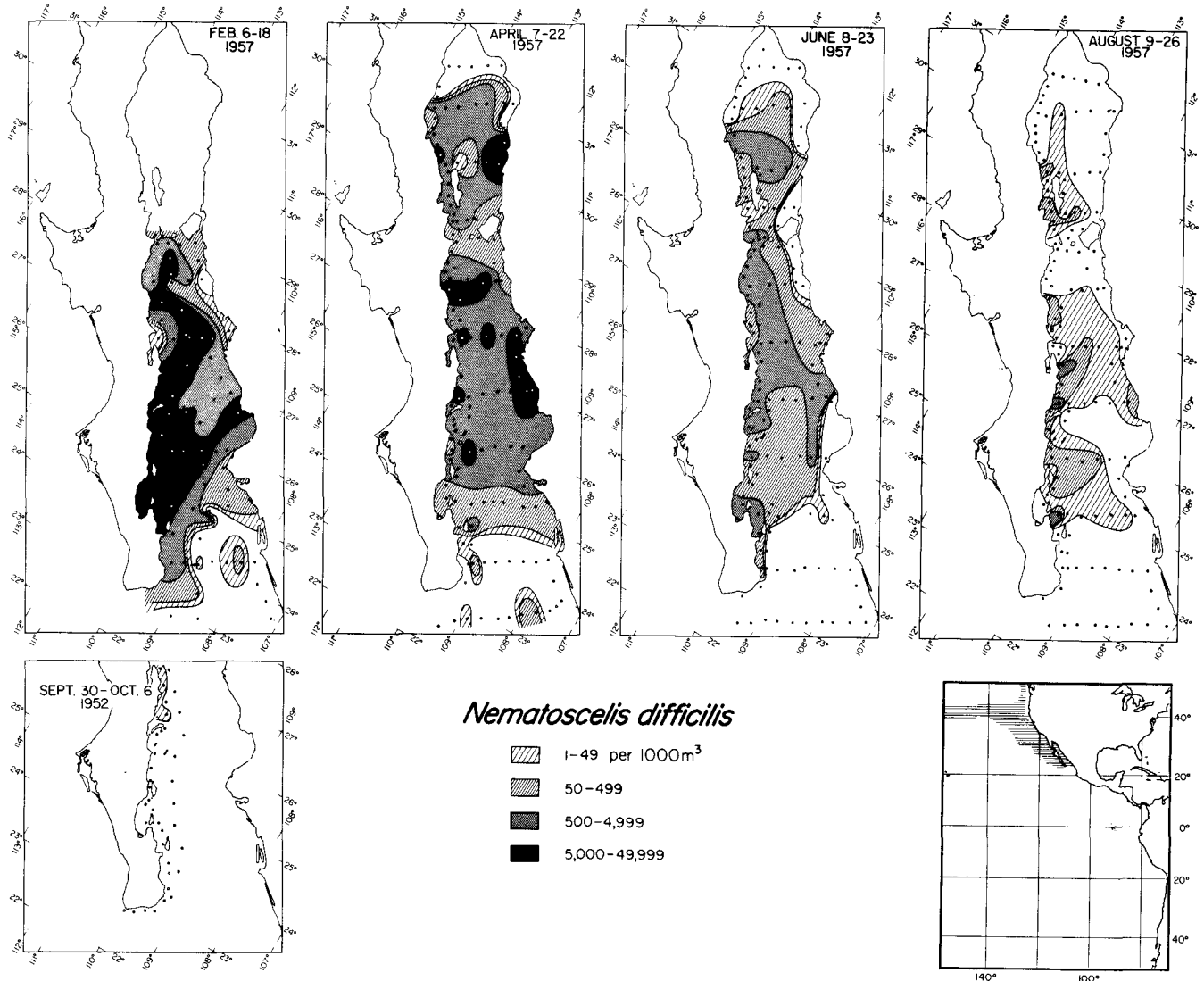


Figure 8. The warm-temperate species, *Nematoscelis difficilis*.

In April, high densities were along the Gulf's margins, particularly the eastern side. These extended as far south as the mouth, 24°N, where surface temperatures of 17-20°C persisted, now due to upwelling. Except for low numbers at the mouth, densities of *N. simplex* were >500/1,000 m³ almost everywhere in the Gulf, as the overall population peaked.

By June the upper water masses of the Gulf were warmer by 3-6°C than in April, and mean flow in the southern half of the Gulf was northerly. Highest densities were then general to the northern Gulf but were infrequent south of the island channels, diminishing to zero at the mouth.

When temperatures increased to 28-31°C in August, the population became reduced. The overall range of *N. simplex* remained unchanged except for retraction from the northernmost shelf region. Highest densities were

now around the island channels where temperatures were lowest, to 28°C. Peak numbers had been outside of these channels during the previous months. Pockets of moderate density were present on the western side of the Gulf to 24°S, evidently associated with summer mixing processes along that coast. The 1952 data on *N. simplex* suggest that those processes persist into October.

***Nematoscelis difficilis* (Figure 8)**

In the oceanic North Pacific *Nematoscelis difficilis* inhabits the temperate-subtropical transition zone of the North Pacific Drift, 40-45° N (= Subarctic-Central in water mass terms). It is also prominent throughout the California Current from southern Oregon to Baja California but is known from the Gulf of California on the basis of three low-density records near Bahia Concepción, September-October 1952 (Figure 8). This popula-

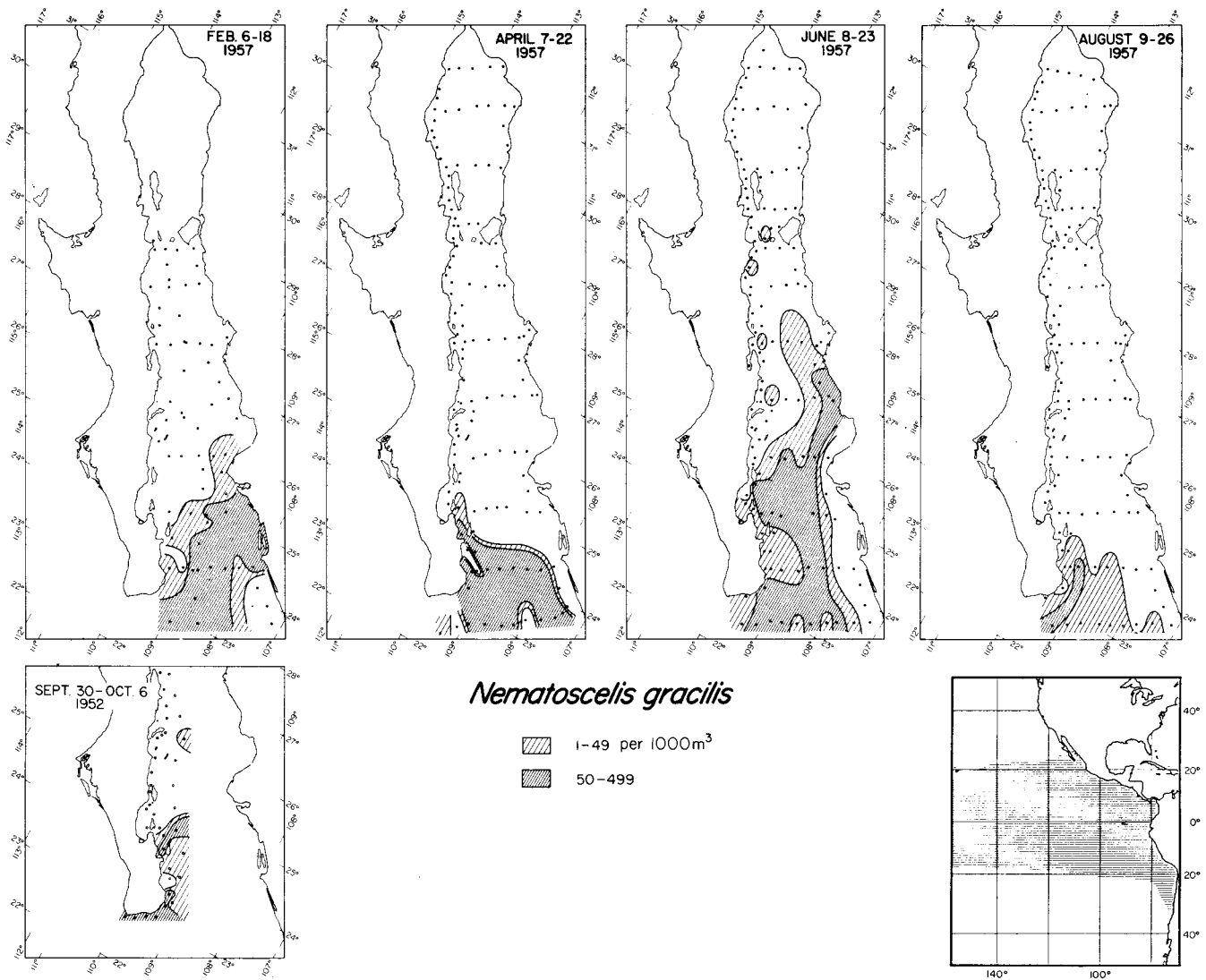


Figure 9. The tropical *Nematoscelis* species, *N. gracilis*.

tion was interpreted (Brinton 1962) as relict—isolated by tropical water at the mouth of the Gulf. However, the range of *N. difficilis* in the Gulf during 1957 nearly overlapped that of *Nyctiphanes simplex*, and this species was second in abundance of the Gulf euphausiids. These were altogether unexpected findings.

It is safe to state that *N. difficilis* lives deeper than *Nyctiphanes simplex*, though their vertical ranges overlap. The profiles for those species to the west of California and Baja California showed *N. simplex* tending to stay above approximately 100 m and adult *N. difficilis* below the mixed layer, except where stratification had broken down, as with upwelling (Brinton 1967a, 1979). (Weibe and D'Abramo [1972] showed that most *Nematoscelis megalops*, a close sibling and geographical analogue in the Atlantic of *N. difficilis*, are below 100 m at night in the Mediterranean Sea. Wiebe and Boyd [1978]

showed that *N. megalops* was spread through the upper 600 to 800 m in Gulf Stream cold core rings and apparently did not engage in diurnal vertical migrations.)

The February 1957 distribution showed *N. difficilis* concentrated toward the western side of the Gulf. High densities extended to the mouth. Though February data were lacking for the northern Gulf, this month is seen to be generally optimal for *N. difficilis*. Penetration into the southeastern Gulf of the 20°C isotherm at 10 m is associated with fewest numbers, but the presence of *N. difficilis* this far south assures exchange with the California Current population (cf. February 1957 distribution to west of Baja California in Brinton 1967b).

In April, instances of >5,000/1,000 m³ were fewer than in February in the southern half of the Gulf but did occur along both coasts to about 26°S.

From June to August, the diminishing population

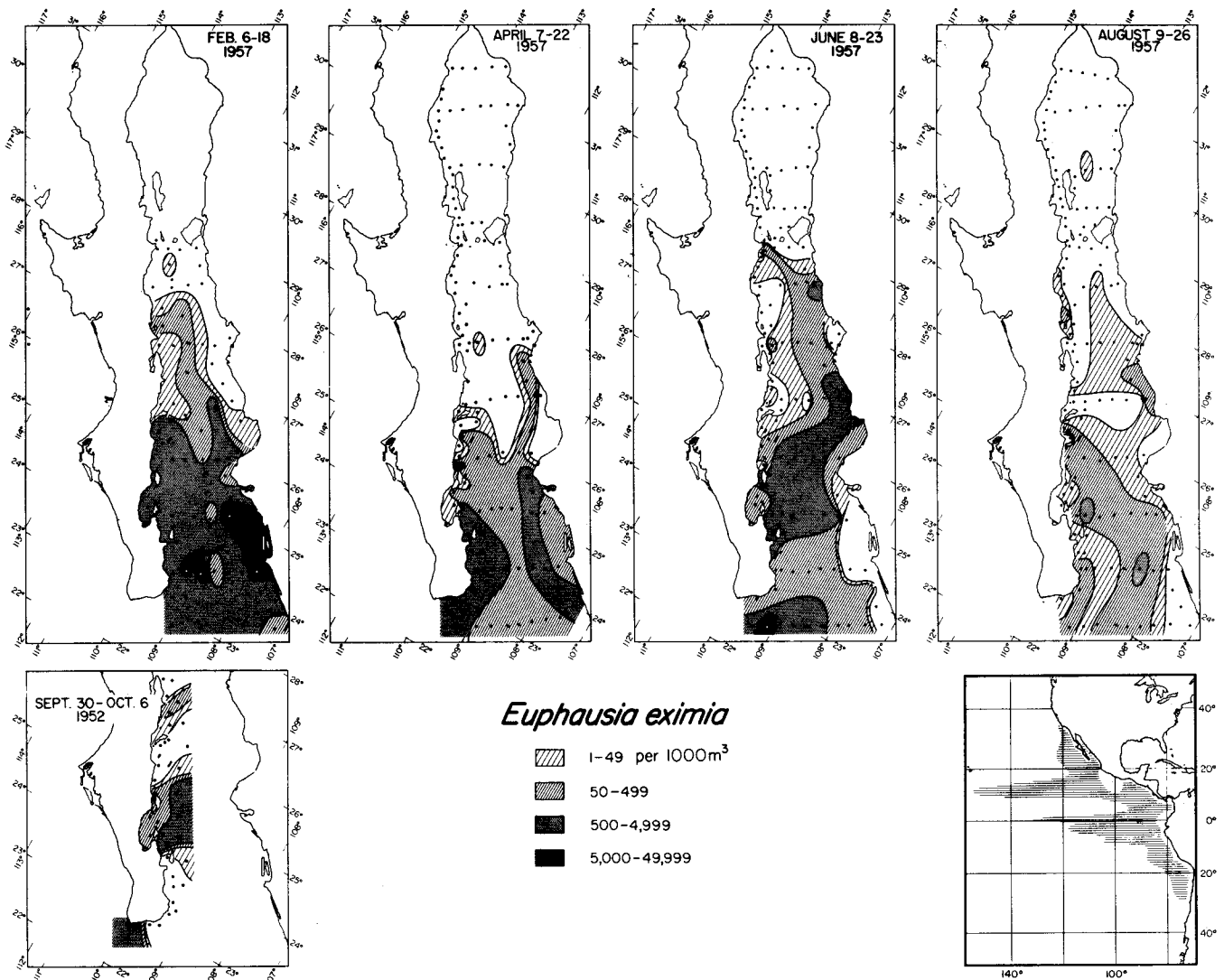


Figure 10. *Euphausia eximia*, which proliferates at margins of the eastern tropical Pacific.

tended to concentrate toward the west where coolest temperatures prevailed. Heated shelf waters to the north and east evidently provided limited refuge there, with occurrences primarily in or near the northern island channels and in the eastern zone south of Bahía Guaymas, 27-28°N. Tropical water entering the mouth of the Gulf—particularly to the east—appears to have compressed the distribution toward the north and west. Larvae, which customarily occur in the upper layer now warmed to 28-30°C, were represented by a single specimen, a furcilia, in the August catches.

If the vertical range of adult *N. difficilis* in the Gulf is greater than 200 m, as was supposed to be the case off southern California, this might induce mortality when the euphausiids are carried into neritic waters. However, in the terminal part of the California Current off Baja California, 23°N, adults migrated through less than 200 m,

apparently limited to strata where [O₂] was greater than about 1.5 ml/liter. Such a vertical range in the Gulf could help to explain the extensive presence of *N. difficilis* shoreward of the basins.

During June and August in the mid- and southern sectors of the Gulf (Figure 3, 4), high temperatures in the upper 100 m would be expected to limit *N. difficilis* to below that depth, and shoaling of the 1.5-ml/liter oxygen surface to less than 100 m could further narrow the vertical range, thereby all but eliminating this organism from the southern Gulf by August.

***Nematoscelis gracilis* (Figure 9)**

This species belongs to the euphausiid assemblage of the eastern tropical Pacific, while also ranging along the equatorial Indo-Pacific belt. The June 1974 data from the mouth of the Gulf of California (Brinton 1979) showed

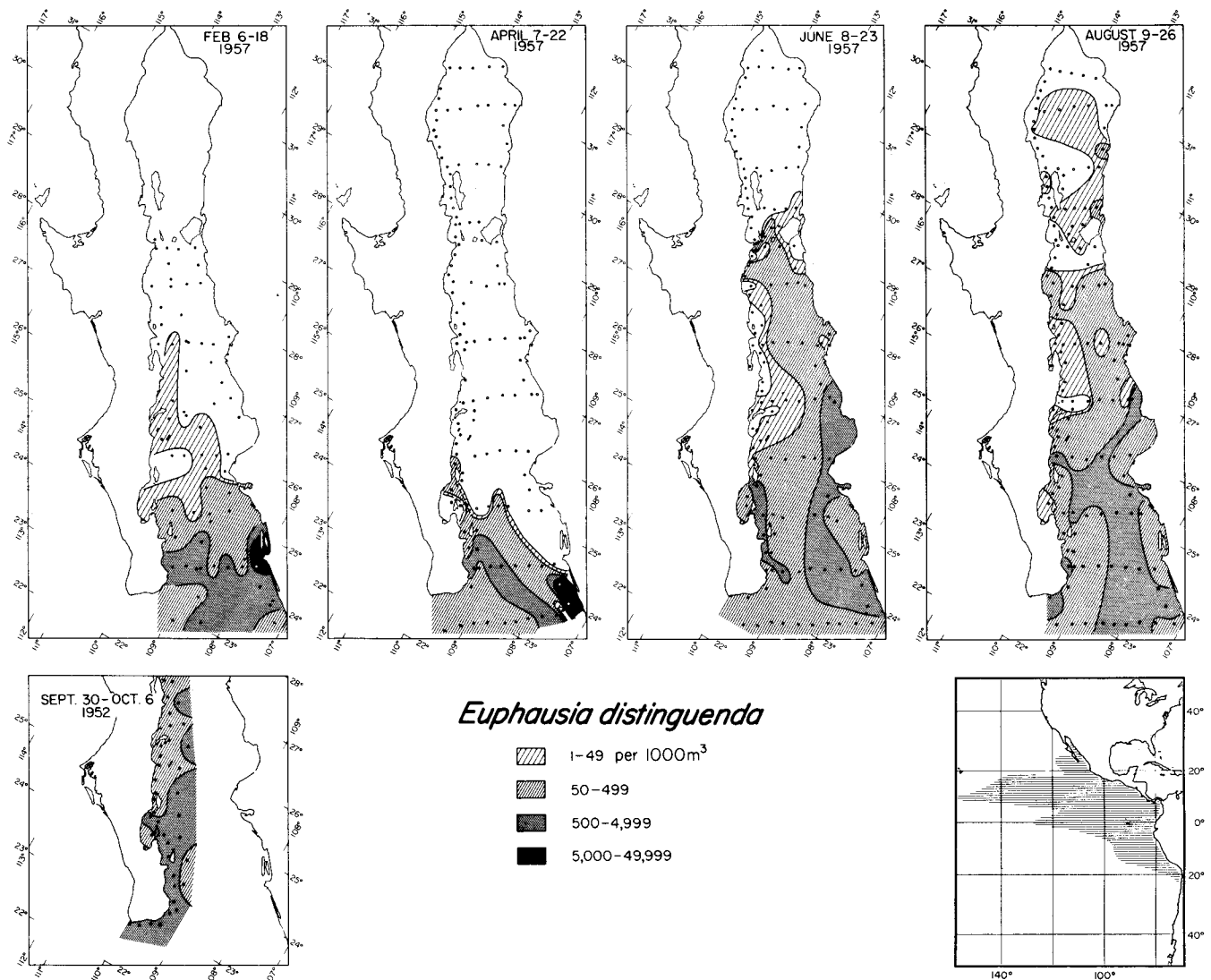


Figure 11. *Euphausia distinguenda*, endemic to the eastern tropical Pacific.

that the northern limit of *N. gracilis* abuts the southern limit of congener *N. difficilis* there. Adults of both species were beneath the 0-40-m layer at night, except at an upwelling locality to the west of Cabo San Lucas. In the daytime *N. gracilis* was within the extreme [O₂] minimum layer, 300-400 m, while *N. difficilis* was above 200 m, apparently limited by the 1.0- or 1.5-ml/liter [O₂] surface. Larvae and juveniles of both species ranged within or into the mixed layer, day and night.

During February of 1957, *N. gracilis* was present only in the southern Gulf. Its most northern presence was to the east where the oxygen minimum was shoalest (Figure 5) and where *N. difficilis* was sparse. Flow at 200-m depth shows this distribution to be within a system of slow eddy circulation. Elsewhere, where *N. difficilis* was dominant, flow was southerly (Figure 6).

The April distribution extended farthest north on the western side, as far as Isla Espiritu Santo, 24½°N. This

was within the warmest waters in the Gulf—>21°C at 10 m (Figure 2) and >14°C at 100 m (Figure 3).

June warming and strong northerly flow in the upper levels (Figure 6) brought *N. gracilis* to the northern island channels, 29°N, though its uninterrupted geographical distribution extended only to the Guaymas Basin, 27½°N.

By August, northerly transport to mid-Gulf was reduced. There, eddy circulation developed, and the range of *N. gracilis* retracted southward. The high temperatures general to the Gulf in August should be suitable for this species, in keeping with its distribution across the eastern tropical Pacific. Hence, a southerly trend in flow within the subsurface habitat of the bulk of *N. gracilis* may be limiting.

***Euphausia eximia* (Figure 10)**

E. eximia is abundant in the California Current to the west of Baja California, 21-30°N. The range extends

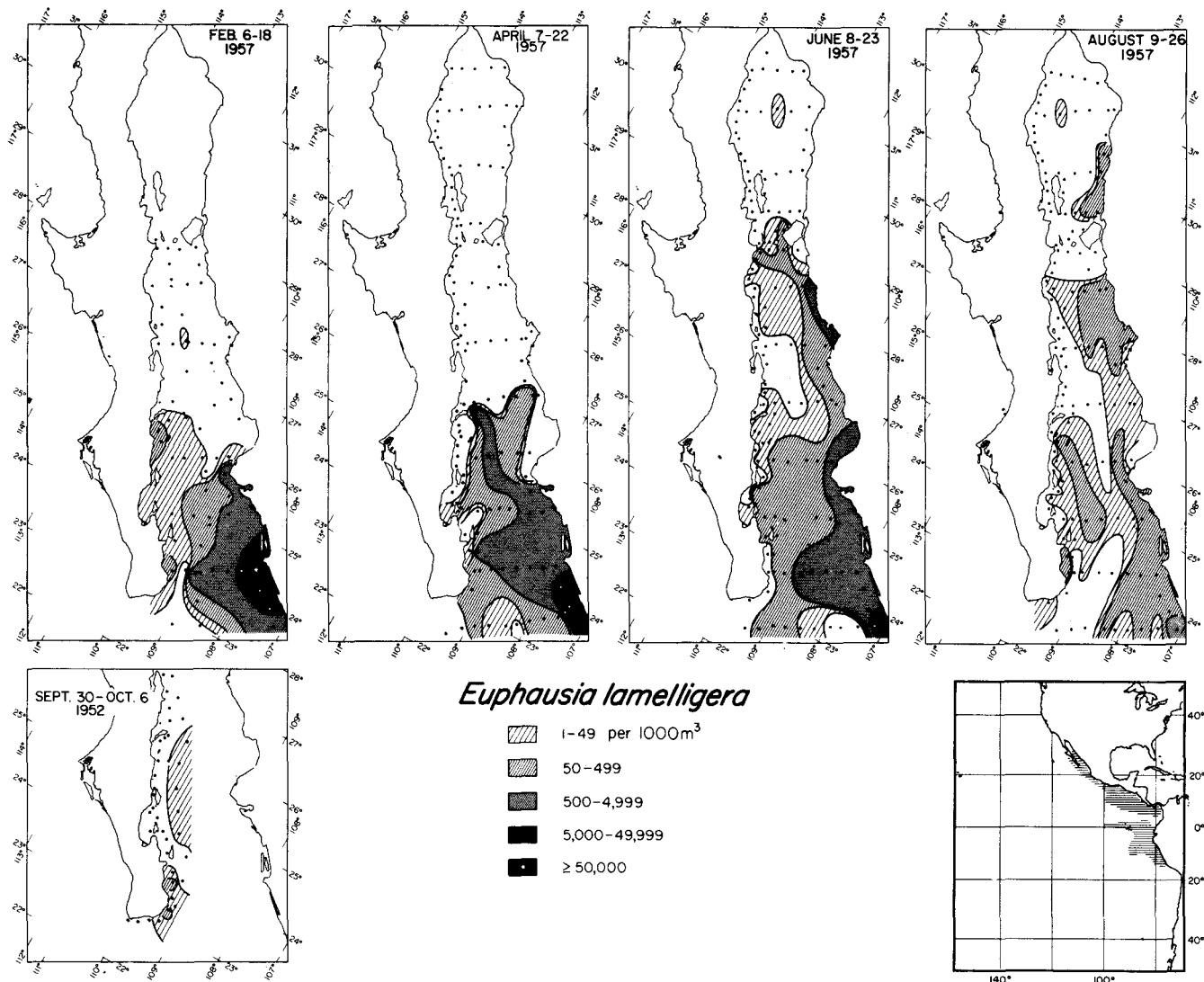


Figure 12. *Euphausia lamelligera*, coastal to the eastern tropical Pacific.

across the eastern tropical Pacific, but the species is sparse, nonreproductive, and avoids the mixed layer in waters where surface temperature exceeds 26°C and/or [O₂] in the minimum layer is <0.1 ml/liter (i.e. low). This includes the region between the equator and 21°N at the mouth of the Gulf.

E. eximia in the Gulf shifted little with season, appearing as a resident population from 28°N southward. As with the two warm-temperate species, *Nematoscelis difficilis* and *Nyctiphanes simplex*, highest densities of *E. eximia* were during February. Maxima for *E. eximia* were in a region of sluggish circulation in the southern Gulf. The most northern presence of significant numbers was in June when upper level flow was strongly toward the north, particularly on the western side. Lowest densities were in August when temperatures >26°C extended to 25-60-m depth (Figure 4).

Euphausia distinguenda (Figure 11)

E. distinguenda is endemic to the eastern tropical Pacific where it is widespread and is the most abundant euphausiid. The vertical range extends up into the warmest layer there and it is also tolerant of lowest [O₂], 0.05 ml/liter, at daytime depths. In both respects, *E. distinguenda* differs from *E. eximia*. It also differs from *E. eximia* in that its distribution in the Gulf fluctuates greatly with season.

In February, *E. distinguenda* was as far north as 27°N off Bahía Concepción. This may be a residual tongue; the August range showed that *E. distinguenda* is distributed nearly throughout the Gulf late in the year. Also, this mid-Gulf presence is to the west of the southerly flow at both the surface and 200 m (Figure 6).

As during February, high densities in April were at the mouth of the Gulf, with maxima over the eastern shelf.

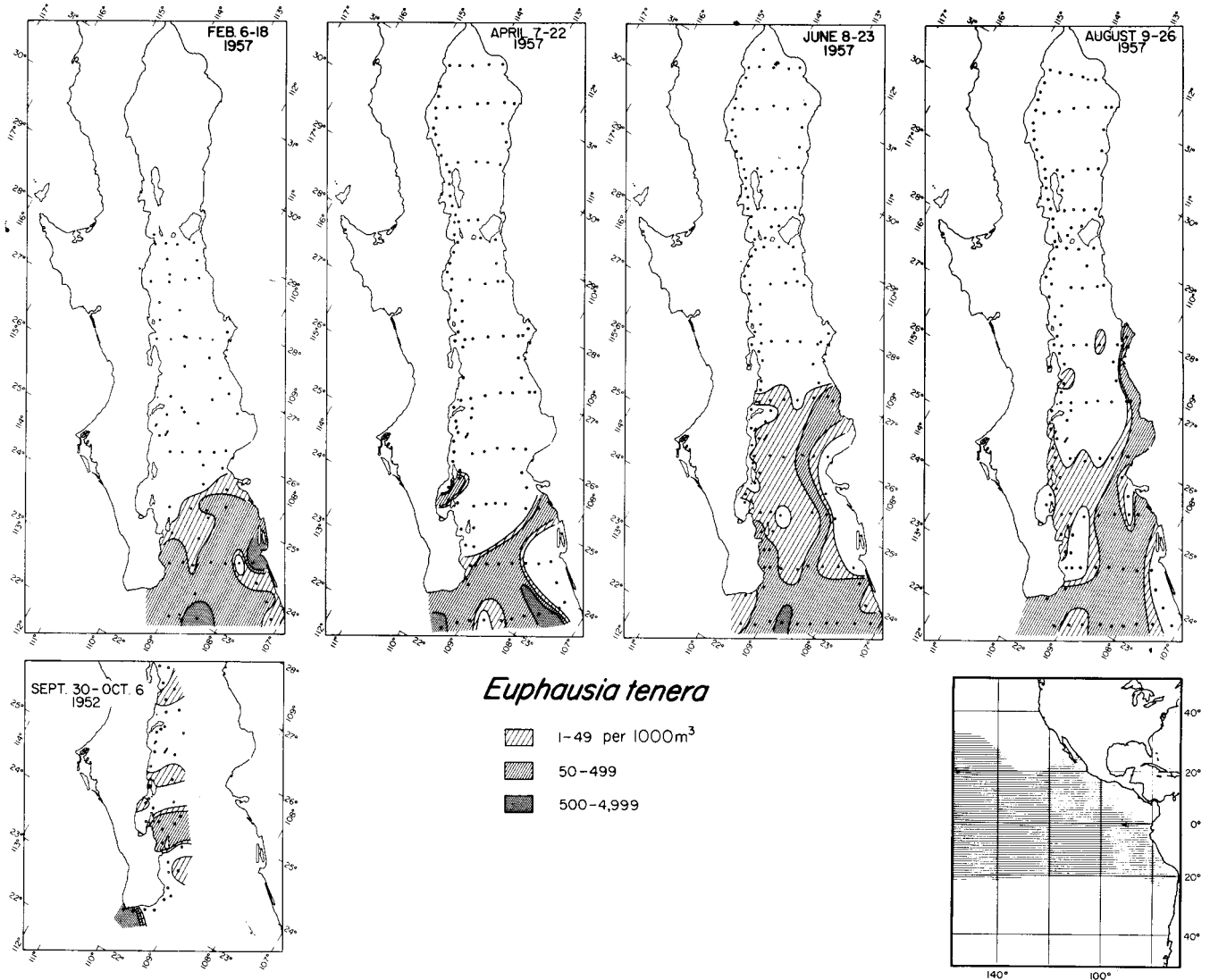


Figure 13. *Euphausia tenera*, oceanic in tropical seas.

E. distinguenda moved up the Gulf during June-August when northerly flow developed, mainly on the western side. Upper level temperatures now exceeded 22°C at 10 m and 15°C at 100 m. Presence of this organism in shelf waters of the northern Gulf in August must have resulted from northward flow through the island channels, followed by branching flow toward the east.

***Euphausia lamelligera* (Figure 12)**

E. lamelligera is more coastal than *E. distinguenda* in the eastern tropical Pacific where both are endemic. The two species are particularly closely related (Brinton 1975, 1979), but their overlapping coastal-versus-oceanic ranges within the tropics indicate incomplete habitat separation.

There appears to be even less separation in the Gulf than farther south. Here there is much shelf and slope area

in relation to basin, and a population having basic affinities with one system could readily be mixed with the other. Thus, the overlapping of *E. distinguenda* and *E. lamelligera* in the Gulf parallels the similarity between the distributions of the Gulf's two warm temperate euphausiids—typically oceanic *Nematoscelis difficilis* and coastal *Nyctiphanes simplex*.

Whereas the February-April range of *E. lamelligera* scarcely reached mid-Gulf, 27°N, the June-August period of northerly flow brought it to the northern shelf, mainly along the eastern slope. Breaks in continuity appeared in the zone of the island channels, near 29°N (cf. *E. distinguenda*). Highest densities were regularly in eastern waters at the mouth of the Gulf.

***Euphausia tenera* (Figure 13)**

E. tenera has a broadly tropical distribution around the globe. It is the smallest *Euphausia* species—slender,

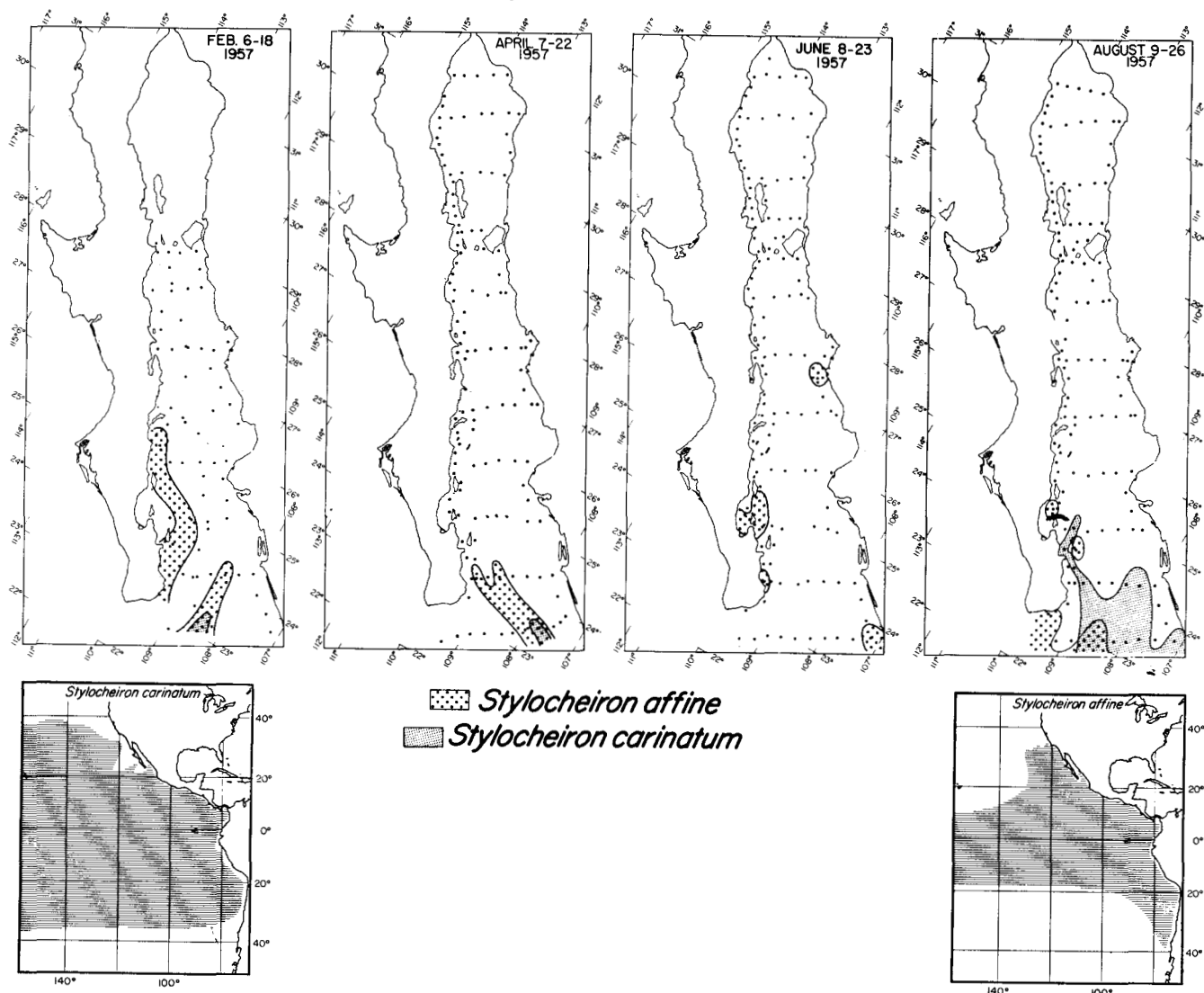


Figure 14. The two *Stylocheiron* species found in the Gulf of California. *S. affine* is present here as the East Equatorial Form. The overall range shown for *S. affine* excludes the relatively divergent Central Form.

rarely reaching 11 mm in length, compared with 12 and 14 mm for the more robust *E. lamelligera* and *E. distinguenda* or with as much as 25 mm for *E. eximia* in the Gulf. However the diurnal vertical migration of *E. tenera*, as determined in the eastern tropical Pacific, is as extensive as that of the others, about 0-300 m for the adult.

During February and April, *E. tenera* was limited to the southern Gulf. During the June and August periods of warming and inflow, the distribution extended barely to mid-Gulf, mainly within the northerly current near the eastern side. This, together with *E. tenera*'s consistently low density over much of the southeastern shelf at the mouth, 24-26°N, contributed to this being the *Euphausia* species at lowest density in the Gulf. These characteristics attest to the midocean, though not necessarily blue-water, affinities of *E. tenera* (Brinton 1962, 1979), relative to the eastern boundary current affinities of the predominant species in the Gulf.

***Stylocheiron affine* and *S. carinatum* (Figure 14)**

During 1957, these euphausiids were few, patchy in occurrence, and restricted to the southern Gulf. They were not present in the September-October 1952 samples. The intrusions show no significant pattern of seasonal change.

S. affine is represented in the general area by a "California Current Form" and an "East Equatorial Form," which have been observed to merge off the mouth of the Gulf (Brinton 1962). These, together with a "West Equatorial Form," are the basis for the composite range shown in Figure 14, inset. There were few adult specimens in the 1957 material, and no analysis of "Form" was attempted.

S. carinatum has been described as particularly sparse off the mouth of the Gulf and, when present there (Brinton 1962, 1979), as derived from tropical water to the south.

S. affine is a nonmigrator, living mainly within the thermocline. *S. carinatum* appears to be a short-distance

migrator, between the mixed layer at night and the thermocline in the day. Thus, both are distributed by upper level flow, being unable to avail of the deep counter-currents which often serve the strong vertical migrators in maintaining range stability.

Nematobranchion flexipes and Euphausia diomedea

Two other euphausiid species (distributions not shown here) were recorded at or near the mouth of the Gulf. Young of *Nematobranchion flexipes* were at 23°N, near the tip of the Baja California peninsula in June (one record) and August (two records). These specimens evidently came from the southernmost part of the California Current, inasmuch as *N. flexipes* has been found lacking in the most oxygen-deficient part of the eastern tropical region to the south.

The virtual absence from the Gulf of the widely tropical species *Euphausia diomedea* was unexpected. Single specimens were found at 23°N, south and southeast of Cabo San Lucas, in April and June. In August there were two records at the mouth of the Gulf and one at 27°N in the northerly stream on the eastern side.

E. diomedea is related to *E. eximia* (e.g. their larvae are almost indistinguishable), more so than to *Euphausia lamelligera*, *E. distinguenda*, or *E. tenera*. Evidently the Gulf is habitable by *E. eximia*, which “proliferates at the margins of the eastern tropical Pacific” (Brinton 1979), and not by its more tropical relative, *E. diomedea*.

EUPHAUSIID BIOMASS

In tropical and subtropical seas, the proportion of euphausiid biomass to total zooplankton biomass (wet displacement volume) retained by our nets varies between about 3% and 50% among localities. However, within oceanographic regions there is less variability. This is seen in the June 1974 values from three regions of the eastern Pacific (Brinton 1979): 1) southernmost California Current, \bar{x} = 12%, range 7-15%; 2) outer Gulf (Cabo San Lucas to Cabo Corrientes), \bar{x} = 8%, range 7-13%; 3) eastern tropical zone (Acapulco to Galapagos Islands), \bar{x} = 21%, range 9-49%.

These means of euphausiid biomass are higher than the 3 to 7% obtained inside the Gulf during 1957 (Figure 15). However, an annual mean of the four monthly means of total zooplankton biomass in the Gulf in 1957 is close to 300 cc/1,000 m³. This compares with the regional 1974 means outside the Gulf of 258, 312, and 305 cc/1,000 m³ for regions 1), 2), and 3) above, respectively. These latter values for total biomass were obtained in June 1974. The June 1957 mean inside the Gulf agreed with the mean of the four 1957 cruises. This indicates that biomass in the Gulf, at least in June, may be of the same order as that in the subtropical-tropical ocean outside.

However, the June 1974 data outside of the Gulf were

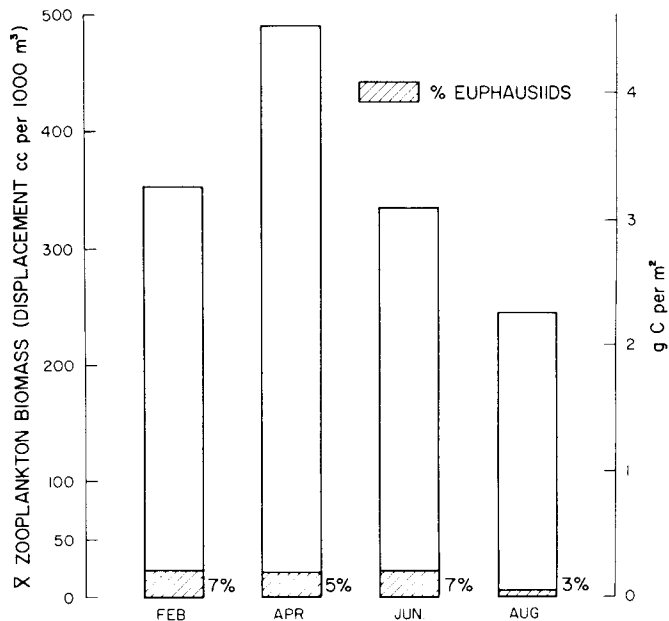


Figure 15. Mean euphausiid biomass shown as a percentage of the mean total biomass for each Gulf of California cruise in 1957.

obtained using a Bongo net, which differs in design from the 1-m ring net used in the Gulf in 1957. The Bongo net has no anterior bridle to signal a warning to the plankton. Bongo nets are proving to be more effective than the 1-m net in catching euphausiids of >8-mm length; smaller sizes are caught in equal number (authors' unpublished observations from California Current samples). Biomass of specimens 7-14 mm (which includes juveniles of all Gulf species + adults of all except *Euphausia eximia* and *Nematoscelis difficilis*) is underestimated by about two times when the 1-m net is used; of specimens 15-20 mm (includes adults of *E. eximia* and *N. difficilis*) by about four times. Hence, most Gulf species may have been substantially undersampled, leading to underestimation of euphausiid biomass by a mean of three times. The estimates of total numbers of euphausiids are much less affected by difference in the kind of net than are estimates of biomass because specimens >8 mm—mostly adults—are few compared with young stages.

Comparisons of biomass among the Gulf cruises and between the Gulf cruises and samplings outside the Gulf may nevertheless aid in placing the Gulf's plankton in perspective with that of the adjacent ocean. Euphausiid biomass in the Gulf was nearly constant at 20 cc/1,000 m³, or 0.2 g carbon/m², during February to June (means for all stations of each cruise; Figure 15). However, expressed as a percentage of the total, euphausiids were most, 7%, in February and June, and down to 5% in April when total biomass peaked.

This nearly uniform euphausiid biomass during February to June resulted from the simultaneous buildup in

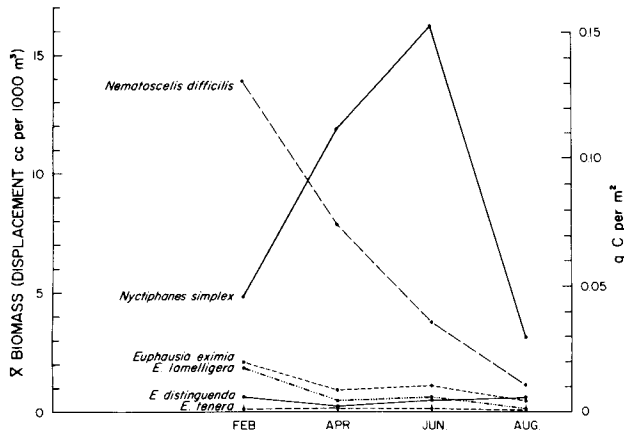


Figure 16. Biomass of six euphausiid species, each determined as a mean of values for all stations of each of the Gulf of California cruises in 1957.

Nyctiphanes simplex and decline from February onwards in *Nematoscelis difficilis* (Figure 16). February peaks in biomass for *Euphausia eximia* and *E. lamelligera* contributed little to the overall euphausiid biomass at that time, through certainly being significant in the southernmost part of the Gulf.

Euphausiids decreased to 3% in August, when the two bulk species were much diminished.

THE DEVELOPMENTAL PHASES— ABUNDANCES AND DISTRIBUTIONS

During 1957 in the Gulf, euphausiid recruitment and survivorship developed in an interpretable way in the three species that appear to be resident—those sufficiently numerous and geographically stable to show some independence from the populations outside the Gulf. These species are *Nyctiphanes simplex*, *Nematoscelis difficilis*, and *Euphausia eximia*.

The tropical species entering the Gulf are centered either 1) in the eastern tropical Pacific to the south (*Euphausia distinguenda* and *E. lamelligera*) or 2) in the ocean-wide equatorial belt to the south and west (*Nematoscelis gracilis* and *Euphausia tenera*, and *E. diomedae* of which one specimen was found north of the mouth, 23° 30'N). *E. distinguenda* and *E. lamelligera* reproduced substantially in the southern Gulf. Few larvae of *N. gracilis* and *E. tenera* (see below, Proportions of Life Phases), and none of *E. diomedae*, were found in the Gulf.

The calyptopis is the youngest larval phase retained by our nets, and its abundance will be used as a measure of recruitment to the populations of the species considered resident. Only general trends in survivorship and growth may be derived from the four bimonthly sets of samples.

There is some information on life-span of species of euphausiids similar to those living in the Gulf. Jörgensen and Matthews (1975) gave one year as the probably life-

span of *Nematoscelis megalops* in a Norwegian fjord. *N. difficilis* is very closely related to *N. megalops* and has the same life-span, or a little longer, based on Brinton and Wyllie's (1976) data from the California Current. Gros and Cochard (1978) interpreted *Nyctiphanes couchii*, a northeastern Atlantic relative of *N. simplex*, as living approximately two and a half years in the Bay of Biscay. *Euphausia pacifica*, in the California Current off southern California, lives to one and a half years, according to Brinton (1976); there is no information on the life histories of the tropical *Euphausia* species.

Nyctiphanes simplex

In the Gulf, *Nyctiphanes simplex* produced most calyptopes in February (Figure 17), the mean being 3,600/1,000 m³, which accounted for 80% of the total for the four 1957 cruises. Calyptopes declined in numbers as the year progressed. However, *N. simplex* was the only species to produce these larvae in significant numbers as late as August. High variances (Appendix I) are associated with these means, and with those below, in the discussion of regional variation in the occurrences of life stages. However, means will nevertheless be used here as indications of seasonal and regional trends in abundances.

Furcilia larvae increased during February-June, while calyptopes decreased, indicating improving larval survivorship as spring progressed. Youngest *N. simplex* calyptopes of 1-mm length (Boden 1951) must grow to oldest furciliæ of 5- or 6-mm length in about a month (cf. *N. couchii*; Le Roux 1973)—certainly in less than the two-month interval between the Gulf cruises. Hence, the June peak in furciliæ derives from calyptopes produced somewhat after the apparent peak in February.

Juvenile *N. simplex*, like the furcilia larvae, were most numerous during April-June, whereas adults showed a steady increase during February-June, with scarcely a decline in August.

Nematoscelis difficilis

Ninety percent of the February-August crop of calyptopes of *Nematoscelis difficilis* were produced in February when the mean density was 900/1000m³ (Figure 17). The coinciding February peak in the older larvae (furciliæ) indicates that maximum recruitment was earlier than February. (Gopalakrishnan [1973] found the larval life of *N. difficilis* to be of the order of 30 days.) Calyptopes declined during April to June and ceased to be produced by August. Adults and larvae were both most numerous in February. Whereas *Nyctiphanes simplex* adults increased through the year, those of *N. difficilis* decreased, though in both species the adult stock remained nearly constant. It appears likely that the numerous larvae of February, or somewhat earlier, led to the April-June peak in juveniles and then to a substan-

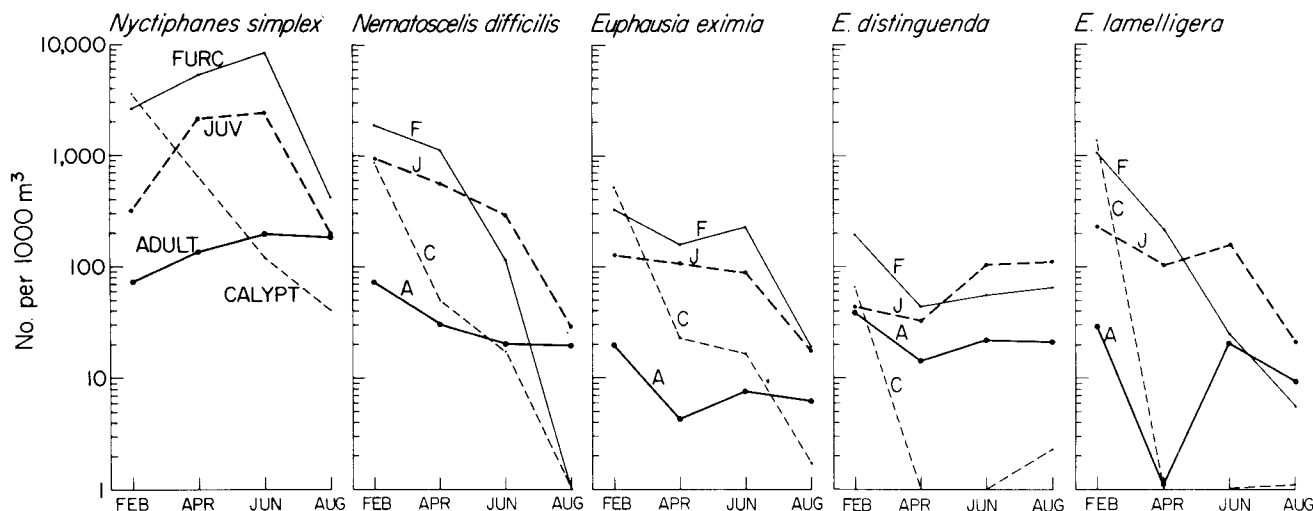


Figure 17. Seasonal variation in abundances of life phases of five predominant euphausiids. Values are means of all values, each Gulf of California cruise in 1957. See Appendix I for data on *Nyctiphanes simplex* and *Nematoscelis difficilis*.

tial stock of young adults in August, clearly the most stressful period for *N. difficilis*. These adults would be expected to reproduce during the ensuing winter.

Euphausia eximia

This species followed nearly the same pattern as *Nematoscelis difficilis*. Ninety-five percent of all calyptopis larvae were observed in February, with their production decreasing nearly to zero by August. In *E. eximia* there were relatively more furciliæ entering the population as late as June. Adults were then at a second peak, following a February maximum. Adults held their numbers into August, evidently receiving input from the June juveniles, whereas the younger phases were much reduced.

Euphausia distinguenda

Of the tropical species, *E. distinguenda* showed the most stability through the year, with furciliæ, juveniles, and adults nearly constant in numbers. However, the youngest larvae (calyptopes) were significantly present only in February inside the Gulf. Substantial recruitment from the south may have occurred during the June-August period of northerly flow.

Euphausia lamelligera

The distribution of *E. lamelligera* (Figure 12) shows that the center of distribution of this coastal species is at the mouth of the Gulf and southward. As in the other species, peak recruitment in the Gulf was in February. Furciliæ steadily declined thereafter. Adults remained nearly constant in numbers, except for a near absence in April at the end of the spring period of outflow.

Regional Differences in Population Structures

The Gulf is considered here to consist of four zones (Figure 18), which roughly reflect common limits of seasonal shifts in zonation of the euphausiids (Figures 7-14).

These zones are modified from those proposed by Gilbert and Allen (1943) that corresponded with differences in diatom abundances and are like those proposed by Round (1967) for phytoplankton floras. Round's northern and southern zones apply to euphausiids. His central zone is subdivided here to separate the distinctive "island channels," 28½-29½°N, from "mid-Gulf."

Although scarcely 100 km apart, the two sides of the Gulf nevertheless differ with respect to 1) extent of continental shelf, hence of neritic mixing through the water column, and 2) nutrient renewal through upwelling in a given season. In the northern Gulf, in the zone of island channels and in the mid-Gulf, mean temperatures (10-m depth) are somewhat lower on the western side throughout the year (except in mid-Gulf in February; Figure 19). In the southern Gulf, the eastern side is cooler during February-April, and the western side during June-August.

Nyctiphanes simplex and *Nematoscelis difficilis*, the two species that utilize most of the area of the Gulf, were examined for east-west differences in population characteristics in the four zones.

Nyctiphanes simplex (Figures 18A, 20A). In the northern Gulf and in the island channels (zones A and B), calyptopis larvae were more abundant on the eastern side throughout the year, except in August when the western island channels became the principal refuge for the presence of calyptopes.

In the southern half of the Gulf (zones C and D) calyptopes were commonest on the eastern side in February, with the maximum shifting to the west during April-August. However, the dominance of zones A and B in the production of calyptopes is seen in Figure 20A, in which the mean value for the eastern Gulf during all of February-June (four zones combined) is well above that for the western side.

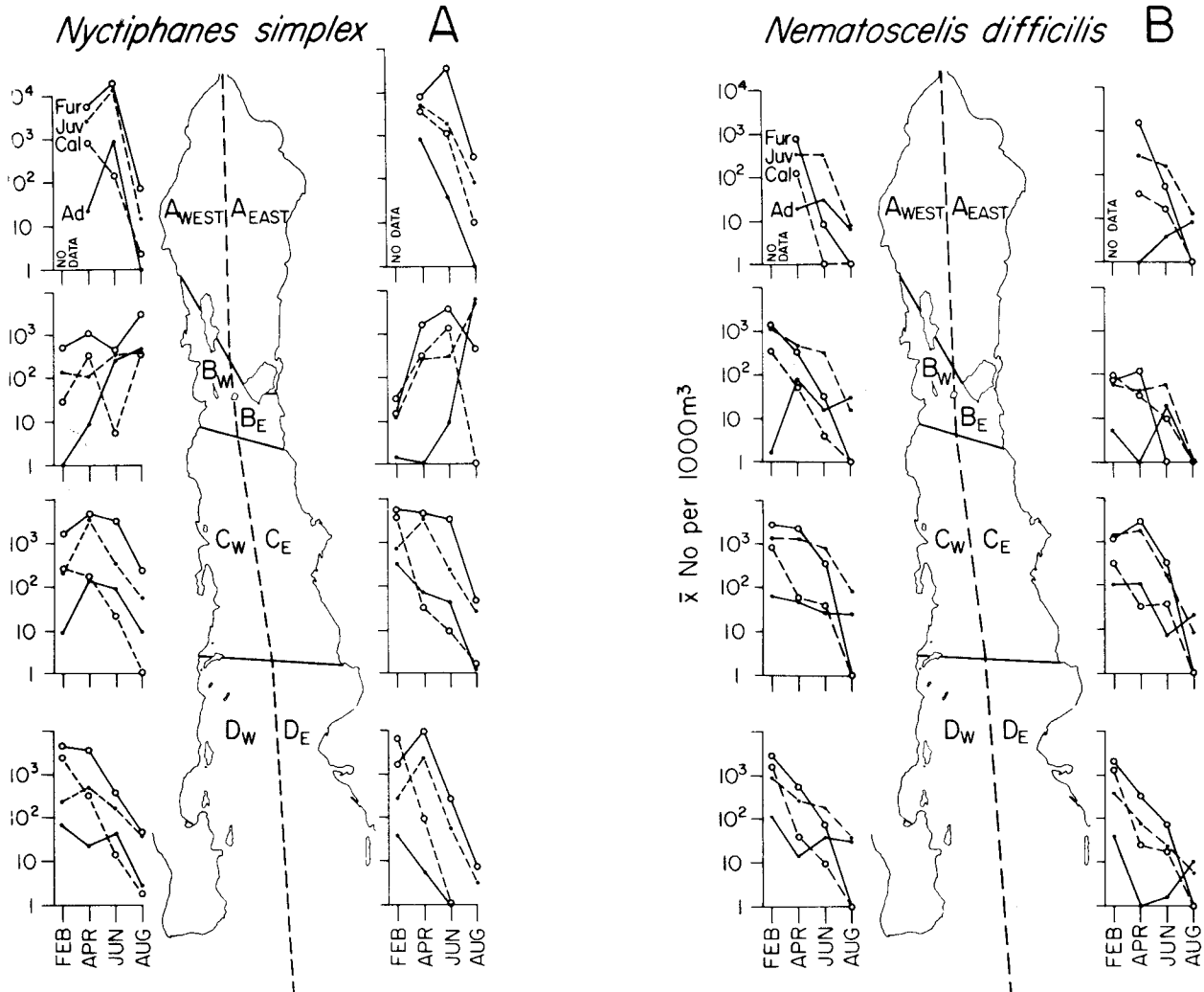


Figure 18. Seasonal changes 1957 in abundances of life phases of a) *Nyctiphanes simplex* and b) *Nematoscelis difficilis* on eastern and western sides of Gulf of California. (See Appendix 1 for data.) Zones are approximated from characteristics of euphausiid distributions: A, northern Gulf; B, zone of island channels; C, mid-Gulf; D, southern Gulf.

Furcilia larvae averaged a little more numerous to the west in February and August (Figure 20A), largely because of higher numbers in the western island channels than in the eastern, zone B (Figure 18A). During April-June the overall maximum moved to the east, affected largely by the distribution in the upper half of the Gulf (zones A and B).

Like calyptopes, juveniles and adults were more concentrated to the east during February-April. The difference was more significant in the adults, due 1) in February to high numbers to the west in zone C, though most adults were then in zone D, and 2) in April to high numbers to the west in zone A, to which zone the maximum for adults had then shifted.

By June the maxima for juveniles and adults had moved toward the west, with the abundances in the northern Gulf (zone A) most strongly affecting the mean values shown in Figure 20A. By August, maxima for both of

these older life phases had shifted back to the eastern side; however, Figure 18A again shows that the easterly shift only took place in the north, though in both zones A and B.

Nematoscelis difficilis (Figures 18B, 20B). In the northern Gulf with its extensive shelf, zone A, most calyptopes were on the western side in April, with the maximum shifting to the east in June (Figure 18B). Somewhat more furciliae were to the east in zone A during both April and June. Juveniles declined almost equally on both sides of the northern Gulf as the year progressed. More adults were to the west during April-June, but by August there was no east-west difference.

In zone B, mixing is to considerable depths in channels between islands and between islands and the mainland. To the west, where the deep Canal de las Ballenas and Canal de Salsipuedes are generally cooler than surrounding waters (Figure 19), larvae were more abundant

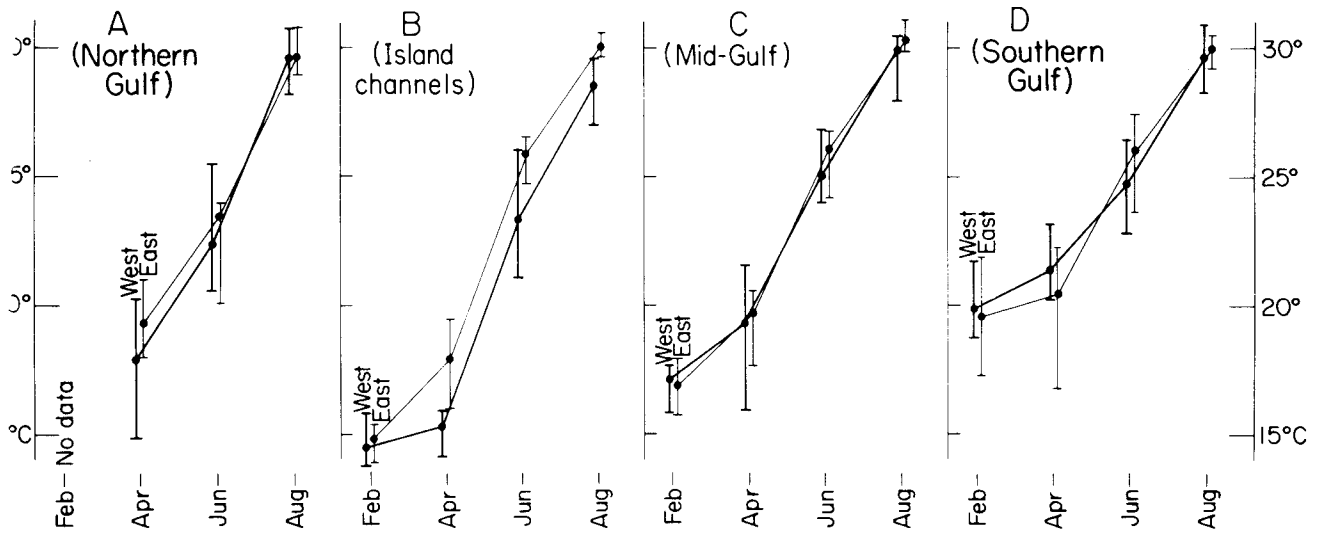


Figure 19. The 1957 10-meter temperatures for eastern and western halves of each zone of the Gulf of California, plotted as means and ranges.

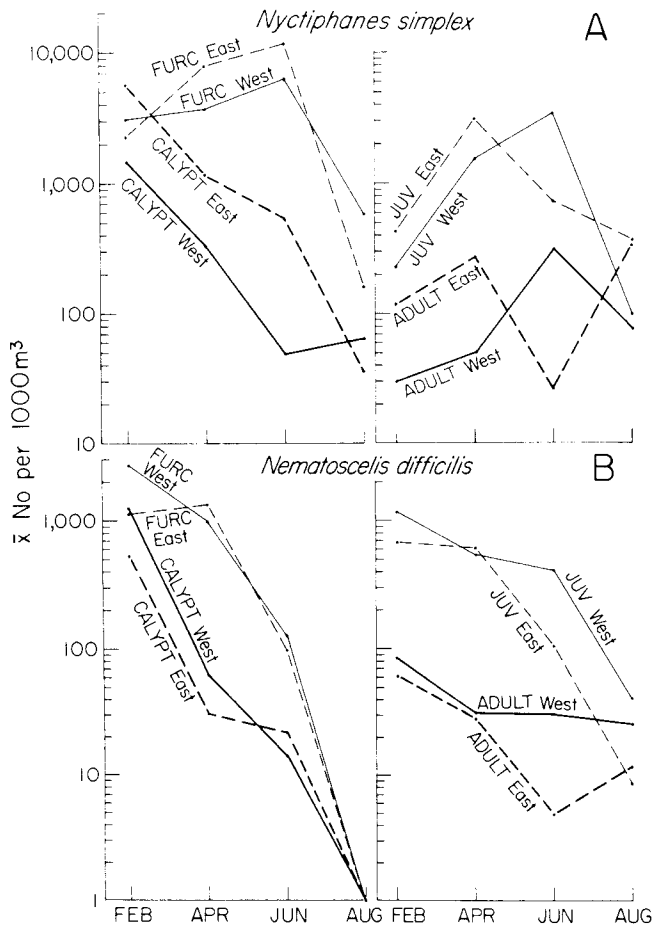


Figure 20. The 1957 seasonal abundances of life phases of the two predominant warm-temperature species, comparing eastern and western sides of the Gulf of California. A. *Nyctiphanes simplex*, B. *Nematoscelis difficilis*. (See Appendix I for data).

throughout the year than to the east, off Isla Tiburón. Juveniles declined progressively through the year on both sides of the zone, while numbers of adults fluctuated.

In zone C, mid-Gulf, there were more calyptopes to the west than to the east during the reproductive period, February-April. Juveniles were more numerous in this zone than to the north, and adults were more consistent in numbers through the year than elsewhere.

On both sides of zone D, the southern Gulf, calyptopis and furcilia larvae steadily decreased to zero as the year progressed. Juveniles and adults were regularly more abundant on the more oceanic, western side.

Thus, significant east-west differences in *N. difficilis* were few:

1) Calyptopes averaged somewhat higher to the west during February-April (Figure 20B), a consequence of higher abundances to the west in all four zones. During June, they were more abundant to the east in three of the zones and were equally distributed in the fourth.

2) Furcilia were more abundant to the west during February, particularly in zones B and C, but were equally distributed during April-June.

3) Juveniles and adults were about four times more abundant on the western side during June-August, with the least such difference in the shallow northern Gulf, zone A.

TEMPERATURES AT WHICH YOUNGEST LARVAE OCCURRED

Temperature at 10-m depth in the Gulf ranged between 13 and 32°C during February-August 1957. The youngest larvae sampled (calyptopes) of one or another euphausiid species were found across the full range of

temperature, except the maximum, $>31^{\circ}\text{C}$ (Figure 21). However, it was evident (Figure 17) that in all species most reproduction was in the winter.

In this discussion, a given $^{\circ}\text{C}$ includes all increments between that $^{\circ}\text{C}$ and the next, i.e. " 14°C " includes $14-14.9^{\circ}\text{C}$.

February temperatures were the lowest observed, $13-20^{\circ}\text{C}$, and in April the range was $15-22^{\circ}\text{C}$. General warming had begun by June.

Nyctiphanes simplex produced 80% of its calyptopis larvae in the mid- and southern Gulf (zones C, D) in February at localities where temperatures were $17-18^{\circ}\text{C}$ (Figures 2, 21). Most of the smaller April crop was where temperatures were $14, 17, \text{ and } 20^{\circ}\text{C}$, with the highest mean at 14°C . These low temperatures no longer prevailed in the upper layers in June when the small number of calyptopes were found mostly at $23-24^{\circ}\text{C}$, near the lower limit of temperature found for that cruise. In August most of the relatively small maximum of calyptopes were found at 27°C —again the lowest temperature encountered.

From the lowest to the highest temperatures there is a declining trend in the percentage of stations at which calyptopis larvae of *N. simplex* were found, regardless of numbers. This trend (Figure 21) is punctuated by spikes at 14°C , 23°C , and $27-28^{\circ}\text{C}$, corresponding to the April, June, and August maxima in absolute numbers.

In *Nematoscelis difficilis* the February and April temperatures at which calyptopis larvae peaked were $17-19^{\circ}\text{C}$ (Figure 21). This range was general to mid-Gulf in February and mainly on the western side in April. The few larvae produced in June were scattered across the full available range of temperature of $22-27^{\circ}\text{C}$. Percentages of stations at which calyptopes were found tended to be highest toward the lower end of the temperature range.

In the three principal *Euphausia* species living in the southern half of the Gulf during their main period of reproduction, February-June, calyptopis larvae were found concentrated at 20°C during the February maximum, again at 20°C in April in the case of *E. eximia*, at $24-26^{\circ}\text{C}$ in June, and at $29-30^{\circ}\text{C}$ in August. These were essentially the prevailing temperatures in the Gulf during the respective seasons. We know nothing of the extent to which these larvae might be at somewhat greater depths as the year progressed, so as to occur at more nearly constant temperatures. However, the simple reduction in numbers of larvae after February in the cases of *E. distinguenda* and *E. lamelligera* and after April in *E. eximia* indicates that the warmer months are not conducive to substantial recruitment in the Gulf.

PROPORTIONS OF LIFE PHASES

For each of seven euphausiid species, the annual proportion of the total made up by each of the four life phases

sampled here is similar. Catch curves, in which means for the four cruises are averaged (Figure 22), show furcilia larvae to be the most numerous phase and adults the least.

There are fewer calyptopes than furciliæ due, in part, to the relative duration of these phases. Data obtained from rearing *Nematoscelis difficilis* (Gopalakrishnan 1973), *Nyctiphanes couchii* (Le Roux 1973), and *Euphausia eximia* (M. Knight personal communication) all indicate that the calyptopis phase lasts about 10-12 days and furcilia phase about twice as long, 18-24 days. Thus, even without considering interphase mortality, mean numbers of calyptopes should be half those of furciliæ. However, calyptopes were found to average about one quarter the number of furciliæ. There is clearly substantial escapement by calyptopes through the 0.55-mm meshes of the net. (Smallest calyptopes of *Nematoscelis difficilis* and

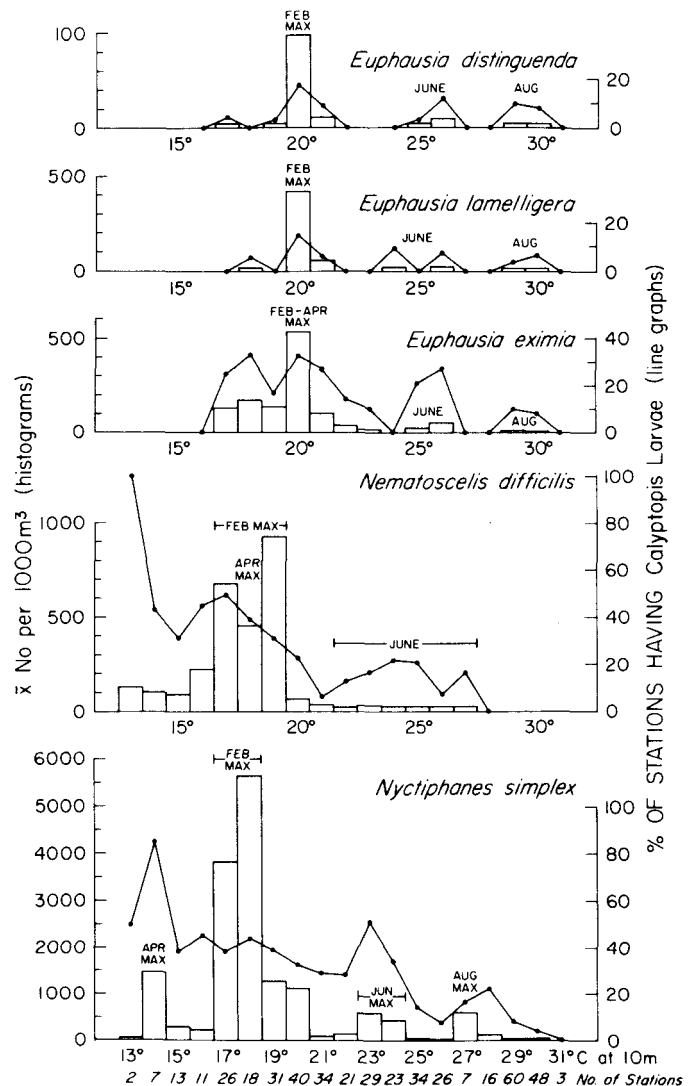


Figure 21. The youngest larvae sampled (calyptopes), all four 1957 cruises of the Gulf of California, plotted as a function of temperature (10-m depth).

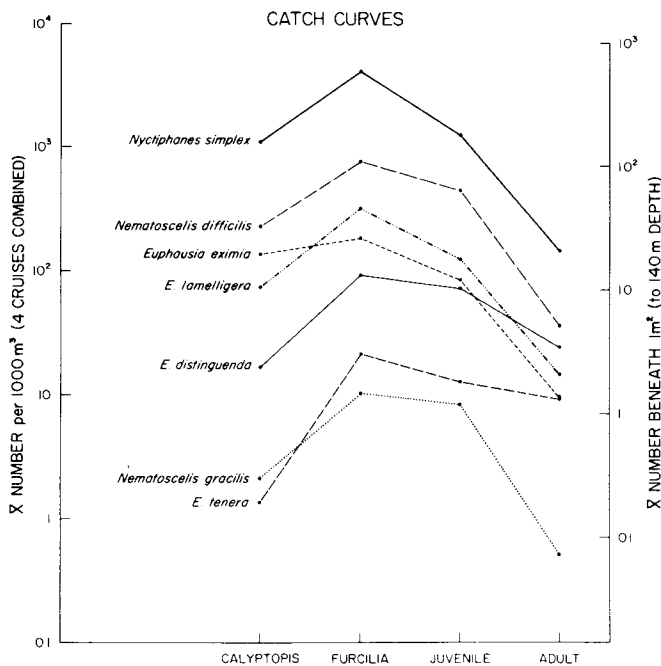


Figure 22. Abundances of life phases, all of the 1957 Gulf of California cruises combined.

Nyctiphanes simplex are about 1.0-1.3 mm in length and about one-half of that in depth or width.)

The juvenile and adult phases in warm-temperate euphausiids are expected to be of the order of six months each, with some adults living to one and one-half or two years of age (Brinton 1976; Gros and Cochard 1978).

The shapes of the curves in Figure 22 reflect a combination of 1) recruitment intensity, 2) duration of life-phase, and 3) survivorship. A rough mean for the ratio of calyptopis:furcilia:juvenile:adult for all seven species is 1:4:3:0.5. *Euphausia eximia* has relatively most calyptopes, indicating both high recruitment and high larval mortality in this largest of the Gulf species. *E. distinguenda* and *E. tenera* have proportionately more adults than the other species, indicating either a relatively long adult phase or a greater influx of adults to the Gulf. The similarities among the curves suggest similarities in life-span—possibly one year in this strongly seasonal regime.

Whereas *Nyctiphanes* and *Nematoscelis* incubate their externally attached eggs for a time, *Euphausia* sheds its eggs directly into the water. This means that the nauplii (not retained by our nets) of *Euphausia* swim freely but those of *Nyctiphanes* and *Nematoscelis*, whose eggs hatch as metanauplii and then develop into calyptopes, are protected. The difference in rearing strategy does not lead to a difference, here, in the ratio of calyptopes that survive to the next phase.

SUMMARY AND DISCUSSION

The mouth of the Gulf of California is located almost exactly on the tropic, 23°27'N. To the west, this line

approximates the zone of mixing of the California Current with the Equatorial Water mass of the eastern tropical Pacific. Hence, through recent time, most tropical euphausiid species and those of the southern part of the California Current have had access to waters of the Gulf. Present-day colonization by species from the California Current system has been made by only three species, representing three genera, whereas tropical species appear as transients, except in the southernmost part of the Gulf.

Nematoscelis difficilis, *Nyctiphanes simplex*, and *Euphausia eximia* are established in much of the Gulf, and their ranges there varied little with season. *Euphausia pacifica* and *Thysanoessa gregaria* are distributed like *N. difficilis* in the California Current, and both may occur as far south as the mouth of the Gulf (Brinton 1979). Their absence in the Gulf is evidently due to inability to accommodate to summer extremes in temperature and to a lack of flow into the Gulf in winter-spring when conditions there might be within their ranges of tolerance. *E. pacifica* is a vertical migrator which enters the surface layer at night in all regions where the species has been observed. This characteristic could be a disadvantage for residence in the Gulf. *N. difficilis* tends to avoid the surface layers where a thermocline is developed, as in the summer in the Gulf. *Thysanoessa gregaria* is a nonmigrator or short-distance migrator inhabiting the depth range of the thermocline itself. Evidently such a stratum is insufficiently stable or constant in temperature to have permitted *T. gregaria* to occur here.

Nyctiphanes simplex and *Euphausia eximia* are logical inhabitants of the Gulf because their ranges are centered in these latitudes. In addition, the extensive shelf in the Gulf is particularly suitable for *N. simplex*.

Many euphausiid species occupy different depths, both in the course of their life histories and diurnally as migrating juveniles and adults. These depths may span hundreds of meters. Distributions of these species are certainly affected by the conservative conditions beneath the sea surface. However, the generally more variable upper level phenomena—currents, temperature, food—may act in a critical way at any stage of an animal's development. Variation in some, if not all, of these parameters is more extreme in the Gulf, particularly the northern half, than in most oceanic regions. The August warming to 29-31°C in the Gulf is more extreme than in the open ocean, and the Gulf euphausiids then enter a resting phase with respect to reproduction, though the ranges of most species are then most expanded.

The biogeographical accommodations that euphausiids in the Gulf of California have made to seasonal changes in temperature and direction of flow include both reciprocal and common responses among the warm-temperate and the tropical species in this partly closed system. Reciprocal responses include the relationships of the ranges of *Nematoscelis difficilis* and *N. gracilis* in the

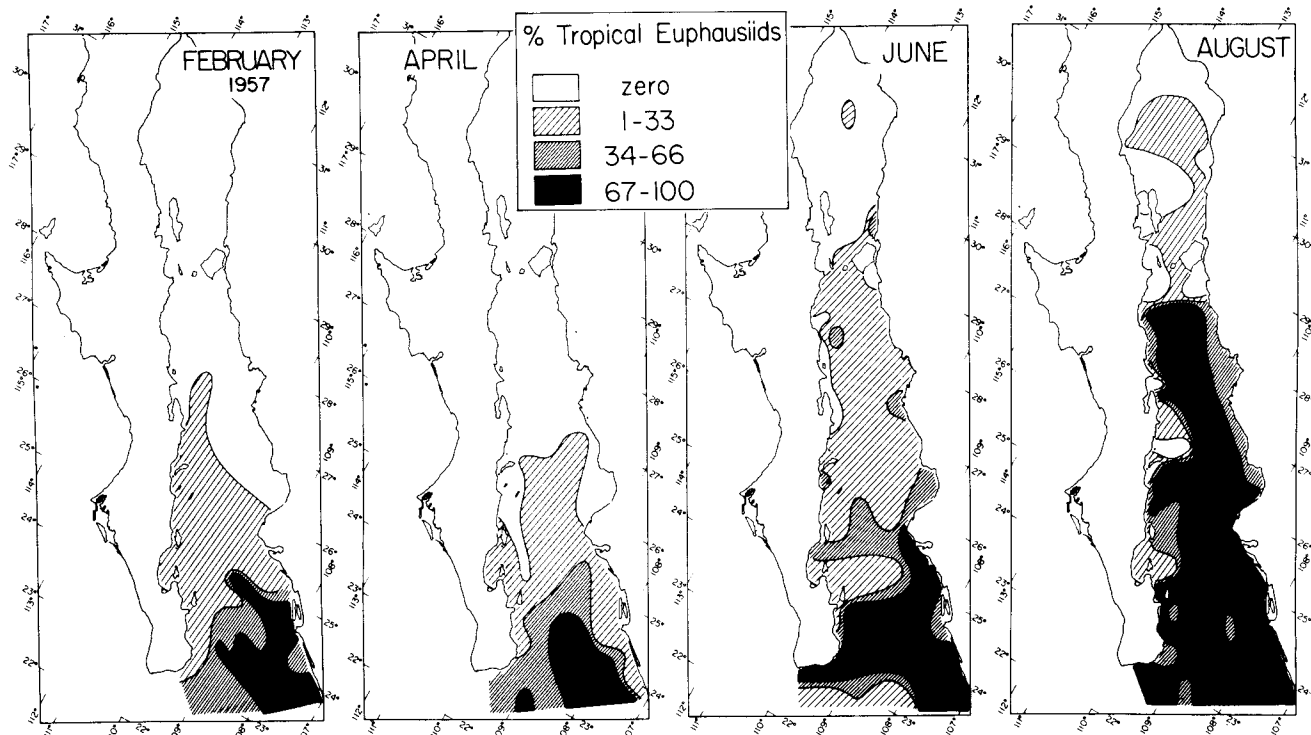


Figure 23. The tropical euphausiids (four species: *Euphausia distinguenda*, *E. lamelligera*, *E. tenera*, and *Nematoscelis gracilis*) shown as % of total euphausiids occurring in the Gulf of California.

southern half of the Gulf during February-April, with tropical *N. gracilis* occupying areas where warm-temperate *N. difficilis* was absent or at low density and moving northward on the eastern side in June as *N. difficilis* receded from there. Both species of *Nematoscelis* showed lowest density and diminished range during the heat of August (Figures 8, 9).

Although the range of *Euphausia eximia* extended northward into mid-Gulf during all seasons, the composite range of the strictly tropical species showed northern range extension after April, reaching the zone of the island channels in June and the northern Gulf in August where their dominance extended northward through mid-Gulf (Figure 23).

The dominant Gulf species, *Nyctiphanes simplex* and *Nematoscelis difficilis*, although both occupying most of the Gulf during all seasons, nevertheless showed certain complementary characteristics. *N. difficilis* was at its peak in mid-Gulf in February, while *N. simplex* was then building for April (western Gulf) and June (northern Gulf) maximum abundances. By June *N. difficilis* was sparse in the northern Gulf (Figures 7, 8). In August, *N. simplex* was most dense in the zone of the island channels, where *N. difficilis* was, for the first time, sparse or absent.²

²An unpublished report by Mundhenke (1969: The relationships between water masses and euphausiids in the Gulf of California and the eastern tropical Pacific, masters thesis, U.S. Naval Postgraduate School, 115 pages) has come to our attention since this paper went to press. This discusses euphausiids from 54 Tucker Trawl samples obtained by R/V *Te Vega* in the Gulf during September 22-November 14, 1967. As in our August samples, *Euphausia eximia* and *E. distin-*

Though there were distinct zonal irregularities in the presence of larvae (Figure 18), there were trends showing that *N. simplex* calyptopes and, to a lesser extent, furciliæ were more abundant along the shallower eastern side of the Gulf during their periods of peak production, whereas maxima for *N. difficilis* were in the generally deeper waters of the western side (Figure 20B). However, the shallow northern Gulf was an important nursery area for both species.

The strong warm-temperate zooplankton community in the Gulf includes, together with the euphausiids *Nematoscelis difficilis* and *Nyctiphanes simplex*, the copepod *Calanus pacificus californicus* Brodskii which bulked as the dominant organism in the Gulf during February-April.

Moser et al. (1974) emphasized the widespread occurrence in the Gulf of two fishes of commercial importance having cold-water affinities. The Pacific mackerel, *Scomber japonicus*, averaged fifth in abundance in the Gulf, and the Pacific sardine, *Sardinops sagax caeruleus*, varied between third and sixth in abundance, depending on the cruise.

According to A. Fleminger (personal communication), most *Calanus* submerge to greater depths than the 0-140m sampled during these 1957 cruises. Evidence that this is not the case with *N. difficilis* consists of the fact that

guenda occurred northward to the island channels, but *Nematoscelis gracilis* was in mid-Gulf, 27°N, as in our June samples. *E. lamelligera*, *E. tenera*, and the *Stylocheiron*s were not recorded, but *E. gibboides* and *Nematobrachion flexipes* were reported inside the Gulf to 28°N, differing significantly from our findings. *Nematoscelis difficilis* was found in all zones, but *Nyctiphanes simplex* only from mid-Gulf northward.

numbers of adult *N. difficilis* did not decrease significantly in August in the 0-140 m layer sampled during the 1957 cruises (Figure 17). Younger stages were then much reduced, but this is consistent with the pattern in all species.

The values in the Gulf for biomass of euphausiids were 25 cc/1,000 m³ during February to June, dropping to 7 cc in August. The higher means are like those in the richer part of the California Current off central California, San Francisco to Point Conception (Isaacs et al. 1969; Fleminger et al. 1974). There, 30-80 cc/1,000 m³ were measured along different lines of stations between San Francisco and Point Conception during April 1956. Mean values of biomass for different east-west transects of the California Current were then 4-9 cc from Point Conception southward along Baja California. During April in the warm year 1958, values were 3-6 cc/1,000 m³ all the way from San Francisco southward.

Summer (July) values for euphausiid biomass during 1955-56 in the California Current were 10-15 cc/1,000 m³ north of Point Conception and 3-10 cc to the south. Values in 1957-59 were slightly lower. The mean proportion of total biomass made up by euphausiids was also nearly the same on opposite sides of the Baja California peninsula. In the southern part of the California Current during 1956-59 it was 10% (January), 7% (April), 6% (July), 10% (October), comparing with 7% (February), 5% (April), 7% (June) and 3% (August) in the Gulf. The richer places along western Baja California for both euphausiids and total biomass are near Punta Banda (31°N), Vizcaino Bay (28-29°N), and Punta Eugenia (29°N) southward along the coast. In the eastern tropical Pacific (Brinton 1979), euphausiids were at maxima of 13 cc and 26 cc beneath 1 m², or 20% and 50% of total volume, at the equator and the northern edge of the North Equatorial Countercurrent. Off the mouth of the Gulf they were 2-7 cc/1,000 m³, or 3-6% of total biomass. The values for cc beneath 1 m² approximately convert to cc per 1,000 m³ by doubling. Longhurst's (1976) data indicated that euphausiids comprise about 5% of total biomass at 14°N in the eastern tropical Pacific, agreeing with proportions observed at the mouth of the Gulf.

Thus, euphausiid biomass and its proportion of the total biomass in the Gulf is intermediate between that found in the richest and poorest parts of either the California Current or the eastern tropical Pacific. Parts of the Gulf having the largest standing stocks correspond to places and times where *Nyctiphanes simplex* and *Nematoscelis difficilis* are most abundant. At such localities, values of 50-200 cc/1,000 m³ for euphausiids and > 1,000 cc for total biomass are as high as any reported from mid- to low latitudes in the Pacific.

Could *Nyctiphanes simplex* be economically harvested in the Gulf? Several localities having densities of >50,000/

1,000m³ were encountered in the northern Gulf during April-June. Such densities of euphausiids are rare in the California Current, although *N. simplex* has been found in such numbers in Bahía Sebastián Vizcaino, 28°N. In the northern Gulf, the mean biomass of this species was at a maximum of 77 g/1,000 m³ in the western sector in June (data converted from Figure 18A). This is somewhat higher than April and June values of 35 g and 48 g from the eastern sector of the northern Gulf.

As stated in the section on euphausiid biomass, a factor of 2 may be applied to these values for *N. simplex* from CalCOFI 1-m net catches so as to equate them with those obtained using an unbridled net. This gives mean biomass values in the range of 70-150 g/1,000 m³ in the sectors in which *N. simplex* is most abundant. Higher local densities would, of course, be encountered.

The range 70-150 g compares with 100-300 g/1,000 m³ for *Euphausia pacifica* in the vicinity of the Strait of Georgia in the inland waterway of British Columbia. There, *E. pacifica* and *Calanus plumchrus* have been the objects of a modest fishery, which expanded from 10 tons/year in 1970 to >100 tons in 1974 (Heath 1977). Mid-water trawls were used.

A next step in addressing the question of practicability of harvesting *N. simplex* would be exploratory fishing in the northern Gulf by means of plankton trawls, possibly in conjunction with acoustic reconnaissance (e.g. Samoto 1972), and a study of population dynamics of the species.

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