EUPHAUSIID DISTRIBUTIONS IN THE CALIFORNIA CURRENT DURING THE WARM WINTER-SPRING OF 1977-78, IN THE CONTEXT OF A 1949-1966 TIME SERIES

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ABSTRACT

Euphausiid species having affinities with warm offshore and southerly waters of the California Current extensively penetrated the region of the southern California eddy during the winter of 1977-78. Coastal *Nyctiphanes simplex* was then more strongly displaced than had previously been observed for that season.

During 1949-1960, three two-year cool periods were interrupted by warm periods of differing duration, timing, and intensity. Euphausiid biogeography off southern California during December 1977 to August 1978 developed much as during November 1959 to April 1960—the wane of the longest warm period, 1957-60. Those three years were uninterrupted by marked spring-summer upwelling and strong southerly flow.

By June-July 1978, as in January-March 1960, water temperatures and species distributions returned to average. The cool-water euphausiids *Euphausia pacifica* and *Nematoscelis difficilis* again were predominant from central California to northern Baja California.

RESUMEN

Especies de eufáusidos con afinidades a las cálidas aguas sureñas y de afuera de la Corriente de California penetraron extensivamente en la región del giro del sur de California durante el invierno de 1977-78. La especie costera *Nyctiphanes simplex* estuvo entonces más fuertemente desplazada de lo que se había observado previamente para aquella estación.

Durante 1949-1960, tres períodos frescos de dos años cada uno fueron interrumpidos por períodos cálidos de duración, tiempo, e intensidad diferentes. La biogeografía de eufáusidos frente al sur de California, desde diciembre de 1977 hasta agosto de 1978, se desarrolló de una manera muy parecida a la del período entre noviembre de 1959 y abril de 1960—a fines del período cálido más largo, desde 1957 hasta 1960. Esos tres años siguieron ininterrumpidos por las surgencias marcadas de primavera-verano y el fuerte flujo hacia el sur.

Ya por junio y julio de 1978, las temperaturas del agua y las distribuciones de especies regresaron al promedio, tal como había sucedido en enero-marzo de 1960. Los eufáusidos de aguas frescas, *Euphausia pacifica* y *Nematoscelis difficilis,* volvieron a ser predominantes desde California central hasta la parte norte de Baja California.

[Manuscript received 1 July 1981.]

INTRODUCTION

Ocean temperatures were 1-2°C above average, and salinities were below average along the California coast during the stormy winter of 1977-78. Northwest winds were unusually strong for that season. Extensive zooplankton collections were obtained during the CalCOFI surveys of December 1977 to August 1978, permitting comparisons with earlier surveys.

Changes in distributions of plankton species generally suggest roles of interactions among species and of changing environment. When changes appear to be particularly related to the environment, they can be aids in understanding variability in climate and circulation, provided that the broad geographical affinities of the species are understood.

Geographical associations of species within the California Current have been variously described (Bieri 1959; Brinton 1962; Johnson and Brinton 1963; McGowan 1968, 1971). If these are presumed to be functional assemblages, they have been documented with less certainty than the distributions of individual constituent species (e.g. Fleminger 1964; Alvariño 1965; Brinton 1967a, 1973; Brinton and Wyllie 1976; McGowan 1967; Berner 1967; Bowman and Johnson 1973; Reid et al. 1978).

Species of Chaetognatha (e.g. *Sagitta hexaptera*), Pteropoda (*Limacina inflata*), and Euphausiacea (*Euphausia hemigibba*) occurring in westerly and southwesterly California Current areas have been shown to be associated with North Pacific Central Water (Fager and McGowan 1963). Other subtropical euphausiids, also occupying offshore parts of the California Current (*Euphausia recurva, E. mutica*), now appear to be particularly adapted to margins of the Central Gyre, when abundance as well as range is a criterion. *Euphausia eximia* was thought to indicate northerly intrusions of Equatorial Water into the California Current (Brinton 1962). *E. eximia* is now understood to be a species that proliferates at cool margins of the eastern tropical Pacific, including Baja

Californian waters (Brinton 1979; Brinton and Townsend 1980). Even the subarctic affinity of the much studied Californian population of *Euphausia pacifica* (Lasker 1964, 1966; Brinton 1976) is uncertain because this species is strongly reproductive all along the California coast.

The California Current system is a zone of hydrographic transition extending from the southern edge of the cool-temperate, Subarctic Water mass of the Gulf of Alaska (ca. 42°N) to equatorial water at the Tropic of Cancer, and from coastal upwelling centers westward toward or into the Central Water mass. A species tends to be most abundant in, or restricted to, a particular sector of the current system: northern, southern, coastal, or offshore. More species overlap off southern California and northern Baja California, 30-35°N, than elsewhere.

Comparisons of 1977-78 distributions with those in a 1949-1966 time series will be made using only the data from a designated area extending westward from southern California. The inshore part of this area includes the Southern California Bight, in which coastal upwelling develops particularly well to the south of promontories, notably Point Conception, in response to northerly winds (Reid et al. 1958; Reid 1960). The offshore part frequently includes a southerly component of the California Current which, on the average, lies 240 km off northern Baja California where it bends shoreward (Hickey 1979). The southern California eddy is formed from the easterly edge of this flow, together with northwesterly flow in the Bight (Figure 1). This eddy supports dense reproductive populations of California Current euphausiids (Brinton 1976).

The distributions of euphausiids show that those species with distinct affinities for Subarctic, Central, or Equatorial Water masses, as defined by Sverdrup et al. (1942), have not massively intruded into the California Current system during the past 30 years of CalCOFI observations. Subarctic *Thysanoessa longipes* and *Tessarabrachion oculatus* have often occurred southward to about 38°N, to the west of San Francisco, but individuals reaching farther south are rare (Brinton 1973). Occurrences off southern California during the cold spring of 1956 will be referred to, below, when the more coastal northern species *Thysanoessa spinifera* is discussed.

Four euphausiids that are numerically important within the current from central California southward (*Nematoscelis difficilis, Euphausia gibboides, E. recurva, Thysanoessa gregaria*) also extend northward into the North Pacific Drift (38-45°N), evidently a biogeographical extension of the California Current Transition Zone. The North Pacific Drift is in the zone 40-45°N. According to Dodimead et al. (1963) the Drift is a part of the Subarctic Zone, though they consider it to be transitional with Central Water. Species of other taxa which appear to be endemic to the North Pacific Drift—California Current Transition Zone are the chaetognath *Sagitta scrippsae* (Alvariño 1962) and the copepod *Eucalanus californicus* (Johnson 1938; Fleminger 1973). California Current endemics include the copepods *Calanus pacificus californicus* (Brodsky 1965) and two species of *Labidocera, L. jollae* and *L. trispinosa* (Fleminger 1978). Newman (1979) summarizes evidence for a Californian Transition Zone.

California Current euphausiids have not been observed to extend into the tropical waters, excepting *Euphausia eximia* mentioned above. Tropical species have sometimes ranged northward into Baja Californian waters, particularly during the "warm years," 1957-59 (e.g. *Nematoscelis gracilis*, Brinton 1967a), when central species were also particularly strong in easterly range extensions.

Thus, the more abundant euphausiids occurring off California and Baja California may be considered to be of a Transition Zone Fauna. Based on the period 1949-1966, these species may be further grouped as follows.

1) Northern, including North Pacific Drift, 35-45°N (with reproductive areas along coastal California):
   Euphausia pacifica (having both transition zone and subarctic populations), and
   Nematoscelis difficilis.
2) Intermediate or Subtropical, including North Pacific Drift (with offshore reproductive tendencies):
   Euphausia gibboides,
   E. recurva, and
   Thysanoessa gregaria.
3) Baja Californian:
   Euphausia eximia, Stylocheiron affine (California Current Form, Brinton 1962)

In addition, there are nearshore euphausiids:

1) the Gulf of Alaska to California species *Thysanoessa spinifera,* and
2) the Baja Californian *Nyctiphanes simplex.*

In mid-year, the two coastal species have shown strongest overlap, particularly off southern California during May-July when *T. spinifera* is reproductive.

The distributions of these euphausiids will be shown for the 1977-78 period. Extents of range and abundance (ubiquitous species) within the southern California area will be compared with earlier CalCOFI collections. Limitations in the data are obvious. Sur-

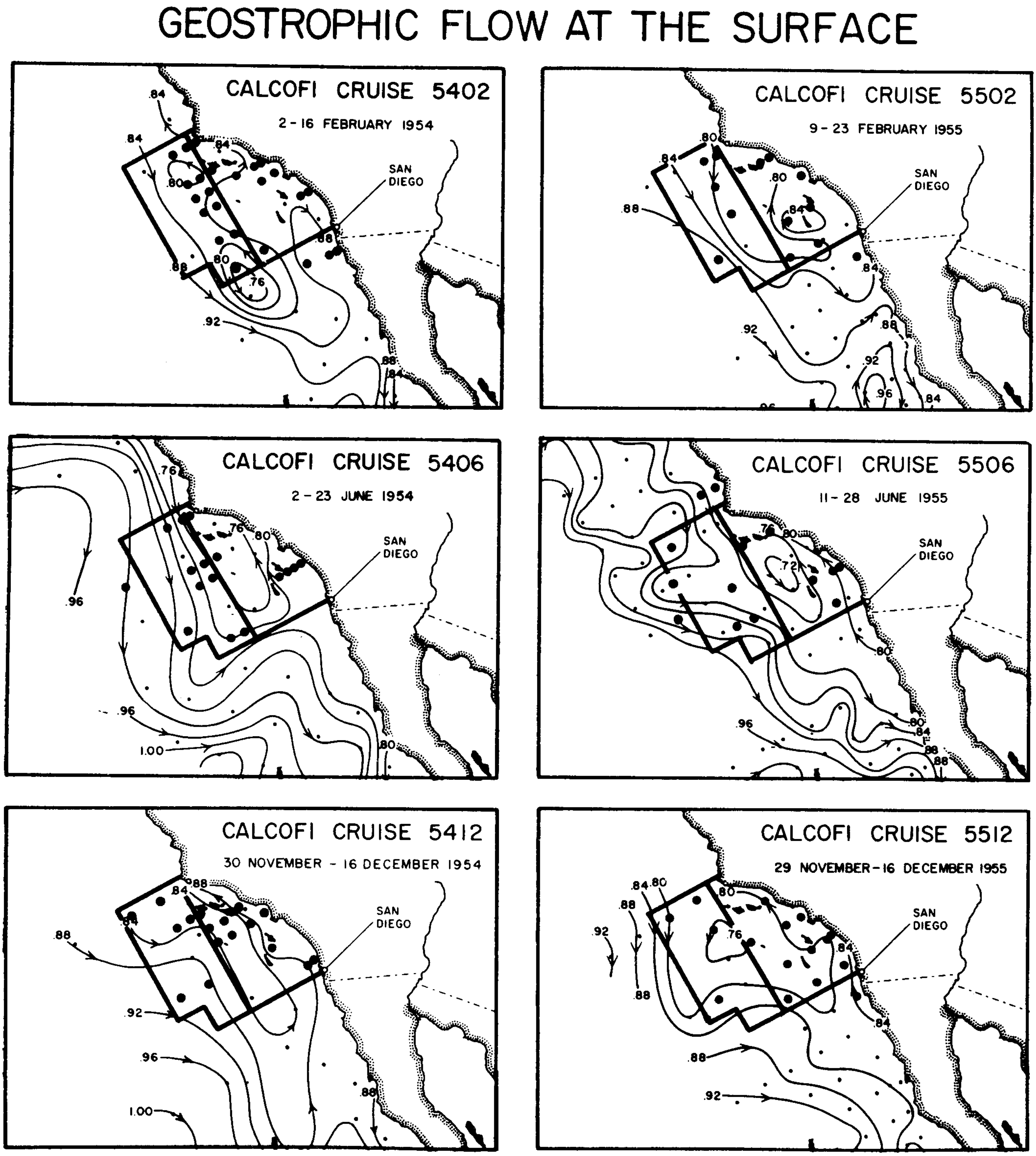

Figure 1. Geostrophic flow at the surface relative to 500 decibars in the southern California region for three months of the warm year 1954 and cool 1955, from Wyllie (1966). The area treated in time series of euphausiid distributions is outlined. Characteristics of inshore and offshore halves are described in text.

veys from the period 1967 to 1977 have yet to be analysed for the distribution of zooplankton species. Cruises differ greatly in the number of samples examined, and the time series does not make adequate use of our information on areal abundances of the species. Nevertheless, it was deemed appropriate to present the more timely and available data as a supplement to a symposium on climatology and biology of the California Current appearing in this volume, particularly Bernal (1981), Chelton (1981), and Eber (1981).

MATERIALS AND METHODS

Sampling during 1949 to 1966 was by means of a CalCOFI 1-m-diameter ring net towed obliquely from 70-m depth during 1949 and 1950, and from 140 m after 1950. Field and laboratory procedures follow those described by Kramer et al. (1972). The 1977-78 samples were obtained by use of 0.71-m-diameter Bongo nets, towed obliquely from 210 m. Brinton and Townsend (1981) show that abundances of given species of euphausiids are not significantly different from replicate Bongo and 1-m net tows. Bongos catch the larger sized animals better, whereas the 1-m net provides the better estimates of larvae, to about 6 mm in length. Subsampling and counting procedures are described in Brinton (1979).

All samples of the 1977-78 cruises were counted. Many of the 1949-1966 cruises were analysed in their entirety. However, only those samples from a southern California study area (Figure 1) are used in the time series upon which this report will focus. In the many cases in which cruises were examined only from the standpoint of the southern California area, only nighttime samples were studied. Such samples provide best estimates of both abundance and presence or absence of rare species. By reducing the number of samples to be studied, it has been possible to obtain data from many more months than would otherwise have been possible. As few as ten samples in a given month and as many as 47 were used to describe distributions in the southern California area.

Much of the data in the time series is presented as the percentage of the southern California area occupied by each species during each month. When only presence or absence is considered, as with six of the eight species in the time series, basic principles of contouring are used in assessing the areas occupied. In the other two species, areas of high abundance are determined in the same way.

Mean temperatures and salinities for the area were obtained by weighting each temperature or salinity increment by the amount of area closer to that isotherm than to any other isotherm, as plotted in CalCOFI Atlas I (Anonymous 1963) and Wyllie and Lynn (1971).

RESULTS

The Temperature and Salinity Environment

The distributions of temperature at 10-m depth reflect states of the California Current during December 1977 to July 1978 (Figure 2). The position of the 15°C isotherm varied little during these seven months of above-average temperatures. The western half of the southern California area was <15°C, and the eastern was >15°C during December-January when temperatures were 2°C warmer than average.

Water having a temperature of 13-14°C was to the north and offshore of Point Conception until early March. It extended into the Santa Barbara Channel in April, as upwelling developed along all of the coast, excepting Los Angeles to San Diego. Coastal cooling continued during May-June. A plume of <14°C water extending well to the west of southern California continued to develop into June-July. East-west temperature gradients indicate that this prominent westerly meander of the cool coastal stream extended 200-300 km southwestward from near Morro Bay (35°N) before returning shoreward into the southern part of the Southern California Bight. Eastward development of 15-16°C temperatures along 35°N, just to the north of this meander, indicate an easterly intrusion of the offshore environment, usually encountered only off northern Baja California.

The 17°C water reached northward well into southern Californian waters in December, complementing the southeasterly penetration of cooler offshore waters. The opposing parallel tongues were associated with intense unseasonal storms from the northwest. The 17°C temperatures retreated to the latitude of Vizcaino Bay (29°N) by February-March. The 17-18°C water returned to the southern California area during May-July as a northeasterly tongue. This lay inshore of the cool-water tongue described above as part of the westerly, then easterly meander of central California coastal waters.

Within the region designated the southern California area (Figure 1), mean temperature at 10-m depth (Figure 3) and ranges of temperature and salinity values across the area (Figure 4) help to describe events of 1977-78 in relation to certain other years. Mean temperature minima were during February-March in the inshore half of the region and during March to May in the offshore half (except 1951). Maxima were in July to October in both places, the values being higher inshore of the prevailing southerly flow.

During December 1977 to May 1978, the mean temperatures were like those of the warm years 1958-59, both offshore and inshore (Figure 3). The offshore means for December 1977 to January 1978 were the highest recorded. Inshore, they were in line with those of the winters of 1957-58 and 1958-59. Only the 1959-60 winter was warmer, after which the 1957-60 warm period lost its extreme characteristics. The similarity of 1977-78 to the warm years disap-

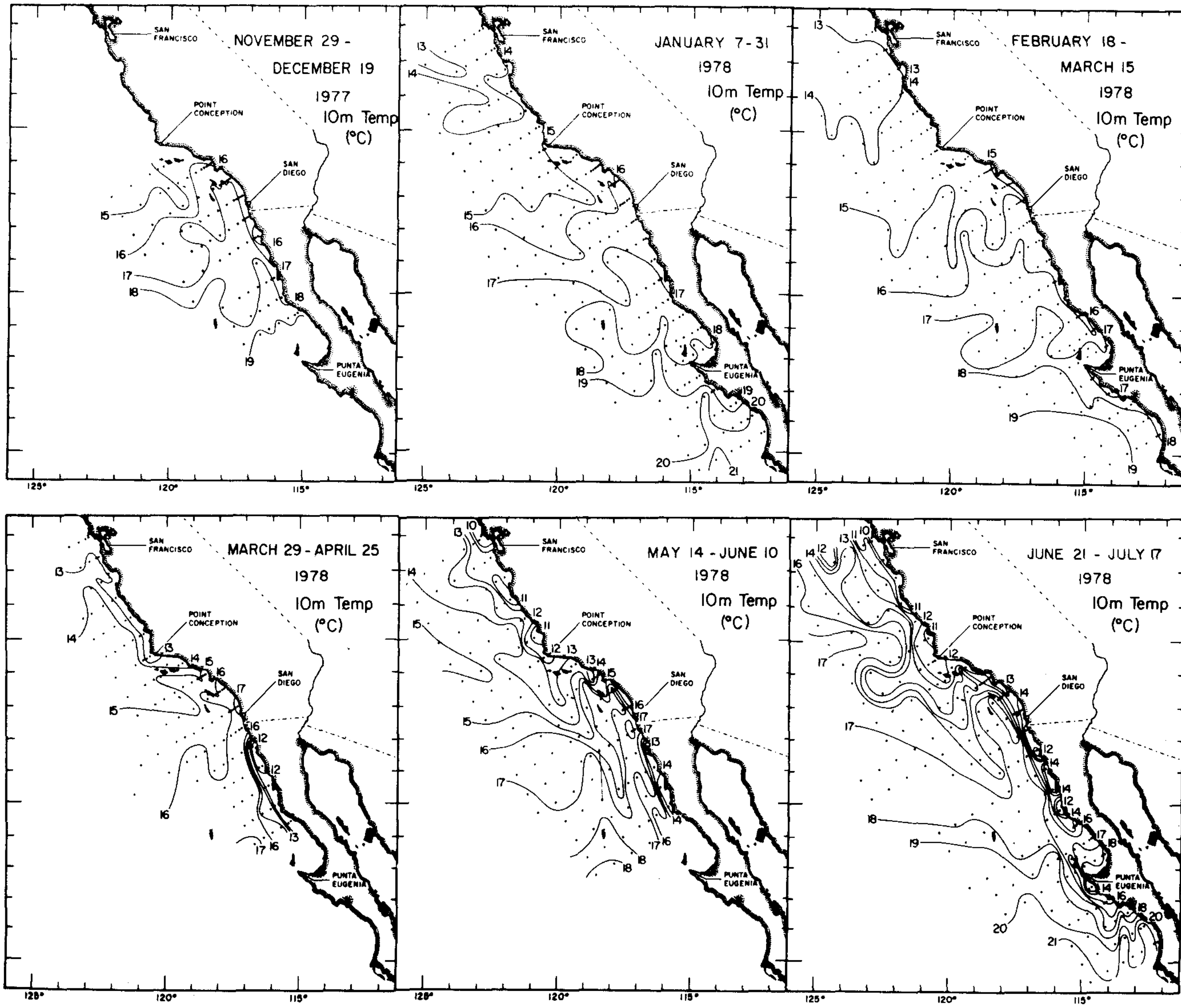

Figure 2. Distributions of temperature (10 m) in the California Current during December 1977 to July 1978.

peared by July 1978.

Three two-year periods stand out in the 1949-1960 temperature distributions plotted in CalCOFI Atlas I as being consistently cooler than average in the southern California area: September 1949 to September 1951, January 1952 to December 1953, and April 1955 to March 1957. During 1953 and 1956, the monthly mean temperatures (Figure 3) were 1-3°C lower than during warm 1958 and 1959 and the warm winter-spring of 1977-78. The year 1951 differed from 1953 and 1956 in being (1) intermediate in temperature in the offshore region during February-May, and (2) like the warm years during October-December, offshore, and September-December, inshore.

Mechanisms behind these variations in mean temperatures are expected to relate to plankton distributions. They may be further inferred through examination of the ranges of temperature and salinity in the offshore and inshore southern Californian regions (Figure 4). For example, spring temperature minima offshore reflect southerly flow from the central California coast, whereas inshore minima reflect local upwelling.

The year 1952-53 was cool, 1958-59 a warm year, 1959-60 a warm December-January followed by a cool February and a near normal spring-summer, and 1977-78 a warm December-May followed by a moderate June-July. The year 1977-78 differed from the other three years in the following ways:

1) During December-March 1977-78, temperature minima (ca. 14.5°C) and maxima (16-17°C) were relatively constant, both onshore and offshore.

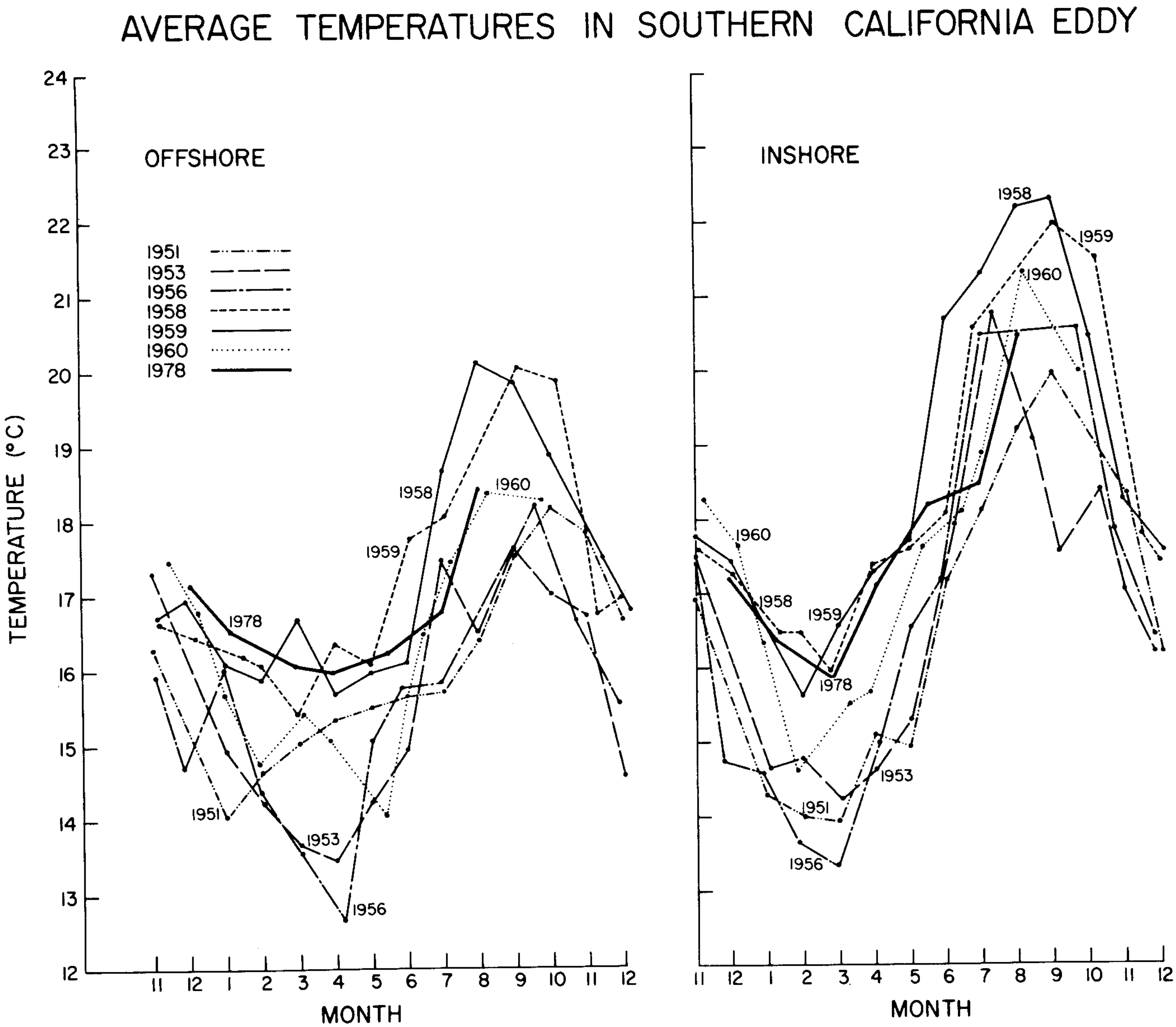

Figure 3. Monthly mean temperatures (10 m) in offshore and inshore parts of the southern California area during years of temperature extremes. Temperature values are from Oceanic Observations of the Pacific (1949-1960) and Wyllie and Lynn (1971).

2) In late 1977, water with salinity as low as 32.9‰ appeared in the offshore region and as low as 33.0‰ in the inshore region. Much of this water of low salinity and high temperature appears to have penetrated well into the Bight.

3) The highest salinities of January-February 1978 were like those of the cool 1952-53 winter, that is, 0.3‰ less than in the warm years 1958-60 when southerly flow and coastal upwelling were depressed.

In the inshore area during May-July 1978, temperature minima of <12°C were associated with salinity maxima to 33.9‰ inshore, indicating the resumption of upwelling. In the offshore area, temperature minima were then <13°C and the salinity range was broad, 33.0-33.8‰, indicating continuing southerly flow, but now of both northern offshore water and of central Californian upwelled water.

In general, inshore temperature ranges were similar to offshore ranges during winter months. Winter temperatures of 1977-78 differed from other years by decreasing little as the season progressed from December to February. Later in 1978, the inshore range of temperature became broader than the offshore range and encompassed it. Upwelling and northerly flow into the Bight appear as causes. Inshore salinities are generally higher than offshore, for the same reasons. But during December 1977 to April 1978, inshore-offshore differences were little.

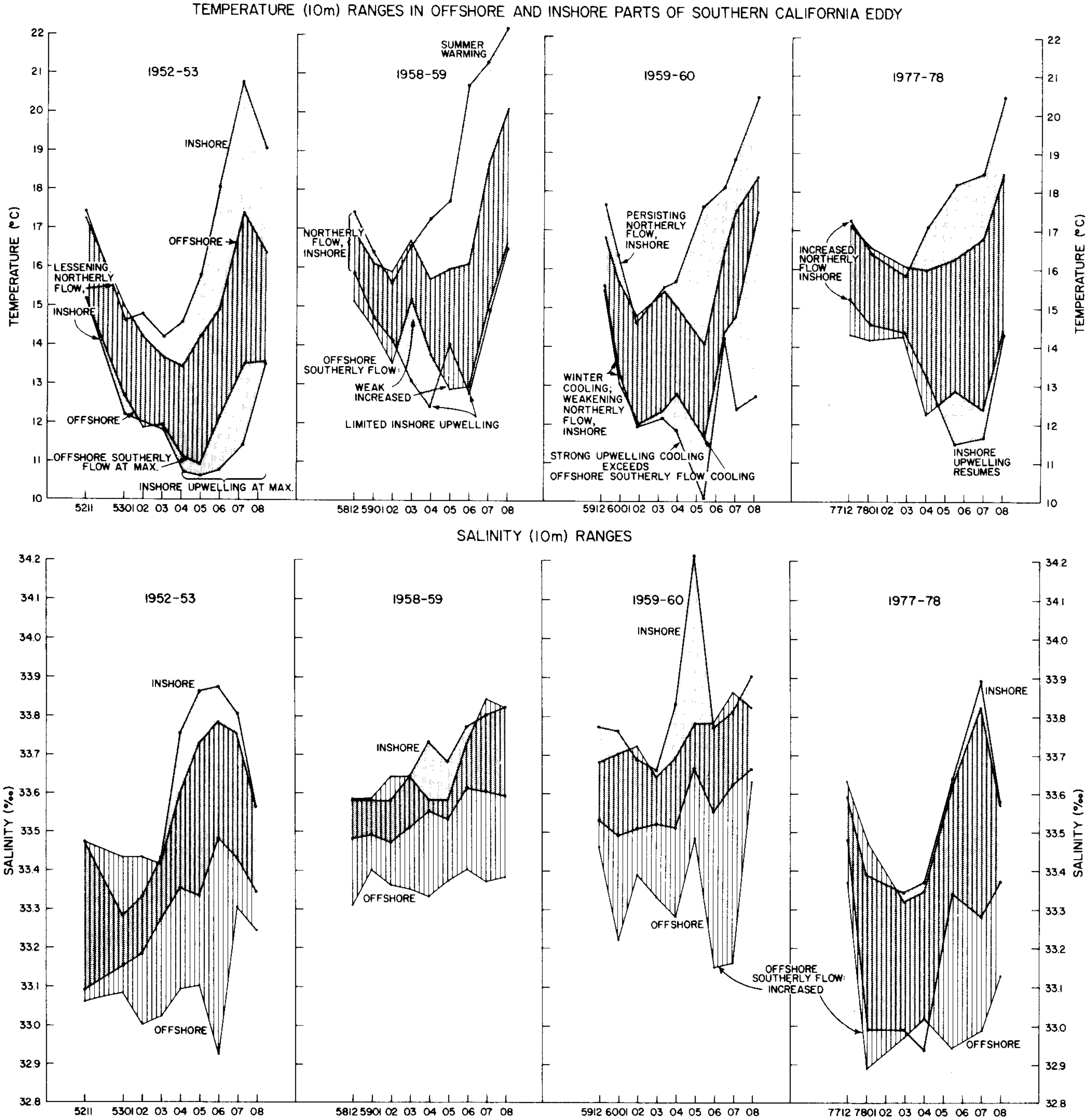

Figure 4. Ranges of temperature and salinity values (10 m) in offshore and inshore parts of the southern California area during cool 1952-53, warm 1958-59, warm, then cool 1959-60 and 1977-78.

Distributions of the Species during December 1977-July 1978

Euphausia pacifica (Figure 5)

During December-January, high densities of *Euphausia pacifica* (>500/1000 m^3) in the southern California area were restricted to a narrow tongue extending southward from the Channel Islands. This was associated with the southwesterly extension of the 15°C isotherm at 10 m. The population was extraordinarily weak to the south, scarcely extending into Baja California waters. Some larvae were nevertheless produced.

As in January, the substantial parts of the February-April distributions were conspicuously coastal along central California. However, they now extended

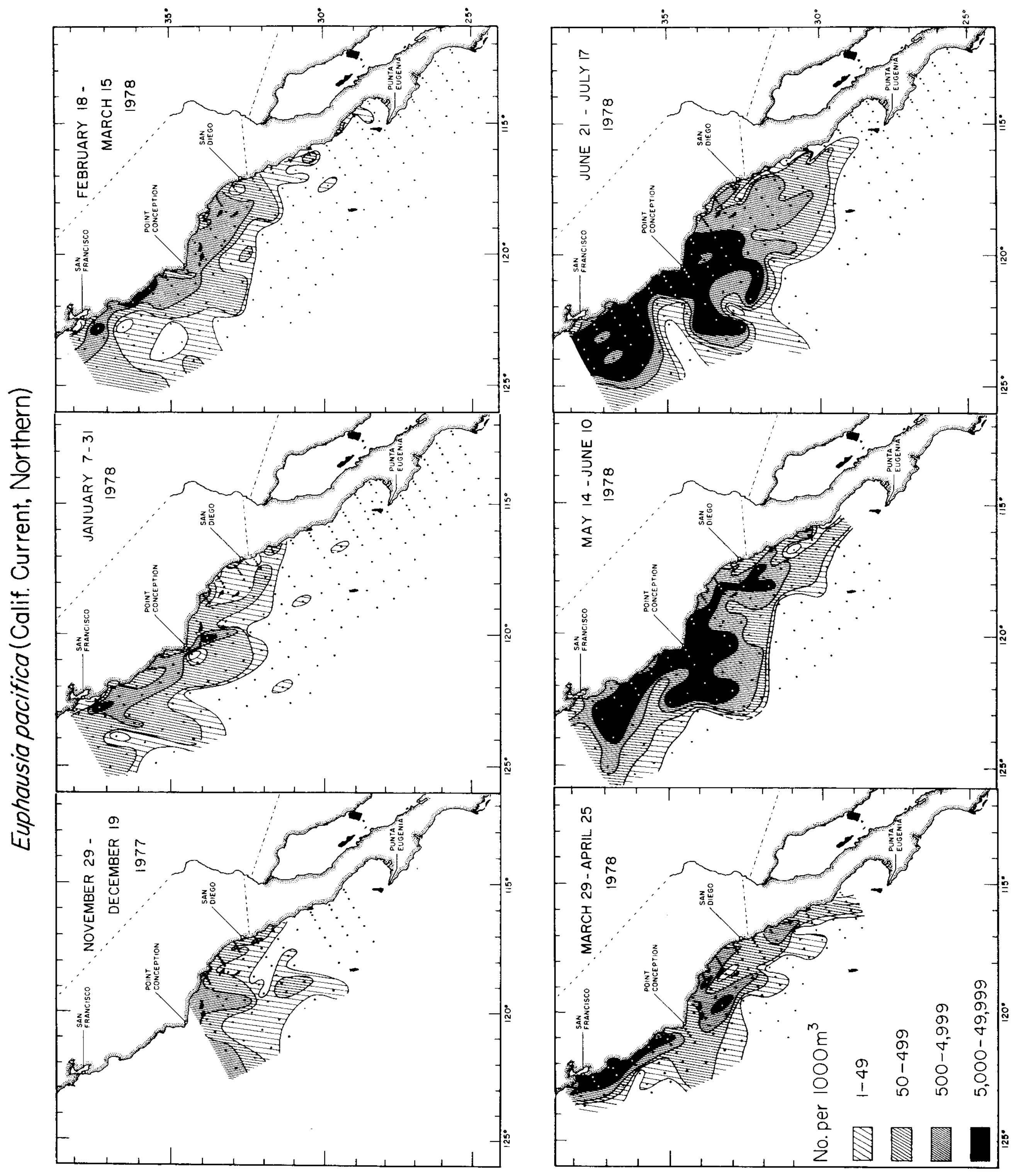

Figure 5. Distributions of the northerly California Current species *Euphausia pacifica* during 1977-78.

well into the Bight. The nearshore Baja California population developed progressively.

The increasingly dense population of May-July appears to be a reproductive response to the development of coastal upwelling. It extended well into Baja California waters and some 250 km seaward of Point Conception. The extensive meanders of isotherms are associated with the contours of abundance. The easterly intrusion of warm water to the north of Point Conception and the reduction of *E. pacifica* there appears more extreme than that observed during April of 1962 and 1963 (Brinton 1967a). It becomes the second aberrant event of this year, following the winter warming and its effects.

***Euphausia gibboides* (Figure 6)**

A Transition Zone species usually centered well offshore, *E. gibboides* ranged far into waters of central California and the Southern California Bight during December 1977 to March 1978. Incursions into the Bight appear to be both from the west and from the south. Coastal occurrences to the north of Point Conception and the generally shoreward displacement of the distributions are reminiscent of 1958 (Brinton 1967a). Retraction from coastal waters appears to have commenced in April as cooling developed. The May-July easterly incursions off central California are complementary to the easterly retraction of the distribution of *E. pacifica* (Figure 5).

Maximum production of larvae by this species is typically well offshore. It has been maximal during spring and summer (Brinton 1967a), as was the case in 1978.

***Euphausia eximia* (Figure 7)**

The extensive occurrences of *E. eximia* along southern California and extending to the north of Point Conception in early 1978 reinforce the significance of a climatological feature of that period already stressed. The offshore and southerly environment of the California Current Transition Zone shifted to the east and somewhat to the north. To a degree, it displaced *E. pacifica* and, as will be seen, the northerly Transition Zone species *Nematoscelis difficilis* and coastal *Nyctiphanes simplex*.

The northerly spread of *E. eximia* from its Baja California center diminished after March. Substantial production of larvae in the southern California and northern Baja California areas stopped at the same time, evidently due to coastal cooling.

***Nyctiphanes simplex* and *Thysanoessa spinifera* (Figure 8)**

Nyctiphanes simplex is a southerly coastal species usually having a northern limit near Point Conception. As in the warm year 1958, *N. simplex* ranged to northern California during the winter and spring of 1977-78. The winter distribution along California was particularly bound to the coast. By June the central California distribution had retracted and the southern California population became dense, extending westward into the region of southerly flow.

Thysanoessa spinifera is northerly and coastal. Its range is clearly complementary to that of *N. simplex*, though its April to June or July peaks in abundance are more seasonal than in *N. simplex*. Winter occurrences off southern California and Baja California were sparse during 1977-78, as is regularly the case. The May-August distribution off southern California, comprised mainly of spring larvae, was the most extensive that has been observed. It was associated with the massive meander of cool water to the west and south of Point Conception.

Springtime expansion of the range of *T. spinifera* off southern California will be shown to have regularly occurred during both warm and cold years. The exception was the particularly cold spring of 1956. Then, two subarctic species having relatively offshore affinities, *Tessarabrachion oculatus* and *Thysanoessa longipes* made rare appearances 90 km south-southwest of Point Conception (Station 83.60) during both April and June.

The Central Pacific Species (Figure 9)

These species have highest densities and reproductive areas in the Central Pacific Gyre, to the west of the California Current. Low densities drift westward into the Transition Zone, particularly during winter when southerly flow is weakest. Composite range and abundance of these nine species varied little during December 1977-July 1978. As with the Transition-Zone species having warm-water affinities (*Euphausia gibboides* and *E. eximia*), the central species were patchily present in the southern California area during December to March, after which they were almost absent. Their association with the easterly incursions of warm water to the north of Point Conception and off northern Baja California are striking (Figure 2).

These species include *Thysanopoda astylata*, *T. obtusifrons*, *Euphausia brevis*, *E. hemigibba*, *Nematoscelis atlantica*, *N. tenella*, *Stylocheiron affine* (Central Form), *S. carinatum*, and *S. suhmii*. Only one of these, *E. hemigibba*, will be plotted in the time series to be described.

A 1949-66 and 1977-78 Time Series of Species Ranges off Southern California

Examples of species distributions in the southern California area are shown in Figure 10. The 1949-1960 period produced three cool episodes and three

Euphausia gibboides (Transition Zone, Offshore)

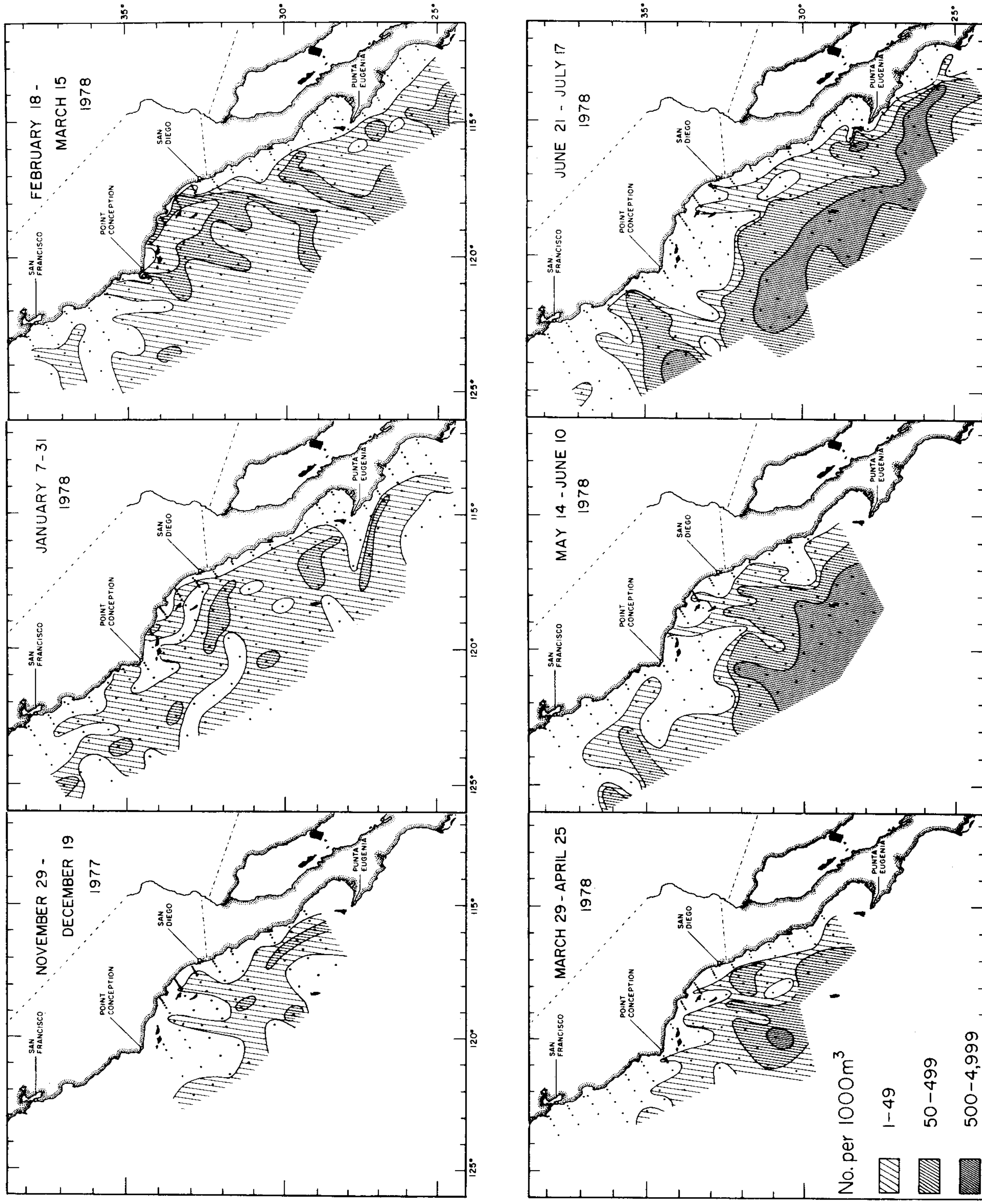

Figure 6. Distributions of the Transition Zone species *Euphausia gibboides* in the California Current during 1977-78.

Euphausia eximia (Transition Zone, Southern)

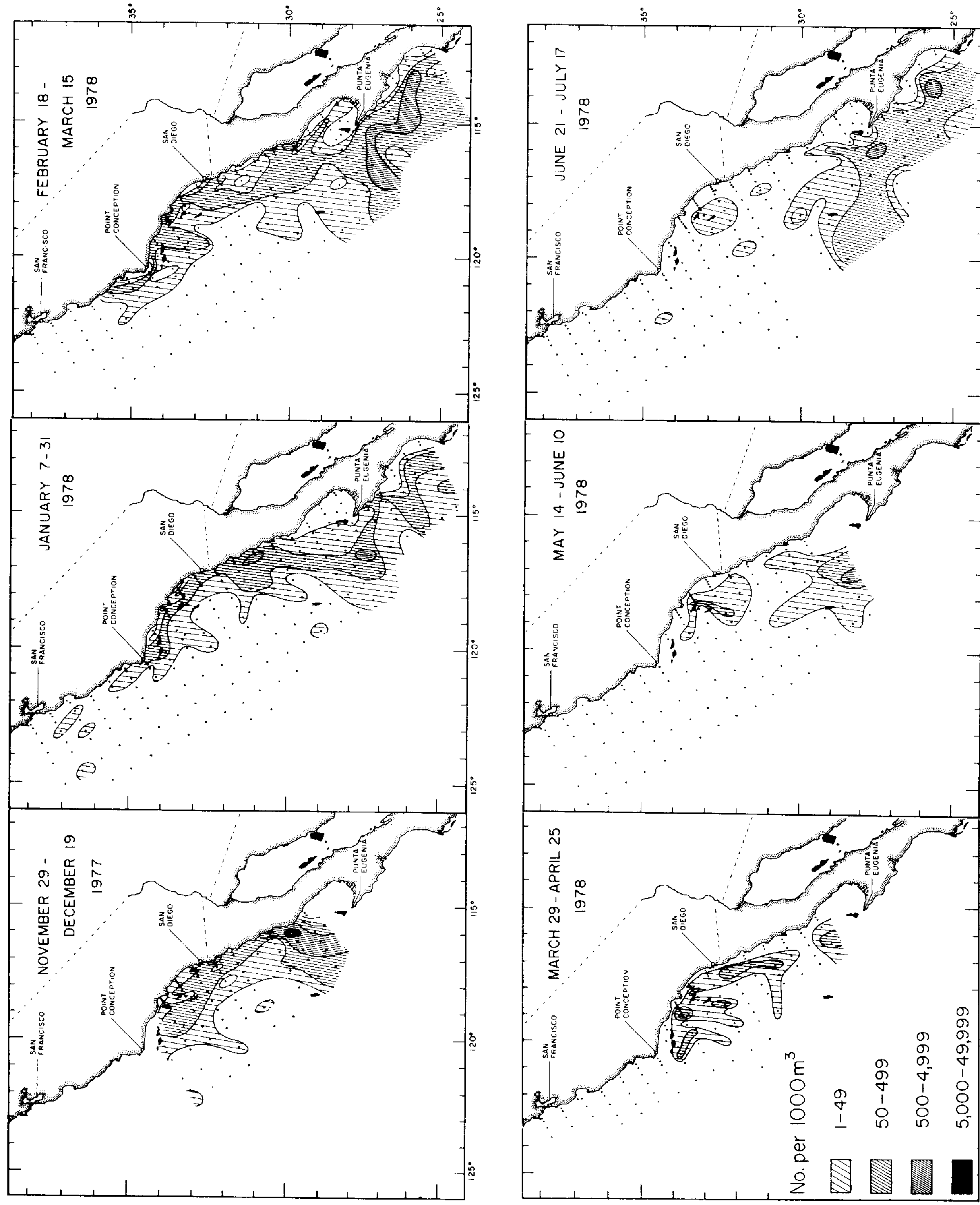

Figure 7. Distributions of the southerly Transition Zone species *Euphausia eximia* in the California Current during 1977-78.

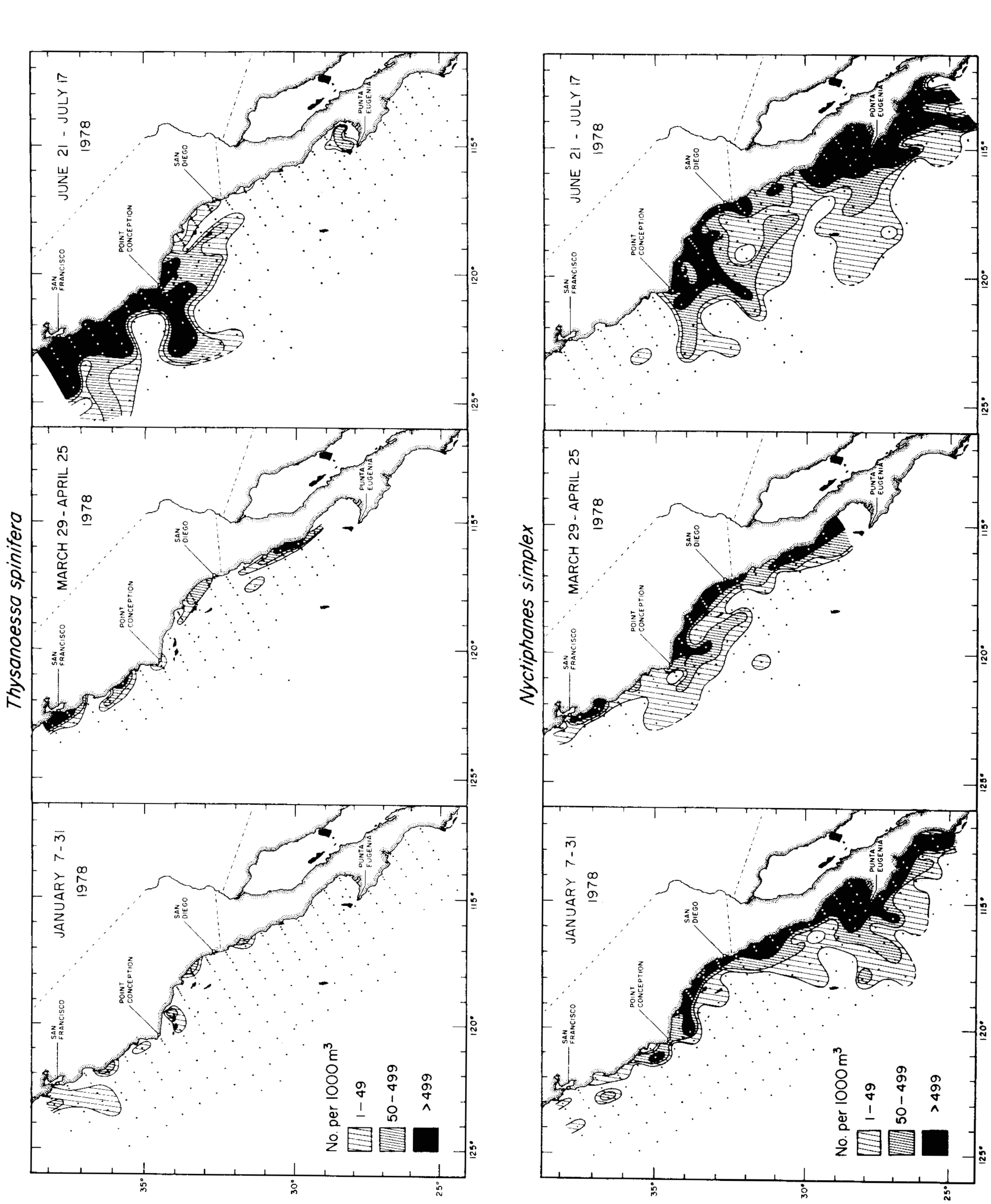

Figure 8. Distributions of coastal species in the California Current during 1978: *Thysanoessa spinifera* (northern) and *Nyctiphanes simplex* (southern).

Central Pacific Group, 9 species combined

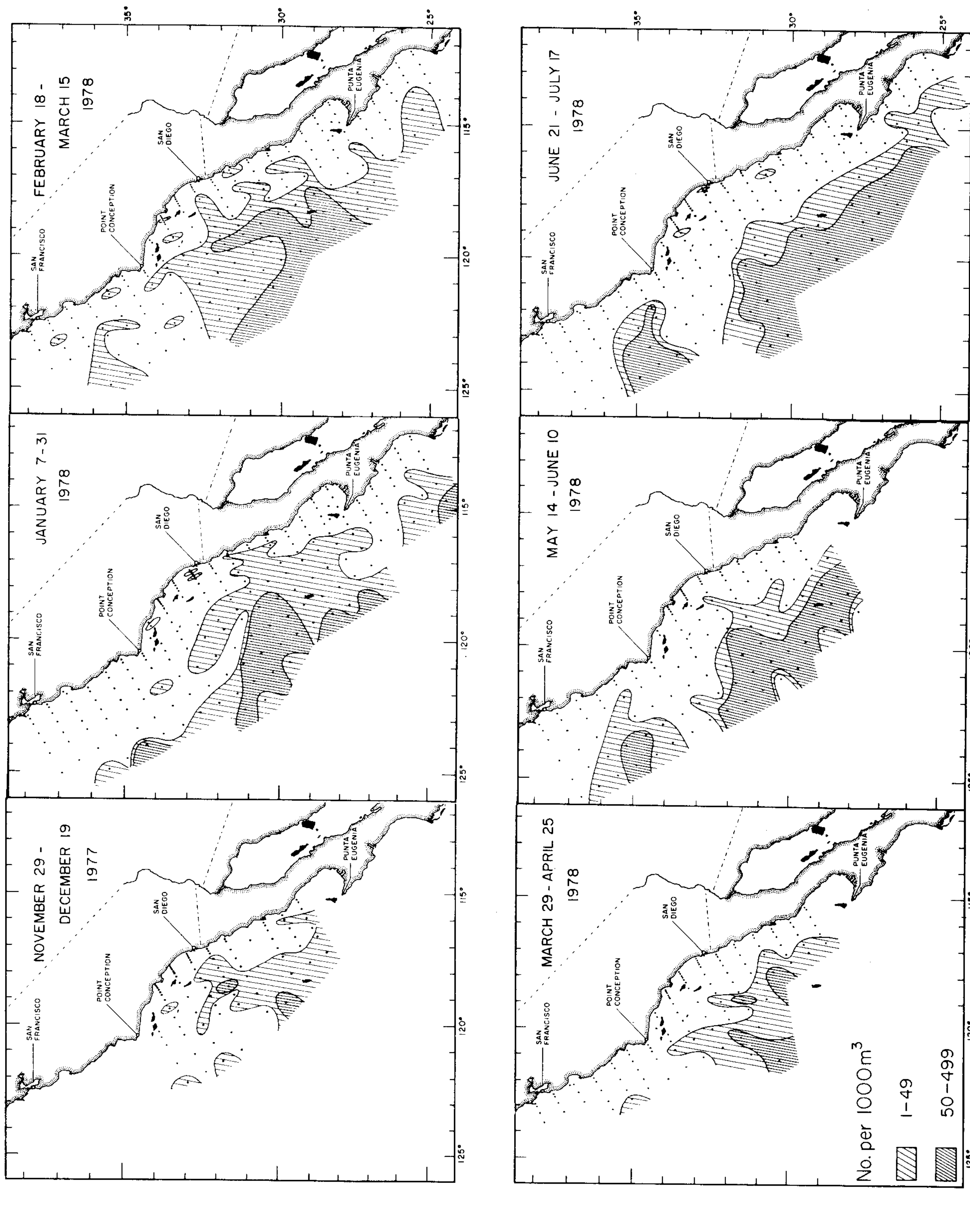

Figure 9. Combined distributions in the California Current of a group of nine Pacific Central Water species, 1977-78.

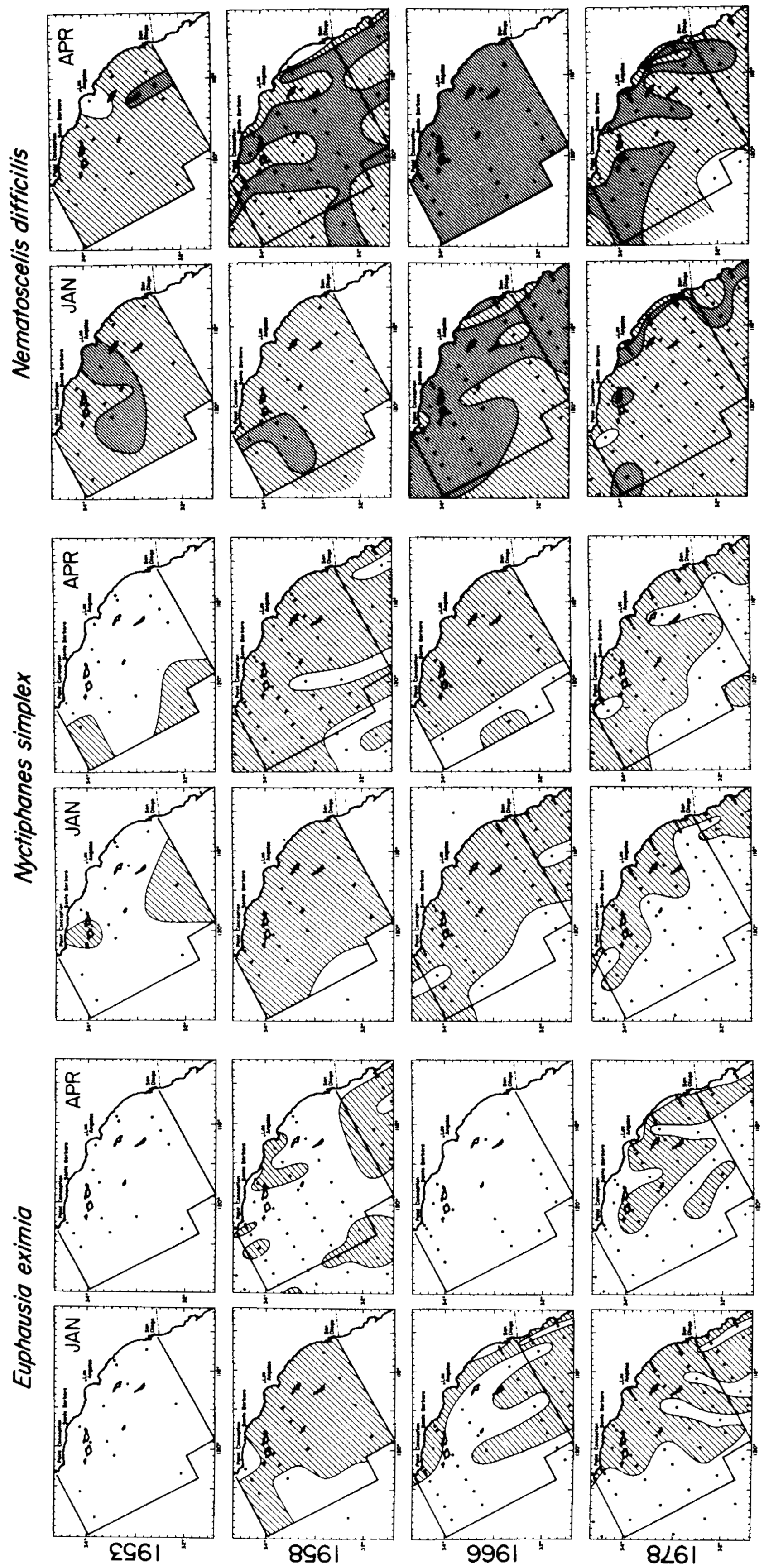

Figure 10. Examples of distribution in the southern California area of species representing the southerly part of the Transition Zone (*Euphausia eximia*), the coastal part (*Nyctiphanes simplex*) and the northerly part (*Nematoscelis difficilis*, for which abundances >500/1,000 m^3 are also shown, as plotted in Figure 11).

warm ones in this area (Figure 11). The standard against which a given month has been measured is the 10-year (1949-1959) monthly mean for that month, determined from data in CalCOFI Atlas I.

The three cool episodes are each of two years' duration: September 1949 to September 1951, January 1952 to December 1955, and April 1955 to March 1957. Late 1955 to mid-1956 was the coldest period.

The first warm episode was brief—October to December 1951, although during April-September 1951, monthly mean temperatures had alternated between normal and subnormal. The second was from February to August 1954, with aftershocks in December 1954 and March 1955. The third lasted 2½ years, from May 1957 to January 1960. Our analysis of the plankton from the 1960s and 1970s is very incomplete. The years 1962 and 1963 were cool and 1966 was near normal, judging by January and April data from those years. Monthly surveys were replaced by quarterly surveys during most of 1961-1977. The reader is referred to Eber (1981) for North Pacific temperature records for those decades. Summers of 1971, 1972, and 1976 were warmest.

The year 1977-78 appears to have been the time of strongest wintertime development of warm water off California subsequent to 1957-60.

The percentage of area off southern California occupied by each euphausiid species was determined as described in MATERIALS AND METHODS. Flow from the east and the south contribute warm-water plankton to this area. The cool-water species *Euphausia pacifica, Thysanoessa gregaria* and *Nematoscelis difficilis* have persistent reproductive populations in the eddy, apparently receiving most infusions from the northwest. Coastal *Nyctiphanes simplex* is usually present, pulsing northward from Baja California centers.

Distributions of northerly *Nematoscelis difficilis,* southerly *Euphausia eximia,* and coastal *Nyctiphanes simplex* (Figure 10) will provide examples of values plotted in Figure 11. Extents of occupancy of the southern California area during January and April in years of contrasting temperature characteristics are shown. Ubiquitous *N. difficilis* is measured in terms of the area in which >500 individuals per 1000 m^3 were present.

During the cool year 1953, *E. eximia* was absent, *N. simplex* occupied <25% of the area, and high abundances of *N. difficilis* were in <25% of the area.

In a warm year, 1958, *E. eximia* was significantly present during January but less so in April. *N. simplex* occurred at nearly all stations both months. *N. difficilis* increased its spread of high abundance from January to April.

Temperatures during 1966 were more nearly normal than in 1953 and 1958. *E. eximia* was present in the winter period of northerly flow but was lacking during April upwelling. *N. simplex* and high abundances of *N. difficilis* were widely present during both months.

During the warm winter of 1977-78, *E. eximia* was present throughout the inshore half of the area. As the system reverted toward normal in April, *E. eximia* began its retreat southward. Over the same period, coastal *N. simplex* increased its range from <40% to >60% of the area. Similarly, *N. difficilis* increased its area of abundance from 5% to 35%.

Before summarizing the warm and cool periods in terms of the eight euphausiids plotted in Figure 11, the general responses of the separate species to the changing temperature regime will be considered.

Euphausia hemigibba, representing the central Pacific group, was present in 20% or less of the area until the period of particularly variable temperature of April 1951 to February 1952. It was then scarce until 1958. Warming in 1954 appears not to have involved central incursions. Only during 1958 and in early and late 1959 was *E. hemigibba* present in much of the area. In 1978 its area increased to 35% by March, before declining to zero by July.

Three species of the warmer offshore waters of the Transition Zone reacted similarly. Occurrences of southern *Euphausia eximia* and offshore *E. gibboides* and *Stylocheiron affine* increased during or following times of average or above-average temperature: July-September 1949, October-December 1951, November 1952 (*E. eximia*'s peak preceded that of *E. gibboides* and *S. affine*), November 1954, January-May 1954 (not *E. gibboides*) and, more significantly, July-November 1954. All three occupied much of the area during July 1957 to January 1960, and again during December 1977 to March 1978.

The typically southern inshore species *Nyctiphanes simplex* closely followed the pattern of the Transition Zone species mentioned above. It differed in showing (1) no significant occurrences during late 1952, when the mean temperatures showed only weak warming, and (2) increased occurrences during December 1977 to July 1978 when *E. eximia* and *S. affine,* and to some extent, *E. gibboides* decreased.

The cold-water nearshore species *Thysanoessa spinifera* seems to have been relatively indifferent to year-to-year changes in ocean climate, because its occurrences were always few during winter, when annual temperature variations were most notable. It became prominent each mid-year as larvae dispersed. The April-July peaks in *T. spinifera* tended to be during or near times of moderate depressions in occurrences of *N. simplex*. This is expected in view of the complementary distributions of these nearshore

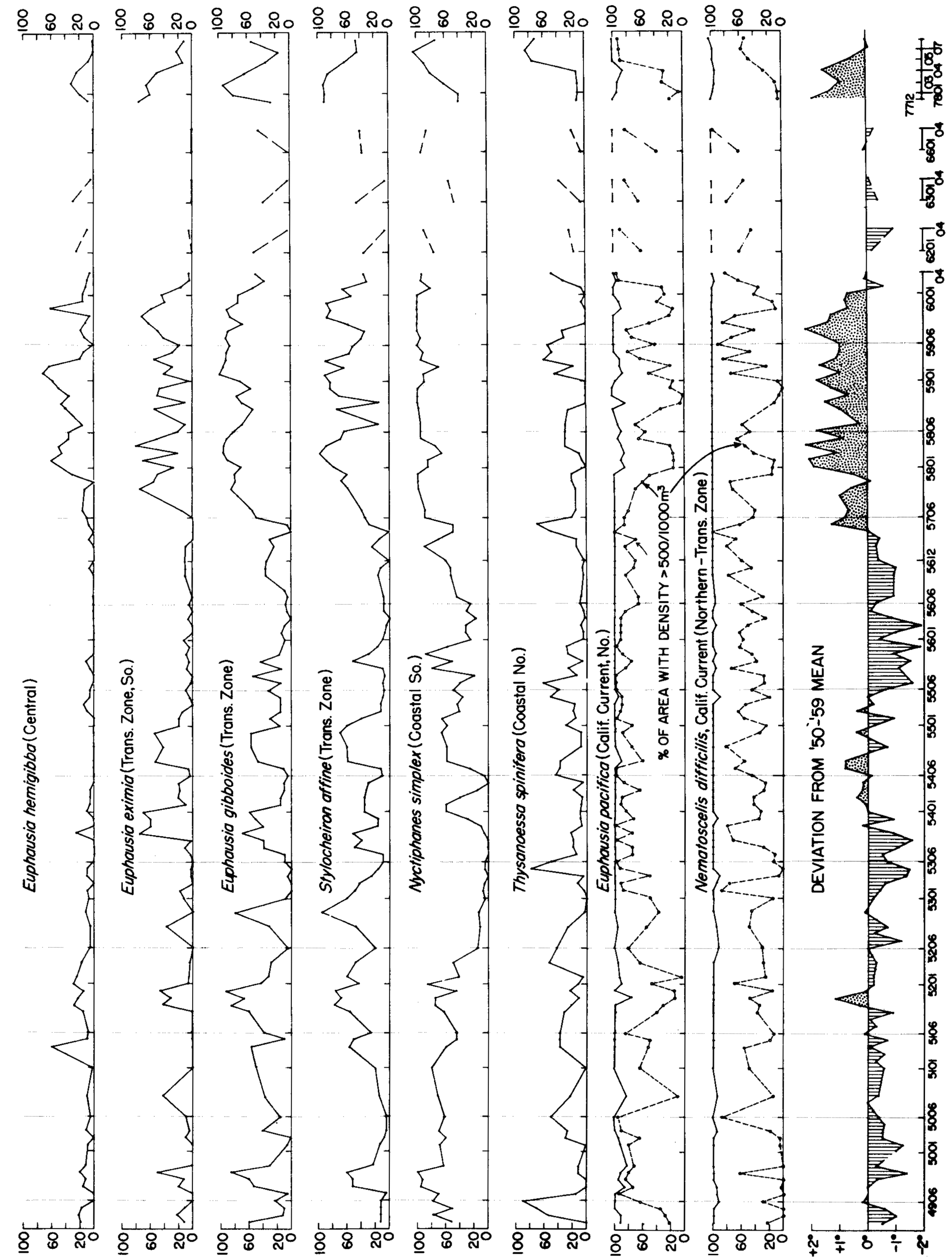

Figure 11. Percentages of the southern California area occupied by species having principal affinities with different parts of the Current are plotted for 1949-1966 and 1977-78. For the two ubiquitous species, the percentage of area with densities >500/1,000 m³ are plotted. Deviations from 10-year monthly means of the mean monthly temperatures for the area are shown.

species, outside of the southern California area of overlap.

Euphausia pacifica has been the dominant euphausiid in the California Current from central California northward during all years of observations. *Nematoscelis difficilis* is predominant somewhat seaward and to the south of *E. pacifica*. Both are usually present throughout the southern California area. Times during which either species is consistently (1) absent from any part of the area or (2) at low density, are considered noteworthy. The 1949-50 sampling, which extended only to 70-m depth, is probably unreliable for these two species (Brinton 1967b), particularly for estimating abundance of *N. difficilis* and daytime presence of *E. pacifica* (Figure 11).

E. pacifica was absent from part of the area during the warm periods of October-December 1951, January 1958-April 1959, November-December 1959, and December 1977-May 1978. These are also times when high densities of *E. pacifica* ($>500/1000^3$ m) were most restricted, approaching 0% of the area during each of the four periods.

N. difficilis appeared to be consistently lacking from part of the area only during 1977-78. This may have been due to particularly thorough sampling of the area (Figures 5-10). The percentage of area occupied by high abundance of *N. difficilis* was generally equal to or greater than for *E. pacifica* during warm periods and less during cool periods. However, the ups and downs of the high abundance curves for the two species agree more often than not.

SUMMARY

During December 1977 to May 1978 there were higher than average ocean temperatures in the California Current. Offshore zooplankton species then reached shoreward, and southerly species ranged far to the north along the coast, much as during the warm year of 1958 (Ahlstrom 1960; Berner 1960; Brinton 1960). In 1978, however, temperatures in the Current returned to average by July-August.

In southern Californian waters, where emphasis has centered in this description, the distributions of euphausiids showed that Transition Zone species having northern affinities were at much reduced abundances during the 1977-78 winter period of temperatures 1-2°C above average. Some easterly incursions of offshore Transition Zone species (e.g. *Euphausia gibboides*) and stronger northerly incursions of southerly *Euphausia eximia* were associated with shoreward and northerly retraction of the usually dominant cool-water *Euphausia pacifica* and *Nematoscelis difficilis*. This also happened during the three winters of the best documented and most pronounced warm-water period of 1957-60. For example, high densities of *N. difficilis* ($>500/1000$ m^3) occupied $<18\%$ of the southern California area during December 1957 to February 1958 and during November 1958 to January 1959, comparing with 5-11% during December 1977 to March 1978.

The 1977-78 winter differed from warm winters during 1957-60 in that even the southerly coastal species *Nyctiphanes simplex* was much compressed shoreward. About half of the southern California area became occupied by this species, compared with 70-80% of the area during winters of 1957-60.

The salinities as low as 32‰ off southern California during 1977-78 (Figure 4) were also anomalous. Such values normally indicate water of northern origin. The high temperatures make this improbable. Substantial precipitation along all of the California coast during December-January certainly contributed. The euphausiid distributions along central and southern California did not then indicate substantial transport from the northwest. The more extensive occurrences in the southern California eddy of *Euphausia eximia* and *Stylocheiron affine,* as compared with *Nyctiphanes simplex,* are evidence of northerly development of the southern part of the Transition Zone, rather than of the southern coastal environment.

Another feature of 1977-78 was the distinct development during spring months of tongue-like extensions of offshore Transition Zone species (Figure 6) and central Pacific species (Figure 9) into the California Current to the north of Point Conception, as well as toward northern Baja California as commonly occurs. This took place as warming tendencies subsided. Easterly incursions of offshore species toward central California have been observed during spring months (Brinton 1967a). However, they were particularly pronounced in 1978, appearing to be associated with extensive springtime meanders in the Current. The cool-water component of the meander brought *Euphausia pacifica* and *Thysanoessa spinifera* far to the west of Point Conception. The dispersion there of *T. spinifera* (Figure 8) was the most extensive yet seen.

The 1949-1966 time series (Figure 11) of euphausiids in southern California waters, against which the events of 1977-78 have been measured, indicated three warm periods separated by two-year cool periods. Only the warm period of 1957-60 was of substantial duration. Nevertheless, April-December 1951 and January-August 1954 permitted local spreading of species with warm-water affinities (e.g. *E. eximia, E. gibboides,* and *Nyctiphanes simplex*).

January, when northerly coastal flow is usually maximal, and April, when southerly, offshore flow and upwelling often develop strongly, are ecologically

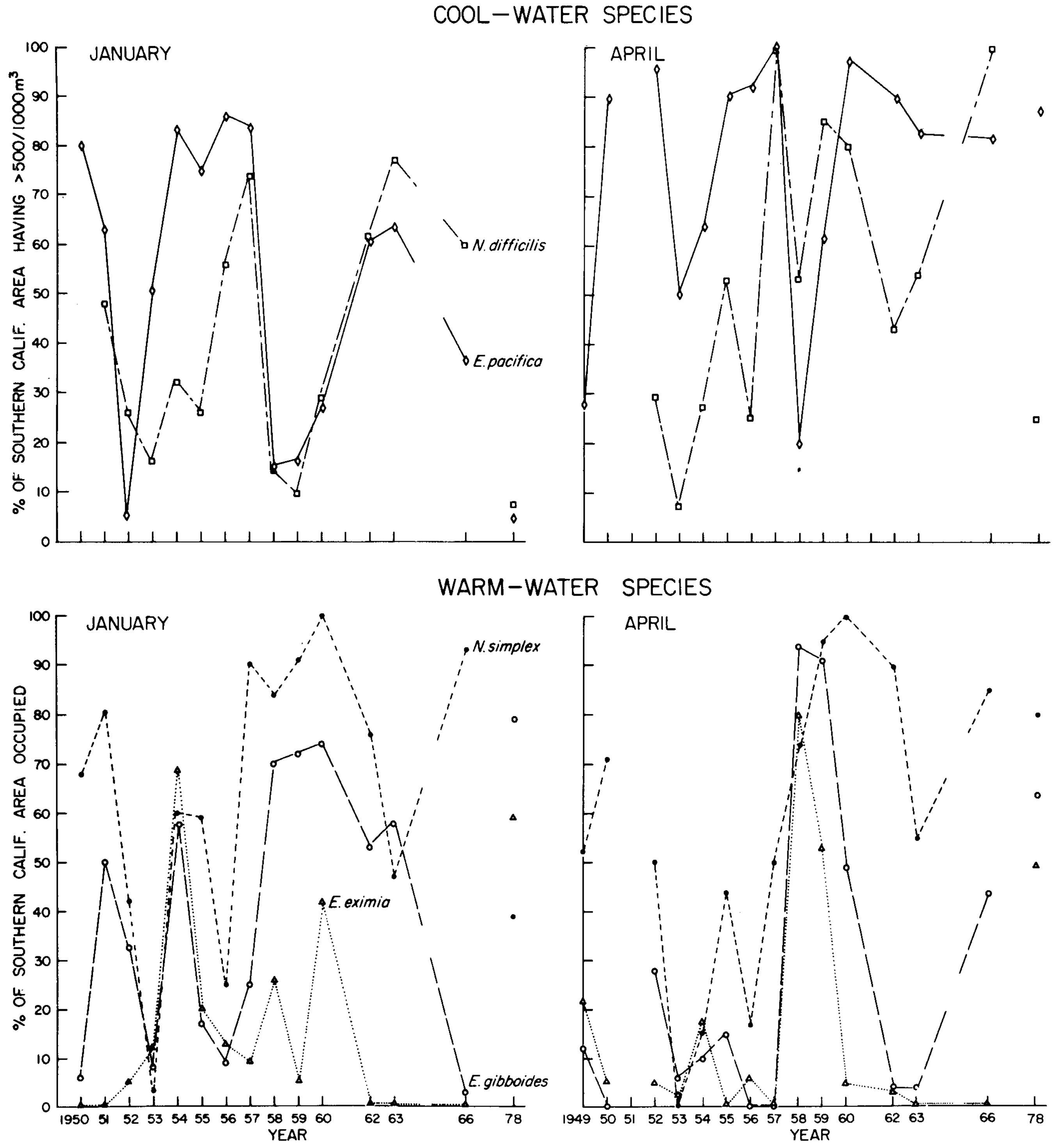

Figure 12. Percentage of southern California area occupied during January and April of 1950-66 and 1978 by the cool-water species *Euphausia pacifica* and *Nematoscelis difficilis* compared with the warm-water species *Euphausia gibboides* (offshore), *E. eximia* (inshore), and *Nyctiphanes simplex* (inshore).

critical times in the annual cycle of climate. Distributions during these months may be used as measures of presence of cool-water and warm-water euphausiids in the southern California area during 1950 to 1978. The generally complementary tendencies of the two groups are evident (Figure 12).

However, there are also some dissimilarities between northern *Euphasia pacifica* and more offshore *Nematoscelis difficilis*. Both show broader though generally parallel distributions of high densities in April compared with February. This is to be expected with the development of upwelling. *E. pacifica* was particularly diminished during January 1952 following warm conditions in late 1951 and was also sparse during warm 1958-59 and January 1978. *N. difficilis* reached a minimum in cool January 1953, as did the several warm-water species, while *E. pacifica* was somewhat less affected. During Januarys of the extended warm period 1958-60, the warm-water species were broadly distributed while the cool-water species were reduced. This was true of April distributions during 1958-59 but not of 1960 by which time cooling had commenced.

Figure 12 also suggests that *Nyctiphanes simplex* persisted widely along California following its northerly proliferation during 1958-60, and that it did not retract southward thereafter to the extent seen during 1953-56. However, in January, 1978, *N. simplex* was more restricted than during Januarys of 1957-60 as well as of 1962, 1963, and 1966.

Diminution in the area of abundances of *E. pacifica* and *N. difficilis* in January 1958 contrasts with the concurrent northerly spread of *E. eximia* and the shoreward spread of *E. gibboides*, as has been emphasized. By April 1958, *E. pacifica* had returned to its normally high density for that season. *N. difficilis* was still much reduced, while April occurrences of the warm-water species (excepting *N. simplex*) were intermediate between the January maxima and mid-1978 minima.

The distributions of temperature and of euphausiids during 1977-78 indicate much zonal transport within the prevailing meridional flow. Clearly, adjacent eddies serve in such transport (e.g. Brinton and Wyllie 1976). Understanding of eddy structure off southern California and in neighboring waters is developing through satellite imagery (e.g. Bernstein et al. 1977; Owen 1980). This will importantly complement conventional means of describing complex coastal environments, in which details of flow are proving to be as important as mean components.

ACKNOWLEDGMENTS

We are pleased to acknowledge the collaboration of the Instituto Nacional de Pesca of Mexico. Portions of these data were collected under authority of the Secretaria de Relaciones Exteriores and the Departamento de Pesca of Mexico.

I thank A. W. Townsend for valuable contributions to this work. Support was provided by the Marine Life Research Program, the Scripps Institution of Oceanography's component of the California Cooperative Oceanic Fisheries Investigations, and by the National Science Foundation, Grant GA-26192.

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