

EFFECTS OF THE 1982–83 EL NIÑO EVENT ON THE EUPHAUSIID POPULATIONS OF THE GULF OF CALIFORNIA

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ABSTRACT

Euphausiid species distributions and abundances in the central and southern Gulf of California were compared during successive springs: March 12–22, 1983 (peak of 1982–83 El Niño) and March 23–April 7, 1984 (relaxation period). Estimates of overall abundance of individual species did not differ significantly between the two years ($p > .05$). Distributions of abundance suggested between-year differences of a much lower order than seasonal changes previously described. Certain of the marginally tropical or tropical species (*Euphausia eximia*, *E. distinguenda*, and *E. tenera*) were found more consistently to the north in March 1983 than in 1984, accompanying surface salinities $<35\text{‰}$ and surface temperatures $>21^{\circ}\text{C}$, which characterized the influence of tropical water in the gulf in spring 1983. Surface warming during El Niño is suggested as the environmental agent most likely to have had biological effects; however, March temperatures of 1983 were only 1° to 2°C over those of 1984.

Youngest observed larvae (calyptopes) of the dominant species, warm-temperate *Nyctiphanes simplex*, exceeded 100,000 individuals/1000 m^3 at 30% of the sampling stations in the gulf during 1984; in 1983, 94% of the stations registered $<7,000$ ind/1000 m^3 . However, due to high variances around means for each year, such observations are interpreted with caution. In 1983, 60% of *N. simplex* postlarvae were at the northernmost stations, near Tiburón Island, where the lowest temperatures were recorded.

RESUMEN

Se compararon las distribuciones y abundancias de las especies de eupáusidos en el Golfo de California central y sur durante dos primaveras sucesivas: del 12 al 22 de marzo de 1983 (período de máxima intensidad de El Niño 1982–83) y del 23 de marzo al 7 de abril de 1984 (fase de relajamiento). Las estimaciones de abundancia total por especie no mostraron diferencias significativas entre años ($p >$

0.05). Las distribuciones de abundancia sugieren que las diferencias entre años fueron de menor orden que la variación estacional previamente descrita. Ciertas especies marginalmente tropicales o tropicales (*Euphausia eximia*, *E. distinguenda*, y *E. tenera*) se encontraron presentes consistentemente más al norte en marzo de 1983 que en 1984, coincidiendo con salinidades en superficie $<35\text{‰}$ y temperaturas en superficie $>21^{\circ}\text{C}$, valores característicos de la masa de agua tropical que invadió el golfo en la primavera de 1983. Se sugiere que el calentamiento superficial del agua durante el evento del Niño pudo haber sido el agente ambiental con mayores efectos biológicos; a pesar que los valores de temperatura registrados en 1983 fueron tan sólo de 1 a 2°C más altos que aquéllos en 1984.

Las larvas más tempranas (caliptopis) de la especie dominante, *Nyctiphanes simplex*, indicadora de aguas templado-cálidas, excedieron los 100,000 ind/1000 m^3 en 30% de las estaciones muestreadas en el golfo durante 1984; en 1983, el 94% de las mismas registraron $<7,000$ ind/1000 m^3 . Sin embargo, estas observaciones deben tomarse con precaución debido a las altas varianzas asociadas a las medias de cada año. En 1983, 60% de las poslarvas de *N. simplex* se encontraron en las estaciones situadas más al norte, cerca de la isla Tiburón, donde se registraron las temperaturas más bajas.

INTRODUCTION

The Gulf of California (figure 1) comprises a series of basins, deepening to the south, which are produced by transform faults (van Andel 1964). It averages approximately 1000 km long and 150 km wide. The benthic and pelagic inhabitants of the gulf have diverse biogeographical affinities. The benthic fauna is probably best regarded as subtropical, with its closest faunal affinity with the tropical "Panamic" region. Northeast Pacific temperate species form a smaller component that increases in abundance northward in the gulf, and also increases during the winter months (Brusca and Wallerstein 1979). Similarly, the pelagic fauna includes tropical, subtropical, and warm-temperate elements (Walker

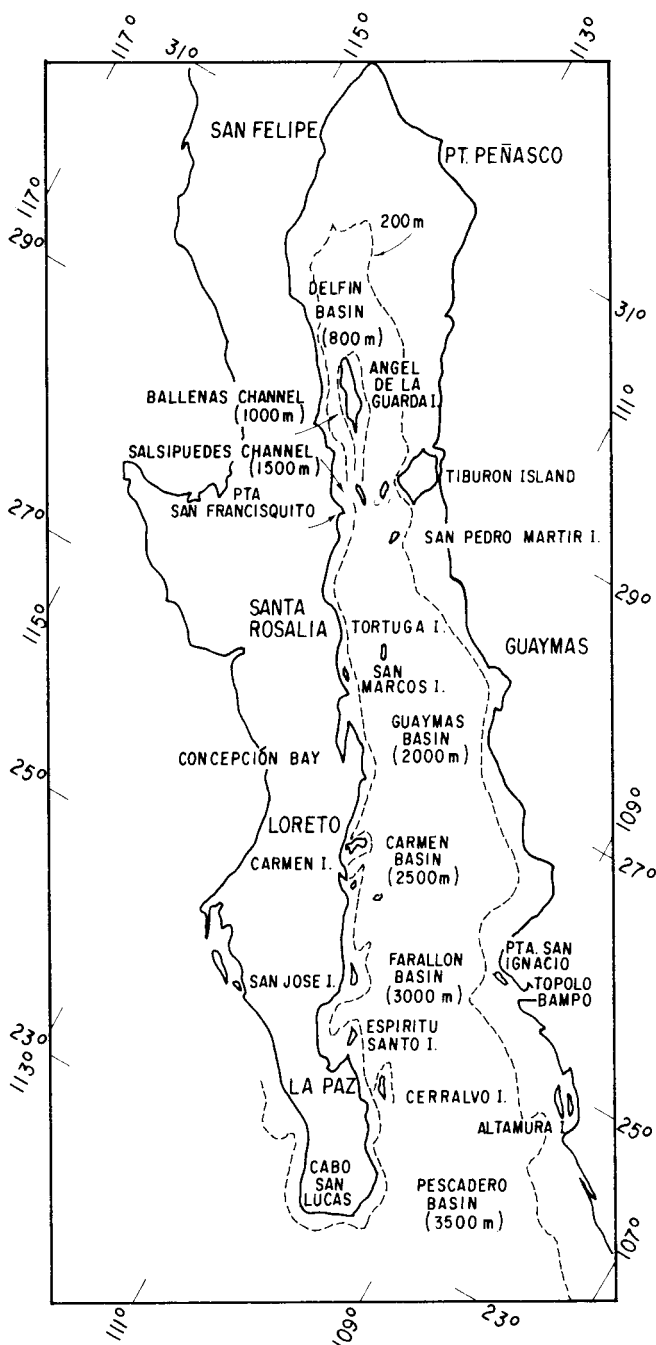


Figure 1. The Gulf of California. Dashed line is 200-m isobath.

1960; Brinton et al. 1986), but interannual changes in distribution or abundance of species have not been described.

Many of the gulf species also occur off the west coast of Baja California, where the California Current meets the equatorial circulation system. The equatorial and the subtropical systems alternately influence the gulf in response to shifts in wind stress (Wyrtki 1966; Baumgartner and Christensen 1985).

The gulf is an evaporation basin, with surface

salinity commonly $>35\%$. However, studies of interannual variability of abiotic conditions in the gulf have confirmed the existence of climatic anomalies resulting from strengthening of the equatorial circulation system as a response to El Niño/Southern Oscillation events (Baumgartner and Christensen 1985; Robles-Pacheco and Marinone 1987).

Analysis of preserved siliceous phytoplankton contained in laminated sediments in a 20-year time series from the central gulf has revealed strong abundance increments of tropical and subtropical diatoms in response to El Niño periods (Baumgartner et al. 1985). Periods of enhancement of phytoplankton microfossils in the deep anoxic basins of the central gulf probably correspond to periods of increased primary productivity and chlorophyll *a* content such as was measured during the 1982–83 El Niño event (Valdez-Holguin and Lara-Lara 1987). Zooplankton volumes were also reported to be high during that event (Jiménez-Pérez and Lara-Lara 1988). This contrasts with the diminished volumes observed in other eastern Pacific systems in 1982–83 (Barber and Chávez 1983, 1986; McGowan 1983, 1984, 1985).

In order to interpret effects of El Niño 1982–83 on euphausiid populations of the Gulf of California, we compared euphausiid species distributions and abundances in March 1983, when the event was intense, with those of March–April 1984, when the system was in transition to what is believed to have been more typical conditions. In an earlier study of seasonal changes in populations of euphausiids in the gulf, based on bimonthly cruises during 1957, Brinton and Townsend (1980) determined that February–April was a peak period of reproduction and abundance of most species. They found a close association of distribution and abundance of species with climatic conditions, particularly temperature.

METHODS

Zooplankton samples were collected from R/V *El Puma* during two cruises extending from Tiburón Island (29°N) southward to the gulf entrance (23°–24°N) during March 12–22, 1983, and March 23–April 7, 1984 (figure 2). Oblique net tows were made from about 200-m depth to the surface, using a 60-cm-mouth-diameter bongo net with 0.333-mm mesh. Volumes of water strained by the nets were determined from flowmeter readings, and abundances of euphausiids were standardized as numbers of individuals per 1000 m³ of water. Samples were preserved in 4% formaldehyde buffered with sodium borate. Stations were sampled at 12-hour intervals, near to noon and midnight.

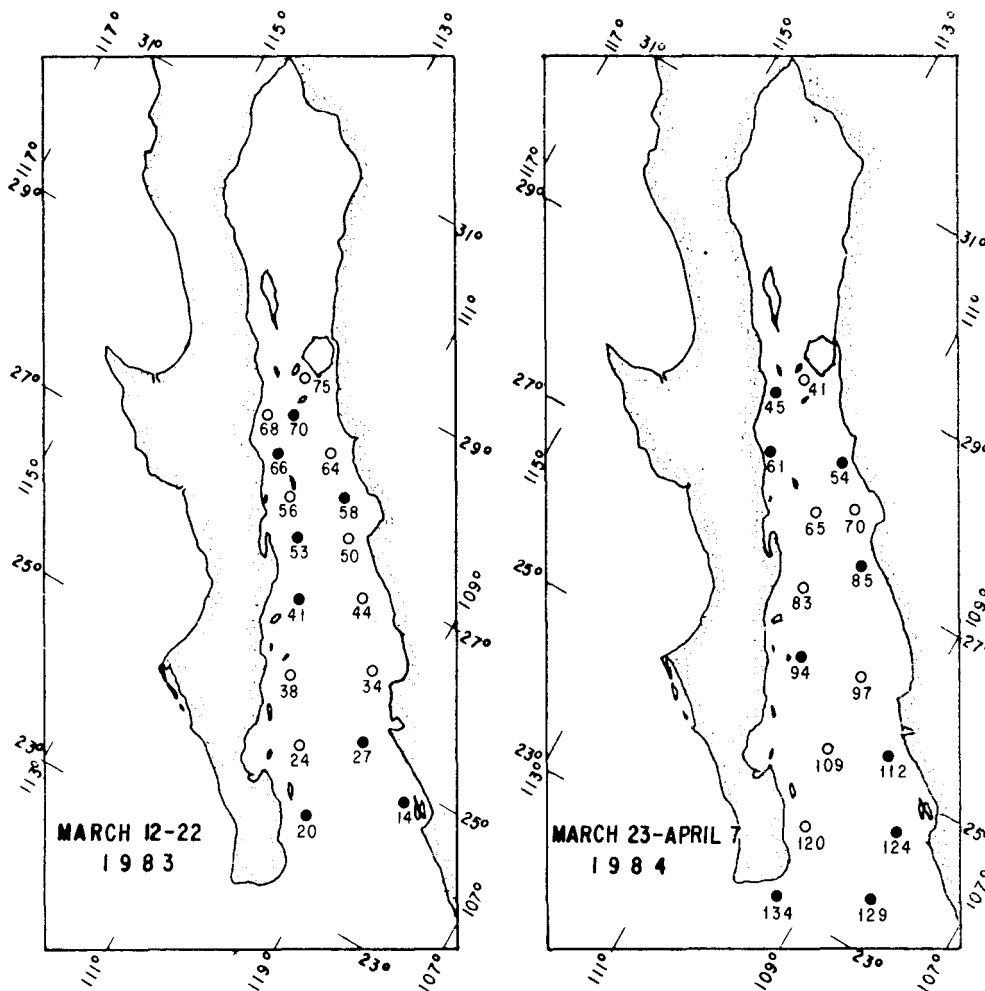


Figure 2. Location of zooplankton tows during CICESE cruises 8303 and 8403/04 (○ = day samples; ● = night samples).

Species were identified and counted in $\frac{1}{32}$ aliquots, fractionated by means of a Folsom splitter. Three life-history stages—calyptopis and furcilia larvae, and postlarvae (juveniles and adults)—were sorted. When a life stage of a species was represented by fewer than three specimens, additional $\frac{1}{32}$ aliquots were used, up to a total of $\frac{1}{8}$ of the original sample. In order to estimate possible combined effects of vertical migration and net avoidance, day abundances of the stages of each species were compared with night abundances by means of Mann-Whitney's U test (Siegel 1980).

Temperature and salinity were measured with a Bissett-Berman CTD at 75 hydrographic stations in March 1983, and at 80 stations in March–April 1984. Dissolved oxygen determinations were done by the Micro-Winkler method at 39 of the 1983 stations. There are no available data for oxygen in 1984.

Frequency distributions of euphausiid abundances were consistently skewed; consequently,

abundances were $\log_{10}(x \pm 1)$ transformed before calculation of means and 95% confidence limits. These values were then antilogged, 1 was subtracted, then reported in the original measurement unit.

RESULTS

The Physical Environment

During March 1983, highest surface salinities (34.9‰–35.2‰) were to the north, near Tiburon Island and along the eastern side of the central gulf (figure 3). Values decreased somewhat toward the south, reaching 34.5‰ in the gulf entrance. In March–April 1984, surface salinities were above 35‰ along the length of the investigated area, except at the mouth of the gulf.

In both years, the surface water temperature showed a gradient of increase from north to south (figure 4). In March 1983 it ranged from 18° to 25.5°C, and in 1984 from 15.8° to 23.8°C. In 1983,

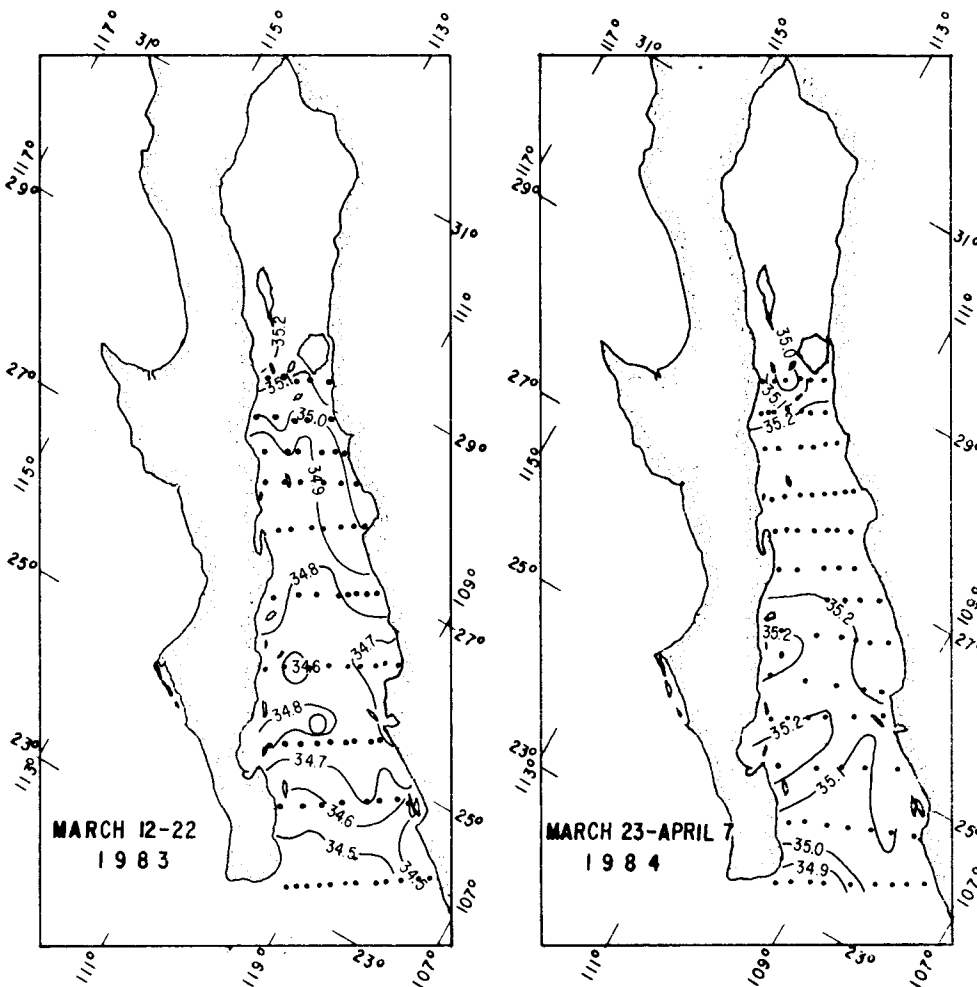


Figure 3. Surface salinity distributions (‰) in the Gulf of California.

tongues of cool water extended along the eastern coast, and in 1984, on both sides of the gulf.

The 1983 temperatures at 30-m depth were 1°C lower than at the surface, but the horizontal gradients were similar at the two levels (figure 5). In contrast, 1984 presented more isotherm distortion at 30-m depth in relation to surface distribution, with temperature differences between coasts as high as 4°C in the southern gulf. The interannual temperature difference persisted at 100-m depth (figure 6), with values about 2°C warmer in 1983 than in 1984.

The depth of the 1.5 ml/l dissolved oxygen isopleth in March 1983 (figure 7) increased northward from the mouth (120 m) to the central gulf (>200 m). There are no available data for 1984.

Distribution

Species populations. Euphausiid mean abundance was 6,869 ind/1000 m³ in March 1983, with eleven species present (table 1). In spring 1984, in the same

geographic area (24° to 29°N), euphausiid mean abundance was 29,921 ind/1000 m³. However, for each species, 95% confidence limits for the abundance estimates significantly overlapped between years (table 1). Two species not found inside the gulf (north of 24°N) in 1984 (*Nematoscelis gracilis* and *Stylocheiron carinatum*) were nevertheless present just outside the mouth, 23°–24°N, in that year.

Significant differences between day and night abundances were found only in postlarval *Nyctiphanes simplex* ($p = 0.042$) and *Euphausia eximia* ($p = 0.002$), with nighttime abundances being greater and, therefore, used to determine abundances of those species. Larvae did not show significant day-night differences in abundance ($p > 0.05$). Therefore, both day and night samples were used to determine abundances of larvae of all species (table 2).

The greater average euphausiid abundance in 1984 was mainly due to the generally coastal species *Nyctiphanes simplex*, since it constituted 60% of the euphausiids sampled in 1983, and 96% in 1984. Five

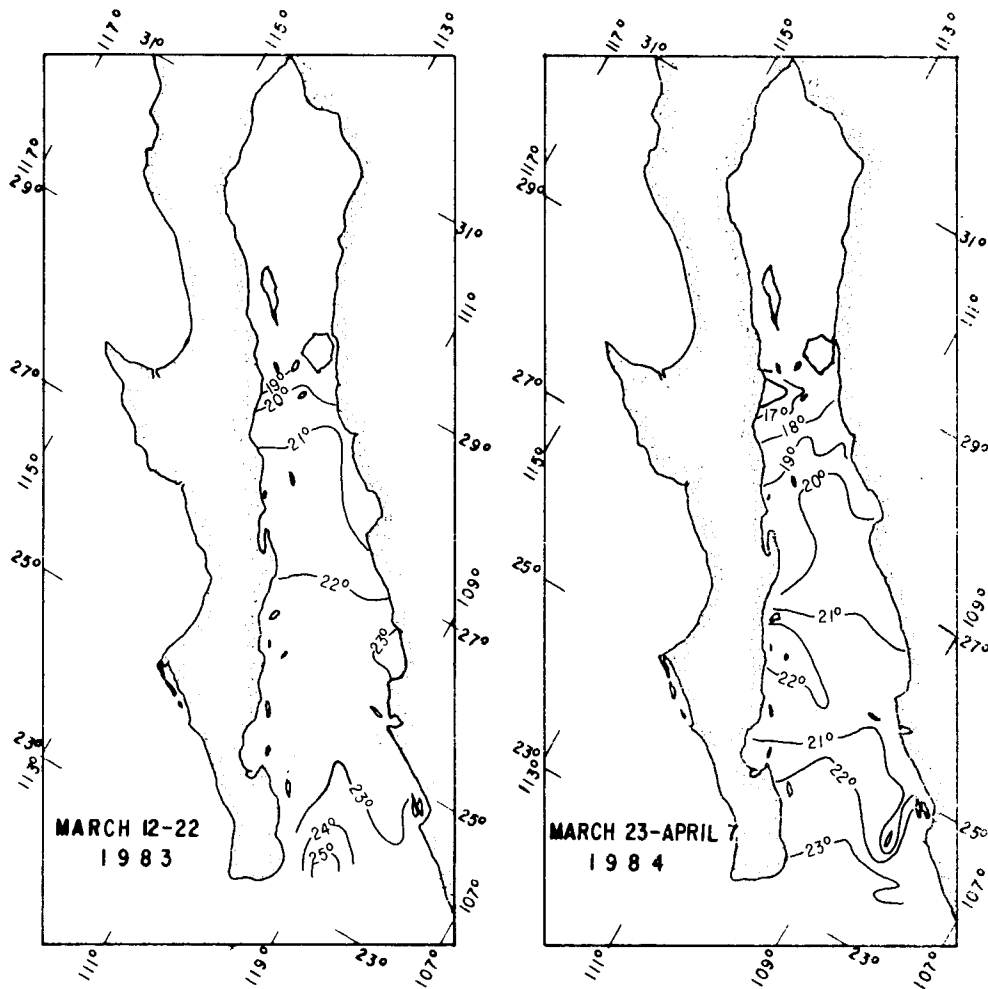


Figure 4. Surface temperature distributions (°C) in the Gulf of California.

TABLE 1
 1983 and 1984 Mean Abundances (Antilogged), Also Showing Lower (LL) and Upper (UL) 95% Confidence Limits

Geographical range ^a	Species	1983 (N = 17)		1984 (N = 14) ^b	
		\bar{x} (LL _{95%} -UL _{95%})	%	\bar{x} (LL _{95%} -UL _{95%})	%
Warm-temperate North Pacific	<i>Nematoscelis difficilis</i>	2,555 (1,432-4,560)	37.2	1,120 (243-5,150)	3.7
Marginal to eastern tropical Pacific	<i>Nyctiphanes simplex</i> ^c	4,133 (995-17,146)	60.2	28,770 (3,108-266,267)	96.1
	<i>Euphausia eximia</i> ^c	110 (16-718)	1.6	9 (0-180)	<0.1
Equatorial Pacific endemics (adapted to regions with subsurface oxygen deficiency)	<i>Nematoscelis gracilis</i>	0 (0-2)	0.1	0 (0-0)	<0.1
	<i>Euphausia diomedea</i>	2 (0-9)	0.1	2 (0-9)	<0.1
	<i>Euphausia distinguenda</i>	56 (12-258)	0.8	9 (1-54)	<0.1
	<i>Euphausia lamelligera</i>	1 (0-2)	<0.1	1 (0-3)	
Cosmopolitan in tropical and subtropical waters	<i>Euphausia tenera</i>	7 (1-31)	<0.1	4 (0-21)	<0.1
	<i>Nematobrachion flexipes</i>	1 (0-3)	<0.1	1 (0-3)	<0.1
	<i>Stylocheiron affine</i>	2 (0-8)	<0.1	5 (0-28)	<0.1
	<i>Stylocheiron carinatum</i>	1 (0-2)	<0.1	0 (0-0)	0
	Total	6,869	100.0	29,921	100.0

^aDefined in Brinton (1962, 1979).

^bExcluding stations at mouth of gulf (23°-24°N).

^cMeans are from night samples only (1983 n = 8; 1984 n = 7), because night and day \bar{x} 's differed significantly.

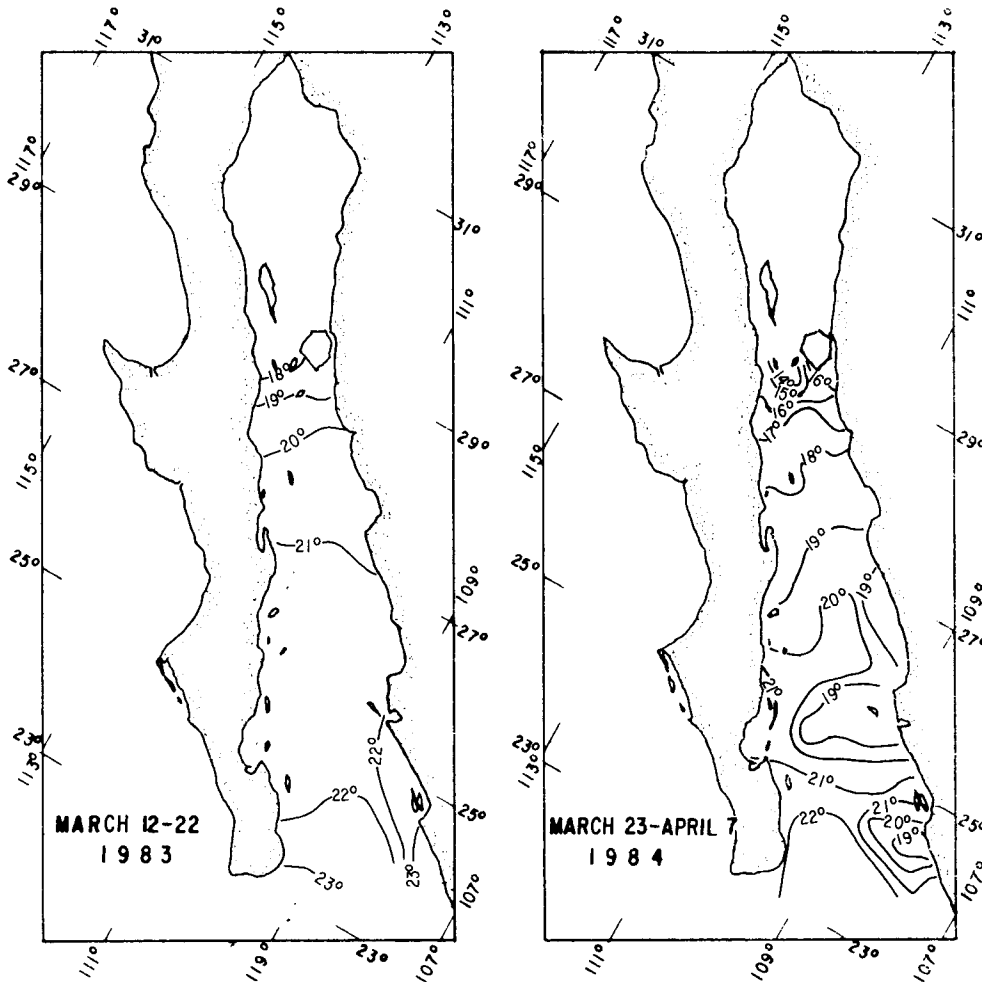


Figure 5. Temperature distributions (°C) at the 30-m depth.

TABLE 2
 1983 and 1984 Mean Abundances (Antilogged), with Lower and Upper 95% Confidence Limits

Species		Calypt.	1983 Furc.	Postlar.	Calypt.	1984 ^a Furc.	Postlar.
<i>Nematoscelis difficilis</i>	\bar{x}	1,240 (726-2,118)	575 (207-1,595)	279 (115-676)	124 (12-1,188)	216 (43-1,063)	90 (14-560)
<i>Nyctiphanes simplex</i>	\bar{x}	835 (189-3,685)	2,046 (874-4,787)	396 ^b (145-1,079)	1,940 (143-26,091)	1,499 (189-11,821)	1,277 ^b (31-50,757)
<i>Euphausia eximia</i>	\bar{x}	3 (0-14)	7 (1-26)	62 ^b (13-294)	1 (0-6)	6 (1-30)	4 ^b (1-60)
<i>E. diomedea</i>	\bar{x}	1 (0-4)	0	1 (0-9)	0	1 (0-4)	1 (0-4)
<i>E. distinguenda</i>	\bar{x}	19 (3-90)	18 (4-75)	4 (0-18)	3 (0-13)	2 (0-8)	5 (0-29)
<i>E. lamelligera</i>	\bar{x}	0	0	1 (0-2)	0	1 (0-1)	1 (0-1)
<i>E. tenera</i>	\bar{x}	2 (0-8)	3 (0-9)	1 (0-5)	1 (0-7)	1 (0-6)	1 (0-3)
<i>Nematoscelis gracilis</i>	\bar{x}	0	1 (0-1)	0 (0-1)	0	0	0
<i>Nematobrachion flexipes</i>	\bar{x}	0	1 (0-3)	0	0	1 (0-3)	0
<i>Stylocheiron affine</i>	\bar{x}	1 (0-4)	1 (0-3)	1 (0-5)	1 (0-6)	4 (0-15)	3 (0-11)
<i>S. carinatum</i>	\bar{x}	0	0	1 (0-2)	0	0	0

^aExcluding stations at mouth of gulf (23°-24°N).

^b \bar{x} 's are from night stations only (1983 n = 8; 1984 n = 7), because night and day \bar{x} 's differed significantly.

Total abundance for each species within a year differs from table 1 because of the properties of the log-normal distribution and, in the cases of *Nyctiphanes simplex* and *Euphausia eximia*, the inclusion of daytime abundance estimates for larval stages in the present table.

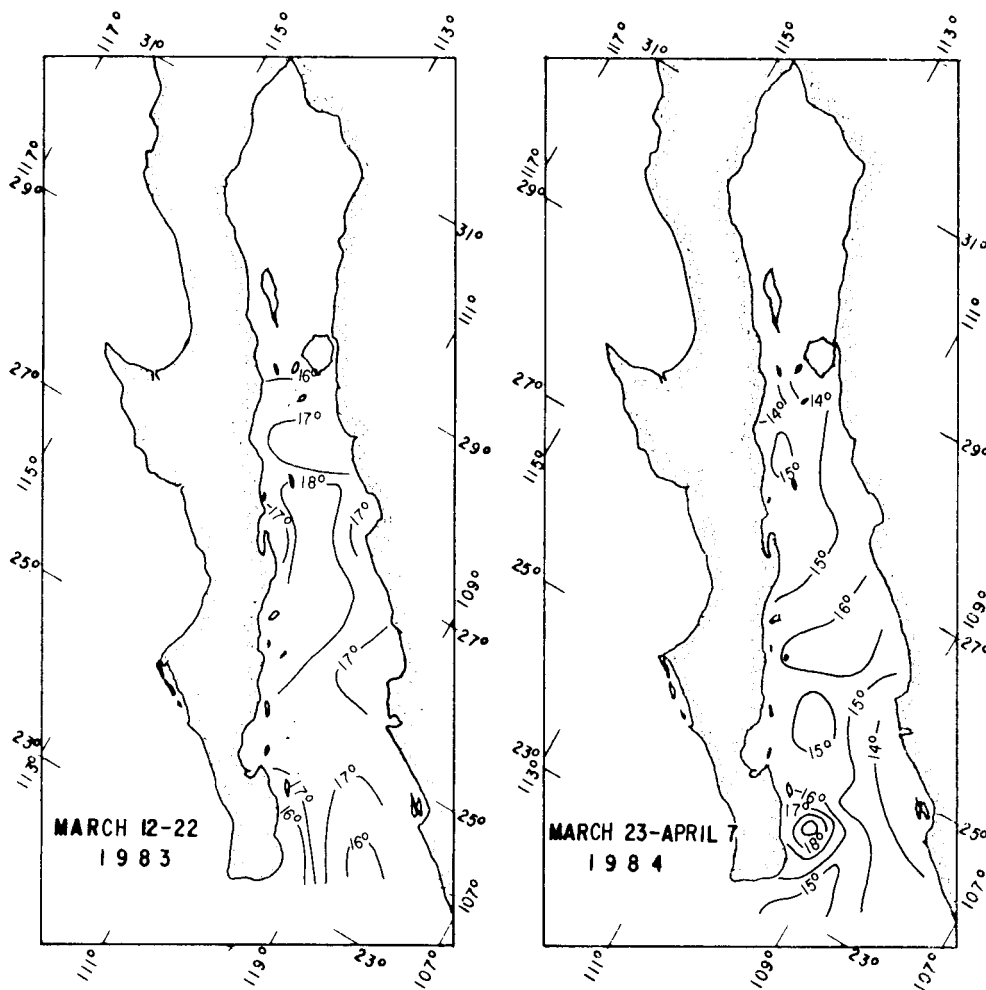


Figure 6. Temperature distributions (°C) at the 100-m depth.

of the six 1983 high abundances of *N. simplex*, >5,000 ind/1000 m³, were to the north, at stations where temperature was less than 21°C (figure 8). In 1984, abundances of >5,000 ind/1000 m³ were more common, with the highest interval, >50,000 ind/1000 m³, extending along much of the eastern coast of the gulf. *Nematoscelis difficilis* was the species second in abundance at 37% of the total euphausiids in 1983, and 4% in 1984 (table 1). Highest abundances in 1984, >5,000 ind/1000 m³, appeared shifted somewhat toward the north in the central gulf with respect to 1983 (figure 9).

The remaining nine species contributed <5% of the total euphausiids in both years (table 1). Their individual mean densities were <200 ind/1000 m³. *E. distinguenda* (figure 10), *E. eximia* (figure 11), *E. tenera* (figure 12), and *E. diomedae* (appendix 1, 2) were more consistently found in the central part of the gulf during 1983, when warm temperatures (e.g., >21°C, surface) and low salinity (<34.9‰, surface) were farther to the north (figures 3, 4). No

specimens of these species were found at the northernmost group of stations, 28°–29°N. *Stylocheiron affine* showed no difference in distribution between the two years (figure 13).

Life-history stages. With the exception of *Stylocheiron carinatum*, of which only postlarvae were present, larvae of all species were present in the gulf. The youngest observed life-history stage, the calyptopis larvae (nauplii not sampled), was found for only seven of the eleven species (table 2). Calyptopes of *Nyctiphanes simplex* and the warm-temperate species *Nematoscelis difficilis* were abundant across the area sampled (appendix 1, 2); maximum densities were associated with surface temperatures of <22°C (figure 14). Recruitment of calyptopes of *N. simplex* was uneven across the sampling grids of both years, as seen in the high variances associated with mean abundance (table 2). However, in spring 1984, densities >100,000 ind/1000 m³ were found at four of the stations (appendix 2), all of which were along the eastern coast, whereas in spring 1983, all

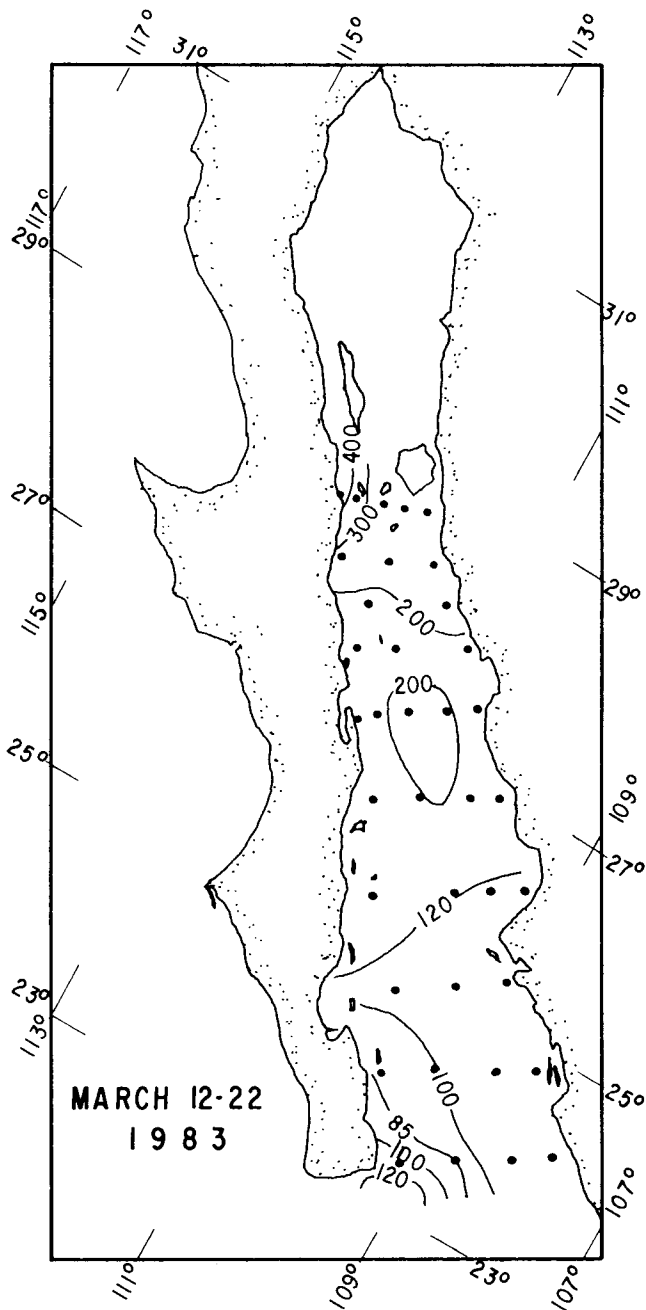


Figure 7. Depth of the 1.5 ml/l oxygen concentration.

but one of the stations yielded <7,000 calyptopes/1000 m³ (appendix 1). Postlarvae of *N. simplex* included more ovigerous females in spring 1984 than in 1983.

In 1983 the northward extensions of the ranges of the two most abundant species from the eastern tropical Pacific, *E. distinguenda* and *E. tenera* (figures 10, 11) were entirely due to larvae (appendix 1), with postlarvae remaining restricted to the gulf entrance, in the zone characterized by the lowest subsurface oxygen levels (figure 7).

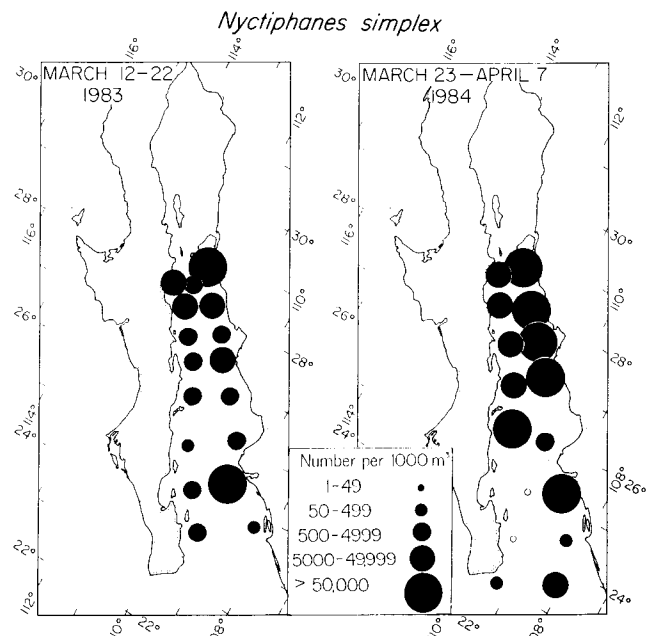


Figure 8. Distribution of *Nyctiphanes simplex*.

DISCUSSION

Environmental conditions in the Gulf of California during March 1983 showed climatic anomalies that can be explained as a response to the El Niño event that affected the eastern Pacific Ocean beginning in fall 1982 (Cane 1983; Rasmusson and Wallace 1983; Simpson 1983; Barber and Chavez 1986). Those anomalies consisted mainly of sea-level rise and surface-water warming, both reaching record values for the last 30 years (Robles-Pacheco and

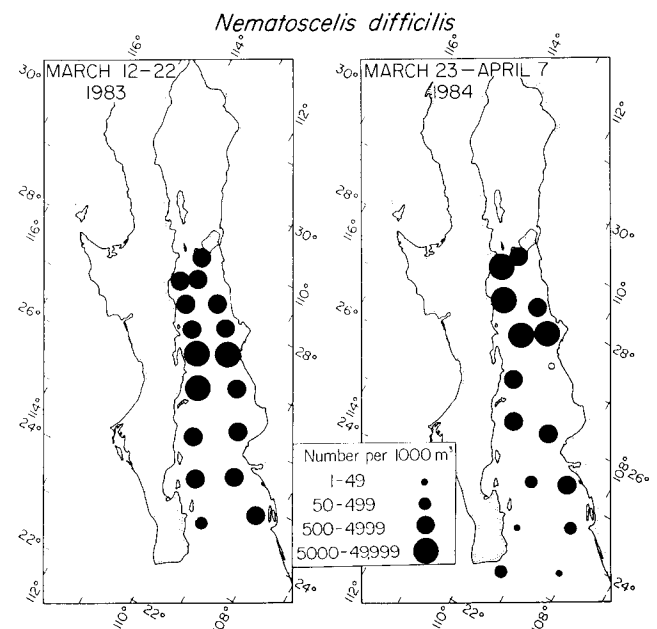


Figure 9. Distribution of *Nematoscelis difficilis*.

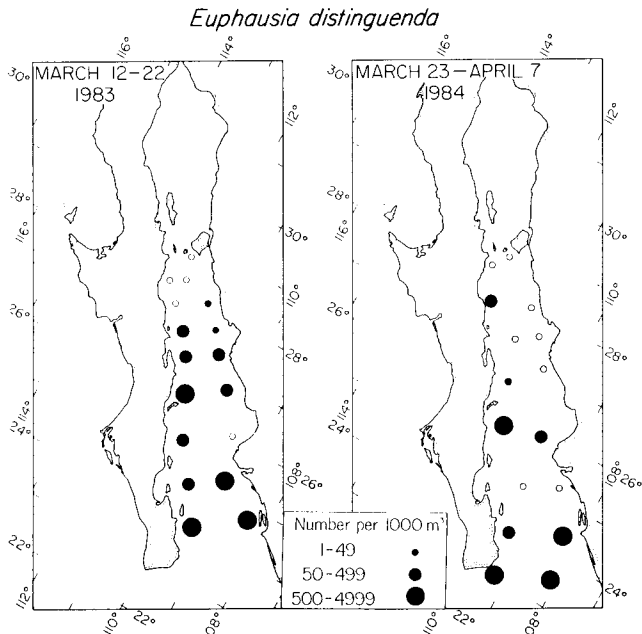


Figure 10. Distribution of *Euphausia distinguenda*.

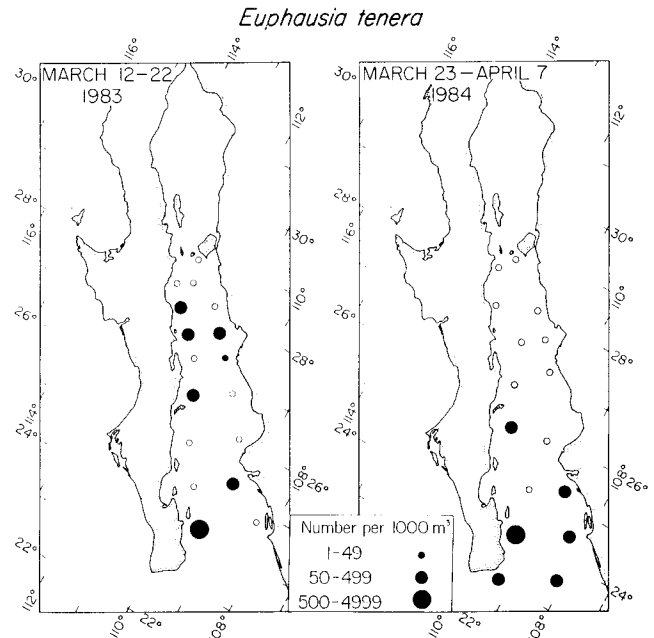


Figure 12. Distribution of *Euphausia tenera*.

Christensen 1984; Robles-Pacheco and Marinone 1987). The observed relatively low surface salinity of 1983 (<35‰) indicated that tropical surface water had invaded the gulf from the south (Robles-Pacheco and Marinone 1987). Subsequently, during spring 1984, surface salinity was reverting toward the more usual values reported by Roden and Groves (1959), Roden (1964), and Alvarez-Borrego and Schwartzlose (1979). Surface temperatures

were 1° to 2°C lower during spring 1984, showing that El Niño had weakened.

Surface temperatures and euphausiid species distributions observed in the gulf in April 1984 were similar to the conditions described for April 1957 (Brinton and Townsend 1980). April 1957 may have been the beginning of El Niño 1957-59, because water temperatures were reported to be 1°C warmer than in April 1956 (Anonymous 1963).

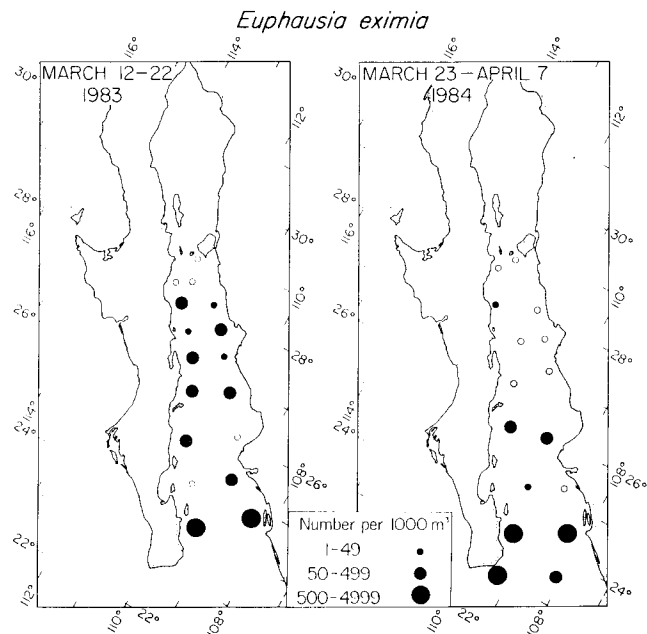


Figure 11. Distribution of *Euphausia eximia*.

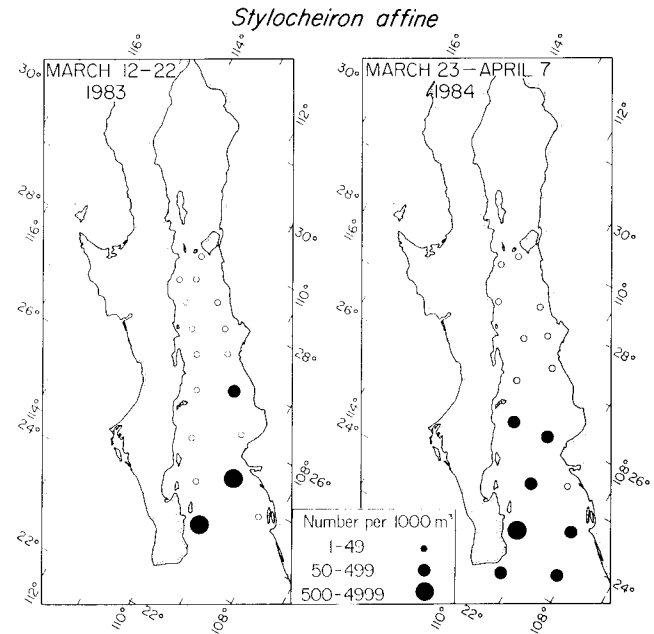


Figure 13. Distribution of *Stylocheiron affine*.

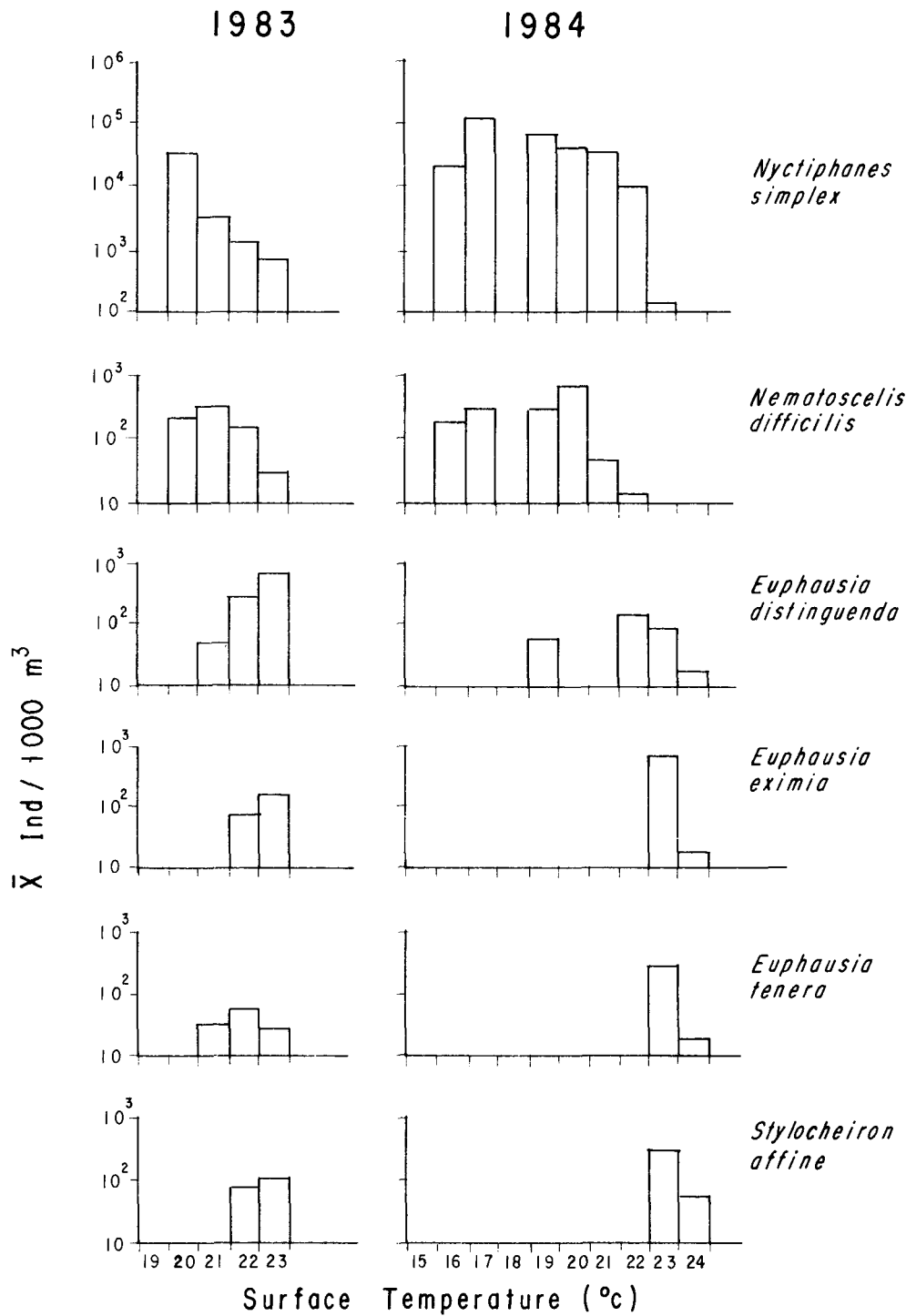


Figure 14. Mean abundances of calyptopis larvae versus surface temperature.

Therefore, the springs of 1957 and 1984 can be considered as transition states—to a warm period in 1957 and to a cool period in 1984. This generally corresponds to conditions reported for the California Current, where longer time series are available (Bernal 1981; Brinton and Reid 1986).

Increased tropical characteristics of gulf water in

1983 were associated with surprisingly indistinct differences in abundance and reproduction of the dominant, widespread species (*Nyctiphanes simplex*) compared with 1984, although there are suggestions of possible differences in abundances of calyptopes and postlarvae (table 2). However, those tropical waters seem to be related to an increased 1983 pres-

ence of *Euphausia eximia*, *E. distinguenda*, and *E. tenera*, species that belong to eastern tropical Pacific adaptative groups (Brinton 1962, 1979). In the following spring (1984), as climatic conditions changed, the *Euphausia* species contracted their distribution somewhat southward.

Between-year differences in euphausiid abundance and distribution suggested by the data can be explained by the changing surface circulation, which is coupled to the large-scale Pacific Ocean circulation (Wyrtki 1966; Baumgartner and Christensen 1985). When El Niño occurs, the North Equatorial Countercurrent is strengthened, causing the Costa Rica Current to reach northward into the Gulf of California. This process resembles an extension into spring of the usual summer-autumn gulf circulation pattern (Baumgartner and Christensen 1985). Northward incursions of the tropical species, interpreted as seasonal, were observed in the summer of 1957 (July–August; Brinton and Townsend 1980) and in the autumn of 1967 (September–November; Mundhenke 1969), when water was transported northward, associated with maximum recorded temperatures for those years.

In the California Current system, *E. distinguenda* and *E. tenera* rarely penetrate north of the tropics (Brinton 1960, 1962), and their occasional northward presence there has been related to El Niño, as in fall 1957 when the strong warming event of 1958–59 became evident in the eastern North Pacific. For example, at that time *E. distinguenda* was found off Punta Eugenia (28°N; Brinton 1960, 1967a). During winter 1982 many *E. distinguenda* and *E. tenera* adults were found off Magdalena Bay lagoons (23°26'–25°35'N), just to the north of the expected limit of the tropical fauna (Green-Ruiz 1986).

E. distinguenda is endemic to the eastern tropical Pacific, and postlarvae perform diel vertical migrations into and out of depths below 150 m, where oxygen concentrations are <1.0 ml/l in this water mass (Brinton 1979). Other species with this capability — *E. lamelligera*, *E. diomedae*, and *Nematoscelis gracilis* — were lower in abundance and steady in geographical range in March of 1983 and 1984 in the gulf. Brinton and Townsend (1980) reported that these species remained near the mouth of the gulf during the cool season of 1957 (February–April) but reached the central gulf and even the northernmost gulf during summer. The extent to which this northward penetration in 1957 may have been enhanced by the midyear onset of El Niño 1958–59 is not known.

All of the above equatorial species and the warm-water cosmopolite *E. tenera*, especially their post-

larval stages, had maximum densities where low concentrations of oxygen were present at shallowest depths (figure 7), while postlarvae of the temperate species *Nematoscelis difficilis* were absent in this region. Warm-water cosmopolite species such as *E. tenera* (40°N–40°S, but absent in eastern boundary currents) are not always good indicators of tropical water mass because of their large geographical ranges. However, the intrusion of *E. tenera* larvae into the gulf certainly results from transport by tropical water, since this species inhabits the eastern tropical Pacific but is usually absent from the adjacent southernmost part of the California Current (Brinton 1962, 1979).

In the spring of 1957, distributions of *Nematoscelis difficilis* and *Nyctiphanes simplex* extended southward to the mouth of the gulf (Brinton and Townsend 1980) as in 1983 and 1984. The summer data from 1957 showed both species still present almost to the mouth of the gulf, though in reduced numbers, even though surface waters were 10°C warmer than in spring. Both species, together with *Euphausia eximia*, are residents of the California Current (Brinton 1962, 1967a, 1973). However, *E. eximia* and *N. simplex* populations are centered in the southernmost part of that current, where they are considered to be midstream and coastal components, respectively, constituting their own subtropical group. On the other hand, *N. difficilis* is a conspicuous element all along the current to the tip of Baja California (23°N) (Brinton 1979). *N. difficilis* did not show strong interannual (1983, 1984) differences in its gulf distribution, despite its association with cooler waters than *Nyctiphanes simplex*. This may have been due to the generic behavior of *Nematoscelis*, whose postlarvae tend to stay beneath the mixed layer (below approximately 50–100 m in summer) day and night (Brinton 1967b, 1979).

Thus *Nematoscelis difficilis* may stabilize its range by avoiding the surface layer with its relatively variable temperatures. In March 1983, the mixed layer of the gulf was very stable, as can be observed in the 30-m temperature distributions (figure 5). There is some evidence, though inconclusive, that *N. difficilis* migrates vertically, possibly to 300–400 m in the California Current, but its migration may be restricted to well-oxygenated waters (Brinton 1967b, 1979). It is nevertheless probable that during spring 1983 many *N. difficilis* remained submerged beneath the warm surface layer of the gulf. This mechanism was observed in the copepod *Calanus pacificus californicus* during summer (Fleminger data in Brinton et al. 1986). However, Brinton and Townsend (1980) considered this possibility un-

likely for *N. difficilis* because they did not find significantly fewer adults in August 1957 than in April 1957, within the 0–140-m depths sampled. Because of the extensive presence of oxygen-deficient waters in the gulf, information on the depth distributions of gulf euphausiids is needed.

Among these species, *Nyctiphanes simplex* showed the longest reproductive period in 1957: at least February through June (Brinton and Townsend 1980). Even though 1983 larvae were found throughout a large range of surface temperature (20°–23°C), they were most abundant to the north, where temperature was lowest (figures 4, 14; appendix 1). This supports the possibility that the warming event of 1983 had a negative effect on calyptopis recruitment. Brinton and Townsend (1980) reported that the best calyptopis recruitment in 1957 occurred in waters of 17°–18°C (10-m depth), which is cooler than any part of the gulf covered in 1983. Calyptopis distribution in April 1957 was very similar to that of April 1984, but surface water temperature was slightly warmer in 1984. However, temperature distribution at 30-m depth in spring 1984 resembled that at 10-m depth in April 1957, with <19°C prevailing at those respective depths in the central and southeastern gulf.

Subsurface warming (down to 100 m) in spring 1983 could also help explain lower abundances of *N. simplex* postlarvae, since this species may perform short vertical migrations (150 m), as observed in the California Current (Brinton 1967b).

Feeding habits of *N. simplex* are not yet known. It seems unlikely that production of this species was limited in 1983 by available food, because much other plankton was then abundant in the gulf. Primary productivity and chlorophyll *a* concentrations were higher in the gulf during El Niño 1982–83 than during other times of observation (Valdez-Holguín and Lara-Lara 1987; Lara-Lara and Valdez-Holguín 1988), contrasting with generally decreased productivity observed in more oceanic, warm-temperate systems affected by El Niño (Dandonneau and Donguy 1983; Barber and Chavez 1983; McGowan 1983). Zooplankton biomass was also high, with March 1983 average amounts (displacement volumes) (Jiménez-Pérez and Lara-Lara 1988) being similar to March–April 1984 averages (Lavaniegos-Espejo 1988) and to those reported for April of 1956 and 1957 (Brinton et al. 1986).

Abundances of *Nyctiphanes simplex* in the gulf during spring 1983 were not low compared with most abundances found in the California Current, where, in uneventful years, this species usually is restrained within the region of about 20°N to 35°N

(Brinton 1962, 1979). During El Niño events this species proved to be a good indicator of northerly transport of coastal water of the California Current, reaching at least to Cape Mendocino (40°N) in 1958 (Brinton 1960) and at least to the Washington–Oregon border (46°N) in 1982–83 (Brodeur 1986). In the southern part of its distributional range, off Magdalena Bay (24°–25°N), *N. simplex* was not found in December 1982, whereas in summer of that year it had been present there in 40% of a set of zooplankton samples, constituting 95% of all euphausiid adults. In February 1983, warm temperatures persisted, and *N. simplex* continued to be scarce at that southern locality (Green-Ruiz 1986).

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APPENDIX 1
 Abundances of Life Phases (Individuals/1000 m³), March 1983

Species	Life-history stage	Sampling stations (D = day; N = night)																
		D 75	N 70	D 64	D 68	N 66	N 58	D 50	D 56	N 53	D 44	N 41	D 34	D 38	N 27	N 14	D 24	N 20
<i>Nematoscelis difficilis</i>	Calypt.	843	2,190	2,831	3,038	2,170	1,822	6,390	1,844	2,744	628	1,795	308	1,812	994	461	840	78
	Furc.	211	313	786	640	723	1,325	3,630	1,418	3,659	63	3,740	231	680	1,293	1,077	2,648	0
	Postlar.	492	1,408	1,258	240	217	455	73	177	1,220	157	1,945	308	113	597	461	388	0
<i>Nyctiphanes simplex</i>	Calypt.	87,117	782	2,674	6,875	5,931	2,981	3,921	1,560	305	0	1,496	925	151	4,077	0	1,421	932
	Furc.	35,409	2,972	5,505	2,238	10,416	828	3,340	2,695	534	2,073	1,496	463	529	92,775	154	840	388
	Postlar.	9,836	352	315	0	615	248	109	71	457	188	1,496	0	151	1,790	231	258	39
<i>Euphausia eximia</i>	Calypt.	0	0	0	0	0	0	0	0	0	126	0	0	151	99	77	0	544
	Furc.	0	0	0	0	0	0	36	0	38	31	37	0	76	50	231	0	932
	Postlar.	0	0	39	0	72	83	0	35	38	0	75	0	0	199	461	0	155
<i>Nematoscelis gracilis</i>	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	78
	Postlar.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	78
<i>E. diomedea</i>	Calypt.	0	0	0	0	0	0	0	0	0	63	0	0	0	0	0	32	117
	Postlar.	0	0	0	0	108	0	0	0	0	0	0	0	0	25	0	0	117
<i>E. distinguenda</i>	Calypt.	0	0	0	0	0	0	0	142	145	126	449	0	154	1,094	538	65	1,320
	Furc.	0	0	39	0	0	41	109	0	38	63	0	0	227	398	231	388	1,476
	Postlar.	0	0	0	0	0	0	0	0	0	0	112	0	76	298	231	0	1,165
<i>E. lamelligera</i>	Postlar.	0	0	0	0	0	0	0	0	0	0	0	38	0	38	0	0	
<i>E. tenera</i>	Calypt.	0	0	0	0	0	166	0	142	0	0	150	0	0	0	0	0	78
	Furc.	0	0	0	0	72	0	36	35	0	0	75	0	0	0	0	0	311
	Postlar.	0	0	0	0	0	0	0	0	0	0	0	0	0	99	0	0	1,243
<i>Nematobranchion flexipes</i>	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	25	0	32	39	
<i>Stylocheiron affine</i>	Calypt.	0	0	0	0	0	0	0	0	0	0	0	0	398	0	0	233	
	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	99	0	0	78	
	Postlar.	0	0	0	0	0	0	0	0	0	63	0	0	75	0	0	272	
<i>S. carinatum</i>	Postlar.	0	0	0	0	0	0	0	0	0	0	37	0	0	0	0	39	
Total		133,908	8,017	13,447	13,031	20,324	7,949	17,644	8,119	9,178	3,581	12,903	2,235	4,158	104,385	4,191	6,912	9,712

APPENDIX 2
 Abundances of Life Phases (Individuals/1000 m³) March–April 1984

Species	Life-history stage	Sampling stations (D = day; N = night)														Outside gulf	
		D 41	N 45	N 54	D 70	N 61	D 65	N 85	D 83	D 97	N 94	N 112	D 109	N 124	D 120	N 129	N 134
<i>Nematoscelis difficilis</i>	Calypt.	2,892	1,763	1,020	11,791	5,172	10,584	0	179	269	0	1,339	0	0	0	0	0
	Furc.	0	1,528	127	3,088	3,735	6,324	0	1,071	806	133	669	67	173	38	0	0
	Postlar.	263	1,763	2,677	0	1,473	161	0	2,142	168	1,339	0	135	138	0	17	85
<i>Nyctiphanes simplex</i>	Calypt.	143,286	25,746	115,615	115,098	9,769	5,679	4,751	3,213	134	18,102	105,774	0	0	0	412	0
	Furc.	1,117	12,343	2,422	10,668	5,172	42,593	82,121	1,071	873	31,279	14,728	0	104	0	6,201	0
	Postlar.	66	0	28,681	1,684	431	645	48,187	13,923	671	4,525	29,456	0	69	0	34	102
<i>Euphausia eximia</i>	Calypt.	0	0	0	0	0	0	0	0	34	0	0	0	1,526	0	0	
	Furc.	0	0	0	0	36	0	0	0	134	67	0	34	1,174	76	0	389
	Postlar.	0	0	0	0	0	0	0	0	0	116	0	0	553	0	189	761
<i>Nematoscelis gracilis</i>	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	68
	Postlar.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	481	68
<i>E. diomedea</i>	Furc.	0	0	0	0	0	0	0	0	0	33	0	0	0	229	69	17
	Postlar.	0	0	0	0	0	0	0	0	0	33	0	0	173	0	52	17
<i>E. distinguenda</i>	Calypt.	0	0	0	0	144	0	0	0	134	133	0	0	69	0	172	17
	Furc.	0	0	0	0	0	0	0	0	34	33	0	0	138	38	567	68
	Postlar.	0	0	0	0	0	0	0	45	269	532	0	0	760	38	756	541
<i>E. lamelligera</i>	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	35	0	17	51
	Postlar.	0	0	0	0	0	0	0	0	0	33	0	0	0	0	0	17
<i>E. tenera</i>	Calypt.	0	0	0	0	0	0	0	0	0	0	0	0	207	458	120	17
	Furc.	0	0	0	0	0	0	0	0	0	0	335	0	0	229	120	118
	Postlar.	0	0	0	0	0	0	0	0	0	67	0	0	35	0	52	186
<i>Nematobrachion flexipes</i>	Furc.	0	0	0	0	0	0	0	0	33	0	0	69	0	0	0	
	Postlar.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	
<i>Stylocheiron affine</i>	Calypt.	0	0	0	0	0	0	0	0	0	0	0	138	458	34	51	
	Furc.	0	0	0	0	0	0	0	0	67	33	0	34	69	343	69	51
	Postlar.	0	0	0	0	0	0	0	0	0	67	0	34	173	114	206	118
<i>S. carinatum</i>	Furc.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	
Total		147,624	43,143	150,542	142,329	25,932	65,986	135,059	21,644	3,593	56,559	152,301	304	4,077	3,547	9,586	2,776