

## THALIACEA OF THE CALIFORNIA CURRENT REGION: RELATIONS TO TEMPERATURE, CHLOROPHYLL, CURRENTS, AND UPWELLING

MAURICE BLACKBURN  
Institute of Marine Resources<sup>1</sup>  
University of California San Diego  
La Jolla, California 92093

### ABSTRACT

Thaliacea are a major component of herbivorous zooplankton biomass in the upper layers of warm seas and are able to colonize areas where conditions are suitable at a faster rate than other herbivores. An attempt was made to relate distribution and abundance of the principal species of the California Current region to distributions of their food (measured as chlorophyll *a*), temperature, surface currents, and indices of upwelling. Data of all cruises made in the region in 1969, when all the required kinds of data were available, were used.

The three most abundant species of Thaliacea were *Dolioletta gegenbauri*, *Doliolum denticulatum*, and *Thalia democratica*. *Dolioletta* is a cool-water form whose southern limit of range approximates the 15°C isotherm at 10 m. It lives in the California Current and is always present close to shore in waters of suitable temperature. Thus, it can become abundant in areas where chlorophyll is most plentiful, and most observations are consistent with such a population increase. The range of *Doliolum* is limited by temperature in a different way, the northern range limit being about the position of the 13°C isotherm at 10 m. It enters the region from the west and becomes abundant when it reaches phytoplankton-rich coastal waters of suitable temperature. *Thalia* occurs in slightly warmer water than does *Doliolum*. It enters the region from offshore but does not reach the coast during most of the year and never attains maximum abundance there. It is most abundant in offshore waters of low chlorophyll, unlike *Dolioletta* and *Doliolum*.

The question was posed as to why Thaliacea do not dominate the zooplankton of coastal upwelling areas. In the region studied, the offshore Ekman transport prevents *Dolioletta* from becoming dominant close inshore in the early part of the upwelling season, although it can become dominant there later. *Doliolum* is sometimes prevented from reaching the coast by the velocity of the California Current, and when it does arrive it is sometimes excluded from the most inshore rich waters by low temperature. *Thalia* seldom reaches the coast, for reasons which are not clear.

### INTRODUCTION

Thaliacea (salps, doliolids, and pyrosomes) are filter-feeding holoplankters, whose diet is mostly phytoplankton. They are frequently a major component of zooplankton biomass in the upper waters of warm and temperate seas (e.g. Thompson, 1948; Tranter 1962; Furnestin

1970; De Decker 1973). Their ecology is less known than that of other major herbivore groups, but several interesting studies have been made recently on salps. Silver (1971) and Heron (1972a, b) demonstrated remarkably high rates of growth of individuals and population in *Salpa fusiformis* and *Thalia democratica*, respectively. Heron found that growth in length was over 10%/hour during much of the life cycle in both the solitary and aggregate forms. The complete cycle of two generations was completed in two days to two weeks, being longer when food was scarce or temperature low. In the 2-day case the population was increasing in numbers up to 2.5 times/day, the highest rate recorded for a metazoan animal.

Silver and Heron characterized salps as opportunists or colonizers, better able than other herbivores to respond to phytoplankton blooms by rapid population growth. Salps often appear in very dense swarms, some of which have been correlated positively with phytoplankton and negatively with crustacean herbivores (Berner 1957; Fraser 1961; Humphrey 1963; Sheard 1965). The ability of salps to increase greatly probably reflects their high efficiency in obtaining food. Rates of filtration can exceed 100 ml/minute in large individuals (Harbison and Gilmer 1976). Food particles from 1 μm to 1 mm are taken unselectively (Madin 1974). On the other hand, salps seem to have few abundant predators, although the list of those known is growing (Silver 1971, 1975; Heron 1973; Hamner et al. 1975).

Assuming that these features of ecology apply to some extent to other Thaliacea as well as salps, it appeared that a study of thaliacean distribution in relation to temperature, phytoplankton, and currents would be of interest. Temperature, food, and currents are generally considered the major determinants of distribution of epipelagic animals both areally and temporally, but I have sometimes experienced difficulties in relating various kinds of animals to them. The animal of interest may have a varied diet, increasing the difficulty of defining the distribution of its food. If it is planktonic, its own distribution can be described from net catches made on a research ship, but relations to the distribution of its food may be obscured by its drift in currents. If the animal is nektonic, it can search for food and aggregate upon it independently of water movements if temperatures are suitable, but its own distribution may be hard to define unless fishing can be done. With Thali-

<sup>1</sup>Present address: 741 Washington Way, Friday Harbor, Washington 98250.

acea it seemed for reasons given above that food distributions could be defined approximately from measurements of chlorophyll *a* and that the animals should remain abundant in the presence of plentiful food (and suitable temperature) even though subject to drift. High abundance of Thaliacea in an area of high phytoplankton concentration would not necessarily signify the drifting in of a swarm but more probably its generation in situ from a diffused "seed" population.

It was hoped that the proposed study would answer a special question; namely, why Thaliacea do not dominate the zooplankton of coastal upwelling areas since they are such efficient herbivores. Charts of their abundance in the California Current region show that they are dominant only occasionally in upwelling areas although Thaliacea is the principal taxon on a biomass basis for the whole region in the upwelling season (Berner 1967; Isaacs et al. 1969, 1971; Fleminger et al. 1974). They tend to be less abundant close inshore, a situation also observed off northwest Africa in the upwelling season (Blackburn 1979).

The material of the 1969 series of CalCOFI cruises appeared suitable for the proposed distribution study. A large part of the California Current region was covered eight times during 1969 with a similar and rather dense station pattern. The cruises yielded collections and measurements of several properties including zooplankton, chlorophyll *a*, temperature, and surface geostrophic current. Although the CalCOFI program began in 1949, 1969 was the first year of reasonably good coverage for chlorophyll *a* or any other measure of phytoplankton. Thus the charts by Berner (1967) of thaliacean distributions in the period 1949-1958 cannot be related to phytoplankton.

## MATERIAL AND METHODS

The materials and data described here refer to all the CalCOFI cruises made in 1969, namely 6901, 6902, 6904, 6905, 6906, 6907, 6908, 6910, and 6912. Figure 1 shows the entire CalCOFI station grid, which, however, was not completely covered on any of the 1969 cruises. The areas actually covered on each cruise are shown with cruise dates in Figures 4 to 20.<sup>2</sup> Within each cruise area all stations shown in Figure 1 were occupied for zooplankton and hydrography, with few exceptions. Chlorophyll *a* was measured at fewer stations. Each station in Figure 1 has a number such as 93.60, where 93 is the identifying number of the line of stations normal to the coast and 60 is the station number within the line. This paper is concerned with lines 60 to 137 (the offing of San Francisco to about 25°N latitude) and stations no farther offshore than number 90, with few exceptions.

<sup>2</sup>Because the author has made his species distribution charts available in the style and size of the CalCOFI Atlas, we are printing them here full size to facilitate the reader for tearing out and overlaying.

Cruise 6902 extended north of line 60, but none of the others did, and so that part of 6902 was ignored in this study. Cruise 6901 omitted lines south of line 120, and cruise 6904 omitted lines north of line 80. The following cruises or pairs of cruises covered the whole area from line 60 to line 137: 6902, 6905 and 6906 combined, 6907, 6908 and 6909 combined, 6910 and 6912. On 6902 lines 60 to 77 were occupied twice, once by R/V *Miller Freeman* and once by R/V *Alexander Agassiz*. The zooplankton from only the *Miller Freeman* lines, which had more stations, was used in the present work.

## Zooplankton Hauls

One oblique non-closing zooplankton haul was made at each station at whatever time it was occupied. Smith (1974) described the methods and charted displacement volumes of total zooplankton in ml/1000 m<sup>3</sup> of water strained. The standard haul was from about 210-m depth to the sea surface, but shallower hauls, depending on the depth of bottom, were necessary close inshore. Nets were of uniform mesh size, 0.505 mm. The mean volume of water filtered per standard haul was 672 m<sup>3</sup>. The actual volumes filtered, haul depths, and other necessary information for all hauls, were obtained from an unpublished list in the computer data files of the Coastal Fisheries Division, Southwest Fisheries Center, National Marine Fisheries Service. The list was kindly provided by Paul Smith.

## Sorting and Counting of Thaliacea

Each plankton sample was examined, and large Thaliacea (over 2 cm) were separately counted. The rest of the sample was divided with a Folsom splitter (McEwen et al. 1954) into aliquots of convenient size. The normal aliquot was about 20 to 30 ml. Aliquots were rarely smaller than that but sometimes larger. The sample fraction they represented ranged from 1/4 to 1/128 and was most frequently 1/16. Thaliacea in each aliquot were identified and counted under a low-power microscope. Those numbers were multiplied by the denominator of the aliquot and added to the numbers removed before splitting, to give an estimated number per haul of each species. Thompson (1948) was the principal reference used for identifications.

There were some difficulties in counting, especially when small doliolids were very numerous and entangled in phytoplankton. Some counts were approximate. Special efforts were made to make accurate counts at inshore stations for reasons made clear later. Numbers of different generations (phorozoid and gonozoid in doliolids, solitary and aggregate in salps) were combined because their distributions appeared to be the same. Berner (their distributions appeared to be the same. Berner (1957, 1967) combined generations for the same reason. Aggregates in strings or whorls were counted if separate from

solitaries but not if attached to them. Doliolid oozoids were counted, although not identifiable by species.

The above-mentioned numbers per haul are used in preference to numbers per standard volume of water strained for some purposes, as explained later. The data summarized in Figures 4 to 20 are in numbers per 1000 m<sup>3</sup> of water, however. This was done to facilitate comparison with the charts of Berner (1967) for the same region. For the same reasons, I used limiting numbers for contours which are the same as some of Berner's limiting numbers, although my charts have fewer contour intervals. In effect Figures 4 to 20 have less contour detail than similar charts by Berner, but show all important features and can easily be compared with his figures. No contours were drawn around single stations.

### Temperature

The principal species of Thaliacea in the California Current region are most abundant near the sea surface, as mentioned later. Berner (1957) compared distributions of Thaliacea and temperatures in the mixed layer. He noted that temperatures measured at 10 m below surface were generally close to mixed-layer temperatures. Berner and Reid (1961) used 10-m temperatures entirely in a similar study, and I have done the same. Wyllie and Lynn (1971) published charts of 10-m temperature for all CalCOFI cruises made in 1969.

### Surface Currents

Information on surface currents was obtained from charts of dynamic height anomalies (0 over 500 decibars), prepared for each CalCOFI cruise of 1969. Charts for cruises 6901 and 6902 are given and methods described in Scripps Institution of Oceanography (1976). Those for the other cruises are unpublished and were lent for this study by John Wyllie, who drew them.

### Chlorophyll *a*

Concentration of chlorophyll *a* as a convenient measurement of total phytoplankton. Owen and Sanchez (1974) listed such concentrations for some stations on each CalCOFI cruise of 1969 and described their methods (fluorometric analysis of acetone extracts). Owen (1974) gave contoured charts of chlorophyll *a* at the sea surface and in the 0-150-m layer for the four 3-month periods of 1969 (January-March, etc.). His charts show maxima and minima in similar locations for the two depth levels. Remarks made subsequently about chlorophyll distribution refer to the surface data of Owen and Sanchez for the specified cruise. Figures 2 and 3 are based on those data and show areas where surface chlorophyll *a* was 0.5 mg/m<sup>3</sup> or higher on each cruise. Owen and Sanchez also listed data on primary production (C<sup>14</sup> uptake) from some cruises, but the areal coverage was too sparse for the measurements to be of use in this study.

### Upwelling Indices

Bakun (1975) calculated mean upwelling indices for each day in 1969 in several areas along the west coast of North America, and some of them are used in this paper. The upwelling index is the component of computed Ekman transport directed offshore, in metric tons of water per sec per 100 m of coastline. Upwelling indices for the inshore end of CalCOFI line 60 were taken from Bakun's table for 39°N latitude, since line 60 was closer to that position than any other position given. Similarly indices for lines 63 to 80 were taken from the table for 36°N; lines 83 to 100 from 33°N; lines 103 to 110 from 30°N; lines 113 to 130 from 27°N; and lines 133 and 137 from 24°N.

### RELATIVE ABUNDANCE OF SPECIES

Table 1 is a summary of all data showing numbers per haul by cruise and principal species for northern, central, and southern parts of the area (A, B, and C). The principal species are Salpidae, except *Dolioletta gegenbauri* and *Doliolum denticulatum* which are Doliolidae.

For the whole area and year the three most abundant forms are *Dolioletta gegenbauri*, *Thalia democratica*, and *Doliolum denticulatum*. They account for 86.4, 6.1, and 2.8%, respectively, of all individuals. Oozoids of Doliolidae make up an additional 3.2%, which probably represents the above-mentioned species of that family. Salps other than *Thalia democratica*, together with negligible numbers of pyrosome fragments, comprise the remaining 1.5%. Most of this residue (1.3% of the total) is the form known as *Salpa fusiformis*.

In the northern area (San Francisco to Point Conception), the relative abundance of principal species is broadly similar to that for the whole region, except that *Doliolum denticulatum* is scarcer than *Salpa fusiformis*. In the central area (Point Conception to Punta Eugenia), *Dolioletta gegenbauri* is much scarcer than in the north, *Doliolum denticulatum* much more abundant, *Thalia democratica* slightly more abundant, and *Salpa fusiformis* less abundant. Numbers of the first three species are comparable for the year as a whole. South of Punta Eugenia, all species are much scarcer than in the other two areas. *Thalia democratica* and *Doliolum denticulatum* might have been taken in larger numbers if lines of stations had extended as far offshore as in the other areas (Figures 14, 18, and 19). *Thalia democratica*, *Doliolum denticulatum*, and oozoids in that order comprise 92.8% of the total numbers per haul, and *Dolioletta gegenbauri* is scarcer than *Salpa fusiformis*.

Although *Dolioletta gegenbauri* is predominantly a northern form, it is most abundant in the warmer months wherever it occurs. This suggests that seasonal changes in its abundance might be related to upwelling, although temperature may determine the limits of range. The peak

TABLE 1  
Cruises<sup>1</sup>, Hauls per Cruise, and  
Mean Numbers of Thaliacea per Haul by Species.

Cruise Number	6905 to 6906			6908 to 6909			6910	6912	Total
	6901	6902	6904	6907	6909	6910			
A. Station Lines 60-77									
Numbers of Hauls	46	58	0	46	47	48	46	47	
<i>Doliolletta gegenbauri</i>	952	242		43,135	11,871	14,021	1,192	284	71,697
<i>Doliolum denticulatum</i>	160	6		<1	<1	36	2	11	215
Oozoids of Doliolidae	182	178		279	332	660	132	28	1,791
<i>Thalia democratica</i>	3	38		1	4	5	0	2,119	2,170
<i>Salpa fusiformis</i>	9	32		8	7	8	130	723	917
<i>Cyclosalpa bakeri</i>	34	7		1	1	0	1	46	90
<i>Iasis zonaria</i>	2	2		8	0	1	0	1	14
<i>Ritteriella picteti</i>	0	<1		1	0	0	0	<1	1
<i>Cyclosalpa affinis</i>	1	0		0	0	0	0	1	2
<i>Pegea confoederata</i>	<1	0		<1	0	0	0	1	1
Others <sup>2</sup>	<1	1		<1	0	0	0	0	1
B. Station Lines 80-120									
Number of Hauls	133	126	136	132	136	132	136	133	
<i>Doliolletta gegenbauri</i>	76	68	491	1,069	1,447	236	53	2	3,442
<i>Doliolum denticulatum</i>	184	412	62	25	996	296	60	54	2,089
Oozoids of Doliolidae	79	89	173	112	393	11	19	10	887
<i>Thalia democratica</i>	5	7	4	5	22	8	1,235	1,694	2,980
<i>Salpa fusiformis</i>	10	6	8	18	16	13	47	39	157
<i>Cyclosalpa bakeri</i>	2	1	18	31	0	<1	7	5	64
<i>Iasis zonaria</i>	2	1	<1	<1	<1	<1	<1	1	4
<i>Ritteriella picteti</i>	2	<1	<1	1	<1	<1	<1	0	3
<i>Cyclosalpa affinis</i>	0	0	<1	0	0	0	1	7	8
<i>Pegea confoederata</i>	<1	<1	0	0	0	0	1	2	3
Others <sup>3</sup>	<1	<1	<1	0	<1	1	1	1	3
C. Station Lines 123-137									
Number of Hauls	0	33	31	31	33	33	33	25	
<i>Doliolletta gegenbauri</i>	0	2	0	0	1	1	0	0	4
<i>Doliolum denticulatum</i>	10	4	0	16	49	14	3	3	96
Oozoids of Doliolidae	6	37	4	18	15	3	2	85	
<i>Thalia democratica</i>	10	18	3	38	24	20	3	116	
<i>Salpa fusiformis</i>	1	1	2	1	5	3	1	14	
<i>Cyclosalpa bakeri</i>	0	0	<1	0	0	0	0	<1	
<i>Iasis zonaria</i>	0	0	0	0	0	0	0	0	
<i>Ritteriella picteti</i>	<1	0	0	0	0	0	0	<1	
<i>Cyclosalpa affinis</i>	0	0	0	0	0	0	0	0	
<i>Pegea confoederata</i>	0	0	0	0	0	0	0	0	
Others <sup>4</sup>	0	0	0	0	5	0	0	5	

<sup>1</sup>See Figure 1 for location of station lines.

<sup>2</sup>*Cyclosalpa strongylenteron*, *Ithlea punctata*, *Thetys vagina*, plus fragments of *Pyrosoma* colonies.

<sup>3</sup>Same as in <sup>1</sup>, plus *Doliolina mülleri*, *Dolioloides rarum*, *Cyclosalpa pinnata*, *Cyclosalpa virgula*, and *Salpa cylindrica*.

<sup>4</sup>*Ithlea punctata*, *Thetys vagina*, and *Salpa cylindrica*.

of the upwelling season in 1969 was March to May in the southern area, April to July in the central area, and June to August in the northern area (Bakun 1975), and this is the usual pattern (Reid et al. 1958). *Doliolum denticulatum* is most abundant in the central area. There seem to be two peaks of abundance, July to September and January to February. *Thalia democratica* is abundant in the central and northern areas but only in October and December. Its peak in the southern area, where it is scarce, in late summer. *Salpa fusiformis*, predominantly northern, is distributed seasonally like *Thalia democratica*. If the three last-mentioned species are related to temperature or upwelling, the relations are probably

more complex than for *Doliolletta gegenbauri*. This matter is discussed later.

The four species mentioned above were also the principal species in the material of Berner (1957, 1967) from the same region. In the rest of this study, only the three most abundant species are considered. The reason for excluding *Salpa fusiformis* is that it may represent a mixture of two species, *S. fusiformis* and *S. aspera*, in the California Current region. Foxton (1961) held this view although others, including Thompson (1948), Berner (1957) and Silver (1975), regarded *S. aspera* as an intergrading variety. I could not use the criteria of Foxton to distinguish *fusiformis* and *aspera* under the conditions of my work. The principal criteria are smoothness of the test (spiny or not) and numbers of fibers in muscle-bands. It was common for the test to be found separated from the rest of the animal in the preserved samples, and time was insufficient to count the numerous muscle fibres in all specimens. All specimens were identified as *S. fusiformis*, but in view of Foxton's opinion I hesitate to regard them as one species. Some tests were spiny and some smooth.

Since *Doliolletta gegenbauri*, *Doliolum denticulatum*, and *Thalia democratica* are the only species of those genera considered here, they are henceforth generally referred to by genus only for convenience.

## DISTRIBUTION OF PRINCIPAL SPECIES

### *Doliolletta gegenbauri*

Berner (1957) regarded this species as characteristic of subarctic or California Current water. In his material from the region shown in Figure 1, it occurred at stations where mixed-layer temperatures ranged from 9.0° to 27.8°C and averaged 11° to 16°C. Comparing my distribution charts with contemporaneous 10-m isotherms, I concluded that the species generally occurred at <14° in the colder months and <16° in the warmer months. The 15° isotherm seemed to delimit the distribution fairly well on a year-round basis and is shown in Figures 4 to 9.

The non-closing CalCOFI zooplankton hauls give no information on bathymetric distribution of *Doliolletta* or other Thaliacea. Berner (1957) reviewed data from various sources and concluded that *Doliolletta* is most common in the 0-100-m layer, especially at 0-50 m. similar distributions near the sea surface are discussed later for *Doliolum* and *Thalia*. Most hauls were made to about 210 m and strained about 670 m<sup>3</sup> of water, as noted earlier. The most inshore one or two hauls on each line were made less deep from necessity, and therefore strained less water. Assuming that each species is concentrated in a layer of more or less uniform depth less than 210 m both offshore and inshore, estimated numbers per 1000 m<sup>3</sup> must be high at the inshore stations where shallow

TABLE 2

Rank Correlation Coefficients Between Upwelling Indices and Ratios<sup>1</sup> of Numbers of *Dolioletta gegenbauri* and *Doliolum denticulatum* for Two Periods in 1969.

	x	x-1	x-2	x-3	x-4	x-5	x-6
January-June (Cruises 6901-6906)							
<i>Dolioletta gegenbauri</i> .....	+0.25	+0.29	+0.46**	-0.05	+0.02	+0.06	+0.07
<i>Doliolum denticulatum</i> .....	+0.21	+0.07	+0.17	+0.22	+0.07	+0.13	+0.19
July-December (Cruises 6907-6912)							
<i>Dolioletta gegenbauri</i> .....	+0.02	-0.14	-0.11	-0.06	-0.08	-0.17	0.00
<i>Doliolum denticulatum</i> .....	+0.03	-0.15	-0.15	0.00	-0.26	+0.05	+0.09

<sup>1</sup>Each ratio was the number taken at Station 2 divided by the number at Station 1 where Station 1 was the most inshore station on a CalCOFI line and Station 2 the one next offshore. Each ratio was compared with 7 upwelling indices for the area of the line: x was the index for the day on which the earlier of the two stations was occupied, and x-1, x-2, etc., were indices for 1, 2, etc., days previously. Coefficients without \* are not significant for the numbers of degrees of freedom used.

hauls were made, relative to such numbers elsewhere. Figures 4 to 20 indicate numbers per 1000 m<sup>3</sup> for reasons given earlier, but those within about 10 miles of the coast are too high by an unknown amount.

Figure 4 shows the distribution of *Dolioletta* on cruise 6901 (January 1969). It occurred almost always on the low side of the 15° isotherm, although not in all parts of that area. It was more plentiful inshore than offshore, which was real because the inshore area extended more than 10 miles from the coast. The area of high abundance shown is broadly congruent with the area in which surface chlorophyll was >0.5 mg/m<sup>3</sup> (Figure 2, A). The population probably grew faster where food was more plentiful. On cruise 6902 in February-March (Figure 5), the 15° isotherm and the population extended slightly farther south. Figure 2 (B) shows four areas of chlorophyll >0.5 mg/m<sup>3</sup> along the coast. *Dolioletta* was relatively abundant in the two northern areas but not in the others, which were probably too warm for it. The small offshore area of abundant *Dolioletta* does not agree so well with chlorophyll concentration, which was low there.

On the April cruise 6904 there were two areas with temperatures <15° at 10 m, one in the main axis of the California Current and one in a coastal upwelling area south of San Diego. The area of occurrence of *Dolioletta* was partially divided in a similar, but not exactly the same, way (Figure 6). In general *Dolioletta* occupied the whole area of <15° water and extended slightly into warmer water. Chlorophyll >0.5 mg/m<sup>3</sup> at the surface occurred almost continuously along the coast (Figure 2, C), and the two high coastal concentrations of *Dolioletta* were in that area. Where *Dolioletta* was missing or scarce near the coast, it was probably because of near-limiting temperatures, with two exceptions: It was absent in a small strip of water near Point Conception and scarce in another strip near San Diego. The temperature was <15° and the chlorophyll >0.5 mg/m<sup>3</sup> at both places. Similar situations are seen in other figures and discussed later.

TABLE 3

Data From Which the Significant Coefficient in Table 2<sup>1</sup> Was Calculated.

Cruise	Line	Ratio	Date x	Index
6901 .....	60	2.17	1-24	30
	63	1.47	1-24	49
	80	0.94	1-17	26
	83	5.00	1-17	16
6902 .....	63	3.24	2-8	58
	67	3.45	2-8	58
	70	18.29	2-14	214
	73	2.00	2-15	61
	83	0.84	2-15	86
	90	0.01	2-16	17
	93	1.00	2-16	17
	97	9.00	2-20	167
6904 .....	100	9.00	2-20	167
	103	2.00	2-23	37
	107	0.03	2-23	37
	80	993.00	4-13	93
	83	157.00	4-12	173
	87	3.88	4-10	64
	90	0.43	4-9	34
	93	22.50	4-4	234
	97	26.67	4-2	203
	100	1.63	4-6	42
6905 .....	103	1.56	4-6	88
	107	3.18	4-9	60
	110	66.40	4-9	60
	63	13.00	5-24	132
	67	0.03	5-23	165
	70	0.59	5-22	200
	73	35.20	5-16	130
	77	212.11	5-15	93
	80	4.10	5-13	182
	83	229.82	5-13	264
6906 .....	87	<0.01	5-10	66
	90	1.61	5-10	66
	93	10.00	5-5	412
	97	1.29	6-9	252
	100	129.00	6-12	221
	103	210.00	6-13	88
	107	23.00	6-15	154
	110	<<0.01	6-15	154

<sup>1</sup>Ratio and date x are explained in Table 2; Index is the upwelling index for the second day before date x.

Figure 7 refers to cruises 6905 and 6906 in May and June, north and south of San Diego respectively. The area of 6905 was almost entirely <15°, and *Dolioletta* occurred over nearly all of it. The general level of abundance was higher than before, but the areas of highest abundance did not agree so well with those of high surface chlorophyll, i.e. >0.5 mg/m<sup>3</sup> (Figure 2, D). Specifically, *Dolioletta* was absent in an area west of San Diego where chlorophyll was high, perhaps because temperature was ≥15°. It was also less abundant in two coastal strips than it was slightly farther offshore, although chlorophyll was high inshore. These situations, reminiscent of the two noted in April, occurred north of Point Conception and off San Diego. The area of cruise 6906 was >15° except in two coastal upwelling areas.

*Dolioletta* occurred in the northern upwelling area but not in the southern one, which it probably did not reach even as a seed population. It was present and even moderately abundant in some of the warmer waters as well. The contours run parallel with those of dynamic height. Chlorophyll measurements  $<0.5$  mg/m<sup>3</sup> were in and near the northern upwelling area (Figure 2, D).

The distribution of *Dolioletta* on cruise 6907 (July) is not shown because it was similar to Figure 7. The areas  $<15^\circ$  were smaller (Figure 18) but included most of the areas where *Dolioletta* was moderately or very abundant. *Dolioletta* occurred at a low level of abundance in several large areas  $>15^\circ$ , as in June. The  $15^\circ$  isotherm followed the limit of the range less well in June and July than in other months. Chlorophyll values for cruise 6907 were mostly  $<0.5$  mg/m<sup>3</sup> even along the coast, although higher near the coast than elsewhere (Figure 3, E).

Temperatures on cruise 6908 in August-September (Figure 8) were about the same as on 6907. The southern limit of *Dolioletta* was north of its July position and agreed better with the temperature. A large northern area of relatively high surface chlorophyll (Figure 3, F) included some of the highest concentrations of *Dolioletta*. An elongate area of very abundant *Dolioletta* touched the coast north of Point Conception. At that point the concentration was one of the highest recorded for *Dolioletta*, and the zooplankton was almost entirely that species. On cruise 6909 (September-October, south of San Diego) almost all waters were  $>15^\circ$ , and *Dolioletta* was scarcely present (Figure 8). High temperature probably excluded it. Surface chlorophyll was high along the coast north of Punta Eugenia (Figure 3, F).

On cruise 6910 (October-November) the total area of *Dolioletta* and water  $<15^\circ$  was about the same as in Figure 8, but *Dolioletta* was generally scarcer (Figure 9). Figure 3(G) shows the distribution of chlorophyll  $>0.5$  mg/m<sup>3</sup>, which agreed fairly well with that of *Dolioletta* in inshore waters. The distribution on cruise 6912 (November-December) is not shown. It was much more restricted than on any other cruise, in an area off San Francisco and a small one of low abundance on the coast east of Point Conception. The first area was in water  $<15^\circ$  and the second was not (see temperature in Figure 20). Chlorophyll concentrations  $>0.5$  mg/m<sup>3</sup> were virtually confined to the San Francisco area (Figure 3, H).

Figures 4 to 9 are broadly similar to some of the charts of Berner (1967) for *Dolioletta* at the same periods in other years. For example, Figures 5, 7, and 8 are comparable with those for the same periods in 1950, 1950, and 1949 respectively. On the other hand, Figures 8 and 9 do not agree well with those for the same periods in 1952, when *Dolioletta* was fairly abundant south of Punta Eugenia.

### *Doliolum denticulatum*

Berner (1957) and Berner and Reid (1961) considered this species characteristic of Central Pacific water, which contributes to the California Current by horizontal mixing from the west (Reid et al. 1958). Thus *Doliolum* enters the current system from the west, not from the north as *Dolioletta* does. In Berner's material from the region of Figure 1, it occurred at stations where mixed-layer temperatures ranged from  $10.6^\circ$  to  $23.5^\circ\text{C}$  and averaged  $15^\circ$  to  $21^\circ\text{C}$ . Berner and Reid considered its areal distribution to be limited by some 10-m temperature slightly below  $14^\circ$  or  $15^\circ$ . They used the  $14^\circ$  isotherm at 10 m as an indicator of the limit of distribution. In their charts and mine, the winter occurrence of *Doliolum* can be quite extensive on the cool side of the  $14^\circ$  and even the  $13^\circ$  isotherm. The  $13^\circ$  isotherm seems to delimit the distribution better than any other throughout the year and is shown in Figures 10 to 14. Data on vertical distribution from various sources indicate that *Doliolum* is most common at 0-100 m, especially 0-50 m (Berner 1957; Berner and Reid 1961). Thus concentrations shown in Figures 10 to 14 at stations very close inshore are too high relative to those at other stations for reasons given under *Dolioletta*.

Figure 10 shows the distribution of *Doliolum* in January. It occurred in several inshore and offshore areas at  $>13^\circ$  and extended north along the coast in slightly cooler water. The area of higher abundance is similar to that of surface chlorophyll  $>0.5$  mg/m<sup>3</sup> (Figure 2, A) but extends farther south along the coast. The general picture is like that shown by Berner and Reid (1961) for January 1958. They regarded the coastal occurrence north of Point Conception as unusual, since it was not seen in earlier winters for which they had data (Berner 1967). They attributed it to transport in the countercurrent, which runs poleward close to the coast in winter. This countercurrent was present in January 1969 but only north of San Diego (Scripps Institution of Oceanography 1976). Together with the temperature and chlorophyll data, it explains the observed distribution of *Doliolum* in inshore waters, including the break south of San Diego.

In February-March (Figure 11) *Doliolum* occurred less extensively to the north of Point Conception than in January. although surface concentrations of chlorophyll  $>0.5$  mg/m<sup>3</sup> were still present (Figure 2, B). The countercurrent was weaker and probably brought in a smaller seed population. The rest of the distribution is consistent with the idea of a population spreading in from offshore, being limited to waters  $>13^\circ$ , and increasing in numbers in coastal locations of relatively high chlorophyll. The areas of relatively abundant *Doliolum* broadly agree with the areas of high chlorophyll, except for one of the latter south of Punta Eugenia. Figure 11 resembles the

chart for March 1958 but is quite unlike that for March 1949 when no *Doliolum* occurred inshore (Berner and Reid 1961). Berner and Reid pointed out that temperatures were higher in 1958 than in the years 1949 to 1956.

The distribution of *Doliolum* for April is not shown here. The species occurred in patches over most of the area from Point Conception to Punta Eugenia, both offshore and inshore, where almost all temperatures were  $>13^{\circ}$ . Highest concentrations were close to the coast in areas of high chlorophyll, which are shown in Figure 2, C. The chart for April 1958 by Berner and Reid is comparable but shows a more continuous distribution over the same area. Charts for April of 1949 and 1954 show no inshore occurrence (Berner 1967).

Figure 12 is for May and June. Most of the area was  $>13^{\circ}$ , but *Doliolum* was scarce, being most abundant in an upwelling area north and south of San Diego where surface chlorophyll was  $>0.5 \text{ mg/m}^3$  (Figure 2, D). Most other high-chlorophyll areas were in inshore waters north of Point Conception, which were probably too cool for *Doliolum*. As noted for *Dolioletta* in Figures 6 and 7, abundance sometimes fell at the most inshore stations. For *Doliolum* this could be caused by low temperature from the upwelling. That would not apply to *Dolioletta*, however, and another explanation is suggested later. Figure 12 shows a distribution much less extensive in inshore waters than in May 1958, but more than in June 1949 (Berner and Reid 1961). The connections between offshore and inshore occurrences seem to have been reduced from a few months earlier (compare with Figures 10 and 11).

The July chart (Figure 13) reveals a more extensive and continuous distribution, although by no means covering the whole area of water  $>13^{\circ}$ . That isotherm delimits the range of *Doliolum* better in cold months than in warm. Abundance was highest along the coast and so in general were the chlorophyll concentrations, but they were lower than usually found with the higher concentrations of doliolids (Figure 3, E). The only other published July chart is for 1949 (Berner 1967), which shows no inshore occurrences.

The chart for cruises 6908 and 6909 (August-October) is similar to Figure 13 and the following Figure 14 and so is not given. It also resembles the situation for September 1952 but not for September 1949 (Berner and Reid 1961). The distribution of *Doliolum* on cruise 6908 (north of San Diego) agreed well with that of chlorophyll, both being relatively abundant in certain inshore waters. The agreement on 6909 (south of San Diego) was poor, however. Figure 3(F) shows the areas of highest chlorophyll.

The October-November distribution (Figure 14) is much the same as the preceding. It resembles those of October-November 1951, 1952, and 1957 but not 1949

(Berner and Reid 1961; Berner 1967). It agrees only partially with chlorophyll distributions (Figure 3, G). The chart for November-December (not given) shows *Doliolum* ranging farther north along the coast from Point Conception, recalling the situation in Figure 10. The countercurrent was not evident on cruise 6912, although it was on the preceding one. *Doliolum* was scarcer on 6912 than on cruises 6910 or 6901. Agreement between areas of high chlorophyll and abundant *Doliolum* was poor. The richest area of chlorophyll was in the offing of San Francisco (Figure 3, H), and *Doliolum* did not reach it.

Concentrations of *Doliolum* were generally lower than those of *Dolioletta* in 1969. Maximum numbers per haul were respectively 48,000 and 264,000. No plankton sample consisted almost entirely of *Doliolum*, but a few samples were almost totally *Dolioletta* or *Thalia*.

#### *Thalia democratica*

According to Berner (1957) this is a species of Central Pacific water. It enters the California Current system by horizontal mixing from the west, like *Doliolum*. In Berner's material it occurred at stations where mixed-layer temperatures ranged from  $10.0^{\circ}$  to  $24.9^{\circ}\text{C}$  and averaged  $14^{\circ}$  to  $21^{\circ}\text{C}$ . It appeared from inspection of all 1969 data that the  $15^{\circ}$  10-m isotherm delimited the distribution of *Thalia* better than any other, and it is shown in Figures 15 to 20. *Thalia* is most common on the warm side of that isotherm and *Dolioletta* on the cool side. The distribution of *Thalia* is in some ways like that of *Doliolum*, but it appears to be slightly less tolerant of cool water and occurs less often at the coast. According to Berner (1957) and the authors he cited, *Thalia* is most common at 0-75 m, especially 0-25 m. Thus, previous remarks about inshore concentrations apply also to this species.

Figures 15 and 16 show distributions of *Thalia* in January and February-March. In these and later figures the contour intervals are not the same as previously used. The species occurred mainly offshore and, unlike *Dolioletta* and *Doliolum*, it hardly ever reached the coast. Thus, its occurrences do not agree at all with those of relatively high chlorophyll concentrations (Figure 2, A and B). *Thalia* was found in areas where surface chlorophyll ranged from 0.1 to  $0.3 \text{ mg/m}^3$  (data of Owen and Sanchez 1974). Charts by Berner (1967) for February and March 1949, 1951, 1952, and 1954 are comparable with Figure 16, but in 1950 *Thalia* was much more abundant and widespread and reached several parts of the coast. Distributions for April 1969 (not given) and May-June (Figure 17) were broadly like the preceding but with diminishing occurrence of *Thalia* on the cool side of the  $15^{\circ}$  isotherm. Relations to chlorophyll (Figure 2, C and D) were about the same as before. Abundance of *Thalia* for the whole area remained at the low levels of



previous months. Berner's (1967) charts of *Thalia* in those months show similar conditions in 1949 but a more widespread distribution and higher abundance in 1950, 1951, 1952, 1954, and 1958.

The July chart (Figure 18) and that for August-October (not given) are alike. They show a slight increase in general abundance of *Thalia*, which occurred over larger areas and sometimes closer to the coast. The 15° isotherm agreed much better with the limits of range of *Thalia* than before and did so for the rest of the year. Surface chlorophyll concentrations in *Thalia* areas were quite low, generally <0.1 mg/m<sup>3</sup> (compare Figure 3, E and F). Distributions of *Thalia* in the same months in 1949, 1951, and 1952 showed some occurrence in coastal waters south of San Diego, but this was not so in 1950 (Berner 1967).

Figures 19 and 20, for October-November and November-December, reveal a wider distribution and much higher general abundance than in other months. *Thalia* reached the coast at several places, although the highest concentrations (maximum 56,000/haul) were offshore in chlorophyll-poor areas. At a few of those stations, the zooplankton was almost entirely *Thalia*. There were a few areas of chlorophyll >0.5 mg/m<sup>3</sup> in water >15° (Figure 3, G and H), but *Thalia* did not occur in them. Berner (1967) gave charts for October-November of 1949, 1951, and 1952. They are similar to mine except that some of the highest concentrations extended to the coast south of San Diego. Temperature charts for those periods show no signs of upwelling at the places where *Thalia* was abundant inshore (Anonymous 1963), so chlorophyll was probably low.

#### ABUNDANCE RELATED TO UPWELLING INDEX

It was noted earlier that *Dolioletta* and *Doliolum* sometimes declined in abundance at the innermost one or two stations of a line. Figures 6, 7, and 12 show this. More instances might be evident but for the fact that numbers per 1000 m<sup>3</sup> tend to be relatively high at inshore stations, as explained previously. Since chlorophyll concentrations were generally highest close inshore (Figures 2 and 3), it seemed that some other property or process at times depressed the inshore abundance of doliolids.

In upwelling situations along the coast, 10-m temperatures were often about 13°C, and occasionally as low as 11°C (Wyllie and Lynn 1971). From previous information, such temperatures would not have been unsuitable for *Dolioletta*, but they would have been slightly adverse for *Doliolum*. Another possibility is that offshore Ekman transport of near-surface water prevented the animals from becoming more abundant close inshore. Since both possibilities are associated with upwelling, it was decided to investigate the relations of inshore abundance to contemporaneous upwelling indices in the same

area. Data on abundance of *Dolioletta* and *Doliolum* were used. *Thalia* seldom occurred inshore.

The number of the species taken at the most inshore station was divided into the number at the station next offshore. The distance between the stations ranged from 4 to 16 nautical miles and averaged 6.9 miles. If one of the two stations had a zero number, 1 was added to each of the two numbers so that a ratio could be obtained. Then, for each line upwelling indices were found from Bakun (1975) for each of the following days:  $x$ , the day on which the earlier of the two stations was occupied;  $x - 1$ , the previous day;  $x - 2$ , the day before that; and so on to  $x - 6$ . The two stations were generally occupied on the same day and were never more than one day apart. Negative or zero values of the upwelling index were not used. The data are copious, and it is only necessary to give them in one case, which serves as an example (Table 3). A Spearman rank correlation coefficient was calculated for each set of paired ratios and indices.

Table 2 lists the 28 correlation coefficients for the two species for January-June and July-December. Only one is statistically significant, but the probability of as high a value by chance is <1%, so the significance is not questionable. Furthermore, the date in that case of the upwelling ( $x - 2$ ) in relation to the date of the observations is reasonable. Typical values for offshore transport near the surface in coastal upwellings are about 10 to 25 cm/second when winds are strong (Huyer 1976). Thus, it would take one or two days for a parcel of water and plankton to be moved from one station to the other. The coefficients for the earlier period are nearly all positive, and those for the later period nearly all negative. Numbers of pairs of observations for January-June ranged from 36 to 43 for *Dolioletta* and from 27 to 33 for *Doliolum*. For July-December the corresponding ranges were 35 to 39 and 41 to 43. It may be concluded that the offshore:inshore ratio of abundance of *Dolioletta* in January-June is positively correlated with the amount of upwelling about two days before the observations. A similar correlation may exist for *Doliolum* at the same period but cannot be demonstrated. No such correlations are found for either species in July-December.

#### DISCUSSION

The distribution of *Dolioletta gegenbauri* seems to be governed by temperature, food (phytoplankton), and water movements in a rather simple way. The southern limit of its range is obviously temperature-dependent. Since it enters the region of interest from the north with the California Current, rather than from offshore, it is always present fairly close to shore in waters of suitable temperature. Thus, it can become abundant fairly quickly in areas where phytoplankton is most plentiful, which are mostly coastal upwelling areas. Most of the observa-



tions are consistent with such growth of population (Figures 4 to 9) in food-rich areas (Figures 2 and 3). A few of the observations are inconsistent, and they cannot all be explained. Some can, as indicated in the previous section. In the first half of the year there is a statistically significant tendency for the offshore:inshore ratio of *Dolioletta* numbers to vary positively with the upwelling index. That is to say, abundance close inshore is lower than expected as a result of the upwelling. The upwelling does not affect the distribution of *Dolioletta* through the low temperature, which that species can tolerate. It probably affects the distribution by transporting some individuals offshore, or retarding the spreading of more offshore individuals toward the shore. After June, however, it is apparently easier for *Dolioletta* to reach very high levels of abundance in food-rich situations close inshore. Upwelling indices begin to decline about that time on the southern and central parts of the coast (Bakun 1975), and the offshore Ekman transport is probably less effective than formerly in depressing numbers of *Dolioletta* close inshore.

The range of *Doliolum denticulatum* is also limited by temperature, as Berner and Reid (1961) pointed out. It occurs with higher temperatures than does *Dolioletta*. The relation to temperature is not as obvious in Figures 10 to 14 as in charts for *Dolioletta*, because there are generally large areas with suitable temperature where *Doliolum* does not occur. *Doliolum* enters the area from the west and reaches the coast as a result of horizontal mixing of waters. When it reaches the coast the population may increase in response to the high abundance of phytoplankton in inshore waters, as with *Dolioletta*. There are more exceptions, however. A few of them very close inshore probably signify effects of low temperatures caused by upwelling. Some may represent effects of offshore Ekman transport, operating as shown above for *Dolioletta*. Some in winter can be explained as a result of transportation along the coast by the countercurrent, as noted also by Berner and Reid (1961). There still remain several unexplained instances of apparent failure of *Doliolum* to become abundant along all parts of the coast where food and temperature conditions are suitable. The reason may be that the species often fails to reach the coast at all, which is much better shown in some charts of Berner and Reid for certain years than in mine. I interpret the distribution in Figure 12, showing discontinuous occurrence from offshore to inshore in May and June, as meaning that the velocity of the California Current posed a barrier to the eastward spreading of *Doliolum*. The current then had a higher velocity and was less meandering than in other months of 1969, a situation seen also in monthly average charts (Wyllie 1966).

Berner and Reid (1961) observed that *Doliolum* extended from offshore to inshore much more frequently in

1957 and 1958 than in the period 1949 to 1955 and that the 1957-58 winter was the first one known to them in which some *Doliolum* remained inshore. They considered these changes to be related to the anomalously high temperatures of late 1957 and 1958. The distributions in 1969 were more like those of 1957 and 1958 than the other years. Temperatures in the California Current region in 1969 were not high as in 1957 and 1958, however, but average (Anonymous 1963; Wyllie and Lynn 1971).

The distribution of *Thalia democratica* is hard to explain. It enters the area from the west like *Doliolum*, and its range from north to south is broadly temperature-dependent in much the same way as that of *Doliolum*. Unlike *Dolioletta* and *Doliolum*, it does not become very abundant or reach the coast until October-December, which is after the upwelling season (Figure 15 to 20). Even then the highest concentrations of *Thalia* remain offshore in areas where chlorophyll values are quite low. According to the charts of Berner (1967), the situation in other years of observation was probably not very different, although no chlorophyll data are available.

Silver (1971, 1975) made observations on stomach contents of *Thalia* and concluded that *Thalia* swarms were associated with a certain assemblage of phytoplankton species in the water. If that assemblage were characteristic of offshore rather than inshore waters in the California Current region, it could be argued that it governs the distribution of *Thalia*. The matter is questionable, however. Silver identified only four species by name, *Nitzschia sicula*, *N. bicapitata*, *Pseudoeunotia doliolus*, and *Thalassionema nitzschoides*. According to Elizabeth Venrick (personal communication), *N. sicula* is frequent but not abundant in offshore waters, and little is known about its abundance inshore; *N. bicapitata* is ubiquitous in distribution; *P. doliolus* can be abundant offshore, and little is known about its abundance inshore; and *T. nitzschoides* is more or less ubiquitous but slightly more abundant inshore.

Harbison and Gilmer (1976) found that salps have the same rates of filtration at different particle concentrations. They also noted that the mucous feeding net became clogged with particles in some of their experiments, which lasted from 2 to 9 hours. They therefore believed that salps would clog in areas of very rich phytoplankton and could not become highly abundant there. The distribution of *Thalia* as shown here might be reconciled with that idea. On the other hand, Heron (personal communication) has found that salps regularly cease production of the mucous net, which might eliminate or relieve clogging. Doliolids can be very abundant in phytoplankton-rich areas as shown in this paper. Clogging has not been reported in them.

The specific question posed at the beginning of the paper was why Thaliacea do not generally dominate the

zooplankton in coastal upwelling situations in the California Current region. For *Doliolletta gegenbauri*, the answer is that offshore Ekman transport prevents the species from becoming dominant in the early part of the upwelling season, although it sometimes does become dominant later. The answer for *Doliolum denticulatum* is probably that the velocity of the California Current makes it hard for the species to reach the coast from offshore in the upwelling season; and when it does arrive it is sometimes excluded from the inshore waters by very low temperature, and perhaps also by the offshore transport. No explanation can be given with confidence for *Thalia democratica*, but a possible one is that the most suitable diet consists of species of phytoplankton that generally occur offshore.

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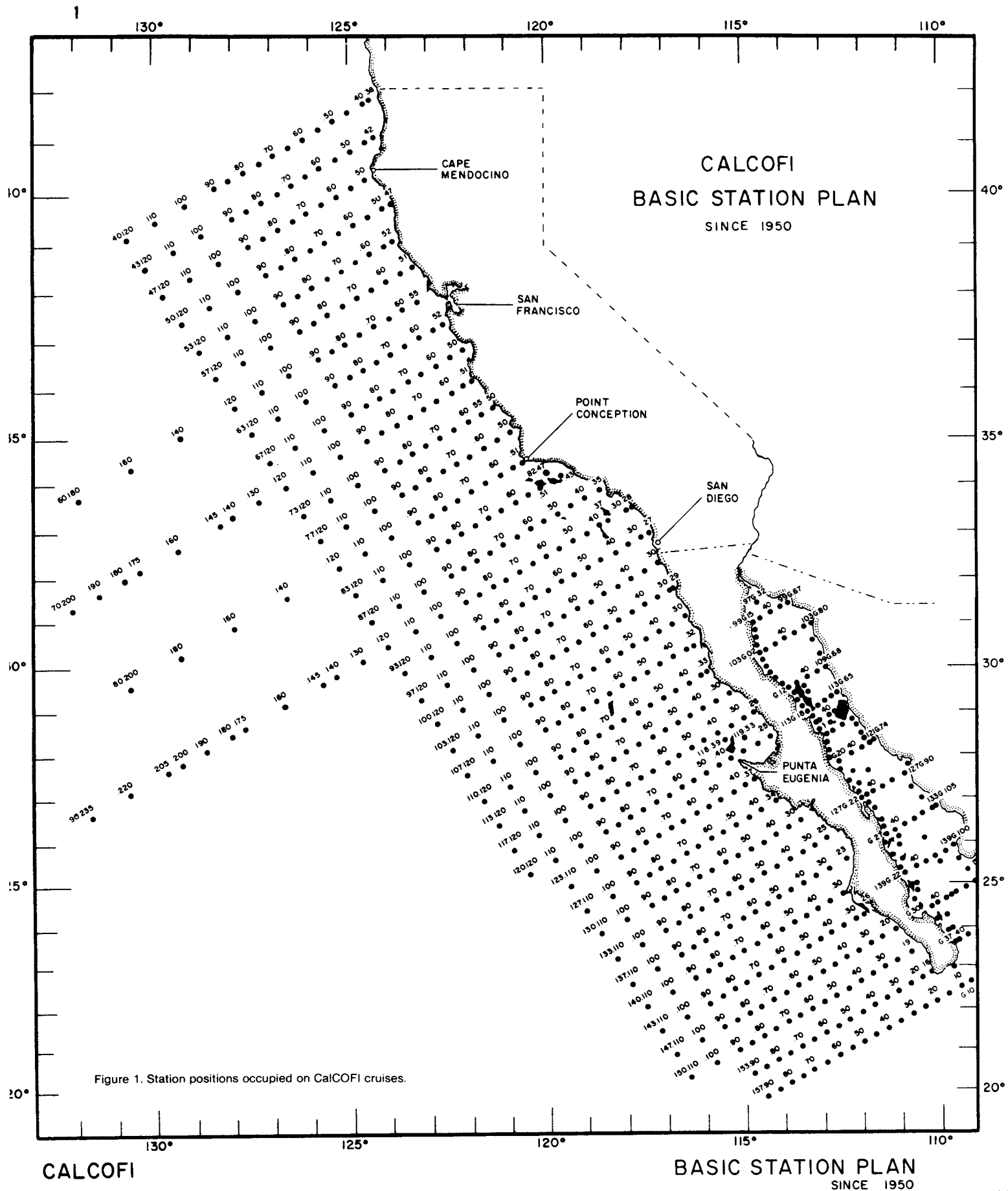


Figure 1. Station positions occupied on CalCOFI cruises.

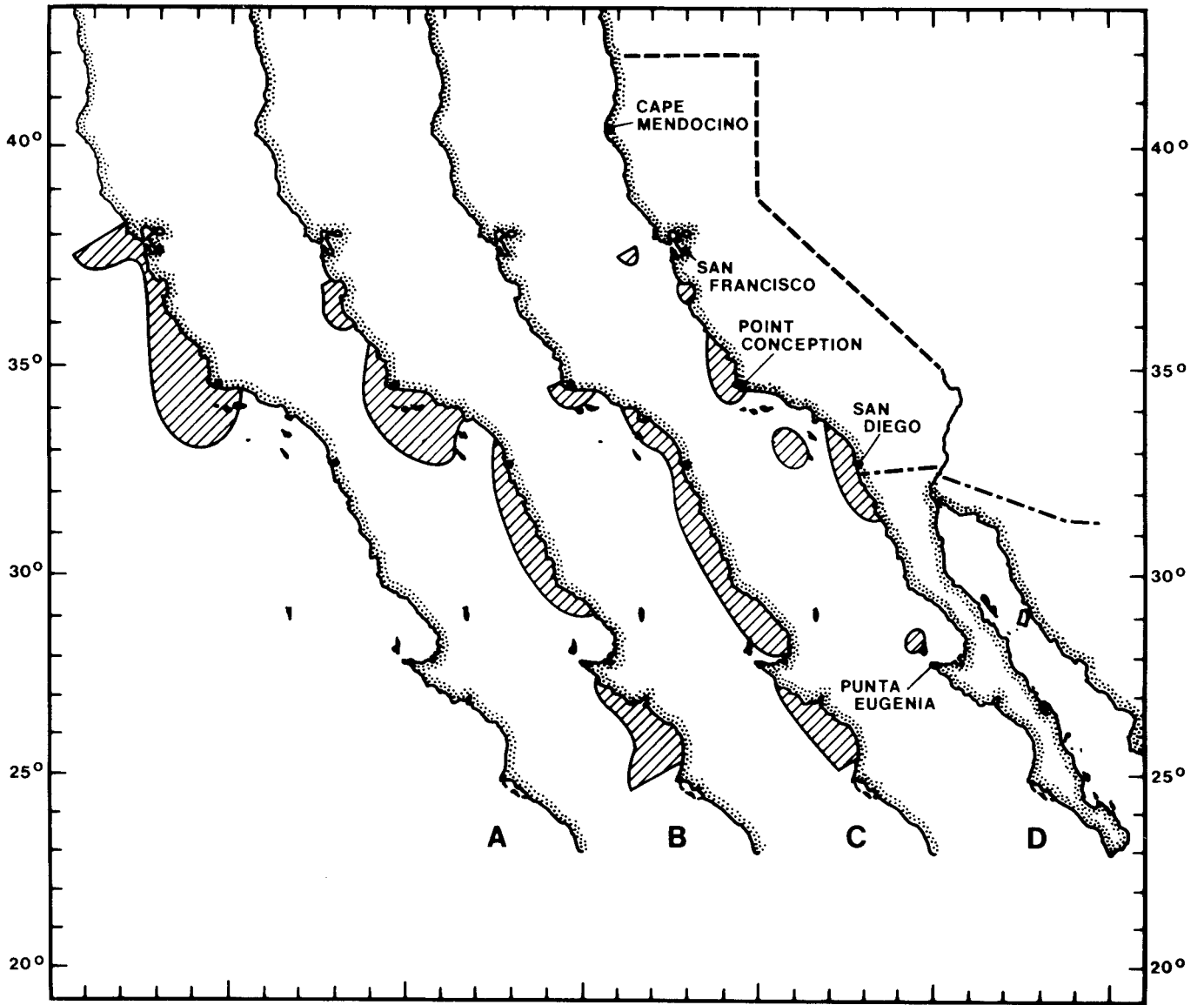


Figure 2. Areas of surface chlorophyll *a*  $\geq 0.5$  mg/m<sup>3</sup> shown by hatching on the following CalCOFI cruises: 6901 (A), 6902 (B), 6904 (C) and 6905-6906 (D).

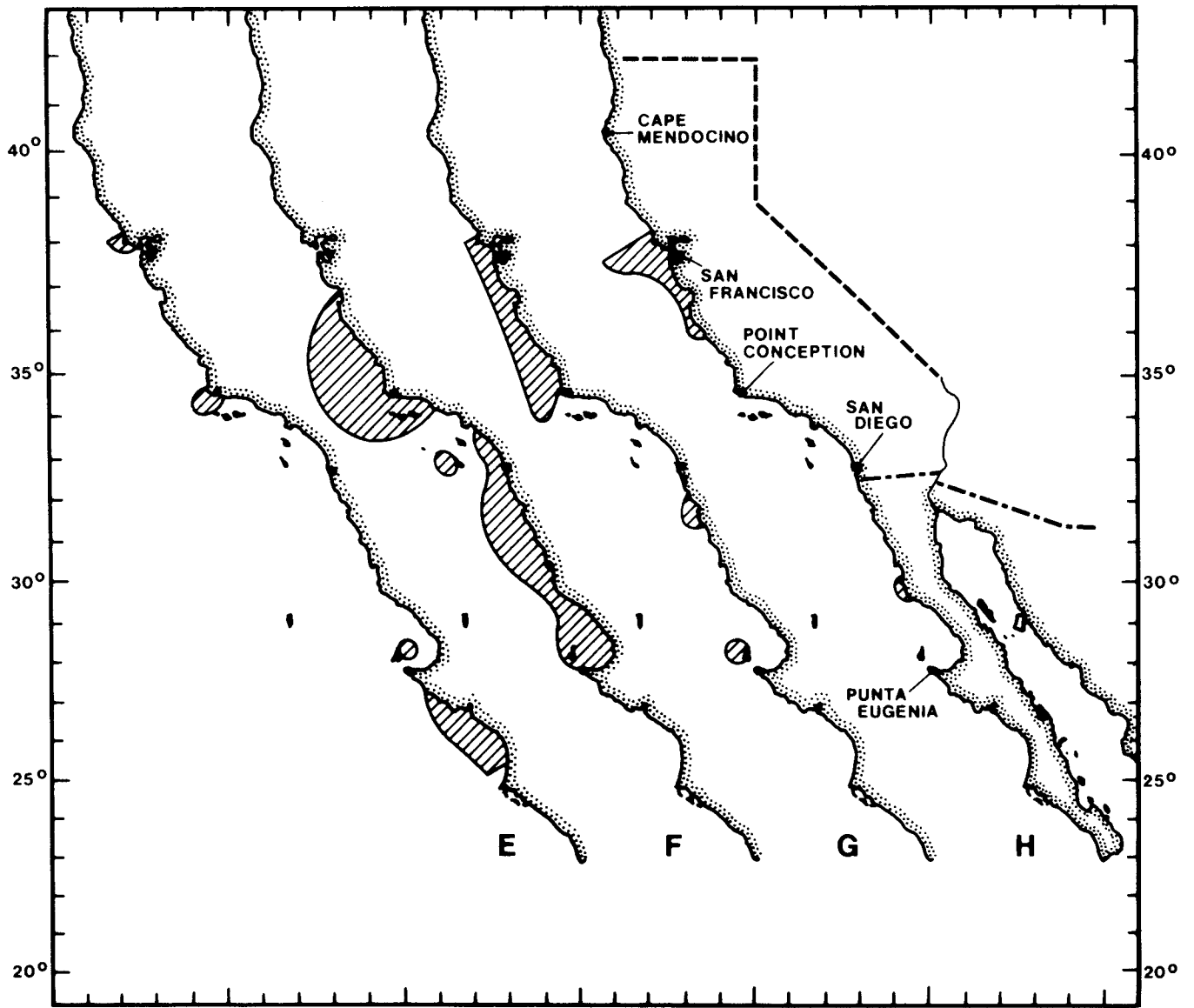
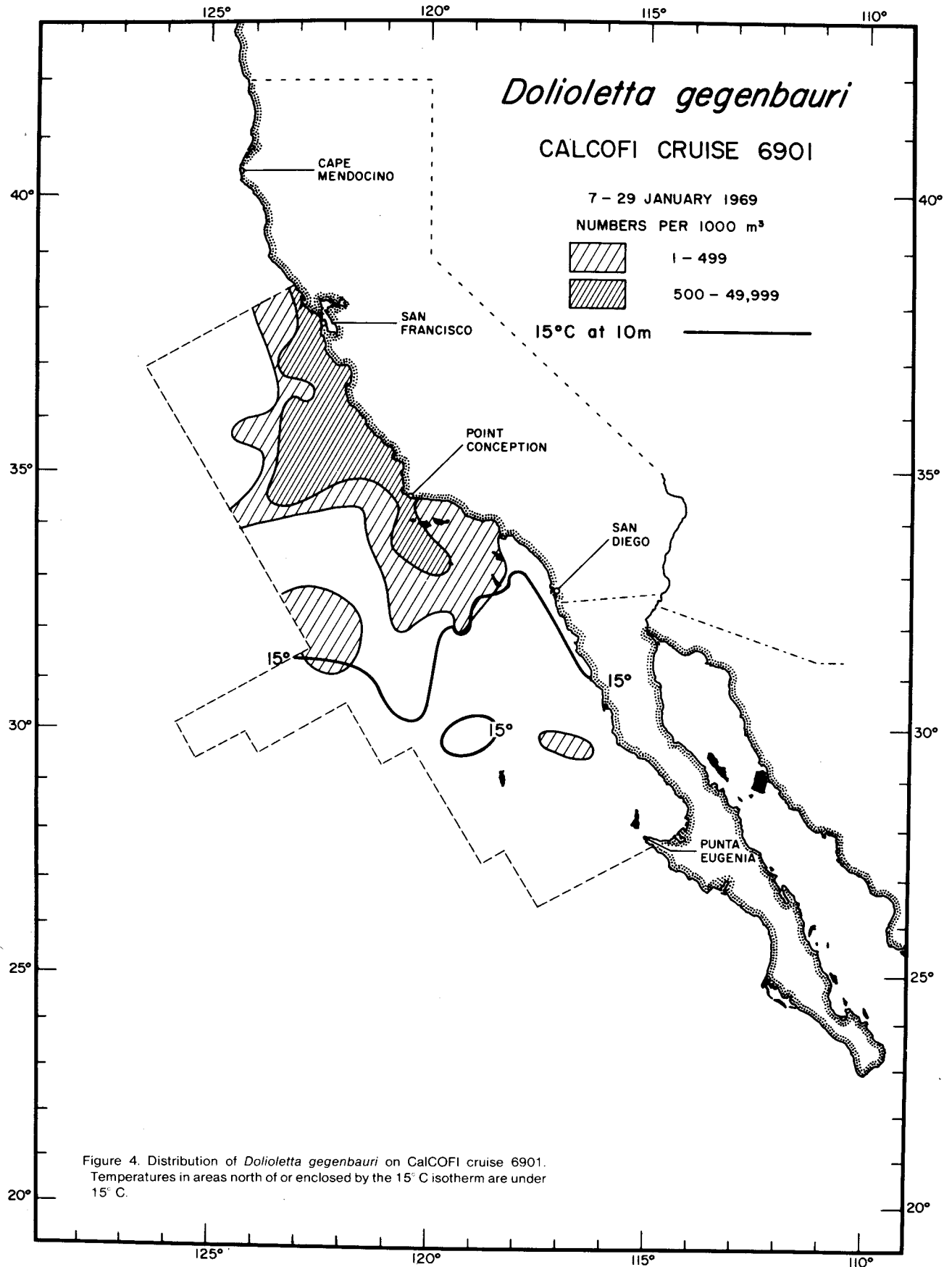
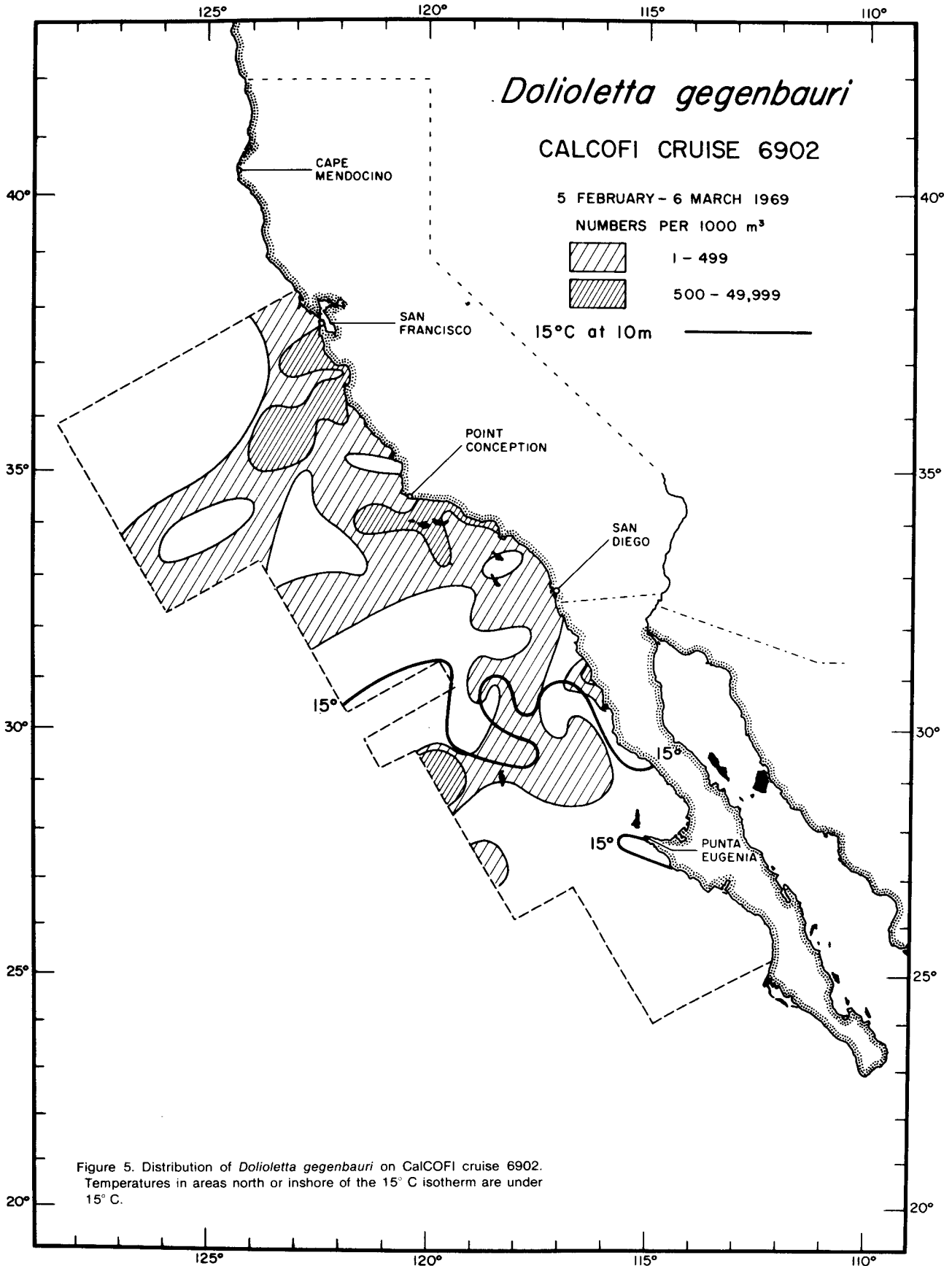
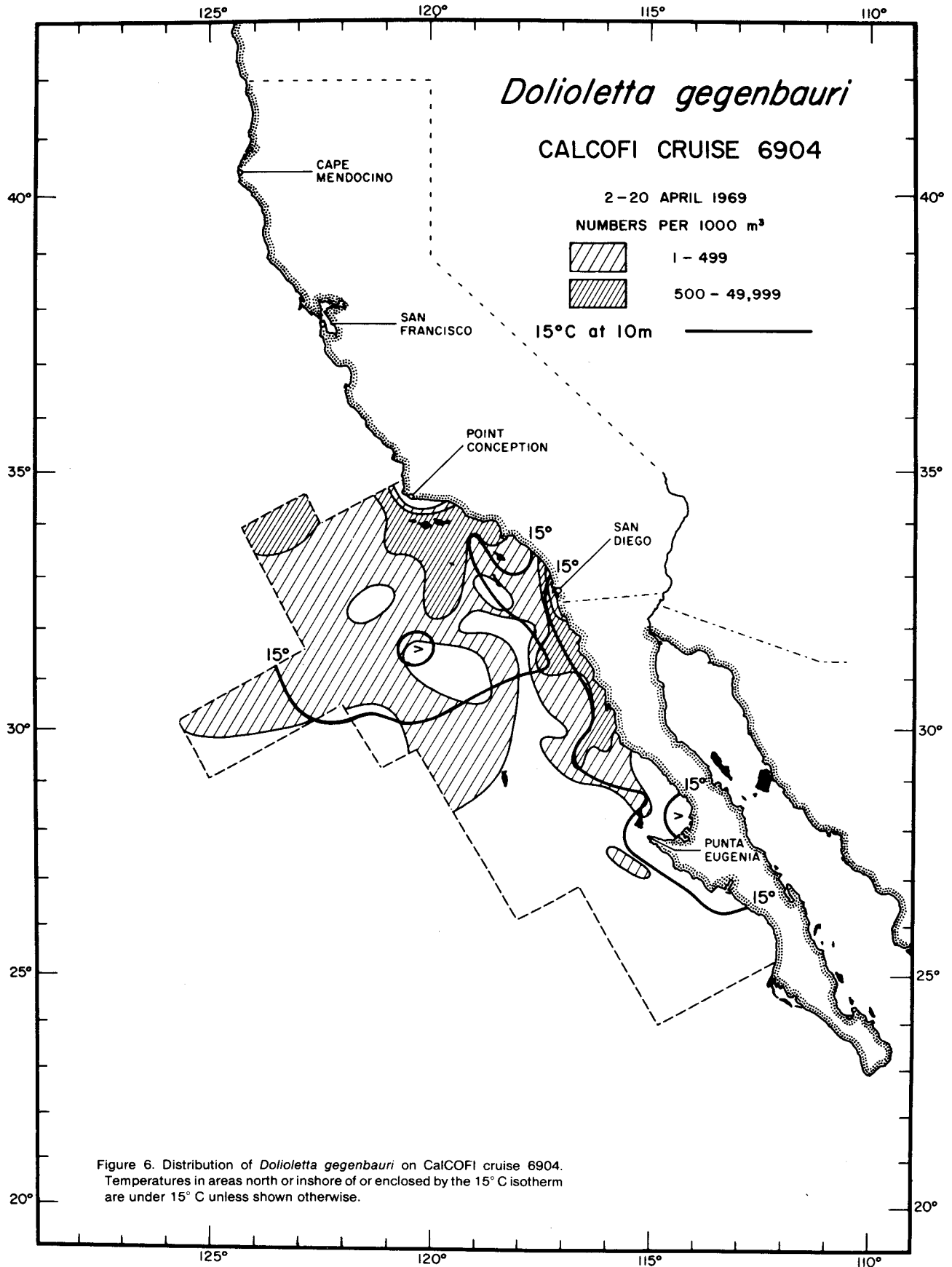


Figure 3. Areas of surface chlorophyll  $a \geq 0.5$  mg/m<sup>3</sup> shown by hatching on the following CalCOFI cruises: 6907 (E), 6908-6909 (F), 6910 (G) and 6912 (H).









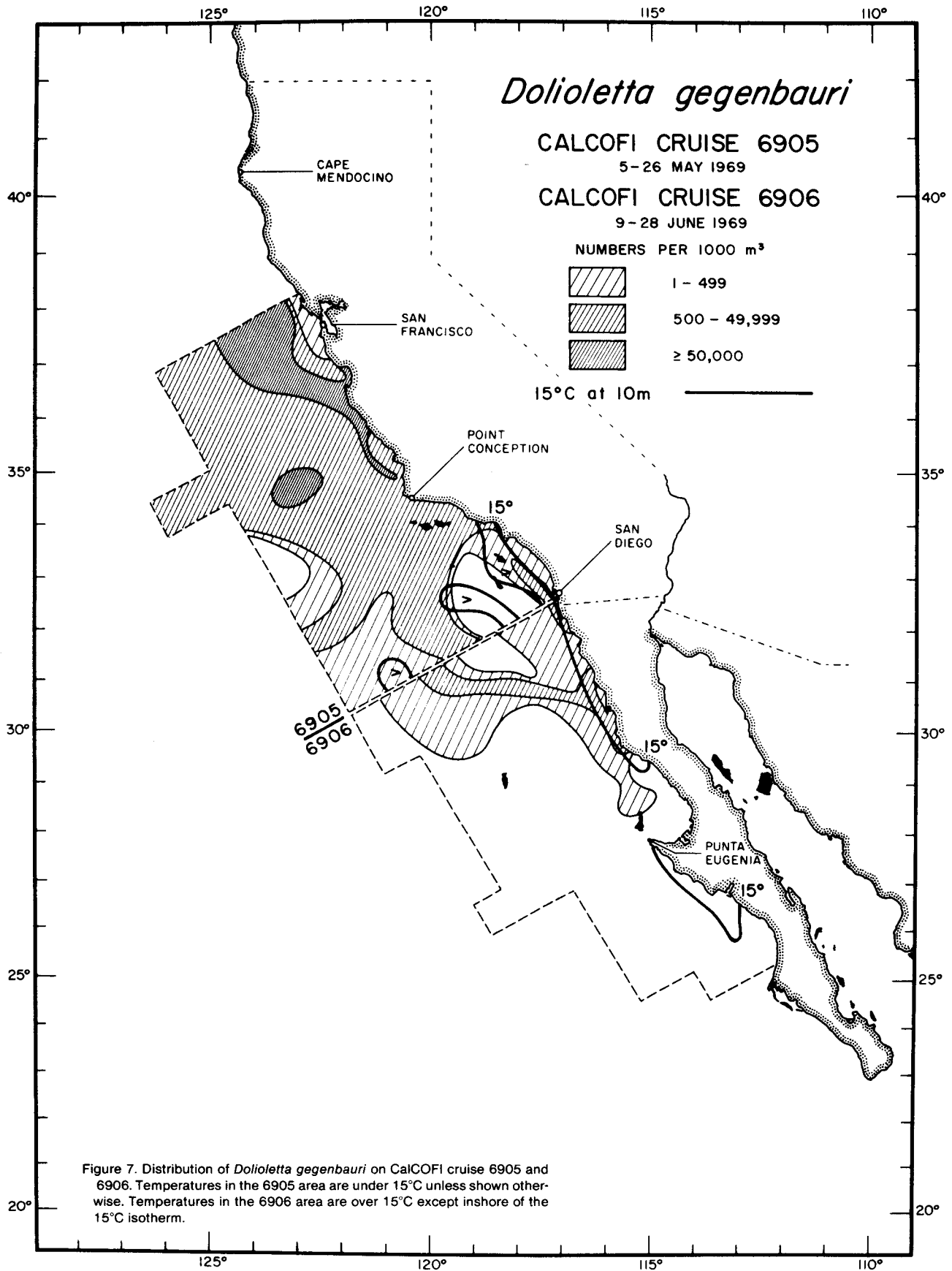
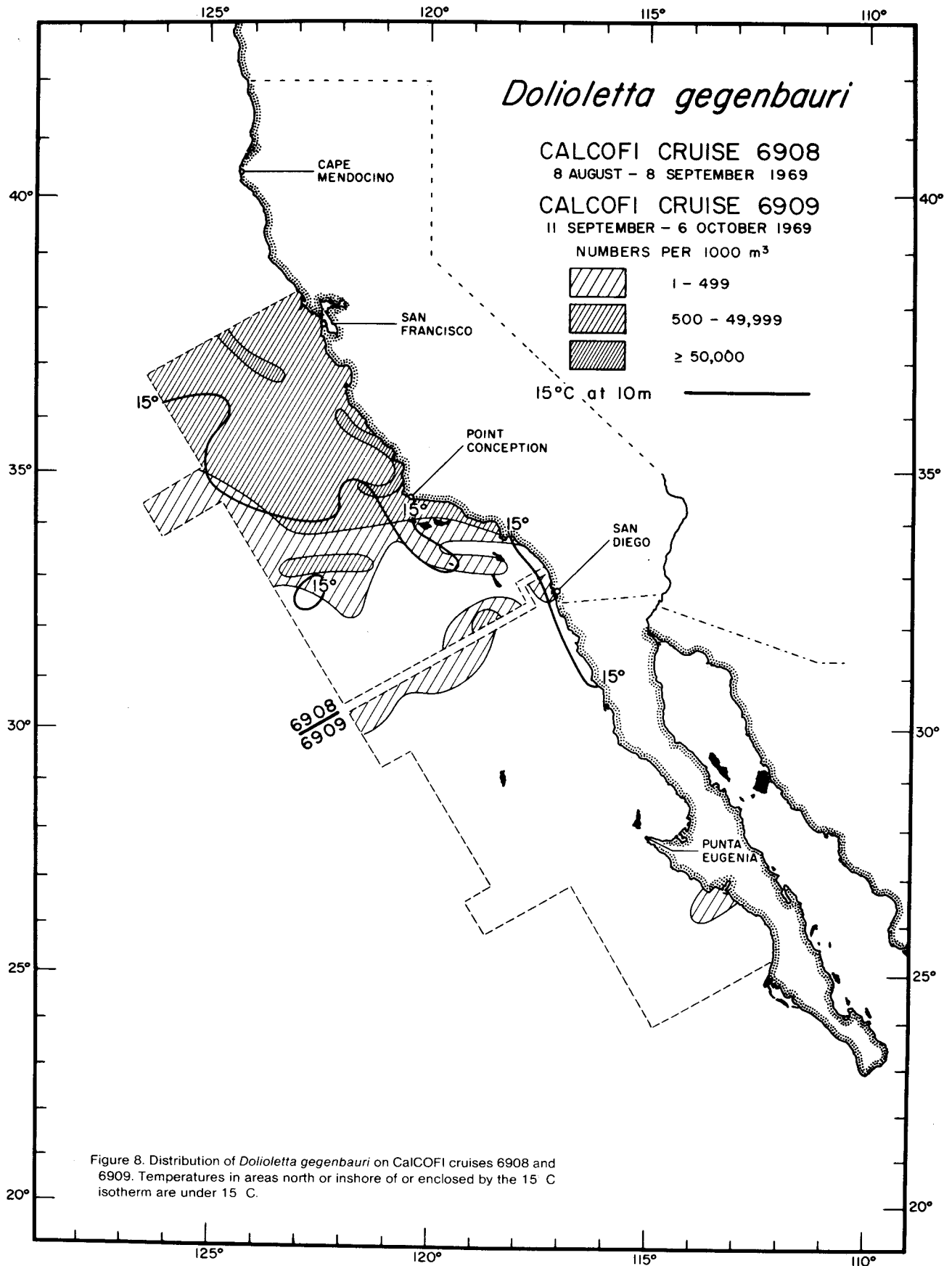
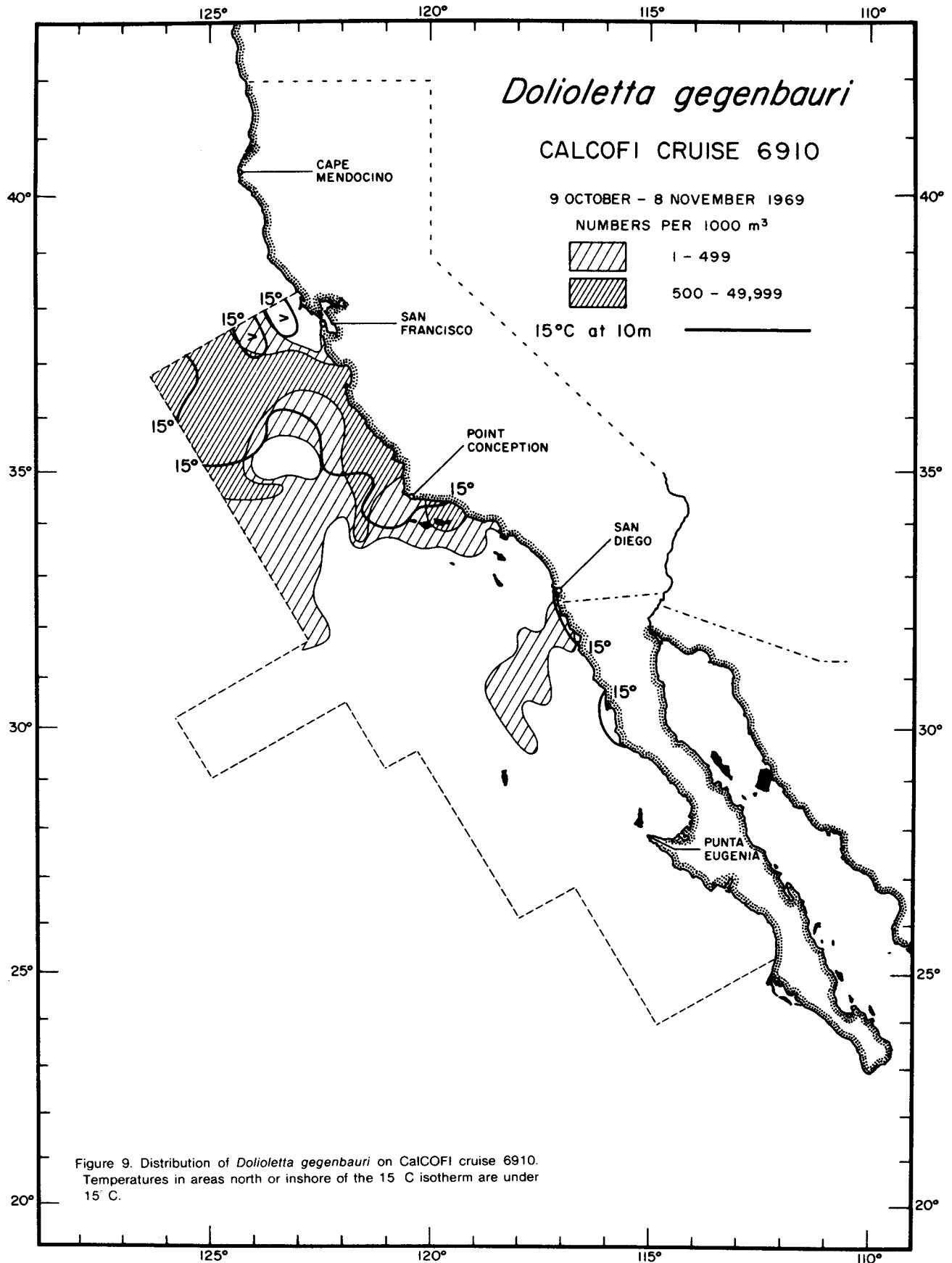
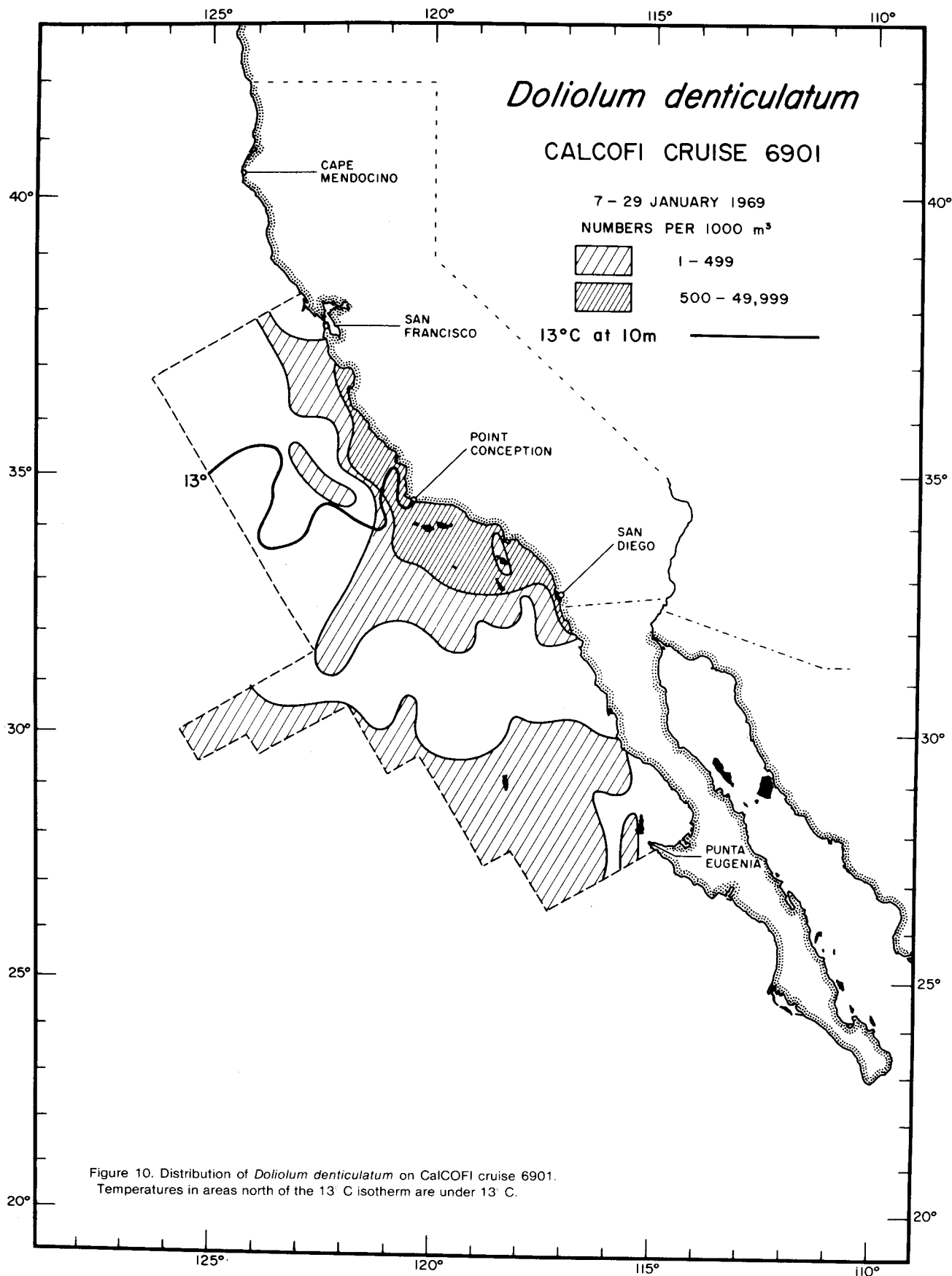
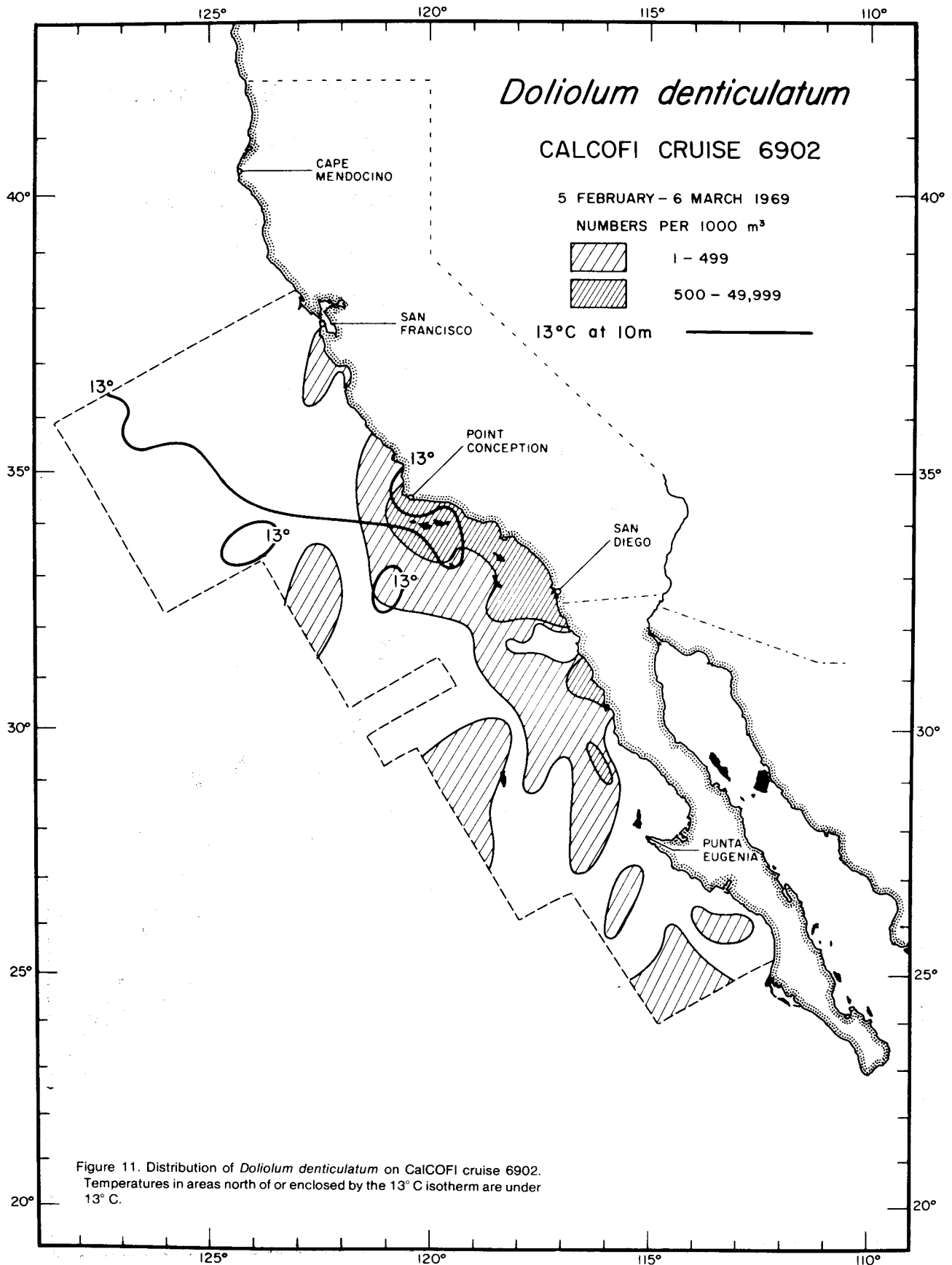


Figure 7. Distribution of *Doliolletta gegenbauri* on CalCOFI cruise 6905 and 6906. Temperatures in the 6905 area are under 15°C unless shown otherwise. Temperatures in the 6906 area are over 15°C except inshore of the 15°C isotherm.

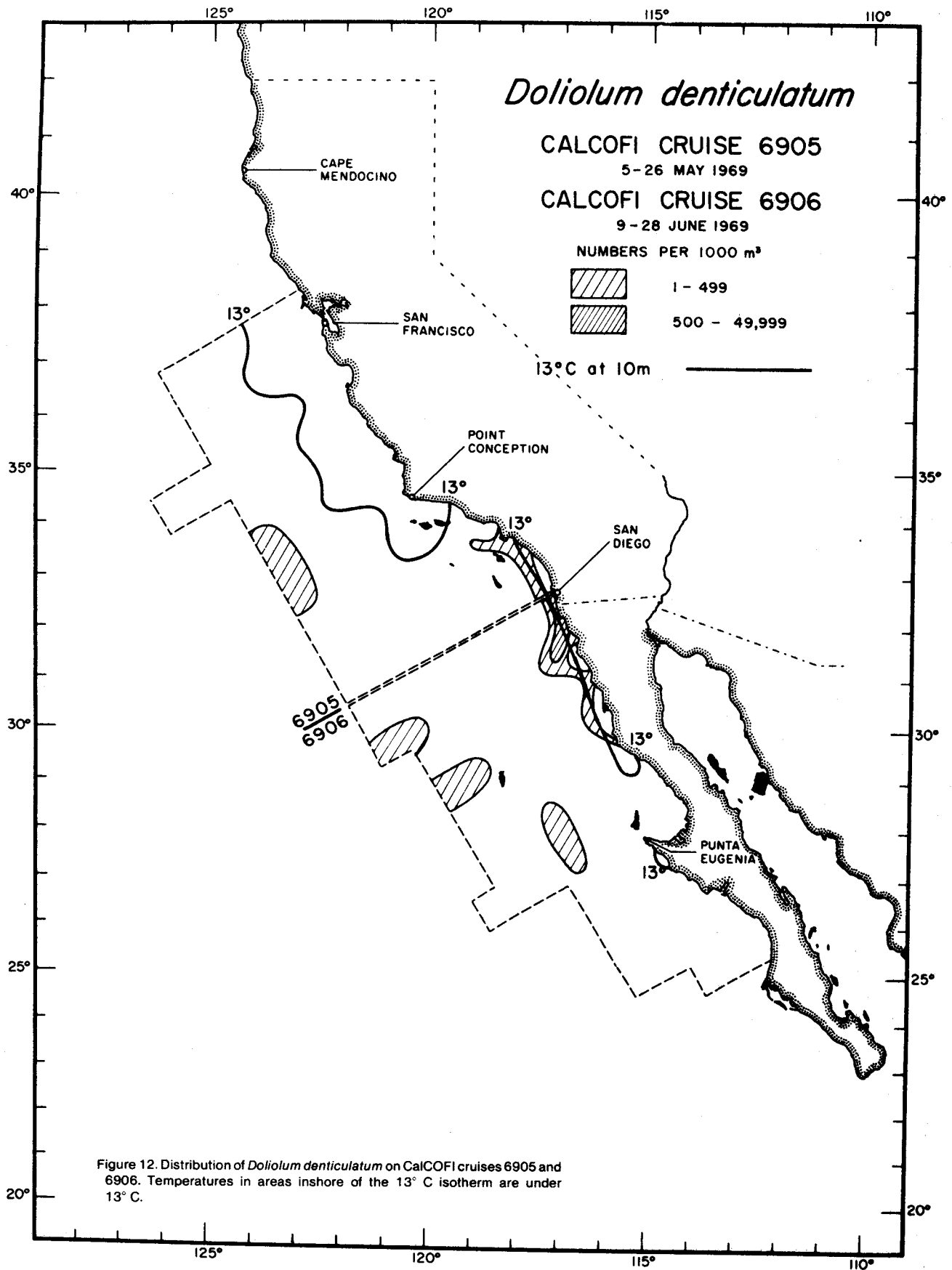


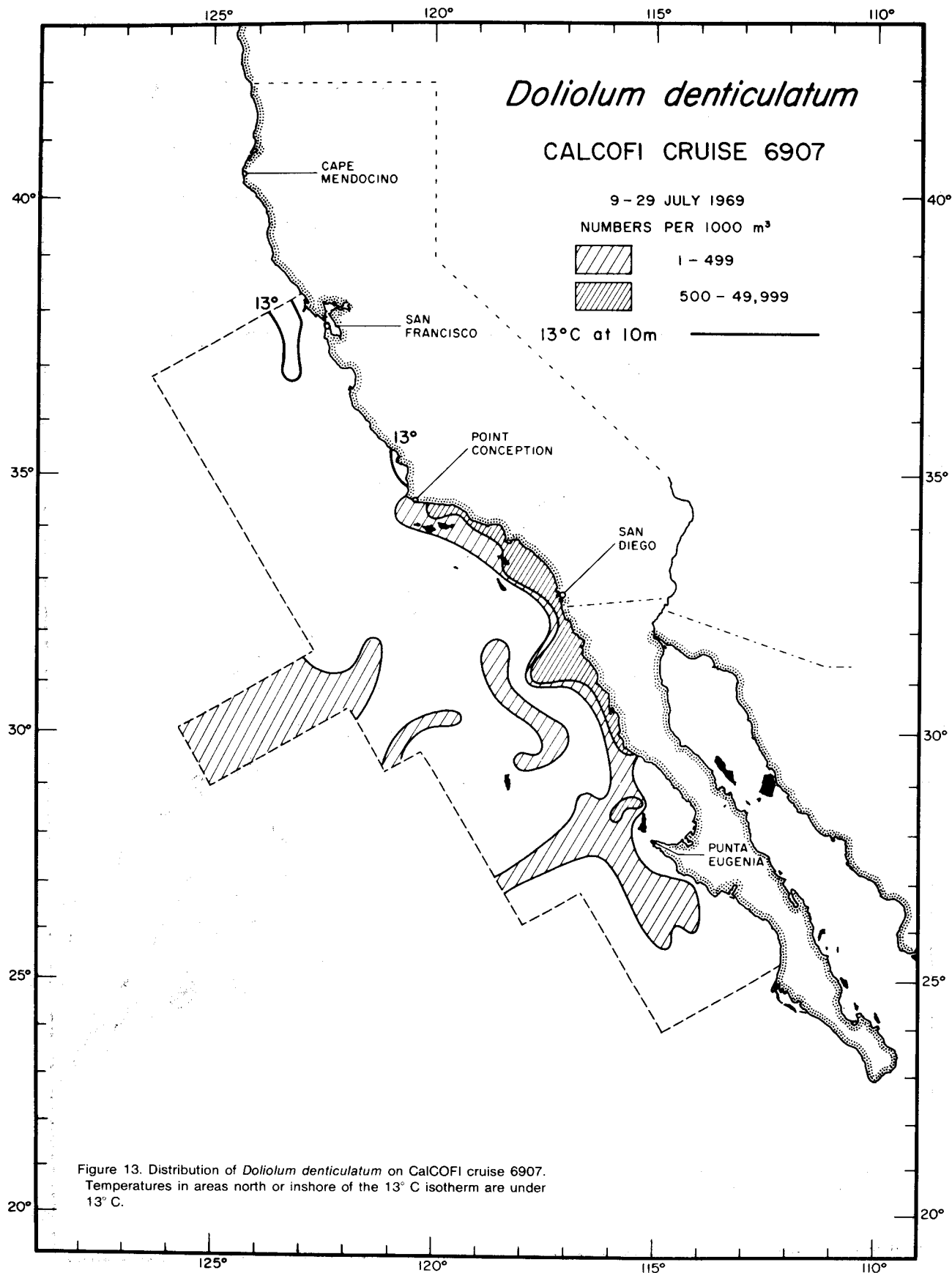


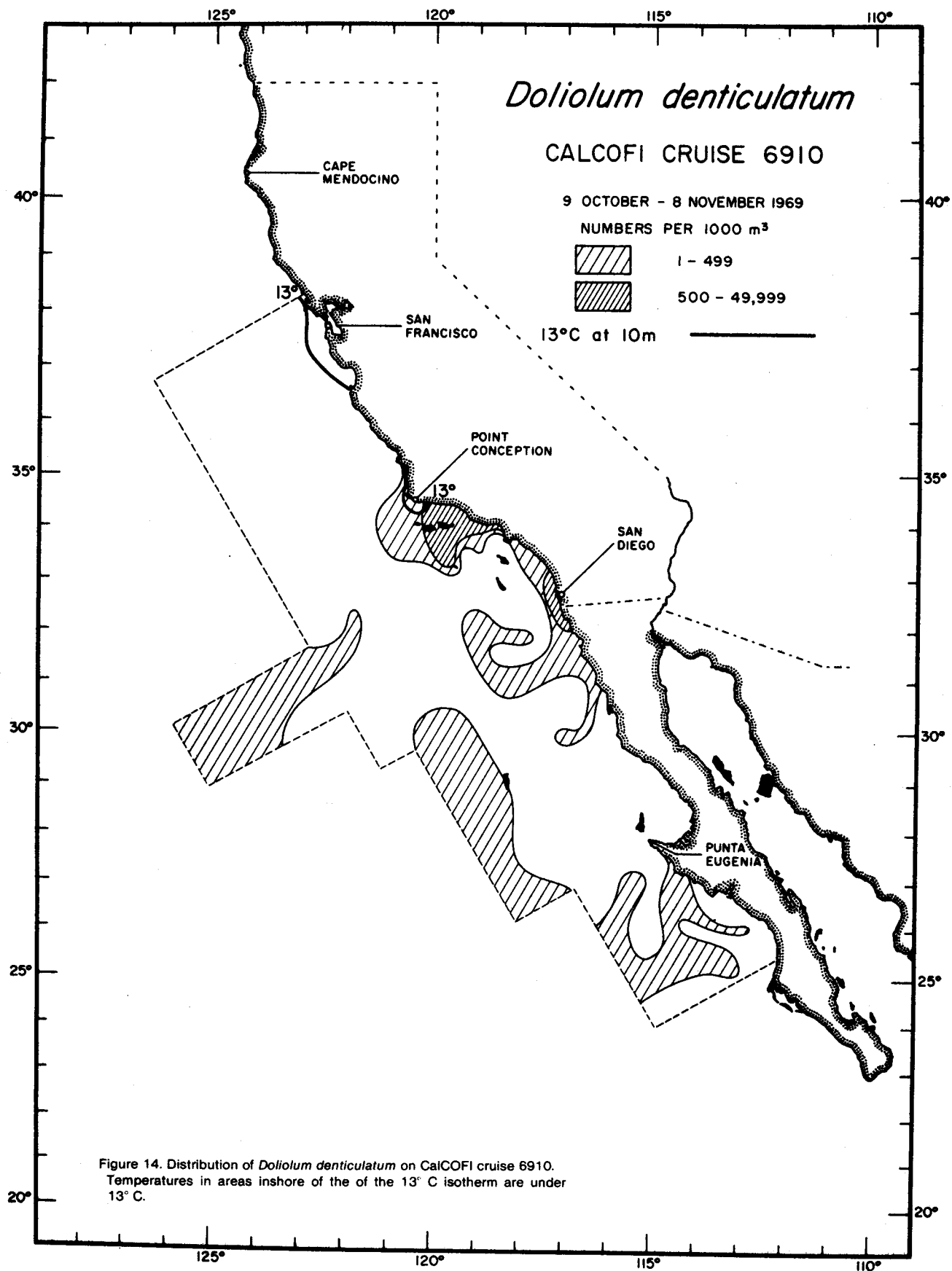












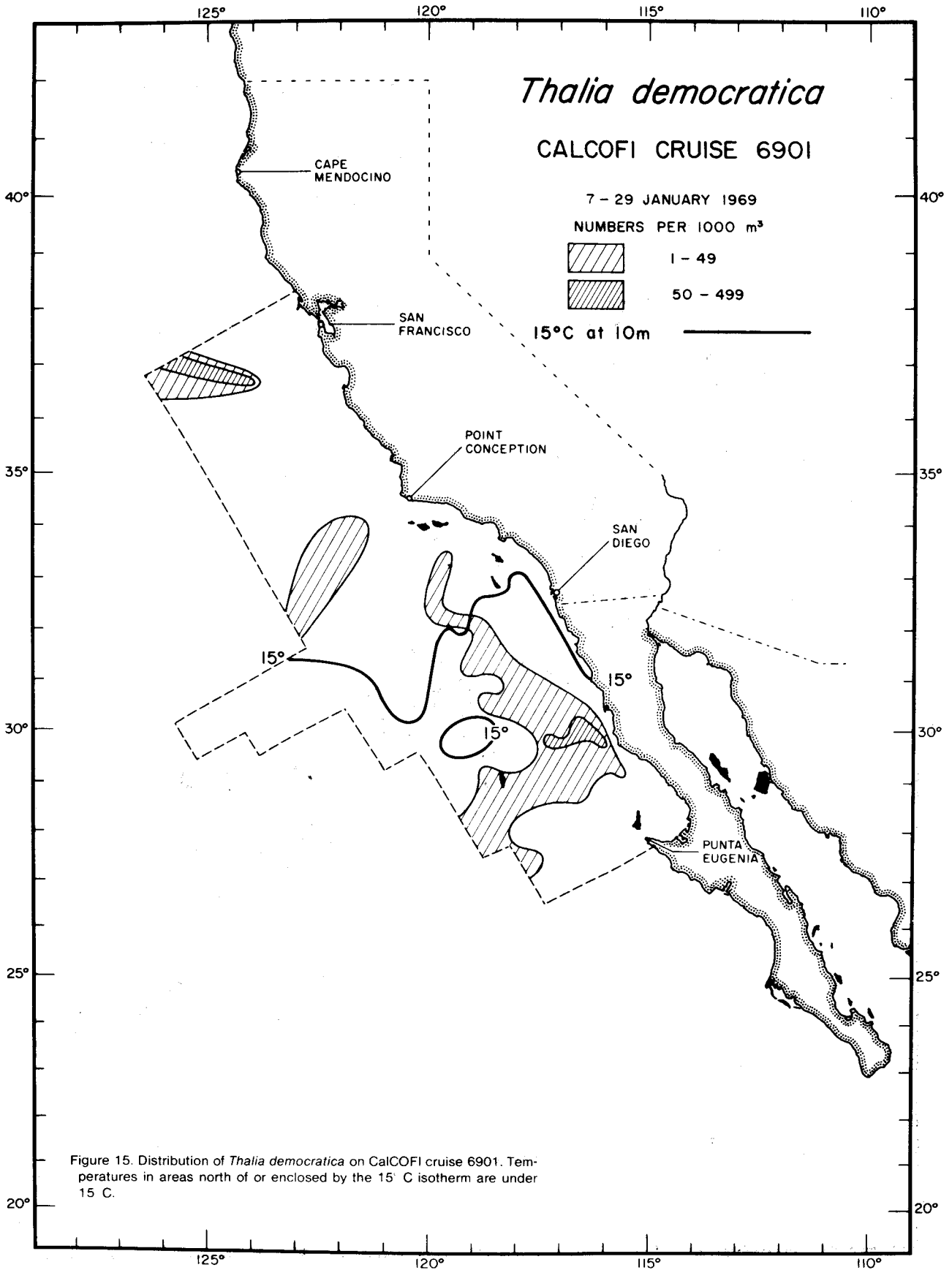


Figure 15. Distribution of *Thalia democratica* on CalCOFI cruise 6901. Temperatures in areas north of or enclosed by the 15° C isotherm are under 15 C.

