Extraordinary abundance of squid paralarvae in the tropical eastern Pacific Ocean during El Niño of 1987

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Abstract.–A two-ship survey of the eastern tropical Pacific collected surface plankton samples during El Niño in August–November 1987. Although the diversity of cephalopods in these samples was low, cephalopod abundance was extremely high. Most of the cephalopods collected were rhynchoteuthion paralarvae of an ommastrephid squid, either *Doscidicus gigas* or *Sthenoteuthis oualaniensis*. High abundances (hundreds of paralarvae in a 15-min tow) were concentrated in a band parallel to the coast, 740–900 km off Central America. This band of high abundance was approximately coincident with the 29°C surface isotherm. Maximum abundance (>12,000 rhynchoteuthions in a 15-min tow) was four orders of magnitude greater than background levels and an order of magnitude greater than any other report of cephalopod abundance. Based on flowmeter readings from the sampler, the anomalous abundance was not a sampling artifact. Size-frequency analysis indicates that this patch cannot be explained as a result of recent hatching from an egg mass. This abundance may have resulted from warm El Niño waters, aggregation by convergence of surface currents, or the interaction of these factors during the squid's spawning season.

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Reports of the effects of El Niño/Southern Oscillation have been widespread in both scientific literature and popular news media. Shifts in distribution and decreases in abundance of marine animals resulting from El Niño have received much attention. Cephalopods are important components of the marine food web, as well as the targets of commercial fisheries. I report here on the serendipitous collection of squid paralarvae during El Niño 1987 at abundances an order of magnitude higher than any previously known.

Materials and methods

A two-ship survey for a visual census of marine mammals was conducted in the eastern tropical Pacific Ocean during August–November 1987. During four cruise legs, the NOAA Ship *David Starr Jordan* surveyed the area between the equator—19°N and 79–121°W, while the NOAA Ship *MacArthur*, also in four legs, covered the region westward of the *Jordan* survey to 148°W and southward to 11°S. Surface plankton samplers (Manta nets; Brown and Cheng, 1981) were towed by both ships almost every day after sunset to collect fish larvae. Surface temperature was measured by bucket thermometer concurrently with each plankton tow. The distance of each tow was estimated by a flow meter mounted below the net. Extremely high numbers of cephalopod paralarvae were found in some of these samples when they were sorted for ichthyoplankton after the conclusion of the cruises.

Results

The diversity of cephalopods in these samples was quite low; only 15 species were identified and >99% of the 15,052 cephalopods collected were a single species of the squid family Ommastrephidae (Table 1). Ommastrephid paralarvae are distinctive and are referred to as rhynchoteuthions because the two tentacles (as opposed to the eight arms) are fused throughout the early life history. Throughout the entire surveyed region, abundance of paralarval ommastrephids, measured as number of rhynchoteuthions collected per 15-min tow, generally was 0–10 squids per tow. Maximum abundance (22 stations with 20–>100 rhynchoteuthions/tow) was found about 740–900 km offshore in a band parallel to the coast of Central America (Fig. 1A). Within this band at three stations during two separate legs, 379, 461, and 12,354 rhynchoteuthions were collected, respectively. Although most of the stations in this band were sampled by the *Jordan*, the northeasternmost *MacArthur* stations were in the eastern end of

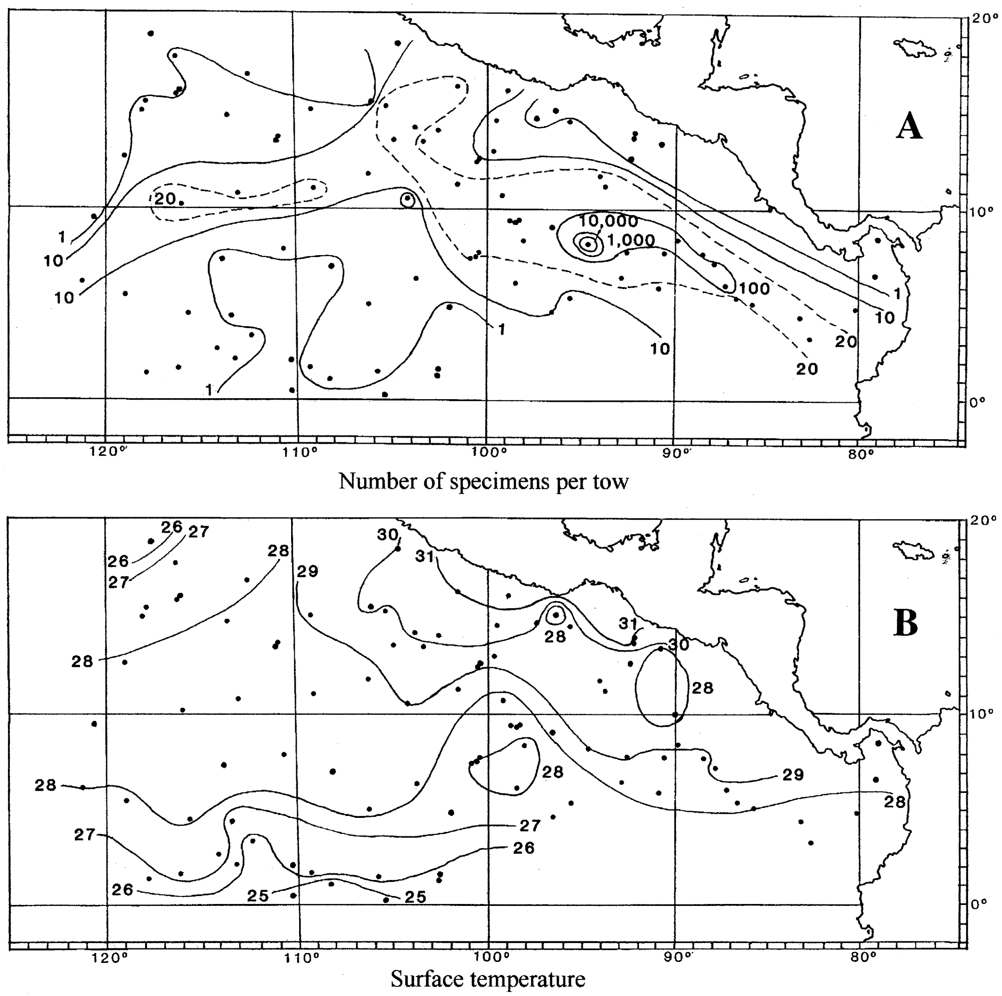

Figure 1

NOAA Ship *D.S. Jordan* cruise 8710, August–November 1987: (**A**) sampling locations and isolines of abundance for rhynchoteuthion squid paralarvae; (**B**) surface isotherms (°C).

the band. A secondary patch of abundance (five stations with 20–90 rhynchoteuthions/tow) was sampled by the *MacArthur* farther to the west (9–13°N, 121–135°W) and appeared to be a westward extension of the band of peak abundance.

The primary band of maximum abundance was approximately coincident with the 29°C surface isotherm (Fig. 1B). Peak abundance was found in the vicinity of a very productive oceanographic upwelling feature known as the Costa Rica Dome (Li et al., 1983). The secondary patch of abundance was in an area with surface temperatures in the mid-28°C range. It may be associated with a westward extension of the Costa Rica Dome, termed the countercurrent ridge (Fiedler et al., 1991). A plot of abundance versus surface temperature shows a clear peak between 27.5° and 31.0°C (Fig. 2). The three stations with highest abundances were all in areas of 29.0–29.5°C surface temperatures (see vertical arrows in Fig. 2). Abundance tapered off late in the survey although surface temperatures remained above 27.5°C (Fig. 3), within the optimum range indicated by peak abundance.

In addition to a biological-oceanographic pattern of abundance, two other alternatives could explain the pattern described here: 1) it could represent concentrated patches of recent hatchlings from isolated egg masses; or 2) it could result from sampling error associated with changes in towing characteristics of the samplers (e.g. speed, duration).

To address alternative 1, I examined size-frequency distributions based on dorsal mantle lengths (DML), both within individual samples and in the total pooled population. For samples with >100 specimens, I measured a subsample of 100. I separated the stations into dusk tows (within one hour after local sun-

Table 1

Cephalopods collected by Manta-net surface zooplankton samples during the two-ship survey of the eastern tropical Pacific, August–November 1987.

	Ship		
	Jordan	*MacArthur*	Total
Ommastrephidae	14,445	495	14,950
Argonauta sp.	16	36	52
unid. squid	9	3	12
Liocranchia sp.	1	9	10
Abraliopsis sp.	9	0	9
Onykia? sp.	4	2	6
Chiroteuthis sp.	3	0	3
Pterygioteuthis sp.	2	0	2
Chtenopteryx sp.	1	1	2
Enoploteuthis? sp.	1	1	2
Abralia? sp.	1	0	1
Thysanoteuthis rhombus	1	0	1
Cranchia scabra	1	0	1
Leachia sp.	1	0	1
Octopodidae	0	1	1
Total	14,495	548	15,043

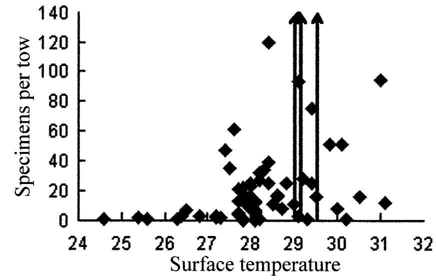

Figure 2

Rhynchoteuthion squid paralarval abundance plotted against surface temperature for NOAA Ship *D.S. Jordan* cruise 8710. Vertical arrows represent samples with maximum numbers of paralarvae.

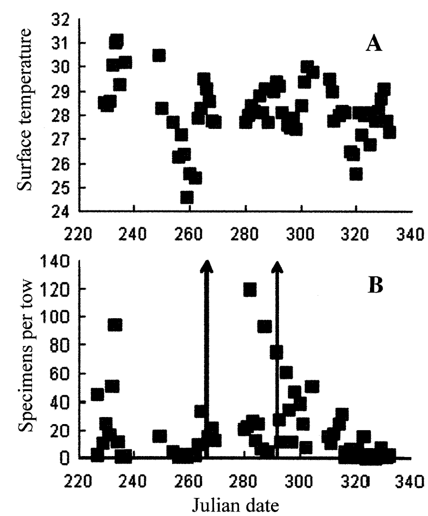

Figure 3

Relationships among water temperature, squid abundance, and date for NOAA Ship *D.S. Jordan* cruise 8710: (**A**) surface temperature plotted against Julian date; (**B**) rhynchoteuthion squid paralarval abundance plotted against Julian date. Vertical arrows represent samples with maximum numbers of paralarvae.

set) and night tows to determine the contribution of diel variability, from either visual avoidance of the net or vertical migration by larger animals, to the size distribution. The overall size distribution was skewed toward the size of newly hatched animals, with the model length 1.0–1.5 mm DML. The size range in dusk samples was 0.5–3.5 mm DML (Fig. 4A). A small second group of larger squid 3.5–8.5 mm DML (modal length ca. 6.0–6.5 mm DML) not present in dusk tows was collected at night in addition to the smaller paralarvae (Fig. 4B). Some stations, such as *Jordan* station IV-05 (Fig. 4D), included only very small squid 1–2 mm DML, as might be expected from a hatching event. The greatest abundance, however, at station III-62, was characterized by a broader range of lengths (Fig. 4C) with a larger modal size of 2.0–2.5 mm DML. On the basis of analysis of growth rings in statoliths from Hawaiian *S. oualaniensis*, a 2.5-mm-ML paralarva is ca. 20 days old (Bigelow, 1991). I therefore conclude that this very high abundance did not result from the net happening upon an egg mass, either just before or just after hatching, but instead an aggregating mechanism must be responsible for this patch.

I examined the second alternative by calculating the variability in flow meter revolutions among tows. The mean and standard deviation for this estimate of sampling efficiency were 2771 and 645, respectively. None of the three outliers from this distribution (one high and two very low) collected >20 rhynchoteuthions. All of the samples with abundances >40 rhynchoteuthions came from tows with 2612–2947 revolutions. Although this parameter can be used to estimate the volume of water filtered by the sample, I did not do this because assumptions about the orientation of the net mouth with respect to the sea surface are required for surface samples and this orientation can change greatly with sea

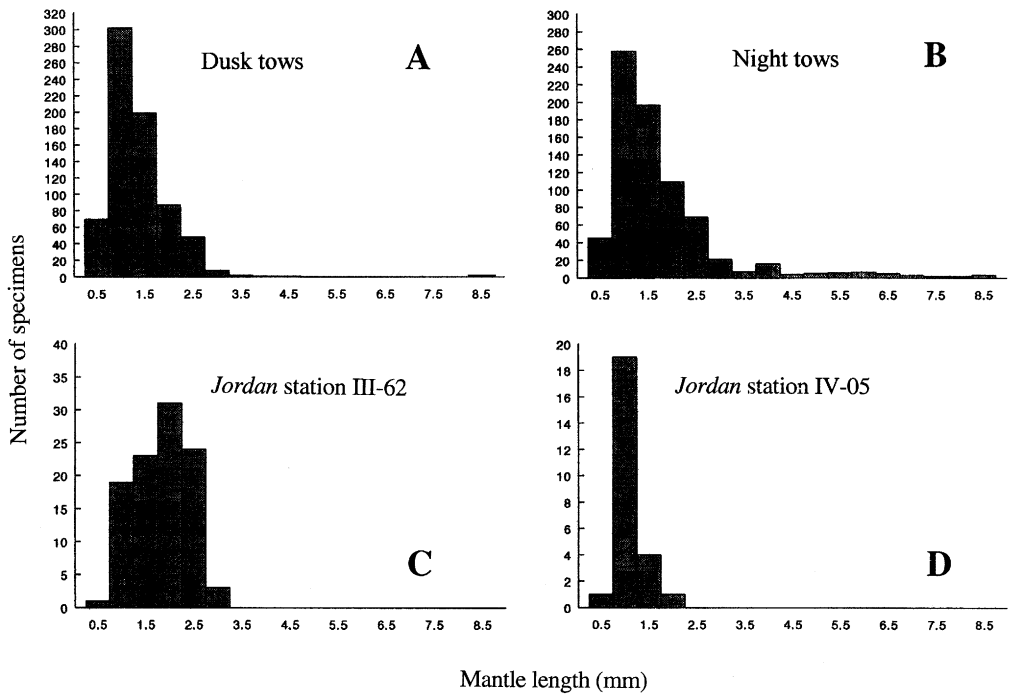

Figure 4

Size-frequency distributions for ommastrephid paralarvae. All specimens were measured from samples that collected <100 rhynchoteuthions. A subsample of 100 specimens was measured from samples containing >100: (**A**) pooled distribution for all dusk tows (samples collected <1 h after local sunset); (**B**) pooled distribution for all night tows (samples collected >1 h after local sunset); (**C**) lengths of 100 specimens from the station that collected maximum abundance; (**D**) example of size-frequency distribution expected from a station that sampled a recent hatching event.

state. The low variability of flow meter counts indicates that observed abundances did not result from sampling artifacts.

Discussion

Aside from the band of high rhynchoteuthion abundance parallel to the coast and coincident with the 29°C isotherm, these collections are not unusual for surface samples of cephalopod paralarvae. The abundance of other cephalopods with paralarvae typically found at the surface, such as *Argonauta*, was not exceptional. Unusually high abundances in these samples were found only in the paralarvae of ommastrephid squids.

The Humboldt squid, *Doscidicus gigas*, is an ommastrephid sufficiently abundant in this area to support commercial fisheries, but descriptions of the paralarvae of this species are not adequate to identify them with confidence. However, the general morphology, morphometrics, and chromatophore patterns of the paralarvae reported here are consistent with those of another widely distributed and abundant ommastrephid, *Sthenoteuthis oualaniensis*, whose paralarvae have been described from off Hawaii (Harman and Young, 1985). It is not possible at this time to be certain which of these species composed the high abundances reported here. Although natural spawning has not been observed directly for either of these species, ommastrephids are known to spawn large egg masses that are gelatinous and pelagic and are very difficult to collect with nets. Spawning aggregations of *S. oualaniensis* and other ommastrephids have been located in other areas. It seems reasonable to assume that either species may aggregate in the study area to produce egg masses.

No information is available on the abundance of these squid paralarvae in subsurface waters of this region. The highest abundance of *S. oualaniensis* in Hawaiian waters is found in the mixed layer from the surface to 20 m depth (Young and Hirota, 1998). Surface abundance therefore appears to be a reasonable indication of overall paralarval distribution of this species. Furthermore, the depth of maximum zooplankton abundance in the eastern tropical

Pacific is generally limited by an oxygen minimum layer beneath the thermocline (Saltzman and Wishner, 1997). Thus, the distribution of these shallow-living paralarvae may have been compressed toward the surface by the oxygen-minimum layer.

Expendable bathythermograph measurements by the *Jordan* during this period showed the mixed-layer depth to be 20–40 m, except where the thermocline was depressed within an anticyclonic eddy located very close to the stations with maximum squid abundance (Hansen and Maul, 1991). Convergence of surface currents associated with the downwelling that depresses the thermocline could aggregate surface plankton such as these paralarvae (Bakun and Csirke, 1998). Although the area of maximum abundance was near the Costa Rica Dome, an upwelling feature where the thermocline typically shoals from 60 m to 30 m depth (Balance et al., 1997), thermal topography in this area was anomalously flat during El Niño of 1987 (Fiedler et al, 1992).

A few other records of cephalopod distribution and abundance are known from this region. In an extensive multicruise survey of the eastern tropical Pacific in 1967–68 (Okutani, 1974), few *S. oualaniensis* or other ommastrephids were collected. Similarly, in a cruise in this region from October 1969 through February 1970, during which surface zooplankton were sampled, no large numbers of paralarvae were encountered, although the most abundant cephalopod family sampled was the Ommastrephidae (Ueynagi and Nonaka, 1993).

Typical numbers of cephalopod paralarvae taken in zooplankton samples worldwide number 0 to perhaps 20 squids per sample, usually about 1–5 squids (Vecchione, 1987). The highest abundance previously reported anywhere of which I am aware was almost 1000 loliginid paralarvae in a 15-min surface plankton tow in the western North Atlantic (Vecchione et al., 1986). The maximum abundance found in the present study was over an order of magnitude greater than that.

The samples reported in this study were collected during the peak of a moderate El Niño event (McPhaden and Hayes, 1990). Surface temperatures in the area averaged 3.5°C warmer than during the same period of the following year (Fiedler et al., 1992). The temperature distribution of these samples indicates that high abundances of rhynchoteuthions would not be expected at temperatures <27.5°C. Therefore, warm El Niño waters probably were the primary reason for the high abundance of squid paralarvae found here. These abundant surface-dwelling paralarvae may have been concentrated to extraordinary densities by convergent surface currents in the vicinity of an anticyclonic eddy. Seasonal occurrence is likely important, because surface temperatures remained high until the end of these cruises, whereas squid abundance decreased dramatically during the final 30 days. The sampling fortunately was conducted during the season when these squid were hatching.

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