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Seasonal abundance of the siphonophore, *Nanomia bijuga*, in Monterey Bay

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Abstract

Quantitative video surveys, conducted in the upper 1000 m in Monterey Bay from an ROV, showed that the year-round population of the siphonophore *Nanomia bijuga* occupied a day-time depth range between 10 and 800 m, with the majority between 200 and 400 m. The time-series transects revealed a repeating pattern of seasonal variations in abundance, with peak abundance during the Oceanic period, about three months after the onset of regional upwelling. The seasonal pattern was consistent over a three-year period from 1993 to 1995. The abundance of *N. bijuga* was significantly correlated with the annual cycle of primary production in Monterey Bay. This study is based on data from the first time series of systematic mesopelagic transects conducted by an ROV. © 1998 Elsevier Science Ltd. All rights reserved.

1. Introduction

In extensive midwater video surveys in Monterey Bay, California, the physonect siphonophore *Nanomia bijuga* is usually the most commonly observed gelatinous animal, year-round. They are frequently seen with euphausiid krill in their gastrozooids, and in Monterey Bay they are important predators of *Euphausia pacifica*, *Thysanoessa* spp., and *Nematoscelis difficilis*. *Nanomia bijuga* occurs broadly in warm and temperate waters along the western coast of North America, from about 25°N to at least 50°N (Alvarino, 1974; Mackie, 1985). The abundance of *N. bijuga* near the northern end of its range was measured with bongo nets at 47 per 1000 m³ (Mapstone

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and Arai, 1992). Net-caught specimens in Monterey Bay were common at 400 m but could not be distinguished from other physonects (Smith-Beasley, 1992).

Accurately assessing the abundance of siphonophores, or any gelatinous mesopelagic animal, has been a challenge to the conventional midwater sampling technologies of nets and acoustics (Harbison, 1983). The fragile structure of siphonophore colonies is easily disrupted by most midwater trawling gear, when abundant they clog nets, and except for those with pneumatophores their watery bodies usually do not reflect sound well. In situ techniques are far more promising (Hamner et al., 1975; Bergstrom et al., 1992; Hamner and Robison, 1992) but few such assessments have been made in deep water. Barham (1963) used the bathyscaphe Trieste to study the contribution of *N. bijuga* to sonic scattering layers in the San Diego Trough and estimated point abundances as high as 300 per 1000 m³. Rogers, et al. (1978) observed concentrations of *N. cara* an order of magnitude higher, in layers just above the bottom of the Gulf of Maine, at depths between 120 and 200 m.

Seasonal variations in the abundance of siphonophores have been indicated in several studies (Moore, 1949; 1953; Mills, 1981; Kirkpatrick and Pugh, 1984; Lo and Biggs, 1996). Both inshore and offshore species have shown changes in abundance associated with water mass changes, but these patterns are complicated by temporal changes in depth, inter-annual differences, short-term hydrographic changes, and horizontal transport (Mackie et al., 1987). Clear-cut, repeating correlations with specific seasonal parameters have not been apparent, particularly in deep water.

Monterey Bay has three, well-defined hydrographic seasons: Upwelling from March to September, followed by an intrusion of oceanic water through October, and then the Davidson Current period when warm water moves northward along the coast (Bolin and Abbott, 1963). These seasons are reflected in characteristic patterns of mixed layer depth (Olivieri and Chavez, 1998) and of primary production (Chavez, 1996). The present study addresses seasonal changes in the abundance of *Nanomia bijuga*, a subsequent paper will deal with predation and vertical migration.

2. Methods

Over the course of three years we studied *Nanomia bijuga* at a single station in Monterey Bay. The site, 36°42'N, 122°02'W, is located over the axis of the Monterey Submarine Canyon, where the water column depth is 1600 m (Fig. 1). Measurements of local primary production and hydrography were made at a moored instrument platform near the midwater transect site (Chavez et al., 1997). Depth declines rapidly down-canyon to the west of the time-series station, and the area is open to oceanic water.

Vertical distribution and abundance measurements were made with the remotely operated vehicle (ROV) Ventana, operated by the Monterey Bay Aquarium Research Institute (MBARI). Ventana is an ISE Hysub 40, outfitted for scientific research

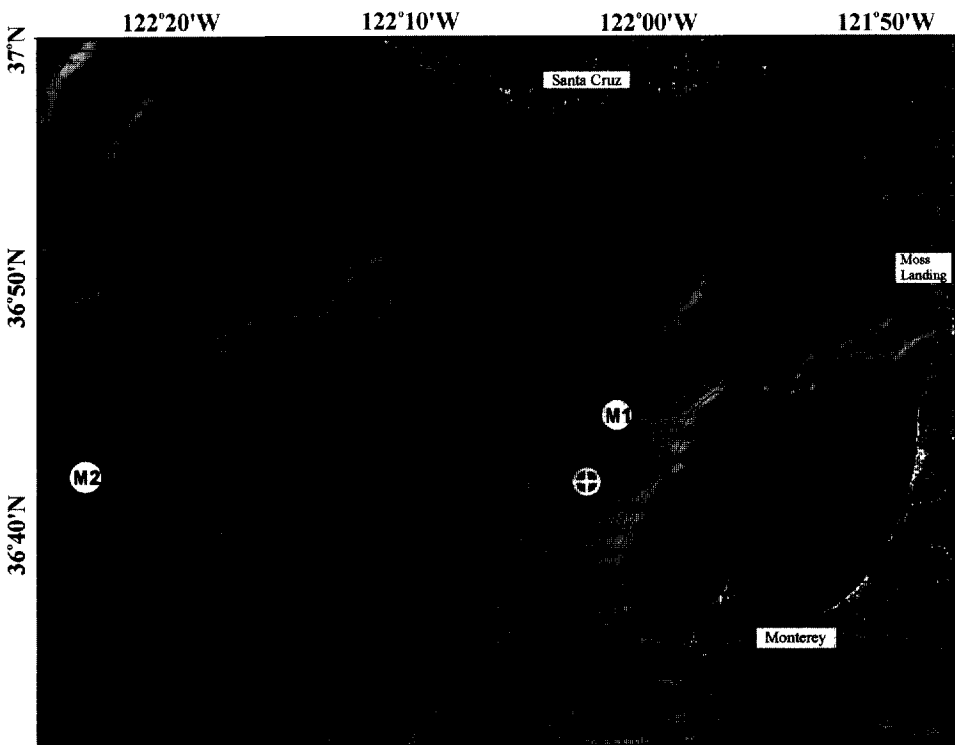


Fig. 1. Location of the midwater time-series survey site (+), over the Monterey Submarine Canyon. M1 and M2 are locations where moorings provide continuous measurements of surface hydrography and primary production (Chavez et al., 1998).

(Robison, 1993). The principal video camera is a broadcast quality, Sony DXC-3000, fitted with a Fujinon 5.5–48 mm zoom lens. For quantitative transecting, lighting was arranged to give broad forward coverage, the lens was set at its widest angle, and focus was adjusted to give the largest depth of field from 1–4 m in front of the vehicle. The camera's field of view at a focal distance of 1.25 m is 2.65 m², and this number was used to calculate transect volumes. Video images were transmitted through optical fibers in the ROV's tether and recorded on high-resolution BetaCam tapes aboard the surface support ship R/V Point Lobos.

During transects the ROV was driven at a mean speed of 0.5 m/s, just slow enough for the moving video images to remain clear. The size range of *Nanomia*, 3–25 cm, was well within the resolution capability of the camera under transecting conditions. Transects were run at a constant heading, at constant depth, for 10 min. Mean transect length was 0.33 km (SD = 28 m), measured in real time by a low-speed, savonius rotor flowmeter. Mean transect volume was 814 m³. Temperature, salinity, depth and oxygen concentration were measured with a SeaBird SBE-9, mounted on the ROV. A Sea Tech 25 cm transmissometer measured particle density at 670 nm.

Time codes link the video data, frame by frame, to the simultaneous CTDO measurements. Ventana also carried a 675 kHz Mesotech scanning sonar system, capable of surveying the water in a 50 m radius around the vehicle.

For assessment of seasonal abundance in the present study, we conducted 257 daytime transects at 100 m intervals between 100 and 1000 m. Transecting dives were made approximately twice each month. For analysis of vertical distribution, depths were categorized in 100 m increments (e.g. 100–199, 200–299, etc.). All depth intervals were sampled at least twice during each hydrographic season between February 1993 and January 1996, and most were sampled seven times per season. We did not include transects made above 100 m in the statistical analyses because ambient sunlight made the viewing conditions there impossible to compare directly with deeper layers. We assessed *Nanomia* abundance in this upper layer during the descent and ascent portions of 72 vertical ROV dive profiles, and with 21 separate horizontal transects.

Transect videotapes were analyzed ashore with an editing deck and a high-resolution monitor. Numbers of *Nanomia*, and nine other midwater species, were counted as they passed through the camera's field of view. While each individual colony was tracked through the entire depth of field, we recorded the number of *Nanomia* present in 15 s (7.5 m) increments. At transecting speed, this allowed us to accurately register each individual. At each depth, counts were normalized based on the total volume of water transected. Effects of hydrographic season and depth were analyzed with a two-way ANOVA (Zar, 1984). For all analyses $\alpha = 0.05$.

3. Results

The transect data included 10,126 *Nanomia bijuga* in a daytime depth range between 10 and 800 m. Over the three years of this study, 70% of the population was concentrated between 200 and 400 m (Fig. 2). There was no significant difference in this pattern between years. While *Nanomia* was rare in the upper 100 m, we have observed viable colonies in the upper 10 m while blue-water diving over the Monterey Canyon and in shallow, inshore waters as well. There was no significant seasonal change in distribution relative to depth, even though the mixed layer thickness ranged from less than 5 to more than 50 m (Olivieri and Chavez, 1998). The corresponding temperature range occupied by *Nanomia* was 5–10°C, and temperature did not appear to be a limiting factor. The decrease in *Nanomia* with depth below 400 m did correlate with declining oxygen ($p < 0.004$, Pearson correlation coefficient; Zar, 1984), and abundance was positively correlated with oxygen ($p < 0.001$). Oxygen content dropped rapidly with increasing depth from about 6 ml/l near the surface to about 1 ml/l or less at 500 m (Fig. 3). At depths between 600 and 900 m dissolved oxygen was usually less than 0.5 ml/l and less than 1% of the population occurred below 600 m. The lowest oxygen level at which we observed *Nanomia* was 0.1 ml/l. In recent dives with the ROV Dolphin 3K in Sagami Bay, Japan, where no comparable oxygen minimum layer occurs, *Nanomia* was observed in abundance to depths of 800 m.

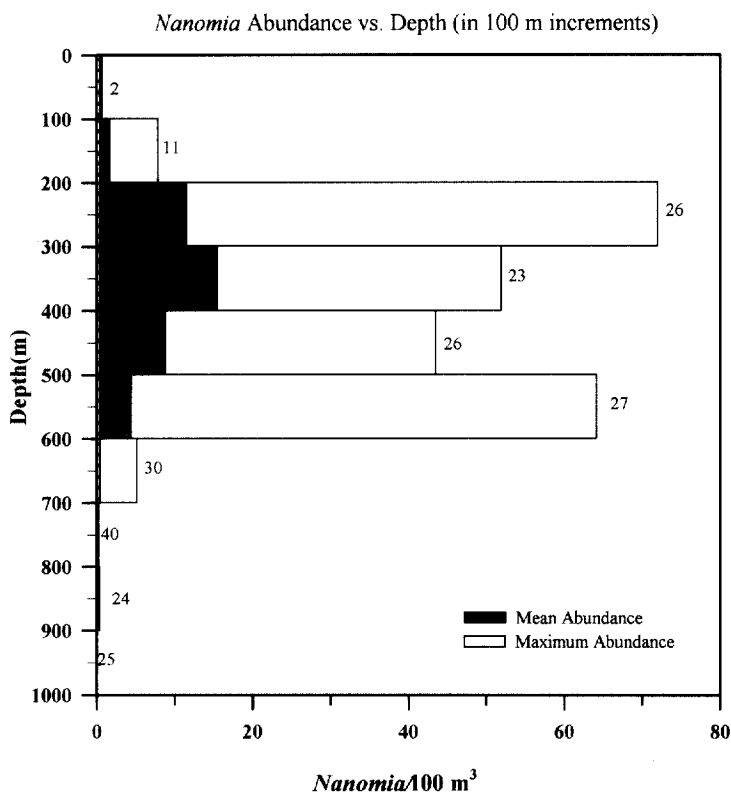


Fig. 2. Vertical distribution of *Nanomia bijuga*; mean and maximum measured abundances, from data gathered in 234 transects over three years (1993–1995). Numbers at the ends of the bars are the number of transects conducted at each depth interval.

Total abundance of *Nanomia bijuga* showed a strong seasonal cycle through all three of the years we surveyed (Fig. 4) and there were no significant differences between years. Peak abundance occurred about three months after the onset of upwelling, during the Oceanic period, and the differences between this season and the other two were significant ($p < 0.001$). *Nanomia* abundance also was linked to peaks of primary production (Fig. 5). Cross correlation of mean productivity values with mean *Nanomia* abundance was significant ($p < 0.01$), with primary production measured as peak chlorophyll values, after a 3–4 month lag (Fig. 5).

Along transect paths within its principal depth range, the mean abundance of *Nanomia* was 5 per 100 m^3 , and peak abundance was 1 colony per cubic meter. Evidence of patchiness from the transect data was statistically equivocal. The index of dispersion and Green's index (Ludwig and Reynolds, 1988) indicated random distributions. On the other hand, two-term local quadrat variance (Ludwig and Reynolds, 1988) calculated for 13 randomly selected transects between 200 and 400 m, indicated horizontal patch dimensions of about 15 m. We also used the scanning sonar to assess

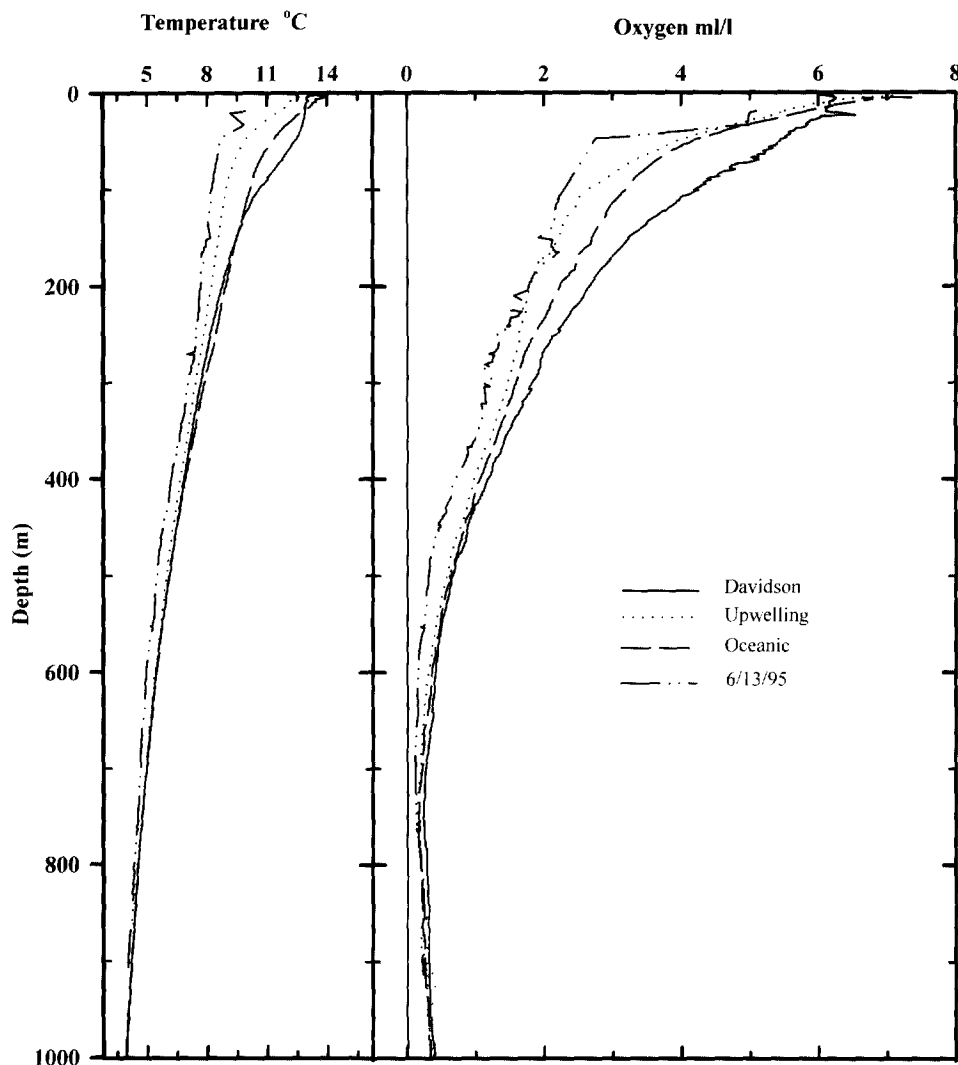


Fig. 3. Temperature and oxygen profiles from data generated by ROV dives made during the present study. The Davidson, Upwelling, and Oceanic profiles are mean values for each season from 1993 through 1995; 6/13/95 is a typical, single dive profile during the Upwelling period.

spatial patterns and patchiness (Fig. 6). Clear sonar targets, reflected from pneumatophores (Barham, 1963), could be readily counted and correlated with video images of individual *Nanomia* colonies. Sonar surveys independent of transects frequently showed clumped targets, subsequently identified with video as groups of *Nanomia*. The most distinct aggregation we measured was about 15 m in largest dimension and contained approximately 300 colonies in 1,500 m³ of water. These

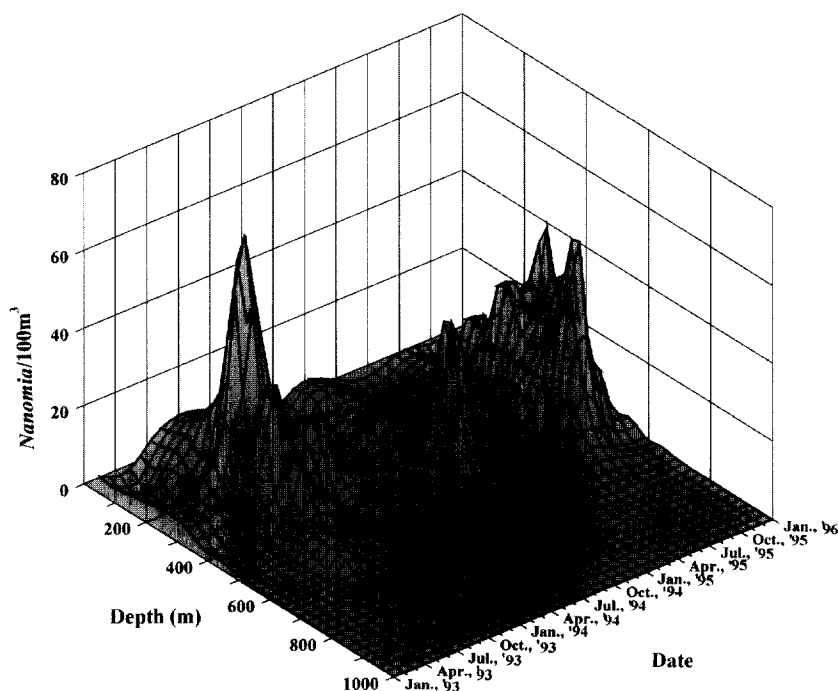


Fig. 4. Abundance and depth distribution of *Nanomia bijuga* in Monterey Bay from 1993 through 1995.

aggregations of *Nanomia* were common, particularly when associated with the presence of krill. Presumably, longer transects would have resolved the aggregation pattern more precisely.

4. Discussion

Nanomia bijuga is an active and highly mobile midwater predator, able to react quickly to mechanical stimuli and to swim rapidly for tens of meters. We have measured top speeds at about 30 cm/s. While the obtrusiveness of the ROV at short range must be considerable, we saw little evidence of avoidance. On the transect runs the great majority of colonies remained in place and did not react to our approach by contracting or swimming away. This observation was confirmed by sonar measurements of *Nanomia* abundance 10 to 20 m in front of the vehicle, which did not alter as the ROV approached and passed through the adjacent water. This is the first time-series data set ever reported for a midwater species, and it demonstrates the ability of the ROV to make high resolution surveys of gelatinous animals.

Nighttime transects indicate an upward shift in the population of *Nanomia* but the data are, as yet, insufficient for statistical treatment and comparison. Barham's (1963)

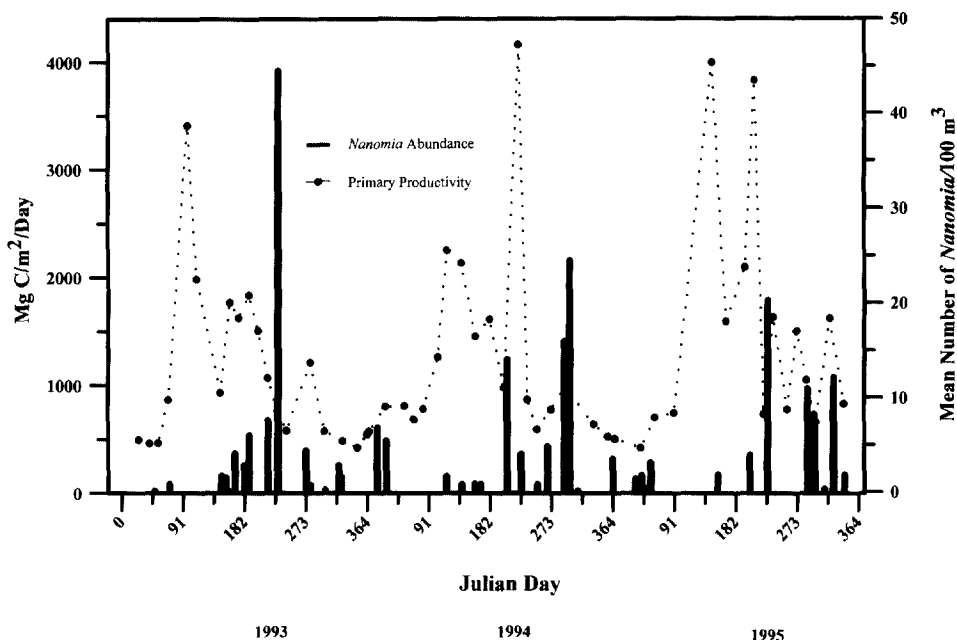


Fig. 5. Abundance of *Nanomia bijuga* plotted with synoptic measurements of primary production from adjacent waters.

in situ observations of *N. bijuga* from Trieste, documented diel vertical migrations of several hundred meters. In Monterey Bay, *Nanomia*'s vertical range overlaps broadly with two calycophoran siphonophores (*Lensia* sp. and *Chuniphyes* sp.) which have a slightly deeper center of distribution at 300–500 m (unpublished data). The calycophorans also show a seasonal cycle of abundance in Monterey Bay that peaks during the Oceanic period. The presence of *Nanomia* is positively correlated in our transect data with the narcomedusa *Solmissus* sp. ($p < 0.001$), and the giant appendicularian *Bathochordaeus* sp. ($p = 0.017$; unpublished data). No synoptic measure of seasonal euphausiid abundance is available, yet like *Nanomia*, they are present year-round in Monterey Bay and along the California coast (Brinton, 1976). Also like *Nanomia*, *Euphausia pacifica* is most common between 200 and 400 m during the day, and its abundance is linked to seasonal upwelling (Brinton, 1976).

We can rule out temporal depth changes as an apparent cause of seasonal changes in *Nanomia* abundance (Bigelow and Sears, 1937) because our transecting pattern consistently sampled below the population through all seasons. Likewise, interannual variations and short-term hydrographic changes (Mackie et al., 1987) do not complicate the analysis because the cyclic patterns we measured were consistent, and there were no significant differences between years. This leaves two likely explanations for the observed seasonality: advection—where the annual intrusion of Oceanic water

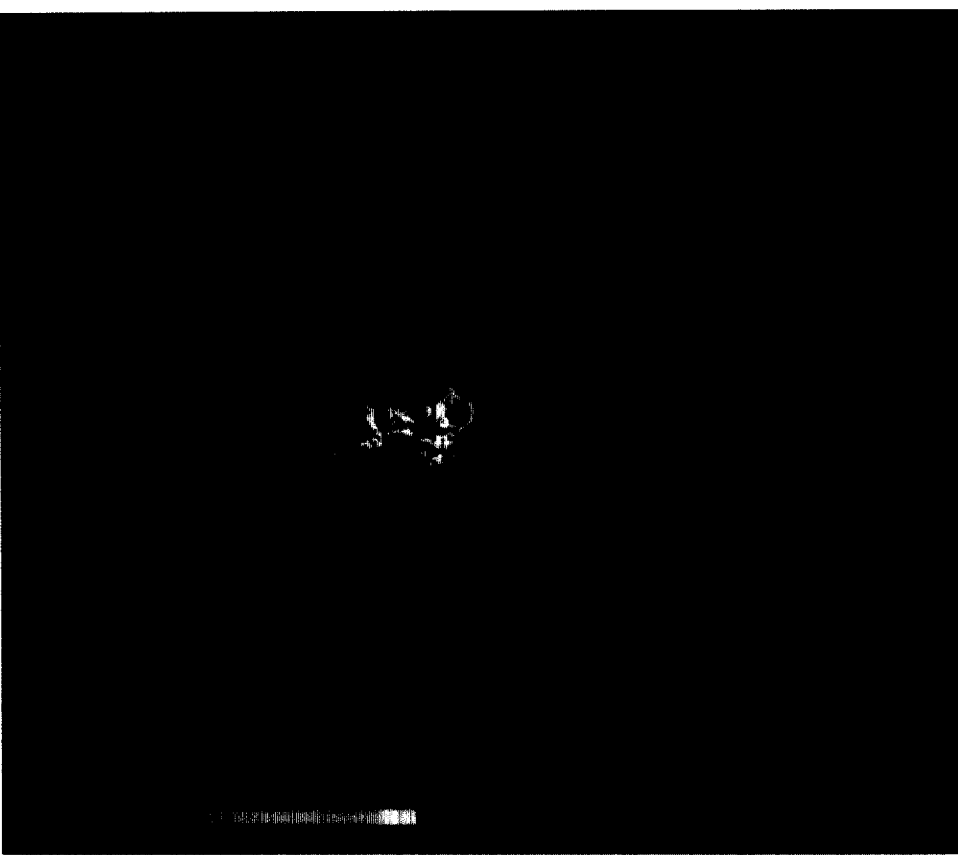


Fig. 6. Scanning sonar image from the ROV Ventana. The radius of the sweep was 10 m, the forward angle of the beam was 60°, and the ensonified volume was about 3500 m³. Individual colonies of *Nanomia bijuga* appear as light-colored spots, indicating sound reflected from their gas-filled pneumatophores. The source identifications were confirmed optically as Ventana passed through this aggregation.

brings with it a higher concentration of *Nanomia* than are resident in Monterey Bay during the Upwelling and Davidson Current periods; or population growth—where the resident *Nanomia* population expands as a result of increases in their principal prey, after the increase of primary production due to upwelling. Whether the source is a seasonally expanding local population or one supplemented by advection from offshore, the end result is a persistent and abundant population of *Nanomia bijuga* in the midwater community over the Monterey Canyon.

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