Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA

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Abstract. The seasonal abundance and vertical distribution patterns of a group of small calycophoran siphonophores (principally *Chuniphyes multidentata* and *Lensia conoidea*) were investigated using a remotely operated vehicle (ROV) deployed in Monterey Bay, California. Abundance was assessed along 295 horizontal transects covering a depth range of 100–1000 m over a three and a half year period. The vertical distribution of the study animals changed seasonally, coupled to the onset and cessation of upwelling in the bay. While numerical abundance peaked after upwelling, there was no significant difference between seasons. The siphonophores were more broadly distributed over the depth range sampled during the upwelling or Shallow Mixed Layer (SML) period, than during the non-upwelling or Deep Mixed Layer (DML) period. There were no significant differences in abundance or distribution patterns between years except in 1993, when there were significantly more siphonophores observed during the SML period than during the DML period. This may reflect effects resulting from the 1992–1993 El Niño event. The abundance of these siphonophores was negatively correlated with that of *Nanomia bijuga*, a physonect siphonophore of similar size and feeding behavior found in the bay. The siphonophores studied here appear from preliminary data to migrate vertically, possibly with two separately migrating groups.

Introduction

Gelatinous animals have long been known to be widespread inhabitants of the world's oceans [e.g. (Haeckel, 1881; Hartman and Emery, 1956; Totton, 1965; Alvariño, 1967, 1971; Pugh, 1975; Biggs, 1977; Gamulin and Krsinie, 1993; Pages and Kurbjeweit, 1994)], yet until the advent of SCUBA, submersibles and remotely operated vehicles (ROVs), their role in marine ecosystems remained largely speculative and poorly studied (Hamner *et al.*, 1975; Robison, 1993). Gelatinous animals are typically so fragile that they are all but destroyed by traditional sampling methods. Siphonophores, with their colonial morphology, are particularly delicate and are usually recovered only as fragments by plankton nets. This has resulted in poor identification and limited quantitative data. As a consequence, relatively little attention has been paid to these ubiquitous predators. With the use of SCUBA, researchers have been able to study these animals *in situ* and to capture the smaller species intact for study in the laboratory (Purcell, 1981). SCUBA, however, is limited by the duration of observations and the depths at which samples may be taken. These limitations are largely overcome by ROVs (Robison, 1993).

Siphonophores are predators. Their feeding ecology varies with mobility, size and taxonomic suborder (Purcell, 1981, 1997). The suborder, Calycophorae, preys on a variety of hard- and soft-bodied organisms (Purcell, 1981, 1997) and is represented by many species ranging in size from centimeters to tens of meters. The size of the colony greatly influences the siphonophore's mobility and

consequently, its feeding strategy. Most large siphonophores are lie-and-wait predators. In Monterey Bay, the larger calycophorans (Praya, Rosacea) feed heavily on low density, mobile prey such as salps, chaetognaths, medusae, larger crustaceans (e.g. sergestids) and occasionally fish and squid (Robison and Silguero, unpublished observations). The smaller species are typically active and agile swimmers that use short bursts of rapid swimming followed by brief periods of tentacle deployment to search out their high density, patchy prey (Mackie et al., 1987; Purcell, 1997; Robison et al., 1998). The dominant prey of the smaller siphonophores are euphausiids and copepods (Purcell, 1981, 1982, 1997; Robison et al., 1998). When abundant, siphonophores can be the 'most important non-crustacean predators' in the surface waters (Purcell, 1981, 1982, 1997), yet little is known about their abundance or vertical distribution patterns, particularly on a seasonal basis [review in (Mackie et al., 1987); (Pugh, 1984)]. Most of the preceding studies of siphonophore distribution and abundance have been based on material collected by nets, which introduce errors in enumeration and identification. Most previous investigations have also been constrained by limited temporal resolution. Information gained from long term, in situ studies on the abundance and distribution of siphonophores is critical for assessing the role of these ubiquitous predators in marine ecosystems. This is the first study of calycophoran seasonal abundance conducted with an ROV, and the first quantitative, deep-sea study of calycophorans in situ.

For three and a half years (1993–1996), the Monterey Bay Aquarium Research Institute (MBARI) used the ROV Ventana to sample the abundance and vertical distribution of gelatinous, mesopelagic animals in Monterey Bay, California. Monterey Bay is a unique environment, with a submarine canyon that bisects the bay, bringing the deep-sea habitat within an hour and a half transit from shore. The bay is a highly seasonal environment where coastal upwelling delivers nutrient-rich water during the spring and summer months (Bolin and Abbott, 1963). This study investigated the seasonality of an important constituent of the bay's mesopelagic fauna by assessing the abundance and vertical distribution patterns of a large and distinct subset of its calycophoran siphonophores.

Method

Study site

The study site was a single dive station in Monterey Bay, California, at 36°42'N, 122°02'W (Figure 1). The site is located over the axis of the Monterey Submarine Canyon in 1600 m of water. Local primary production measurements were made from an instrument platform moored in deep water (Figure 1) near the midwater transect site (Chavez et al., 1997).

Bolin and Abbott defined three seasons in Monterey Bay as Upwelling, Oceanic and Davidson Current periods (Bolin and Abbott, 1963). While these three periods are very distinct hydrodynamically, their salinity, oxygen and nutrient concentrations do not show a three-season cycle. These parameters vary with the presence or absence of upwelling and show just two distinct stages—upwelling and non-upwelling (Bolin, 1964). This two-season characterization of Monterey
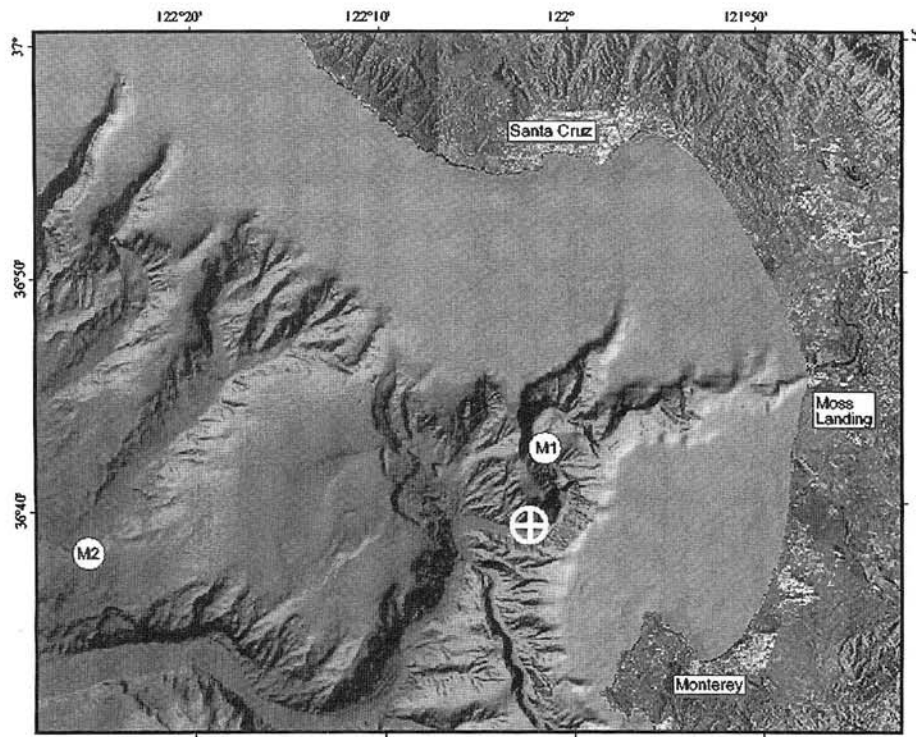
Fig. 1. Monterey Bay, showing locations of the transect survey site (+) over the Monterey Submarine Canyon, and the M1 and M2 moorings which collect continuous measurements of surface hydrography and primary production (Chavez *et al.*, 1997; Robison *et al.*, 1998).

Bay is very important to the study of the ecology of the area, since phytoplankton and zooplankton abundance vary chiefly in relation to nutrient levels (Loeb *et al.*, 1983). During the upwelling season, upwelling intensity may vary, but a shallow thermocline is persistent and deepens only when upwelling ceases completely. The seasons of Monterey Bay are defined in this paper by mixed layer depth. The shallow mixed layer (SML) season is marked by the onset of upwelling around Julian day 92 (April 1), and the deep mixed layer (DML) season is marked by the cessation of upwelling around Julian day 305 (November 1) (Olivieri, 1997).

The circulation, seasons and upwelling characteristics of Monterey Bay have been studied since Bigelow and Leslie's (Bigelow and Leslie, 1930) description based on surveys of temperature, salinity, oxygen, nutrients and plankton. Since that time, efforts have focused chiefly on characterizing the upper level (0–300 m) circulation patterns (Skogsberg, 1936; Bolin and Abbott, 1963; Bolin, 1964; Broenkow and Smethie, 1978; Graham *et al.*, 1992; Graham, 1993; Rosenfeld *et al.*, 1994; Paduan and Rosenfeld, 1996). Although some of these studies addressed the evidence of deeper (300+ m) circulation patterns, little has been done to

specifically address deep circulation in the bay (Lynn and Simpson, 1987; Koehler, 1990; Breaker and Broenkow, 1994; Ramp *et al.*, 1997). Breaker and Broenkow offer a model of bay circulation with the surface layer having a predominant cyclonic (northward) flow, intermediate depths with anticyclonic flow, and depths below 200–300 m reversing again to cyclonic flow (Breaker and Broenkow, 1994). Koehler (Koehler, 1990) and Ramp *et al.* (Ramp *et al.*, 1997) found that the deep circulation in Monterey Bay may be related to the strength of the California Undercurrent, with seasonal fluxes following seasonal changes in the undercurrent's intrusion into the Bay. The California Undercurrent is strongest in the winter months, then weakens or completely reverses when upwelling begins (Lynn and Simpson, 1987).

Description of Ventana and transect methods

Quantitative, horizontal transects were conducted using MBARI's ROV, Ventana, an ISE Hysub 40 that has been outfitted for scientific research (Robison, 1993). It is equipped with a SeaBird SBE-9 CTDO for salinity, temperature, oxygen concentration and depth measurements. The main video camera on Ventana was a broadcast quality Sony DXC-3000, fitted with a Fujinon 5.5–48 mm zoom lens. Transects were conducted with the lens set at its widest angle and focus set to give the largest depth of field at a distance of 1–4 m in front of the camera. Lighting was adjusted to give broad forward illumination. The camera's field of view at 1.25 m from the lens was 2.65 m^2, and this value was used to calculate the volume of water sampled in each transect. Transects were traversed at constant heading and depth for 10 min, at an average speed of 0.5 m s^{-1}.

Time codes linked the CTDO measurements to simultaneous video data. Video images were carried up the vehicle's tether via optical fibers to the surface support ship, the RV 'Point Lobos', and were recorded on high-resolution BetaCam tapes. The mean transect length was 305.4 m, measured by a low-speed, savonius rotor flowmeter. This equates to an average measured volume of 809.2 m^3 per transect. Calycophoran abundance was recorded post-dive from 15 s tape increments. Averages of CTDO data were calculated from the corresponding 15 s intervals. All animal counts were normalized to the volume of water transected.

Assessment of seasonal abundance and distribution

Over the course of the study, 295 daytime transects were conducted, approximately twice each month, at 100 m intervals at depths between 100 and 1000 m. Abundance data were binned into 100 m depth increments for data analysis (e.g. 100–199, 200–299 etc.). All depth increments were sampled at least seven times each season, with an average of 15 transects per season (Table I). Twenty-eight night transects were also conducted, at depths between 100 and 1000 m, during the SML periods of 1994 and 1995 (Table II). The data were analyzed for seasonal patterns in vertical distribution, abundance and inter-annual changes. Correlation of peak siphonophore abundance with peak primary production was tested by binning data into 1-week intervals by Julian day, and advancing the primary

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Table I. Number of transects conducted and the total water volume sampled for the seasonal abundance and vertical distribution comparisons in the shallow mixed layer (SML) and deep mixed layer (DML) periods of 1993–1996

Depth (m)	SML		DML	
	No. transects	Vol. sampled (m^3)	No. transects	Vol. sampled (m^3)
100	7	5947	8	6741
200	16	15576	14	11916
300	18	16411	10	8258
400	18	16688	12	10970
500	20	18481	12	9044
600	16	14514	16	13932
700	25	20007	20	16969
800	13	10047	15	12252
900	13	10108	15	13190
1000	14	9877	11	8053

Table II. Number of transects conducted and the total water volume sampled for the daytime versus night-time vertical distribution and abundance comparisons. All data are from the shallow mixed layer (SML) period of 1994 and 1995

Depth (m)	SML 1994 and 1995			
	Daytime		Night-time	
	No. transects	Vol. sampled (m^3)	No. transects	Vol. sampled (m^3)
100	4	3463	6	4795
200	7	6464	3	2409
300	7	6080	4	3333
400	5	5030	2	1550
500	9	7524	4	3277
600	4	3508	3	2523
700	14	11455	3	2510
800	11	9246	1	907
900	4	3223	1	924
1000	6	4707	1	830

production data in time by week-long intervals until maximum correlation (maximum R) was reached with the siphonophore abundance data. Primary production data were taken from Robison et al. (Robison et al., 1998) and are available for 1993–1995 only.

The correlation between the abundance of the calycophorans we investigated and that of a potential competitor, the physonect siphonophore *Nanomia bijuga*, was tested for the depth range in which their populations overlap. *Nanomia bijuga* abundance was binned into 50 colonies/1000 m^3 intervals and the maximum observed calycophoran abundance was also recorded for each interval.

The study animals

In the suborder Calycophorae, there are three families (Diphyidae, Clauso-phyidae and Abylidae) of small species whose nectophores resemble the shape

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of a rocket, earning them the common name 'rocketship'. They are fast swimmers of small size, up to 40 mm bell (nectophore) length (Totton, 1965), which use comparable feeding strategies to capture similar prey items (Purcell, 1981, 1997). The two principal species in Monterey Bay are *Chuniphyes multidentata* (Family Clausophyidae) and *Lensia conoidea* (Family Diphyidae). The rocketship siphonophores are identifiable to genus level from the ROV video when stationary close-ups are taken. Genus level identification was not possible when moving at transect speed, so these species are grouped in this analysis. Although another calycophoran siphonophore, *Praya*, was among the animals catalogued for the ROV transects, it was not included in this study because its great size and passive feeding strategy makes it ecologically distinct from the smaller calycophroans investigated here.

Results

There were 1755 rocketship calycophorans observed over the study period. They occurred in all depth intervals sampled, over a temperature range of 3.9 to 11.2°C and an oxygen range of 0.072 to 2.285 ml l^{-1} (Figure 2). The only significant correlation between these physical factors and the vertical distribution of the siphonophores was an increase in animal abundance with decreasing oxygen concentration and increasing depth in the SML period (R^2 = 0.384). Rocketship calycophorans have been observed in trawl collections in Monterey Bay and the California Current all the way up to the surface (J.M.B.Silguero, unpublished data), and with the ROV, down to 1675 m, the deepest Ventana has been taken. High light levels in the surface waters make observation of these small, transparent animals almost impossible with the ROV at daytime depths above 100 m.

Abundance, distribution and seasonality

The cumulative abundance and depth distribution of the target siphonophores over all three years of the study is shown in Figure 3. Interactions of abundance with depth, season and year were subsequently tested by a three-way ANOVA. There was a significant difference in vertical distribution between seasons, with a broader and deeper depth distribution in the SML period (P = 0.002). Further analysis by *a priori* student t-tests (α = 0.05) showed significantly higher numbers of these siphonophores during the DML period at the depth interval of 300–400 m (P < 0.01), and significantly more during the SML period at the 700–800 m (P < 0.01) and 900–1000 m (P < 0.05) depth intervals. Although the SML had an average of 9.5 rocketship calycophorans per 1000 m^3 (integrated over the water column from the surface to 1000 m) and the DML period had an average abundance of 6.7 per 1000 m^3, this difference was not statistically significant. The siphonophores' distribution was concentrated in the upper 500 m during the DML period of low productivity, then shifted deeper during the productive SML period without a significant change in overall abundance between the two seasons. This pattern held for all years except 1993, when their abundance was significantly higher in the SML period than in the DML period (P = 0.01). Results
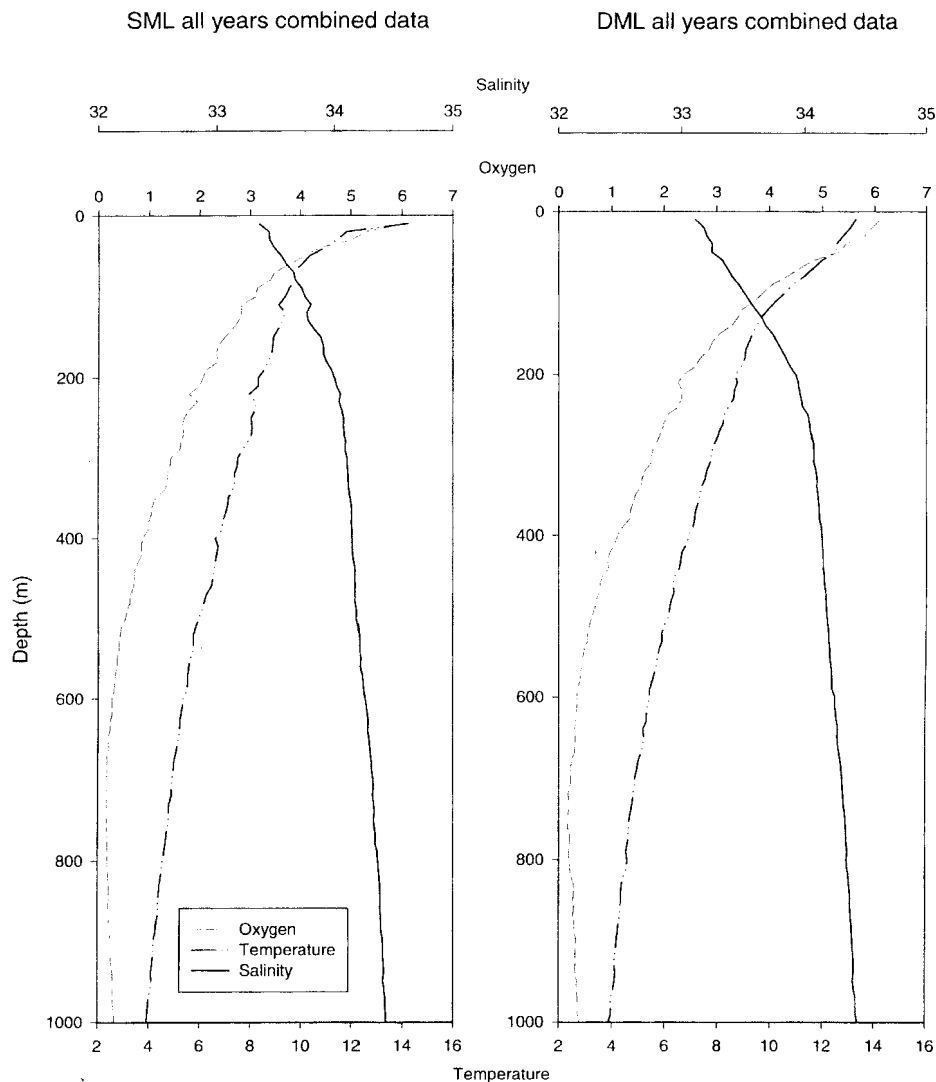
Fig. 2. CTDO data for upwelling (SML) and non-upwelling (DML) periods. Data are averaged over the time period of the study (1993–1995). Oxygen (ml l⁻¹), temperature (°C), salinity (‰).

showed no significant difference of overall abundance or vertical distribution between years.

When the data were examined by Julian day in correlation with the measurements of primary production (Robison *et al.*, 1998), the peak in rocketship calycophoran abundance occurred 42 days (6 weeks) after the initial phytoplankton bloom ($R^2 = 0.547$, Figure 4).
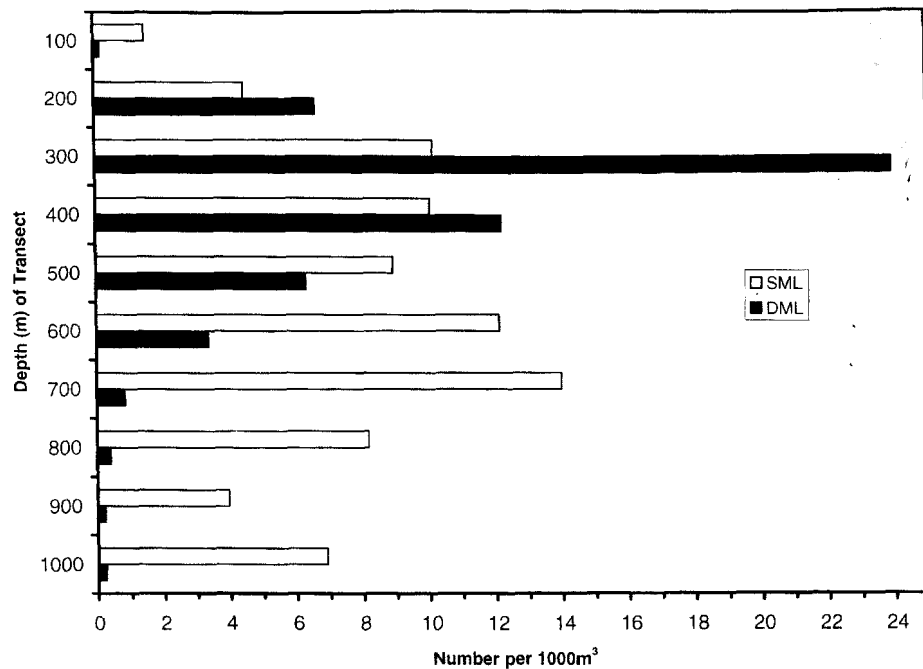
Fig. 3. Rocketship calycophoran seasonal abundance and vertical distribution data combined over the three years of the study. The deeper depth distribution in the SML period is significant (R^2 = 0.384). Differences during the DML period at the 300–400 m depth interval, and during the SML period at the 700–800 and 900–1000 m intervals, were significant, ($P < 0.01$, $P < 0.01$ and $P < 0.05$ respectively).

Correlation with Nanomia bijuga

The abundance of rocketship siphonophores peaked 48 days before the maximum abundance of *N.bijuga*, which occurred 90 days after the peak of primary production (Robison *et al.*, 1998). Rocketship calycophorans co-occurred with *N.bijuga* over its full depth range of 10–800 m (Robison *et al.*, 1998). There was a negative correlation between the rocketship siphonophores and *N.bijuga* abundance in the depths where they overlapped (R^2 = 0.689, Figure 5).

Diel vertical migration

When nighttime transect data were compared with daytime data from the same season (SML) and years (1994 and 1995) (Figure 6), two distinct vertical distribution patterns appeared. The daytime pattern generally reflected the overall vertical distribution shown in Figure 4. The nighttime pattern was bi-modal, with peaks centered at 300 and 650 m. These data are considered preliminary, and no statistical analysis was done.
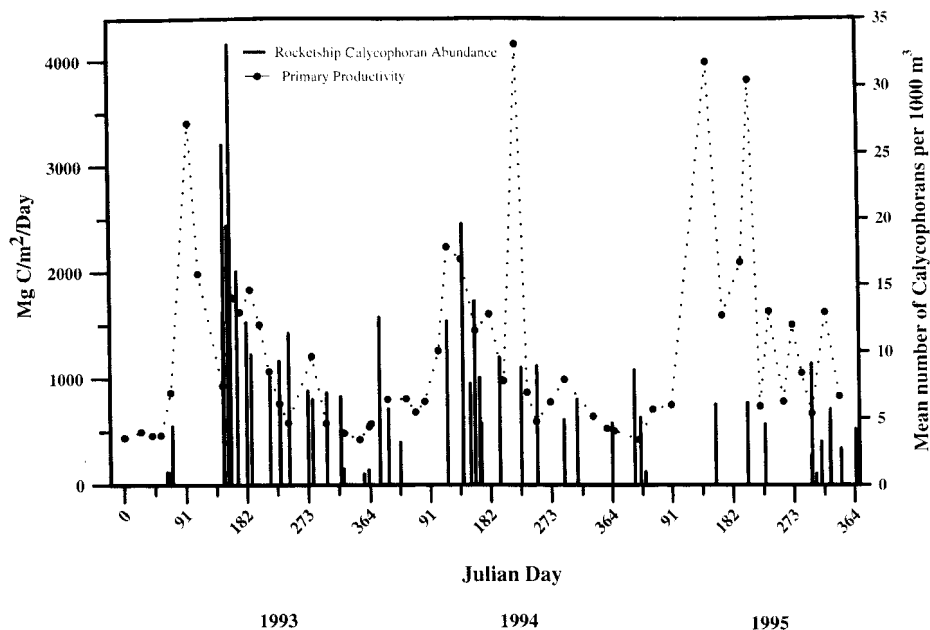
Fig. 4. Rocketship calycophoran abundance and primary production by Julian day for 1993–1995. There is a 42 day lag between peak primary production and peak siphonophore abundance over all years ($R^2 = 0.547$).

Discussion

Abundance and distribution

These siphonophores are found throughout the water column in Monterey Bay, but there are currently no quantitative data on their abundance in the epipelagic zone, above 100 m. Studies on rocketship siphonophores living in neritic and epipelagic waters of Friday Harbor, Washington (Purcell, 1982), and over the Santa Barbara Basin, California (Purcell and Kremer, 1983), report abundances an order of magnitude higher than those reported here for mesopelagic species. We found a significant variation between seasons in overall rocketship abundance only in 1993, when there were significantly more individuals present during the upwelling season. This observed increase in abundance may be a result of the 1992–93 El Niño, which was ending as our field work began (Lenarz et al., 1995; Lynn et al., 1995).

There was a positive correlation between calycophoran abundance and decreasing oxygen concentration during the SML season. This relationship was probably an artifact of oxygen concentration decreasing with depth, coupled with the siphonophores' center of distribution shifting deeper during this season.
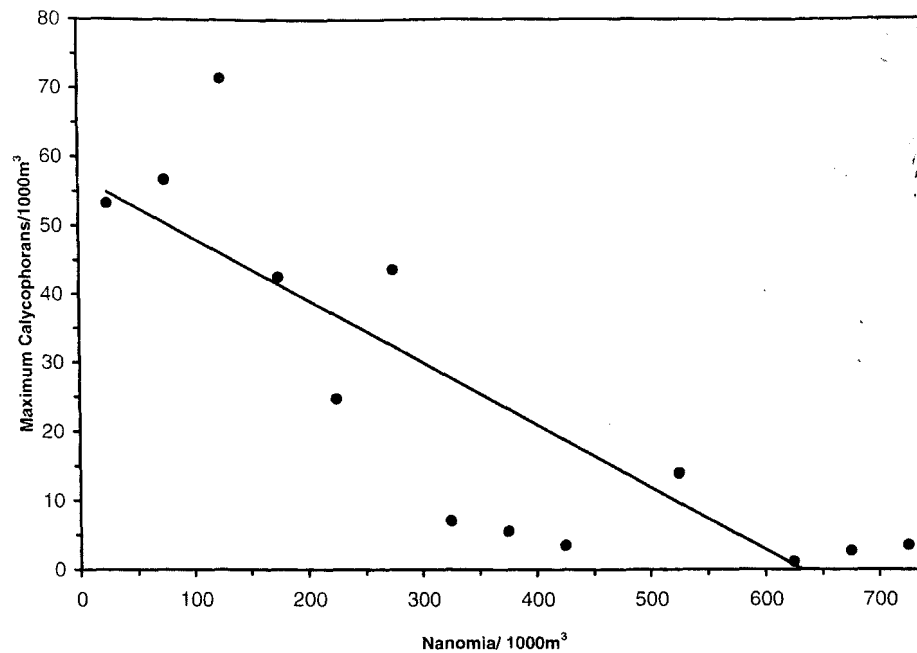
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Fig. 5. Calycophoran versus *Nanomia bijuga* abundance. Solid line is the linear trendline for the data with *N.bijuga* abundance binned into 50 animal/1000 m³ increments and plotted against the maximum calycophoran abundance in that bin. This correlation is highly significant; $R^2 = 0.689$, $P = 0.0003$.

Seasonality

The onset of upwelling in Monterey Bay brings a peak in primary production that is commonly an order of magnitude higher than during non-upwelling periods (Olivieri, 1997). This peak in primary production is likely to bring about a succession of species over time, from increased populations of herbivores to peaks of primary and secondary predators. The increase in food in the surface layers should lead to an increase in food at all depths via the ladder of vertical migrations and vertical particle flux. It is this increase in food availability that we believe leads to the observed peak in abundance of rocketship calycophorans 6 weeks after peak primary production, and the overall increase in their depth distribution during the SML period. Seasonal changes such as these have been documented previously for several siphonophore species. However, the seasonal changes reported were best correlated with temperature, not food availability (Mackie *et al.*, 1987). In contrast, the present study did not find a significant correlation between temperature and the distribution of the siphonophores. This is most likely because the majority of the siphonophores studied live well below the levels of the water column that are cooled by upwelling.

Data on community succession following nutrient enrichment in Monterey Bay are sparse. Loeb *et al.* found an increased abundance of crustacean zooplankton during the SML period of Monterey Bay in 1975, but there were few samples
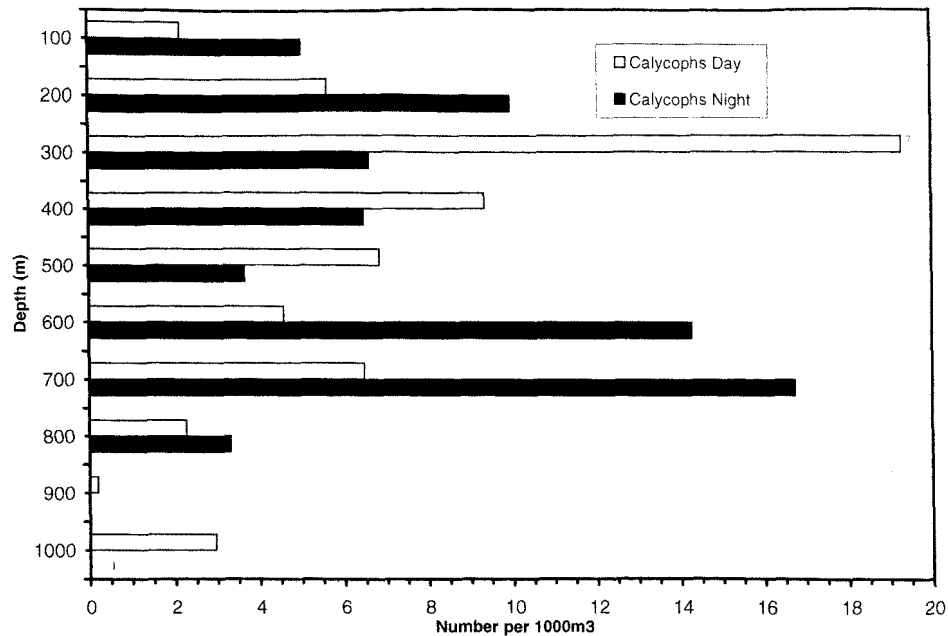
Fig. 6. Day and night abundance and vertical distribution of rocketship calycophorans in the SML periods of 1994 and 1995. Possibly two separately migrating populations: one with a daytime depth distribution of 300–400 m migrating up to 100–200 m at night, and the other with a daytime distribution of 800+ m migrating up to 600–700 m at night.

taken and no species identification was done (Loeb *et al.*, 1983). However, succession such as that indicated here has been observed in systems similar to the one found in Monterey Bay.

Devassy *et al.* studied community succession following phytoplankton blooms along the Goa coast in the Arabian Sea (Devassy *et al.*, 1979). Their study tracked succession from a *Chaetoceros* spp. bloom on the 19th of April to a bloom of copepods 28 days later, and subsequent development of a tertiary community of gelatinous predators dominated by siphonophores 40 days after the initial *Chaetoceros* bloom. Sreekumaran-Nair *et al.* assessed the response of phytoplankton and zooplankton to eutrophication along the west coast of India and found similar results, with a peak in gelatinous zooplankton, including siphonophores, about 2–3 months after nutrient enrichment (Sreekumaran-Nair *et al.*, 1992). These patterns are consistent with the data from the present study, and lend weight to the theory that the peak in calycophoran abundance is due to community succession following the infusion of nutrients which accompanies upwelling in the SML period (Olivieri, 1997).

The observed 6 week lag between peak primary production and peak calycophoran abundance may be explained by linking the calycophoran life cycle within the sequence of community succession. The calycophoran life cycle alternates between large numbers of polygastric colonies (the stage studied here) and

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large numbers of reproductive eudoxids (Moore, 1949; Mackie *et al.*, 1987). Purcell found that eudoxids mature to release gametes only when they are able to feed (Purcell, 1982). It is likely that when the rocketship calycophorans of Monterey Bay encounter low food availability during the DML period of late fall and winter (Loeb *et al.*, 1983), the polygastric stage may not develop eudoxids until nutrient-rich upwelled waters rejuvenate the food supply in spring (SML). The peak 'in primary production from upwelling, and the subsequent rise in crustacean zooplankton, undoubtedly provide an increase in food for the overwintering poly-gastric stages. This would trigger eudoxid production and ripening, leading to peak numbers of colonies some 6 weeks after peak primary production.

As this study sampled at only one station, observed variations in siphonophore abundance may also be the result of advective processes in the Bay. Schlining (Schlining, 1998) proposed that *Nanomia bijuga* may be transported into the bay by the seasonal intrusion of equatorial waters (California Undercurrent). He found a strong correlation between peak numbers of *Nanomia* and peak in-trusion of the California Undercurrent (200 m deep). Lynn and Simpson (Lynn and Simpson, 1987) and Ramp *et al.* (Ramp *et al.*, 1997) indicate that deep circu-lation in Monterey Bay is tied to the seasonal intrusion of the California Under-current. However, Schlining's model was unable to account for the peak of *Nanomia* abundance at 400 m, which lies considerably below the depth of the California Undercurrent. As the bulk of the rocketship siphonophores examined in the present study also live below the depth of the California Undercurrent's intrusion into the Bay, Schlining's model may not apply. Further, the rocketship population peak occurs before the California Undercurrent Intrusion. A more complete understanding of deep circulation patterns in Monterey Bay is critical to an assessment of their role in the variable abundance of all mesopelagic zooplankton.

Diel vertical migration

It appears from the day–night comparison data (Figure 6) that the rocketship siphonophores aggregate at two separate levels in the water column, with evidence of moderate diurnal vertical migrations. This pattern may reflect the combined depth distributions and migratory movements of the two most commonly observed mesopelagic species in the bay: *Lensia conoidea* and *Chuni-phyes multidentata*. Although the vertical distribution ranges of the two most common species overlap, *L.conoidea* is found in shallow water (100–500 m), and *C.multidentata* is found deeper (400–1000+ m) (Alvariño, 1967; Pugh, 1984; J.M.B.Silguero, unpublished data).

Evidence from previous research supports this interpretation of our limited dataset. In a study of siphonophore populations in the northeast Atlantic, Pugh (Pugh, 1984) found evidence that rocketship siphonophores migrated vertically. His data for *C.multidentata* were somewhat equivocal, but data for the vertical migration of *L.conoidea* were strong. (Alvariño, 1967) found evidence of a small shift in the distribution of *L.conoidea* off San Diego, California (300–500 m daytime depth versus 250–500 m night-time depth). *Chuniphyes multidentata*

showed a larger nighttime shift in Alvariño's study of animals living at bathy-pelagic depths (1850–2350 m daytime versus 1450–1700 m night-time). As Alvar-iño did not sample between 525 m and 1340 m during the day (but did at night), it was not possible to determine whether the *C.multidentata* she found in this depth zone at night were migrators. It is useful to know that the population she observed was migrating at both shallow (400–500 m) and bathypelagic depths. Extrapolating from this information, it is possible that the animals we found between 500 and 1000 m were also migrators, as our data seem to indicate.

Correlation with Nanomia bijuga

Nanomia bijuga is also a small [up to 45 cm (Totton, 1965)], agile siphonophore which preys on small crustacean zooplankton (Robison *et al.*, 1998). *Nanomia* feed predominantly on euphausiids and copepods, while rocketship caly-cophorans eat mostly copepods [(Robison *et al.*, 1998; Purcell, 1997), respec-tively]. Copepods generally have rapid life cycles, some less than 30 days, with several generations in a single year (e.g. *Calanus pacificus*). Euphausiids have more complex and longer life cycles (e.g. *Euphausiia pacifica* has a generation time of a year) (Parsons *et al.*, 1984). *Nanomia bijuga* is the most abundant species of siphonophore in the bay and is typically an order of magnitude higher in abun-dance than the rocketship siphonophores at all depths where their distributions overlap. Its peak of abundance is about 6 weeks after that of the rocketships (Robison *et al.*, 1998). In this study, a negative correlation in the abundance of these two siphonophores was found. When *N.bijuga* numbers were high, rocket-ship numbers were low and vice versa. This pattern may reflect competitive exclu-sion, predation on the rocketship siphonophores by *Nanomia* (although we have never observed it) or interactions of each siphonophore with factors not measured in this study. The difference in population peaks of the rocketships and *N.bijuga* was probably linked to the life cycles of their principal prey. Further investigation is needed to fully understand the observed negative correlation.

The seasonal broadening of the vertical distribution of rocketship siphonophores in Monterey Bay was correlated with the high productivity of the spring and summer months, which is brought on by upwelling. During the DML period, when primary production was low, these siphonophores were found chiefly in the upper few hundred meters of their distribution range. When high productivity during the SML period increased food availability, the siphono-phores' vertical range expanded into deeper water. The peak of their abundance occurred on a time scale too short to be discerned by seasonal analysis, and only by examining the data in relation to primary productivity can their abundance changes be seen. Further investigation is needed to fully understand these patterns.

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