



## The impact of El Niño events on populations of mesopelagic hydromedusae

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### Abstract

For over 10 years, the midwater ecology group at MBARI has compiled video and accompanying physical data with the ROV *Ventana* operating in mesopelagic depths of Monterey Bay, CA in order to elucidate patterns in midwater ecology. Two El Niño events have occurred during this time period, in 1991–92 and in 1997–98. The oceanographic metric of spiciness combines temperature and salinity data into one sensitive measurement. Although temperature and salinity measurements alone revealed no clear patterns, clear signals of spiciness were observed that corresponded to water mass intrusions into the deep waters of the bay during the two El Niño events. During these events, some seldom-seen species were observed in high numbers in the midwater, while historically common species became rare. During non-El Niño years, the leptomedusa *Mitrocoma cellularia* (A. Agassiz, 1865) was common in the surface waters (0–50 m) of Monterey Bay, but it was not abundant at depth, while the trachymedusa *Colobonema sericeum* Vanhöffen, 1902 was found in relatively high numbers at mesopelagic depths. During the last two El Niño events, *M. cellularia* was observed in higher numbers at mesopelagic depths, whereas *C. sericeum* was scarce. *M. cellularia* was found in a wider range of temperatures, salinities, and dissolved oxygen values than was *C. sericeum*. Transport and tolerance hypotheses are proposed to explain differences in the presence and numerical density of the medusae.

### Introduction

El Niño events are associated with a variety of physical oceanographic phenomena that affect the distribution, abundance, growth and reproduction of marine organisms throughout the Pacific basin. It is now known that the El Niño-Southern Oscillation is the single most important factor in governing interannual oceanic variability on the sub-decadal to decadal time scale in the Pacific (Chavez, 1996; Chavez et al., 1999). This variability is often expressed off California as unusually warm surface ocean temperatures. The consequences of this mass transport of warm water are primarily a reduction of upwelling and a concomitant reduction in phytoplankton productivity (Glynn, 1988; Chavez, 1996).

During the 1997–98 El Niño, a weakening and reversal of trade winds preceded the generation of high temperature surface waters in the equatorial Pacific

(Chavez et al., 1999). One of the consequences of this warming was the cessation of equatorial upwelling. Normal upwelling did not recur until the trade winds abruptly returned in the eastern Pacific in mid-May of 1998, at which time the cold subsurface waters were upwelled to the surface (Chavez et al., 1999).

Pennington & Chavez (2000) present a long-term (1989–1996) characterization of the physical and biological (primary production) properties of Monterey Bay, California. Primary productivity in Monterey Bay during the 1991–92 El Niño showed a 25% decrease from the 1989 to 91 period (Lenarz et al., 1995). In addition, the beginning of the productive season was delayed by several months (Lenarz et al., 1995; Pennington & Chavez, 2000). This delay and reduction in primary productivity and the elevated temperatures caused substantial changes in local marine populations. Graham (1994) found that the scyphozoan *Chrysaora fuscescens* Brandt, 1835 in

Monterey Bay was several orders of magnitude less abundant during the 1991–92 El Niño event than in the preceding non-El Niño years. He suggested that *C. fuscescens* may have shifted north, although the data to support this contention was inconclusive.

El Niño events have also affected the distribution and abundance of fish throughout the Pacific (Barber & Chavez, 1983, 1986; Glynn, 1988; Bailey et al., 1995; Dorn, 1995; Hammann et al., 1995; Lenarz et al., 1995). The most widely discussed El Niño impact is the crash of the Peruvian anchovy, *Engraulis ringens*, once the world's largest fishery, with the 1972–73 and 1982–83 El Niño events (Barber & Chavez, 1983, 1986; Glynn, 1988). In addition to those on fishes, there are well documented studies of the effects of El Niño on surface-dwelling populations of marine reptiles, birds, and mammals (Barber & Chavez, 1983; Gibbs & Grant, 1987; Glynn, 1988; Laurie, 1990; Ainley et al., 1995; Culik & Luna-Jorquera, 1997).

The effects of El Niño events on mesopelagic communities are not understood, however, recent studies have shown that the surface waters and the mesopelagic community are inextricably linked. Robison et al. (1998) and Silguero & Robison (2000) have shown that the physonect siphonophore, *Nanomia bijuga*, and calycophoran siphonophores have seasonal cycles that are significantly correlated with both the onset of upwelling in the surface waters, and with peaks in primary production. *N. bijuga*'s seasonal peaks were found to follow the peak chlorophyll values by a 3–4 month lag, while the calycophoran siphonophores lagged by 1–2 months. The dominant prey of *N. bijuga* were euphausiid krill, which were able to feed directly on the phytoplankton. This short, trophic link between the surface waters and the mesopelagic gelatinous community shows that physical changes in the epipelagic waters can have a direct and dramatic impact on the organisms of the mesopelagic.

Many of the dominant macroscopic organisms in the mesopelagic depths of Monterey Bay are cnidarians (Widder et al., 1989; Raskoff, 1998; Robison et al., 1998; Silguero & Robison, 2000). Hydromedusae are often the most abundant organism in the lower mesopelagic depths, especially in low oxygen regions (Purcell et al., 2001). Medusae typically occupy high trophic positions, which are normally thought of as dominated by fish (Mills, 1995), and thereby play an important role in the overall cycling of nutrients in the deepsea.

*Mitrocoma cellularia* is a hydromedusa (Lepidomedusae: Mitrocomidae) found from the Bering

Sea to southern California (Kramp, 1968; Arai & Brinkmann-Voss, 1980). It reaches a maximum diameter of 100 mm and has over 300 fine tentacles. In Friday Harbor, Washington it is found seasonally from April–November (Arai & Brinkmann-Voss, 1980; Mills, 1983, 1993). In Monterey Bay, *M. cellularia* is a common member of the epipelagic gelatinous community (surface to 100 m) from fall to early-spring (Wrobel & Mills, 1998), but it can be found in low numbers at other times of the year (Raskoff, pers. obs.). *Colobonema sericeum* is a hydromedusa (Trachymedusae: Rhopalonematidae) found in the mesopelagic depths of the Pacific, Atlantic and Indian Oceans (Kramp, 1968; Wrobel & Mills, 1998). Its bell diameter reaches 45 mm and it has 32 thick tentacles.

This study focused on two important medusae in the mesopelagic gelatinous community of Monterey Bay, California. Observations were made with the Monterey Bay Aquarium Research Institute's (MBARI) remotely operated vehicle (ROV) over a 9 year time period (1990 through 1998). Temperature, salinity and dissolved oxygen measurements taken in tandem with the video observations have permitted physical characterization of the midwater habitat. The ROV observations overlapped the El Niño events of 1991–92 and 1997–98. The resultant MBARI video database has permitted evaluation of patterns of abundance of midwater medusae as they relate to El Niño events.

## Materials and methods

### Midwater study site

The MBARI midwater time-series site (MWTS) is located at 36° 42' 00" N – 122° 02' 00" W, at the mouth of Monterey Bay (Robison et al. 1998). This site lies over the meandering axis of the Monterey Submarine Canyon in 1600 m of water. This location allows access to deepwater, as it enters the bay, yet permits transport of organisms back to the laboratory within 1.5 h. The canyon head is at Moss Landing, and the canyon stretches west southwest through the bay to join the continental rise at 3000 m, roughly 80 km off shore. The deep water currents of Monterey Bay are not well understood. The flow is thought to be primarily up-canyon at the mesopelagic depths, with across canyon currents with differing directions depending on depth (Breaker & Broenkow, 1994). The MWTS site

was sampled with a ROV twice a month, on average, from 1989 to the present. Data for this study are from 1990 to 1998.

#### *Remotely Operated Vehicle (ROV) data and spiciness*

The R/V *Point Lobos* and the ROV *Ventana* have been in operation at MBARI since 1988. Since that time, an active research program on the ecology of the mesopelagic zone (100–1000 m in depth) has been underway at the MWTS site. The *Ventana* has completed over 290 mesopelagic dives at this MBARI midwater site, making it the most visited location in the world for mesopelagic studies. The sub is an ISE Hysub 40 with a variety of sensors and modifications added for midwater research (Robison, 1993). A Falmouth Scientific, Inc. Micro-CTD (conductivity, temperature and depth) sensor and a Sea-Bird Electronics SBE 13 dissolved oxygen (DO) sensor with Beckman oxygen electrode, recorded data every 4 s. The data were then automatically averaged and logged into the database in 15 s intervals. CTD-DO data were collected starting at the end of 1990, therefore only data from 1991 to 1998 are presented. The ROV dove no deeper than 400–500 m until the middle of 1991, at which point it began regular dives to 1000 m. Secondary processing of the CTD data determined that the information from June, 1995 to June, 1996 were erroneous and those data were excluded from analysis.

Individual plots of temperature and salinity data were insufficient to detect differences in water masses brought into Monterey Bay by El Niño events at mesopelagic depths (Raskoff, unpubl. data). It was necessary to look at an oceanographic metric that was more sensitive to changes in water masses than either temperature or salinity individually. The dynamic interaction of temperature and salinity can be described by the calculation of a metric called spiciness (Flament, 1986; Lynn et al., 1995). This metric has been used in the past to identify water mass intrusions and the onset of El Niño events (Lynn et al., 1995). Warm, salty water has a high spiciness, while cold, fresh water has a low spiciness (Jackett & McDougall, 1985; Flament, 1986; Lynn et al., 1995; Ramp et al., 1997; Schlining, 1999; Schmitt, 1999). Spiciness calculations were created from ROV CTD data from the dives at the MWTS site between 1990 and 1998 (excluding June 1995–June 1996). Missing data are shown in Figure 1 as blank areas. Twenty meter depth strata were binned and averaged over weekly intervals. From this, an average CTD profile was created by averaging all

the binned depth strata over the 9 years. From this average profile, anomalies of spiciness, in terms of standard deviations from the mean, were calculated and plotted onto a contour graph. Spiciness anomalies were used to elucidate the very subtle differences found in water masses at these mesopelagic depths. The calculations and graphing of spiciness were performed in Matlab (MathWorks, Inc., Version 5.3) and are based on the algorithms of Flament (1986) as modified and programmed by Schlining (1999). Contours of spiciness were gridded using the Kriging method (Keckler, 1995).

BetaCam video tapes were annotated by the MBARI video lab staff and all resulting records of organisms were placed into a database. Individual annotations were linked to their corresponding CTD-DO data by timecode. The database was queried for organisms of interest and the resulting numbers were normalized to a proxy of abundance, number observed  $h^{-1}$ . Normalization was accomplished by dividing the number of organisms observed in a particular parcel of water by the amount of time the ROV spent in that same parcel. Data were then binned into 100 m depth strata by month, for the 9 years of the study (1990–1998). Contour plots of medusae vertical distributions (Fig. 2) were constructed for analysis with the inverse distance gridding method (SPSS Inc., 1998).

The CTD-DO data associated with the individual organisms of interest were culled from the data base. The organism-based temperature ( $^{\circ}C$ ), salinity, and dissolved oxygen ( $ml\ l^{-1}$ ) bubble plots (Fig. 3) were created from weekly averaged data over the 9-year time period. This provides a descriptive way of depicting the physical parameters of the water in which the organisms were found. In addition, the values for each species were compared statistically to test for differences in the means with the nonparametric Mann–Whitney  $U$  two-sample test. These nonparametric tests were used because of the data's violation of parametric tests requirement of equal variances (Zar, 1996).

## **Results**

### *ROV CTD data*

Contours of spiciness anomalies for the MWTS site over the 9-year period showed rapid and marked changes in the waters of the mesopelagic depths when warm, salty waters were brought into the bay during

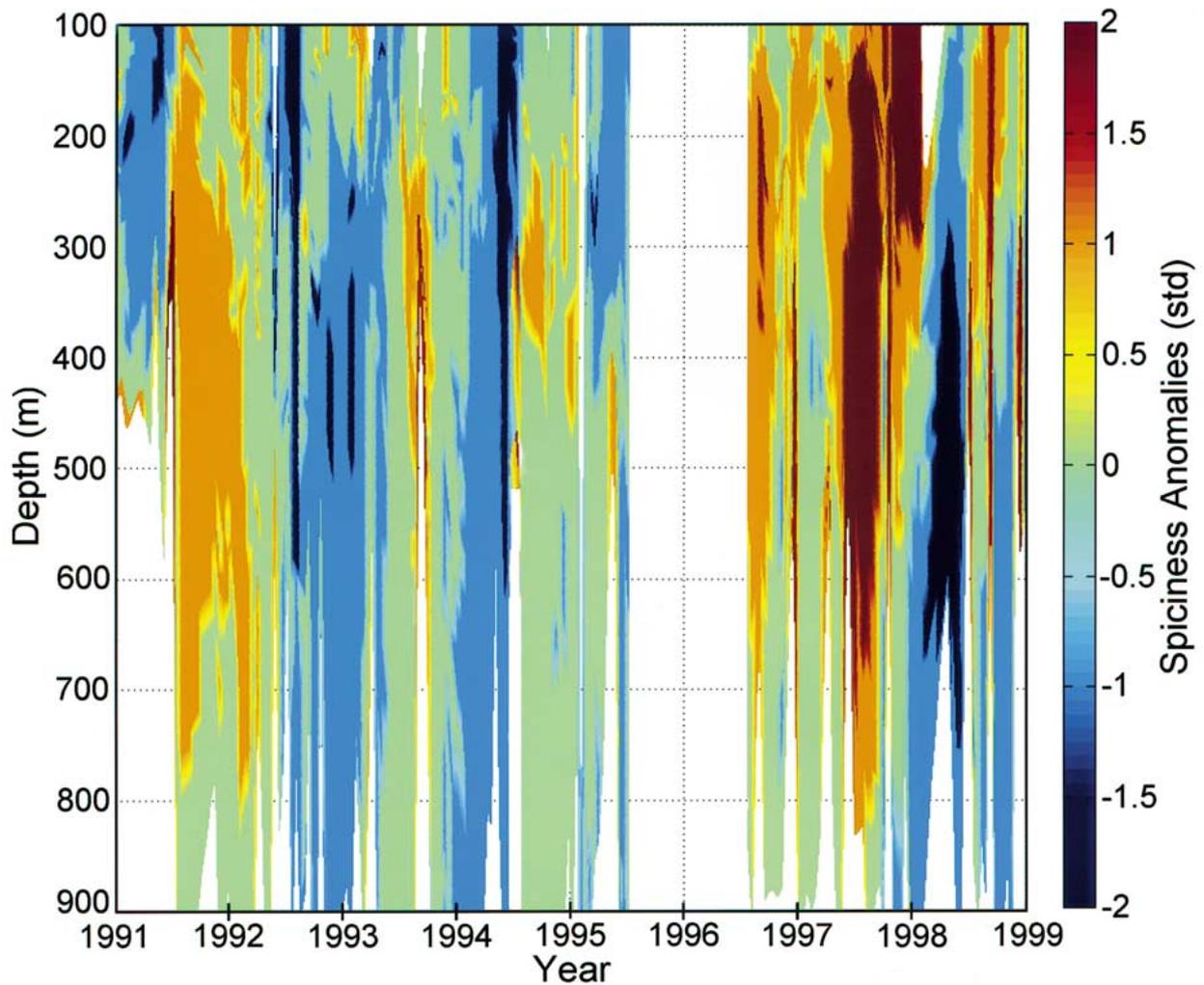


Figure 1. Contour of spiciness anomalies for the MWTS site in Monterey Bay, California from 1991–1998. Contours are spiciness anomalies in standard deviations from the mean (see text for details). Red/Orange areas are high in spiciness, blue areas are low.

the two El Niño events, as indicated by the orange/red coloration in Figure 1. Although consistent data collection was not deeper than 400–500 m from January, 1990 to June, 1991, the onset of the 1991–92 El Niño in June/July, 1991 apparently was captured with the ROV's CTD. The near instantaneous onset of the spiciness signal is observed from the surface waters down to 800 m in the middle of 1991. The collapse of the spiciness signal showed a gradual decline in spice in the surface waters down to 300 m over a 3 month period from October to December, 1991. During this time, there were still high spice waters in the 300–600 m depth range, which finally left abruptly in February, 1992. The overall magnitude of the 1991–92 El Niño was moderate as determined by the

spiciness anomalies (averaged 1.0 standard deviation (SD) from the mean). The years following the 1991–92 El Niño were marked with a fairly regular pattern of elevated spiciness from July to October. These results correspond to those found by Schlining (1999), who observed that these elevations were the signature of the California Undercurrent, which seasonally runs up the coast. An unusually strong undercurrent signal was seen at the end of 1996, but missing data in the CTD record for the beginning of that year make interpretation difficult.

The onset of the 1997–98 El Niño was observed in the midwaters in June, 1997. This strongly positive anomaly signal was found from near-surface waters down to 800 m and was nearly twice as strong as the

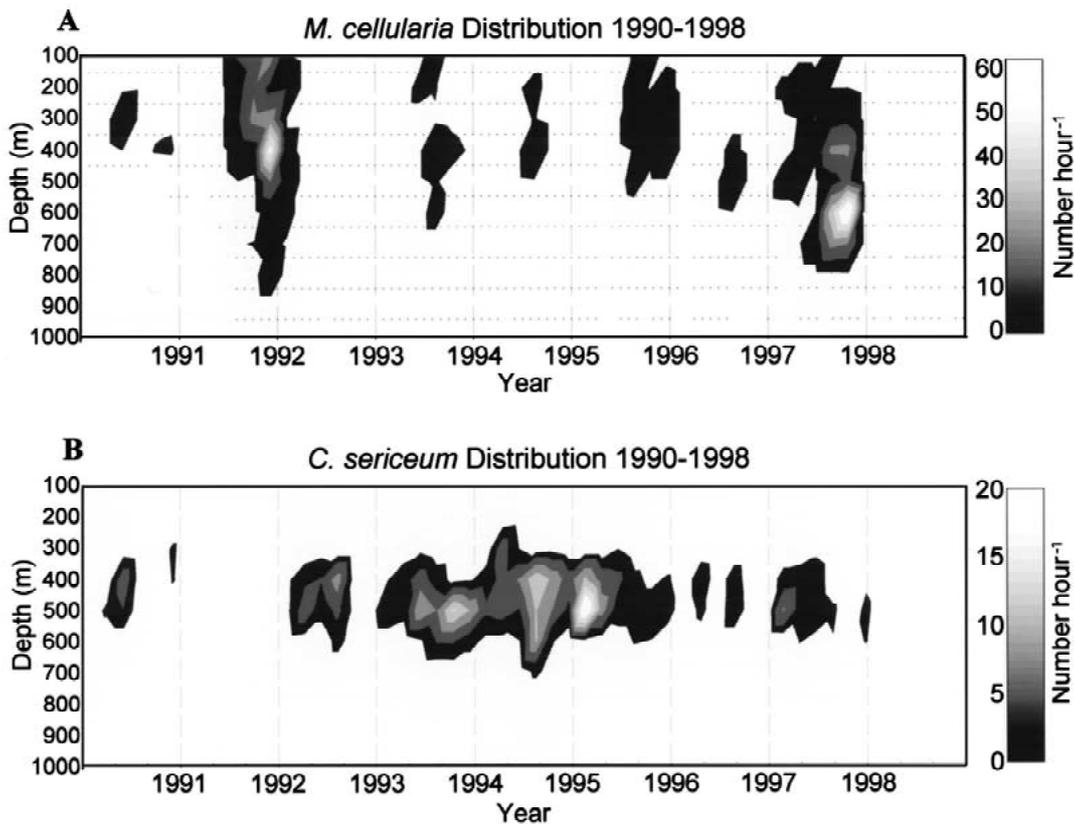


Figure 2. Vertical distribution and abundance of *Mitrocoma cellularia* (A) and *Colobonema sericeum* (B) from 1990 to 1998 in Monterey Bay, California. Abundance axes (number h<sup>-1</sup>) are scaled differently for each species. Dots in plot A show sampling opportunities by the ROV.

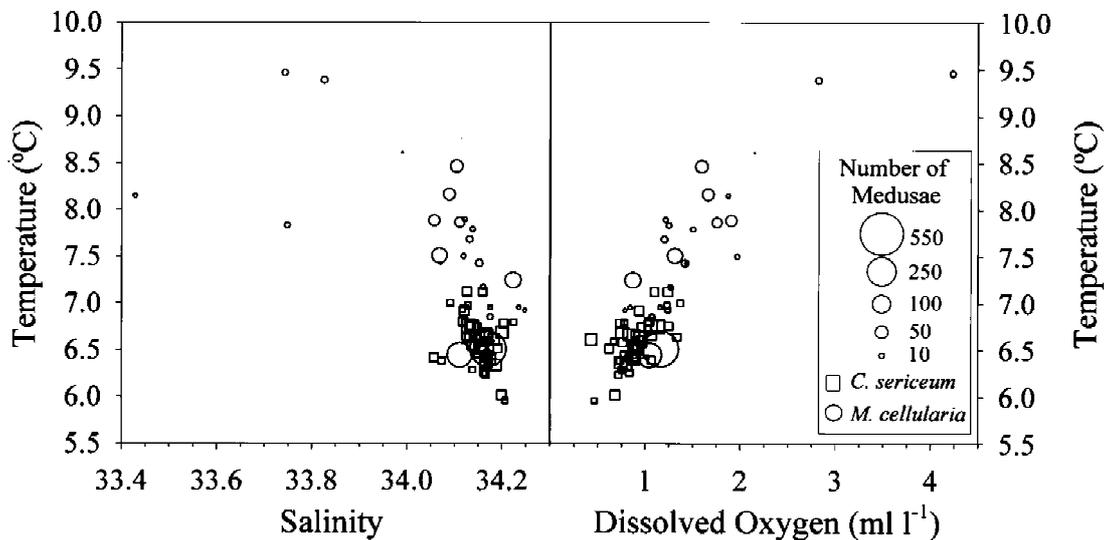


Figure 3. Temperature, salinity and dissolved oxygen plots for *Mitrocoma cellularia* and *Colobonema sericeum* in Monterey Bay, California from 1991 to 1998. Bubble plots show the number of medusae observed in waters with listed physical characteristics.

1991–92 El Niño (average of 2.0 SD from the mean). Like the 1991–92 El Niño, the 1997–98 signal had a rapid onset. The decline of the 1997–98 signal was, however, much different than in the previous El Niño. Whereas in 1991–92, the deep mesopelagic waters were the last to recede back to normal spiciness values, in 1997–98 they were the first to fall. There was a gradual decline in spiciness from October, 1997 to January, 1998. Unlike the 1991–92 El Niño, the 1997–98 El Niño was followed not by a period of average spiciness, but by a very strong negative spiciness signal (dark blue), which could be indicative of a major upwelling event.

#### *Mitrocoma cellularia* distribution

The population of *Mitrocoma cellularia* experienced a pronounced increase (Fig. 2A) that coincided with the El Niño signatures found in the ROV CTD physical data (Fig. 1). Both the onsets of the population increase and the elevated spiciness signal from the 1991 to 92 El Niño were first observed in June/July, 1991. Medusa abundance decreased in February of 1992. The high spiciness signals also began to decrease at this same time. High medusa abundance in 1992 reached from the surface waters down to >500 m, with a peak abundance of 36 ind. h<sup>-1</sup>, centered at 300–400 m in November, 1991. From 1992 to 97, there were low numbers of *M. cellularia* in the midwaters, with a few medusae appearing in summer/fall. High abundance of medusae recurred in June/July, 1997 (Fig. 2A) at the same time that the spiciness signal from the 1997 to 98 El Niño was also first observed. Medusa abundance declined in November. In 1997–98, the *M. cellularia* population was abundant from the surface waters down to 900 m, with peak abundance in October, 1997 of 52 ind. h<sup>-1</sup>, centered at 600–700 m. The decrease of medusae in 1997 was correlated with the spiciness decrease, as it was in 1991–92. Although the onset of the *M. cellularia* blooms in the bay closely matched the onset of the spiciness signals, the peaks in abundance for both the 1991–92 and 1997–98 blooms did not correspond to the beginning of the spice signal but instead they followed the onset of the spice signal by several months.

#### *Colobonema sericeum* distribution

The vertical distribution of *Colobonema sericeum* was very different from that found for *M. cellularia*. *C. sericeum*'s vertical distribution (Fig. 2B) appeared to

be inversely related to high spice events (Fig. 1). In years with a high spiciness signal, 1991–92 and 1997–98, *C. sericeum* were scarce, whereas during the years in-between these El Niño events *C. sericeum* were abundant. March/April, 1993 began a 3-year period of relatively high abundance. Peaks in abundance were observed from September to November in both 1993 and in 1994, while 1995 showed an early peak in February, with over 20 medusae observed h<sup>-1</sup>. By July, 1995 the numbers of *C. sericeum* had dropped to more typical levels. With the onset of the 1997–98 El Niño, *C. sericeum* populations dropped to very low levels in the mesopelagic waters of the bay. Over the entire nine years of the study, the depth range of *C. sericeum* varied little, with the population centered around 400–500 m.

#### Organismal T-S-DO plots

Analysis of temperature, salinity and dissolved oxygen (T-S-DO) plots provide information on the physical parameters of the water mass in which the medusae are associated (Fig. 3). The axis scales represent the minimum and maximum values the medusae are subject to in their natural environment.

The T-S-DO bounding values for *M. cellularia* were: temperature, 4.21–14.09 °C (mean = 7.36, SD = 1.69); salinity, 32.39–34.70 (mean = 34.09, SD = 0.23); dissolved oxygen, 0.30–6.75 ml l<sup>-1</sup> (mean = 1.55, SD = 1.23). The bounding values for *C. sericeum* were: temperature, 3.78–7.64 °C (mean = 6.49, SD = 0.57); salinity, 34.16–34.78 (mean = 34.16, SD = 0.09); dissolved oxygen, 0.07–3.42 ml l<sup>-1</sup> (mean = 0.90, SD = 0.43). Thus *M. cellularia* was found to occupy a wide range of temperature and dissolved oxygen values. Conversely, *C. sericeum* was found in a narrow range of temperature and dissolved oxygen values. The temperature, salinity and dissolved oxygen values found with the two medusae were compared with a Mann–Whitney *U* test to examine the hypothesis that the means were equal for both species. The resulting *P* values: temperature (°C) was found to be significantly different (*P* < 0.001), salinity was not found to be different (*P* = 0.239), and dissolved oxygen (ml l<sup>-1</sup>) was found to be significantly different (*P* < 0.001). The standard deviations of the three physical parameters were consistently much greater for *M. cellularia* than for *C. sericeum*. In summary, *M. cellularia* could be found in waters almost twice as warm, of lower salinity, and with twice the dissolved oxygen than *C. sericeum*.

## Discussion

CTD data recorded from nine years of ROV dives at the MWTS site were used to characterize the mesopelagic environment of Monterey Bay. These data, when examined with the sensitive calculation of spiciness, permit visualization of the El Niño water masses as these enter the bay (Fig. 1). The quick onset of both the 1991–92 and 1997–98 El Niños was observed. In addition to the quick onset, spice signals were found down to depths of 800 m and these signals persisted for many months. Further analysis is needed to determine the origin of these intruding water masses, as high-spiciness water masses could have been transported northward from off southern California or could represent an on-shore transport of waters residing initially far off the coast of central California. A similar temperature signal was observed down to 200 m (the limit of the sensors) from mooring data during the 1991–92 El Niño (Pennington & Chavez, 2000). These results show that the spiciness metric can be of great value in finding and visualizing subtle changes in water masses, which can be biologically important.

Patterns of change in the vertical distribution and abundance of both species are associated, both directly and inversely, with the two El Niño events measured (Fig. 2). *Mitrocoma cellularia* vertical distribution and abundance closely mirrored the spiciness signals of the two El Niño events (Fig. 2A). In both 1991–92 and 1997–98 the *M. cellularia* population had a sudden increase in numbers as well as a widening of depth range. During the El Niño events, the depth range of the population extended from the surface waters down to 800 m. Conversely, *Colobonema sericeum* vertical distribution and abundance were inversely related to the El Niño events (Fig. 2B). During the two El Niño events, *C. sericeum* vertical abundance dropped to very low levels. In the years between the two events, *C. sericeum* was found in high numbers.

A comparison of the physical properties of the water in which the two medusae were found was performed to ascertain the possibility of physiological differences which might lead to the differing responses to the El Niño events. The ROV CTD-DO measurements which corresponded with the individual medusae observed were used to construct T-S-DO bubble plots of abundance related to the various physical parameters. *M. cellularia* showed a much wider tolerance for temperature, salinity and dissolved oxygen ranges than did *C. sericeum* (Fig. 3). Although the means for the three parameters were similar between the two

medusae, the amount of variation exhibited by *M. cellularia* proved to be large enough for temperature and dissolved oxygen to be significantly different from each other. *M. cellularia* was found over a much wider range of physical values than *C. sericeum*. A large part of this variation was due to the fact that *M. cellularia* was found over a wider range of depths (surface to 900 m) compared with *C. sericeum* (200–700 m). These results indicate there may be distinct physiological differences in the two medusae with respect to their preferred habitat and their tolerance of changing water properties.

A number of hypotheses for the different distribution patterns of the two medusae can be considered. The first, a tolerance hypothesis, supposes that the medusae are limited by their physiological tolerance to various physical parameters. This premise has some support from the T-S-DO plots. *C. sericeum* occurred within a much narrower range of salinity, temperature and dissolved oxygen values than did *M. cellularia*. *M. cellularia* was not found in the midwaters of Monterey Bay all year long, yet its observed T-S-DO ranges should allow it to effectively live in the deep waters of the bay nearly year-round. It is not known what affect changes in T, S and DO would have on the reproduction and survivability of these species. Experimental data are needed to assess the relative importance of each of these factors.

Other researchers have found that variation in physical parameters can have a pronounced effect on the reproductive success of jellyfish. Purcell et al. (1999) found that changes in temperature and salinity had significant affects on ephyra and polyp production in the scyphozoan *Chrysaora quinquecirrha*. Increasing temperature, in combination with high salinity, provided for increased ephyra production, while decreasing temperature delayed the strobilation event. Salinity was also important, with more ephyra and polyps produced at intermediate salinities than at the low or high end. Dawson et al. (2001) found that high temperatures associated with the 1997–98 El Niño caused a prolonged crash of the rhizostome *Mastigias* sp. in the marine “Jellyfish Lake” of Palau. Both reproduction and survivability of the medusae and the scyphistomae decreased dramatically, partly due to bleaching of the zooxanthellae in the polyps. Only after the waters started to cool down did the population start to rebound.

A second possible explanation for the differences in patterns of abundance is related to transport, with medusae carried into or out of the bay with

the intruding water masses, as was suggested for the scyphomedusa *Chrysaora fuscescens* during the 1991–92 El Niño (Graham, 1994). In both 1991–92 and 1997–98 El Niños, the *M. cellularia* bloom onset corresponded with the beginning of the spice signal (intrusion event), however peaks of abundance were not observed for several months thereafter. This delay could be explained if the jellies were advected and then reproduce locally in the months following their arrival in the bay. *M. cellularia* is a medusa with a benthic polyp stage which could settle from free-spawned eggs and sperm and reproduce additional medusae asexually within the 3–4 month period. Alternatively, the medusae could have been produced from resident polyps in the bay, which responded to the physical changes in the water by increasing medusa production, as was found for *C. quinquecirrha* (Purcell et al., 1999). Barring a detectable genetic signature which could delineate between *M. cellularia* of southern or local origin, these two possibilities would be very difficult to separate. The transport hypothesis also best explains the *C. sericeum* data reported in this study. These populations declined during the El Niño events, but that may simply represent a northward transport of medusae.

There are also potentially significant life cycle differences between these two medusae. *C. sericeum* exhibits holoplanktonic, direct development, while *M. cellularia* has a benthic polyp form in its life cycle. Little is known about reproduction and development time in *C. sericeum*. Without a resident benthic polyp stage, it may be that it would take *C. sericeum* longer to re-colonize the bay if the population was advected away, regardless of how quickly this holoplanktonic species can reproduce. Whereas the benthic reservoir of *M. cellularia* polyps might enable this species to not only remain in the area, but react quickly to advantageous environmental change. More research is needed to understand the importance of life cycles in relation to population fluctuations.

Although the reasons for these different patterns of distribution are not well understood, it is clear that there are pronounced differences in the gelatinous community with respect to episodic events such as El Niño. More *in situ* research must be done, at even greater depths, if we are to fully understand the link between large scale oceanic and atmospheric events and the ecology of deep sea organisms.

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## References

- Ainley, D. G., R. L. Veit, S. G. Allen, L. B. Spear & P. Pyle, 1995. Variations in marine bird communities of the California Current, 1986–1994. CALCOFI Rep. 36: 72–77.
- Arai, M. N. & A. Brinckmann-Voss, 1980. Hydromedusae of British Columbia and Puget Sound. Can. Bull. Fish. aquat. Sci. 204: 1–192.
- Bailey, K. M., J. F. Piatt, T. C. Royer, S. A. Macklin, R. K. Reed, M. Shima, R. C. Francis, A. B. Hollowed, D. A. Somerton, R. D. Brodeur, W. J. Ingraham, P. J. Anderson & W. S. Wooster, 1995. ENSO events in the northern Gulf of Alaska, and effects on selected marine fisheries. CALCOFI Rep. 36: 78–96.
- Barber, R. T. & F. P. Chavez, 1983. Biological consequences of El Niño. Science 222: 1203–1210.
- Barber, R. T. & F. P. Chavez, 1986. Ocean variability in relation to living resources during the 1982–83 El Niño. Nature 319: 279–285.
- Breaker, L. C. & W. W. Broenkow, 1994. The circulation of Monterey Bay and related processes. Oceanogr. mar. Biol. 32: 1–64.
- Chavez, F. P., 1996. Forcing and biological impacts of onset of the 1992 El Niño in central California. Geo. Phys. Res. Let. 23: 265–268.
- Chavez, F. P., P. G. Strutton, G. E. Friederich, R. A. Feely, G. C. Feldman, D. G. Foley & M. J. McPhaden, 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997–98 El Niño. Science 286: 2126–2131.
- Culik, B. M. & G. Luna-Jorquera, 1997. Satellite tracking of Humboldt penguins (*Spheniscus humboldti*) in northern Chile. Mar. Biol. 128: 547–556.
- Dawson, M. N., L. E. Martin & L. K. Penland, 2001. Jellyfish swarms, tourists and the Christ-child. Hydrobiologia 451 (Dev. Hydrobiol. 155): 131–144.
- Dorn, M. W., 1995. The effects of age composition and oceanographic conditions on the annual migration of Pacific whiting, *Merluccius productus*. CALCOFI Rep. 36: 97–105.

- Flament, P., 1986. Subduction and fine structure associated with upwelling filaments. Ph.D. dissertation, University of California, San Diego.
- Gibbs, H. L. & P. R. Grant, 1987. Ecological consequences of an exceptionally strong El Niño event on Darwin's finches. *Ecology* 68: 1735–1746.
- Glynn, P. W., 1988. El Niño-Southern Oscillation 1982–1983: nearshore population, community and ecosystem responses. *Ann. Rev. Ecol. Syst.* 19: 309–345.
- Graham, W. M., 1994. The physical oceanography and ecology of upwelling shadows. Ph.D. dissertation, University of California, Santa Cruz.
- Hammann, M. G., J. S. P. Nayar & O. S. Nishizaki, 1995. The effects of the 1992 El Niño on the fisheries of Baja California, Mexico. *CALCOFI Rep.* 36: 127–133.
- Jackett, D. R. & T. J. McDougall, 1985. An oceanographic variable for the characterization of intrusions and water masses. *Deep Sea Res.* 32: 1195–1207.
- Keckler, D., 1995. *Surfer for Windows, Version 6 User's Guide*. Golden Software, Inc., Golden, CO, 480 p.
- Kramp, P. L., 1968. The hydromedusae of the Pacific and Indian Oceans. Sect. II and III. Dana-Rep. Carlsberg Found. 72: 1–200.
- Laurie, W. A., 1990. Population biology of marine iguanas (*Amblyrhynchus cristatus*). I. Changes in fecundity related to a population crash. *J. anim. Ecol.* 59: 515–528.
- Lenarz, W. H., F. B. Schwing, D. A. Ventresca, F. Chavez & W. M. Graham, 1995. Explorations of El Niño events and associated biological population dynamics off central California. *CALCOFI Rep.* 36: 106–119.
- Lynn, R. J., F. B. Schwing & T. L. Hayward, 1995. The effect of the 1991–1993 ENSO on the California current system. *CALCOFI Rep.* 36: 57–71.
- Mills, C. E., 1983. Vertical migration and diel activity patterns of hydromedusae: studies in a large tank. *J. Plankton Res.* 5: 619–635.
- Mills, C. E., 1993. Natural mortality in NE Pacific coastal hydromedusae: Grazing predation, wound healing and senescence. *Bull. mar. Sci.* 53: 194–203.
- Mills, C. E., 1995. Medusae, siphonophores and ctenophores as planktivorous predators in changing global ecosystems. *ICES J. mar. Sci.* 52: 575–581.
- Pennington, J. T. & F. P. Chavez, 2000. Seasonal fluctuations of temperature, salinity, nitrate, chlorophyll and primary production at station H3/M1 over 1989–1996 in Monterey Bay, California. *Deep Sea Res.* II 47: 947–973.
- Purcell, J. E., J. R. White, D. A. Nemazie & D. A. Wright, 1999. Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. *Mar. Ecol. Prog. Ser.* 180: 187–196.
- Purcell, J. E., D. L. Breitburg, M. B. Decker, W. M. Graham, M. J. Youngbluth & K. A. Raskoff, 2001. Pelagic cnidarians and ctenophores in low dissolved oxygen environments. In Rabalais, N. N. & R. E. Turner (eds), *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*. American Geophysical Union. Coastal and Estuar. Stud. 58: 77–100.
- Ramp, S. R., J. L. McClean, C. A. Collins & A. J. Semtner, 1997. Observations and modeling of the 1991–1992 El Niño signal off central California. *J. Geophys. Res.* 102: 5553–5582.
- Raskoff, K. A., 1998. Distributions and trophic interactions of mesopelagic hydromedusae in Monterey Bay, CA: *In situ* studies with the MBARI ROVs *Ventana* and *Tiburón*. *Ocean Sciences - San Diego, CA. Eos, Transactions, American Geophysical Union.* (abstracts) 79: OS1.
- Robison, B. H., 1993. Midwater research methods with MBARI's ROV. *Mar. Tech. Soc. Jour.* 26: 32–39.
- Robison, B. H., K. R. Reisenbichler, R. E. Sherlock, J. M. B. Silguero & F. P. Chavez, 1998. Seasonal abundance of the siphonophore, *Nanomia bijuga*, in Monterey Bay. *Deep Sea Res.* II 45: 1741–1751.
- Schlining, B., 1999. Seasonal intrusions of equatorial waters in Monterey Bay and their effects on mesopelagic animal distributions. Masters thesis, Moss Landing Marine Laboratories.
- Schmitt, R. W., 1999. Spice and the demon. *Science* 283: 498–499.
- Silguero, J. M. B. & B. H. Robison, 2000. Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. *J. Plankton Res.* 22: 1139–1153.
- SPSS, Inc., 1998. *SigmaPlot 5.0 User's Guide*. SPSS Science Marketing Department, Chicago, IL, 448 p.
- Widder, E. A., S. A. Bernstein, D. F. Bracher, J. F. Case, K. R. Reisenbichler, J. J. Torres & B. H. Robison, 1989. Bioluminescence in the Monterey Submarine canyon: image analysis of video recordings from a mid-water submersible. *Mar. Biol.* 100: 541–551.
- Wrobel, D. & C. Mills, 1998. *Pacific Coast Pelagic Invertebrates: a Guide to the Common Gelatinous Animals*. Sea Challengers/Monterey bay Aquarium, Monterey, 108 pp.
- Zar, J. H., 1996. *Biostatistical Analysis*. Simon and Schuster, Upper Saddle River, 662 pp.