

Hydromedusa blooms and upwelling events in the Bay of Panama, Tropical East Pacific

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Seasonal upwelling events dominate the coastal areas of some regions of the Tropical East Pacific. The effects of upwelling on gelatinous zooplankton are largely unknown and undocumented for this or any region, although upwelling is known to shape phytoplankton dynamics. Small hydromedusae, the most widespread and diverse representatives of gelatinous plankton, are often neglected in plankton ecology as they are inconspicuous and escape direct observation. Their occurrence is seasonal and standard plankton sampling techniques easily overlook their blooms. In order to investigate whether upwelling affects hydromedusae dynamics, we monitored their abundance and diversity in the Bay of Panama, a region on the Pacific Coast of Panama characterized by seasonal upwelling events. Our results show that, although the number of species is relatively constant throughout the year, hydromedusa abundance in the Bay of Panama can be up to two orders of magnitude higher during upwelling than non-upwelling conditions. The difference in the numbers of hydromedusae between the two seasons is mostly due to temporally short medusa blooms that occur only during the upwelling season. Our results point to a link between hydromedusa blooms and upwelling events, and the increased productivity associated with them. The results are consistent with a scenario in which upwelling events act on the benthic colonies thus inducing medusa production.

INTRODUCTION

Upwelling is one of the most important processes in coastal regions. It sustains high phytoplankton production that propagates up the food chain, thus supporting rich coastal marine ecosystems and some of the most productive fisheries in the world (Pauly and Christensen, 1995). Upwelling events occur on the Eastern sides of major oceans, and the Bay of Panama, a shallow wide-mouth bay located on the Pacific coast of Panama, is a regional center of upwelling. The Bay is characterized by strong upwelling in the dry season from January to April, when the displacement of the surface water mass by northern winds induces the rise of cold, deep and nutrient-rich water that fertilizes the

euphotic zone (Forsberg, 1963; 1969; D’Croz *et al.*, 1991; D’Croz and Robertson, 1997). During the wet season, from May to December, there is no upwelling and this season is characterized by warm, low salinity, nutrient-poor water (Fleming, 1939; Schaefer *et al.*, 1958; D’Croz *et al.*, 1991). Although it is known, both in the Bay of Panama (Forsberg, 1963; 1969; D’Croz *et al.*, 1991) and elsewhere (Anderson, 1964; Hecky and Kilham, 1988), that upwelling events shape the phytoplankton community, influencing ecosystem productivity, their effect on gelatinous zooplankton, and especially on medusa blooms, is still mostly unexplored.

Gelatinous zooplankton represents one of the driving forces of the marine ecosystem. Its components, salps, medusae and ctenophores, undergo seasonal pulses in

response to favorable conditions and rapidly produce biomass that sustains the marine food chain (Boero *et al.*, 2008). Since gelatinous zooplankton is mainly composed of top predators that feed on a variety prey, relying mostly on larvae from copepods to fish, these pulses can have important top-down impacts on the entire marine community. Medusae (jellyfish) of the orders Scyphozoa, Cubozoa and Hydrozoa represents one main component of gelatinous zooplankton and their blooms are important events controlling plankton dynamics in coastal waters worldwide (Decker *et al.*, 2007). Although generally neglected in the literature (Lynam *et al.*, 2005a, b), they have a significant predatory impact on fish populations (and thus on fishery industries), both via predation and competition (Purcell, 1994a, b; Purcell and Arai, 2001; Purcell, 2003; see also Brodeur *et al.*, 2002; Volovik, 2004 for ctenophores).

Despite this ecological and economic importance, the factors that cause population fluctuations of gelatinous zooplankton are not well understood, and blooms are mostly unpredictable (but see Decker *et al.*, 2007). This lack of knowledge is mainly due to the intrinsic difficulties of studying organisms that occur in temporally and spatially restricted peaks of abundance (CIESM, 2001; Kawahara *et al.*, 2006). Even more difficult is the study of the most abundant but least noticeable component of gelatinous zooplankton, the Hydromedusae (order Hydrozoa). These tiny medusae are usually overlooked in plankton ecology because they escape direct observation and standard plankton sampling techniques cannot detect their blooms (Boero *et al.*, 2008). Moreover, species-level identification is difficult and requires extensive taxonomic knowledge of the group, which contains 842 species in 222 described genera (Bouillon and Boero, 2000). Correct identification also relies on live adult specimens, as juvenile medusae of different species, or even genera, can look remarkably alike and often lack diagnostic features (Boero and Bouillon, 1987).

The population dynamics of hydromedusae in tropical regions are poorly known and the effect of upwelling on medusa production by the colonial polyps has not been examined. We monitored the hydromedusae in the Panama Bay during 2006 in order to document seasonal changes in abundance and diversity and to ultimately understand the effect of upwelling on their population dynamics.

METHODS

Medusa collection

Medusae were collected using a 153 μm plankton net, 45 cm long and with a 12.7 cm mouth.

The small size of the plankton net, and the collecting bottle attached to the net, allowed for the collection of delicate hydromedusae without damaging them. Plankton tows were conducted within a holding pool (9 m \times 3 m) at the Smithsonian Tropical Research Institute's (STRI's) Naos Laboratory (8°55'N, 79°32'W) (Fig. 1). The pool receives unfiltered water from the Bay of Panama (located just few meters away from the laboratory and from the pool itself) through a pump (7.6 cm in diameter) at a speed of 65/70 gallon of water/min.

Two tows per day were conducted twice a week from February to December 2006. Tows were conducted during the morning when the net was towed along the long side of the pool 15 times (by walking up and down at constant speed). The net was kept completely submerged in the water during the tow. This ensured that approximately the same amount of water was filtered for each sample. The plankton collected during the two consecutive tows was combined and considered as a single daily sample. The plankton was examined in the laboratory under a stereomicroscope and hydromedusae were isolated from other planktonic organisms using a glass pipette. Medusae were photographed and identified using a Nikon Eclipse E600 microscope. Medusae were identified to the lowest possible taxonomic level and preserved in ethanol for subsequent molecular analysis. When species level identification was not possible, especially for new born and juvenile medusae, the species were identified to genus or sometimes family. The number of species and total number medusae were recorded.

Abiotic factors

Seawater temperature is monitored in the Bay of Panama as part of a long-term environmental monitoring project conducted by STRI. During 2006, temperature was measured daily at two locations within the Bay: Isla Pacheco (Archipelago de Las Perlas) and Isla Tabougilla (Fig. 1). Temperature was measured by permanent thermometers located at 6 m (Pacheco) and 12 m (Tabougilla) depth. The temperature profiles from Isla Tabougilla and Pacheco did not differ significantly (correlation coefficient = 0.98), therefore the data from Isla Tabougilla (the location closest to the site of medusa collection) alone were used.

Because upwelling events are normally correlated with low temperature, we used the temperature profiles from Isla Tabougilla to identify the start and end of the upwelling season. The starting date was set to 15 January when the water temperature began to fall, and the ending date was set to 28 April when the

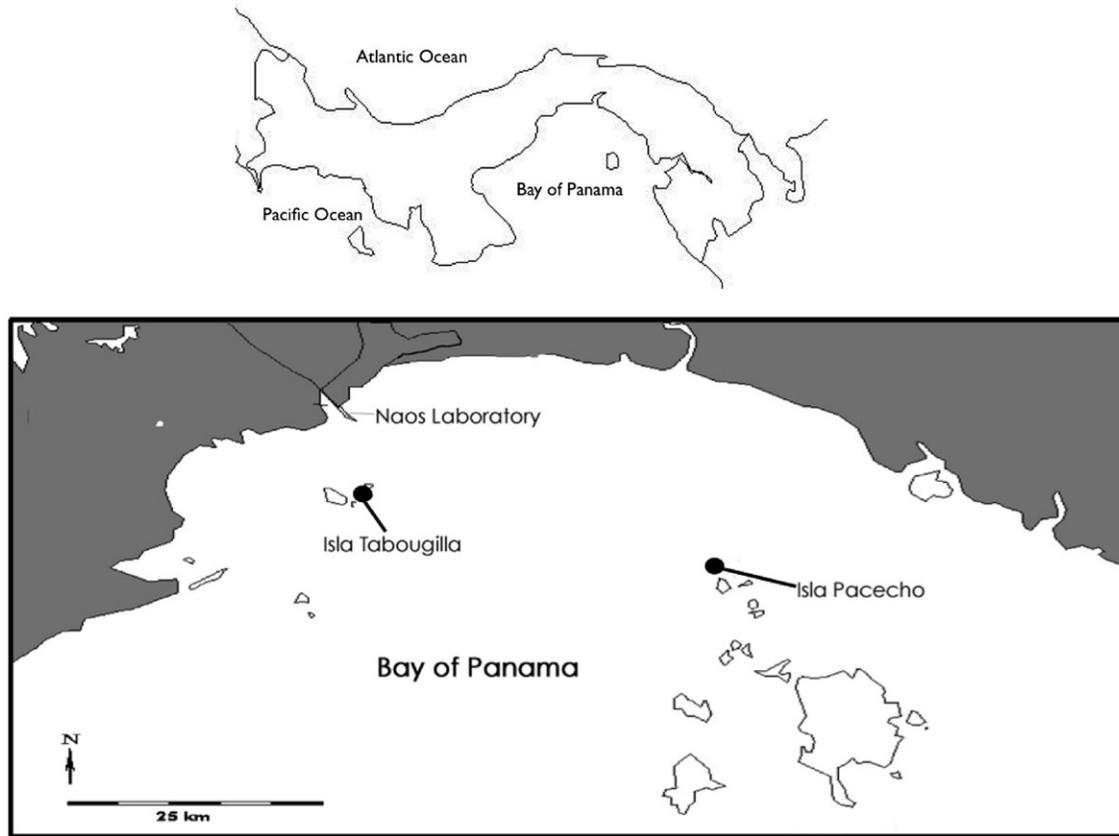


Fig. 1. Map of Panama (top) and of the Bay of Panama (bottom).

temperature rose back to non-upwelling levels. These dates are similar to the upwelling dates (13 January–28 April) calculated by the Meteorological and Hydrological Branch of the ACP (Panama Canal Authority) in 2006, using a metric based on 11 variables (see: http://striweb.si.edu/esp/physical_monitoring/summary_seasons.htm for details). Salinity was measured daily at the Naos Laboratory seawater system using an electronic salinometer.

Precipitation brings fresh water that stratifies the surface of the ocean and can have an immediate negative influence on the number of medusae in the surface water. Therefore, rainfall could affect the abundances in our surface collections, without reflecting the overall abundance of hydromedusae in the bay. We examined this possibility by counting the number of days when sampling was conducted within 10 h of rainfall (as recorded at STRI's Culebra Point Outreach Center, a few hundred meters from the STRI laboratory at Naos). Precipitation occurred prior to sampling on 9 days. During two of them, the precipitation was insignificant (<0.5 mm). The remaining 7 days represent only 6.8% of sampling days. These days did not have a different

abundance and therefore the effect of stratification due to rainfall was not further considered in this study.

Data analyses

To determine if there is a significant difference in medusa abundance and diversity between the upwelling and non-upwelling periods, we divided the samples into two groups: an upwelling group (9 February–28 April) and a non-upwelling group (28 Apr–30 December). A *t*-test was performed to determine if the mean number of medusae collected per day in the upwelling period is different from the mean number of medusae collected per day in the non-upwelling period. The *t*-test was implemented under the alternative assumptions of constant and group-specific variance.

Pearson's correlation coefficients between medusa abundance and temperature and salinity were calculated using SAS. Correlations were first calculated across the entire sample (February–December). Finer correlations were also examined by treating upwelling and non-upwelling seasons separately.

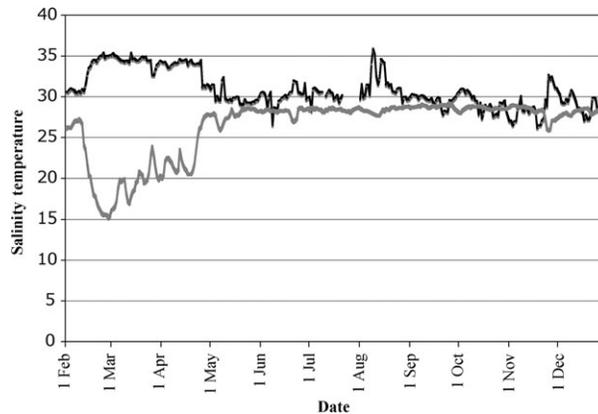


Fig. 2. Temperature (in °C, in gray) and salinity (in ‰, in black) values in the Bay of Panama during the study period (February–December 2006). Temperature and salinity varied significantly between upwelling and non-upwelling periods.

RESULTS

Abiotic factors

Water temperature was significantly cooler [average 22.13°C; standard deviation (s.d.) = 3.04] during the upwelling season than the non-upwelling season (average 28.39°C; s.d. = 0.49) (Fig. 2). Salinity was higher (33.85‰; s.d. = 1.26) during the upwelling season than the non-upwelling season (29.61‰; s.d. = 1.42) (Fig. 2). Salinity and temperature were negatively correlated over the entire year (Pearson’s correlation coefficient = -0.86; $P < 0.05$) and within each season (Pearson’s correlation coefficient = -0.24 during non-upwelling and -0.89 during upwelling; $P < 0.05$). These results are consistent with salinity and temperature values observed during several previous non-El Niño years in the Bay of Panama (D’Croz *et al.*, 1991).

Medusa abundance

A total of 2844 individual medusae were collected in 113 days; 1971 during the 34 days of sampling during upwelling (average/day 57.97; s.d. = 104.92; Table I) and 873 during the 79 non-upwelling days (average/day 11.05; s.d. = 12.07; Table I). The difference in abundance between the two seasons is significant ($P < 0.01$). The daily number of medusae and a box plot of the medusae grouped by month are shown in Fig. 3.

Medusa abundance correlated negatively with temperature (Pearson’s correlation coefficient = -0.386; $P < 0.01$; Fig. 4) and positively with salinity (Pearson’s correlation coefficient = 0.306; $P < 0.01$; Fig. 4) across the entire year (Table II). There was no significant correlation between abundance and either temperature or salinity within each season (Table II).

A histogram showing the number of days with different medusa abundance shows that most days (90%) had fewer than 50 medusae and on only 13 days (11.5%) were no medusae collected (Fig. 5). The 8 days with the highest medusa abundance all fell above 1 s.d. from the mean daily abundance. All of these “blooms” occurred during the upwelling season.

Medusa diversity

Although it was clear how many different morphotypes of medusae were present, assigning taxonomic names to them all was not possible. Some of the individuals were identified to species (*Cladonema pacificum*, *Amphynema dynema*, *Bougainwillia muscus* or *Turritopsis dohrnii*). Medusae in the genera *Obelia*, *Campalecium*, *Amphynema* and *Clytia* could only be identified to genus and these categories may, therefore, include more than a single species. Finally, a few juveniles were identified to family (i.e. family Amphynematidae) or left unidentified as Leptomedusae or Anthomedusae (see Bouillon and Boero, 2000 for taxonomic classification). All of the species, genera and families identified are usually found in shallow coastal waters and most of their benthic

Table I: Summary of medusa counts per sample during the upwelling and non-upwelling periods

	Mean	Standard deviation	Minimum	Maximum
Total sample	25.168	61.742	0.000	405.000
Non-upwelling	11.051	12.070	0.000	56.000
Upwelling	57.971	104.919	0.000	405.000

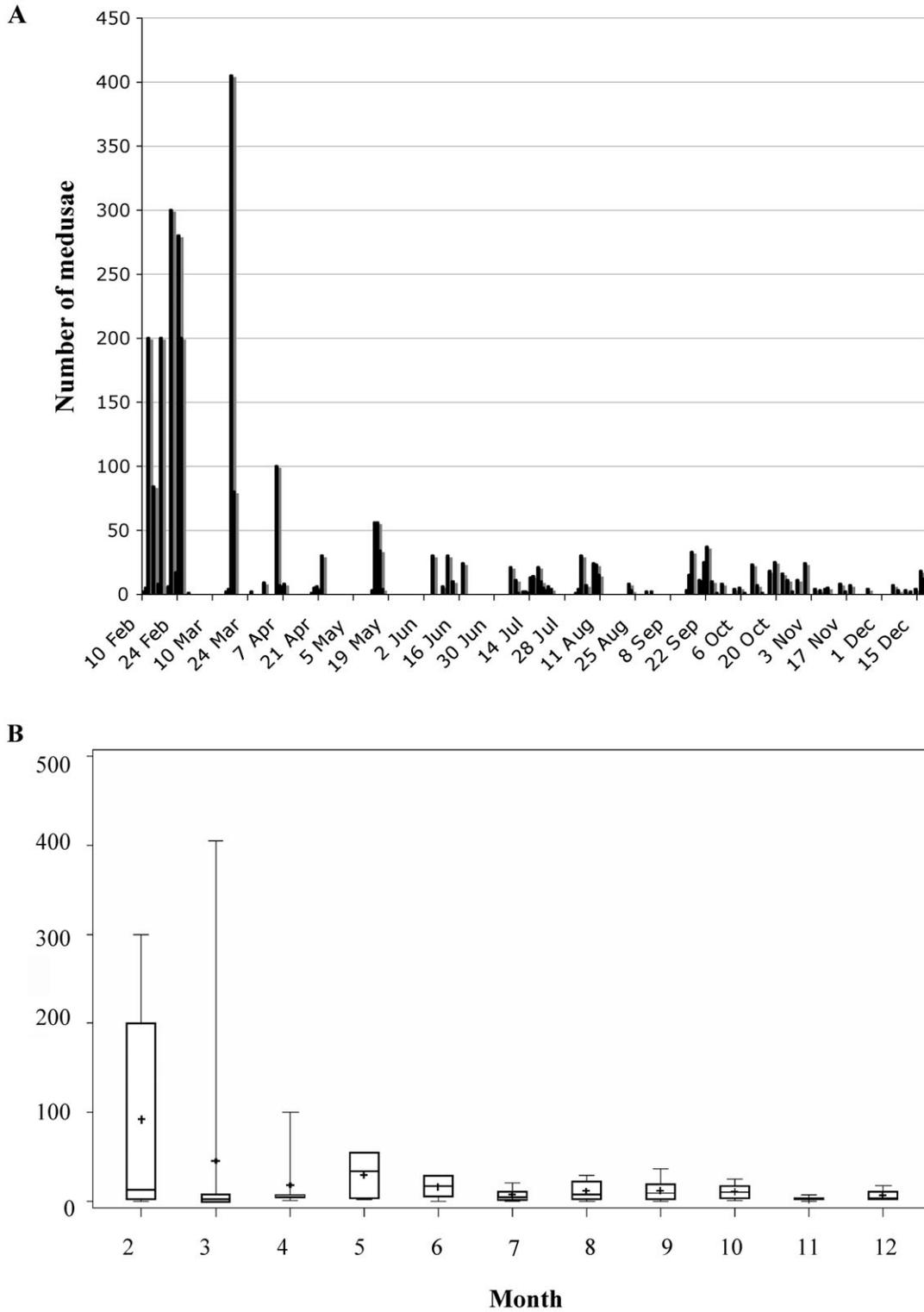


Fig. 3. Monthly averages and daily abundance of medusae. **(A)** Number of medusae collected on each day. **(B)** Number of individuals grouped by month. Rectangular boxes represent the interquartile range, the line dividing each box represents the median and the cross represents the average. The bars extending from each box represent the spread of 95% of the data.

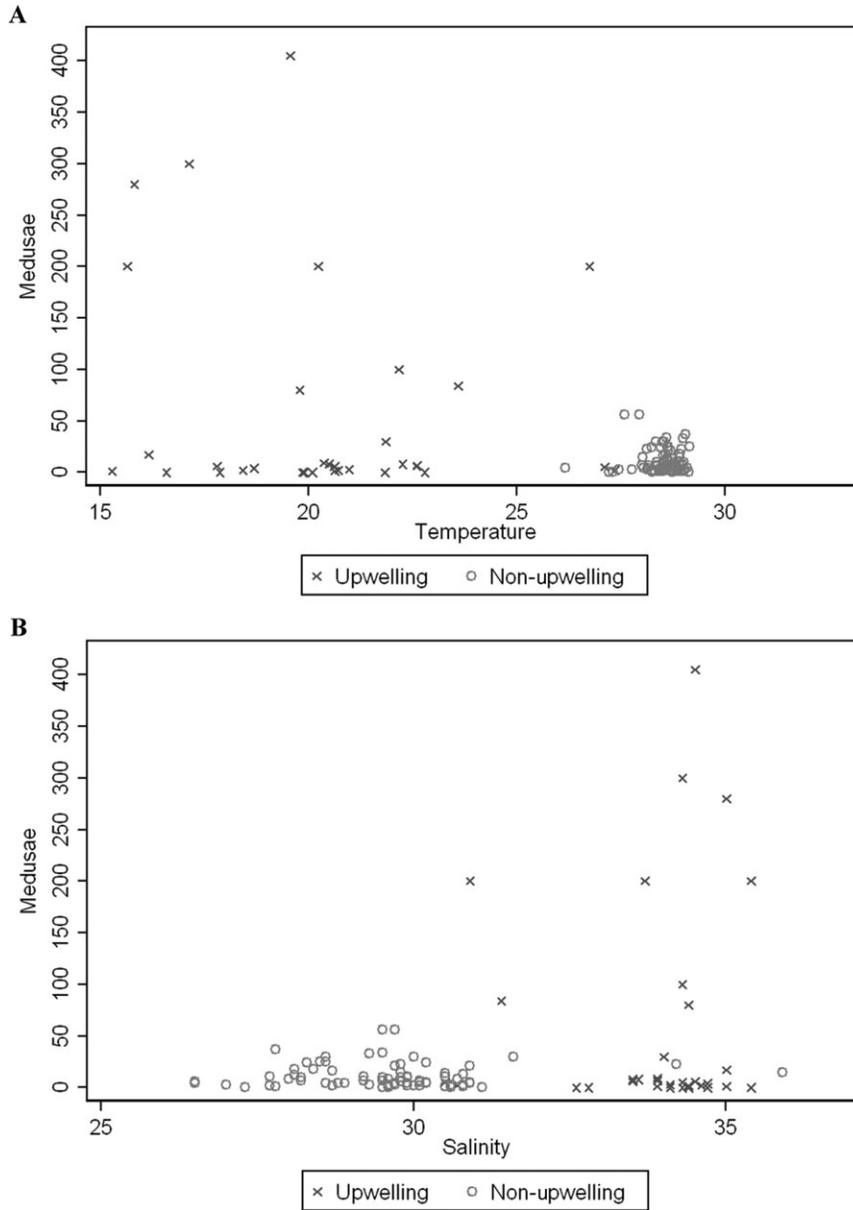


Fig. 4. Numbers of individual medusae with (A) temperature and (B) salinity. Circles and “x” refer, respectively, to non-upwelling and upwelling periods. Medusa abundance correlated negatively with temperature (Pearson’s correlation coefficient = -0.386 ; $P < 0.01$) and positively with salinity (Pearson’s correlation coefficient = 0.306 ; $P < 0.01$).

colonies have been found in shallow waters in the Bay of Panama (Miglietta, unpublished results).

A total of seven taxa were identified at the species level, nine taxa at the genus level and six morphotypes were left as *Leptomedusa* or *Anthomedusa* (Table III). The most abundant taxa were *Bougainvillia muscus*, *Turritopsis dohrnii*, *Clytia* spp., *Obelia* spp., *Campalecium* sp. *Ectopleura dumortieri* and *Proboscidactyla ornata*. All but a few rare morphotypes were found during both non-upwelling and upwelling seasons. The number of

identifiable taxonomic units collected on a single day ranged from 0 to 7 (Fig. 6) and the average number of species per samples did not differ significantly between upwelling and non-upwelling periods.

Blooms, the days with extraordinary abundance during the upwelling period, were not usually the result of a massive increase in the abundance of a single species. Blooms were generally composed of one to three species with *Bougainvillia muscus* being the major component followed by *Clytia* spp., *Campalecium* sp. and

Table II: Pearson's correlation coefficients between the number of medusae and temperature and salinity during the entire year and during the non-upwelling and upwelling seasons

	Temperature	Salinity
Total sample	-0.386	0.306
Non-upwelling	-0.018	0.029
Upwelling	-0.182	0.071

Amphinema dinema. However, the blooms varied in the relative representation of these species, they did not always co-occur and these were also found in non-bloom samples.

DISCUSSION

The number of hydromedusae collected per sample in the Bay of Panama varied over two orders of magnitude, due primarily to short periods of very high abundance (blooms) that occurred during the upwelling season. The difference in frequency of blooms between the two seasons resulted in a highly significant statistical effect of season on medusa abundance. No blooms

occurred during the non-upwelling season. The blooms during the upwelling were separated by periods of low abundance similar to levels during the non-upwelling season, showing that abundance was not uniformly higher throughout the season. The differences in abundance between the seasons were not explained by changes in taxonomic composition, which remained constant through the year, as most of the taxa were found in both the upwelling and non-upwelling seasons. This is consistent with what observed by Gibbons and Buecher (Gibbons and Buecher, 2001) in another upwelling region, the Benguela ecosystem, where medusae species composition did not vary during the three upwelling events recorded in a short-term (28 days) survey. The present study is the first to observe a correlation between upwelling and quantified medusa abundance.

The fact that blooms were not usually the result of a massive increase in the abundance of a single species but were often composed of two or three species suggests the possibility that they result from a habitat-wide rather than a single species response to upwelling conditions.

Across the year, medusa abundance was negatively correlated with temperature and positively correlated with salinity (Table II; Fig. 4). These correlations

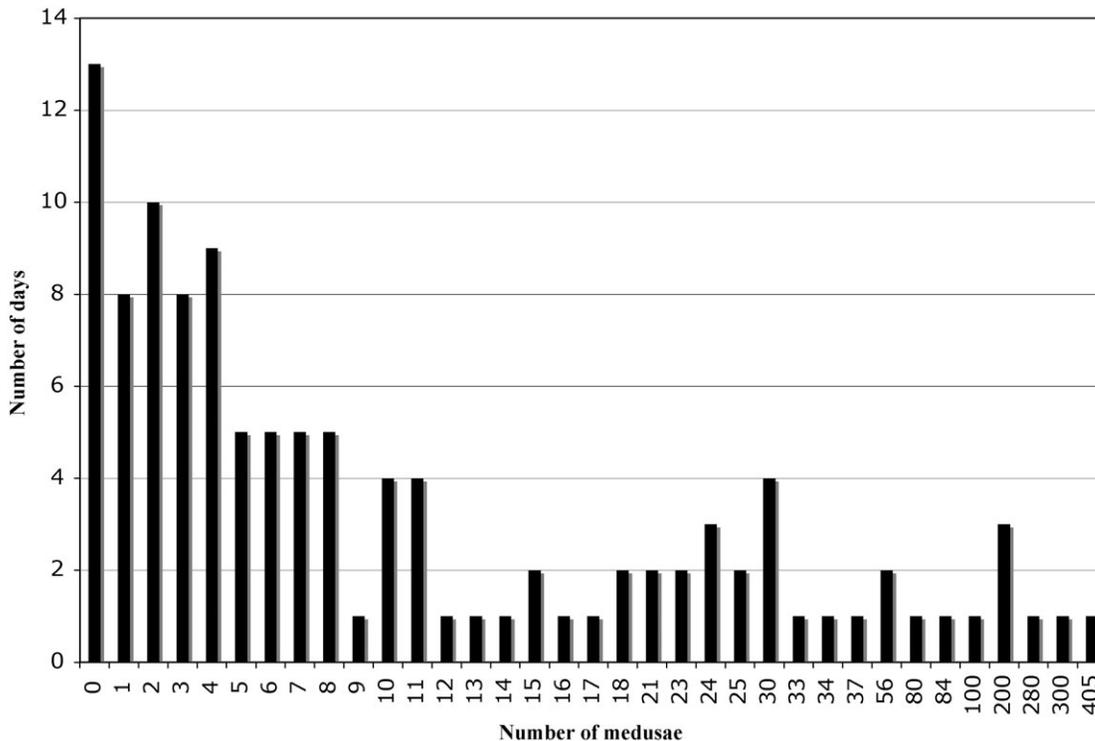


Fig. 5. Histogram of medusa abundance, showing the frequency distribution of the abundances. Fewer than 50 medusae were collected on most days.

Table III: Hydromedusae collected in the Bay of Panama during 2006

Taxon	Month
<i>Bougainvillia muscus</i>	2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12
<i>Amphinema dinema</i>	2, 4, 5, 6, 7, 8, 9, 10
<i>Cladonema pacificum</i>	5, 7, 12
<i>Turritopsis dohrnii</i>	2, 3, 4, 7, 8, 10, 11, 12
<i>Proboscidactyla ornata</i>	3, 4, 6, 8, 9, 10, 11, 12
<i>Ectopleura dumortieri</i>	4, 6, 7, 8, 9, 10, 11
<i>Podocorynoides minima</i>	4, 5, 7, 11
<i>Campalecium</i> sp.	2, 4, 5, 6, 7, 8, 9, 10, 12
<i>Amphinema</i> sp.1	4
<i>Coryne</i> spp.	4, 8, 9, 10, 11
<i>Amphynema</i> sp.2	5, 8
<i>Obelia</i> spp.	2, 5, 6, 7, 9, 10, 11, 12
<i>Clytia</i> spp.	2, 3, 4, 7, 8, 10, 11
<i>Zanclaea</i> sp.	2, 10
<i>Sarsia</i> sp.	11, 12
<i>Coryna</i> sp.2	6, 7
Leptomedusa	4
Anthomedusa 1	5, 11
Anthomedusa 2	6
Anthomedusa 3	6, 7
Anthomedusa 4	2
Anthomedusa 5	4, 5

Months are indicated by numbers (2–12 = February–December). Upwelling months are indicated in bold.

disappear when each season is considered separately, showing that the overall relationship is due to differences between the seasons. Although the average number was significantly higher during the upwelling season, ideal conditions for medusa blooms seem to change with the season. Whether this is due to a shift in the physiological response of the species to external condition, or it is induced by the difference in food availability between the two seasons is unclear, it represents an interesting direction for future investigations. During the non-upwelling season, medusae were most abundant at temperatures above 28°C and salinity below 30‰. During the upwelling season, on the other hand, the highest number of medusae (blooms) was found during periods of strongest upwelling, with temperatures below 20°C and salinity above 34‰ (Fig. 4). In the Bay of Panama, upwelling-induced low temperatures are tightly correlated with increased productivity, measured both as chlorophyll *a* concentration and phytoplankton density (D’Croz *et al.*, 1991), suggesting that these hydromedusa blooms are also associated with increased productivity.

The medusae identified in this study belong to shallow water hydroid species and were therefore produced in local coastal waters rather than being brought to the surface by the upwelling itself. In addition, during upwelling, a northeastern wind generally blows, resulting in a current running from onshore to offshore (D’Croz and Robertson, 1997). Therefore it seems

unlikely that medusae were carried onshore (where the sampling occurred) by surface water currents. Unfortunately, little oceanographic information is available for the Republic of Panama, and a map of the small scale, local hydrographic regime in the Bay of Panama is necessary to put the available biological information into an oceanographic context.

Because planktonic medusae are produced by benthic colonies, medusa blooms are most likely associated with events that trigger medusa production by the benthic colony. It has been shown that medusa production can be triggered by circannual rhythms, temperature or lunar phase (Elmhirst, 1925; Werner, 1954; Edwards, 1978; also see Brock, 1975 on the production of gonophores in *Laomedea flexuosa*), although each of these factors was tested on one species only. Our results suggest that some aspect of upwelling is such a trigger. However, the nature of the trigger of medusa production cannot be inferred from our data, as blooms could represent a response of the benthic colonies to several factors (temperature, salinity, productivity, food abundance, etc.). In addition, differences between species in the time it takes from initiation of a medusa bud to release of the medusa may desynchronize the appearance of medusa from species whose medusa production was triggered by the same cue.

It is unclear if the pattern of hydromedusa blooms associated with upwelling can be generalized for other upwelling sites. In the Monterey Bay Region (CA, USA), Robison *et al.* (Robison *et al.*, 1998) and Silguero and Robison (Silguero and Robison, 2000) found that the siphonophore *Nanomia bijuga* has seasonal cycles of abundance correlated with the onset of upwelling and Raskoff (Raskoff, 2001) reported the decrease in abundance of the medusa *Colobonema sericerum* during El Niño years, while in Friday Harbor (WA, USA), Mills (Mills, 1981) recorded a high biomass of medusae during summer months. A few other studies have investigated the gelatinous zooplankton in upwelling regions such as South Africa and Chile (Pagès and Gili, 1991; Pagès *et al.*, 2001; Buecher and Gibbons, 2000). Because these studies mostly refer to sampling effort concentrated during 1 or 2 months per year (Buecher and Gibbons, 2000; Gibbons and Buecher, 2001), or multiple samplings from different locations during a single season (Pagès and Gili, 1991; Pagès *et al.*, 2001), they are not directly comparable to our study and cannot be used to compare abundance and diversity between upwelling and non-upwelling periods. The drastic changes in abundance from day to day during the upwelling season, found in our study, suggests that it will be difficult to get a representative view of medusa abundance with small numbers of seasonal samples.

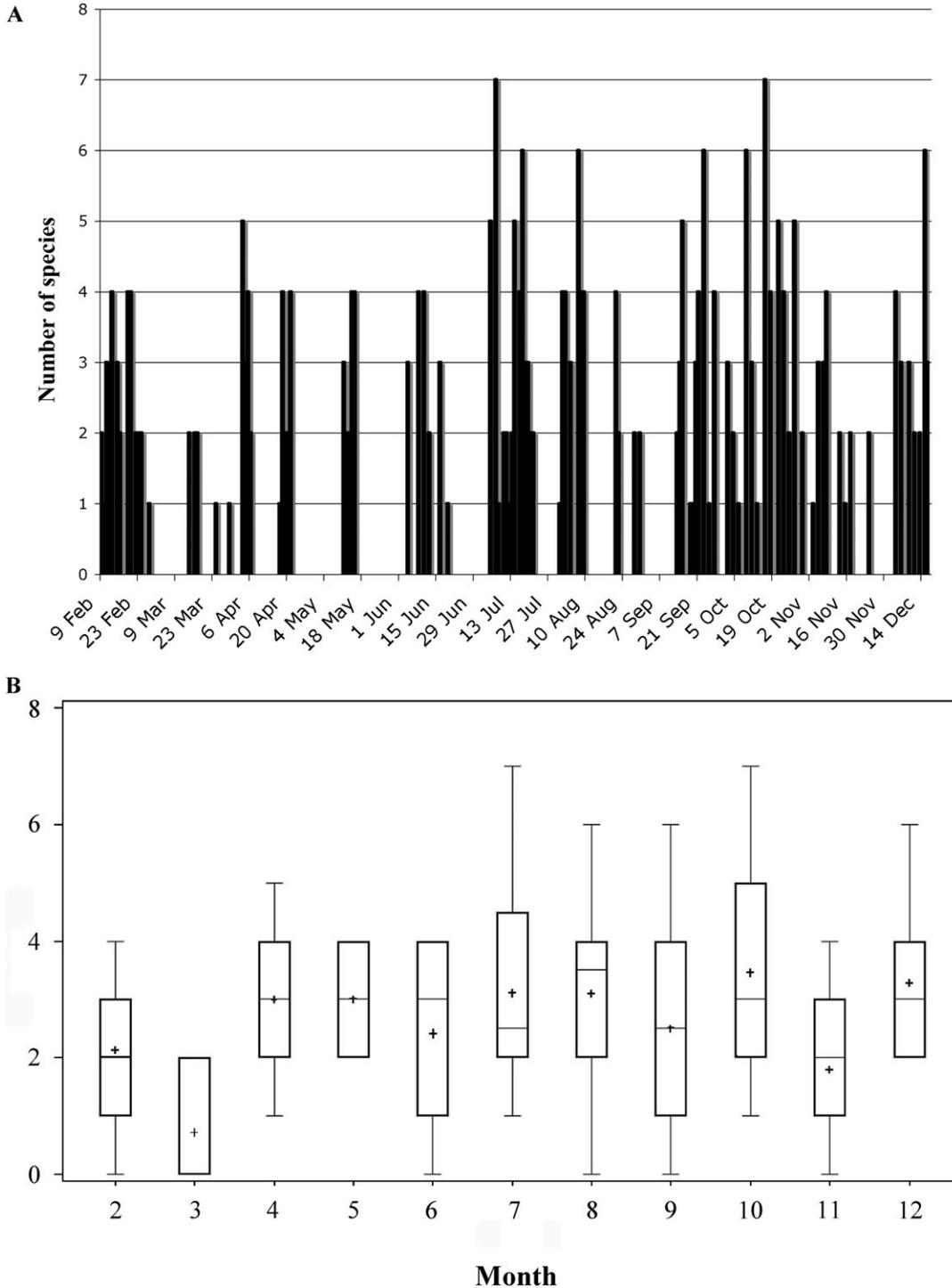


Fig. 6. Monthly averages and daily number of taxa of medusae. **(A)** Number of taxa collected on each day. **(B)** Number of taxa grouped by month. Rectangular boxes represent the interquartile range, the line dividing each box represents the median and the cross represents the average. The bars extending from each box represent the spread of 95% of the data.

The medusa blooms associated with upwelling in the Bay of Panama can be compared with previous studies of hydromedusa dynamics in non-upwelling

sites, the majority of which come from non-tropical regions. Our results associate increased medusa abundance with upwelling, and thus relatively decreased

temperatures, but in temperate regions hydromedusa and scyphomedusa blooms are usually associated with increased temperatures. The scyphomedusa *Chrysaora quinquecirrha* blooms in the Chesapeake Bay at the upper end of the local temperature range (Decker *et al.*, 2007). *Pelagia noctiluca* blooms are best predicted by high temperature, lack of rainfall and high atmospheric pressure in the Mediterranean Sea (Goy *et al.*, 1989). Mean densities of the hydromedusa *Aequorea victoria* in the Northeast Pacific were positively and significantly related to mean temperatures and salinities during a 4-year survey (see Purcell, 2005 for a review of species whose blooms are correlated with high temperature). A 6-year survey of 17 hydromedusa species off northeast England found that peaks in abundance and diversity occur during late spring, which is also the time of highest productivity (Nicholas and Frid, 1999).

These superficial differences between tropical and temperate systems could be produced by the same causal element: seasons of high productivity. On the Atlantic coast of North America, phytoplankton blooms occur in the spring and early summer (Brown *et al.*, 1985) and warmer conditions trigger phytoplankton blooms in the North Atlantic (Irigoiien *et al.*, 2000). In most cases, the hydromedusa blooms also occur during warmer temperatures. Most likely, blooms are the response to the increased productivity that propagates up the food chain and translates into higher food abundance for both the benthic polyps and the planktonic medusae. Pelagic–benthic interactions, and how they are influenced by physical processes in near-shore environment are rather poorly understood (Menge *et al.*, 1997). It is known that primary production affects the benthic productivity (Thiel, 1981), and Menge *et al.* (Menge *et al.*, 1997) elegantly demonstrated how rocky intertidal communities are affected by a bottom-up effect of phytoplankton. Both studies link the increased abundance of phytoplankton (and thus zooplankton) with more food for filter feeders and faster benthic growth. Consistent with this “bottom-up” hypothesis, our data suggest a possible indirect effect of upwelling, and plankton enrichment, on benthic organisms.

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REFERENCES

- Anderson, G. C. (1964) The seasonal and geographic distribution of primary productivity off the Washington and Oregon coasts. *Limnol. Oceanogr.*, **9**, 284–302.
- Boero, F. and Bouillon, J. (1987) Inconsistent evolution and paedomorphosis among the hydroids and medusae of the Athecatae/Anthomedusae and the Thecatae/Leptomedusae (Cnidaria, Hydrozoa). In Bouillon, J., Boero, F., Cicogna, E., Cornelius, P. F. S. *et al.* (eds), *Modern trends in the Systematics, Ecology and Evolution of Hydroids and Hydromedusae*, Oxford University Press, Oxford, pp. 229–250.
- Boero, F., Bouillon, J., Gravili, C. *et al.* (2008) Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series*, **356**, 299–310.
- Bouillon, J. and Boero, F. (2000) Phylogeny and classification of Hydroidomedusae The Hydrozoa: a new classification in the light of old knowledge. *Thalassia Salentina*, **24**, 1–46.
- Brock, M. A. (1975) Circannual rhythms—I. Free-running rhythms in growth and development of the marine cnidarian. *Campanularia flexuosa*. *Comp. Biochem. Physiol.*, **51**, 377–383.
- Brodeur, R. D., Sugisaki, H. and Hunt, G. L. (2002) Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Mar. Ecol. Prog. Ser.*, **233**, 89–103.
- Brown, O. B., Evans, R. H., Brown, J. W. *et al.* (1985) Phytoplankton blooming off the U.S. East Coast: A satellite description. *Science*, **229**, 163–167.
- Buecher, E. and Gibbons, M. J. (2000) Interannual variation in the composition of the assemblages of medusae and ctenophores in St. Helena Bay, Southern Benguela Ecosystem. *Sci. Mar.*, **64**, 123–134.
- CIESM (2001) Gelatinous zooplankton outbreaks: theory and practice. *CIESM Workshop Series 14*, p. 1–112.
- D’Croz, L. and Robertson, R. D. (1997) Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. In Lessios, Harilaos, A. and Macintyre, I. G. (eds), *Proceedings of the 8th International Coral Reef Symposium*.
- D’Croz, L., Del Rosario, J. B. and Gomez, J. A. (1991) Upwelling and phytoplankton in the Bay of Panama. *Revista de Biología Tropical*, **39**, 233–241.

- Decker, M. B., Brown, C. W., Hood, R. R. *et al.* (2007) Predicting the distribution of the Scyphomedusa *Chrysaona quinquecirrha* in Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, **329**, 99–113.
- Edwards, C. (1978) The hydroids and medusae *Sarsia occulta* sp nov, *Sarsia tubulosa* and *Sarsia loveni*. *J. Mar. Biol. Assoc. UK*, **58**, 291–311.
- Elmhirst, R. (1925) Lunar periodicity in *Obelia*. *Nature*, **116**, 358–359.
- Fleming, R. H. (1939) A contribution to the oceanography of the Central America Region. In *Proceedings of the 6th Pacific Science Congress*, **Vol. 3**, 167–176.
- Forsberg, E. D. (1963) Some relationship of meteorological, hydrographic and biological variables in the Gulf of Panama. *Bull. Inter.-Amer. Trop. Tuna Comm.*, **7**, 1109.
- Forsberg, E. D. (1969) On the climatology, oceanography and fisheries of the Panama Bight. *Bull. Inter.-Amer. Trop. Tuna Comm.*, **14**, 49–259.
- Gibbons, M. J. and Buecher, E. (2001) Short-term variability in the assemblage of medusae and ctenophores following upwelling events in the southern Benguela ecosystem. *Mar. Ecol. Prog. Ser.*, **220**, 169–177.
- Goy, J., Morand, P. and Etienne, M. (1989) Long term fluctuation of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables. *Deep-Sea Res.*, **36**, 269–279.
- Hecky, R. E. and Kilham, P. (1988) Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effect of enrichment. *Limnol. Oceanogr.*, **33**, 789–822.
- Irgoien, X., Harris, R. P., Head, R. N. *et al.* (2000) North Atlantic Oscillation and spring bloom phytoplankton composition in the English Channel. *J. Plankton Res.*, **22**, 2367–2371.
- Kawahara, M., Uye, S., Ohtsu, K. *et al.* (2006) Unusual population explosion of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters. *Mar. Ecol. Prog. Ser.*, **307**, 161–173.
- Lynam, C. P., Heath, M. R., Hay, S. J. *et al.* (2005a) Evidence for impacts by jellyfish on North Sea herring recruitment. *Mar. Ecol. Prog. Ser.*, **298**, 157–167.
- Lynam, C. P., Hay, S. J. and Brierley, A. S. (2005b) Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. *J. Mar. Biol. Assoc. UK*, **85**, 435–450.
- Menge, B. A., Daley, B. A., Wheeler, P. A. *et al.* (1997) Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? *Proc. Natl Acad. Sci.*, **94**, 14530–14535.
- Mills, C. E. (1981) Seasonal occurrence of planktonic medusae and ctenophores in the San Juan Archipelago (NE Pacific). *J. Biol.*, **39**, 6–29.
- Nicholas, K. R. and Frid, C. L. J. (1999) Occurrence of hydromedusae in the plankton off Northumberland (western central North Sea) and the role of planktonic predator. *J. Mar. Biol. Assoc. UK*, **79**, 979–992.
- Pagès, F. and Gili, J. M. (1991) Effects of large-scale advective processes on gelatinous zooplankton populations in the Northern Benguela ecosystem. *Mar. Ecol. Prog. Ser.*, **75**, 205–215.
- Pagès, F., Gonzalez, H. E., Ramon, M. *et al.* (2001) Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Brassia bassensis* (Siphonophora: Calycophorae). *Mar. Ecol. Prog. Ser.*, **210**, 13–24.
- Pauly, D. and Christensen, V. (1995) Primary production required to sustain global fisheries. *Nature*, **374**, 255–257.
- Purcell, J. E. (2003) Predation on zooplankton by large jellyfish (*Aurelia labiata*, *Cyanea capillata*, *Aequorea aequorea*) in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.*, **246**, 137–152.
- Purcell, J. E. (2005) Climate effect on formation of jellyfish and ctenophore blooms: a review. *J. Mar. Biol. Assoc. UK*, **85**, 461–476.
- Purcell, J. E. and Arai, M. N. (2001) Interactions of pelagic cnidarians and ctenophores with fishes: A review. *Hydrobiologia*, **451**, 27–44.
- Purcell, J. E., Nemazie, D. A., Dorsey, S. E. *et al.* (1994a) Predation mortality of bay anchovy (*Anchoa mitchilli*) eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, **114**, 47–58.
- Purcell, J. E., White, J. R. and Roman, M. R. (1994b) Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay. *Limnol. Oceanogr.*, **39**, 263–278.
- Raskoff, K. A. (2001) The impact of El Niño events on populations of mesopelagic hydromedusae. *Hydrobiologia*, **451**, 121–129.
- Robison, B. H., Reisenbichler, K. R., Sherlock, R. E. *et al.* (1998) Seasonal abundance of the siphonophore, *Nanomia bijuga*, in Monterey Bay. *Deep-Sea Res. II*, **45**, 1741–1751.
- Schaefer, M. B., Bishop, X. M. and Landa, G. V. (1958) Some aspects of upwelling in the Gulf of Panama. *Bull. Inter.-Amer. Trop. Tuna Comm.*, **3**, 77–130.
- Silguero, J. M. B. and Robison, B. H. (2000) Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. *J. Plankton Res.*, **22**, 1139–1153.
- Thiel, H. (1981) Benthic investigations in the Northwest African upwelling area. Report on the cruises 26, 36, 44 and 53 of RV Meteor. *Forsch. Ergebn.*, **33**, 1–15.
- Volovik, S. P. (ed.) (2004) Ctenophore *Mnemiopsis leidyi* (A Agassiz) in the Azov and Black seas: its biology and consequences of its intrusions. **Vol. 17**, Turkish Marine Research Foundation, Istanbul.
- Werner, B. (1954) On the development and reproduction of the anthomedusan *Margelopsis haeckeli* Hartlaub. *Trans. NY Acad. Sci.*, **2163**, 143–146.