



The bathypelagic community of Monterey Canyon

Bruce H. Robison*, Rob E. Sherlock, Kim R. Reisenbichler

Monterey Bay Aquarium Research Institute, 7700 Sandholdt Rd., Moss Landing, CA 95039 USA

ARTICLE INFO

Article history:

Received 15 March 2009

Accepted 22 December 2009

Available online 7 March 2010

Keywords:

Bathypelagic zone

Community composition

Unmanned vehicle

Monterey Canyon

ABSTRACT

We used a quiet, deep-diving remotely operated vehicle (ROV) to conduct oblique, quantitative video transects of the bathypelagic fauna at depths between 1000 and 3500 m at a site over the Monterey Submarine Canyon, in the eastern North Pacific off central California. Fifteen such dives were made over a two-year period. Analyses of the video data revealed a rich and diverse fauna dominated by gelatinous animals. In particular, the holopelagic polychaete *Poeobius meseres* was an important detritivore in the upper half of this depth range. As *Poeobius* abundance eventually declined with increasing depth, larvacean abundance increased. In contrast, the relative numbers of crustacean grazers, principally copepods and mysids, remained relatively constant with depth. Medusae were most abundant and most diverse among the gelatinous predators, which also included ctenophores, and siphonophores. Chaetognaths occurred chiefly in the upper half of the depth range. While there is considerable overlap, the bathypelagic fauna can be separated into upper (1000 to 2300 m) and lower (2400 to 3300 m) zones, as well as a distinct and populous benthic boundary layer. Within the overall bathypelagic community is a complex web of trophic links involving gelatinous predators that feed on both gelatinous and hard-bodied particle feeders, as well as on each other. The amount of organic carbon contained in this jelly web is substantial but its ecological fate is uncertain. The assessment of bathypelagic communities will be important for establishing baselines to conserve deep pelagic biodiversity within high-seas protected areas.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Historically, our knowledge of the bathypelagic fauna has been based on specimens collected by net tows. As a consequence bathypelagic animals have been characterized chiefly by calanoid copepods, black fishes, and red shrimps (Marshall, 1954). In 1956 Hartman and Emery published “Bathypelagic Coelenterates,” based on images from a film camera and strobe they deployed in Otis Barton’s *Benthoscope* in deep water off southern California. They captured images of unknown medusae and siphonophores and they speculated about why these animals lived at particular depths and what they ate. Subsequently, Bernard (1958) and Peres (1958) using the bathyscaphe *F.N.R.S. III* documented the occurrence of deep-living gelatinous animals in the Mediterranean off Toulon. These early glimpses of an alternative fauna in deep water were largely forgotten as attention was focused on the mesopelagic depth zone and its sonic scattering layers (Clarke and Backus, 1956; Barham, 1966; Isaacs et al., 1974).

Typically, studies of deep-living animals have been conducted piecemeal, focused on taxonomic groups such as crustaceans (Mauchline, 1972; Burghart et al., 2007), or on constituent

ecological or biological categories such as zooplankton or jellies (Koppelman et al., 2003; Lindsay and Hunt, 2005). Attempts to assess an entire bathypelagic community have been rare (Vereshchaka and Vinogradov, 1999; Bergstad et al., 2008). Technological advances have enabled substantial progress in our understanding of bathypelagic ecology, beginning with brief sightings during benthic submersible dives (Barham et al., 1967) and deep-towed echosounders (Wishner, 1980). Split-beam echosounders now allow the resolution of scattering layers at depths as great as 3000 m (Opdal et al., 2008) while video profilers and plankton recorders are reaching down to 1000 m (Stemmann et al., 2008). Research in the deep water column is going through an essential transformation from indirect to direct methods as manned and unmanned undersea vehicles provide unprecedented access, new capabilities, and new perspectives (Robison, 2004; Vinogradov, 2005; Youngbluth et al., 2008). What follows is the assessment of a bathypelagic community from the perspective of a state-of-the-art remotely operated vehicle.

2. Methods

The study site is located at 36.33°N, 122.90°W; where the 3500-m isobath crosses the axis of the Monterey Submarine Canyon, about 90 km west of Point Sur, California (Fig. 1). Fifteen

* Corresponding author. Tel.: +18317751721; fax: +18317751645.

E-mail addresses: robr@mbari.org (B.H. Robison), robs@mbari.org (R.E. Sherlock), reki@mbari.org (K.R. Reisenbichler).

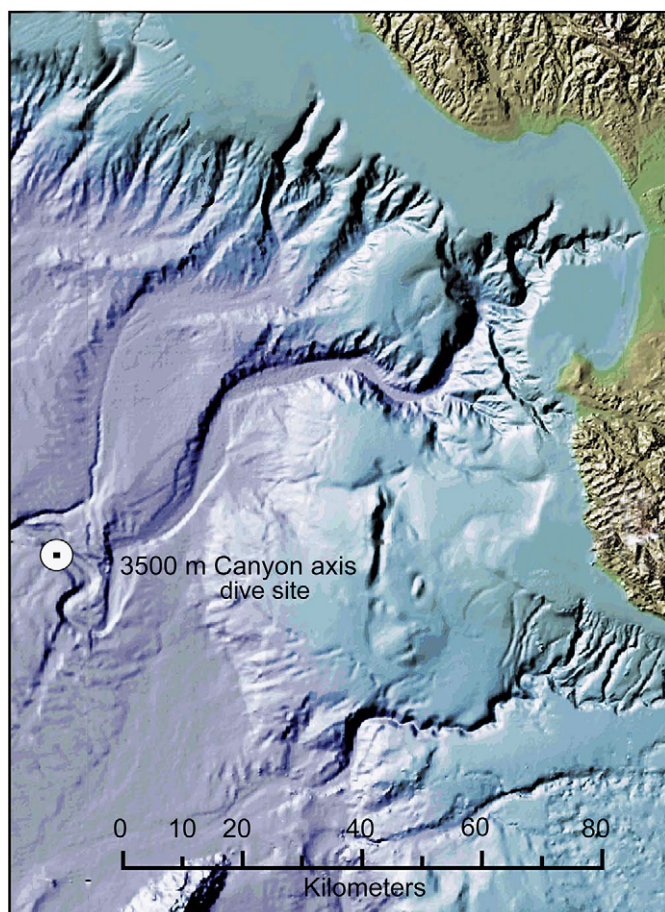


Fig. 1. Monterey Submarine Canyon. The bathypelagic survey site is approximately 115 km down-canyon from the canyon head in the center of Monterey Bay, California, USA. The survey site is located at 36.33°N, 122.90°W, where the water depth is 3500 m. Seafloor color transition on the map is at the 2000 m isobath.

quantitative video transects were conducted during six cruises of the R/V *Western Flyer* between October 2003 and September 2005. Transects were run during each of the region's three hydrographic seasons (Breaker and Broenkow, 1994).

Measurements of the vertical distribution and abundance of bathypelagic animals were made with the ROV *Tiburon*; a purpose-built research vehicle with electric thrusters that reduce its acoustic signature when compared with hydraulic ROVs. The primary video camera was a broadcast-quality, Panasonic WV-E550 (800 TVL resolution) fitted with a Fujinon S8.5 × 4.2BERM-16B zoom lens. For quantitative transecting, four HMI lights were arranged to give broad coverage in the direction of travel, the lens was set at its widest angle, and focus was adjusted to give the largest depth of field from 1–4 m in front of the vehicle. The camera's field of view at a focal distance of 1.5 m was 2.43 m², and this number was used to calculate transect volumes. Video targets smaller than about 3 mm could not be reliably identified with this system; however after this survey was completed, new high-definition video cameras have lowered this threshold to 2 mm. The largest animal we measured was a brooding squid, 4.52 m in total length (Seibel et al., 2005). Video images were transmitted through optical fibers in the ROV tether and recorded on high-resolution BetaCam tapes aboard the *Western Flyer*.

The quantitative video surveys were run as continuous oblique transects between 1000 and 3500 m depth, during daylight hours. The mean average speed through the water was 0.42 m s⁻¹, just slow enough to keep the moving video images sharp. This was achieved by moving the ROV forward at an average speed of

0.31 m s⁻¹, and down at 0.28 m s⁻¹. The camera was tilted down at a 27° angle in order to align with the direction of travel. This maximized the amount of time an animal was in the field of view. Transects were conducted in a descending, zigzag pattern, with the surface vessel proceeding at about the same forward speed as the ROV and along the same forward vector. This deployment pattern was necessary in order to prevent the vehicle's long, heavy tether from dragging the ROV off course. No stops were made mid-transect to observe or collect specimens.

The average time required to conduct a complete transect profile was 147 min (range = 110 to 310 min). Mean water volume observed per transect was 9000 m³ (range = 7620 to 10138 m³) between 1000 and 3500 m depth. A Falmouth Scientific 3D-ACM acoustic current meter was used to monitor transect speeds in real time and to record the transect speed and 3-D vector data for determining distance traveled, after the dive. Temperature, salinity, and depth were measured with Falmouth Scientific OTM, OCM, and OPM modules; oxygen concentration was measured with a SeaBird sbe 43 instrument, and all sensors were monitored directly by the ROV data management system. A Sea Tech 25-cm transmissometer measured particle densities at 660 nm. Time codes linked the video data, frame by frame, to the simultaneous CTDO and transmissometer measurements.

For analysis of vertical distribution and abundance, faunal data were categorized into 100-m depth bins (e.g. 1000–1099, 1100–1199, etc.). Transect videotapes were analyzed ashore with a Sony BetaCam editing deck and a high resolution monitor. Individual animals were identified and counted as they passed through the camera's field of view and were logged in MBARI's video database using the VARS video annotation and reference system (MBARI, 2009). For each 100-m depth bin, animal counts were standardized based on the total volume of water transected. For the present analysis, common bathypelagic fauna were placed into taxonomic groups. Their abundance was standardized by volume transected and square-root transformed. Square root transformation was used in order to lessen the contribution from rare species, without excluding them entirely. Multi-dimensional scaling was utilized to elucidate patterns in faunal composition, abundance, and distribution over depth and time (Clarke and Warwick, 2001; Clarke and Gorley, 2006).

The volume of water measured by each of these video transects is roughly equivalent to the water volume sampled by an RMT-8 trawl towed at 2 knots for 25 minutes. Relatively speaking then, these are small-volume, high-resolution assessments. Net tows have long been known to undersample gelatinous animals (Hartman and Emery, 1956; Madin and Harbison, 1978; Robison, 2004) while favoring hard-bodied fishes, squids, and crustaceans. ROV-based video sampling has its own potential biases, including avoidance, attraction, and the observation that many more animals are seen during descents than during ascents. The identities of target species were determined during non-transect dives at the same site, either by extended close-up observation in situ or by collecting specimens for examination in the laboratory. The identification of gelatinous taxa is incomplete here because so many species, genera, and even families of bathypelagic gelata have yet to be described and named (Haddock, 2004). Likewise, with animals smaller than 3 mm and because of the many cryptic species among the gelata, identifications from a moving vehicle can be a challenge.

3. Results

3.1. Water column profiles

The hydrographic characteristics of the water column between 1000 and 3500 m at the study site were conservative throughout

our surveys. In a profile from a typical dive (Fig. 2) temperature declined from 4.0 °C to about 1.5 °C at the bottom; salinity increased from 34.4 to 34.7; oxygen increased from 0.8 to 2.6 ml l⁻¹; and % light transmission, as an inverse proxy for particle density and particulate organic carbon (Bishop, 1999), ranged from 82 to 83.5%. A benthic boundary layer (BBL) of particulate matter, from 100 to 300 m thick, was evident in all transmissometer profiles, and to the eye.

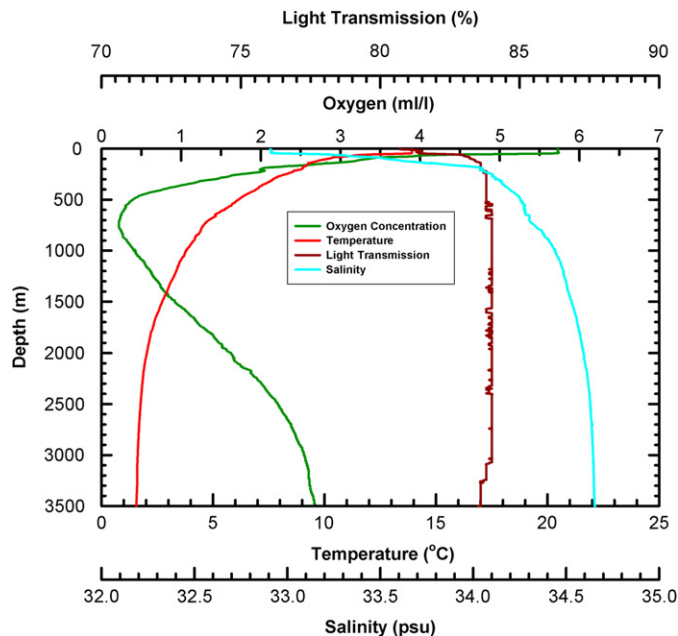


Fig. 2. Hydrographic depth profile of temperature, salinity, oxygen, and % light transmission from a typical ROV dive at the bathypelagic survey site.

Descent through the water column from 1000 m to the seafloor at 3500 m revealed several patterns of animal distribution. Overall abundance was greatest between 1500 and 2000 m, and was least from 2600 to 3000 m (Fig. 3). In general, the diversity of observed taxa declined with depth, followed by a sharp increase in both the number of taxa and overall animal abundance in the BBL.

3.2. Particle feeders

The most striking feature of the vertical distribution patterns of the bathypelagic fauna was the high abundance of *Poeobius meseres*, which was a consistent, repeating pattern seen on all 15 dives. *Poeobius* is an atypical, holopelagic polychaete worm found also at mesopelagic depths in Monterey Bay where it feeds on a variety of particulate food (Utall and Buck, 1996). This species is widely distributed throughout the eastern North Pacific (McGowan, 1960). In its bathypelagic depth range, *Poeobius* abundance at our study site peaked at 1800 m, which corresponded with a marked decline in particle abundance (Fig. 4).

Doliolids occurred between 1000 and 2000 m; most are undescribed doliopsid species but *Dolioletta gegenbauri* was a prominent constituent of this group. Salps were uncommon and were found chiefly between 1000 and 1600 m. Larvaceans were abundant and continuously distributed through the entire bathypelagic depth range (Fig. 3). At depths below 2300 m, the deepest occurrence of *Poeobius*, larvaceans were dominant and their numbers increased with depth; the highest counts were in the BBL. Similar patterns were observed in a deep BBL in the North Atlantic by Vinogradov (2005). The house sizes we recorded ranged from 2 cm to more than 35 cm, and most are undescribed species of the families Oikopleuridae and Fritillariidae; the common exception was *Fritillaria rex* (Hopcroft and Robison, 2005).

Crustacean detritivores included some copepods, mysids, and munnopsid isopods (Osborn, 2007, 2009). Their overall

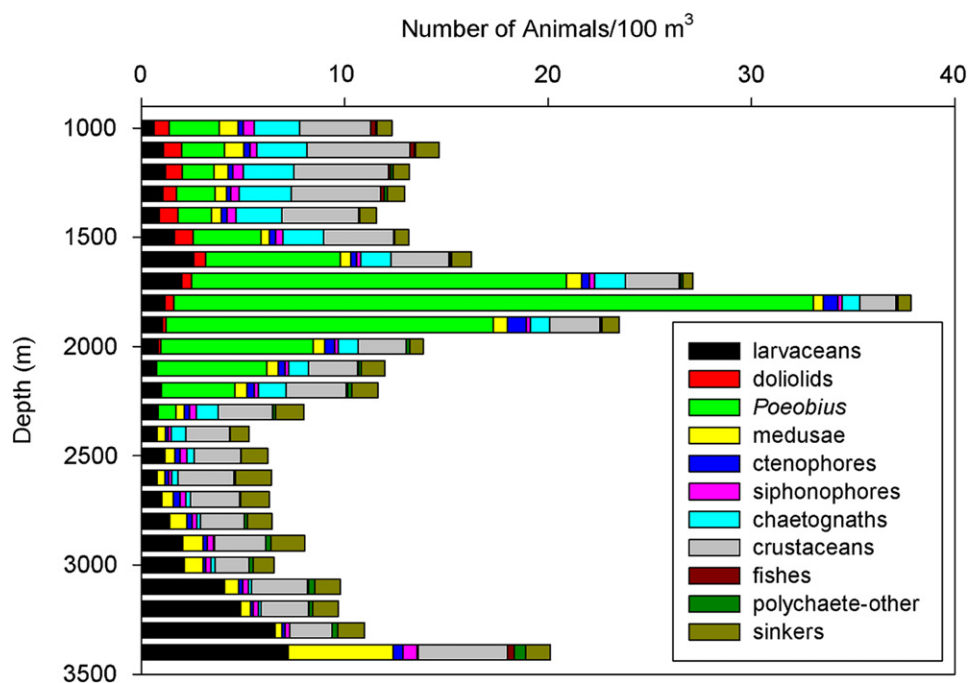


Fig. 3. Bathypelagic fauna recorded during oblique video transects over the Monterey Canyon. Animals were categorized into common groups, counted, and binned (pooled) within 100 m depth increments from 1000 to 3500 m. Volume for each transect was calculated using a 3-dimensional acoustic flowmeter. Colored bars represent the number of individuals recorded from each faunal group, normalized by the total volume transected within each depth increment. A total of 15 transects are represented.

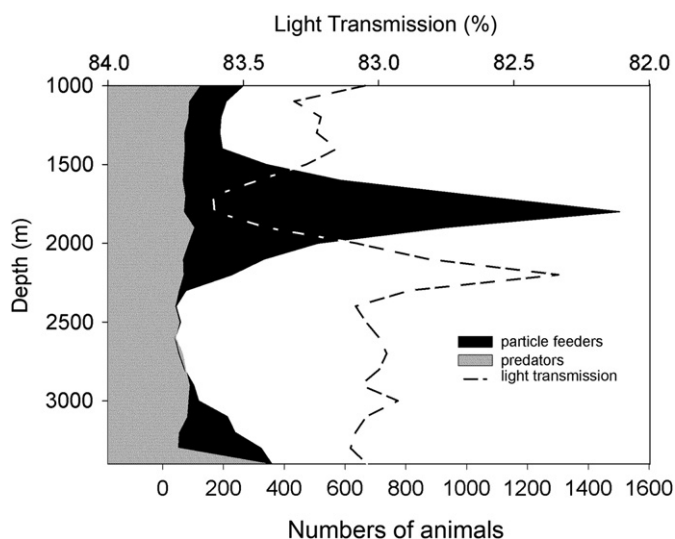


Fig. 4. Relative abundances of bathypelagic predators (chaetognaths, ctenophores, fishes, medusae, polychaetes, and siphonophores) and particle feeders (chiefly *Poeobius meseres*, copepods, larvaceans, salps, and doliolids). Total numbers of animals recorded from 15 video transects are plotted along with readings of % light transmission from an ROV-mounted transmissometer. The axis of the transmissometer data has been reversed, relative to that in Fig. 2. Light transmission is an inverse proxy for particle density; in this case, particle density increases from left to right.

abundance declined with depth to about 1800 m as *Poeobius* abundance peaked (Fig. 3); then remained relatively constant, with a spike in the BBL. Copepods showed a gradual decline in abundance with increasing depth. Mysids, although less abundant, mirrored the distribution of the copepods, and showed a large increase in the BBL. Munnopsid distribution was bi-modal around a dearth of observations from 1500 to 2800 m.

3.3. Predators

Gelatinous predators dominated the bathypelagic depth range and as a group they were consistently abundant from 1000 to 3500 m, with a spike in the BBL (Fig. 4). Chaetognaths were most abundant in the upper half of the bathypelagic depth range. Siphonophores were present within every depth interval. The great majority of these were small, diphyid calycophorans. Physonect siphonophores were widely distributed as well, and like the calycophorans they peaked in the BBL. A diverse group of medusae was also distributed throughout the surveyed depth range (Fig. 3) and there was considerable taxonomic variability with depth. One exception was the narcomedusa *Aegina* spp., which was observed at all depth levels. Lobate ctenophores were also widespread, with *Bolinopsis infundibulum* distribution centered at 1700 m and *Bathocyroe fosteri* centered at 2100 m. *Thalassocalyce inconstans*, while far less common, was also widely distributed in the vertical plane (Swift et al., 2009).

Fishes, while relatively uncommon, showed three vertical distribution patterns. *Bathylagus milleri*, *Serrivomer sector*, *Chauliodus macouni*, and *Cyclothone acclinidens/microdon* are all known from lower mesopelagic depths above 1000 m, and they were found in this bathypelagic survey as deep as 1800 m. Deep-living fishes that were found between 1200 and 2500 m included *Cyema atrum*, *Oneirodes acanthius/eschrichtii*, and *Cetostoma regani*. Fishes that were most common in the BBL but which were also found at least 800 m above the bottom included *Coryphaenoides* spp., *Careproctus* sp., and *Lycodapus mandibularis*. Squids, while common at mesopelagic depths, were rarely seen below 1000 m. The exception was *Gonatus onyx*, which descends to depths

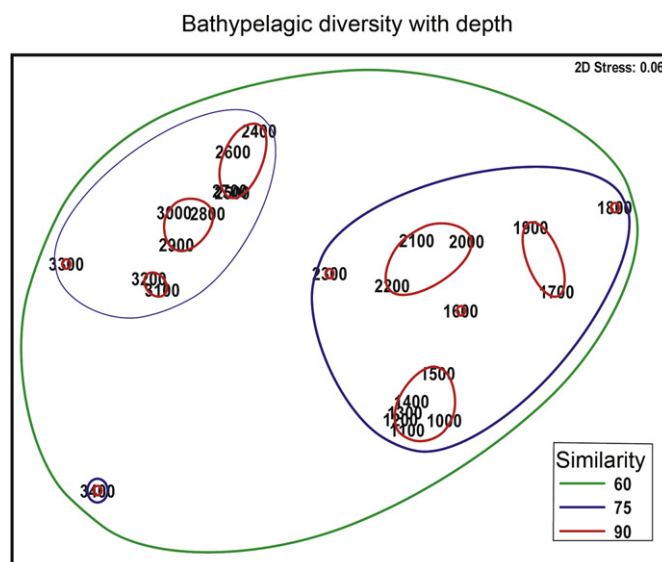


Fig. 5. Multi-dimensional scale (MDS) plot from 15 oblique bathypelagic transects conducted between the years 2003 and 2005. Bathypelagic fauna were standardized by volume, grouped, then binned over 100-m depth increments from 1000 to 3500 m. Each plotted number represents a 100-m depth bin and the 15 faunal counts made within that bin. Proximity indicates a given depth bin's similarity to any other depth bin in terms of faunal composition and abundance, for the groups of organisms presented in Fig. 3. Contours are used to group the depth bins by degree of similarity: 60, 75, and 90%. Data were normalized by volume transected, then square-root transformed prior to applying the MDS. Stress value indicates how well the n-dimensional data fit within a 2-dimensional representation. A stress value < 0.1 generally corresponds to a very good fit (Clarke and Warwick, 2001). The plot shows three principal faunal groups: upper bathypelagic, lower bathypelagic, and benthic boundary layer.

between 1500 and 2500 m to brood its eggs (Seibel et al., 2005). Predatory polychaete worms included tomopterids, which occurred above 1500 m, *Pelagobia* sp., found throughout the bathypelagic range, and the flabelligerid *Flota vitjasi* which was found in the BBL and up to 2800 m. Non-parasitic amphipods were observed in low numbers all through the depth range.

3.4. Other targets

The discarded mucus feeding filters of large larvaceans ("sinker") were observed throughout the water column (Fig. 3) as well as abundantly on the seafloor at 3500 m. These large, fast-sinking, nutrient-rich particles were observed being consumed by both benthic and pelagic animals. The constancy of sinker abundance in the depth profile suggests a steady rate of production. Sinkers provide a substantial portion of the organic carbon supplied to the deep benthos off Monterey Bay (Robison et al., 2005a, 2005b) although on a larger geographic scale their role in vertical carbon flux remains unmeasured (Burd et al., 2010). In addition to egg masses that were attended by squid, unattended gelatinous egg cases of several different sizes and configurations were observed.

3.5. Patterns of abundance and vertical distribution

Multi-dimensional scaling (MDS) analysis (Clarke and Warwick, 2001; Clarke and Gorley, 2006) showed broad similarities of faunal composition and abundance within each of three depth zones: upper bathypelagic, from 1000 to 2300 m; lower bathypelagic, from 2400 to 3300 m; and benthic boundary layer, below 3300 m (Fig. 5).

Smaller scale vertical distribution patterns were also apparent within the two bathypelagic zones (Fig. 3). From 1000 to 1500 m

the relative proportions of the gelatinous particle feeders, the crustacean particle feeders, and the gelatinous predators were constant. From 1600 to 1900 m, *Poeobius meseres* became the dominant species, while doliolids and larvaceans declined in importance. The proportional abundance of crustaceans and of gelatinous predators was similar to the layer above. The MDS faunal dissimilarities between 1600 m and 1900 m shown in Fig. 5 were due chiefly to the large spike in *Poeobius* abundance. From 2000 to 2200 m the numbers of *Poeobius* declined but it remained the most abundant faunal element. This changed at 2300 m (Fig. 3).

Beginning at 2400 m the lower bathypelagic zone showed a pattern of increasing abundance of larvaceans. Medusae also increased between 2400 and 3000 m; then declined from 3100 to 3300 m. At 3400 m the MDS analysis showed the beginning of the distinctly different benthic boundary fauna (Fig. 5). This group includes animals that feed only above the seafloor, such as lobate ctenophores, trachymedusae, diphyid and physonect siphonophores, larvaceans, and mysids; and those which feed both on and above the benthic interface, including the medusa *Benthocodon* sp., the polychaete *Flota vitjasi*, the isopod *Munneurycope*, the macrourid *Coryphaenoides acrolepis*, liparid fishes, and cydippid ctenophores.

MDS was also applied to transect data by dive series and by month. The results showed no apparent indication of seasonality. Over the 24 months of the survey, dive results tended to be more like those of dives made within days of each other than with those made months apart, but there were exceptions. These results suggest a slight change in faunal composition over time but a clear case of transition cannot yet be made.

4. Discussion

These oblique video transects are a new means of assessing the bathypelagic fauna. Like most emerging methodologies they arrive with both advantages and disadvantages. On the positive side, they provide accurate, high-resolution, quantitative data on the distribution and abundance of a much broader range of taxa than standard net tows. On the negative, samples of individual organisms are not collected because to do so would require stopping the ROV and breaking the continuity of the transect. For common animals it is usually possible to go back and collect samples after a transect; for a rare or exceptional specimen the options are to pass it by or break the transect.

Because their dominant vector is vertical, these transects resemble CTD profiles more than net tows, where the strongest component is horizontal. While this characteristic limits quantification along a depth horizon, it greatly improves resolution in the vertical plane. With multiple dives the needs of quantification can be met while retaining the benefits of precise vertical resolution. Our repeated observations that many more animals are seen during descents than ascents probably reflects disturbances caused by the vehicle's tether while rising, as well as the heightened defenses of animals to predatory threats from below (Barham, 1972; Herring, 2002).

Our 15 transects revealed a rich and diverse bathypelagic fauna above the outer extent of the Monterey Canyon. Gelatinous forms were abundant through the entire depth range. These animals constitute a substantial portion of the bathypelagic biomass and they dominate both of the trophic tiers they occupy. *Poeobius*, the larvaceans, and doliolids feed on particles and while at some depths their numbers are roughly equivalent to those of crustacean grazers, overall their soft-bodied architecture predominates. Chaetognaths, medusae, ctenophores, and siphonophores all feed on both hard- and soft-bodied detritivores, as well as on each other. Because these gelatinous predators are

frequently observed consuming other gelatinous predators, we cannot estimate the number of trophic steps involved in this portion of the bathypelagic food web. Nor can we yet assess the ultimate fate of the organic carbon in their bodies; except to invoke the poetry of Eugene Field's gingham dog and calico cat – who “ate each other up.”

The vertical patterns of relative abundance of trophic types that we measured do not reflect the patterns typical of data collected by net tows; where bathypelagic carnivores give way to omnivores, with increasing depth (e.g., Vinogradov and Tseitlin, 1983). The reason for this is most likely the selective differences between nets and in situ observations (Koppelman and Frost, 2008); nets sample larger volumes of water and select against gelatinous forms, while an ROV surveys smaller volumes of water and thus records fewer hard-bodied animals.

The principal faunal distinction between the upper and lower bathypelagic zones in our surveys was the shift from *Poeobius* to a variety of larvacean species as the dominant particle feeders (Fig. 3). Correlated with this depth-linked shift is a dramatic increase in particle density as the numbers of *Poeobius* declined (Fig. 4) followed by a gradual decrease in particles as the abundance of larvaceans increased.

The composition of the bathypelagic biota is noticeably different from the mesopelagic community above, although the two are inextricably linked (Burghart et al., 2007; Robinson et al., 2010). The absence of squids, except for brooding females, probably reflects their dependence on vision as a primary sensory system. On the other hand, fishes that have adapted to the bathypelagic habitat, without mesopelagic or benthic associations (e.g. *Cyema*, *Oneirodes*, and *Cetostoma*), typically have greatly reduced eyes and they rely on their other senses (Marshall, 1979). Other adaptations include maximizing the range of food types that can be utilized, as is the case with the carnivorous doliolid *Pseudusa bostigrinus* (Robison et al., 2005a). Another difference, when compared with the mesopelagic community, is the absence of predatory crustaceans like sergestids, which prey upon other metazoans.

A comparison of the bathypelagic community we observed, with assessments made using other methods in other regions, leaves little doubt that what we see is a function of how we look. Vereshchaka and Vinogradov (1999) surveyed bathypelagic plankton through the windows of the *Mir* submersibles over the Mid-Atlantic Ridge (MAR). They found patterns of depth-related abundance roughly similar to our data for fishes, chaetognaths, and gelatinous predators between 1000 and 3000 m. In contrast, they also found a large biomass of radiolarians, few larvaceans, and an overall planktonic fauna dominated by crustaceans. ROV surveys of gelatinous zooplankton reported by Youngbluth et al. (2008) found different patterns of relative abundance in different locations over the MAR; although like our study and that of Vinogradov (2005), larvaceans were found in increasing abundance approaching the bottom. No single technology is ideal for surveying all bathypelagic animals (Hosia et al., 2008) but the value of repeated ROV dives to study a resident community seems clear.

The deep pelagic biota is the largest and least known major faunal group on Earth. These animals represent an incomparable reservoir of global biodiversity, although we have yet to discover and describe the majority of the species. Protecting marine biodiversity on the high seas is common language in most international agreements regarding marine protected areas. But existing agreements focus almost exclusively on the deep seabed, while ignoring the great majority of species in the water column above. A principal reason for this situation is that we still lack an adequate understanding of these communities on a global scale. What we need is a biodiversity baseline, built upon data from

several geographic regions, that will allow us to determine the rates and directions of ongoing changes in deep pelagic systems, and to identify and quantify the ecosystem services they provide (Robison, 2009).

5. Summary and conclusions

1. Gelatinous animals dominated the bathypelagic fauna we observed.
2. *Poeobius meseres* played a major role in determining the characteristics of the bathypelagic community.
3. Discarded larvacean houses constituted a consistent source of large, nutrient-rich particles throughout the bathypelagic depth range.
4. The benthic boundary layer contained a large contingent of gelatinous animals, both particle feeders and predators.
5. Oblique, quantitative video transects provided an excellent small-volume, high resolution assessment of the bathypelagic fauna.
6. Biodiversity baselines of bathypelagic species are needed for conservation efforts.

Acknowledgments

We thank: Karen Osborn, Stephanie Bush, Susan von Thun, Annette Gough, Kyra Schlining, Kris Walz, Captain Ian Young and the crew of the R/V *Western Flyer*, and Chief Pilot Robert Reynolds and the pilots of the ROV *Tiburon*, for their contributions to this project. We also thank Steve Etchemendy, MBARI's Director of Marine Operations. This work was supported by the David and Lucile Packard Foundation.

References

- Barham, E.G., 1966. Deep scattering layer migration and composition: observations from a diving saucer. *Science* 151, 1399–1403.
- Barham, E.G., 1972. Deep-sea fishes: lethargy and vertical orientation. In: Farquhar, G.B. (Ed.), *Proceedings of an International Symposium on Sound Scattering in the Ocean*. Maury Center for Ocean Science, Washington, D.C., pp. 100–118.
- Barham, E.G., Ayer Jr., N.J., Boyce, R.E., 1967. Macrobenthos of the San Diego Trough: photographic census and observations from bathyscaphe, *Trieste*. *Deep-Sea Research* 14, 773–784.
- Bergstad, O.A., Falkenhaus, T., Astthorsson, O.S., Byrkjedal, I., Gebruk, A.V., Piatkowski, U., Priede, I.G., Santos, R.S., Vecchione, M., Lorange, P., Gordon, J.D.M., 2008. Towards improved understanding of the diversity and abundance patterns of the mid-ocean ridge macro- and megafauna. *Deep-Sea Research II* 55, 1–5.
- Bernard, F., 1958. Plancton et benthos observes durant trois plongees en bathyscaphe au large de Toulon. *Annales de l'Institut Oceanographique* 35, 287–326.
- Bishop, J.K.B., 1999. Transmissometer measurement of POC. *Deep-Sea Research I* 46, 353–369.
- Breaker, L.C., Broenkow, W.W., 1994. The circulation of Monterey Bay and related processes. *Oceanography and Marine Biology: an Annual Review* 32, 1–64.
- Burd, A.B., Hansell, D.A., Steinberg, D.K., Anderson, T.R., Aristegui, J., Baltar, F., Beupre, S.R., Buesseler, K.O., DeHairs, F., Jackson, G.A., Kadko, D.C., Koppelman, R., Lampitt, R.S., Nagata, T., Reinthaler, T., Robinson, C., Robison, B.H., Tamburini, C., Tanaka, T., 2010. Assessing the apparent imbalance between geochemical and biochemical indicators of meso- and bathypelagic biological activity: what the @#! is wrong with present calculations of carbon budgets? *Deep-Sea Research II* 57 (16), 1557–1571.
- Burghart, S.E., Hopkins, T.L., Torres, J.J., 2007. The bathypelagic Decapoda, Lophogastrida, and Mysida of the eastern Gulf of Mexico. *Marine Biology* 152, 315–327.
- Clarke, G.L., Backus, R.H., 1956. Light conditions in the sea in relation to the diurnal vertical migration and records of luminescence of deep-sea animals. *Deep-Sea Research* 4, 1–14.
- Clarke, K.R., Warwick, R.M., 2001. *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation* 2nd ed. PRIMER-E Ltd., Plymouth, UK.
- Clarke, K.R., Gorley, R.N., 2006. *PRIMER v6: User Manual/ Tutorial*. PRIMER-E Ltd., Plymouth, UK.
- Haddock, S.H.D., 2004. A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia* 530/531, 549–556.
- Hartman, O., Emery, K.O., 1956. Bathypelagic coelenterates. *Limnology and Oceanography* 4, 304–312.
- Herring, P., 2002. *The Biology of the Deep Ocean*. Oxford University Press, Oxford.
- Hopcroft, R.R., Robison, B.H., 2005. New mesopelagic larvaceans in the genus *Fritillaria* from Monterey Bay, California. *Journal of the Marine Biological Association of the United Kingdom* 85, 665–678.
- Hosia, A., Stemann, L., Youngbluth, M., 2008. Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. *Deep-Sea Research II* 55, 106–118.
- Isaacs, J.D., Tont, S.A., Wick, G.L., 1974. Deep scattering layers: vertical migration as a tactic for finding food. *Deep-Sea Research* 21, 65–656.
- Koppelman, R., Fabian, H., Weikert, H., 2003. Temporal variability of deep-sea zooplankton in the Arabian Sea. *Marine Biology* 142, 959–970.
- Koppelman, R., Frost, J., 2008. The ecological role of zooplankton in the twilight and dark zones of the ocean. In: Mertens, L.P. (Ed.), *Biological Oceanography Research Trends*. Nova Science Publishers, New York, pp. 67–130.
- Lindsay, D.J., Hunt, J.C., 2005. Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and northwestern Pacific. *Journal of the Marine Biological Association of the United Kingdom* 85, 503–517.
- Madin, L.P., Harbison, G.R., 1978. *Bathocyroe fosteri* gen. et sp. nov., a mesopelagic ctenophore observed and collected from a submersible. *Journal of the Marine Biological Association of the United Kingdom* 58, 559–564.
- Marshall, N.B., 1954. *Aspects of Deep Sea Biology*. Hutchinson, London.
- Marshall, N.B., 1979. *Developments in Deep-Sea Biology*. Blandford, Poole.
- Mauchline, J., 1972. The biology of bathypelagic organisms, especially Crustacea. *Deep-Sea Research* 19, 753–780.
- MBARI (Monterey Bay Aquarium Research Institute), 2009. Video Annotation and Reference System (VARS). MBARI, Moss Landing, CA Available at: <<http://www.mbari.org/vars/>>.
- McGowan, J., 1960. The relationship of the distribution of the planktonic worm, *Poeobius meseres* Heath, to the water masses of the North Pacific. *Deep-Sea Research* 6, 125–139.
- Opdal, A.F., Godø, O.R., Bergstad, O.A., Fiksen, Ø., 2008. Distribution, identity, and possible processes sustaining meso- and bathypelagic scattering layers on the Mid-Atlantic Ridge. *Deep-Sea Research II* 55, 45–58.
- Osborn, K.J., 2007. *Phylogenetics and ecology of pelagic munnopsid isopods (Crustacea, Asellota)*. Ph.D. Thesis, University of California, Berkeley.
- Osborn, K.J., 2009. Relationships within the Munnopsidae (Crustacea, Isopoda, Asellota) based on three genes. *Zoologica Scripta*, doi:10.1111/j.1463-6409.2009.00394.x.
- Peres, J.-M., 1958. Remarques generales sur un ensemble de quinze plongees effectuees avec le bathyscaphe F.N.R.S. III. *Annales de l'Institut Oceanographique* 35, 259–286.
- Robinson, C., Steinberg, D.K., Koppelman, R., Robison, B.H., Anderson, T.R., Aristegui, J., Carlson, C.A., Frost, J.R., Ghiglione, J.-F., Hernandez-Leon, S., Jackson, G.A., Queguiner, B., Ragueneau, O., Rassoulzadegan, F., Tamburini, C., Tanaka, T., Wishner, K.F., Zhang, J., 2010. Mesopelagic zone ecology and biogeochemistry – a synthesis. *Deep-Sea Research II* 57 (16), 1504–1518.
- Robison, B.H., 2004. Deep pelagic biology. *Journal of Experimental Marine Biology and Ecology* 300, 253–272.
- Robison, B.H., 2009. Conservation of deep pelagic biodiversity. *Conservation Biology* 23, 847–852.
- Robison, B.H., Raskoff, K.A., Sherlock, R.E., 2005a. Adaptations for living deep: a new, bathypelagic doliolid from the eastern North Pacific. *Journal of the Marine Biological Association of the United Kingdom* 85, 595–602.
- Robison, B.H., Reisenbichler, K.R., Sherlock, R.E., 2005b. Giant larvacean houses: rapid carbon transport to the deep sea floor. *Science* 308, 1609–1611.
- Seibel, B.A., Robison, B.H., Haddock, S.H.D., 2005. Post-spawning egg care by a squid. *Nature* 438, 929.
- Stemann, L., Hosia, A., Youngbluth, M.J., Søiland, H., Picheral, M., Gorsky, G., 2008. Vertical distribution (1–1000 m) of macrozooplankton, estimated using Underwater Video Profiler, in different hydrographic regimes along the northern portion of the Mid-Atlantic Ridge. *Deep-Sea Research II* 55, 94–105.
- Swift, H.F., Hamner, W.M., Robison, B.H., Madin, L.P., 2009. Feeding behavior of the ctenophore *Thalassocalyce inconstans*: revision of anatomy of the order Thalassocalycida. *Marine Biology* 156, 1049–1056.
- Uttall, L., Buck, K.R., 1996. Dietary study of the midwater polychaete *Poeobius meseres* in Monterey Bay, California. *Marine Biology* 125, 333–343.
- Vereshchaka, A.L., Vinogradov, G.M., 1999. Visual observations of vertical distribution of plankton through the water column above Broken Spur vent field, Mid-Atlantic Ridge. *Deep-Sea Research I* 46, 1615–1632.
- Vinogradov, M.E., Tseitlin, V.B., 1983. Deep-sea pelagic domain (aspects of bioenergetics). In: Rowe, G.T. (Ed.), *The Sea, Deep-Sea Biology*, Vol. 8. John Wiley & Sons, New York, pp. 123–165.
- Vinogradov, G.M., 2005. Vertical distribution of macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible “Mir-1”. *Marine Biology* 146, 325–331.
- Wishner, K.F., 1980. Near-bottom sound scatterers in the Ecuador Trench. *Deep-Sea Research* 27A, 217–223.
- Youngbluth, M., Sornes, T., Hosia, A., Stemann, L., 2008. Vertical distribution and relative abundance of gelatinous zooplankton, *in situ* observations near the Mid-Atlantic Ridge. *Deep-Sea Research II* 55, 119–125.