

THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

# Oceanography

## CITATION

Robison, B.H., K.R. Reisenbichler, and R.E. Sherlock. 2017. The coevolution of midwater research and ROV technology at MBARI. *Oceanography* 30(4):26–37, <https://doi.org/10.5670/oceanog.2017.421>.

## DOI

<https://doi.org/10.5670/oceanog.2017.421>

## COPYRIGHT

This article has been published in *Oceanography*, Volume 30, Number 4, a quarterly journal of The Oceanography Society. Copyright 2017 by The Oceanography Society. All rights reserved.

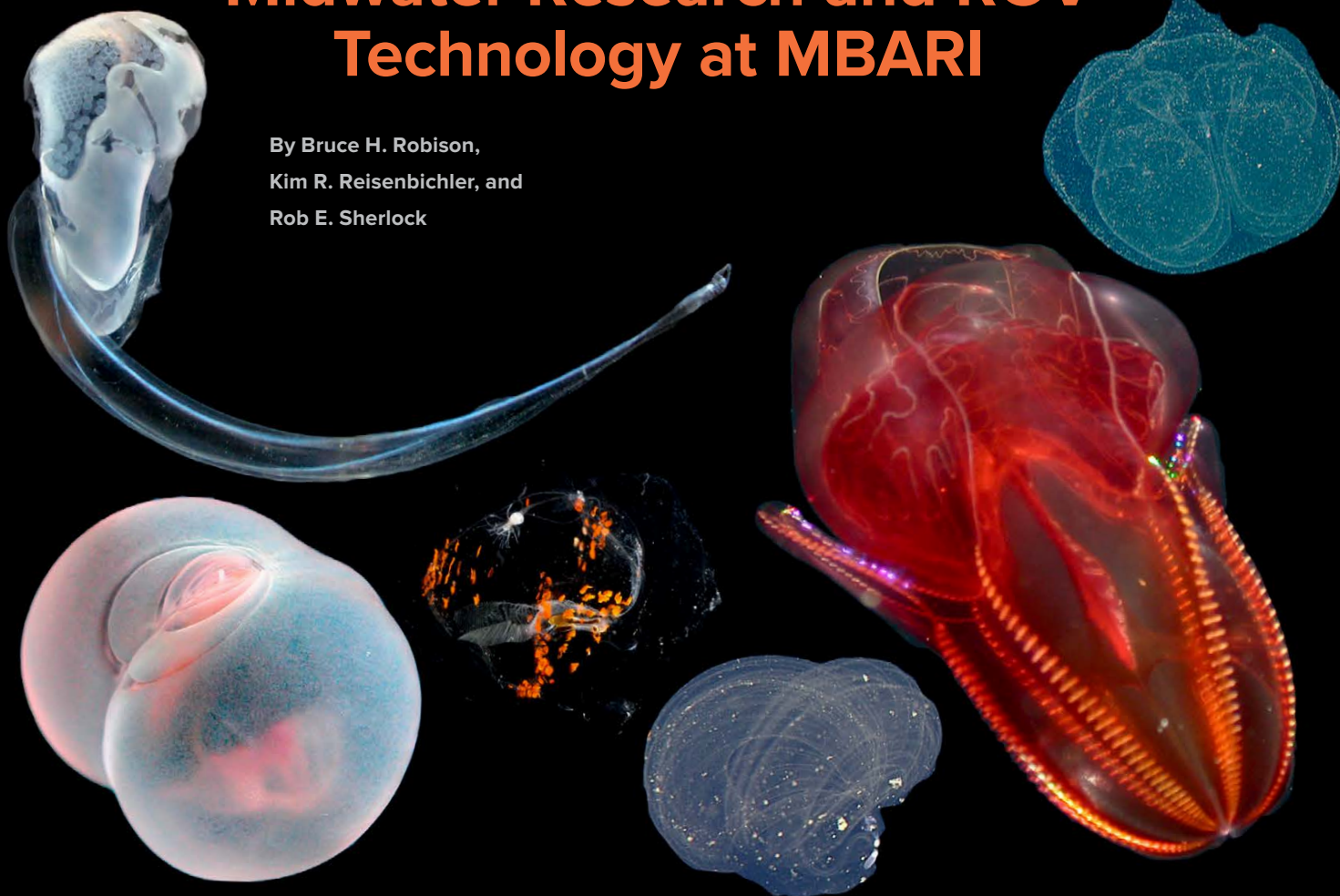
## USAGE

Permission is granted to copy this article for use in teaching and research. Republication, systematic reproduction, or collective redistribution of any portion of this article by photocopy machine, reposting, or other means is permitted only with the approval of The Oceanography Society. Send all correspondence to: [info@tos.org](mailto:info@tos.org) or The Oceanography Society, PO Box 1931, Rockville, MD 20849-1931, USA.



## The Coevolution of Midwater Research and ROV Technology at MBARI

By Bruce H. Robison,  
Kim R. Reisenbichler, and  
Rob E. Sherlock



Some of the “new” species, genera, and families described from MBARI’s midwater ROV program. Clockwise from upper left: *Kiyohimea usagi*, *Stellamedusa ventana*, *Pseudusa bostigrinus*, *Tiburonia granrojo*, *Mesochordaeus erythrocephalus*, *Lampocteis cruentiventer*, *Fritillaria rex*, *Doliolula equus* and *Bythotiara dolioequis*, *Chaetopterus pugaporcinus*, and *Bathochordaeus mcnutti*.

**ABSTRACT.** Coevolution is a process through which two interactive systems mutually influence each other's development. Midwater research and remotely operated vehicle technology are two such interactive systems, and at the Monterey Bay Aquarium Research Institute they have been coevolving for 30 years. As the technology has matured, the scope, scale, and complexity of the research has also advanced, particularly in such areas as observing animal behavior and in situ experimentation, which were virtually impossible before we gained direct access to the environment. Here we examine midwater research domains and the technologies that enable them: how new instrumentation enables in situ respiration and fluid dynamics measurements; how imaging and data handling systems build data sets that allow long-term analyses of seasonal, episodic, and anthropogenic environmental changes; and how variable ballast and thruster controls have allowed us to make close-up observations and conduct delicate experimental manipulations without disturbing the animals we are studying. The coevolution continues and future developments will focus on integrating diverse sensor systems to provide new perspectives for midwater ecology, and on automating research processes to expand the scale of operations, improve efficiency, and promote technology transfer.

## INTRODUCTION

Prior to the creation of the Monterey Bay Aquarium Research Institute (MBARI), no remotely operated vehicle (ROV)-based midwater research program had ever been attempted. We began our test dives in September 1988 and became operational before the end of that year. Our platform was *Ventana*, a 40 hp electro-hydraulic, work-class vehicle, purpose-built for MBARI by ISE in Canada. David Packard's mandate was that we would develop this oil rig support vehicle into a broadly capable research platform to serve both pelagic and benthic science needs. In 2017 *Ventana* made its 4,000<sup>th</sup> dive, a testament to Packard's vision and a record that exceeds the dive total of all other work-class scientific ROVs combined. Roughly a quarter of those dives were made for research in midwater.

What follows is an assessment of midwater research and development at MBARI as a coevolutionary process. Coevolution is a term coined by Ehrlich and Raven (1964) to define the interactive influence of two species, with each affecting the evolution of the other—the original case involved butterflies and plants. This concept can be readily applied beyond biology to include such things as the relationship between language and symbols, or between science and technology (Robison, 2000).

## GETTING STARTED

With no established research guidelines to follow, we developed our own, largely based on our experience with the one-person submersibles *WASP* and *Deep Rover* (Robison, 1983; Alldredge et al., 1984; Widder et al. 1989; Reisenbichler and Robison, 1991). An important early decision was that scientist and pilot would sit side-by-side in the control room of the ROV's surface support vessel, and that scientists would be an integral part of the operation: controlling cameras, sampling systems, instruments, and logging video data. Another critical decision was the commitment to an accessible, well-organized video database, which ultimately led to the development of VARS (Video Annotation and Reference System; Schlining and Stout, 2006).

The first rush of midwater discoveries was based on simple observation using a high-resolution video camera coupled to a high-quality 10x zoom lens. Our ROV video systems have evolved steadily over the years, and at present we are employing a high-definition Insite Zeus Plus (1080i) that gives us an 86° field of view at wide angle. Likewise, the lighting systems have matured from early quartz-halogen lamps to today's LEDs.

Once it became possible to work regularly at mesopelagic depths, the overwhelming realization was that the

number of gelatinous animals had been grossly underestimated by conventional midwater sampling methods, and that in general, the biomass of the world ocean's midwaters had been underestimated by at least a quarter (Pugh, 1989; Haddock, 2004; Robison, 2004). In addition, it was clear that the midwater realm was far more densely populated, complex, active, and ecologically structured than could have ever been appreciated by traditional methods employing nets and acoustics.

Coupled with our new observational capabilities was the need to collect specimens for identification and for the description of new forms. Many species observed in situ looked nothing like the illustrations of preserved specimens that accompanied their published descriptions, and this was particularly the case for gelatinous animals. For collecting purposes, we needed to look no further than two tools developed by the Harbor Branch Oceanographic Institute (HBOI) for use on their *Johnson-Sea-Link* submersibles: detritus or "D" samplers, and a suction sampler that feeds into a carousel of rotating sample containers. Over the years, we have improved the capabilities and reliability of these samplers, but the fundamental designs remain those of HBOI (Youngbluth, 1984; Robison, 1993).

*Ventana* is still in operation although its original support ship, the 110-foot (33.5 m) R/V *Point Lobos* has been replaced by the 135-foot (41.1 m) R/V *Rachel Carson*. In 1997, MBARI added the ROV *Tiburón* to our stable of undersea assets (Newman and Robison, 1993). *Tiburón* was an electric vehicle with a 4,000 m depth range, built in-house by MBARI engineers (Kirkwood et al., 2009). Deployed from our 117-foot (35.7 m) SWATH ship R/V *Western Flyer*, *Tiburón* made more than a thousand dives during its 10-year operational life, and while it was an excellent midwater research platform, its power and payload were judged to be inadequate for heavy benthic work. Its replacement, ROV *Doc Ricketts*, which came aboard in 2009, is a large, 75 hp electro-hydraulic vehicle with a 4,000 m

depth range, launched through the *Flyer*'s central moon pool (Figure 1). Like its predecessors, *Ricketts* is deployed as a single-body system. Without the complexities imposed by a tether management clump system, the single-body ROV has much greater maneuverability and responsiveness, particularly in midwater.

## LOCATION

MBARI's proximity to Monterey Submarine Canyon allowed us to adopt a unique operational mode for *Ventana*—day trips. *Rachel Carson* and *Ventana* typically leave the dock each morning at 0700 hrs and arrive at our reference dive site at about 0830. This allows for a full, six-hour dive day and gets us back to our home dock in Moss Landing by 1630 hrs. Because of the relatively short run back to shore after each dive, we are able to quickly bring freshly caught specimens into the controlled conditions of the seawater lab ashore, a factor that greatly enhances their long-term survival.

Our principal midwater dive site (Midwater One, at 36°42'N, 122°02'W) is located over the axis of the Monterey Submarine Canyon where the water

column depth is approximately 1,600 m. Seafloor depth declines rapidly to the west as the canyon descends, and the site is fully open to oceanic water. In 1928, Henry Bryant Bigelow conducted the first reconnaissance survey of the waters and plankton of Monterey Bay (Bigelow and Leslie, 1930), and this specific location was one of his deep stations. The site was subsequently occupied by Tage Skogsberg, who initiated the first long-term hydrobiological survey of Monterey Bay, which ran from 1929 to 1937 (Skogsberg, 1936; Skogsberg and Phelps, 1946). Rolf L. Bolin surveyed deep waters over the Monterey Canyon, including this station, in the 1950s (Bolin, 1964), and Eric G. Barham used acoustics and net tows to study midwater animal distribution patterns over the Canyon, also at this site (Barham, 1957). In addition, the midwater fauna at this location was sampled with nets in the 1970s (Robison, 1972) and in the 1980s with the submersible *Deep Rover* (Widder et al., 1989). The historical record of oceanographic conditions and biological patterns in the water column of Monterey Bay at this particular location reaches back over 80 years, and because

of this long record, we selected the site as MBARI's midwater reference station.

When we compare data from the historic surveys with the present day, we find both similarities and differences in the hydrography, species composition, relative abundance, and vertical distribution of animals in the deep water column—patterns that tell us how the midwater community has changed over the long term. The modern time-series data set has also revealed significant short-term variations that appear to reflect an accelerated rate of change due to human influence.

The need to expand the geographic scope of MBARI's operations led to the design and development of a second, more capable ROV support vessel, with longer endurance. Purpose-built for MBARI in 1995, R/V *Western Flyer* permits extended operations at greater distances from home than permitted by day trips, and we typically deploy for week-long midwater expeditions. During these trips, the ROV dive time increases to 12 hours each day, and we frequently operate in water depths down to 3,500 m. Due to the inherent stability of SWATH vessels, *Flyer* is an exceptionally suitable support ship for long, deep ROV operations. *Flyer*'s range has enabled us to make comparative surveys of the midwater communities in the Gulf of California, off the coasts of Washington and Oregon, and as far west as Hawai'i.

## TIME SERIES

In order to establish a database for investigating temporal patterns in the composition and dynamics of the Monterey Canyon midwater community, we initiated a time-series program based on quantitative video transects. Our approach is to fly the ROV at a constant depth and at a constant speed ( $55 \text{ cm s}^{-1}$ ) for 10 minutes. The first transect is run at a depth of 50 m, the second at 100 m, and subsequently at 100 m intervals down to 1,000 m. The main video camera is set at its widest angle and the distance traveled during each transect is measured with an acoustic current meter. Lighting is configured to fully illuminate the entire

a

b

c

d

**FIGURE 1.** MBARI's three work-class remotely operated vehicles (ROVs). (a) *Ventana* as originally configured, in 1988. (b) Upgraded *Ventana* in 2005. (c) *Tiburón* in the test tank. (d) *Doc Ricketts* launching through the moon pool of R/V *Western Flyer*.

viewing angle of the lens, up to 3 m in front of the vehicle.

In volumetric terms, each single-depth transect run is the visual equivalent of a four-minute haul with a trawl net that has a 10 m<sup>2</sup> mouth opening, or 1,270 m<sup>3</sup>. Over a 20-year span of the time series, the average number of animals annotated per transect, across all depth bins is 445 (range = 156–811). The most populous depth is 300 m. While the resolution of the video camera is adequate to resolve animals as small as copepods when the vehicle is moving slowly or stopped, at transect speeds targets smaller than about 8 mm are difficult to identify.

We conduct the transecting at a single site, our Midwater One reference station (above). The average frequency of transect dives has been about one per month since 1993. Transect videos are annotated within MBARI's VARS system. In the laboratory ashore, scientists annotate the video, identifying and logging all of the animals in each video frame. Each identification is then linked to that frame's timecode, along with all of the ancillary data collected simultaneously by the ROV: conductivity, temperature, oxygen, depth, particle density, date, and time. The midwater time series project has yielded a unique 25-year data set of the mesopelagic community in Monterey Bay; there is nothing else like it in the world. Further details of these transecting methods can be found in Robison et al. (2005b) and Katija et al. (2017b).

Data from the midwater time series have been used in a broad range of publications to provide a measure of the temporal variability of the patterns and processes being investigated. For example, the consistency with which giant larvaceans of the genus *Bathochordaeus* rapidly deliver high-quality organic carbon to the deep seafloor through their discarded filter houses was shown to comprise about a third of the food necessary to support the deep benthic communities in Monterey Bay (Robison et al., 2005b). Time-series data allowed us to quantify this carbon flux over a 10-year span and thus to

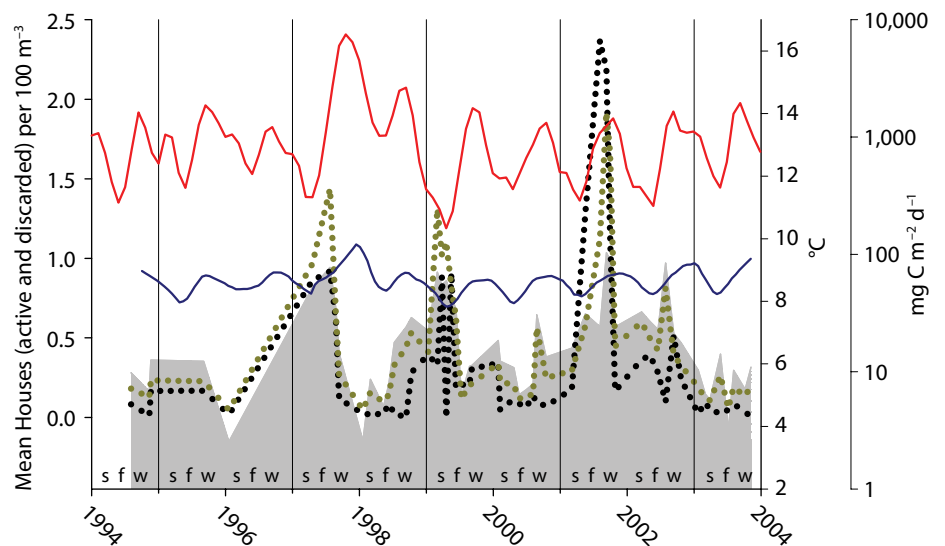
establish that it is an enduring, integral component of the regional deep-sea food web (Figure 2). As more is learned about the geographical distribution of giant larvaceans (Sherlock et al., 2016), it is becoming apparent that this process may be a global-scale carbon transport vector.

## TEMPORAL DYNAMICS

The time-series database also allows us to investigate patterns of distribution and abundance that reflect the temporal variability of populations, as well as changes in the composition of the midwater community. The abundant physonect siphonophore *Nanomia bijuga*, which is a principal predator of euphausiid krill, shows a clear pattern of seasonality in abundance and depth distribution (Figure 3) that is linked to the regional cycle of upwelling and primary production (Robison et al., 1998). The depth range of another group of small siphonophores, the rocketship calycophorans, that feed on copepods, was found to change seasonally in concert with upwelling, while their abundance did not (Silguero and Robison, 2000). In contrast, the vertical distribution of the foraminiferan *Hastigerinella digitata*, another copepod predator,

remained rigidly centered around 300 m between 1997 and 2008 without significant seasonal changes in abundance (Hull et al., 2011). Non-seasonal, episodic changes in hydrographic characteristics, such as those associated with El Niño events, are also reflected in the changing patterns of species composition and abundance in the midwater community (Raskoff, 2001).

Another kind of ecological dynamic revealed by the time-series data is that of an invasive species, the Humboldt squid, *Dosidicus gigas*. While *D. gigas* had occasionally occurred in Monterey Bay prior to the initiation of our ROV surveys, it did not appear in our transects until the El Niño event of 1997–1998. It disappeared as the waters cooled only to return again in 2002, after which it remained as a key predator in the pelagic community for the next five years (Figure 4). During this time, *D. gigas* abundance was strongly correlated with a significant decline in the commercially important ground fish—Pacific hake—*Merluccius productus* (Zeidberg and Robison, 2007; Stewart et al., 2014), and with a decrease in the population of the market squid *Doryteuthis opalescens*.



**FIGURE 2.** Carbon flux (gray area) to the deep seafloor and the abundance of active (dotted black line) and discarded (dotted green line) giant larvacean houses. Data collected in a 10-year ROV-based time series in Monterey Bay show a consistent supply of carbon over summer (s), fall (f), and winter (w) seasons. Integrated temperatures (at the surface, solid red line; at 200 m depth, solid blue line) were taken at a permanent mooring adjacent to the transect site. After Robison et al. (2005b)

## LIVE STUDIES

The ability to collect living animals in pristine condition and quickly return them to the lab ashore for long-term maintenance has led to unprecedented opportunities for experimental work in the laboratory. This capability gave rise to several significant advances in our understanding of the biological processes of midwater animals. Examples include: (1) measuring the effects of temperature on development in the siphonophore *Nanomia bijuga* (Sherlock and Robison, 2000); (2) determining that the medusa *Mitrocoma cellularia* responds to water-borne chemical cues for feeding (Tamburri et al., 2000); (3) learning that *Aequorea victoria* requires a dietary

source of luciferin for bioluminescence, despite its long-standing reputation for being an intrinsic source for this photoprotein (Haddock et al., 2001); (4) discovering new bioluminescent systems in *Vampyroteuthis infernalis* (Robison et al., 2003); (5) demonstrating the direct uptake of dissolved organic matter by gelatinous animals (Skikne et al., 2009); and (6) establishing that deep-sea squid species grow more slowly and live longer than their shallow-water counterparts (Hoving and Robison, 2017).

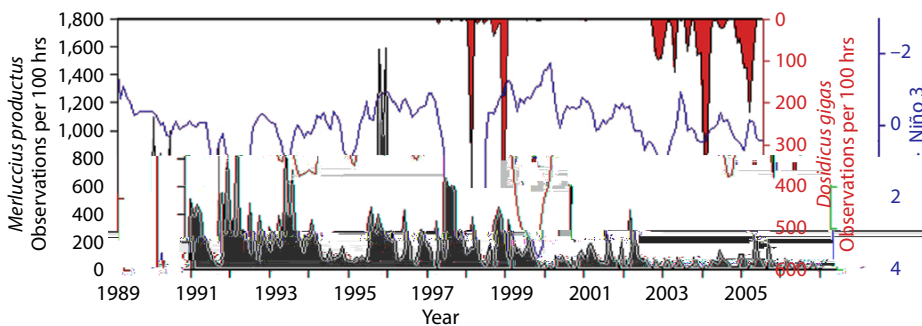
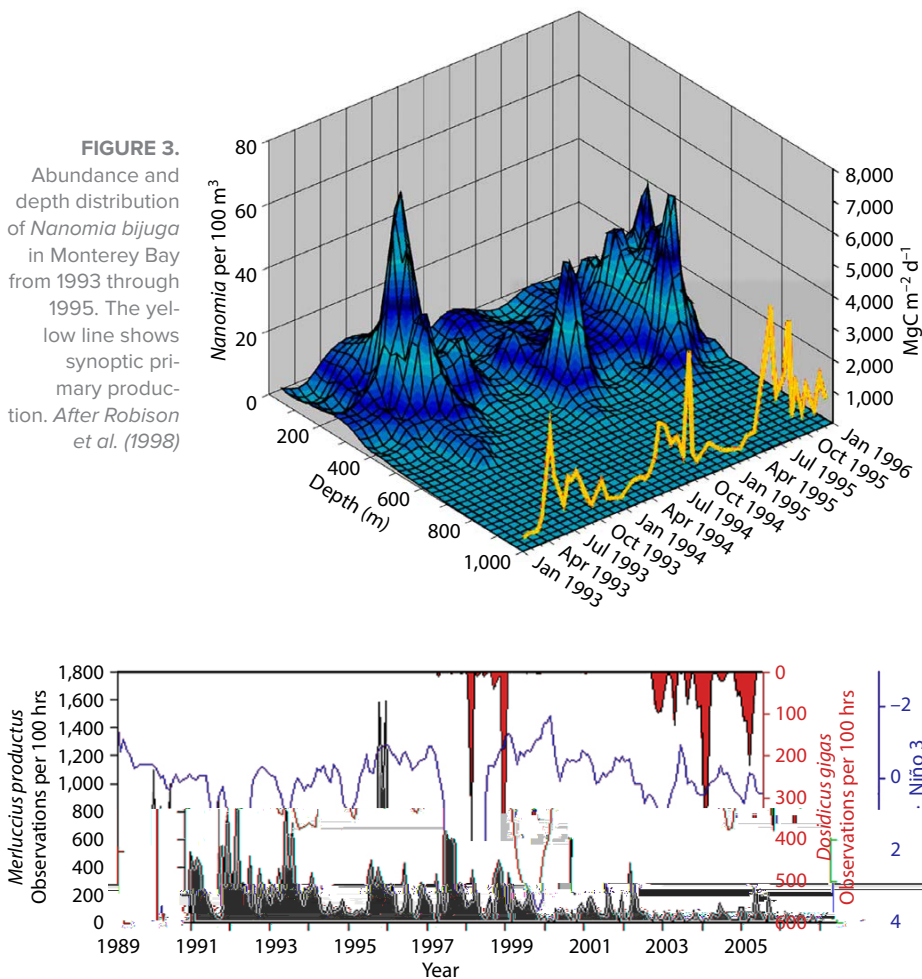
MBARI's ROVs also enable manipulative, experimental work to be conducted on live specimens in situ, following the institutional priority to “take the laboratory into the ocean.” In some cases,

this approach is used to confirm or refute hypotheses that have been tested first in the laboratory ashore (e.g., Tamburri et al., 2000; Bush, 2012). Another approach is to conduct the entire operation at depth with the ROV. An example of the latter is the deployment of an instrument—Deep Particle Image Velocimeter (DeepPIV)—to directly measure the grazing rates of giant larvaceans, which construct large mucus feeding filters that are too delicate to be investigated in the lab. The instrument uses a collimated laser sheet and a high-resolution camera to measure filtration rates by tracking fluid motion and particle trajectories within the highly structured filter (Katija et al., 2017b). When coupled with long-term abundance data from the midwater time series, the results show that the grazing impact of giant larvaceans far exceeds previous estimates for any pelagic filter feeder. Here again, the long-term data set affirms that this is yet another important and enduring carbon flux process in the food web of Monterey Bay, which probably occurs broadly in the world ocean.

A corollary, in situ DeepPIV investigation has shown that giant larvaceans are able to filter a range of microplastic particles from the water column, then ingest and package these particles into their fecal pellets. Microplastics also become embedded in the larvaceans' mucus filtration houses, which are regularly discarded to sink to the seafloor. Thus giant larvaceans can contribute significantly to the vertical flux of microplastics through the rapid sinking of their abandoned houses and their fecal pellets (Katija et al., 2017a).

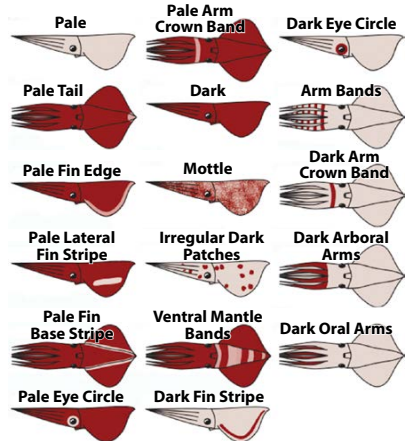
## BEHAVIOR

With our ROVs as platforms for observation, we have published a series of papers that define a new discipline of midwater research—animal behavior (e.g., Hunt et al., 2000; Drazen and Robison, 2004; Bush and Robison, 2007; Hoving et al., 2013). Because there is only so much that can be learned about behavior from a net-caught specimen, being able to accumulate behavioral observations in situ has



yielded a windfall of new kinds of information. In terrestrial behavior studies, different kinds of animals require different approaches for observing their behaviors, and the same applies in mid-water. Over time, MBARI scientists and pilots have learned how best to deal with certain species to enable our observations and manipulations. Variable ballast systems on our ROVs allow them to be trimmed to neutral buoyancy, minimizing vertical thruster use to hold position, while also increasing vehicle stability and stealth. Likewise, the ROV's control system can be shifted to utilize only the aft thrusters for maneuvering when close to an animal, thus reducing water disturbance around the target.

Results from our behavioral studies include the first ethograms ever published for deep pelagic species (Bush et al., 2009; Trueblood et al., 2015; Burford et al., 2015). These papers show how three squid species from different families all



**FIGURE 5.** *Octopoteuthis deletron* in a typical posture at depth; light and dark variations in chromatic pigmentation patterns as behavioral components in *O. deletron*. After Bush et al. (2009)

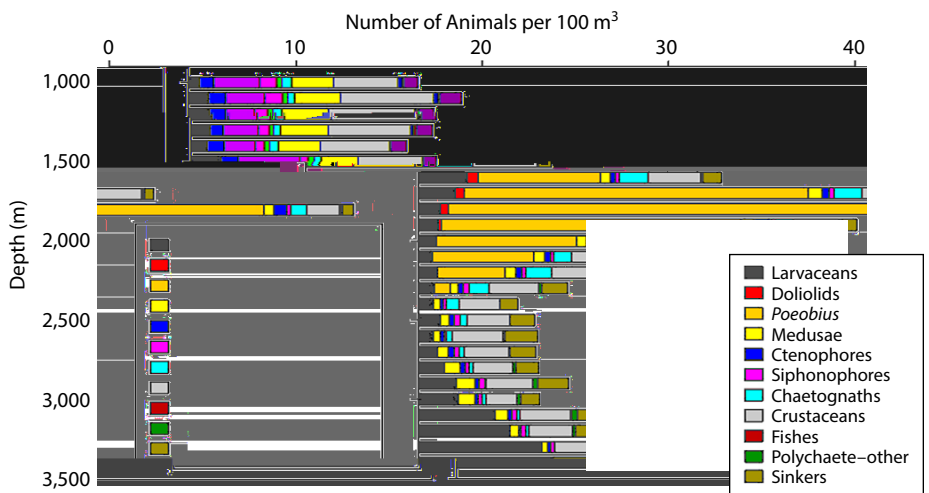
use pigmentation patterns, posture, locomotion, bioluminescence, and inking to communicate visually—this despite the low light levels of their environment. Specific combinations of these five components of communication are associated with particular behaviors. The observed communication patterns are like seeing the words in a text conversation but not knowing, yet, what the words mean (Figure 5). This is an intriguing area for future research in nonhuman communication, particularly because cephalopods are not known to communicate with each other acoustically (Moynihan, 1985).

In addition to species identifications and abundance, VARS annotations also include behavioral data (e.g., feeding, inking). Thus, it is possible to search the database and accumulate observations from throughout our long series of dive records. For example, the tails of juvenile squid *Chiroteuthis calyx* are typically oriented in the same direction as the siphosomes of the siphonophore *Nanomia bijuga* when they co-occur in the water column during periods of diel vertical migration (Burford et al., 2015). The squid tails closely resemble the nematocyst-laden siphosomes of the more numerous siphonophores (Vecchione et al., 1992), and statistical analyses strongly indicate that this

behavior is a case of mimicry. Likewise, the curling behavior of some zoarcid midwater fishes, chaetognaths, and tomopterid worms has also been identified as Batesian mimicry of medusae, as unpalatable models (Robison, 1999).

## BATHYPELAGIC

Midwater surveys below 1,000 m have been conducted principally by our deeper diving ROVs, *Tiburion* and *Doc Ricketts*. Transecting horizontally below 1,000 m is a challenge because of the drag and weight of the armored tether and the need to keep *Western Flyer* almost directly above the ROV. As a consequence, we conducted oblique video transects to quantify the fauna of Monterey Canyon between 1,000 m and 3,500 m depth to create the first-ever description of a bathypelagic community (Robison et al., 2010). These transects revealed a community dominated by gelatinous forms, with the aberrant polychaete *Poebobius meseres* playing an important role in structuring the vertical pattern of particle distribution. Larvaceans were also significant as detritivores, and their discarded feeding structures or “sinkers” were a consistent source of large, nutrient-rich particles throughout the bathypelagic depth range (Figure 6).



**FIGURE 6.** Bathypelagic fauna recorded during oblique video transects over Monterey Canyon. Animals were categorized into common groups, counted, and binned (pooled) within 100 m depth increments from 1,000 m to 3,500 m. Volume for each transect was calculated using a three-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. After Robison et al. (2010)

As a general rule, we have found that most bathypelagic animals do not long survive transit to the surface. Thus, we have had relatively little success in maintaining them in the lab. The few exceptions are crustaceans such as the mysid *Boreomysis californica*, some hyperiid amphipods, the asselote isopod *Munnopsis abyssali* that migrates regularly up to the lower mesopelagic, and (surprisingly) the bobtail snipe eel *Cyema atrum*. Adaptations to life in the bathypelagic habitat have resulted in some remarkable evolutionary transformations, such as that of the predatory doliolid *Pseudusa bostigrinus* (Robison et al., 2005a), which has assumed the apparently more appropriate body form of a medusa, as well as the medusa's appetite for copepods. Additional surprises among the residents of the water column below 1,000 m include an as yet unnamed bathypelagic nudibranch (Figure 7), five new polychaete species that release green bioluminescent "bombs," presumably as deterrents to predation (Osborn et al., 2009), and an extraordinary pelagic example of a typically benthic worm family that uses a combination of larval and adult features to remain permanently in the water column (Osborn et al., 2007).

## PHYSIOLOGY

Respiration rates are a proxy for metabolic rates, and as such they are valuable for characterizing the flow of nutrient



**FIGURE 7.** Figure 7. An undescribed bathypelagic nudibranch from Monterey Bay.

energy through a food web. In the past, respiration rates were measured on animals collected at depth and then subjected to decompression and thermal stress during trawl or vehicle recovery and their transfer to lab-based respirometers at surface pressures. In order to mitigate these problems we developed the Midwater Respirometry System (MRS), an instrument that measures oxygen consumption at depth—another example of “taking the laboratory into the ocean.”

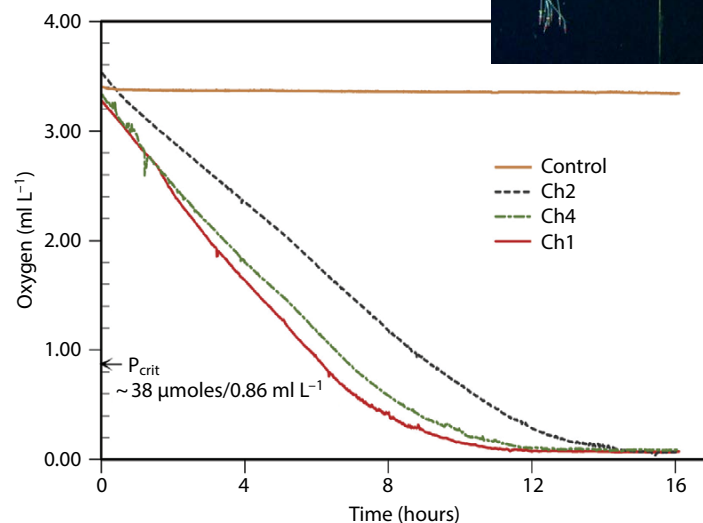
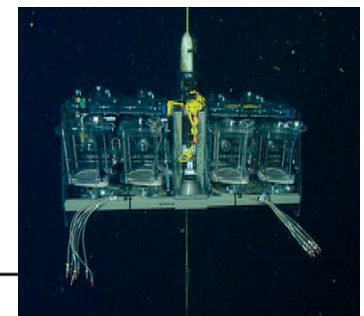
The MRS consists of eight chambers, each with an optode to measure oxygen concentration, a pumping system to flush and re-fill the chambers, and a computer to record data and control the instrument's functions. The chambers are derived from the D-samplers we use for animal collection. In operation, with the MRS attached to the front of the ROV, animals are collected in six of the chambers, while two are reserved as controls. Once the chambers are filled, the ROV flies to a mooring, the MRS hydraulics are decoupled, and the instrument is attached to a “hanger” at a depth similar to that at which the specimens were collected. The ROV flies away and typically returns 24 to 48 hours later, after one or more programmed incubations have taken place.

One goal of the respiration measurements is to determine the critical partial pressure of oxygen below which a

species can no longer regulate its oxygen consumption ( $P_{crit}$ ). Results to date indicate that some species show the same  $P_{crit}$  values in situ as they do when measured at one atmosphere; others have different values. We have used the  $P_{crit}$  value for the mesopelagic forage shrimp *Sergestes similis* to correlate the upward shift of its vertical distribution with the vertical expansion of Monterey Bay's well-developed oxygen minimum zone (Figure 8). Another MRS-based in situ study is examining how controlled changes in pH within the chambers affect the oxygen uptake patterns of squid, shrimp, and jellies.

## FEEDING AND FOOD WEBS

Feeding interactions and the assembly of trophic links into a food web are critical for understanding ecosystem structure, function, and energy flow. Data on feeding and food webs gathered by in situ methods is preferred over the traditional approach based on post-capture stomach content analyses, because the latter can be biased by net feeding, stomach



**FIGURE 8.** The Midwater Respirometry System deployed on its mooring; and oxygen consumption rate curves for *Sergestes similis*.



eversion, and rapid digestion of gelatinous prey. Our long-term access to the midwater habitat has yielded a series of publications that deal with the feeding patterns of individual species as well as of the midwater community as a whole. One of the principal ecological advances enabled by our ROVs was the discovery and documentation of an extensive and complex gelatinous fauna in deep water. As much as a quarter of total pelagic biomass may be incorporated into the bodies of these animals, and they can seasonally dominate the second and third trophic levels of midwater communities. These animals were substantially undersampled by conventional methodologies, and with the advent of undersea vehicles, the “jelly web” is now recognized as a significant component of midwater ecosystems worldwide (Robison, 2004).

Multiple observations of feeding by individual species reveal striking differences in the ways that different predators consume the same type of prey. Both the siphonophore *Nanomia bijuga* and the ctenophore *Thalassocalyce inconstans* feed on euphausiid krill. The former uses nematocyst batteries on its tentacles to stun and capture, while the latter gently enfolds the same prey in a soft, sticky lobe (Robison 2004; Swift et al., 2009). In contrast, the Humboldt squid, *Dosidicus gigas*, uses its highly dexterous arm tips to pluck individual krill from the water.

In situ observations have also revealed similarities and subtle distinctions in feeding by disparate species. The munnopsid isopod *Acanthamunnopsis milleri* collects particulate matter from the surrounding water using fine, stiff bristles distributed along its elongate arms, then draws the arms past its mouth to remove the accumulated food (Osborn, 2008). We have observed the pelagic red crab *Pleuroncodes planipes* feeding in a similar manner. In contrast, another munnopsid isopod, *Munneurycope murrayi*, collects aggregated marine snow such as discarded larvacean houses (Osborn, 2008) from the water column. The long, retractile filaments of the vampire squid,

*Vampyroteuthis infernalis*, were widely believed to be sensory structures until they were observed in situ being used to collect detritus and marine snow aggregates, which were subsequently drawn through the arms and to the mouth for ingestion (Hoving and Robison, 2012). In all of these cases, gut content analyses alone would not have allowed us to distinguish between these feeding modes and food types.

A detailed investigation of the feeding of abundant squids in the genus *Gonatus* involved mining the VARS database for adventitious observations of feeding, as well as targeted dive time to seek out these predators. The surprising results showed that in addition to the micronektonic fishes we expected them to consume (Figure 9), gonatid squids also exhibited a high degree of cannibalism upon their own species as well as on congeners (Hoving and Robison, 2016). Searching the VARS database with a much broader scope has yielded a detailed description of the deep pelagic food web of Monterey Bay (Choy, et al., 2017). Based on 743 independent feeding events, the results indicate that gelatinous predators—siphonophores, medusae, and ctenophores—are key carnivores, comparable to fish and squid in their importance within the food web. This study also examines how gelatinous predators, once believed to be a trophic “dead-end,” are fully integrated into overall food web structure.

## REPRODUCTION

The ability to make in situ observations has revealed unanticipated aspects of reproduction among squids. The first case of parental care by a squid was confirmed by ROV *Tiburón* when it came upon a female *Gonatus onyx* brooding a clutch of 2,000–3,000 eggs at a depth of 2,500 m (Seibel et al., 2005). Prior to this discovery, all squids were believed to either deposit their eggs on the seafloor or to release them in floating egg masses; in either case, the eggs were left to develop on their own. Subsequent dives by *Tiburón* and *Doc Ricketts* confirmed that a



**FIGURE 9.** Black-eyed squid *Gonatus onyx* manipulating its prey, the larger owlfish *Bathylagus milleri*, so that it can sever the fish’s spinal cord with its beak to render it immobile for consumption.

brooding *G. onyx* descends to depths well below the normal depth range of this species and once there, carries her eggs in her arms for the six- to nine-month brooding period. Another squid, *Bathyteuthis berryi*, was later found to brood its eggs in a similar fashion (Bush et al., 2012), and we now believe that this reproductive mode is common among deepwater squid species. Additional discoveries have confirmed same-sex sexual behavior in *Octopoteuthis deletron* (Hoving et al., 2012) and a pulsed semelparous reproductive strategy in *Vampyroteuthis infernalis* that is unique among coleoid cephalopods (Hoving et al., 2015).

## “NEW” SPECIES

An inevitable result of exploring the midwater habitat with our ROVs has been the discovery of many animals that were previously unknown to science. Most of them have been gelatinous forms—delicate, often ephemeral creatures that were so damaged during capture by nets as to be unrecognizable. Because our vehicles can trim to neutral buoyancy and

attenuate their forward thrusters, we can observe and collect specimens without disrupting or damaging them. One benefit of seeing these animals in their natural habitat, before collecting and describing them, is that we can determine how various body parts fit together and function. Examining an unknown species in context, watching it swim, feed, and react, provides an invaluable perspective when it comes to describing it. In the case of an animal that has radically changed its configuration while adapting to an extreme habitat (e.g., the bathypelagic doliolid that looks and acts like a medusa; Robison et al., 2005a), these clues are vital.

Some midwater species are so fragile that they are virtually uncollectable. After being brought to the surface and gently placed into a container for preservation, the specimens disintegrate, and we are left with what looks like a jar of water. A case in point includes the lobate ctenophores *Kiyohimea usagi* and *Lampocteis cruentiventer* (Matsumoto and Robison, 1992; Harbison et al., 2001). Museum jars containing the holotypes of these species appear to have nothing in them but preservative and a scattering of ctenes across the bottom. For both of these “new” animals, it is the detailed video

footage, deposited along with the type “specimens,” that provides the vouchers for verification. For large larvacean species, the external feeding filters can be critical criteria for characterization, but these structures are likewise so delicate that they can only be described from in situ observations (Hamner and Robison, 1992; Hopcroft and Robison, 1999; Sherlock et al., 2017).

## SUBJECTIVE RESULTS

Much of what we have learned during 30 years of in situ midwater research cannot be, or has not yet been, quantified. Nevertheless, some of what we have observed bears repeating, if not as objective data, then at least as hard-won glimpses into the workings of midwater communities.

- Midwater animals anticipate threats from below. Many daytime predators align their bodies vertically and direct their sightlines upward to detect the silhouettes of potential prey. This aspect of community behavior is illustrated in Figure 10, which shows no response from animals in a sonic scattering layer when approached laterally or from above. When approached from below, however, the aggregation disperses.

- A correlate observation is that we see more animals when descending with the ROV than we see during ascent—surely a consequence of the tether above the vehicle. This is why we run our transect series from the top, down.
- We see more animals, particularly fishes, from electrically powered vehicles than from hydraulic ones. The reason is undoubtedly the loud and high-pitched noise produced by hydraulic pumps.
- We are well aware that the presence of a large, loud object that projects unnatural levels of light into an otherwise dim and quiet habitat will surely bias some of our observations. Using the ROV scanning sonar we can see that some targets hang just outside the vehicle’s light field, while others are just as clearly drawn in to the light. Efforts to measure this effect have been somewhat successful (Widder et al., 2005) but overall the impact of our presence must always be kept in mind when interpreting our results.

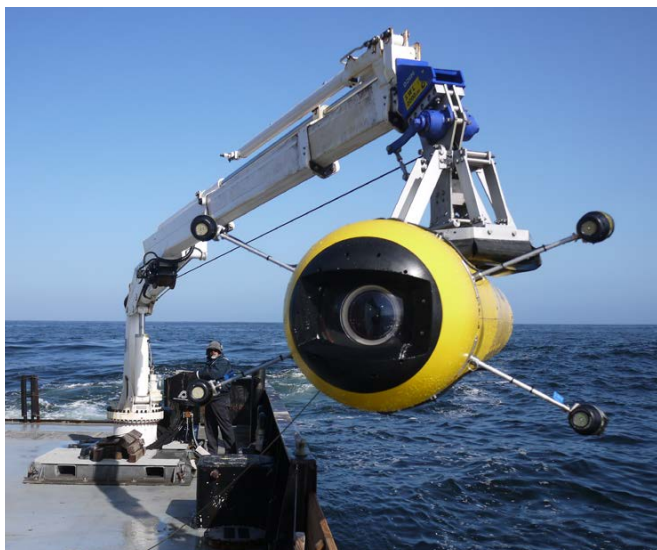
## LOOKING FORWARD

Despite the global significance of the deep pelagic fauna and the obvious benefits of preserving its biodiversity, the basic information necessary to do so is still lacking. A long-term goal of MBARI’s midwater research projects is to resolve the basic characteristics of pelagic community structure and dynamics, such that we can identify and model the fundamental ecological components. While the species that occupy these ecological niches may vary over time and from place to place, the basic structural patterns should remain consistent. This model will be a baseline that can be monitored to assess the impacts of climate change. It can also be used to identify appropriate areas for deep pelagic marine protected areas. This new knowledge may also serve as the foundation for comparative studies of change and ocean health in other geographic regions, with communities comprised of different species yet fundamentally similar in their basic ecological structure.

**FIGURE 10.** A 38 kHz acoustic profile of the path of ROV *Tiburón* (red line) through a sonic scattering layer in the Gulf of California. The ROV track runs chiefly from 250 m to 350 m depth. The parallel blue track is backscatter from the system’s compass, which rides the tether about 50 m above the vehicle. Observations from *Tiburón* revealed the layer to be composed principally of the myctophid fish *Triphoturus mexicanus*.

The scientific and conservation value of MBARI's midwater time series is well established, and in order to ensure its continuation we have developed the means to reduce its cost through automation. We have tested an imaging system (i2MAP) mounted on an autonomous underwater vehicle (AUV) that can be programmed to conduct video transects with the same depth and duration profiles as those we run with the ROVs. The camera and lights mounted on a *Dorado* AUV provide transect images of equal or better quality than we have obtained with the ROVs (Figure 11). Because the battery-powered AUV is significantly quieter than the hydraulic ROVs, it appears that this new approach reduces avoidance. Likewise, increasing the frame rate at which the video is recorded allows the AUV to travel faster than an ROV does while transecting, which also appears to reduce avoidance. We anticipate that ongoing, side-by-side comparisons of the two systems will show an overall improvement in the number and diversity of animals recorded. Reducing the costs of fielding an automated video transecting system should facilitate technology transfer, so that other institutions can conduct midwater surveys to suit their interests, or generate comparable data from their own regions, and contrast them with the reference community in Monterey Bay. It will also allow MBARI to expand its regional midwater survey coverage beyond our single site (Reisenbichler et al., 2016).

The next step forward for this technology will be to integrate our optical imaging systems with acoustic systems on the same platform. The goal of this effort will be to provide simultaneous measurements of the midwater community from these two complementary sensory perspectives. Acoustic imaging will give us the broad picture because of its ability to insonify a large volume of water. The optical imaging will allow us to identify the sources of the backscatter signals that comprise the acoustic targets. Preliminary tests conducted with the two systems mounted on ROV *Ventana* have



**FIGURE 11.** *Dorado* AUV with the i2MAP imaging package mounted in the vehicle's nose. LED lights ride the X-mounts.

the eventual goal of combining them on a *Dorado* AUV for autonomous surveys. This hybrid approach will allow us to investigate new categories of questions, such as the apparent, order-of-magnitude discrepancies between mesopelagic fish biomass as measured by acoustics and by trawling (Irigoién, et al., 2014).

MBARI is working with colleagues from Stanford University and the Woods Hole Oceanographic Institution, with funding from the National Science Foundation, to develop *Mesobot*, an AUV designed for mesopelagic missions. *Mesobot* is a new class of small, agile vehicles that is specifically designed to enable unprecedented scientific access to the midwater habitat. The vehicle will use cameras to non-invasively follow individuals and aggregations of midwater animals. With endurance exceeding 24 hours, survey tasks will follow animals as they undertake diel vertical migrations. Use-case missions include: watching a giant larvacean build, use, and discard a filter-house; following a predatory siphonophore or medusa to measure feeding frequency and prey diversity; measuring the daily ambits of migratory and non-migratory grazing salps. For many missions, *Mesobot* will begin with a lightweight tether that will enable control by a human pilot. After acquiring a target of interest, the tether will be disconnected and the vehicle will complete

the mission autonomously.

Future directions for technology development in support of midwater research also encompass the following: expanding the DeepPIV instrument from planar to volumetric measurements, thus providing for three-dimensional analyses; developing a bioelectric field sensor to afford an entirely new sensory perspective on the midwater habitat; developing automated image recognition software to speed up the VARS annotation process; using red-light imaging systems to increase the stealthiness of our vehicles; developing chemosensory instruments; and deploying swarms of stealthy, integrated microbots to survey the three-dimensional midwater habitat from a three-dimensional perspective.

## PREDICTIONS

Declining oxygen concentrations (Gilly et al., 2013) will have a substantial impact on midwater communities. Based on our results to date, we can make the following predictions about the future of the mesopelagic community in Monterey Bay:

- Hypoxia-tolerant species will find their habitats expanded both vertically and horizontally.
- Shoaling of the oxygen minimum zone will expose some mesopelagic species to greater pressure from visually cued predators as they relocate nearer to the surface.


- Species that do not undertake diel vertical migrations will shift their depth distributions or face continuous exposure to lower ambient oxygen at their preferred depths.
- Some species will be displaced vertically; others will not. This will result in the fragmentation and reassembly of community groups, establishing new patterns of competition and interaction.
- Gelatinous predators, because of their apparent tolerance of hypoxia, may increase in relative abundance.
- High-performance top predators with high oxygen requirements (e.g., tunas, salmon) may relocate geographically as oxygen declines, while opportunistic, hypoxia-tolerant species (e.g., squid) may replace them.

## CONCLUSIONS

The ocean's midwaters comprise the largest living space on Earth, and within this vast habitat are the planet's largest and least-known major animal communities (Robison, 2009). MBARI's midwater ecology projects provide the world's only community baseline for measuring the effects of climate change on the ecology of the deep water column. The continuing coevolution of our technology and science promises higher resolution, larger scales, and greater precision for understanding the structure and dynamics of these communities—as well as breakthroughs we can only imagine.

In his welcoming remarks at the inaugural meeting of The Oceanography Society, David Packard (1989) said: "As I am sure you all know, progress in scientific research is highly dependent on the instrumentation and equipment available to the scientists doing the research. To deal with this problem more effectively, we have established a management structure in which the scientists and engineers are working in parallel with each other, in personal contact on a daily basis. This arrangement greatly facilitates communication, eliminates reams of paper work, and as I had hoped, is working extremely well." Whether or not we realized it at the

time, coevolution has been at MBARI's core from the outset. What we've also learned from these collaborations, beyond the technological and scientific advances themselves, is that it's not just the tools that enable us, but how we use them.

During MBARI's early years, one of our institutional challenges was the question—"does science drive technology or is it the other way around?" With regard to midwater research, we can confidently say that at MBARI, science challenges technology and technology inspires science. 

## REFERENCES

- Allredge, A.L., B.H. Robison, A. Fleminger, J.J. Torres, J.M. King, and W.M. Hamner. 1984. Direct sampling and in situ observation of a persistent copepod aggregation in the mesopelagic zone of the Santa Barbara Basin. *Marine Biology* 80:75–81, <https://doi.org/10.1007/BF00393130>.
- Barham, E.G. 1957. *The Ecology of Sonic Scattering Layers in the Monterey Bay Area*. PhD thesis, Stanford University, Palo Alto, CA.
- Bigelow, H.B., and M. Leslie. 1930. Reconnaissance of the waters and plankton of Monterey Bay, July 1928. *Bulletin of the Museum of Comparative Zoology at Harvard College* 52:430–581.
- Bolin, R.L. 1964. Hydrographic data from the area of the Monterey Submarine Canyon, 1951–1955. Final Report, Stanford University, Hopkins Marine Station, Pacific Grove, CA, 12 pp.
- Burford, B.P., B.H. Robison, and R.E. Sherlock. 2015. Behaviour and mimicry in the juvenile and subadult life stages of the mesopelagic squid *Chiroteuthis calyx*. *Journal of the Marine Biological Association of the United Kingdom* 95:1,221–1,235, <https://doi.org/10.1017/S0025315414001763>.
- Bush, S.L. 2012. Economy of arm autotomy in the mesopelagic squid *Octopoteuthis deletron*. *Marine Ecology Progress Series* 458:133–140, <https://doi.org/10.3354/meps09714>.
- Bush, S.L., H.J.T. Hoving, C.L. Huffard, B.H. Robison, L.D. Zeidberg. 2012. Brooding and sperm storage by the deep-sea squid *Bathyteuthis berryi* (Cephalopoda: Decapodiformes). *Journal of the Marine Biological Association of the United Kingdom* 92:1,629–1,636, <https://doi.org/10.1017/S0025315411002165>.
- Bush, S.L., and B.H. Robison. 2007. Ink utilization by mesopelagic squid. *Marine Biology* 152:485–494, <https://doi.org/10.1007/s00227-007-0684-2>.
- Bush, S.L., B.H. Robison, and R.L. Caldwell. 2009. Behaving in the dark: Locomotor, chromatic, postural, and bioluminescent behaviors of the deep-sea squid *Octopoteuthis deletron* Young 1972. *Biological Bulletin* 216:7–22, <https://doi.org/10.1086/BBLv216n1p7>.
- Choy, C.A., S.H.D. Haddock, and B.H. Robison. 2017. Deep pelagic food web structure as revealed by in situ feeding observations. *Proceedings of the Royal Society B* 284:20172116, <https://doi.org/10.1098/rspb.2017.2116>.
- Drazen, J.C., and B.H. Robison. 2004. Direct observations of the association between a deep-sea fish and a giant scyphomedusa. *Marine and Freshwater Behaviour and Physiology* 37(3):209–214, <https://doi.org/10.1080/10236240400006190>.
- Ehrlich, P.R., and P.H. Raven. 1964. Butterflies and plants: A study in coevolution. *Evolution* 18:586–608, <https://doi.org/10.1111/j.1558-5646.1964.tb01674.x>.
- Gilly, W.F., J.M. Beman, S.Y. Litvin, and B.H. Robison. 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annual Review of Marine Science* 5:393–420, <https://doi.org/10.1146/annurev-marine-120710-100849>.
- Haddock, S.H.D. 2004. A golden age of gelata: Past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia* 530/531:549–556, <https://doi.org/10.1007/s10750-004-2653-9>.
- Haddock, S.H.D., T.J. Rivers, and B.H. Robison. 2001. Can coelenterates make coelenterazine? Dietary requirement for luciferin in cnidarian bioluminescence. *Proceedings of the National Academy of Sciences of the United States of America* 98(20):11,148–11,151, <https://doi.org/10.1073/pnas.201329798>.
- Hamner, W.M., and B.H. Robison. 1992. In situ observations of giant appendicularians in Monterey Bay. *Deep Sea Research* 39:1,299–1,313, [https://doi.org/10.1016/0198-0149\(92\)90070-A](https://doi.org/10.1016/0198-0149(92)90070-A).
- Harbison, G.R., G.I. Matsumoto, and B.H. Robison. 2001. *Lampocteis cruentiventer* gen. nov., sp. nov.: A new mesopelagic lobate ctenophore, representing the type of a new family (Phylum Ctenophora (Class Tentaculata, Order Lobata, Family Lampoctenidae, fam. nov.). *Bulletin of Marine Science* 68:299–311.
- Hopcroft, R.R., and B.H. Robison. 1999. A new mesopelagic larvacean, *Mesochordaeus erythrocephalus*, sp. nov., from Monterey Bay, with a description of its filtering house. *Journal of Plankton Research* 21:1,923–1,937, <https://doi.org/10.1093/plankt/2110.1923>.
- Hoving, H.J.T., S.L. Bush, and B.H. Robison. 2012. A shot in the dark: Same-sex sexual behavior in a deep-sea squid. *Biology Letters* 8(2):287–290, <https://doi.org/10.1098/rsbl.2011.0680>.
- Hoving, H.J.T., V.V. Laptikhovskiy, and B.H. Robison. 2015. Vampire squid reproductive strategy is unique among coleoid cephalopods. *Current Biology* 25(8):R322–R323, <https://doi.org/10.1016/j.cub.2015.02.018>.
- Hoving, H.J.T., and B.H. Robison. 2012. Vampire squid: Detritivores in the oxygen minimum zone. *Proceedings of the Royal Society B* 279(1747):4,559–4,567, <https://doi.org/10.1098/rspb.2012.1357>.
- Hoving, H.J.T., and B.H. Robison. 2016. Deep-sea in situ observations of gonatid squid and their prey reveal high occurrence of cannibalism. *Deep Sea Research Part I* 116:94–98, <https://doi.org/10.1016/j.dsr.2016.08.001>.
- Hoving, H.J.T., and B.H. Robison. 2017. The pace of life in deep dwelling squids. *Deep Sea Research Part I* 126:40–49, <https://doi.org/10.1016/j.dsr.2017.05.005>.
- Hoving, H.J.T., L.D. Zeidberg, M.C. Benfield, S.L. Bush, M. Vecchione, and B.H. Robison. 2013. First in situ observations of the rare deep-sea squid *Grimalditeuthis bonplandi* reveal unique use of tentacles. *Proceedings of the Royal Society B* 280:20131436, <https://doi.org/10.1098/rspb.2013.1463>.
- Hull, P.M., K.J. Osborn, R.D. Norris, and B.H. Robison. 2011. Seasonality and depth distribution of a mesopelagic foraminifer, *Hastigerinella digitata*, in Monterey Bay, California. *Limnology and Oceanography* 56(2):562–576, <https://doi.org/10.4319/lo.2011.56.2.0562>.
- Hunt, J.C., L. Zeidberg, W.M. Hamner, and B.H. Robison. 2000. The behavior of *Loligo opalescens* (Mollusca: Cephalopoda) as observed by a remotely operated vehicle. *Journal of the Marine Biological Association of the United Kingdom* 80:873–883.
- Irigoien, X., T.A. Klevjer, A. Rostad, U. Martinez, G. Boyra, J.L. Acuña, A. Bode, F. Echevarria, J.I. Gonzales-Gordillo, S. Hernandez-Leon, and others. 2014. Large mesopelagic fishes biomass

- and trophic efficiency in the open ocean. *Nature Communications* 5, 3721, <https://doi.org/10.1038/ncomms4271>.
- Katija, K., C.A. Choy, R.E. Sherlock, A.D. Sherman, and B.H. Robison 2017a. From the surface to the seafloor: How giant larvaceans transport microplastics into the deep sea. *Science Advances* 3(8):e1700715, <https://doi.org/10.1126/sciadv.1700715>.
- Katija, K., R.E. Sherlock, A.D. Sherman, and B.H. Robison. 2017b. New technology reveals the role of giant larvaceans in oceanic carbon cycling. *Science Advances* 3(5):e1602374, <https://doi.org/10.1126/sciadv.1602374>.
- Kirkwood, W.J., M. Chaffey, E. Mellinger, D. Au, S. Etchemendy, and B.H. Robison. 2009. An ocean research platform: ROV *Tiburón*. *The Journal of Ocean Technology* 4(1):16–30.
- Matsumoto, G.I., and B.H. Robison. 1992. *Kiyohimea usagi*, a new species of lobate ctenophore from the Monterey Submarine Canyon. *Bulletin of Marine Science* 51:19–29.
- Moynihan, M. 1985. Why are cephalopods deaf? *The American Naturalist* 125(3):465–469, <https://doi.org/10.1086/284353>.
- Newman, J.B., and B.H. Robison. 1993. Development of a dedicated ROV for ocean science. *Marine Technology Society Journal* 26:46–53.
- Osborn, K.J. 2008. *Phylogenetics and Ecology of Pelagic Munnopsid Isopods (Crustacea Asellota)*. PhD dissertation, UC Berkeley, Berkeley, CA, UMI Microform 3306283.
- Osborn, K.J., S.H.D. Haddock, F. Pleijel, L.P. Madin and G.W. Rouse. 2009. Deep-sea swimming worms with luminescent “bombs”. *Science* 325:964, <https://doi.org/10.1126/science.1172488>.
- Osborn, K.J., G.W. Rouse, S.K. Goffredi, and B.H. Robison. 2007. Description and relationships of *Chaetopterus pugaporcinus*, an unusual pelagic polychaete (Annelida, Chaetopteridae). *The Biological Bulletin* 212(1):40–54, <https://doi.org/10.2307/25066579>.
- Packard, D. 1989. Welcoming remarks to The Oceanography Society at its inaugural meeting. *Oceanography* 2(2):46–47, <http://doi.org/10.5670/oceanog.1989.15>.
- Pugh, P.R. 1989. Gelatinous zooplankton—the forgotten fauna. *Progress in Underwater Science* 14:67–78.
- Raskoff, K.A. 2001. The impact of El Niño events on populations of mesopelagic hydromedusae. *Hydrobiologia* 451:121–129, [https://doi.org/10.1007/978-94-010-0722-1\\_11](https://doi.org/10.1007/978-94-010-0722-1_11).
- Reisenbichler K.R., M.R. Chaffey, F. Cazaneve, R. McEwen, R. Henthorn, R.E. Sherlock, and B.H. Robison. 2016. Automating MBARI’s mid-water time-series video surveys: The transition from ROV to AUV. Pp. 3,027–3,035 in *Proceedings, MTS IEEE Oceans 2016 Conference*, September 19–23, 2016, Monterey, CA, <https://doi.org/10.1109/oceans.2016.7761499>.
- Reisenbichler, K.R., and B.H. Robison 1991. Deep sea diving from an armchair: Using an ROV for mesopelagic research. Pp. 75–78 in *Proceedings, AAUS, 11th Annual Symposium*, Honolulu, HI.
- Robison, B.H. 1972. *Distribution and Ecology of the Midwater Fishes of the Eastern North Pacific Ocean*. PhD dissertation, Stanford University, Palo Alto, CA.
- Robison, B.H. 1983. Midwater biological research with the WASP ADS. *Marine Technology Society Journal* 17:21–27.
- Robison, B.H. 1993. Midwater research methods with MBARI’s ROV. *Marine Technology Society Journal* 26:32–39.
- Robison, B.H. 1999. Shape change behavior by mesopelagic animals. *Marine and Freshwater Behaviour and Physiology* 32:17–25, <https://doi.org/10.1080/10236249909379034>.
- Robison, B.H. 2000. The coevolution of under-sea vehicles and deep-sea research. *Marine Technology Society Journal* 33:65–73.
- Robison, B.H. 2004. Deep pelagic biology. *Journal of Experimental Marine Biology and Ecology* 300(1–2):253–272, <https://doi.org/10.1016/j.jembe.2004.01.012>.
- Robison, B.H. 2009. Conservation of deep pelagic biodiversity. *Conservation Biology* 23:847–858.
- Robison, B.H., K.R. Reisenbichler, J.C. Hunt, and S.H.D. Haddock. 2003. Light production by the arm tips of the deep-sea cephalopod *Vampyroteuthis infernalis*. *Biological Bulletin* 205(2):102–109, <https://doi.org/10.2307/1543231>.
- Robison, B.H., K.A. Raskoff, and R.E. Sherlock. 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(3):595–602, <https://doi.org/10.1017/S0025315405011525>.
- Robison, B.H., K.R. Reisenbichler, and R.E. Sherlock. 2005b. Giant larvacean houses: Rapid carbon transport to the deep sea floor. *Science* 308:1,609-1,611, <https://doi.org/10.1126/science.1109104>.
- Robison, B.H., K.R. Reisenbichler, R.E. Sherlock, J.M.B. Silguero, and F.P. Chavez. 1998. Seasonal abundance of the siphonophore, *Nanomia bijuga*, in Monterey Bay. *Deep Sea Research Part II* 45(8–9):1741–1751, [https://doi.org/10.1016/S0967-0645\(98\)80015-5](https://doi.org/10.1016/S0967-0645(98)80015-5).
- Robison, B.H., R.E. Sherlock, and K.R. Reisenbichler. 2010. The bathypelagic community of Monterey Canyon. *Deep Sea Research Part II* 57(16):1,551–1,556, <https://doi.org/10.1016/j.dsr2.2010.02.021>.
- Schlining, B.M., and N.J. Stout. 2006. MBARI’s Video annotation and reference system. Pp. 1–5 in *Proceedings of the Marine Technology Society/ Institute of Electrical and Electronics Engineers Oceans Conference*, September 18–21, 2006, Boston, MA, <https://doi.org/10.1109/oceans.2006.306879>.
- Seibel, B.A., B.H. Robison, and S.H.D. Haddock. 2005. Post-spawning egg care by a squid. *Nature* 438:929, <https://doi.org/10.1038/438929a>.
- Sherlock, R.E., and B.H. Robison. 2000. Effects of temperature on the development and survival of *Nanomia bijuga* (Hydrozoa, Siphonophora). *Invertebrate Biology* 119(4):379–385, <https://doi.org/10.1111/j.1744-7410.2000.tb00106.x>.
- Sherlock, R.E., K.R. Walz, and B.H. Robison. 2016. The first definitive record of the giant larvacean, *Bathochordaeus charon*, since its original description in 1900 and a range extension to the northeast Pacific Ocean. *Marine Biodiversity Records* 9(79):1–10, <https://doi.org/10.1186/s41200-016-0075-9>.
- Sherlock, R.E., K.R. Walz, K.L. Schlining, and B.H. Robison. 2017. Morphology, ecology, and molecular biology of a new species of giant larvacean in the eastern North Pacific: *Bathochordaeus mcnutti* sp. nov. *Marine Biology* 164:20, <https://doi.org/10.1007/s00227-016-3046-0>.
- Silguero, J.M.B., and B.H. Robison. 2000. Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. *Journal of Plankton Research* 22:1,139–1,153, <https://doi.org/10.1093/plankt/22.6.1139>.
- Skikne, S.A., R.E. Sherlock, and B.H. Robison. 2009. Uptake of dissolved organic matter by ephyrae of two species of scyphomedusae. *Journal of Plankton Research* 31(12):1,563–1,570, <https://doi.org/10.1093/plankt/31.12.1563>.
- Skogsberg, T. 1936. Hydrography of Monterey Bay, California. Thermal conditions. *Transactions of the American Philosophical Society* N.S. 29:1–152.
- Skogsberg, T., and A. Phelps. 1946. Hydrography of Monterey Bay, California. Thermal conditions, Part II (1934–1937). *Proceedings of the American Philosophical Society* 90(5):350–386, <https://doi.org/10.2307/1005510>.
- Stewart, J.S., E.L. Hazen, S.J. Bograd, J.E.K. Byrnes, D.G. Foley, W.F. Gilly, B.H. Robison, and J.C. Field. 2014. Combined climate- and prey-mediated range expansion of Humboldt squid (*Dosidicus gigas*), a large marine predator in the California Current System. *Global Change Biology* 20(6):1,832–1,843, <https://doi.org/10.1111/gcb.12502>.
- Swift, H.F., W.M. Hamner, B.H. Robison and L.P. Madin. 2009. Feeding behavior of the ctenophore *Thalassocalyce inconstans*: Revision of anatomy of the order Thalassocalycida. *Marine Biology* 156:1,049–1,056, <https://doi.org/10.1007/s00227-009-1149-6>.
- Tamburri, M.N., M.N. Halt, and B.H. Robison. 2000. Chemically regulated feeding by a midwater medusa. *Limnology and Oceanography* 45(7):1,661–1,666, <https://doi.org/10.4319/lo.2000.45.7.1661>.
- Trueblood, L.A., S. Zylinski, B.H. Robison, and B.A. Seibel. 2015. An ethogram of the Humboldt squid *Dosidicus gigas* Orbigny (1835) as observed from remotely operated vehicles. *Behaviour* 152(14):1,911–1,932, <https://doi.org/10.1163/1568539X-00003324>.
- Vecchione, M., B.H. Robison, and C.F.E. Roper. 1992. A tale of two species: Tail morphology in paralarval *Chiroteuthis*. *Proceedings of the Biological Society of Washington* 105:683–692.
- Widder, E.A., S.A. Bernstein, D.F. Bracher, J.F. Case, K.R. Reisenbichler, J.J. Torres, and B.H. Robison. 1989. Bioluminescence in the Monterey Submarine Canyon: Image analysis of video recordings from a midwater submersible. *Marine Biology* 100(4):541–551, <https://doi.org/10.1007/BF00394831>.
- Widder, E.A., B.H. Robison, K.R. Reisenbichler and S.H.D. Haddock. 2005. Using red light for in situ observations of deep-sea fishes. *Deep Sea Research Part I* 52:2,077–2,085, <https://doi.org/10.1016/j.dsr.2005.06.007>.
- Youngbluth, M.J. 1984. Manned submersibles and sophisticated instrumentation: tools for oceanographic research. Pp.335–344 in *Proceedings of SUBTECH, 1983*, The Society for Underwater Technology, November 15–17, London, England.
- Zeidberg, L.D., and B.H. Robison. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences of the United States of America* 104(31):12,948–12,950, <https://doi.org/10.1073/pnas.0702043104>.

## ACKNOWLEDGMENTS

We are grateful to the many colleagues, interns, students, and postdocs who shared their enthusiasm, expertise, and insights with us during a thousand research dives. We thank the ROV pilots, the ships’ crews, MBARI’s Video Lab, and particularly Annette Gough and Steve Etchemendy for their long-term support. Thanks to Karen Osborn for reviewing and improving the manuscript. Sponsored by the David and Lucile Packard Foundation.

## AUTHORS

**Bruce H. Robison** (robr@mbari.org) is Senior Scientist, **Kim R. Reisenbichler** is Research Specialist, and **Rob E. Sherlock** is Senior Research Technician, all at the Monterey Bay Aquarium Research Institute, Moss Landing, CA, USA.

## ARTICLE CITATION

Robison, B.H., K.R. Reisenbichler, and R.E. Sherlock. 2017. The coevolution of midwater research and ROV technology at MBARI. *Oceanography* 30(4):26–37, <https://doi.org/10.5670/oceanog.2017.421>.