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Biological Explorations in the Mid-Ocean Realm: Food Webs, Particle Flux, and Technological Advancements

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I. INTRODUCTION

The ocean realm covers 99% of this planet by volume; therefore, it is not surprising that models developed to predict cycles of biological production lack rigor (Childress, 1983). Part of the uncertainty stems from the available base of oceanographic data. For decades, biologists have relied on collections made with plankton nets and water bottles to obtain fundamental insights about the behavior, distribution and abundance of pelagic organisms. Information gained from this ship-based methodology has been important, but it lacks the dimension of direct observation (Hamner, 1977; Hamner *et al.*, 1987). Submersibles overcome this constraint by providing *in situ* opportunities to distinguish where fauna are concentrated and how they interact with their environment, their prey or their mates.

Both manned and remotely operated vehicles have been used to conduct undersea investigations in the water column and near the sea floor (Allmendinger, 1982). The history and hardware of manned submersibles are well reviewed in an exhaustive handbook (Busby, 1976). Deep-sea craft under development have been described in other publications (Earle, 1986; Takagawa, 1987). Commercial news magazines, *Sea Technology*, *Subnotes*, *Underwater Systems Design*, highlight the activities of submersibles and the availability of undersea accessory equipment. *In Situ News*, a quarterly pamphlet issued by the University of Rhode Island, serves to summarize recent scientific accomplishments, describe new tools, and announce upcoming meetings.

Undersea vehicles used for scientific purposes today vary considerably in their complexity and capabilities (Hanson and Earle, 1987; Rechnitzer, 1986). They range from special purpose craft that conduct photographic surveys or perform retrieval tasks to multi-purpose submersibles that utilize state-of-the-art instruments (Tietze and Clark, 1986; Tusting, 1986, Youngbluth, 1984). In the last decade, manned submersibles working in water column environments have enhanced substantially the ability to observe, capture and experiment with pelagic fauna at all depths of the ocean (Alldredge *et al.*, 1984; Barnes *et al.*, 1976; Smith and Laver, 1981; Youngbluth *et al.*, 1988). One of the most important contributions has been the ability to examine critical trophic and behavioral relationships among pelagic fauna on the appropriate spatial scales (cm to m) (Harbison, 1987; Janssen *et al.*, 1987; Mackie and Mills, 1983; Mills, 1987). These accomplishments signal that continued use of submersibles and the technically advanced instruments they carry, will help oceanographers decide where and when to perform measurements and conduct experiments.

This paper provides examples of how deep-diving, manned submersibles facilitate investigations of zooplankton at mid-ocean depths. Gelatinous zooplankton are featured in some detail because they represent a group of ecologically important animals that are sampled poorly by other methods (Alldredge, 1984). Most of the information presented has been obtained with the JOHNSON-SEA-LINK submersibles. Ongoing projects in water column environments are reviewed and topics as yet unstudied are suggested.

II. SPECIES DIVERSITY DISCOVERIES

The limited, but exciting water column work with manned submersibles has demonstrated clearly that more kinds of gelatinous zooplankton exist in the deep-sea than recognized previously. Some of the most conspicuous midwater animals are carnivorous ctenophores, medusae and siphonophores. New species of ctenophores have been recognized (Madin and Harbison, 1978a; Madin and Harbison, 1978b; Mills, 1987) and more than a dozen other specimens, which have been photographed and collected at depths ranging to 1000 m, are undescribed (Harbison, 1985; Harbison pers. comm.). Many of these comb-jellies are often relatively numerous ($>1 \cdot m^{-1}$) and one unnamed, crimson cydippid-like species makes daily vertical migrations of at least 300 m in the canyons south of Georges Bank.

Mills and colleagues (Mills *et al.*, 1987) have classified a new species of coronate scyphomedusa using specimens captured from a submersible. Larson and colleagues (Larson, *et. al.*, in press) have captured and described a large (60 cm bell diameter), unusual ulmarid scyphomedusa. Another ten undescribed species of mesopelagic hydromedusae have been collected (C. Mills, R. Larson, pers. comm.).

At least six new species of siphonophores are known to exist under tropical seas (Pugh and Harbison, 1987; Pugh and Youngbluth, 1988a; Pugh and Youngbluth, 1988b). Several other unusual and infrequently collected physonect siphonophores have not yet been described (Pugh, pers. comm.) In addition to these taxonomic studies, the morphology and behavior of a physonect species *Lycnagalma utricularia*, have been noted in some detail (Pugh and Harbison, 1986). This study represents one example of the fact that many animals, previously considered quite rare based on net tow data, are in fact commonly encountered on submersible dives to mesopelagic depths.

Several new or poorly documented deep-sea appendicularians in the genera *Oikopleura, Pelagopleura* and *Fritillaria* have been collected and are being described (R. Fenaux, pers. comm.). Furthermore, it is likely that the genus *Bathochordaeus* will be revised on the basis of new specimens obtained with submersibles. One conclusion to be drawn from studies of gelatinous zooplankton is that the composition of food webs in midwater environments is still being defined.

III. VERTICAL DISTRIBUTION PATTERNS

In situ observations have also shown that many zooplankton live within certain depth zones; zones much narrower than have routinely sampled by tow nets (Mackie, 1985). For example, prior to 1981, the giant appendicularian *Bathochordaeus charon* was known from less than 20 specimens collected over a period of 80 years (Galt, 1979). All samples had been obtained from continuously open nets and consequently the vertical distribution of this species was not well documented. Since 1981, several specimens of this appendicularian have been observed and collected *in situ*, some near 400 m but mostly from 45-65 m within the Gulf Stream (Youngbluth, 1984). The presence of numerous *B. Charon* (up to $9 \cdot m^{-1}$) in their 30-cm diameter, mucoid filter-houses, has always coincided with a strong pycnocline and a high standing biomass of chlorophyll and detritus. Examinations of particles found in the guts of this appendicularian have revealed biogenic debris from phytoplankton and crustaceans.

In situ work with the one-person vehicle WASP off southern California showed that stage V copepodites of *Calanus pacificus californicus* become torpid and overwinter in 20-m bands extending for kilometers at a depth of 450 m during non-upwelling periods. Presumably, this is a response to low food availability (Alldredge *et al.*, 1984). Densities of these diapausing copepods averaged ca. 10^7 individuals$\cdot m^{-3}$, about three orders of magnitude higher than abundance estimates made using nets in surface waters. Both of these distribution patterns indicate that there is more biological structure in the pelagic environment than suspected from remote sampling.

IV. PARTICLE FLUX

Particulate matter is ubiquitous in the oceans. One of the major objectives in oceanographic sciences has been to chronicle and quantify processes that regulate the distribution and sedimentation of biogenic particles in the sea (Platt and Sathyendranath, 1988). Of particular interest, in terms of mechanisms and rates, is the relationship between primary production in the euphotic zone and the downward flux of surface-derived, organic detritus to the deep sea. Large particles, such as the fecal pellets and marine snow aggregates produced by zooplankton, are principal vectors for vertical transport (Knauer *et al.*, 1984). Fecal pellets can sink rapidly (10-1000 $m \cdot d^{-1}$) (Fowler and Knauer, 1986). Marine snow aggregates fall more slowly (10-150 $m \cdot d^{-1}$) (Alldredge and Gotschalk, 1988). Variations in settling rates are related to a host of physical and biological factors, e.g, advection, viscosity, diet and decomposition. As a result, mathematical models developed to predict regional and global flux rates of biogenic material require detailed information about production and distribution of these important particles (Hargrave, 1985).

Most existing data about particle transport events have been based on *in situ* sampling with sediment traps, pump-supported equipment, optical techniques or scuba (Alldredge *et al.*, 1987; Bishop *et al.*, 1985; Lampitt, 1985; Urerre and Knauer, 1981). Data obtained from sediment traps and optical devices can be misleading in that the amount of material measured may be a mixture of particles transported by vertical sinking, lateral advection and periodic resuspension. Similarly, information derived from filtration systems may include both suspended and fast-sinking particles. Scuba assessment of the sizes, sources and sinking of particulate material are depth limited. Direct observation and sampling from submersibles can overcome some of these constraints.

A. Fecal Pellet Transport and Zooplankton Behavior

Quantification of the production, sinking rate, distribution, and abundance of large particles need to be considered in conjunction with feeding and migratory behaviors of zooplankton (Gilmer and Harbison, 1986; Harbison and Gilmer, 1986). Observations and sampling with submersibles have begun to ascertain the depths at which such particles are concentrated. For example, euphausiid fecal pellets can stall at pycnoclines, and this adds to the complexity of predicting sinking rates. Dives made within the Gulf of Maine and the canyons south of Georges Bank revealed that high densities of fecal pellets (50-325 particles·m^{-3}) accumulated at night in 5-24 m thick layers coincident with the pynocline (15-30 m) (Youngbluth *et al.*, 1988). These cylindrical (0.2 mm OD x 3-10 mm long) particles sank rapidly (ca. 200 m·d^{-1}) and could transport substantial amounts of organic matter (7-12 mg C·m^{-2}·d^{-1}) to the bottom. Vertically migrating euphausiids *Meganyctiphanes norvegica* produced the pellets. These individuals represented only part of enormous aggregations (up to 10^{4} individuals·m^{-3}) of adults (25-35 mm long) that remained within 10 m of the seabed day and night and appeared to forage in the benthic boundary region (Greene *et al.*, 1988; Youngbluth *et al.*, 1988). Direct observations of *M. norvegica* near the sea floor also support scattered, anecdotal data from trawls and submersibles (Bigelow, 1928; Mauchline, 1980; Peres *et al.*, 1957; Tregouboff, 1961) which have suggested that epibenthic aggregation and near-bottom feeding by this species occurs in nearshore waters from the western North Atlantic to Mediterranean seas. If consumption of biogenic detritus in the epibenthic region is common among these euphausiids, this species may account for considerable repackaging and bioturbation. Assuming that epibenthic populations feed more or less continuously, those individuals that migrate vertically each night may introduce recycled biogenic and inorganic materials back into the mixed layer when they release fecal pellets. These discoveries are significant because they demonstrate the extent to which environmental factors and zooplankton behaviors can interact to influence the rate and amount of particle transport.

Fecal pellets and carcasses of gelatinous zooplankton called salps have also been implicated as significant sources of particle flux. An occasionally cited, but as yet unquantified observation, was made several years ago from the ALVIN submersible. Cacchione and colleagues (1978) reported that "windrows" of salp bodies were numerous at ca. 3000 m along the sea floor of Hudson Canyon. Presumably these aggregations were formed by *Salpa aspera*, a diel-migrating, midwater species known to attain very high densities (Wiebe *et al.*, 1979). Knowing also that salps can grow and reproduce rapidly and that they can produce fast-sinking fecal pellets (Madin, 1982) suggests that this species must contribute substantially in several ways to the export of particles from the photic zone.

B. Marine Snow Aggregates and Gelatinous Plankton.

The term marine snow has been applied to describe large (1 mm to 1.5 m in diameter or length), aggregated mucoid particles, many of which are formed by gelatinous zooplankton to collect small (down to 0.1 μm) particulate food. Microscopic and chemical examinations of marine snow have indicated that aggregates serve as important sites of nutrient regeneration by microbes, primary production by autotrophs, and phagotrophic growth by microflagellates (Alldredge and Cox, 1982; Caron *et al.*, 1982; Knauer *et al.*, 1982). This information prompted oceanographers to propose that microbe-enriched aggregates constitute a major contribution to the primary level of oceanic food webs. Furthermore, these aggregates may flux within the water column or sink to the sea floor (Asper, 1986).

Because marine snow aggregates are extremely fragile and easily disintegrated, the only successful means of assessing the abundance and obtaining recognizable samples of marine snow aggregates has been with *in situ* methods, either by scuba (Alldredge *et al.*, 1986; Shanks and Trent, 1980) or submersibles (Alldredge and Youngbluth, 1985; Barham, 1979; Silver and Alldredge, 1981). Ecological investigations, which relate marine snow aggregates to the gelatinous zooplankton that produce the aggregates, are rare (Davoll and Silver, 1986). Field observations from submersibles at midwater depths have identified at least three recognizable sources for globular, sheet-like, and string-shaped aggregates. For example, many mucoid globs and sheets, 1-30 cm in greatest dimension, are the discarded filter-houses produced by appendicularians. Masses of these ruptured aggregates typically occur just below the subsurface chlorophyll maximum layer of the Gulf Stream, from 50 to 100 m. Depending on the prevailing currents, these masses can intrude onto the continental shelf of the South Atlantic Bight within plumes of upwelled water. Microbial activity associated with appendicularian filter-houses produced below 200 m may act to recycle biogenic particles in this region of the water column (Davoll and Youngbluth, 1984). Further investigations of these zooplankton are needed to improve predictions about particle enrichment and flux.

Dense concentrations of mucoid material in the form of strings, 3-90 cm long, have appeared at depths of 90-120 m in the Bahamas. These strings have also been noted to occur from 5-600 m. Most strings were oriented vertically and many remained attached to the filamentous rhizopodia of the foraminiferan *Hastigerina pelagica* (Youngbluth, 1984). Estimates of foraminiferan abundance ranged from 5-100 individuals$\cdot$m^{-3}.

Mucous feeding webs of pseudothecosome pteropods (Lalli and Gilmer, 1989), 5 to 80 cm in diameter, can be numerous at depths of 90-120 m in the Bahamas. The rates at which these strings and sheets are produced, sink, and decompose are unknown.

These records of appendicularians, foraminiferans and pteropods are but a few of many observations which indicate that gelatinous zooplankton can produce masses of marine snow. The biological contribution of the particulate material to pelagic and benthic communities is a subject of ongoing investigations.

Recent observations of gelatinous phytoplankton provide yet another example that relates to particle transport. During a series of dives made along the coast of Florida in the summer of 1987, gelatinous colonies (0.5-3 mm in diameter and 5-100 mm in length) of the diatom *Thalassiosira subtilis*, reduced visibility from the submersible to less than 1 m at depths ranging from the base of the thermocline (ca. 5 m) to the sea floor (30-80 m). The dense clusters of colonies (up to 300/liter with dry weight biomass reaching 2 mg$\cdot$liter^{-1}) appeared only in the nutrient-rich, subsurface waters of the Gulf Stream that upwelled over the continental shelf. In a 10-day period these mucoid algal colonies began to decompose, forming globular and comet-shaped aggregates. Preliminary calculations, based on the vertical distribution and standing stock of the colonies and on the area covered by the upwelling event (1.3×10^3 km^2), indicated a biomass of ca. 10^7 kg C. Within a two-day period, a shift in wind direction deepened the mixed layer and forced the intrusion off the shelf into the Gulf Stream. This regional, but nonetheless large-scale mass exchange between coastal waters and the open ocean must affect the productivity of the open ocean (Rudyakov, 1987). *Thalassiosira spp.* are known to occur in upwelled waters around the world (Elbrachter and Boje, 1978; Jimenez, 1981). On a global scale, the magnitude of organic flux associated with the growth of these colonial diatom species will elude satellite reconnaissance because the bulk of primary production occurs deeper than such remote sensing can detect.

V. METABOLISM OF PELAGIC FAUNA

A fundamental requirement for comprehending the dynamic nature of food webs in oceanic regimes is quantification of energy use by major faunal components. These rates can be estimated from measurements of metabolism, since this process generally accounts for the largest fraction of an animal's energy use (Childress, 1977). To date, physiological studies of gelatinous zooplankton taken from mesopelagic environments are rare principally because these fragile animals are difficult to collect and maintain with conventional techniques. The first measurements of oxygen consumption by the midwater ctenophore *Bathocyroe fosteri* (Youngbluth *et al.*, 1988), have revealed rates about half those of shallow water ctenophores (Kremer *et al.*, 1986). However, the accuracy of these results remains unknown. Individuals were collected carefully in special chambers from a submersible but metabolic data were recorded in a shipboard laboratory. Stresses associated with removing an animal from its natural habitat were unquantified and argue for developing an *in situ* approach: e.g., change in pressure and temperature, exposure to light, and transfer from collecting to experimental chambers. Some experiments of this type have been conducted with free-vehicles placed in bathypelagic environments using the manned submersible ALVIN (Smith and Baldwin, 1983).

VI. SUBMERSIBLE AS A MOBILE LABORATORY

Behavior of captive animals is abnormal, and their survival under laboratory conditions is usually limited. However, although nature cannot be duplicated in a laboratory, it is possible to take laboratory tools into the field to facilitate investigations. In this context, significant progress in pelagic research will depend in part on the extent direct visual observations from submersibles can be enhanced with recording devices.

One important trend for future research with manned submersibles, and to an extent remotely operated and autonomous underwater vehicles, will be to expand and extend the quality and range of perception. Human vision is the primary sensor for information in many undersea studies. Records of what can be seen have been made primarily with high definition still and video cameras (Miller and Pawson, in press; Youngbluth, 1984). To date, most images are still collected under bright, white light. Optical equipment of the future will take advantage of low light, filtered light, laser light and stereoscopic technology to provide more realistic and unobtrusive assessments of animal behavior as well as particle abundance and morphology.

The newest color CCD cameras, have high line resolution (up to 700 lines horizontal) and lack ghosting image distortion. The latter quality is essential for critical examinations of shape and movement. Some new video recorders are capable of 400-500 lines, about double the usual limit of playback quality. Experimental stereo-imaging video systems, capable of tracking complex swimming and feeding movements of relatively large zooplankton (>3 cm), are undergoing field trials in an effort to provide a basis for analyzing the adaptive importance and energetic costs of specific behaviors (Hamner *et al.*, in press; Price *et al.*, 1987). A laser-based video system with high resolution (ca. 15 μm) is being tested (R. Strickler and G. Paffenhofer, pers. comm.). Optical gear that can record particle size, density and movement over small (mm to cm) distances (e.g. laser holography, Betzer *et al.*, 1987; camera/transmissometer profiler, Gardner *et al.*, 1987), if adapted to submersibles, would also help to define how the behaviors of zooplankton effect the cycling of organic matter at physical chemical interfaces.

If currently available electronic image intensifiers can be improved and used in concert with low-light SIT and ISIT cameras (Wood and Potts, 1987), observations and measurements could be made at ambient, dim-light conditions within the photic zone. This practice would reduce unnatural phototactic responses associated with using incandescent light in the deep sea and could document a wide variety of normal swimming, feeding and breeding behaviors. ISIT video recordings made in midwater from the submersible DEEP ROVER have shown that bioluminescent displays produced by animals *in situ* differed considerably from displays emitted by captive individuals (Widder *et al.*, in press). This result clearly illustrates that measurements and experiments must be conducted *in situ* to obtain unbiased understanding of the communication value of these signals between and among species. In the latter and previous studies, bioluminescent records indicated that a large proportion of such emissions were produced by organisms smaller than 0.5 mm. Identification of these organisms awaits development of imaging equipment with better magnification and resolution.

Manned submersible diving involves being isolated from a high pressure environment inside a capsule. There is no smell, no taste, no sound from the environment. In an effort to compensate for the absence of such information, environmental data, such as depth, temperature, conductivity, and turbidity can be recorded automatically by a sensor and data logger package (Voyles and Clayton, 1986). Two new sensors have recently been added to the JOHNSON-SEA-LINK submersible system: (1) a SeaTech fluorescence sensor, capable of measuring chlorophyll *a* concentrations ranging from 0.05-50 $mg{\cdot}m^{-3}$, and (2) a novel radiometer

(F. Caimi pers. comm.), that can measure photosynthetically active flux to 500 m. The radiometer works within a spectral range of 400-700 nm and provides nearly instantaneous readings over seven decades of illumination (.003 to 3000 $\mu E \cdot s^{-1} \cdot m^{-2}$) with spatial integration over nearly a 2π-steradian field. Chemical nutrients (NO_3-N, SO_4-S, SiO4, PO_4-P) have been measured from manned submersibles by modified flow injection analysis (Johnson *et al.*, 1986). Access to some or all of these environmental parameters during the course of a dive and the period between consecutive dives is often crucial for planning sampling strategies and conducting *in situ* experiments on a given cruise.

Both the panoramic range and the distance component of visibility are limited from submersibles in direct proportion to the absorption of light in seawater. Another way to interrogate the surrounding environment is with acoustics. Sonar systems can scan large volumes of water in a short period of time. For example, high frequency (420 kHz to 1 MHz) dual-beam acoustical equipment holds promise for obtaining quantitative data on the size and abundance of zooplankton. These data can complement visual records of distribution and migration patterns of individuals and populations (Jefferts *et al.*, 1987) and extend them up to 60 m from the submersible (Green *et al.*, in press). This acoustic technique mitigates two important sampling problems: first, biases associated with animal avoidance of sampling gear (in this case a submersible) and, second, labor intensive enumeration of animals in different size classes. The Japanese are reported to be working on a sonar system that will display video images of targets within a range of 200 m (Tagawa, 1987).

Near real-time detection of zooplankton distribution patterns should clarify how pelagic animals select patchy food resources. In this context, pre-dive shipboard surveys of current shear zones, which can influence the distribution of microzooplankton (Townsend and Cammen, 1985), may be possible with an acoustic doppler profiler (Flagg, 1987).

As the use of *in situ* incubation equipment becomes routine, highly versatile and dextrous manipulator arms will improve the efficiency of deep-sea investigations. In this respect, two features of existing arms deserve special mention. A tool interchange mechanism has been designed to accommodate flexible jaws, clam-shell grab or a cutting blade (C. Tietze, pers. comm.). The advantages of this mechanism include: 1) the ability to index a tool in any of 360 degrees axially, 2) the capability of holding a tool whether or not power is maintained to the arm, and 3) the versatility of using hydraulic power or air pressure to exchange tools. Acoustical signals incorporated into at least one manipulator arm (Hawkes, 1984) indicate force and texture. Knowledge of these factors can be critical when grasping instrumented packages.

VII. SOME RECOMMENDATIONS

Significant progress in water column research will depend on contemporaneous use of submersibles, ships and satellites. In order to implement this strategy, manned submersibles must incorporate at least the following features and equipment to be effective for biological investigations at midwater depths:

1. Variable-speed, ultra-quiet thrusters to rapidly and precisely regulate fine-scale movements in horizontal and vertical directions.
2. A variable ballast system to quickly adjust trim and pitch throughout the depth range of the submersible.
3. High resolution still cameras. High definition video cameras (color and low light, both with zoom capability) mounted on pan-and-tilt platforms. Real-time overlay of alpha-numeric data on the video monitor should become standard, e.g., date, depth, time, environmental parameters.
4. Multiple sampling chambers that can capture delicate, slow-moving creatures as well as more robust, fast-swimming zooplankton.
5. Data logging systems (preferably solid-state) for real-time and recorded measurements of environmental parameters, i.e., depth, temperature and salinity (via conductivity), and the option to adapt additional sensors, e.g., turbidity, chlorophyll, light intensity, oxygen and nutrients, as required by research projects.
6. Efficient, long-life battery system or capability of battery change-out to allow a 12-h term of operation at sea per day.

A factor often overlooked, but critically needed, for effective operation of a submersible is a proper support vessel (Tagawa, 1987). The ship should be capable of operating and launching the submersible in unsettled sea conditions. The concept of using ships or platforms of opportunity, while attractive from the perspective of reduced cost and geographic mobility for the submersible, may, in practice, limit the success of a given mission for several reasons. Possible problems include: a crew's lack of experience in handling the submersible, inadequate cranes for launch and retrieval, disturbance of the submersible's acoustical communication/location/data acquisition gear by ship-generated noise, lack of spare parts, a ship's lack of station-keeping and submersible-tracking equipment, and lack of scientific laboratory space. More attention should be given to blending the facilities of a modern oceanographic ship (dynamic positioning system, winches, laboratories, temperature-controlled rooms) and the features of a submersible tender (launching gear, tracking equipment) to maximize the use of expensive seatime.

VIII. FACILITIES, PROGRAMS AND PROJECTS

Presently, few national or international opportunities exist for long-term research with manned submersibles. Excursions into the midwater realm with manned submersibles are still relatively infrequent, principally because of the number of adequate, currently active vehicles is limited (JOHNSON-SEA-LINKS, DEEP ROVER, PISCES IV & V, CYANA, NAUTILE, ALVIN). In the last five years, federal research support has come primarily from the National Oceanic and Atmospheric Administration (NOAA), the National Science Foundation and the Office of Naval Research, along with occasional funding from Minerals Management Service, Department of Energy and Sea Grant. Funding has increased in direct proportion to the reliability and versatility of submersibles. The recent establishment of regional National Undersea Research Centers by NOAA (in Connecticut, North Carolina, St. Croix and Hawaii and the likely creation of at least one more Center on the west coast of the United States) should increase the number of investigators and programs that focus on *in situ* investigations. The Harbor Branch Oceanographic Institution has promoted science from submersibles, both manned and unmanned, since 1971 by fostering interdisciplinary cooperation among scientists, engineers and operators. The Monterey Bay Aquarium Research Institution (MBARI), founded in 1987, has adopted a similar, multi-talented team approach and plans to conduct projects in midwater (B. Robison, pers. comm.). MBARI, however, has chosen to concentrate on the development of an unmanned, deep-diving vehicle (HYSUB ROV). As the goals and objectives of *in situ* pelagic research broaden among the current and future generations of oceanographers in the United States, it is likely that international collaboration will be based on research initiatives with Japan (JAMSTEC, Mayama, 1987) and France (IFREMER, Grandvaux, 1986).

Current multi-investigator programs in the Gulf of Maine, South Atlantic Bight and the Great Lakes exemplify how manned submersibles can serve fundamental roles as technological resources (Babb and DeLuca, 1988). Projects for the future, that will require *in situ* approaches, have been addressed at several workshops. In a meeting devoted to outlining the properties of aggregated particles and the mechanisms responsible for their formation, it was clear that the importance of these particles to organic flux must be based on *in situ* assessments of their distribution, abundance and utilization (Alldredge *et al.*, 1986). At a symposium on zooplankton behavior, it was concluded that answers to major questions concerning the evolution of natural responses to environmental conditions can be best explored by applying novel optical and acoustic technology *in situ* (Price *et al.*, 1987). Recently, ocean scientists emphasized that optical and acoustical methods (see section on Submersible as a Mobile Laboratory) can produce complementary information about the identity, abundance and distribution of pelagic fauna (Remote Optical and Acoustic Mapping of Ocean Waters, Monterey Bay Aquarium, 20-21, May 1988, B. Robison, pers. comm.). Integration of both methods is a goal for the future and will involve various schemes for the collection, analysis and storage of large data streams.

In an effort to define unsolved problems and chart new directions, studies of marine zooplankton were segregated by time-scale strategies (Marine Zooplankton Colloqium, Lake Arrowhead, 18-22 April 1988, G. Paffenhofer, pers. comm.). One set of recommendations from this colloquium encouraged *in situ* deployments of instruments capable of recording high volumes of data over brief or extended periods to investigate behaviors of individuals and populations. At an earlier conference (22-23 October 1986, Doelling and Harding, 1987), alliances between scientists and engineers from academia and industry were encouraged to facilitate the development of advanced instruments for undersea applications, e.g., robotic tools with artificial intelligence and manipulator devices with tactile sensing systems.

IX. SUMMARY AND CONCLUSIONS

In the last decade, undersea studies with manned submersibles have produced unprecedented records of natural behavior for well-known and undescribed pelagic animals and have shown that many species live in specific depth zones, zones much narrower than have been measured by traditional methods. Such distributional patterns probably reflect preferred feeding areas in many cases and suggest that there is considerably more biological organization in the pelagic ecosystem than recognized previously. These discoveries have indicated new problems to study in the dark, cold and hyperbaric environments that characterize the deep sea.

Over the next decade new discoveries about the behavior and distribution of zooplankton will undoubtedly emanate from submersible-based investigations, principally because of the high potential for coupling direct visual observations of behavior (individuals and populations) with simultaneous measurements of environmental variables. Fragile, gelatinous zooplankton, in particular, require more *in situ* studies to determine their roles in processes associated with biogeochemical cycling of particulate matter.

The conclusion to be drawn from this review is that undersea investigations with manned submersibles need to be an integral part of pelagic research programs, not a separate component. Submersibles have investigated phenomena on temporal and spatial scales not addressable with remote sampling from ships or satellites. Continued use of these vehicles will help oceanographers to optimize where and when to perform ecological investigations in water column environments. Problems of broad significance can be addressed if target organisms in specific geographical regions are selected carefully and a repertoire of physical, chemical and biological factors are studied concurrently.

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