Océanis, Vol. 15, Fasc. 1, 1989
pp. 9-15

SPECIES DIVERSITY, VERTICAL DISTRIBUTION, RELATIVE ABUNDANCE AND OXYGEN CONSUMPTION OF MIDWATER GELATINOUS ZOOPLANCTON: INVESTIGATIONS WITH MANNED SUBMERSIBLES.

Marsh J. Youngbluth
Harbor Branch Oceanographic Institution
5600 Old Dixie Highway, Fort Pierce, Florida 34946, USA

Key words: gelatinous zooplankton, Atlantic Ocean, manned submersibles, marine snow, oxygen consumption.
Mots-clés : zooplancton gélatineux, océan Atlantique, submersibles maniables, neige marine,consommation d'oxygène.

Abstract

Gelatinous zooplankton, including salps, foraminiferans, appendicularians, pteropods, ctenophores, and siphonophores, have been observed, photographed and collected from Johnson-Sea-Link submersibles. Experimental operations using these vehicles within the uppermost 800 m of tropical and temperate regions in the Atlantic Ocean have revealed: (1) the existence of undescribed species; (2) an abundance of species previously considered to be rare; (3) the persistence of large standing stocks of single species distributed within relatively narrow depth intervals; (4) the production of marine snow aggregates by gelatinous plankton; and (5) low rates of oxygen consumption by midwater species. These data support the belief that soft-bodied zooplankton are more diverse, numerous and widespread than several decades of sampling with plankton nets have shown. Furthermore, these data demonstrate that *in situ* investigations with technically advanced vehicles are necessary to fully understand the life histories of pelagic animals.

Résumé

Diversités des espèces, distribution verticale, abondance relative et consommation d'oxygène du zooplancton pélagique gélatineux : recherches effectuées en submersibles maniables.

Le zooplancton gélatineux, comprenant les salpes, les appendiculaires, les ptéropodes, les cténophores et les siphonophores, a été observé, photographié et récolté depuis les sous-marins de poche Johnson-Sea-Link. Les plongées utilisant ces engins dans les premiers 800 mètres des régions tropicales et tempérées de l'océan Atlantique ont montré : (1) l'existence d'espèces inconnues à ce jour, (2) une abondance d'espèces considérées jusqu'alors comme rares, (3) l'existence d'importantes populations monospécifiques dans des couches d'épaisseur relativement limitée, (4) la production de la neige marine par le plancton gélatineux, et (5) les faibles taux de consommation d'oxygène par les espèces des couches moyennes. Ces données montrent que le plancton gélatineux est plus diversifié, plus abondant et plus répandu, que ce qu'avaient montré de nombreuses décades de récoltes effectuées à l'aide de filets à plancton. En outre, ces données montrent que les recherches *in situ*, à l'aide d'engins techniquement évolués sont nécessaires pour bien comprendre le cycle vital des animaux pélagiques.

Introduction

The ocean realm is so vast, covering 99% of this planet by volume, that it is not surprising that models developed to predict cycles of biological production and fluxes of particulate material lack rigor (Childress 1983). Part of the uncertainty stems from the available base of oceanographic data. For decades biologists have relied on plankton nets to provide fundamental insight into the structural and functional relationships among pelagic fauna. While the information gained from this methodology has been important, it has also been misleading. Without the dimension of direct observation, it is difficult to know where fauna are concentrated or how they interact with their environment, their prey or their mates (Hamner 1977; Hamner *et al.* 1987).

The use of research submersibles in the last decade for water column studies has enhanced substantially the ability to observe, capture and experiment with pelagic fauna at all depths of the oceans (Barnes *et al.* 1976; Smith and Laver 1981; Alldredge *et al.* 1984; Youngbluth et al., 1988). One of the most important contributions has been the ability to study pelagic fauna on scales (cm to m) which are appropriate for examining predators prey, metabolic and reproductive relationships required for their survival.

The objective of this paper has been to provide a succinct review of previously published, submersible-based studies that emphasize the ecological importance of gelatinous zooplankton. Since many of these fragile, soft-bodied zooplankton have not often been photographed *in situ*, representatives of several taxa are figured to illustrate their natural appearance in the dark or dimly lit depths of the sea. Much of the information presented has been obtained with the JOHNSON-SEA-LINK submersibles (Youngbluth 1984a).

Spècies Diversity Discoveries

The limited but exciting water column work with manned submersibles has demonstrated clearly that there are more kinds of gelatinous zooplankton in the deep-sea than recognized previously. Some of the most conspicuous midwater animals are the carnivorous ctenophores and siphonophores. Probably more than a dozen of the ctenophores, which have been photographed and collected at depths ranging to 800 m, are undescribed species (Harbison 1985; personal communication). Many of these comb-jellies are often very numerous and one unnamed species makes daily vertical migrations of at least 300 m. At least six new species of siphonophores are known to exist under tropical seas (Pugh and Harbison 1987; Pugh and Youngbluth 1988, in press). Furthermore, the morphology and behavior of a commonly encountered but supposedly rare physonect species have been noted in some detail (Pugh and Harbison 1986). Other unusual and infrequently encountered physonect siphonophores have not yet been described. Mills *et al.*, (1987) have classified a new species of coronate scyphomedusa. Several new or poorly documented deep-sea appendicularians in the genera *Oikopleura, Pelagopleura* and *Fritillaria* will be defined (R. Fenaux, personal communication).

Vertical Distribution Patterns

In situ observations have shown that many gelatinous zooplankton live in certain depth zones, zones much narrower than have been routinely sampled by tow nets (Mackie 1985). Such distribution patterns reflect preferred feeding areas in many cases and suggest that there is considerably more community structure in the pelagic environment than suspected. 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 of the samples had been obtained from continuously open nets and consequently the vertical distribution of this species was not known. Since 1981 several specimens of this appendicularian have been observed and collected *in situ*, some near 400 m but most from 45-65 m (Youngbluth 1984b). This shallow depth interval within the Gulf Stream, where up to 9 individuals per cubic meter have been recorded, 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. The pseudothecate pteropod *Gleba cordata* (Figure 6) and the foraminiferan *Hastigerina pelagica*, have also been numerous from 90-110 m in areas where particulate matter was conspicuous (Youngbluth 1984b). These two zooplankton produce mucous webs or strings, respectively, and feed on the particles that adhere to these substrata (Gilmer 1972; Youngbluth 1984b).

Marine Snow Aggregates

Macroscopic (1 mm to 1.5 m in diameter or length) aggregates of mucoid material occur everywhere in the oceans. The term" marine snow" has been applied to describe these particles, many of which are formed by gelatinous zooplankton. Microscopic and chemical examinations of marine snow have indicated that aggregates serve as important sites of nutrient regeneration by microbes, for primary production by autotrophs, and for phagotrophic growth by microflagellates (Alldredge and Cox 1982; Caron *et al.* 1982; Knauer *et al.* 1982). These kinds of information have prompted scientists 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).

The most successful means of assessing the abundance and obtaining recognizable samples of marine snow aggregates has been with *in situ* methods, either by scuba (Shanks and Trent 1980; Alldredge *et al.* 1986) or submersibles (Silver and Alldredge 1981; Alldredge and Youngbluth 1985). However, 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 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 largest 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 may intrude onto the continental shelf of the South Atlantic Bight within plumes of upwelled water. Strings of mucoid material, 3-20 cm long, have appeared in dense concentrations at depths of 90-120 m in the Bahamas and have also been noted to extend from 5-600 m. Most of the strings were oriented vertically and many remained attached to the filamentous rhizopodia of the foraminiferan *Hastigerina pelagica* (Youngbluth 1984b). Estimates of foraminiferan abundance ranged from 5-100 individuals per cubic meter. The rates at which this mucoid material sinks and decomposes is unknown. These records of appendicularians and foraminiferans are but two of many observations which have indicated that gelatinous zooplankton can produce substantial masses of marine snow. The biological contribution and the vertical flux of this particulate material to pelagic and benthic communities are subjects of ongoing investigations.

Photo 1.

Generation after generation of salps alternate between solitary (asexual) and aggregate (sexual) forms. Shown here is a solitary salp *Helicosalpa virgula*, spawning an aggregate strand of individuals linked side by side. This species from 365 m is ca. 15 cm long, Bahamas. This herbivorous animal feeds by pumping water through the inside of its hollow body. The inner surface of the body is lined with a sticky mucous sheet which accumulates small particles of food

D'une génération à la suivante, les salpes alternent une forme solitaire (asexuée) et une forme agrégée (sexuée). Cette figure montre une forme solitaire de *Helicosalpa virgula*, pondant une chaîne d'individus liés côte à côte. Cette espèce, provenant de 365 m de profondeur aux Bahamas, mesure environ 15 cm de longueur. Cet animal herbivore se nourrit en filtrant l'eau pompée à l'intérieur de son corps creux, dont la surface interne est garnie d'un film muqueux collant qui accumule les petites particules alimentaires.

Photos 2 & 3

Undescribed physonect siphonophores from 700 m, ca. 46 cm long, North Atlantic and Bahamas, respectively. These deep-sea carnivores are actually colonies of swimming, feeding and reproducing animals cemented together in a mucoid matrix. The anterior tube-shaped individuals, which provide locomotion and buoyancy (**2**), are connected to a contractile stem from which a myriad of poisonous tentacles can extend to feed on mm-sized zooplankton (**3**).

Siphonophores physonectes non décrits, trouvés à 700 m de profondeur, mesurant environ 46 cm de longueur, et observés respectivement en Atlantique Nord et aux Bahamas. Les carnivores marins profonds sont en fait des colonies d'animaux qui nagent, se nourrissent et se reproduisent collés ensemble dans une matrice muqueuse. Les individus antérieurs de forme tubulaire,qui assurent la locomotion et la flottabilité, (**2**) sont reliés à un stolon contractile à partir duquel des filaments pêcheurs munis de myriades de cellules venimeuses peuvent s'étendre pour se nourrir de zooplancton de l'ordre du millimètre (**3**).

Photo 4

Undescribed cydippid ctenophore from 550 m, ca. 5 cm long, Bermuda. This animal captures small crustacean prey with two long, sticky tentacles, which are contracted into the two yellow masses in the lower half of the body. The rainbow-colored bands that radiate down along the body result from the refraction of light of many rapidly flapping, locomotory organs called ctenes.

Cténophore cydippide non décrit, provenant de 550 m de profondeur aux Bermudes, mesurant environ 5 cm de longueur. Cet animal capture de petits crustacés à l'aide de deux longs tentacules collants qui sont rétractés dans les deux masses jaunes de la moitié inférieure du corps. Les bandes couleur d'arc-en-ciel qui rayonnent vers le bas du corps proviennent de la réfraction de la lumière à partir de nombreux organes locomoteurs appelés ctènes, qui battent rapidement.

Photo 5

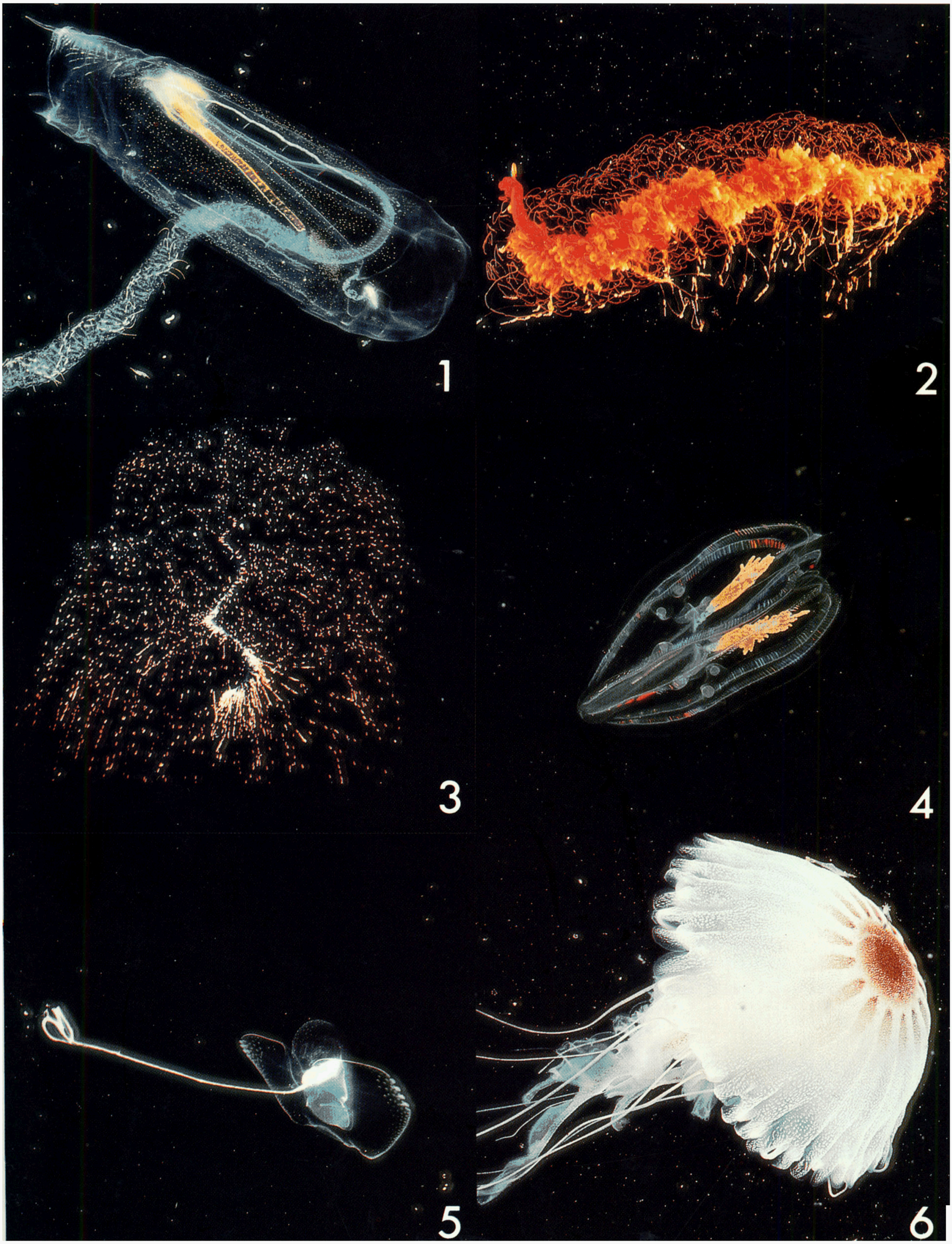
The pseudothecate pteropod *Gleba cordata* from 115 m, ca. 7 cm long, Bahamas. The long esophagus extending upwards from this marine snail has a prehensile mouth that is adapted to select tiny particles of food that adhere to free-floating mucous webs.

Gleba cordata, ptéropode pseudothécosome provenant de 115 m de profondeur, aux Bahamas, mesurant environ 7 cm de longueur. Le long oesophage qui s'étend vers le haut de ce mollusque marin possède une bouche préhensile adaptée à la sélection de très petites particules alimentaires qui adhèrent à des réseaux muqueux flottants.

Photo 6.

This common jellyfish can become very numerous in the coastal waters of the western Atlantic Ocean where it captures little copepods, shrimps and fish larvae with special stinging-cells distributed along its 4-m long tentacles.

Chrysaora quinquecirrha, scyphoméduse, provenant de 50 m de profondeur; diamètre de l'ombrelle d'environ 10 cm. Cette méduse commune peut devenir très abondante dans les eaux côtières de l' océan Atlantique Ouest où elle capture de petits copépodes, des crevettes et des


1
2
3
4
5
6

larves de poissons avec des cellules urticantes spéciales réparties le long de ses tentacules de 4 mètres.

Oxygen Consumption Rates

A basic requirement for comprehending the dynamic nature of food webs in oceanic regimes is the quantification of energy utilization rates by the 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). Metabolic rates have been determined for several midwater crustaceans (Hiller-Adams and Childress 1983), cephalopods (Belman 1978), and fishes (Donnelly and Torres 1988). However, similar 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 a midwater ctenophore *Bathocyroe fosteri* have revealed rates about half as great as those of shallow water ctenophores (Youngbluth *et al.* 1988). These metabolic characteristics complemented *in situ* observations of poor locomotor ability and passive feeding behavior. Calculations based on average metabolic demand (ca. 7% body carbon per day) indicated that a medium-sized (40 mm) *B. fosteri* (260 mg dry weight) would need an input of 150 µg carbon per day. This requirement was smaller (up to 4 times) than rates measured for epipelagic ctenophores (Kremer et *al.* 1986).

Future research on the metabolism of many deep-sea gelatinous animals will probably require the development of *in situ* instrumentation. An *in situ* approach, i.e, conducting measurements in the natural environments of the deep sea, should reduce the variability of metabolic data since experimental animals will not be exposed to abrupt changes in water quality (e.g., temperature, salinity, oxygen and pressure) and light intensity or subjected to undue physical manipulation (Smith and Baldwin 1983).

Summary

The conclusion to be drawn from this review should be that undersea investigations need to be an integral part of zooplankton research programs, not a separate component. Data collected from manned submersibles have provided information, on temporal and spatial scales, about phenomena not addressable with traditional techniques. Continued use of manned submersibles will help oceanographers to optimize where and when to perform ecological investigations in water column environments.

Literature Cited

Alldredge, A.L. 1984. - The quantitative significance of gelatinous zooplankton as pelagic consumers, pp. 407-433. In: *Flows of energy and materials in marine ecosystems*(M.J.R. Fasham ed.). New York, Plenum Press.

Alldredge, A.L. and J.L. Cox. 1982. - Primary productivity and chemical composition of marine snow in surface waters of the Southern California Bight. - *J. Mar. Res*, 40: 517-527.

Alldredge, 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. - *Mar. Biol*, 80: 75-81.

Alldredge, A.L. and M.J. Youngbluth. 1985. - The significance of macroscopic aggregates (marine snow) as sites for heterotrophic bacterial production in the mesopelagic zone of the subtropical Atlantic. - *Deep-Sea Res*, 32: 1445-1456.

Alldredge, A.L., J. Cole and D.A. Caron. 1986. - Heterotrophic production of bacteria inhabiting macroscopic organic aggregates (marine snow) from surface waters. - *Limnol. Oceanogr*, 31 : 68-78

Asper, V.L. 1986. - Accelerated settling of particulate matter by 'marine snow' aggregates. Ph.D. Thesis, Woods Hole Oceanographic Institution/MIT. 189 pp.

Barnes, A.T., L.B. Quetin, J.J. Childress and D.L. Pawson. 1976. - Deep-sea macroplanktonic sea cucumbers: Suspended sediment feeders captured from deep submergence vehicle. - *Science*, 194 : 1083-1085.

Belman, B.W. 1978. - Respiration and the effects of pressure on the mesopelagic vertically migrating squid *Histioteuthis heteropsis*. - *Limnol. Oceanogr*, 23 : 735-739.

Caron, D.A., P.G. Davis, L.P. Madin and J. McN. Sieburth. 1982. - Heterotrophic bacteria and bacterivorous protozoa in oceanic macro-aggregates. - *Science*, 218 : 795-797.

Childress, J.J. 1977. - Physiological approaches to the biology of midwater organisms, pp. 301-324. In: *Oceanic Sound Scattering Prediction* (N.R. Anderson and B.J. Zahuranec eds.), Plenum, New York.

Childress, J.J. 1983. - Oceanic biology: lost in space?, pp. 127-135. In: *Oceanography, the Present and Future* (P.G. Brewer ed.). Springer-Verlag, New York.

Davoll, P.J. and M.W. Silver. 1986. - Marine snow aggregates: life history sequence and microbial community of abandoned larvacean houses from Monterey Bay, California - *Mar. Ecol. Prog. Ser*, 33 : 111-120.

Donnelly, J. and J.J. Torres. 1988. - Oxygen consumption of midwater fishes and crustaceans from the eastern Gulf of Mexico. - *Mar. Biol*, 97 : 483-494.

Galt, C.P. 1979. - First records of a giant pelagic tunicate, *Bathochordaeus charon* (Urochordata, Larvacea) from the eastern Pacific Ocean, with notes on its biology. - *Fish. Bull*, 77 : 514-519.

Gilmer, R.W. 1972. - Free-floating mucous webs: A novel feeding adaptation for the open ocean. - *Science*, 176 : 1239-1240.

Hamner, W.M. 1977. - Observations at sea of live, tropical zooplankton, pp. 284-296. In: *Proceedings of the Symposium on Warm Water Zooplankton*, UNESCO.

Hamner, W.M., S.W. Strand, G.I. Matsumoto, and P.P. Hamner. 1987. - Ethological observations on foraging behavior of the ctenophore *Leucothea* n.sp. in the open sea. - *Limnol. Oceanogr*,. 32 : 645-652.

Harbison, G.R. 1985. - On the classification and evolution of the Ctenophora, pp. 78-100. In: *The origins and relationships of lower invertebrates* (S.C. Morris, J.D. George, R. Gibson and H.M. Platt ,eds.). Oxford, Oxford University Press.

Hiller-Adams, P. and J.J. Childress. 1983. - Effects of season on the bathypelagic mysid *Gnathophausia ingens*: water content, respiration, and excretion. - *Deep-Sea Res.*, 30 : 629-638.

Knauer, G.A., D. Hebel and F. Cipriano. 1982. - Marine snow: major site of primary production in coastal waters. - *Nature*, 300 : 630-631.

Kremer, P., M.F. Canino and R.W. Gilmer. 1986. - Metabolism of epipelagic tropical ctenophores. - *Mar. Biol.*, 90 : 403-412.

Mackie, G.O. 1985. - Midwater macrozooplankton of British Columbia studied by submersible PISCES IV. - *J. Plank. Res.*, 7 : 753-777.

Mills, C.E., R.J. Larson and M.J. Youngbluth. 1987. - A new species of coronate scyphomedusa from the Bahamas, *Atorella octogonos*, new species. - *Bull. Mar.Sci.*, 40 : 423-427.

Pugh, P.R. and G.R. Harbison. 1986. - New observations on a rare physonect siphonophore, *Lycnagalma utricularia* (Claus, 1879). - *J. Mar. Biol. Ass. U.K.*, 66 : 695-710.

Pugh, P.R. and G.R. Harbison. 1987. - Three new species of prayine siphonophore (Calycophorae, Prayidae) collected by submersible, with notes on related species. - *Bull. Mar. Sci.*, 41 : 68-91.

Pugh, P.R. and M.J. Youngbluth. 1988. - A new species of *Halistemma* (Siphonophora, Physonectae, Agalmidae) collected by submersible. - *J. Mar. Biol. Ass. U.K.*, 68 : 1-14.

Pugh, P.R. and M.J. Youngbluth. in press. - Two new species of prayine siphonophore (Calycophorae, Prayidae) collected by the submersibles *'Johnson-Sea-Link'* I and II. - *J. Plank. Res.*

Silver, M.W. and A.L. Alldredge. 1981. - Bathypelagic marine snow: deep-sea algal and detrital community. - *J. Mar. Res.*, 39 : 501-530.

Shanks, A.L. and J.D. Trent. 1980. - Marine snow: sinking rates and potential role in vertical flux. - *Deep-Sea Res.*, 27 : 137-143.

Smith, K.L.,Jr. and M.B. Laver. 1981. - Respiration of the bathypelagic fish *Cyclothone acclinidens*. - *Mar. Biol.*, 61 : 261-266.

Smith, K.L.,Jr. and R.J. Baldwin. 1983. - Deep-sea respirometry: *in situ* techniques, pp. 298-319. In: *Polarographic Oxygen Sensors* (E. Gnaiger and H. Forstner eds.). Springer-Verlag, Berlin.

Youngbluth, M. J. 1984a. - Manned submersibles and sophisticated instrumentation: Tools for oceanographic research, pp. 335-344. In: *Proceedings of SUBTECH 1983 Symposium.* London, Society of Underwater Technology.

Youngbluth, M. J. 1984b. - Water column ecology: *in situ* observations of marine zooplankton from a manned submersible. In: *Divers,* Mem. Univ. Newfld. Occ. Pap. Biol. (N.C. Fleming ed.), Vol. 9 : 45-57.

Youngbluth, M.J., P. Kremer, T.G. Bailey and C.A. Jacoby. 1988. - Chemical composition, metabolic rates and feeding behavior of the midwater ctenophore *Bathocyroe fosteri*. - *Mar. Biol.*, 98 : 87-94.