



A golden age of gelata: past and future research on planktonic ctenophores and cnidarians[☆]

Steven H.D. Haddock

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

E-mail: haddock@mbari.org

Key words: siphonophore, jellyfish, bioluminescence, biodiversity, blue-water diving, submersible

Abstract

The study of the natural history of gelatinous zooplankton ('gelata') reached a high point at the end of the 19th century, when scientists first began to understand the phylogenetic and ecological links between cnidarians and ctenophores. Siphonophores, carefully figured in their entirety, and gauze-like lobate ctenophores too fragile to touch, were described by the dozens. In the ensuing years, focus on zooplankton shifted toward more 'industrial' goals such as quantitative sampling using plankton nets. While plankton scientists were busy summing tattered parts, they lost sight of the whole jellies themselves, and a crustaceocentric view of the ocean came to dominate. During this period, the most dramatic breakthroughs in cnidarian research came from laboratory studies of neurobiology, physiology, and development, particularly of certain model organisms. Now, at the turn of this century, we have the opportunity to bring gelata back into primacy. Submersibles and remotely operated vehicles allow us to study entire life histories of organisms that we did not even know existed. The tools of molecular biology allow us to answer questions about development, evolution, and phylogeny that had reached a stalemate. Even in the surface waters, where it might be thought that there is little left to learn, *in situ* observations have revealed unexpected interactions and hidden diversity. The critical roles that these organisms play in the health of the oceans, their position at the crux of many evolutionary debates, and the tools for biotechnology that they provide, have led to resurgent public appreciation and awareness. Although advanced tools do not necessitate good science, we have few excuses for failing to bring about another golden age of gelata.

Introduction

The name 'coelenterata' has long been employed as a convenient way to describe organisms from the two phyla Ctenophora and Cnidaria. Because it implies a degree of relatedness which is now considered inaccurate, this word is typically avoided in a rigorous taxonomic or phylogenetic context. An alternative term – more encompassing but with less implication of shared common ancestry – is the phrase 'gelatinous zooplankton'. This term has the

advantage of emphasizing the convergent features of transparency, fragility, and planktonic existence that unite these disparate creatures, without the taxonomic baggage associated with other terms. On the other hand, it is a polysyllabic mouthful. Here the term *gelata* is offered as a collective noun to describe the polyphyletic assemblage of medusae, siphonophores, ctenophores, radiolarians, urochordates, molluscs, and worms that eke out a planktonic existence (Fig. 1). It is meant to have no taxonomic implication, but rather to evoke these diverse groups of non-crustacean macroplankton that are too fragile to sample with conventional oceanographic methods.

[☆]A plenary address of the 7th International Conference on Coelenterate Biology.

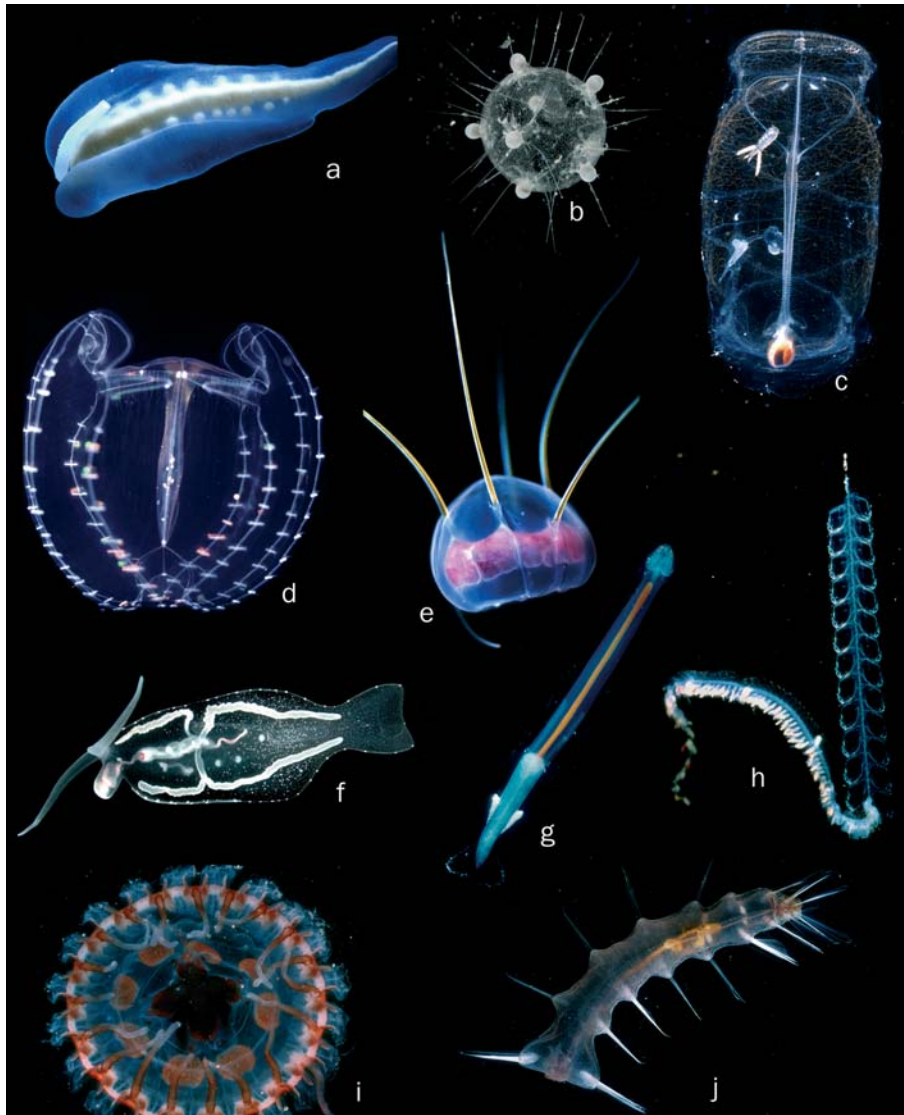


Figure 1. Representative members of gelatinous zooplankton. Organisms from at least eight phyla are included among the gelata. (a) Nemertean. (b) Phaeodarian radiolarian. (c) Salp with parasitic copepod. (d) Lobate ctenophore. (e). Narcomedusan hydrozoan. (f) Nudibranch mollusc. (g). Chaetognath. (h) Physonect siphonophore. (i) Coronate scyphozoan. (j) Polychaete.

The first golden age

Two of the most prominent yet under-appreciated members of the gelata are siphonophores (Cnidaria, Hydrozoa) and comb jellies (Ctenophora). At the end of the 19th century, these taxa occupied more conspicuous positions in both public and scientific consciousness (Winsor, 1972). Comb jellies had several champions in the early 1900s; between 1900 and 1909, twice as many ctenophore

species were described than in any other ten-year period before or since (Fig. 2). The observations conducted by Chun (1880) are so unique that only in the last 20 years have some of his species been 're-discovered.'

Because of their apparently intermediate position between benthic hydroids and planktonic medusae, siphonophores elicited a special fascination from those grappling with the implications and mechanisms of Darwinian evolution. The

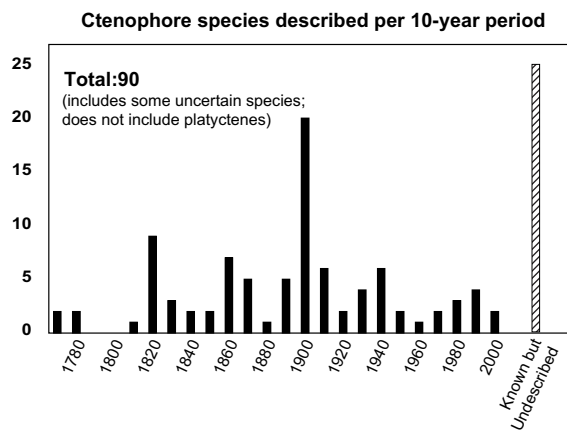


Figure 2. Ctenophores described by decade. The majority of known ctenophore species were described around 1900, with the maximum occurring from 1900 to 1909. Presently there many known deep-sea species, 70% of which are cydippids, which await description. Numbers adapted from Mills (1998), with unpublished data from Harbison, Mills, Haddock, Matsumoto, Lindsay.

great biologists of the time, including Huxley, Haeckel, Vogt, Leuckart, Agassiz, and Darwin himself, enthusiastically enlisted siphonophores in

their debates. Deservedly, all these pioneers have had multiple species of gelata named after them.

Illustrations from this time were inspired as much by the beauty of the organisms as by functional scientific interpretation. Haeckel, fresh from his monumental and still unsurpassed treatise on Radiolaria (1887), created detailed illustrations showing entire siphonophore colonies (1888, 1904) with the apparent intent of demonstrating how such diverse specialized parts could serve a united function (Fig. 3b). His representations from this era compare favorably with living specimens captured by a submersible (Fig. 3a). Another champion of siphonophores, Huxley (1856), asserted that 'living nature is not a mechanism but a poem.' Although some artwork of this time has been said to be distorted by ideological predispositions (e.g. Mechnikov, 1874, as cited in Winsor, 1972), these criticisms cannot detract from their many important positive effects: The predominant attitude was a concern with the whole animal, not merely its parts. This is linked to the desire to understand the origins of life, and the perceptions that cnidarians and ctenophores played key roles in answering basic questions of evolution.

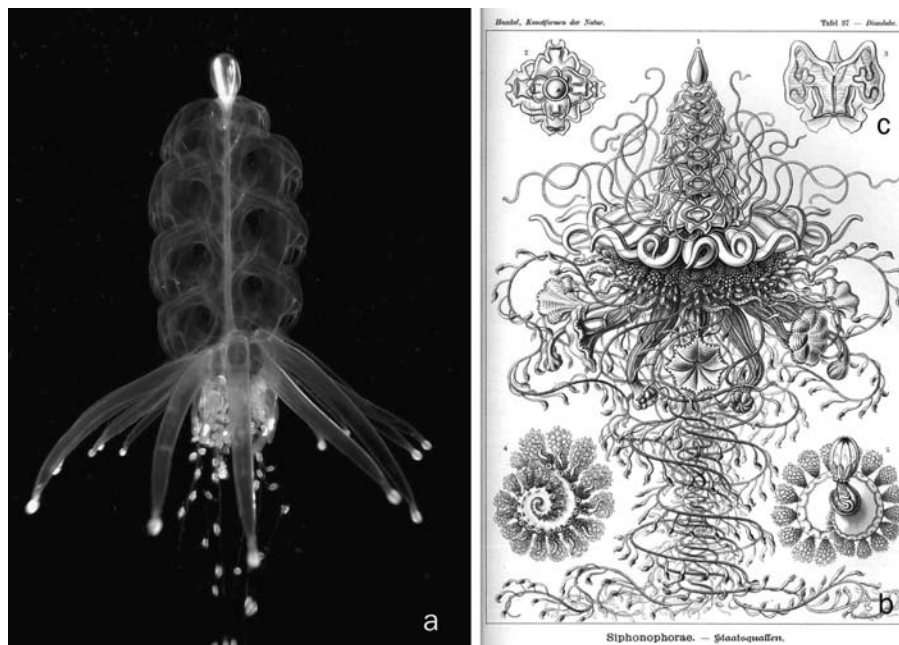


Figure 3. Two views of the siphonophore *Physophora*. (a) Photo of a live specimen collected by submersible. (b) Illustration of whole colony by Haeckel (1904). (c) Detail of isolated nectophore.

Public awareness and fascination with cnidarians followed suit. Haeckel and others presented siphonophores in popular lectures to general audiences. Best-selling books of the time were natural history treatises of Wood (1890), whose encounter with a scyphomedusa inspired a Sherlock Holmes mystery, and Gosse (1853), who described a species of bioluminescent hydromedusa and coined the term 'aquarium' while helping fuel the Victorian aquarium craze with his how-to guides. Siphonophores, medusae, and even radiolarians were depicted in popular glass sculptures by the Blaschkas, who strived for a *tromp l'oeil* degree of realism. Intact living specimens could be obtained because the pace of the sampling, at times using buckets over the side of sailing ships, or dipping from the sea at Mediterranean laboratories, allowed it.

The 'industrial' age

Two shifts occurred in the mid-1900s that contributed to the stagnation of research on gelatinous zooplankton. Ships became larger and faster, and scientists' interest turned to important global questions such as carbon flux. These oceanographic-scale cruises led scientists to ask of the jellies 'how many?' and 'how much?' before having answered 'who?' and 'how?'

In contrast to the drawings of the late 1800s, the depictions of isolated siphonophore bits by mid-20th-century taxonomists show only dissociated parts (Fig. 1c). This was by necessity, as researchers, forced to use nets and other conventional sampling devices, could not obtain intact specimens (cf. Alldredge, 1984; Pugh, 1989; Harbison, 1992; Dennis, 2003). Although this piece-by-piece research is an integral part of our present knowledge (e.g. Totton, 1965), it sheds little light on how the intact organism actually functions.

The situation was worse in lobate ctenophores, where there were not even pieces available for examination. During this period, it seems that if an organism could not be fixed in formalin, it was not studied. Figures in textbooks have been copied generation after generation without reference to living animals, like a visual game of 'Telephone.' A result of this piecemeal approach to examining gelata is that even invertebrate zoologists had very

little understanding of the organisms themselves. For example, the best-known ctenophore genus, *Pleurobrachia*, is depicted upside-down in a majority of scientific and educational illustrations. Although the early taxonomists began this unfortunate convention, there has been little effort to correct it in the intervening 100 years. This seems like a harmless and arbitrary choice, but depicting comb jellies as though they encounter the world with their aboral end perpetuates false affinities with medusae, and impairs our understanding of their distinct non-jellyfish-like modes of feeding (Greve, 1970; Harbison et al., 1978; Moss & Tamm, 1986).

Another result of the difficulty of sampling ctenophores is that their diversity has been underestimated. Three genera (*Pleurobrachia*, *Beroë*, *Mnemiopsis*) have received the vast majority of attention because they are common in shallow coastal waters or because they are robust enough to come up in plankton tows. The lobate genus *Bathocyroe* is extremely abundant throughout the deep ocean – arguably more common than any of the better known genera – yet it was only described 25 years ago (Madin & Harbison, 1978a). The diversity of ctenophores and planktonic cnidarians seems to reside in the higher taxonomic levels. Rather than a few speciose genera, these phyla have many monotypic genera, and families or even orders with only a handful of members. Within the comb jellies, the diversity is demonstrated in the variety of body shapes, sizes, and feeding specializations. Nearly every permutation possible (with or without lobes, auricles, tentacles, tentilla) occurs within the phylum (Fig. 4).

At least in the ctenophores there has been some representation of their many body plans; siphonophores are much more poorly depicted. The aberrant cystonect *Physalia* is generally used to represent the group, although it possesses few traits in common with any other siphonophore genus. (This is similar to the use of *Obelia* as the 'textbook' example of hydromedusan life-cycles, when it is one of the least representative members of the group.) Although it should be rectified, this bias is understandable given that the truly abundant siphonophores are fragile, transparent, and difficult to collect, whereas in certain regions the Portuguese Man o'War, like the ctenophore *Pleurobrachia*, can be washed conspicuously onto beaches.

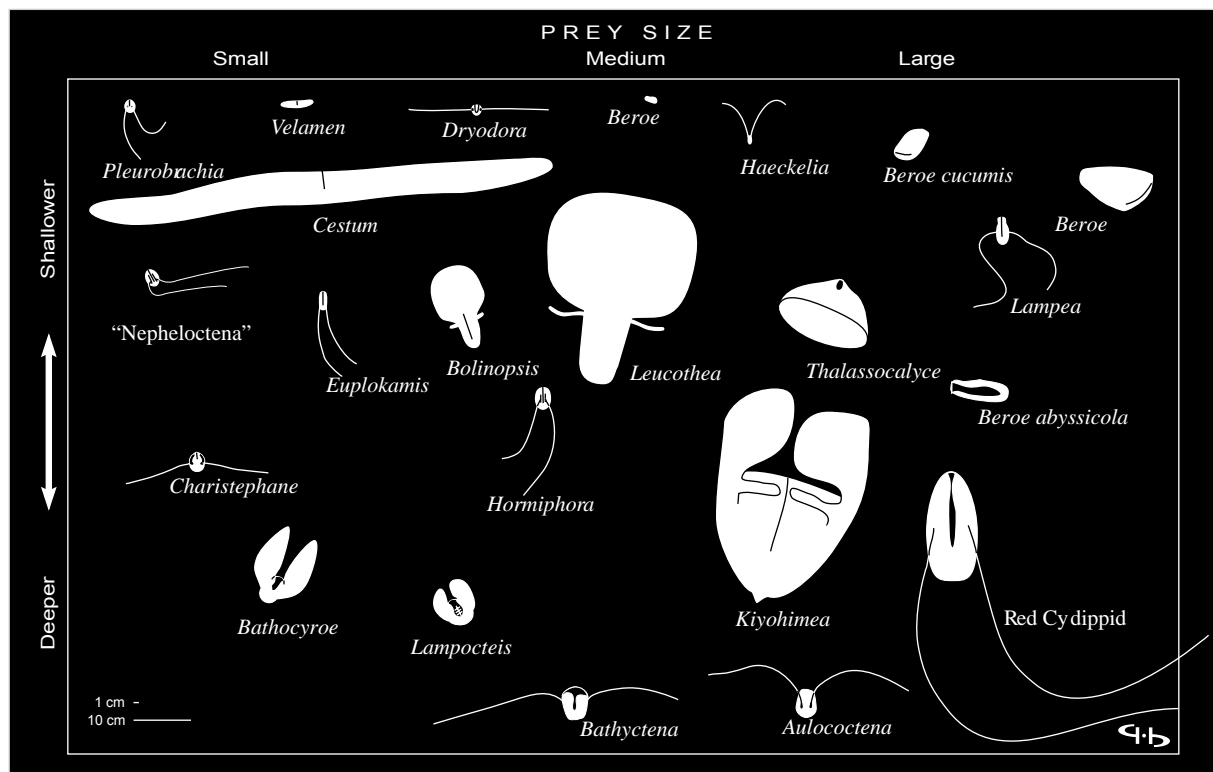


Figure 4. Diversity of ctenophore shapes and sizes. Ctenophores range in size from a few millimeters to nearly a meter. They are found to great ocean depths and eat a range of prey types, from small copepods to shrimp, and even other jellies.

A new golden age

Are we indeed poised for a resurgence in interest and understanding of gelata? There are several reasons why this is an opportune time for significant advances in our understanding of these creatures.

Collection techniques

With the exception of pioneers like Bieri (1966) and Ceccaldi (1972), few people attempted to observe plankton in their natural environment before Hamner and students pioneered the technique of blue-water SCUBA diving (Hamner, 1975; Hamner et al., 1975). This is a system of tethers and procedures for making *in situ* observations on water-column organisms and processes. Although it can not be said to be commonplace, this method has found broad applicability in examinations of marine snow (Silver et al., 1978; Alldredge & Silver, 1988), microbes (Delong et al., 1993), diatoms

and cyanobacteria, in addition to gelata (Harbison et al., 1978; Haddock & Case, 1999). This intimate view of the shallow open water has been extended to the deep-sea by the use of submersibles and ROVs (e.g. Pugh & Harbison, 1987; Widder et al., 1989; Hamner & Robison, 1992; Lindsay et al., 2000). In addition to improved video capabilities, the major development in understanding deep-sea midwater biology has been to equip submersibles with specialized samplers that collect fragile organisms and the water surrounding them undisturbed (Youngbluth, 1984).

These collection methods paint a dramatically different picture of planktonic diversity from typical net tows. Fragile lobate ctenophores, long physonects, large medusae, and species that live just above the bottom are among the groups which are exclusively available to submersibles. Submersible- or hand-collected specimens can be described in their natural state, not just based on a few fragments. A mini-resurgence of ctenophore descriptions began in the late 1970s with the first

reports of submersible-caught specimens (Madin & Harbison, 1978a, b), and this has continued to date (Harbison et al., 2001). (Interestingly, the first ctenophore described during this time appears to have been originally depicted as a juvenile lobate by Chun in 1880.) Presently, there are known to be at least two dozen new species of ctenophores, mostly in new genera, which are awaiting official description (Fig. 2; Harbison, Mills, Haddock, Matsumoto, Lindsay, personal communication; Mills, 1998). Similar situations occur in the siphonophores, although the recent efforts of Phil Pugh have gone a long way toward clarifying this group. There is one widely known species of *Apoemia*, yet at least a dozen other species are being worked up. These descriptions will have an impact on diversity similar to what occurred a hundred years ago.

Another advantage of *in situ* observations by both SCUBA and submersible is the ability to see the natural interactions between organisms in their environment. As Richard Harbison is fond of stating, sampling with plankton nets is akin to flying over London with a grappling hook. You might pick up hats and umbrellas and a few tree branches, but you can only speculate as to where hats belong, and what umbrellas are good for. Many types of predator-prey (notably gelatinous jellies) and symbiont-host relationships (notably parasitic hyperiid amphipods) have been revealed by direct observations, and by collection of specimens with their associated hosts (Harbison et al., 1977; Purcell, 1991; Lindsay et al., 2001; Raskoff, 2002; Gasca & Haddock, 2004).

Finally, these collection techniques provide access to specimens which can be used in natural experiments, and not just poorly enumerated. Specimens typically arrive at the surface alive, with their bioluminescent ability, gut contents, brooded young, and behavioral responses intact. This is essential to any study of their natural history, physiology, and ecology, and is perhaps the most significant impact of modern collection techniques.

Molecular (and other) tools

Advances in laboratory methodology have opened up areas of research that have not been possible for gelatinous creatures. At their most powerful, they convey the ability to get good information

even from damaged specimens. One such technique is to perform enzyme assays to determine aerobic and anaerobic respiratory potential from tissue samples (Thuesen & Childress, 1994; Seibel et al., 1997). Analyses of stable isotope from isolated tissues can also place an organism in an approximate trophic position, although the resultant picture is sometimes softly focused. Of course the truly powerful tools are those of molecular biology; examinations of DNA, RNA, and protein provide views of the present and past lives of organisms that have never before been available.

Molecular phylogenies give additional ways to clarify relationships within phyla, but they can also allow comparisons between organisms which have few or no morphological traits in common. These analyses have revealed severely polyphyletic taxonomic groups within ctenophores and cnidarians, and have provided much of what we now know about the deep divergences in phylogenetic trees – origins which have vexed biologists for the past 150 years (Podar et al., 2001; Collins, 2002).

Molecular tools have also proven to be the keys to discovering and characterizing new fluorescent proteins and photoproteins from species which cannot be collected in large numbers. Presently it is quite possible to clone a gene from a piece of a single specimen, rather than the thousands which were required for protein purification, and this ability broadens the horizon for discovery of these and other novel proteins.

Public interest

Research takes place within the larger context of human society, and as with any research, one must consider potential benefits that justify support using public funds. Fortunately, the beauty and mystery of these organisms has sparked broad interest, and the importance of gelata is appreciated now perhaps more than ever before. Their effect on the health of the ocean has been demonstrated by the devastating impact that invasive species have had on local fisheries (Vinogradov, 1989). There has also been a suggestion that planktonic cnidarians in particular will move into the higher trophic levels which are forcibly vacated through fishing pressure (Mills, 2001). Not only will medusae thrive on the newly available prey, but they will suppress recovery of fish populations

by consuming their larvae. In addition to their danger, beauty, and effects on fisheries, jellies have provided fluorescent proteins (GFP) and photo-proteins (aequorin), which are now standard and indispensable molecular and biomedical tools. Few would have anticipated the significant benefits that have come about through basic research on cnidarians.

In terrestrial systems, one must travel to remote lands to find a new species of vertebrate, yet 100 km offshore of New York, Sydney, Tokyo, or Lisbon is biologically uncharted territory, with entire families of gelata yet to be discovered. The diversity gap (the difference between known and extant species) appears to be greatest in the deep-sea and microbial realms. Thus any complete survey of diversity requires appropriate sampling of fragile deep-sea fauna.

Conclusions

Although we appear to be in an ideal time for dramatically expanding our understanding of gelata, problems still remain. Foremost among these is the lack of respect and support for the taxonomic arts. We cannot assess the impacts of environmental change (natural or anthropogenic) without narrowing the biodiversity gap through surveys of deep and formerly unattainable biota. In addition, without proper taxonomy, we cannot create robust phylogenies, and ecological studies have little validity beyond ‘species X eats species Y’. An additional impediment is that the appropriate collection methods (ROVs and submersibles) are not widely available to the scientific community, and funding to explore the midwater is minimal. However, those with access to the vehicles are almost always willing to share specimens of the various phyla with other scientists. None of these problems are insurmountable; in fact, there is one overriding reason why another golden age seems inevitable: the global community of scientists devoting their immense talents to research on these fascinating organisms.

Acknowledgments

I am indebted to Alice Alldredge, Jim Case, Jim Childress, Richard Harbison, Claudia Mills, Phil Pugh, Bruce Robison, Edie Widder, and others for

their guidance and for opportunities to study gelata. Erik Thuesen provided gentle criticism (‘AGAIN, AWKWARD’) which improved an early draft.

References

- Allredge, A. L., 1984. The quantitative significance of gelatinous zooplankton as pelagic consumers. In Fasham, M. J. R. (ed.), *Flows of Energy and Materials in Marine Ecosystems*. Plenum, New York: 407–433.
- Allredge, A. L. & M. W. Silver, 1988. Characteristics, dynamics and significance of marine snow. *Progress in Oceanography* 20: 41–82.
- Bieri, R., 1966. Feeding preferences and rates of the snail, *Ianthina prolongata*, the barnacle, *Lepas anserifera*, the nudibranchs *Glaucus atlanticum* and *Fiona pinnata*, and the food web in the marine neuston. *Publications of the Seto Marine Biological Laboratory* 14: 161–170.
- Ceccaldi, H. J., 1972. Observations biologiques de *Cestus veneris*. *Tethys* 4: 707–710.
- Chun, C., 1880. *Die Ctenophoren des Golfes von Neapel*, Vol. 1. Wilhelm Engelmann, Leipzig.
- Collins, A. G., 2002. Phylogeny of Medusozoa and the evolution of cnidarian life cycles. *Journal of Evolutionary Biology* 15: 418–432.
- Delong, E. F., D. G. Franks & A. L. Alldredge, 1993. Phylogenetic diversity of aggregate-attached versus free-living marine bacterial assemblages. *Limnology and Oceanography* 38: 924–934.
- Dennis, C., 2003. Close encounters of the jelly kind. *Nature* 426: 12–14.
- Gasca, R. & S. H. D. Haddock, 2004. Associations between gelatinous zooplankton and hyperiid amphipods (Crustacea: Peracarida) in the Gulf of California. *Hydrobiologia* 530/531: (Dev. Hydrobiol. 178): 529–535.
- Gosse, P. H., 1853. *A Naturalist’s Rambles on the Devonshire Coast*. John van Voorst, London.
- Greve, W., 1970. Cultivation experiments on North Sea ctenophores. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 20: 304–307.
- Haddock, S. H. D. & J. F. Case, 1999. Bioluminescence spectra of shallow and deep-sea gelatinous zooplankton: ctenophores, medusae and siphonophores. *Marine Biology* 133: 571–582.
- Haeckel, E., 1887. Report on the Radiolaria collected by the H. M. S. Challenger during the years 1873–1876. Report on the scientific results of the voyage of the H. M. S. Challenger. *Zoology* 18: 1–1803.
- Haeckel, E., 1888. Report on the Siphonophorae collected by H. M. S. Challenger during the years 1873–1876. Report on the scientific results of the voyage of the H. M. S. Challenger. *Zoology* 28: 1–380.
- Haeckel, E., 1904. *Kunstsformen der Natur*. Bibliographisches Institut, Leipzig and Vienna.
- Hamner, W. M., 1975. Underwater observations of blue-water plankton: logistics, techniques, and safety procedures for divers at sea. *Limnology and Oceanography* 20: 1045–1051.
- Hamner, W. M. & B. H. Robison, 1992. *In situ* observations of giant appendicularians in Monterey Bay. *Deep Sea Research* 39: 1299–1313.

- Hamner, W. M., L. P. Madin, A. L. Alldredge, R. W. Gilmer & P. P. Hamner, 1975. Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behavior. *Limnology and Oceanography* 20: 907–917.
- Harbison, G. R., 1992. The gelatinous inhabitants of the ocean interior. *Oceanus* 35: 18–23.
- Harbison, G. R., D. C. Biggs & L. P. Madin, 1977. The associations of Amphipoda Hyperiidea with gelatinous zooplankton. II. Associations with Cnidaria, Ctenophora and Radiolaria. *Deep-Sea Research* 24: 465–488.
- Harbison, G. R., L. P. Madin & N. R. Swanberg, 1978. On the natural history and distribution of oceanic ctenophores. *Deep-Sea Research* 25: 233–256.
- Harbison, G. R., G. I. Matsumoto & B. H. Robison, 2001. *Lampocteis cruentiventer* gen. nov., sp. nov.: a new mesopelagic lobate ctenophore, representing the type of a new family (Class Tentaculata, Order Lobata, Family Lampoctenidae, fam. nov.). *Bulletin of Marine Science* 68: 299–311.
- Huxley, T. H., 1856. On natural history, as knowledge, discipline, and power. *Proceedings of the Royal Institution. Scientific Memoirs* 1: 305–314.
- Lindsay, D. J., J. C. Hunt, J. Hashimoto, Y. Fujiwara, K. Fujikura, H. Miyake & S. Tsuchida, 2000. Submersible observations on the deep-sea fauna of the south-west Indian Ocean: preliminary results for the mesopelagic and near-bottom communities. *JAMSTEC Journal of Deep Sea Research* 16: 23–33.
- Lindsay, D. J., J. C. Hunt & K. Hayashi, 2001. Associations in the midwater zone: the penaeid shrimp *Funchalia sagamiensis* Fujino 1975 and pelagic tunicates (Order: Pyrosomatida). *Marine and Freshwater Behaviour and Physiology* 34: 157–170.
- Madin, L. P. & G. R. Harbison, 1978a. *Bathocyroe fosteri* gen. nov., sp. nov.: a mesopelagic ctenophore observed and collected from a submersible. *Journal of the Marine Biological Association of the United Kingdom* 58: 559–564.
- Madin, L. P. & G. R. Harbison, 1978b. *Thalassocalyce inconstans*, new genus and species, an enigmatic ctenophore representing a new family and order. *Bulletin of Marine Science* 28: 680–687.
- Mechnikov, I., 1874. Studien über die Entwicklung der Medusen und Siphonophoren. *Z. Wiss. Zool.*
- Mills, C. E., 1998. Phylum Ctenophora: list of all valid species names. Electronic internet document available at <http://faculty.washington.edu/cemills/Ctenolist.html>. Published by the author, web page established March 1998, last updated November 2003.
- Mills, C. E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451: 55–68.
- Moss, A. G. & S. L. Tamm, 1986. Electrophysiological control of ciliary motor responses in the ctenophore *Pleurobrachia*. *Journal of Comparative Physiology A* 158: 311–330.
- Podar, M., S. H. D. Haddock, M. Sogin & G. R. Harbison, 2001. Molecular phylogenetic framework for the phylum Ctenophora based on 18s rRNA sequences. *Molecular Phylogenetics and Evolution* 21: 218–230.
- Pugh, P. R., 1989. Gelatinous zooplankton – the forgotten fauna. *Progress in Underwater Science* 14: 67–78.
- Pugh, P. R. & G. R. Harbison, 1987. Three new species of prayine siphonophore (Calycophorae, Prayidae) collected by a submersible, with notes on related species. *Bulletin of Marine Science* 41: 68–91.
- Purcell, J. E., 1991. A review of cnidarians and ctenophores feeding on competitors in the plankton. *Hydrobiologia* 216: 335–342.
- Raskoff, K. A., 2002. Foraging, prey capture, and gut contents of the mesopelagic narcomedusa *Solmissus* spp. (Cnidaria: Hydrozoa). *Marine Biology* 141: 1099–1107.
- Seibel, B. A., E. V. Thuesen, J. J. Childress & L. A. Gorodezky, 1997. Decline in pelagic cephalopod metabolism with habitat depth reflects differences in locomotory efficiency. *Biological Bulletin* 192: 262–278.
- Silver, M. W., A. L. Shanks & J. D. Trent, 1978. Marine snow: microplankton habitat and source of small-scale patchiness in pelagic populations. *Science* 201: 371–373.
- Thuesen, E. V. & J. J. Childress, 1994. Oxygen consumption rates and metabolic enzyme activities of oceanic California medusae in relation to body size and habitat depth. *Biological Bulletin* 187: 84–98.
- Totton, A. K., 1965. A Synopsis of the Siphonophora. British Museum, London.
- Vinogradov, M. Y., 1989. A newly acclimated species in the Black Sea: the ctenophore *Mnemiopsis leidyi* (Ctenophora: Lobata). *Oceanology* 29: 220–224.
- Widder, E. A., S. Bernstein, D. F. Bracher, J. F. Case, P. Hiller-Adams, K. R. Reisenbichler, J. J. Torres & B. H. Robison, 1989. Bioluminescence in the Monterey Submarine Canyon: image analysis of video recordings from a midwater submersible. *Marine Biology* 100: 541–551.
- Winsor, M. P., 1972. A historical consideration of the siphonophores. *Proceedings of the Royal Society of Edinburgh, Section B* 73: 315–323.
- Wood, J. G., 1890. Out of Doors, a Selection of Original Articles on Practical Natural History. Longmans, Green and Co., London.
- Youngbluth, M. J., 1984. Manned submersibles and sophisticated instrumentation: tools for oceanographic research. SUBTECH '83 Proceedings: Society for Underwater Technology, London: 335–344.