

THEME SECTION

First marine zooplankton research—a perspective

Marine Zooplankton Colloquium 2*

Georgia Coastal Center for Education, Savannah, Georgia 31401, USA
8–10 February 1999

ABSTRACT: During the Second Marine Zooplankton Colloquium (MZC2) 3 issues were added to those developed 11 yr ago during the First Marine Zooplankton Colloquium (MZC1). First, we focused on *hot spots*, i.e., locations where zooplankton occur in higher than regular abundance and/or operate at higher rates. We should be able to determine the processes leading to such aggregations and rates, and quantify their persistence. Second, information on the *level* of individual *species*, even of highly abundant ones, is limited. Concerted efforts should be undertaken with highly abundant to dominant species or genera (e.g., *Oithona* spp., *Calanus* spp., *Oikopleura* spp., *Euphausia superba*) to determine what governs their abundance and its variability. Third, zooplankton clearly influence *biogeochemical cycling* in the ocean, but our knowledge of the underlying processes remains fragmentary. Therefore a thorough assessment of variables that still need to be quantified is required to obtain an understanding of zooplankton contributions to biogeochemical cycling. Combining studies on the 7 issues from MZC1 with the 3 from MZC2 should eventually lead to a comprehensive understanding of (1) the mechanisms governing the abundance and existence of dominant zooplankton taxa, and (2) the control of biodiversity and biocomplexity, for example, in the tropical ocean where diversity is high. These recommendations come from an assemblage of chemical, physical and biological oceanographers with experience in major interdisciplinary studies, including modeling. These recommendations are intended to stimulate efforts within the oceanographic community to facilitate the development of predictive capabilities for major biological processes in the ocean.

KEY WORDS: Marine zooplankton · Significant research issues

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Marine zooplankton function at many levels in ocean food webs, as consumers, producers and prey. Ranging in size from microns (protozooplankton) to centimeters and meters (metazooplankton, including chains of Thaliacea), they are also major contributors to elemental cycling and vertical fluxes. Despite more than 100 yr of research on these organisms, our knowledge of their ecological function in their natural environment has increased only modestly. Presently we possess methods to quantify at least the abundances and distributions of hard-bodied metazooplankton with

*Participating scientists: U. Bathmann, M. H. Bundy, M. E. Clarke, T. J. Cowles, K. Daly, H. G. Dam, M. M. Dekshe-nieks, P. L. Donaghay, D. M. Gibson, D. J. Gifford, B. W. Hansen, D. K. Hartline, E. J. H. Head, E. E. Hofmann, R. R. Hopcroft, R. A. Jahnke, S. H. Jonasdottir, T. Kjørboe, G. S. Kleppel, J. M. Klinck, P. M. Kremer, M. R. Landry, R. F. Lee, P. H. Lenz, L. P. Madin, D. T. Manahan, M. G. Mazzocchi, D. J. McGillicuddy, C. B. Miller, J. R. Nelson, T. R. Osborn, G.-A. Paffenhöfer, R. E. Pieper, I. Prusova, M. R. Roman, S. Schiel, H. E. Seim, S. L. Smith, J. J. Torres, P. G. Verity, S. G. Wakeham, K. F. Wishner.

Corresponding author: G.-A. Paffenhöfer, Skidaway Institute of Oceanography, 10 Ocean Science Circle, Savannah, Georgia 31411, USA. E-mail: cmp@skio.peachnet.edu

accuracy, but have only coarse measures, acoustics for example, to locate dense aggregations and determine their temporal changes/variability. For neither protozoa nor metazooplankton have we definitive methods to determine key rates *in situ*, and most of the former remain inaccessible to study at the species level. Therefore it is not so much a lack of ideas but inadequate methodologies and instrumentation that limits the pace of advances in understanding marine zooplankton. Our ability to predict abundances and distributions, even of the most studied species, is still at an early stage. That realization resulted in the first Marine Zooplankton Colloquium (MZC1) in April 1988 and led to a second Marine Zooplankton Colloquium (MZC2) in February 1999. Several of the participants of MZC1, after consultations with colleagues, decided to organize MZC2, which addressed the following questions: (1) Which major issues have emerged as additional critical topics during the past decade in our field? (2) How can these issues be studied?

In the sections below, we first briefly consider the progress made on research issues initially raised in MZC1 (1989). While these issues remain significant for

now and the near future, the bulk of this report focuses on 3 additional challenges that emerged in discussions at MZC2.

PREVIOUS ISSUES

The 7 research issues of MZC1 are listed in Table 1, each with several citations reflecting progress in that area over the past 12 yr. Neither the references selected for the table nor the brief comments below are meant to be complete. They are only meant to illustrate some of the ways in which advances have been realized. A definitive evaluation of recent progress in marine zooplankton ecology, requiring a more intensive review of all 7 issues, would be an appropriate way to mark the 20th anniversary of MZC1 in 2008.

Issue 1 (small-scale behaviors of individual zooplankters) was stimulated by our lack of understanding about how individual zooplankters behave and interact with other organisms at scales of relevance in their natural environment. Our citations of progress include *in situ* observations as well as experimental studies

(Table 1). Notable is the promising technology that enables *in situ* behavioral observations of individual copepods *Acartia discaudata* being preyed upon by individual juvenile herring, moving obliquely upwards as a school (Kils 1992).

Issue 2 (effects of environmental variability on individual physiology and behavior) stemmed from several studies suggesting that zooplankton behaviors respond more to the magnitude of variance of the conditions encountered, rather than their average. Although this issue has not received a major amount of research attention, demonstrated behavioral responses include the almost immediate response of *Acartia hudsonica* to the introduction of predatory fish into enclosures (Bolens & Frost 1991).

Issue 3 (relationship of growth, fecundity and mortality to environmental conditions, past and present) has received considerable attention. For example, Peterson et al. (1991) revealed how to obtain environmentally realistic rates of growth and reproduction of copepods. Obtaining comparable quantitative information on zooplankton mortality rates continues to be a major stumbling block, but the approach by Ohman & Wood (1995) is promising. A comprehensive field study in a stable physical environment (e.g. with *Calanus finmarchicus* as a likely predator of *Oithona*) could provide quantification and some understanding of *in situ* mortality of a major copepod genus (Nielsen et al. 1999).

Issue 4 (definition of nutritional requirements) was addressed in a recent workshop (Kleppel 2001). We emphasize here recent observations on the effects of specific phytoplankton taxa on calanoid reproduction. For example, aldehydes produced by 3 different species of diatoms negatively affected calanoid egg viability (Miralto et al. 1999, Pohnert 2000); however, other phytoplankton may be nutritionally inadequate, rather

than toxic to zooplankton (e.g. Kleppel 1993, Jonasdottir et al. 1995).

Issue 5 (long-term observations of population and community dynamics and variability) has been investigated in several field studies. Aebischer et al. (1990) showed the parallel trends of changes in the abundance of phytoplankton, zooplankton and herring off NE Great Britain over more than 30 yr, yet they stated 'The mechanisms behind the parallelism in trends

platform: <https://doi.org/10.2354/zooplankton-workshop.04.iu-23.21>

NEW ISSUES

Of the 3 new issues identified at MZC2, the first relates to *zooplankton hot spots*, which in this context are defined as volumes of water characterized by enhanced biological activity and/or concentrations of zooplankton. Zooplankton hot spots are often dominated by 1 or only a few species as, for example, the dominance of zooplankton biomass and part of the food-web interactions by the copepod *Calanoides carinatus* during the Arabian Sea SW Monsoon (Smith et al.

information on spatial extent and longevity exists (Fig. 1), the results are over-generalized. Recent advances in instrumentation and deployment techniques have led to the discovery of thin layers of phytoplankton and zooplankton ranging in thickness from a few tens of cm to a few m, extending horizontally for several km and persisting for >24 h (Hanson & Donaghay 1998, Holliday et al. 1998). Changes in temporal and spatial environmental features lead to variability in abundance, distribution and activity of zooplankton (MZC1 Issue 2). The extent of those features will be of special interest in attempting to understand the formation of zooplankton hot spots.

(2) What are the mechanisms that lead to the formation, maintenance and dispersion of zooplankton hot spots? For example, Price (1989) demonstrated that many specimens of the euphausiid *Thysanoessa raschii* returned to feed on a patch of phytoplankton (i.e. the phytoplankton provided a signal which resulted in the aggregation of the euphausiid). Reproduction responses to enhanced food can also provide a mechanism of patch formation, as illustrated by the calanoid copepod *Temora turbinata* in a phytoplankton-rich mass of upwelled water (Paffenhöfer et al. 1987). Calanoid copepods prefer strata of high primary productivity to those of high-chlorophyll concentrations (Herman et al. 1981). Thus, food quality may be more important than quantity (Kleppel 1993).

(3) Are zooplankton hot spots optimal habitats for some species of zooplankton and/or their predators? The study of Herman et al. (1981) seems to indicate that *Calanus* and other copepods can choose vertically the most favor-

spots are critical to biogeochemical coupling, since much of the material flux may occur at very specific times and locations.

Species level

Within the context of a species-level focus 2 goals are essential to the future research on marine zooplankton: (1) understanding biodiversity and mechanisms of biological interactions, and (2) developing predictive modeling capability. The first goal is oriented towards curiosity-driven basic science. The second goal requires a research agenda facilitating appropriate environmental and biological data sets for models.

The working group recommended an integrative and concerted approach that includes multiple levels of biological analyses, from large-scale environments and populations to cellular and molecular levels (Fig. 2). The intent is to generate an understanding of a particular species and the associated relevant pro-

metazooplankton taxa (e.g. *Oithona*, *Oncaea* and small calanoids) can affect processes underlying marine ecosystem function because of their numerical or biomass dominance and their critical role as intermediaries between the classical and microbial food webs (Gonzalez et al. 1994). Changes in marine ecosystems, due to either natural or human-induced variability, could be observed through changes in communities of marine zooplankton, including composition, diversity and abundance.

Zooplankton taxa of significance

Examples of marine zooplankton taxa that could be considered for study include the copepod *Calanus finmarchicus*, a dominant species in part of the North Atlantic, and *Calanoides carinatus* from the northwestern Indian Ocean and ocean margins of Africa. The TransAtlantic Study of *Calanus finmarchicus* (TASC) was an initial effort in an attempt to perform a species-level study, as was the Subarctic Pacific Ecosystem Research (SUPER) study, which focused mainly on 3 species of the genus *Neocalanus* (Miller 1993).

The small copepod genus *Oithona* occurs ubiquitously and abundantly in the sea, from estuaries to the open ocean and from tropical to polar regions (e.g. Paf-

Future models will require not only improvements in the representation of physics but also species-specific performances of the respective abundant zooplankton genera/species. Nested models that include parameterizations of individual and population processes have not been developed. They will require better field and experimental measuring capability, and advances in computer resources.

Any environmentally oriented species-level model will have to be interdisciplinary. Species-level models and hot spot models both occur in an environment affected by physical variables and numerous biological and chemical parameters, usually including several other zooplankton species as well, because no pelagic environment exists where one zooplankton species is exclusively abundant.

Zooplankton and biogeochemical cycles

Zooplankton directly affect the elemental stoichiometry and material fluxes between particulate and dissolved matter through various processes associated with the selective consumption and subsequent processing of their food resources. The most widely recognized link to biogeochemical fluxes is the repackaging of digestive by-products into fast sinking fecal pellets by relatively large animals (Noji 1991). Given the full spectrum of pelagic consumers (including protists) and the extent of their interactions within food webs, however, this is by no means the only way in which zooplankton can regulate the efficiency of the biological carbon pump or influence elemental cycles.

In the subsections below, we briefly consider the implications of zooplankton-mediated processes in modifying sinking particulate fluxes, in recycling and distributing inorganic and organic materials throughout the water column, and in determining the complex dynamics of food-web structure and trophic flows. Implicit in this discussion is a necessary progression of approaches that might begin with simple theory and experimental studies in bottles, but must extend to measurable phenomena in natural settings and system-level coupled models.

Modification of the downward POM flux

To achieve a mechanistic understanding of the decrease in particulate organic fluxes with depth, both within and below the euphotic zone, we need to know to what extent this decrease is due to the activities of zooplankton versus other consumers such as bacteria (Banse 1990) or physical/chemical processes. Furthermore, we need to know the rates and selectivities of zooplankton

in modifying the chemical makeup of sinking particulate organic matter (POM) (Wakeham & Lee 1993). Since most of the downward POM flux is in the form of relatively large particulates (fecal pellets and aggregates; Fowler & Knauer 1986), future research must also address how zooplankton find and colonize such particles and how fast they consume them (Kjørboe 2000). First, however, we ought to find out which proto- and meta-zooplankton taxa are the main colonizers and feeders. Since grazing processes can also stimulate the metabolic activity of bacteria, and in turn the microbial role in particle disaggregation, this is an area of research that potentially involves synergistic influences of micro- and macro-consumers that are no less complicated than food-web interactions in the epipelagic zone.

One exciting possibility for investigating how zooplankton modify the quality of the sinking POM is the use of biomarkers to distinguish organic matter sources and alteration processes (e.g. Brasell 1993, Wakeham & Lee 1993). Progress in this area is presently limited, however, by the relative scarcity of unique biomarkers for phytoplankton prey, notable exceptions being dinosterol for dinoflagellates and long-chain alkenones for certain haptophytes (Brasell 1993). There are, however, virtually no biomarkers for zooplankton. The situation is further complicated by rapid digestive and biosynthetic alteration of dietary organic matter by the zooplankton themselves, as well as their assemblages of gut flora. Consequently, zooplankton nutritional physiologists need to collaborate closely with organic biogeochemists and microbiologists in developing useful new biomarkers for studying the fate of organic matter.

Numerous previous studies have focused on the role of zooplankton feeding on the packaging and vertical flux of particulate organic materials (Noji 1991, Feinberg & Dam 1998). Much less effort has been directed at examining the impacts of zooplankton on the recycling of biogenic materials in the upper water column. By influencing the efficiency of recycling, zooplankton plays a critical role in determining the rate of regenerated production. This provides a direct linkage between zooplankton, primary production, and biogeochemical cycles. Thus, future studies should place greater emphasis on the mechanisms and processes by which zooplankton recycle nutrients and organic matter.

Dissolved inorganic and organic matter (DIM and DOM): recycling and export

A multi-level protistan grazing chain is the dominant trophic pathway in most open-ocean food webs, its length ensuring that primary production will largely be recycled rather than transferred to larger animals or

exported. Although less important in absolute rates of material cycling, larger animals have the unique ability, in such deep-water systems, to deposit their metabolic by-products several hundreds of meters deeper than their food source in the euphotic zone. In addition, the active flux of both inorganic and organic carbon and nitrogen due to diel vertical migrators and the mortality of migrators below the pycnocline can significantly increase the exported production (Longhurst et al. 1989, Dam et al. 1995, Zhang & Dam 1997). Data on this topic remain scarce, however. Further studies along gradients of latitude and productivity, similar to that of Ikeda (1985), are essential to establish global generalizations of the role of migrator-mediated fluxes of DIM and DOM.

A related realization is that zooplankton-generated DOM may be as important as that of phytoplankton in enhancing bacterial biomass and productivity (Hygum et al. 1997, Strom et al. 1997). These observations suggest several questions for future research: (1) What are the roles of zooplankton in supporting the microbial loop, and are they fundamentally different for protistan versus metazoan consumers? (2) What is the relative importance of alternate mechanisms of DOC production by zooplankton (e.g. excretion, sloppy feeding, fecal leaching) in the economy of the sea? (3) Is the biochemical composition of the DOC produced by zooplankton different from that produced from algal exudation, and if so, what are the consequences for bacterial production?

Additionally, we need to understand in much greater detail how direct grazing and the altered digestive products of zooplankton influence specific elemental cycles and greenhouse-relevant gases. Some challenges related to this topic include studies of zooplankton gut and fecal pellets as a habitat for anaerobic processes such as methanogenesis (Tilbrook & Karl 1995), grazing influences on DMS production and transformations (Dacey & Wakeham 1986, Wolfe & Steinke 1996, Tang et al. 2000), and grazer control of the redox

search but in biological oceanography *sensu strictu* towards understanding community and eventually ecosystem functioning, and its variability, will be a function of setting priorities. We will not be able to develop a solid predictive capability on the significance of zooplankton in the pelagic environment, and therefore a general understanding of its functioning, until we can determine the mechanisms of the zooplankton's contribution (e.g. Aebischer et al. 1990). Determining such mechanisms and developing predictive capabilities depends on (1) *continuous long-term observations* not just on abundant zooplankton taxa but also of the major physical, chemical and biological variables governing their occurrence, distribution and abundance, (2) *in situ rate quantifications* of feeding, growth, mortality etc., accompanying the long-term observations, and (3) parallel interdisciplinary *modeling* (e.g. Hofmann & Lascara 1998, Carlotti et al. 2000).

Acknowledgements. This colloquium was made possible by the commitment of more than 40 marine scientists who selflessly provided time and funds. The Skidaway Marine Science Foundation under the direction of Carol Megathlin supported the colloquium financially. The Georgia Coastal Center for Education provided meeting facilities. We gratefully acknowledge their support. This report was composed using a framework established at the meeting and repeatedly revised by several participants, who spent numerous hours to improving it.

LITERATURE CITED

- Aebischer NJ, Coulson JC, Colebrook JM (1990) Parallel long-term trends across four marine trophic levels and weather. *Nature* 347:753–755
- Ambler JW, Ferrari FD, Fornshell JA (1991) Population structure and swarm formation of the cyclopoid copepod *Dioithona oculata* near mangrove cays. *J Plankton Res* 13: 1257–1272
- Ban S, Burns C, Castel J, Chaudron Y and 19 others (1997) The paradox of diatom-copepod interactions. *Mar Ecol Prog Ser* 157:287–293
- Banse K (1990) New views on the degradation and the disposition of organic particles as collected by sediment traps in the open ocean. *Deep-Sea Res* 37:1177–1195
- Barbeau K, Moffett JW (2000) Laboratory and field studies of colloidal iron oxide dissolution as mediated by phagotrophy and photolysis. *Limnol Oceanogr* 45:827–835
- Batchelder HP, Williams R (1995) Individual-based modelling of the population dynamics of *Metridia lucens* in the North Atlantic. *ICES J Mar Sci* 52:469–482
- Bollens SM, Frost BW (1991) Diel vertical migration in zooplankton: rapid individual response to predators. *J Plankton Res* 13:1359–1365
- Brassell SC (1993) Applications of biomarkers for delineating marine paleoclimate fluctuations during the Pleistocene. In: Engel MH, MrB-375 Tw [(us:2(ilDation of o)s C,w [(7:287)-56l, -rasuor)-22.6lj /F3 17m vid1a3(--. ICES ersoeladailD,0ng)1eiras me

- Haurly LR, McGowan JA, Wiebe PH (1978) Patterns and processes in the time-space scales of plankton distributions. In: Steele JH (ed) Spatial pattern in plankton communities. NATO Conference Series, Series IV: Marine Sciences, Plenum Press, New York, p 277-327
- Herman AW, Sameoto DD, Longhurst AR (1981) Vertical and horizontal distribution patterns of copepods near the shelf-break south of Nova Scotia. *Can J Fish Aquat Sci* 38: 1065-1076
- Heron AC (1972) Population ecology of a colonizing species: The tunicate *Thalia democratica*. I. Individual growth rate and generation time. *Oecologia* 10:269-293
- Hofmann EE, Lascara CM (1998) Overview of interdisciplinary modeling for marine ecosystems. In: Brink KH, Robinson AR (eds) *The sea*, Vol 10. John Wiley & Sons, Inc., New York, p 507-540
- Holliday DV, Pieper RE, Greenlaw CF, Dawson JK (1998) Acoustical sensing of small-scale vertical structures in zooplankton assemblages. *Oceanography* 11:18-23
- Hopcroft RR, Roff JC, Bouman HA (1998) Zooplankton growth rates: the larvaeceans *Appendicularia*

- Paffenhöfer GA, Lee TN, Sherman BK (1987) Summer upwelling on the southeastern continental shelf of the USA during 1981. Abundance, distribution and patch formation of zooplankton. *Prog Oceanogr* 19:403–436
- Paffenhöfer GA, Strickler JR, Lewis KD, Richman S (1996) Motion behavior of nauplii and early copepodid stages of marine planktonic copepods. *J Plankton Res* 18: 1699–1715
- Peterson WT, Tiselius P, Kiørboe T (1991) Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. *J Plankton Res* 13:131–154
- Pohnert G (2000) Wound-activated chemical defense in unicellular planktonic algae. *Angew Chem Int Ed* 39: 4352–4354
- Price HJ (1989) Swimming behavior of krill in response to algal patches: a mesocosm study. *Limnol Oceanogr* 34: 649–659
- Robinson AR, Lermusiaux RFJ, Sloan NQ III (1998) Data assimilation. In: Brink KH, Robinson AR (eds) *The sea*, Vol 10. John Wiley & Sons, Inc., New York, p 541–594
- Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California Current. *Science* 267:1324–1326
- Smith S, Roman M, Prusova I, Wishner K, Gowing M, Codispoti L, Barber R, Marra J, Flagg C (1998) Seasonal response of zooplankton to monsoonal reversals in the Arabian Sea. *Deep-Sea Res II* 45:2369–2403
- Strom SL, Benner R, Dagg MJ (1997) Planktonic grazers are a potentially important source of marine dissolved organic carbon. *Limnol Oceanogr* 42:1364–1374
- Strom SL, Miller CB, Frost BW (2000) What sets lower limits to phytoplankton stocks in high-nitrate, low-chlorophyll regions of the open ocean. *Mar Ecol Prog Ser* 193:19–31
- Tang KW, Visscher PT, Dam HG (2000) DMSP-consuming bacteria associated with the calanoid copepod *Acartia tonsa* (Dana). *J Exp Mar Biol Ecol* 256:185–198
- Tang X, Stewart K, Vincent L, Huang H, Marra M, Gallager SM, Davis CS (1998) Automatic plankton image recognition. *Artif Intell Rev* 12:177–199
- Tilbrook BD, Karl DM (1995) Methane sources, distributions and sinks from California coastal waters to the oligotrophic north Pacific gyre. *Mar Chem* 49:51–64
- Ueda H, Kuwahara A, Tanaka M, Azeta M (1985) Underwater observations on copepod swarms in temperate and subtropical waters. *Mar Ecol Prog Ser* 11:165–171
- US GLOBEC (1994) Secondary production modeling workshop report. US Global Ocean Ecosystem Dynamics, Report No. 13, US GLOBEC, Berkeley, CA
- Uye S, Sano K (1995) Seasonal reproductive biology of the small cyclopoid copepod *Oithona davisae* in a temperate