Journal of
Plankton Research
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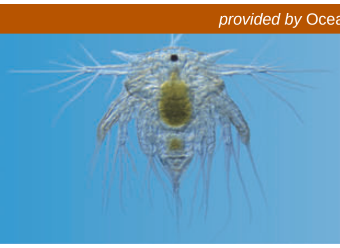

J. Plankton Res. (2015) 37(5): 985–988. First published online August 25, 2015 doi:10.1093/plankt/fbv068

Contribution to the ICES/PICES Theme Session: ‘Interactions of Gelatinous Zooplankton within Marine Food Webs’

INTRODUCTION

Interactions of gelatinous zooplankton within marine food webs

Gelatinous zooplankton (GZ) comprise a taxonomically and functionally diverse group of marine organisms which includes ctenophores, cnidarians and pelagic tunicates, sharing a soft, mostly transparent body texture, a high body water content and a lack of exoskeleton. They range in size from less than a millimetre to nearly 2 m for the cnidarian jellyfish *Nemopilema nomurai*, and comprise some of the fastest growing metazoans on Earth (Hopcroft *et al*., 1998), sometimes surpassing crustacean zooplankton in their contribution to secondary production (i.e. in subtropical waters; Jaspers *et al.*, 2009). They feed on a wide range of prey sizes, with predator–prey ratios comparable in some cases to those of baleen whales and krill (Deibel and Lee, 1992), and with prey removal rates which are similar to those of their non-gelatinous competitors (Acuña *et al.*, 2011). In spite of early work pointing to gelatinous zooplankton as a trophic dead end (Verity and Smetacek, 1996), evidence is rapidly accumulating which shows that they may potentially channel energy from the picoplankton-sized, microbial loop organisms up to the higher trophic levels, including fish (Llopiz *et al.*, 2010). However, this pathway is still largely neglected in most food web investigations even though it is now becoming clear that GZ represent a major fraction of the diet of several commercially important fish species such as bluefin tuna (*Thunnus thynnus*) (Cardona *et al.*, 2012).

Research during the last two decades has shown that GZ blooms are increasing in magnitude and frequency in several areas of the world’s ocean, e.g. in the Black Sea (Kideys, 2002); in the East Asian marginal seas (Uye, 2008); in the Benguela Current (Lynam *et al.*, 2006); in the eastern Bering Sea (Brodeur *et al.*, 2008); in fjord systems around northern Europe (Riisgård *et al.*, 2012), with cascading socio-economic consequences for fisheries and tourism (Richardson *et al.*, 2009; Purcell, 2012). These trends have been blamed on the increasing influence of anthropogenic stressors, such as eutrophication, over-fishing, establishment of artificial hard substrata, climate change and species translocations, which has led to the paradigm that GZ will increase in the future (Richardson *et al.*, 2009; Purcell, 2012). In spite of such growing concerns, international attempts at collating all available information have not supported the paradigm, at least at a global scale (the JEDI jellyfish dataset initiative, Condon *et al.*, 2012a). Rather, these exercises show a patchwork pattern, with increasing, decreasing or no trends in different parts of the world (Condon *et al.*, 2012b). Importantly, this concerted effort has revealed the existence of major knowledge gaps while pointing to directions for future endeavour.

Beyond a need to further elucidate trends in GZ biomass, there is clearly an urgency to understand the

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role of GZ within marine food webs. This knowledge is essential to forecast the implications of future increases in GZ, whether at global or regional scales. For this reason, a special Theme Session was held at the ICES Annual Science Meeting in A Coruña, Spain, in September 2014, which attracted 45 contributions from 18 countries around the world. Here, 10 papers from the Theme Session are compiled, each contributing to the understanding of the role and interaction of gelatinous zooplankton within marine ecosystems.

Highlights

GZ are defined by their high water content. However, this very fundamental trait remains very poorly constrained, and data compilations all revolve around just a few, similar, sometimes redundant coefficients to convert among the different body size proxies. In this issue, Molina-Ramírez *et al.* (Molina-Ramírez *et al.*, 2015) have supplemented available data on body water, carbon and nitrogen content with observations from the global MALASPINA 2010 expedition. Their analysis reveals a high variability in the water content of gelatinous zooplankton, which is body size independent in the carnivores (ctenophores and cnidarians) and body size dependent in the filter-feeders (tunicates). They provide formulas to deal with transformations among body size currencies for food web studies, and point to some paradoxical theoretical implications of these results for the evolution of gelatinous bodies.

To assess the role of gelatinous zooplankton in the marine ecosystems, it is important to understand what environmental factors drive their physiology and population dynamics. Such studies are best conducted under controlled conditions. The Themed Section contains three papers which address physiological limits in the abiotic and biotic environment defining the range within which ctenophores survive and reproduce. Gambill *et al.* (Gambill *et al.*, 2015) show that the larvae of the invasive northern European *Mnemiopsis leidyi* ctenophore population has a broad realized temperature growth range between 8 and 27°C with maximum growth rates of $\mu = 0.9\ \text{day}^{-1}$ at 27°C. Similarly, starvation experiments reported by Granhag and Hosia (Granhag and Hosia, 2015) in this issue confirm that native and invasive lobate ctenophores present in northern Europe, namely *Bolinopsis infundibulum* and *M. leidyi* adults, kept at 6°C, can survive for 10 weeks without food. They do so by reducing their body carbon content to 20–40% of original values (Granhag and Hosia, 2015). Reducing the body size under food shortage is a unique trait of gelatinous organisms. In this issue, Jaspers *et al.* (Jaspers *et al.*, 2015) show that "degrowth" in *M. leidyi* underlies its high reproduction rates. They also show that animals keep reproducing for up to 12 days without food and that low food levels, generally below those characteristic of summer food concentrations in invaded areas of northern Europe, are sufficient for egg production. Together, these life history traits and broad environmental tolerances allow *M. leidyi* to survive, reproduce and thrive under variable conditions in invaded northern Europe.

The importance of coastal estuaries in contributing to jellyfish production is poorly known. In this issue, Marques *et al.* (Marques *et al.*, 2015) report on the population dynamics of the scyphomedusan genus *Aurelia* in three contrasting lagoons in terms of anthropogenic impacts along the Mediterranean Coast of France. Temperature and food availability (or quality) have been shown to regulate growth and production during the pelagic life cycle, although the presence of predatory *M. leidyi* in certain lagoons may impact *Aurelia* production through competitive interactions. Also in this issue, Morais *et al.* (Morais *et al.*, 2015) report on the diet and physiological condition of the non-indigenous jellyfish *Blackfordia virginica* in the temperate Mira estuary (Portugal). Unlike other jellyfish species, *B. virginica* seems to rely not only on metazooplankton as prey, but also on significant amounts of phytoplankton, ciliates and detritus. This may explain observations of sustained growth even during post-bloom situations when the abundance of metazooplankton is low, a phenomenon with potential implications for the functioning of estuarine food webs.

While several recent studies have shown that gelatinous plankton can exert strong top-down control in the ecosystem, their bottom-up role is underappreciated. In this issue, Hosia *et al.* (Hosia *et al.*, 2015) show that the jellyfish *Cyanea capillata* has a shifting role in the food web, from exerting top-down control during most of its pelagic life to fuelling bottom-up processes during bloom senescence in autumn. Decaying *C. capillata* carcasses stimulate bacterial production, thereby impacting the productivity and structure of lower trophic levels, and mediating a significant vertical carbon flux to the benthos.

The trophic role of neustonic gelatinous zooplankton is also understudied. Purcell *et al.* (Purcell *et al.*, 2015) report in this issue on predation rates of the surface-dwelling cnidarian *Velella velella* during 2 years in the Ligurian Sea off Italy. This species consumed euphausiid larvae, copepods, and to a lesser extent fish eggs and larvae, with small differences between day and night. *Velella velella* selected euphausiid larvae positively and copepods negatively, based upon comparisons of gut contents and available prey. As an interesting corollary, Purcell *et al.* (Purcell *et al.*, 2015) also document the utility of citizen science in reporting location and magnitude of *V. velella* strandings on both the European and Pacific North American coastlines in recent years.

One of the most understudied life stages of the metagenic life cycle of many cnidarians is the planula larvae prior to settlement on the bottom. Their small size and pelagic existence makes them highly vulnerable to many planktivores in coastal waters. Using planulae of the cnidarian *Cyanea capillata* as prey, Kuplik *et al.* (Kuplik *et al.*, 2015) report in this issue their laboratory observations on potential consumption by pelagic (ctenophores) and benthic (ascidians and mussels) predators. The tactile predating ctenophores fed on the planulae but showed a preference for copepods when provided. In contrast, the filter-feeding ascidians and mussels consumed significant numbers of planulae when fed solely or in the presence of alternative food source.

Modelling studies were also a prominent component of the session. Building on an Australian tradition of excellence initiated by Andy Heron, Henschke *et al.* (Henschke *et al.*, 2015) incorporated food and temperature into size-structured models to reproduce the population dynamics of the salp *Thalia democratica* in the Tasman Sea. Their work, presented in this issue, goes beyond demonstrating the role of environmental forcing, and confirms that factors promoting the survival of the asexual stage are key to the development of dense salp populations. This line of endeavour will help address the role of salps in ocean food webs.

In summary, the ICES/PICES jellyfish session provided many scientific advances in different fields of GZ research going on around the world and this special volume has been an extraordinary showcase of this vibrant, relevant and fascinating field of research. As is often the case, many new questions arose during the discussions that will challenge future researchers in this field and provide fertile areas of research for many years to come. Future meetings (e.g., 5th International Jellyfish Blooms Symposium to be held in the summer of 2016 in Barcelona, Spain) will hopefully address these questions and provide a forum for additional exchange of information and ideas in this relatively young field of marine research.

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ACKNOWLEDGEMENTS

We thank the sponsors of this session, the International Council for the Exploration of the Sea (ICES) and the North Pacific Marine Science Organization (PICES), for their financial support in organizing the session, Dr Roger Harris for his encouragement and editorial assistance in putting together this special issue, the anonymous referees who helped evaluate the papers and contributed to their improvement, and to the many participants who contributed to the overall success of the session.

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