

HORIZONS

Evolution of the Arctic *Calanus* complex:
an Arctic marine avocado?JØRGEN BERGE^{1,2*}, TOVE M. GABRIELSEN¹, MARK MOLINE^{1,3} AND PAUL E. RENAUD^{1,4}¹UNIVERSITY CENTRE ON SVALBARD, PB 156, N-9171 LONGYEARBYEN, NORWAY, ²FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS, UNIVERSITY OF TROMSØ, N-9037 TROMSØ, NORWAY, ³CENTER FOR COASTAL MARINE SCIENCES, BIOLOGICAL SCIENCES DEPARTMENT, CALIFORNIA POLYTECHNIC STATE UNIVERSITY, SAN LUIS OBISPO, CA 93407, USA AND ⁴AKVAPLAN-NIVA, FRAM CENTRE FOR CLIMATE AND THE ENVIRONMENT, N-9296 TROMSØ, NORWAY

*CORRESPONDING AUTHOR: jorgen.berge@unis.no

Received August 5, 2011; accepted in principle November 23, 2011; accepted for publication December 5, 2011

Corresponding editor: Mark J. Gibbons

Before man hunted the large baleen whales to near extinction by the end of the nineteenth century, Arctic ecosystems were strongly influenced by these large predators. Their main prey were zooplankton, among which the calanoid copepod species of the genus *Calanus*, long considered key elements of polar marine ecosystems, are particularly abundant. These herbivorous zooplankters display a range of adaptations to the highly seasonal environments of the polar oceans, most notably extensive energy reserves and seasonal migrations to deep waters where the non-feeding season is spent in diapause. Classical work in marine ecology has suggested that slow growth, long lifespan and large body size in zooplankton are specific adaptations to life in cold waters with short and unpredictable feeding seasons. Here, we challenge this understanding and, by using an analogy from the evolutionary and contemporary history of the avocado, argue that predation pressure by the now nearly extinct baleen whales was an important driving force in the evolution of life history diversity in the Arctic *Calanus* complex.

KEYWORDS: Arctic; *Calanus*; evolution; baleen whales; life history strategy; predation pressure; avocado analogy

INTRODUCTION

The three main *Calanus* species found in the Arctic today, *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, are morphologically similar but show marked differences in lifespan and body size (see Falk-Petersen *et al.*, 2009 for

a review). Due to their ability to synthesize and bioaccumulate lipids, *Calanus* can concentrate energy, both individually and collectively through synchronized seasonal and diel (Hays, 2003) vertical migration, which makes them unique sources of energy for higher trophic level predators such as fish (Varpe *et al.*, 2005) and



Fig. 1. The three Arctic *Calanus* spp.: *C. hyperboreus* (top), *C. glacialis* and *C. finmarchicus* (bottom). The relative larger size, longer life and larger lipid sac of the high Arctic *C. glacialis*, compared to that of the more boreal *C. finmarchicus*, are generally assumed to be adaptive traits evolved in response towards the strong seasonality of the high Arctic. Photo: Dag Altin (with permission).

seabirds (Karnovsky *et al.*, 2003). All three species have distinct life histories, with *C. hyperboreus* having the longest lifecycle lasting up to five or more years, whereas *C. finmarchicus* generally completes its lifecycle within 1 year (Falk-Petersen *et al.*, 2009) (Fig. 1). *Calanus glacialis*, on the other hand, seems to have a lifecycle ranging between 1 and 3 years (Falk-Petersen *et al.*, 2009). One well-documented feature regarding the distribution of these species is the higher abundances of the large *C. hyperboreus* in the Arctic basins, contrasted with the more short-lived *C. glacialis* commonly associated with Arctic shelf seas. The reason for this difference in distribution is not well understood, although it has been suggested that the *larger* forms can better buffer their seasonally more stochastic feeding environment (Scott *et al.*, 2000). The same explanation is implied for the plastic life cycle of *C. glacialis*, with longer life cycles and larger size in areas of lower productivity and shorter life cycles and smaller size in more productive regions (Falk-Petersen *et al.*, 2009). However, could these relatively long and variable life cycles (both inter- and intraspecifically) be regarded as strategies developed either in areas generally characterized by low predation pressure or under recently lifted constraints (i.e. absence of a strong predation pressure)? If so, the comparably shorter life cycle of *C. glacialis* may represent an adaptive response in the evolutionary arms race against a large and effective predator that allowed it (and not the larger *C. hyperboreus*) to inhabit the shelf seas. This corresponds well with both the historical distributional patterns of whales and the current abundance of macrozooplankton and fish in shelf regions where *Calanus glacialis* thrive. In contrast, whales and other

predators were, and still are, in low abundance in the Arctic Ocean, where the larger and more long-lived *Calanus hyperboreus* dominates. Such a shift in perspective would influence our understanding of polar systems: what we previously believed (McLaren, 1966) were specific adaptive traits (long life, resultant large body size) towards a polar environment may rather be seen as plesiomorphic, whereas the shorter life cycles and smaller body sizes the more apomorphic characteristics evolved under former selection regimes enforced by the now nearly extinct baleen whales.

PREDATION

Our argument centers on the principle that evolution of short life cycles and/or higher fecundity may be an adaptive response to increased predation pressures (Stearns, 1992). First, for this to be feasible, we assume an overall predation risk that is lower in the Arctic Ocean compared with more moderate latitudes where large populations of visual predators such as pelagic fish are common (e.g. Kaartvedt, 2008). Secondly, life history theory predicts (Stearns and Koella, 1986) larger, longer-lived species to be most abundant in areas of low predation risk. This is, in fact, what we observe today with *C. hyperboreus* widely distributed in the Arctic Ocean and *C. glacialis* dominating areas recently inhabited by baleen whales. Even under high predation pressures, short life cycles and high fecundity may maintain high standing stocks of prey despite considerable removal of biomass. A similar, contemporary relationship was recently hypothesized for the Southern Ocean, focusing on the interaction between whales and krill (Smetacek, 2008). A third piece of evidence supporting our alternative view comes from comparison of regions of different levels of whale harvesting. Following the “extinction” of Arctic baleen whales, it has been suggested that a regime shift occurred (Renaud *et al.*, 2008), with a corresponding redirection of the main flow of energy through the food web (Weslawski *et al.*, 2000; Pershing *et al.*, 2010), similar to the trophic cascading effect observed in the Black Sea as a result of overfishing (Daskalov, 2002). A contemporary analogy of such ecological changes may be detected when comparing (although confounded by difference in latitude and water masses) the Svalbard area with the Disko Bay on the western coast of Greenland. The former area, where whales are strongly depleted and seabirds dominate (Steen *et al.*, 2007 and references therein) stands in stark contrast with Disko Bay where Bowhead whales are still numerous (Heide-Jørgensen *et al.*, 2007) and little auks, for example, are comparably very few in numbers (Berge, personal observations). However, an

important distinction between these predators is that while the whales provided a relatively uniform and size-independent predation pressure (Lowry, 1993), the “new” visual predators feed selectively on large individuals (Steen *et al.*, 2007). It should, however, be noted that the presence and relative importance of macrozooplankton taxa such as the visually predatory *Themisto libellula* and *Thysanoessa* spp. is not considered herein. Clearly, these taxa are important predators on early stages of *Calanus* spp., but their feeding rates and potential impact on their prey are poorly known within the Arctic. Our arguments represent circumstantial evidence that does not necessarily invalidate current theory, but we argue that it provides strong support for an equally likely alternative evolutionary mechanism. Evolution of short life cycles, and hence increasing fecundity as a response in an evolutionary arms race with a predator, is only possible provided a sufficiently long coexistence between predators (baleen whales) and prey. Our alternative view is not contradicted by the few available molecular phylogenies, showing that in spite of their morphological similarity, the Arctic *Calanus* species have a long evolutionary history of being distinct (Bucklin *et al.*, 1995; Hill *et al.*, 2001).

AVOCADOS, WHALES AND CALANUS

Classical work (Hutchinson, 1957) defines the niche of a species as the sum of external factors affecting a species simultaneously. More recent work (Crisp *et al.*, 2009) has pointed to the general trend of organisms to shift their distribution as a response to changes in the environment, rather than evolving *in situ* (Ji *et al.*, 2010 and references therein). This may be a valid general statement for planktonic marine organisms that are not limited by physical geographical boundaries, as e.g. the Arctic *Calanus* spp., for which both extensive and rapid shifts in distribution have been observed (Beaugrand, 2002) and predicted (Slagstad *et al.*, 2011). Just as the avocado has been considered an evolutionary anachronism left without its natural vector for seed dispersal after the extinction of the terrestrial frugivore megafauna some 10 000 years BP (Janzen and Martin, 1982), the Arctic *Calanus* may be regarded as left in a similar evolutionary vacuum following the “extinction” of the large baleen whales. Furthermore, current environmental conditions are most likely characterized by other predators such as fish, macrozooplankton and seabirds that may have increased in abundance as a direct response to reduced competition after the removal of the whales (Weslawski *et al.*, 2000). In fact, one may

hypothesize that this accompanying ecological change is likely to lead to further selection towards high fecundity, short life cycles and smaller size, enabling the Arctic *Calanus* to occupy areas currently dominated by abundant and visually searching predators (Kaartvedt, 2008).

Evolutionary “just-so” stories (Gould and Lewontin, 1979) can often be regarded as being strictly of academic interest, as it is the evolutionary end product that determines how organisms and ecosystems function today irrespective of the pathway towards the current regime. However, in a time when polar ecosystems are on the verge of large changes over an unprecedentedly short timescale (Moline *et al.*, 2008), it is of paramount importance to understand *how* and *why* organisms in the system function and interact in order to be able to gain insight into how the system might change as a direct consequence of the ongoing climate change. During the times of the baleen whales, an estimated one to four million tons of these valuable prey species were consumed each year by bowhead whales around the Svalbard Archipelago alone (Weslawski *et al.*, 2000). This consumption equates to between 7 and 25% of the available zooplankton production (Weslawski *et al.*, 2000) in the same region. Following the extinction of these predators, the consumption by alternative predators (seabirds and polar cod) increased from an estimated 1–7% of the total zooplankton production (see Weslawski *et al.*, 2000 for details and calculations). Although the maximum values of these estimates were based on the unlikely scenario that the entire stock of Bowhead whales restricted their feeding to the waters around Svalbard, the impact on the contemporary stock of *Calanus* prey would still have been substantial, especially considering the proposed inverse relationship between predator body size and prey biomass as shown by Shackell *et al.* (Shackell *et al.*, 2010) from the Northwest Atlantic. We argue that the predator perspective provided herein offers an analogy with other systems changed by anthropogenic removal of, for example, megafauna (Janzen and Martin 1982), key predators (Estes *et al.*, 1998) or fish stocks (Jackson *et al.*, 2001), and how selection pressure might change and in some cases render the adaptations of the past difficult to understand in the “new” environment. In our case, indiscriminate predators such as the baleen whales induced a generally *high* predation pressure on their zooplankton prey, whereas the visual predators (which may have increased in abundance) enforce a *changed* pressure through increased size-specific predation risk (Steen *et al.*, 2007; Kaartvedt, 2008). Also, if there were no predators replacing the whales, which may be the case in the Arctic Ocean proper, then there is an overall reduction in mortality. Life history theory thus predicts

evolution towards later age at maturation and more modest reproductive effort per reproductive event, hence a development towards long-lived, larger and iteroparous life history traits such as those observed for *C. hyperboreus* in the central Arctic Ocean today.

FUTURE DIRECTIONS

Although a bottom-up control is generally assumed in oceanographic systems (Daskalov, 2002), rather than the top-down view more often taken in studies of terrestrial and limnological ecosystems, polar oceanographic habitats could be conceived differently (Smetacek and Nicol, 2005). This may partly be a direct consequence of the current lack of large baleen whale populations in the Arctic, which may have directed focus to the food source rather than the predators' role, when explaining evolution and adaptations towards a polar environment. In the Antarctic, following the decline of baleen whales that occurred up until the mid-1960s, krill stocks have over the past three decades declined by an estimated 80% (Smetacek, 2008). Such a counter-intuitive response may be directly linked to the function of the previous polar "food-chain of giants" (Smetacek, 2008), but does nevertheless indicate that the high predation pressure previously occurring in both the Arctic and Antarctic marine systems can have had a top-down effect on the prey population (Roman and McCarthy, 2010). Hence, in a period with rapid changes in the Arctic, we argue that it will be imperative to reconsider the Arctic calanoid copepods and their functional and phenotypic responses to shifts in the ecosystem in order to make reliable predictions concerning not only the future distribution and abundance of the Arctic *Calanus* spp. themselves, but to future changes in ecosystem function in general. Testing hypotheses concerning evolutionary pathways and adaptations require improved knowledge about both the inter- and intra-specific phylogenetic relationships. As our current understanding of the evolutionary history of *Calanus* is presently weakly developed, hypotheses concerning adaptations, biogeography and phenology are at the moment not testable. However, for a genus comprising merely 16 contemporary species (Boxshall and Halsey, 2004) of such a high ecological importance, developing a thorough understanding of their evolutionary relationships should not be a daunting or impossible task.

ACKNOWLEDGEMENTS

The authors wish to thank Dr Ø. Varpe for his valuable input and discussions while developing these ideas, and

three anonymous reviewers for their constructive comments. Prof W. Vader is thanked for providing inspiration to develop the herein outlined ideas.

FUNDING

This work was supported by the Research Council of Norway. Funding to pay the Open Access publication charges for this article was provided by the University Centre in Svalbard.

REFERENCES

- Beaugrand, G. (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, **296**, 1692–1694. doi:10.1126/science.1071329.
- Boxshall, G. A. and Halsey, S. H. (2004) *An Introduction to Copepod Diversity*, vols 1–2, Ray Society, London, pp. 1–996.
- Bucklin, A., Frost, B. and Kocher, T. (1995) Molecular systematics of 6 *Calanus* and 3 *Metridia* species (Calanoida, Copepoda). *Mar. Biol.*, **121**, 655–664.
- Crisp, M. D., Arroyo, M. T. K., Cook, L. G. *et al.* (2009) Phylogenetic biome conservatism on a global scale. *Nature*, **458**, 754–756.
- Daskalov, G. (2002) Overfishing drives a trophic cascade in the Black Sea. *Mar. Ecol. Prog. Ser.*, **225**, 53–63.
- Estes, J., Tinker, M., Williams, T. *et al.* (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, **282**, 473–476.
- Falk-Petersen, S., Mayzaud, P., Kattner, G. *et al.* (2009) Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.*, **5**, 18–39. doi:10.1080/17451000802512267.
- Gould, S. J. and Lewontin, R. C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Pro. R. Soc. Lond. B*, **205**, 581–598.
- Hays, G. (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, **503**, 163–170.
- Heide-Jørgensen, M. P., Laidre, K., Borchers, D. *et al.* (2007) Increasing abundance of bowhead whales in West Greenland. *Biol. Lett.*, **3**, 577–580.
- Hill, R., Allen, L. and Bucklin, A. (2001) Multiplexed species-specific PCR protocol to discriminate four N. Atlantic *Calanus* species, with an mtCOI gene tree for ten *Calanus* species. *Mar. Biol.*, **139**, 279–287.
- Hutchinson, G. E. (1957) Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.*, **22**, 415–427.
- Jackson, J. B., Kirby, M. X., Berger, W. H. *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629–637. doi:10.1126/science.1059199.
- Janzen, D. H. and Martin, P. S. (1982) Neotropical anachronisms: the fruits the Gomphotheres ate. *Science*, **215**, 19–27.
- Ji, R., Edwards, M., Mackas, D. L. *et al.* (2010) Marine plankton phenology and life history in a changing climate: current research

- and future directions. *J. Plankton Res.*, **32**, 1355–1368. doi:10.1093/plankt/fbq062.
- Kaartvedt, S. (2008) Photoperiod may constrain the effect of global warming in arctic marine systems. *J. Plankton Res.*, **30**, 1203–1206. doi:10.1093/plankt/fbn075.
- Karnovsky, N., Kwasniewski, S., Weslawski, J. *et al.* (2003) Foraging behavior of little auks in a heterogeneous environment. *Mar. Ecol. Prog. Ser.*, **253**, 289–303.
- Lowry, L. F. (1993) Foods and feeding ecology. In Burns, J. J., Montague, J. J. and Cowles, C. J. (eds), *The Bowhead Whale*. Soc. Mar. Mammal. 2 (Spec. Pub.). Allen Press Inc., Lawrence, KS, pp. 201–238.
- McLaren, I. (1966) Adaptive significance of large size and long life of the chaetognath *Sagitta elegans* in the arctic. *Ecology*, **47**, 852–855.
- Moline, M. A., Karnovsky, N., Brown, Z. *et al.* (2008) High latitude changes in ice dynamics and their impact on polar marine ecosystems. In: *The Year in Ecology and Conservation Biology 2008*. R. S. Ostfeld and W. H. Schlesinger (eds.). *Annals New York Acad. Sci.*, **1134**, 267–319. doi: 10.1196/annals.1439.010.
- Pershing, A. J., Christensen, L. B., Record, N. R. *et al.* (2010) The impact of whaling on the ocean carbon cycle: why bigger was better. *PLoS ONE*, **5**, e12444. doi:10.1371/journal.pone.0012444.
- Renaud, P. E., Carroll, M. L. and Ambrose, W. G. Jr. (2008) Effects of global warming on Arctic sea-floor communities and its consequences for higher trophic levels. In Duarte, C. M. and Agusti, S. (eds), *Impacts of Warming on Polar Ecosystems*. FBBVA Press, Madrid.
- Roman, J. and McCarthy, J. J. (2010) The whale pump: marine mammals enhance primary productivity in a coastal basin. *PLoS ONE*, **5**, e13255. doi:10.1371/journal.pone.0013255.
- Scott, C. L., Kwasniewski, S., Falk-Petersen, S. *et al.* (2000) Lipids and life strategies of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard. *Polar Biol.*, **23**, 510–516.
- Shackell, N. L., Frank, K. T., Fisher, J. A. D. *et al.* (2010) Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. *Proc. R. Soc. B*, **277**, 1353–1360. doi:10.1098/rspb.2009.1020.
- Slagstad, D., Ellingsen, I. H. and Wassmann, P. (2011) Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: an experimental simulation approach. *Prog Oceanogr.*, **90**, 117–131. doi:10.1016/j.pocan.2011.02.009.
- Smetacek, V. (2008) Are declining Antarctic krill stocks a result of global warming or of the decimation of the whales? In Duarte, C. M. and Agusti, S. (eds), *Impacts of Warming on Polar Ecosystems*. FBBVA Press, Madrid.
- Smetacek, V. and Nicol, S. (2005) Polar ocean ecosystems in a changing world. *Nature*, **437**, 362–368.
- Stearns, S. C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stearns, S. C. and Koella, J. C. (1986) The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution*, **40**, 893–913.
- Steen, H., Vøgedes, D., Broms, F. *et al.* (2007) Little auks (*Alle alle*) feeding in Isfjorden, Svalbard; dual feeding trip length as a response to poor food quality. *Polar Res.*, **26**, 118–125.
- Varpe, Ø., Fiksen, Ø. and Slotte, A. (2005) Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia*, **146**, 443–451.
- Weslawski, J., Hacquebord, L. and Stempniewicz, L. (2000) Greenland whales and walrus in the Svalbard food web before and after exploitation. *Oceanologia*, **42**, 37–56.