

NOTE

# Overwintering of gelatinous zooplankton in the coastal Arctic Ocean

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**ABSTRACT:** Jellyfish and ctenophore blooms are of increasing concern for human enterprise in marine waters, although bloom development remains poorly understood. A key factor in population dynamics of blooms is individual lifespan, which for most gelatinous zooplankton is assumed to be only a few months, often from spring to autumn. Accumulating evidence, however, indicates that some species may overwinter. In this study, we used video photography to quantify medusae and ctenophores beneath land-fast sea ice in the Chukchi Sea near Utqiagvik (Barrow), Alaska, USA, from May to June, 2011–2014. Our data show large *Chrysaora melanaster* medusae overwintering near the bottom, which could contribute to multiyear population increases suggested for this species. *C. melanaster* medusae were observed dragging their tentacles along the bottom, possibly feeding on epibenthic macrofauna. This highlights an underappreciated mechanism for benthic–pelagic coupling by gelatinous zooplankton. Additionally, numerous individuals of 3 ctenophore and 1 hydrozoan species were seen primarily at the sea–ice interface rather than near the bottom. We hypothesize that overwintering of medusae and ctenophores under sea ice is favored by the continued availability of prey, related to high productivity in the coastal Arctic, including production by ice algae. Successful overwintering may also relate to physical sheltering and low water temperatures. Overwintering may be a common life-history trait for gelatinous zooplankton, with important implications for understanding annual and interannual population trends in many environments and has important implications for models including jellyfish and ctenophore populations and ecosystem dynamics.

**KEY WORDS:** Jellyfish · Ctenophore · Benthic–pelagic coupling · Bloom · Macrobenthos · Population dynamics

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## INTRODUCTION

Pelagic cnidarians and ctenophores are important predators in marine ecosystems, feeding on prey ranging from micro- to macrozooplankton, including other gelatinous zooplankton, as well as fish eggs and larvae (Purcell 1997). They are also increasingly appreciated as an important dietary staple for both

commercial and non-commercial fish species, turtles, birds, and invertebrates (Arai 2005). Their potential ecological importance in recycling nutrients and consuming zooplankton and ichthyoplankton has been recognized for nearly 100 yr, with quantitative studies since the mid-twentieth century showing significant effects on the plankton community (e.g. Purcell 1997). Although jellyfish and ctenophores are tradi-

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tionally perceived as planktonic predators, their use of benthic trophic pathways is increasingly apparent (Pitt et al. 2008, Ceh et al. 2015). These data, and the realization that large masses of gelatinous species settle on the sea floor globally ('jellyfalls;' e.g. Lebrato et al. 2012) and are quickly recycled, have renewed interest in their role in benthic–pelagic coupling of the oceanic carbon cycle (e.g. Sweetman et al. 2016).

Many gelatinous species are renowned for forming blooms, which stimulated interest in their population dynamics centuries ago (see Goy et al. 1989). The combination of factors, including favorable climate and food conditions that probably lead to bloom formation, may affect different stages of their life cycles. The life cycle of most jellyfish species includes asexually reproducing attached stages that can live for multiple years. In contrast, ctenophores (except benthic platyctenes) are holoplanktonic. The sexually reproductive, swimming jellyfish and ctenophores generally are assumed to live only a few weeks to months. Nevertheless, available evidence suggests that the jellyfish and ctenophores of some species can live through the winter (Costello et al. 2006, Ceh et al. 2015). Evidence for overwintering includes the presence of only large medusae in early spring, medusae being continually present throughout the year, and medusae caught in deep water during winter (Ceh et al. 2015). Overwintering could allow blooms to develop earlier and more rapidly in spring than would otherwise be predicted. In addition, the overwintering individuals may contribute to winter-time ecological processes.

Most jellyfish and ctenophore studies have occurred in north temperate latitudes in coastal waters where these organisms are likely to interact with large human populations (Purcell 2012). Environments that are difficult to access, such as the deep sea and polar oceans, have received less attention until recently. Sampling of jellyfish in Arctic and sub-Arctic waters that are ice covered in winter has mostly been restricted to summer and autumn. Those studies have shown that the gelatinous communities in ice-free waters are diverse and abundant (e.g. Purcell et al. 2010, Raskoff et al. 2010). Information on jellyfish and ctenophore ecology, including parameters as fundamental as presence/absence, during the ice-covered period has been limited because of sampling difficulties. In the eastern Bering Sea during the open-water period, large jellyfish have been collected for decades in bottom trawls as bycatch in annual sampling for walleye pollock. Although the sampling was only in summer, multi-year increases

(1990–2000 and 2006–2012) suggested that the jellyfish biomass (mainly *Chrysaora melanaster*) accumulated over 2 or more years, and that overwintering under the ice might occur (Brodeur et al. 2008).

Winter was once perceived to be a highly demanding period significantly affecting plankton performance and survival in the Arctic Ocean (Węśławski et al. 1991, Bandara et al. 2016); however, the importance of biological activity during Arctic winter is becoming increasingly apparent (Berge et al. 2015). Although winter-limited food availability, low temperatures, and low light undoubtedly affect Arctic marine organisms, they are able to survive by relying on alternative food sources or accumulated energy (Lundberg et al. 2006, Berge et al. 2015).

In this study, we summarized video recordings made beneath land-fast sea ice in May–June in 2011–2014 in the Chukchi Sea near Utqiaġvik (formerly Barrow, Alaska, USA) showing that *C. melanaster* medusae and other gelatinous zooplankton overwinter beneath Arctic sea ice. The recordings also suggested that large medusae feed epibenthically by dragging their tentacles along the bottom.

## MATERIALS AND METHODS

Field sampling occurred from May to early June 2011–2014 at multiple locations on first-year, land-fast sea ice located within 10 km of Point Barrow, Alaska, USA (71.38° N, 156.48° W), on the nearshore Chukchi Sea. All sites were within 3 km of land with 6–10 m water depth. The general sampling location and typical under-ice salinities of 28–30 measured during our sampling are consistent with Alaskan Coastal Water, which is carried northward from the eastern Bering Strait by the Alaskan Coastal Current (Brugler et al. 2014), although with possible dilution from local freshwater sources. The sampling period coincided with the time of the ice-algae bloom and subsequent export of material from the ice, which preceded the annual ice breakup by several weeks.

At each sampling location, holes through the ice were drilled using a Jiffy ice auger or a Kovacs ice corer. Water temperature and salinity under the ice were measured using a YSI 30 T/S meter. Cameras (Aqua-vu 410 and a Go-Pro Hero3), mounted on a submersible underwater vehicle, were lowered through the ice holes and maintained in position viewing the under-ice or epibenthic communities. Gelatinous animals were identified and counted from the digital recordings. Counts were standardized by time spent at each location for each recording session.

**RESULTS**

All scyphomedusae observed by video were near the bottom each year (Table 1). We emphasize that all medusae seen were intact, pulsing, and apparently healthy. A total of 55 *Chrysaora melanaster* medusae were observed being carried by the weak current, often with their tentacles dragging along the bottom (see the video in the Supplement at [www.int-res.com/articles/suppl/m591p281\\_supp/](http://www.int-res.com/articles/suppl/m591p281_supp/)). Numerous tracks left behind on the sediment surface by jellyfish tentacles were observed in 2011 and 2013. One *C. melanaster* was observed dragging an isopod (*Saduria entomon*) in its tentacles along the bottom (see the Supplement video). A single *C. melanaster* medusa captured by seine on 27 May 2014 (71.37° N, 156.60° W) had a bell diameter of 22–23 cm and 80 cm long oral tentacles apparently coated by sediment. In addition, 2 large *Cyanea* sp. medusae were seen swimming a few meters above the bottom in 2014.

Most of the other gelatinous species were ctenophores (primarily *Mertensia ovum*, *Bolinopsis infundibulum*, and *Beroë cucumis*; Table 1). Although some *M. ovum* were observed near the bottom in 2013 and 2014 (23.8 and 4.8%, respectively), most were seen just beneath the ice, sometimes with

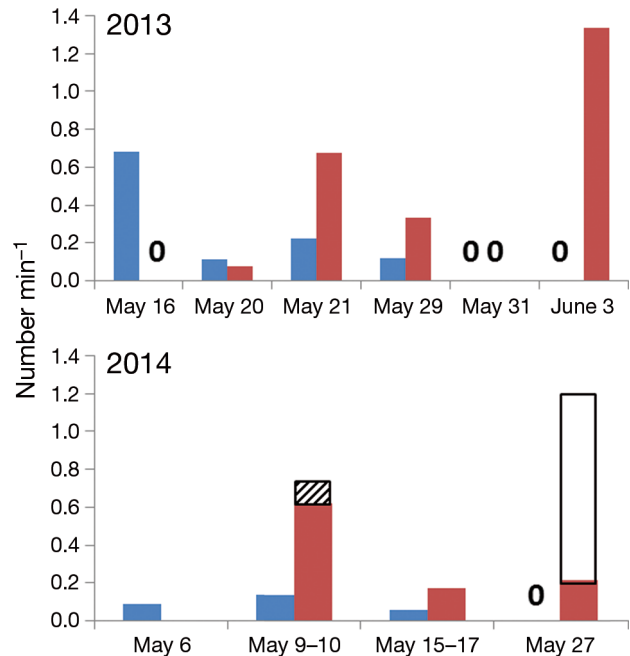


Fig. 1. *Chrysaora melanaster* medusae at the sediment surface (blue) and ctenophores (red bars: *Mertensia ovum*, striped bar: *Bolinopsis infundibulum*, open bar: *Beroë cucumis*, 0: none seen; see Table 1) at the ice-bottom in 2013 and 2014 near Utqiaġvik (Barrow), Alaska, USA. The data for *M. ovum* on 3 June 2013 were from only a 3 min video segment and should be interpreted cautiously

Table 1. Data from video photography beneath land-fast sea ice near Utqiaġvik (Barrow), Alaska, USA. Scyphomedusae were *Chrysaora melanaster* and a single *Cyanea* sp. (marked by an asterisk, \*). Ctenophores were *Mertensia ovum* (*Mo*), *Bolinopsis infundibulum* (*Bi*), and *Beroë cucumis* (*Bc*, which was seen only on 27 May 2014)

Date	Duration (d)	Video records (min/no. of sessions)	Number	Number min <sup>-1</sup> (± SD)
<b>Medusae near bottom</b>				
21–26 May 2011	5	121.4/4	4	0.2 ± 0.3
26 May–4 June 2012	8	333.3/6	3*	0.01 ± 0.02
16 May–3 June 2013	18	151.1/13	42*	0.3 ± 0.6
6–27 May 2014	21	83.7/6	6	0.07 ± 0.08
<b>Ctenophores near bottom</b>				
21–26 May 2011	5	121.4/3	0	0
26 May–4 June 2012	8	333.3/6	0	0
16 May–3 June 2013	18	151.1/13	<i>Bi</i> 1	0.01
6–27 May 2014	21	83.7/7	<i>Mo</i> 10	0.2 ± 0.3
			<i>Mo</i> 2	0.1
<b>Ctenophores under ice</b>				
21–26 May 2011	5	34.2/5	<i>Bi</i> 5	0.15
			<i>Mo</i> 5	0.05 ± 0.06
26 May–4 June 2012	8	54.8/4	<i>Mo</i> 3	0.2 ± 0.3
16 May–3 June 2013	18	60.0/8	<i>Mo</i> 35	0.5 ± 0.5
6–27 May 2014	21	79.3/4	<i>Bi</i> 10	0.2 ± 0.1
			<i>Mo</i> 42	0.9 ± 1.0
			<i>Bc</i> 43	2.3

their tentacles sweeping the ice undersurface. *B. cucumis* was very abundant only once, on the last day of sampling (27 May) in 2014 (Fig. 1). Hydromedusae (*Aglantha digitale*) were observed under the ice (1 in 2011, 2 in 2013) and 1 near-bottom in 2013. In both 2013 and 2014, medusa sightings near-bottom were greater in early May, while ctenophore sightings were more common in late May (Fig. 1). More medusae were seen in 2013 than in other years (Figs. 1 & 2).

**DISCUSSION**

**Overwintering of gelatinous species**

Our data show that large *Chrysaora melanaster* medusae were living under complete ice cover at the winter–spring transition in the coastal Chukchi Sea near Point Barrow,

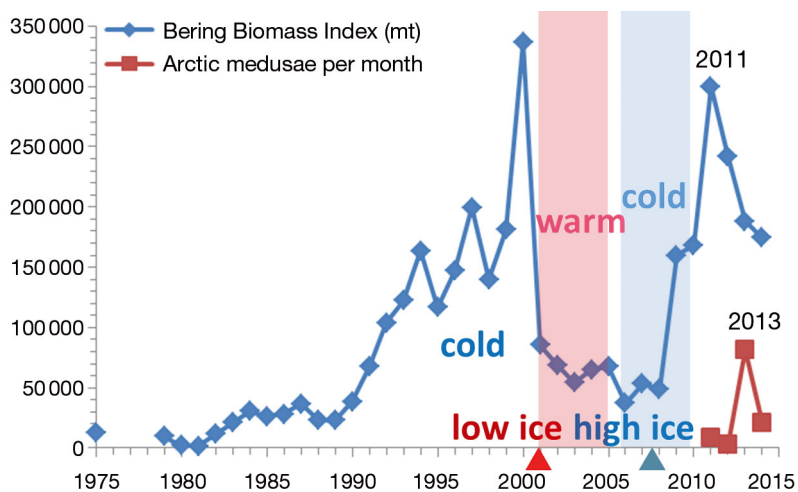


Fig. 2. *Chrysaora melanaster* medusa biomass bycatch in bottom trawls in the eastern Bering Sea (1975–2015) (courtesy of R. D. Brodeur 2013–2015, unpubl. data) and video counts in the Arctic Ocean near Utqiagvik (Barrow), Alaska, USA (2011–2014), adjusted to no. mo<sup>-1</sup> to show on the same scale. Unusually warm (pink) and cold (light blue) periods are shown with colored bars (from Decker et al. 2014). Unusually low (red) and high (blue) sea ice extents are marked by triangles (from Stabeno et al. 2012)

Alaska, USA. Multiple individual medusae were observed dragging their tentacles along the bottom, and additional evidence of this behavior was seen in the abundance of ‘tracks’ on the bottom. Furthermore, an epibenthic isopod was observed in the tentacles of 1 medusa, suggesting feeding on epibenthic macrofauna. Overwintering copepods and euphausiids also are probable food sources for the medusae (Berline et al. 2008, Decker et al. 2014). The medusae we observed have also been reported during winter from the Bering Sea (*C. melanaster*) and the North Sea (*Cyanea capillata*; reviewed by Ceh et al. 2015).

Our observations that Arctic ctenophores and hydromedusae overwinter are also consistent with prior studies. *Mertensia ovum* is present all year in eastern Canadian and Norwegian Arctic surface waters, as well as in the Baltic Sea (Siferd & Conover 1992, references in Purcell et al. 2010, Jaspers et al. 2012, Bandara et al. 2016). Overwintering stocks were typically low (0.1 ctenophores m<sup>-3</sup>), compared to densities (4.0 m<sup>-3</sup>) in the summer after plankton production increased (Siferd & Conover 1992). Interestingly, we recorded some *M. ovum* ctenophores dragging their tentacles along the ice undersurface. Although we have no proof of their feeding, large copepods were observed near the ice. The ctenophore *Beroë cucumis*, which feeds primarily on *M. ovum*, was also found under the sea ice (Webster et al. 2015, Bandara et al. 2016). Another ctenophore, *Bolinopsis infundibulum*, that we recorded near the ice also overwinters in other northern areas (Siferd &

Conover 1992, Båmstedt & Martinius 2015). Previous reports of overwintering hydromedusae (*Aglantha digitale*) in the Arctic (Węśławski et al. 1991, Webster et al. 2015, Bandara et al. 2016) also showed that their populations were far smaller in winter than in summer (Węśławski et al. 1991).

Other observations of overwintering medusae often come from either deep or sheltered waters (Ceh et al. 2015). Our observations of overwintering gelatinous zooplankton in the Arctic may share some similarities with those previous observations of overwintering, in that sea ice may provide physical shelter from winter storms, and the constant, low temperature (approximately -2°C) would minimize metabolic demands. In that context, the numerous epibenthic organisms, including crustaceans, annelids, and fish (Bell et al.

2016), could provide a critical food source during the winter. Epibenthic feeding may in fact be a particularly effective strategy for jellyfish in the Arctic because biogenic sedimentation is greater than at lower latitudes, leading to high biomass benthic communities that are stable and active through the winter (Berge et al. 2015). Ice algae, which grow inside and on the bottom of sea ice and then are exported from the ice to the bottom (Juul-Pedersen et al. 2008, Juhl et al. 2011), also provide a seasonal source of primary production that is unique to ice-covered seas. Although food availability in the coastal Arctic Ocean is still probably lower during winter than other seasons, this may not prevent individuals from reproducing in the spring because jellyfish can regrow gonads when food availability increases (Hamner & Jenssen 1974), and even larval ctenophores can sexually reproduce (Jaspers et al. 2012). Thus, overwintering could be an effective strategy for individuals with the potential to mature to consume the abundant zooplankton food available in spring and increase their sexual reproductive output. Determining how long overwintering jellyfish and ctenophores live and if they reproduce would significantly increase our understanding of the contribution of overwintering to their population dynamics. The presence of reproductive jellyfish and ctenophores during high plankton productivity in spring has important repercussions for population dynamics and models, which depend on inputs and outputs of individuals (e.g. Pauly et al. 2009).

The observations suggest behavioral differences between taxa, as well as possible changes in behavior during the annual observation periods. For example, medusae were exclusively observed near the sea floor, while ctenophores were primarily observed near the ice bottom, locations with access to different food resources. Temporal shifts in the sighting frequency of ctenophores and medusae (Fig. 1) could be related to advection or could be explained by behavioral changes in each population. Both phytoplankton and ice algae biomass typically increase during May in the study area (e.g. Juhl et al. 2011), providing a dramatic change in the quantity and location of food resources within the water column for prey of gelatinous zooplankton. Unfortunately, the temporal trends in observations cannot be explained with the available data.

### Overwintering and multiyear increases in *C. melanaster* populations

We conclude that the large *C. melanaster* medusae observed near the bottom before the ice melted in the nearshore Chukchi Sea had overwintered from the previous year. In the southeastern Bering Sea, newly produced scyphomedusae (ephyrae) were present from May to August, indicating their production during late spring through summer (Decker et al. 2014), which supports our conclusion that the large medusae in the video we analyzed could not have been produced in the same year. If medusae overwinter in the Bering Sea as they do in the Chukchi Sea, we hypothesize that overwintering contributes to the multi-year *C. melanaster* population increases that have been observed in the Bering Sea. We furthermore suggest that the Bering Sea population is directly connected to the overwintering populations we observed in the Chukchi Sea during this study.

Data from the Bering Sea show sequential peaks of large jellyfish, consisting mostly of *C. melanaster*, which suggest multi-year accumulations such as in 2009–2011 (Fig. 2). Analyses of those data from 1975–2004 showed that jellyfish biomass in the northwest middle shelf region was highly correlated ( $R^2 = 0.938$ ) with jellyfish biomass in the southeast region the preceding year, as well as summer sea-surface temperature, ice cover, zooplankton biomass, and current lagged by 1 yr (Brodeur et al. 2008). Thus, in the Bering Sea, cold years with high ice cover were favorable for jellyfish, which would be transported from south to north, following the direction of prevailing currents. Those currents continue northward

through the Bering Strait to the central and coastal Chukchi Sea (Stabeno et al. 2012).

The medusae observed in the coastal Arctic in May 2013 of this study were produced in 2012 or before, following a summertime peak of medusae in the Bering Sea in 2011 (Fig. 2). Thus, we hypothesize that medusae in the Bering Sea and Arctic Ocean live through the winter and that Bering Sea jellyfish are carried north to the Chukchi Sea in prevailing currents. The medusae could originate from polyps on any rocky substrate in the Bering Sea, such as the Alaskan Peninsula and the Pribilof Islands (Decker et al. 2014), and perhaps north of the Bering Strait. Sigler et al. (2017) found *C. melanaster* medusae to be widespread in the northern Bering Sea through the northern Chukchi Sea. Berline et al. (2008) estimated that transport of euphausiids from the Anadyr Gulf and Shpanberg and Bering Straits to the Barrow region took 4 to 20 mo, which corresponds with the suggested transport time of medusae in our study.

### CONCLUSIONS

We believe that the prevalence of jellyfish and ctenophores living through the winter is greater than generally appreciated. Survival through the winter is likely facilitated by protection from rough seas in sheltered waters, reduced metabolic needs from low temperatures, and the continued availability of prey. Recognition that gelatinous zooplankton can overwinter under sea ice is important for understanding their current population dynamics and ecological impacts in Arctic seas. Moreover, jellyfish and ctenophore populations will be more sensitive to changing ice conditions than otherwise anticipated. Understanding the implications of changing sea-ice conditions will become increasingly important as coastal Arctic seas become more open to transportation, commercial fishing, oil and gas exploration, and other forms of commercial exploitation.

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## LITERATURE CITED

- ✦ Arai MN (2005) Predation on pelagic coelenterates: a review. *J Mar Biol Assoc UK* 85:523–536
- ✦ Båmstedt U, Martinussen MB (2015) Ecology and behavior of *Bolinopsis infundibulum* (Ctenophora; Lobata) in the Northeast Atlantic. *Hydrobiologia* 759:3–14
- ✦ Bandara K, Varpe Ø, Søreide JE, Wallenschus J, Berge J, Eiane K (2016) Seasonal vertical strategies in a high-Arctic coastal zooplankton community. *Mar Ecol Prog Ser* 555:49–64
- ✦ Bell LE, Bluhm BA, Iken K (2016) Influence of terrestrial organic matter in marine food webs of the Beaufort Sea shelf and slope. *Mar Ecol Prog Ser* 550:1–24
- ✦ Berge J, Daase M, Renaud PE, Abrose WG Jr and others (2015) Unexpected levels of biological activity during the polar night offer new perspective on a warming Arctic. *Curr Biol* 25:2555–2561
- ✦ Berline L, Spitz YH, Ashjian CJ, Campbell RG, Maslowski W, Moore SE (2008) Euphausiid transport in the Western Arctic Ocean. *Mar Ecol Prog Ser* 360:163–178
- ✦ Brodeur RD, Decker MB, Ciannelli L, Purcell JE and others (2008) The rise and fall of jellyfish in the Bering Sea in relation to climate regime shifts. *Prog Oceanogr* 77:103–111
- ✦ Brugler ET, Pickart RS, Moore GWK, Roberts S, Weingartner TJ, Statscewich H (2014) Seasonal to inter annual variability of the Pacific water boundary current in the Beaufort Sea. *Prog Oceanogr* 127:1–20
- ✦ Ceh J, Gonzalez J, Pacheco AS, Riascos JM (2015) The elusive life cycle of scyphozoan jellyfish — metagenesis revisited. *Sci Rep* 5:12037
- ✦ Costello JH, Sullivan BK, Gifford DJ, Van Keuren D, Sullivan LJ (2006) Seasonal refugia, shoreward thermal amplification and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Limnol Oceanogr* 51:1819–1831
- Decker MB, Cieciel K, Zavalokin A, Lauth R, Brodeur RD, Coyle KO (2014) Population fluctuations of jellyfish in the Bering Sea and their ecological role in this productive shelf ecosystem. In: Pitt KA, Lucas CH (eds) *Jellyfish blooms*. Springer, Dordrecht, p 153–183
- ✦ Goy J, Morand P, Etienne M (1989) Long-term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables. *Deep-Sea Res* 36:269–279
- ✦ Hamner WM, Jenssen RM (1974) Growth, degrowth, and irreversible cell differentiation in *Aurelia aurita*. *Am Zool* 14:833–849
- ✦ Jaspers C, Haraldsson M, Bolte S, Reusch TBH, Thygesen UH, Kjørboe T (2012) Ctenophore population recruits entirely through larval reproduction in the central Baltic Sea. *Biol Lett* 8:809–812
- ✦ Juhl AR, Krembs C, Meiners KM (2011) Seasonal development and differential retention of ice algae and other organic fractions in first-year Arctic sea ice. *Mar Ecol Prog Ser* 436:1–16
- ✦ Juul-Pedersen T, Michel C, Gosselin M, Seuthe L (2008) Seasonal changes in the sinking export of particulate material under first-year sea ice on the Mackenzie Shelf (western Canadian Arctic). *Mar Ecol Prog Ser* 353:13–25
- ✦ Lebrato M, Pitt KA, Sweetman AK, Jones DOB and others (2012) Jelly-falls historic and recent observations: a synthesis to drive future research directions. *Hydrobiologia* 690:227–245
- ✦ Lundberg M, Hop H, Eiane K, Gulliksen B, Falk-Petersen S (2006) Population structure and accumulation of lipids in the ctenophore *Mertensia ovum*. *Mar Biol* 149:1345–1353
- ✦ Pauly D, Graham WM, Libralato S, Morissette L, Palomares MLD (2009) Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia* 616:67–85
- ✦ Pitt KA, Clement AL, Connolly RM, Thibault-Botha D (2008) Predation by jellyfish on large and emergent zooplankton: implications for benthic-pelagic coupling. *Estuar Coast Shelf Sci* 76:827–833
- Purcell JE (1997) Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates and effects on prey populations. *Ann Inst Oceanogr* 73:125–137
- ✦ Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annu Rev Mar Sci* 4:209–235
- ✦ Purcell JE, Kosobokova KN, Hopcroft RR, Whitledge TE (2010) Distribution, abundance, and predation effects of epipelagic ctenophores and jellyfish in the western Arctic Ocean. *Deep-Sea Res II* 57:127–135
- ✦ Raskoff KA, Hopcroft RR, Purcell JE, Kosobokova KN, Youngbluth MJ (2010) Jellies under ice: ROV observations from the Arctic 2005 Hidden Ocean Expedition. *Deep-Sea Res II* 57:111–126
- ✦ Siferd TD, Conover RJ (1992) Natural history of ctenophores in the Resolute Passage area of the Canadian High Arctic with special reference to *Mertensia ovum*. *Mar Ecol Prog Ser* 86:133–144
- Sigler MF, Mueter F, Bluhm BA, Busby MS and others (2017) Late summer zoogeography of the northern Bering and Chukchi seas. *Deep-Sea Res II* 135:168–189
- Stabeno PJ, Kachel NB, Moore SE, Napp JM, Sigler M, Yamaguchi A, Zerbin A (2012) Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. *Deep-Sea Res II* 65–70:31–45
- ✦ Sweetman AK, Chelsky A, Pitt KA, Andrade H, van Oevelen D, Renaud PE (2016) Jellyfish decomposition at the seafloor rapidly alters biogeochemical cycling and carbon flow through benthic food-webs. *Limnol Oceanogr* 61:1449–1461
- ✦ Webster CN, Varpe Ø, Falk-Petersen S, Berge J, Stubner E, Brierley AS (2015) Moonlit swimming: vertical distributions of macrozooplankton and nekton during the polar night. *Polar Biol* 38:75–85
- ✦ Węśławski JM, Kwaśniewski S, Wiktor J (1991) Winter in a Svalbard fiord ecosystem. *Arctic* 44:115–123