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Author for correspondence:
Sue E. Moore
e-mail: sue.moore@noaa.gov

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Marine biology

Is it 'boom times' for baleen whales in the Pacific Arctic region?

Sue E. Moore

Office of Science and Technology, NOAA/Fisheries, Seattle, WA, USA

SEM, 0000-0002-3104-1740

The marine ecosystem in the Pacific Arctic region has experienced dramatic transformation, most obvious by the loss of sea ice volume (75%), late-summer areal extent (50%) and change in phenology (four to six weeks longer open-water period). This alteration has resulted in an opening of habitat for subarctic species of baleen whales, many of which are recovering in number from severe depletions from commercial whaling in the nineteenth and twentieth centuries. Specifically, humpback, fin and minke whales (*Megaptera novaeangliae*, *Balaenoptera physalus* and *Balaenoptera acutorostrata*) are now regularly reported during summer and autumn in the southern Chukchi Sea. These predators of zooplankton and forage fishes join the seasonally resident grey whale (*Eschrichtius robustus*) and the arctic-endemic bowhead whale (*Balaena mysticetus*) in the expanding open-ocean habitat of the Pacific Arctic. Questions arising include: (i) what changes in whale-prey production and delivery mechanisms have accompanied the loss of sea ice, and (ii) how are these five baleen whale species partitioning the expanding ice-free habitat? While there has been no programme of research specifically focused on these questions, an examination of seasonal occurrence, foraging plasticity and (for bowhead whales) body condition suggests that the current state of Pacific Arctic marine ecosystem may be 'boom times' for baleen whales. These favourable conditions may be moderated, however, by future shifts in ecosystem structure and/or negative impacts to cetaceans related to increased commercial activities in the region.

1. Introduction

A 'new normal' climate is emerging in the Pacific Arctic marine ecosystem [1], coincident with the dramatic loss of sea ice at a rate which accelerated after 2000 [2]. Overall, the region has lost 75% of sea ice by volume and 50% in late-summer surface cover, coincident with the extension of the open-water period by four to six weeks. The marine ecosystem north of the Bering Strait is warmer, fresher and stormier than in the past, with annual inflow of Pacific waters roughly 50% higher now than prior to 2001 [3]. Satellite data suggest that this biophysical transformation supports increased rates of phytoplankton net primary production (NPP) by 42% in the Chukchi Sea and 53.1% in the Beaufort Sea, probably in response to reduced sea ice thickness and extension of the open-water period [4]. However, satellites cannot sample subsurface peaks in NPP, which are common throughout the Arctic Ocean [5]. Thus, a full accounting of changes to regional primary productivity remains elusive.

Whether owing to habitat expansion, increasing whale numbers, or both, subarctic species of baleen (mysticete) whales are now commonly reported in the Chukchi Sea. Specifically, humpback, fin and minke whales were seen between Bering Strait and 69° N latitude during aerial surveys conducted from July through to September 2009–2012, where none were seen during surveys conducted from 1982 to 1991 [6]. These three species appear to have expanded their range in late summer to now join the Arctic-endemic bowhead whale and

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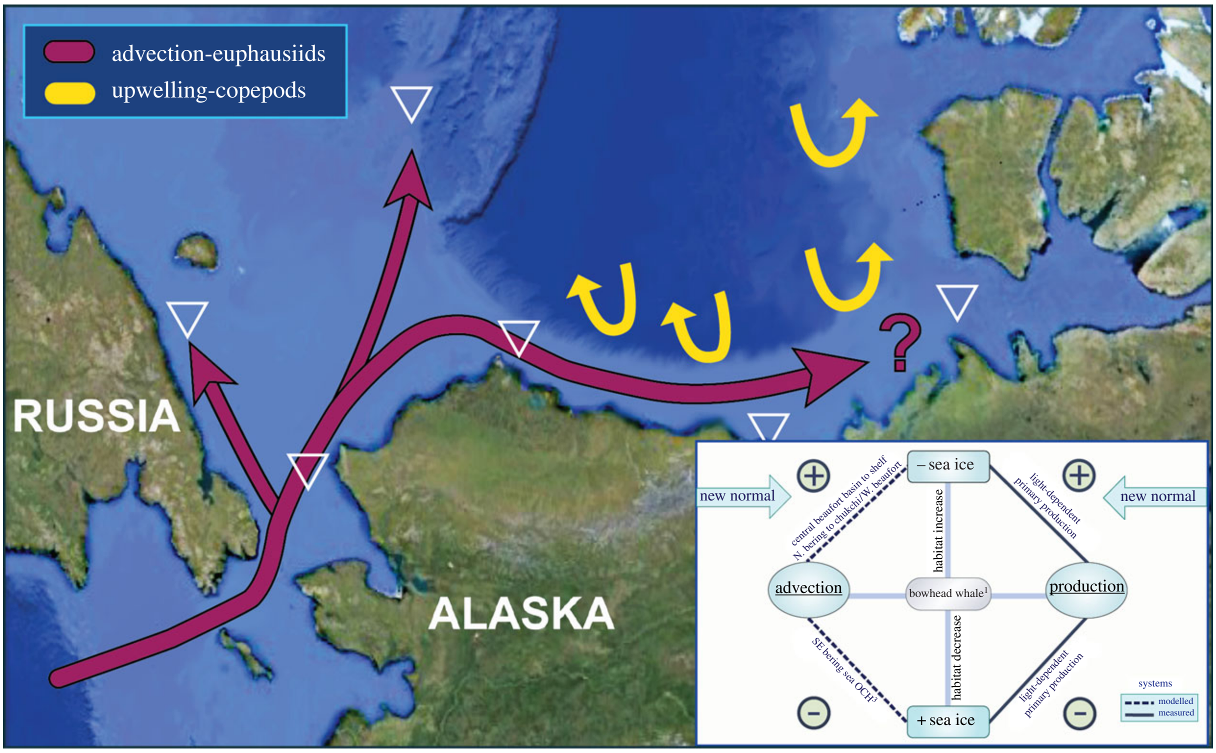

Figure 1. Advection of euphausiids (red) into the Chukchi Sea and upwelling of copepods (yellow) from the basin to the continental shelf in the Beaufort Sea are prey-delivery pathways that are probably enhanced by increased transport through the Bering Strait and wind-forcing combined with the loss of sea ice. Both enhanced production and increased advection common in the 'new normal' Pacific Arctic marine ecosystem deliver food to bowhead whales (inset). This graphic is a composite of revised figures [14,15]; triangles indicate areas where whale-prey associations have been reported [14]. (Online version in colour.)

the seasonally resident grey whale [7] in the rapidly changing marine ecosystem of the Pacific Arctic. Detections of whale calls at an autonomous recorder deployed from 2009 to 2012 revealed that humpback and fin whales remain in southern Chukchi waters through October and in some years into November [3]. Of note, detections of humpback and fin whale calls ceased near the onset of sea ice formation each year, coincident with the onset of bowhead whale call detections. In other words, the subarctic species departed as the Arctic-endemic species arrived, along with seasonal sea ice.

The pan-Arctic reduction in sea ice evident early in the twenty-first century triggered a number of reviews regarding the impact of this loss of habitat on marine mammals [8–10]. Polar bears (*Ursus maritimus*), walruses (*Odobenus rosmarus*) and ice seals appear to be particularly vulnerable because they rely on sea ice as a platform for key life-history functions such as birthing, nursing young, hunting and resting. Conversely, with the loss of sea ice, ocean habitat for cetaceans has expanded both spatially and temporally. This expansion of habitat coincides with the ongoing recovery of most populations of baleen whales from decades of commercial harvest in the nineteenth and twentieth centuries [11,12]. It also facilitates offshore commercial activities, including shipping and oil and gas development, which can have significant negative impacts on cetaceans [13].

In this opinion piece, I summarize observations and offer plausible explanations regarding changes to baleen whale-prey production and delivery coincident with the dramatic loss of sea ice, increased transport through the Bering Strait and amplified upwelling along the Beaufort Sea slope. This synoptic description, coupled with an overview of recent baleen whale seasonal occurrence in the Pacific Arctic, underpins a schematic of habitat partitioning among the five species. The diagram is intended as a first-step in recognizing the current status and role of baleen whales in the changing ecology of the Pacific Arctic.

2. Changes to baleen whale-prey production and delivery

Two well-documented alterations to the Pacific Arctic ecosystem that probably have changed production and delivery of baleen whale-prey in the twenty-first century are the aforementioned loss of sea ice and the increased inflow of Pacific water through the Bering Strait (figure 1). The thinning and extensive seasonal retreat of sea ice has fostered increased NPP, which probably supports higher rates of secondary production, including the mesozooplankton and forage fish prey of baleen whales. This suggested link between sea ice loss and increased prey production is supported by limited observations in the Chukchi Sea [16], where the abundance and biomass of mesozooplankton was higher in reduced-ice years (2007/2008) compared with years with extensive sea ice (1991/1992). The delivery of mesozooplankton prey from the northern Bering to the Chukchi Sea has also probably increased with the more robust northward transport at the Bering Strait since 2001 [3]. Corroborating evidence that prey are advected through the Strait includes the report of grey whales feeding on euphausiids in the southern Chukchi Sea in 2003 [17], and the description of large copepods and euphausiids abundant in the cold, nutrient-rich Bering Sea Anadyr Water advected into the southern and central Chukchi Sea in 2007 [18]. Humpback, fin and minke whales are efficient predators of these mesozooplankton as well as of forage fishes that may follow this plankton stream.

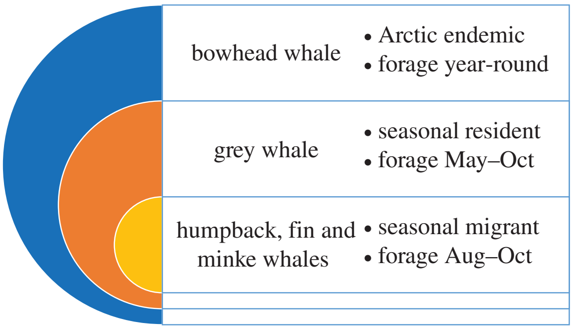

Figure 2. Schematic of habitat partitioning for five species of baleen whales in the Pacific Arctic. Bowhead whales feed on pelagic and epibenthic zooplankton from the northern Bering to Beaufort Sea (blue); grey whales feed on pelagic, epibenthic and benthic prey from the northern Bering through the Chukchi Sea (orange); humpback, fin and minke whales feed on zooplankton and forage fishes primarily in the Bering and southern Chukchi seas (yellow). (Online version in colour.)

The extreme retreat of sea ice combined with upwelling-favourable winds has also probably increased localized abundance of copepods and other mesozooplankton upwelled onto the Beaufort Sea shelf. Notably, the number and strength of upwelling events in the Alaskan Beaufort Sea has increased over the past 25 years [19]. In the western Beaufort, a sudden cessation of upwelling-favourable winds can spring a 'prey trap', which concentrates zooplankton for efficient foraging by bowhead whales [20]. Combined, the recent 'new normal' conditions in the Pacific Arctic seemingly provide Arctic-endemic bowhead whales with optimal foraging opportunities, both from increased upwelling of copepod prey in the Beaufort Sea and robust advection of copepod and euphausiids prey through the Bering Strait into the Chukchi and western Beaufort Sea (figure 1: inset). A suite of observations, including the seasonal ecology of bowhead whale core-use areas [21] and improved whale body condition coincident with sea ice loss [22], support this assertion.

3. Habitat partitioning among baleen whales in the Pacific Arctic

Habitat partitioning among the five baleen whale species is accomplished largely through temporal separation, underpinned by species-specific migration cycles and dissimilar prey preferences (figure 2). Bowhead whales occupy Bering Sea waters in winter, migrating though the Bering Strait in spring and feeding in the Beaufort and then Chukchi seas from late spring through to autumn [7,21]. Grey whales arrive in the northern Bering Sea in late spring and feed there and in the Chukchi Sea through to autumn [7]. Sightings and acoustic detections of humpback, fin and minke whales over the past decade suggest that they occupy the southern Chukchi Sea roughly from August through to October [3,6].

Foraging capability and prey selection can amplify habitat partitioning among the five species. The long, finely fringed baleen of bowhead whales are specialized for filtering zooplankton, while the coarse and short baleen of grey whales provide the means to filter out benthic prey from sediments sucked up from the seafloor—a capability unique to this species. Humpback, fin and minke whales are lunge feeders, adapted with variable length baleen and throat pleats for gulping both mesozooplankton and forage fishes. It is important to note that all five species can and do consume euphausiids or krill. While the role of krill as a key trophic-link in the Pacific Arctic is poorly understood, its importance as prey for baleen whales is well established in Atlantic Arctic and Antarctic marine ecosystems (e.g. [23,24]).

At present, conditions in the Pacific Arctic appear to be favourable (i.e. 'boom times') for all five species of baleen whales. Although the seasonal influx of subarctic species may result in some resource competition with bowhead and grey whales, migration timing and species-specific foraging capabilities will probably curtail inter-specific prey competition. More important is the capability of these species to act as sentinels to alterations in the marine ecosystem [25]. Specifically, baleen whales can provide clues as to the nature, direction and mechanisms of ecosystem shifts, such as where, when and how 'new' NPP is cycled. Whether new production is channelled to pelagic or benthic trophic pathways will restructure the ecosystem in ways that will be reflected in the distribution and relative abundance of these large consumers. Baleen whales also act as ecosystem engineers and their recovering numbers may actually buffer the marine ecosystem from destabilizing stresses associated with rapid change [26]. With more baleen whales recycling nutrients vertically and horizontally and, with increasing numbers of bowhead and grey whales re-suspending sediments during epibenthic and benthic foraging, the Pacific Arctic marine ecosystem will probably continue to change in ways now difficult to predict. A much needed circumpolar assessment of Arctic marine ecosystems (e.g. [14]) could be achieved by comparing changes in the Pacific Arctic to those in other regions, especially where sea ice loss has been quantified (e.g. [10]).

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