

# 1 **Baleen Whale Ecology in Arctic and Subarctic Seas in an Era of** 2 **Rapid Habitat Alteration**

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## 10 **ABSTRACT**

11 Biophysical changes in marine ecosystems of the Arctic and subarctic sectors of the Atlantic and  
12 Pacific are now evident, driven primarily by sea ice loss, ocean warming and increases in  
13 primary productivity. As upper trophic species, baleen whales can serve as sentinels of  
14 ecosystem reorganization in response to these biophysical alterations, via changes in their  
15 ecology and physiological condition. This paper is the first to review baleen whale ecology in  
16 high-latitude marine ecosystems of both the north Atlantic and north Pacific. Oceanographically,  
17 these sectors offer four contrasting habitats to baleen whales: (i) a broad-deep-strait and deep-  
18 shelf inflow system in the Northeast Atlantic (NEA), (ii) a combination of inflow and outflow  
19 systems north of Iceland in the central North Atlantic (CNA), (iii) an outflow shelf and basin in  
20 the Northwest Atlantic (NWA), and (iv) a narrow-shallow-strait inflow shelf system in the  
21 Pacific sector. Information on baleen whale ecology from visual and passive acoustic surveys,  
22 combined with available telemetry and diet studies, show contrasting patterns of baleen whale  
23 occurrence among sectors. In brief, arctic and subarctic waters in the Atlantic sector support a  
24 far greater number of seasonally-migrant baleen whales than the Pacific sector. Thousands of  
25 humpback, fin and common minke whales occupy the diverse habitats of the Atlantic sector.  
26 These species all exhibit flexible diets, focused primarily on euphausiids (krill) and forage fishes  
27 (e.g., capelin, herring, sand lance), which are now responding to ecosystems altered by climate  
28 change. Conversely, the Pacific sector supports a far greater number of arctic-endemic bowhead  
29 whales than the Atlantic sector, as well as a large population of seasonally-migrant gray whales.  
30 Currently, differences in migratory timing and, to a lesser extent, foraging behaviors, serves to  
31 restrict prey competition between the arctic-endemic bowhead whale and seasonally migrant  
32 baleen whale species in both sectors. Regional aspects of changes in prey type and availability  
33 will likely impact future migratory timing, habitat selection, body condition and diet of baleen  
34 whales. Tracking variability in these attributes can provide valuable input to ecosystem models  
35 and thereby contribute the sentinel capability of baleen whales to forecasts of future states of  
36 high latitude marine ecosystems.

37 **Running Title: Baleen whale ecology, Arctic seas**

38 **Keywords: Arctic, Subarctic, baleen whales, marine ecosystems, climate change**

## 39        **1. Introduction**

40            Marine ecosystems in arctic and subarctic seas are undergoing rapid transformation due  
41 to sea ice loss, ocean warming and regional increases in primary productivity (e.g., Wassman,  
42 2015; Moore and Stabeno, 2015; Moore et al., 2018b). The loss of sea ice, both in seasonal  
43 extent and thickness, is an iconic signal of climate change (Zhang et al., 2018; Meier et al.,  
44 2014), with an ice-free summer season anticipated by 2040 (Wang and Overland, 2012). An  
45 overall increase in net primary production has accompanied ice thinning and early retreat (Arrigo  
46 and van Dijken, 2015; Frey et al., 2015; Hill et al., 2017), although observed changes vary  
47 significantly with region. Although global reviews of responses of marine organisms to climate  
48 change often provide scant coverage of polar seas (e.g., Poloczanska et al., 2016), there have  
49 been several reviews focused on marine mammals and sea ice loss in arctic regions (e.g. Laidre  
50 et al., 2015; Kovacs et al., 2011). Notably, a recent special issue focused on impacts of climate  
51 change on marine top predators (Frederiksen and Haug, 2015). However only two papers  
52 reported on cetacean responses to climate change (Víkingsson et al., 2015; Nøttestad et al.,  
53 2015). Responses of arctic marine mammals to climate change was the focus of an earlier  
54 volume of papers, which included a schematic relating marine mammal ecology to sea ice and  
55 projected anticipated climate-related changes for ice-obligate, ice- associated and seasonally  
56 migrant species (Moore and Huntington, 2008). This paper is the first to review baleen whale  
57 ecology in high-latitude marine ecosystems of both the north Atlantic and north Pacific. As  
58 such, it establishes a baseline for future assessments of how these species are faring in a region  
59 of the world that is changing rapidly.

60            Baleen whales, once the target of intense commercial hunting, are now recovering in  
61 many ocean regions (Thomas et al., 2016). The bowhead whale (*Balaena mysticetus*) is the only

62 species endemic to the Arctic, with four distinct populations recognized, two in the Pacific  
63 (Bering-Chukchi-Beaufort and Sea of Okhotsk) and two in the Atlantic (E Canada-W Greenland  
64 and Svalbard-Barents). Seasonally migrant species common to all sectors include humpback  
65 whales (*Megaptera novaeangliae*), fin whales (*Balaenoptera physalus*) and common minke  
66 whales (*Balaenoptera acutorostrata*). Blue whales (*Balaenoptera musculus*) occur in moderate  
67 to low numbers in the Atlantic sector, while gray whales (*Eschrichtius robustus*) are common in  
68 Pacific subarctic and arctic waters. All baleen whales must find dense concentrations of prey to  
69 feed efficiently (Piatt and Methven, 1992) and thereby can identify localized areas of high  
70 productivity (Moore et al., 2014). In this way, they can be considered sentinels to shifting  
71 ecological patterns in marine systems, with shifts in habitat selection and migration timing  
72 leading to changes in diet and body condition (Moore, 2018).

73         Here, we review recent accounts of baleen whale ecology in arctic and subarctic seas of  
74 the Atlantic and the Pacific, and relate patterns of occurrence with observed changes in the  
75 physical and biological oceanography and prey resources of each region. The work is largely  
76 drawn from recent reviews of ecosystem status published as special issues (e.g., Frederiksen and  
77 Haug, 2015; Moore and Stabeno, 2015; Wassman 2015; Moore et al., 2018a, b), as well as  
78 comprehensive individual papers (e.g., Haug et al., 2017; Eriksen et al., 2017; Laidre et al.,  
79 2015). We focus on high-latitude seas, including Icelandic waters and areas offshore East  
80 Greenland (Laidre et al., 2015: region 10), the Labrador Sea (Laidre et al., 2015: region 9),  
81 waters north of 52<sup>0</sup>N offshore Newfoundland (Rice, 2002), and the subarctic portion of the  
82 Bering Sea north of 60<sup>0</sup> N latitude (Stabeno et al., 2012). A comprehensive and comparative  
83 summary of baleen whale ecology in these regions is achieved in three steps: (1) first we set the  
84 stage with a review of the physical and biological oceanography and in four distinct high-latitude

85 regions, (2) the animals are then put in the context of the regional ecosystems via a compilation  
86 of baleen whale population estimates, distribution and phenology, leading to (3) a presentation of  
87 current knowledge of baleen whale prey and where available, how those prey are or may be  
88 impacted by climate change. By comparing subarctic and arctic regions in Atlantic and Pacific  
89 sectors, we can both evaluate the concept of baleen whales as ecosystem sentinels and provide a  
90 basis for including information on these species when forecasting possible future states of these  
91 high-latitude marine ecosystems. We close the paper with some specific recommendations on  
92 next steps toward the goal of routine inclusion of aspects of baleen whale ecology in marine  
93 ecosystem models.

## 94 **2. Physical and Biological Oceanography**

95 The Atlantic and Pacific arctic and subarctic regions are a study in oceanographic  
96 contrasts. In the Atlantic, the broad Gulf Stream carries warm saline water along the coast of  
97 North America, turns east becoming the North Atlantic Current as it passes south of Iceland, then  
98 branches in the Northeast Atlantic (NEA) to enter the Barents Sea and to flow north into the  
99 Arctic Ocean along the eastern side of Fram Strait (**Figure 1A**). The Barents Sea is an inflow  
100 shelf sea (mean depth ca 200m), where Atlantic and Arctic waters meet. Warm and nutrient rich  
101 Atlantic water enters the Barents Sea primarily through its western entrance and influences the  
102 southern region, while cold arctic water penetrates from the east and north and dominates the  
103 northern Barents Sea (see Hunt et al., 2013). The Atlantic Water that flows northward west of  
104 the Barents Sea enters the Arctic Ocean through the broad and deep (450 km x 2,500 m) Fram  
105 Strait and continues eastward north of Svalbard (Haug et al., 2017).

106 In the Central North Atlantic (CNA), Iceland and Jan Mayen sit at the meeting point of  
107 submarine ridges along the Mid Atlantic Ridge, which influences ocean circulation pattern

108 **(Figure 1B)**. In combination with energetic atmospheric circulation this leads to a highly  
109 variable environment on the boundary between colder and warmer water. The East Greenland  
110 Current and East Icelandic Current bring colder water from the north while the North Atlantic  
111 Current and the Irminger Current carry warmer waters from the south. With the polar front lying  
112 through the Denmark Strait, this results in highly variable climatic condition with various  
113 proportions of Polar, Arctic and Atlantic Water, especially north of Iceland but also in the  
114 Irminger Sea southwest of Iceland (see Víkingsson et al., 2015). The shelves along East  
115 Greenland and around Iceland are relatively narrow, while both the Greenland- and Norwegian  
116 Seas are deep water areas, descending to over 5,000m.

117 In the Northwest Atlantic (NWA), arctic and subarctic regions are comprised primarily of  
118 the Labrador Sea and Baffin Bay **(Figure 1C)**. Davis Strait (sill depth *ca.* 800m), separates the  
119 Labrador Sea (maximum depth > 3,500m) from Baffin Bay (maximum depth > 2,000m), to the  
120 north. The NWA is primarily an outflow shelf, with cold saline waters exiting Nares Strait,  
121 Lancaster and Jones Sounds to flow along Baffin Island as the Baffin Island Current. The  
122 Labrador Current brings cold arctic water down the wide (>150 km) Labrador and  
123 Newfoundland shelves to the Grand Banks, the southernmost penetration of polar waters in the  
124 northern hemisphere (Rice, 2002). There it meets the warm Gulf Stream coming from south,  
125 resulting in a rich mixing environment that provides an area of high productivity that influences  
126 the abundance and distribution of subarctic species. Relatively warm water also enters the  
127 Labrador Sea as the West Greenland Current and runs along the narrow (generally <75 km) West  
128 Greenland shelf as the West Greenland Shelf Current. Around the Davis Strait, it branches into a  
129 westward component that crosses over to Baffin Island and a northward current that continues

130 around Baffin Bay. During the winter, ice can cover much of the NWA shelf areas, particularly  
131 down the Labrador Shelf as far south as 52°N latitude.

132 The Pacific sector extends from the northern Bering Sea, across the Chukchi Sea to the East  
133 Siberian and Beaufort seas (**Figure 1D**). The northern Bering, Chukchi and East Siberian seas  
134 are comprised of broad-shallow (~ 50m) continental shelves, while the Beaufort Sea has a  
135 narrow shelf and steep slope culminating in the deep (~3,000m) Canadian Basin. Sea ice covers  
136 this region for 5-7 months of the year, typically reaching maximum and minimum areal extent in  
137 March and September, respectively. The narrow and shallow (85 km wide x 50 m depth) Bering  
138 Strait is the only gateway for Pacific water to enter the Arctic. Transport is primarily northward  
139 and comprised of three water masses, the Alaska Coastal Water, Bering Shelf Water and Anadyr  
140 Water. The volume of transport through Bering Strait (~1Sv) is small (Woodgate et al., 2015)  
141 compared to large transport through the broad-deep Fram Strait (~5 Sv) and Barents Sea.  
142 (Carmack and Wassmann, 2006). Inflow transports heat, nutrients and plankton into both  
143 regions, with a strong summer-season pulse through Bering Strait in the Pacific sector  
144 (Woodgate, 2018; Moore et al., 2016).

145 Rapid sea ice loss has been evident in both the Atlantic and Pacific sectors. The highest  
146 rate of loss was nearly 3 weeks/decade in the Barents Sea compared to roughly 1.5-2  
147 week/decade elsewhere, for the period 1979-2013 (Table 1; Laidre et al., 2015). In the NEA,  
148 dramatic reductions in sea ice thickness and extent have been reported in all seasons (Haug et al.,  
149 2017). Specifically, Divine and Dick (2006) found the ice edge has retreated 250-375 km in the  
150 Greenland Sea in spring and about 250-350 km in the Barents Sea in late summer. Overall,  
151 despite high inter-annual variability, the ice extent in the Barents Sea has decreased by 60% over  
152 the last 200 years, with a larger reduction in maximum ice extent noted in August (40%) than

153 April (12%) (Vinje, 2001). This recent loss of sea ice has resulted in an overall increase in ocean  
154 heat content such that the northern Barents Sea seems now in transition from a cold and stratified  
155 Arctic to a well-mixed Atlantic-dominated system (Lind et al., 2018). In the NWA, much of the  
156 Labrador Shelf, and parts of the West Greenland shelf are covered by seasonal ice. Maximum ice  
157 extent occurs in late February and can be as far south as the northern Grand Banks, sometimes  
158 extending over 100 km from the coast (e.g. Stenson and Hammill, 2014). While the NWA has  
159 undergone periods of relative cooling and warming, overall the trend has been for warmer  
160 temperatures and a deterioration in ice conditions similar to those seen in the NEA (Johnston *et*  
161 *al.*, 2005; Friedlander *et al.* 2010; Stenson and Hammill, 2014). In the Pacific sector, sea ice  
162 extends south to the northern Bering Sea in March, then retreats to the Beaufort Sea in  
163 September (Frey et al. 2015). Until 2018, dramatic reductions in sea ice persistence was driven  
164 more by late ice formation than early ice retreat in this sector, with a seasonal ice-free state  
165 predicted by 2040 (Wang et al., 2018; Wang and Overland 2012). In 2018 and 2019, there was  
166 exceptionally low ice-cover in the Bering Sea and it remains to be seen if this represents a  
167 ‘tipping point’ in winter sea ice persistence ([https://uaf-iarc.org/2019/04/11/bering-strait-sea-ice-](https://uaf-iarc.org/2019/04/11/bering-strait-sea-ice-conditions-winter-2019/)  
168 [conditions-winter-2019/](https://uaf-iarc.org/2019/04/11/bering-strait-sea-ice-conditions-winter-2019/)).

169 Primary production appears to be increasing in some, but not all regions in the Arctic,  
170 coincident with sea ice loss (Arrigo and van Djiken, 2015). From 1998-2012, trends in mean net  
171 primary productivity (NPP) were greatest in the Barents (+28.3%), Chukchi (+42.1%) and  
172 Beaufort (+53.1%) seas, while productivity changes in the NWA were not significant and a  
173 negative trend (-15.2%) was reported for the E Greenland/Iceland area (Table 1). These  
174 measures are similar to those reported in a comparison of Arctic Ocean primary productivity for  
175 2017 compared to 2003-2016 (Frey et al., 2017). Strong positive anomalies in chlorophyll-*a*

176 occurred in the southeastern Chukchi Sea in May, and in the northern Barents Sea in June. These  
177 positive anomalies are in contrast to widespread negative chlorophyll-*a* anomalies reported  
178 across the Barents Sea and Baffin Bay in May (Frey et al., 2017). In the Pacific sector,  
179 reductions in sea ice persistence have been accompanied by increases in SST and Chl-*a*, as  
180 measured from satellites (Frey et al., 2015). Seasonal integrated primary production was  
181 calculated from a 62 year (1950-2012) record of *in situ* measurements and found the Chirikov  
182 Basin in the northern Bering Sea and the Chukchi Shelf to be the most productive areas (Hill et  
183 al., 2017). Increases in the magnitude of integrated primary production were coincident with  
184 changes in vertical distribution, with the subsurface peak described in 1959/60 no longer evident  
185 in the 2000s. The phytoplankton surface bloom in the NE Chukchi Sea was reported to occur  
186 several weeks earlier now compared to 1993, linked with increases in light due to earlier sea ice  
187 retreats.

188

### 189 **3. Baleen whale population estimates, distribution and phenology**

190 There are no comprehensive nor comparable estimates of population sizes for baleen  
191 whales in arctic and subarctic seas due to differences in survey timing and methodologies among  
192 regions. However, a compilation of available estimates demonstrates that, while the number of  
193 arctic-endemic bowhead whales is greater in the Pacific sector, the numbers of seasonally  
194 migrant species are at least an order of magnitude higher in the Atlantic sector (Table 2; **Figure**  
195 **2**). Most of what is known about baleen whale high-latitude distribution and phenology  
196 (seasonal movements) comes from whaling data and sighting surveys from planes and ships;  
197 both generally conducted during the summer-autumn season. Over the past three decades, the  
198 use of satellite telemetry and passive acoustic techniques has expanded year-round sampling



199 capability and supported a fuller understanding of whale habitat selection and movements in  
200 some areas. Combined, sighting surveys, telemetry and passive acoustic detections support  
201 descriptions of changes in baleen whale distribution and phenology coincident with the  
202 biophysical changes seen in the Atlantic and Pacific sectors, as briefly summarized below.

### 203 3.1 *NEA and CNA*

204 Bowhead whales have been reported recently in East Greenland and Svalbard waters  
205 (Boertmann et al., 2015; Storrie et al. 2018), and in the northeastern parts of the Barents Sea (see  
206 Wiig et al., 2007; Vacquie-Garcia et al., 2017). The current Svalbard-Barents population likely  
207 number several 100s of whales (Table 2). The peak period of whaling near Svalbard  
208 (approximately 1680–1790) coincided with a period of reduced ice extent, during which the  
209 summer ice edge retreated north of 79°N, (Allen and Keay, 2006). This period was followed by a  
210 rapid increase in the extent of summer (August) sea ice commencing around 1790, when the ice  
211 edge moved southwards to the southern tip of Spitsbergen (around 76°N) within just a few years.  
212 The current reduction in sea ice, in combination with observed mid-winter upwelling of nutrient-  
213 rich waters, may have created conditions similar to those at the peak of the whaling period (Falk-  
214 Petersen et al., 2014), resulting in the increased observations of bowhead whales in the area.  
215 Results of passive acoustic sampling in Fram Strait supports this idea, based on detection of  
216 bowhead calls throughout the year September 2008-2009, with call rates peaking during winter  
217 months (Moore et al., 2012). A more detailed analysis of a second acoustic dataset revealed  
218 complex songs recorded nearly every hour from October 2008-April 2009, suggesting Fram  
219 Strait may be an important wintering and reproductive ‘display’ area for the Svalbard-Barents  
220 bowhead population (Stafford et al., 2012; 2018). This suggestion was bolstered by results from  
221 a satellite tag deployed on a single female whale, who returned to Fram Strait in December after

222 swimming south from there in April to steep-slope waters offshore east Greenland during the  
223 summer period (Lydersen et al., 2012). These seasonal movements were consistent with patterns  
224 described by commercial whalers in the 16<sup>th</sup> and 17<sup>th</sup> centuries (Southwell, 1898).

225 Common minke, fin, humpback and blue whales migrate into NEA and CNA waters each  
226 spring to feed from summer to early autumn (**Figures 3 A, B**). Minke whales are the most  
227 abundant species numbering around 122,000 whales north of 60°N (Table 2) and occurring in  
228 almost all shelf areas off Greenland, Iceland and Norway. Minke whale numbers have shown  
229 large variations in subareas within NEA and CNA in recent decades (IWC 2016, Víkingsson and  
230 Heide-Jørgensen, 2015, Víkingsson et al., 2015). While the number of fin whales (~23,000  
231 animals north of 60°N) is less than a quarter of that of minke whales, they exceed the later  
232 species in terms of total biomass. The largest concentrations of fin whales are found in waters  
233 around Iceland and East Greenland, where sighting surveys in 2015 supported a population  
234 estimate of about 36,800 individuals (Pike et al. 2018), indicating that this stock has increased  
235 substantially since the sighting surveys in 1987 when the number was about 15,000 whales  
236 (Víkingsson et al., 2009, 2015). Concurrent with the apparent population increase, fin whales  
237 have also expanded their distribution into deeper water including aggregations in continental  
238 shelf-slope habitat west and north of Spitsbergen (Vacquie-Garcia et al., 2017), and of Norway,  
239 with sporadic sightings throughout the Norwegian Sea and into the Barents Sea in summer (Øien,  
240 2009; Nøttestad et al., 2015).

241 The number of humpback whales in the NEA and CNA is estimated in the range of  
242 10,000-15,000 animals, (Table 2), with the largest feeding aggregations near Iceland. Humpback  
243 whales were rare in Icelandic waters throughout most of the 20<sup>th</sup> century, but a significant and  
244 rapid increase (12% p.a.) occurred in the CNA between 1970 and 2001 (Pike et al. 2009a); since

245 1995, abundance seems to have stabilized (Víkingsson *et al.*, 2015). In Norwegian waters, the  
246 number of humpback whales seems to have been fairly stable, with whales commonly found in  
247 the areas around Bear Island south of Svalbard during summer, moving into the Barents Sea later  
248 in the season to feed on capelin (Christensen *et al.*, 1992; Øien, 2009). Hundreds of humpback  
249 whales remain offshore Iceland and northern Norway through mid-winter, to feed on capelin and  
250 herring (Víkingsson *et al.* 2015; Ancieto *et al.* 2018). In recent years, humpback whale songs  
251 have been recorded in North Icelandic waters during winter (Magnúsdóttir *et al.*, 2014). Whether  
252 this late migratory and/or overwintering strategy has any relation to the recent success of  
253 humpback whales compared to other baleen whales (Víkingsson *et al.* 2015) in the North  
254 Atlantic is an unresolved matter of discussion. Blue whales are observed primarily around  
255 Iceland (Pike *et al.* 2009a) and, to a lesser degree, near Svalbard (Vacquie-Garcia *et al.*, 2017).  
256 The population of blue whales in the NEA was estimated to be around 900 animals, based on  
257 sightings surveys data from 1987-2001 (Pike *et al.* 2009b); a new estimate that accounts for the  
258 recent sightings near Iceland and Svalbard indicate that this estimate is now considerably higher  
259 (Table 2; Pike *et al.* 2018,). Passive acoustic sampling revealed a strong seasonal presence of fin  
260 and blue whales in Fram Strait and the Greenland Sea (Moore *et al.*, 2012; Klinck *et al.*, 2012).  
261 Fin whale calls were detected over a prolonged period (August through March/May), with blue  
262 whale calls recorded over a much shorter (June/July-September/October) time frame.

### 263 3.2 NWA

264 While the general distribution of baleen whales in the NWA, particularly along the  
265 coasts, is reasonably well known (**Figure 3C**), estimates of population size are extremely limited  
266 and data on trends in abundance are absent. The only large-scale survey for bowhead whales was  
267 conducted in 2013 (Doniol-Valcroze *et al.*, 2015), and there have been only two comprehensive

268 surveys for large cetaceans along the Canadian continental shelf carried out in 2007 and 2016  
269 (Lawson and Gosselin, 2018). These later surveys estimated the total number of cetaceans from  
270 the northern tip of Labrador down to the southern Scotian Shelf and Gulf of St. Lawrence during  
271 a similar time period. However, the abundance estimates of many of the species were quite  
272 different between surveys, likely due to changes in distribution.

273         Although originally considered to be two stocks, bowhead whales that occupy Baffin Bay  
274 are now recognized as a single East Canada-West Greenland population (Laidre et al., 2015).  
275 This population summers in western Baffin Bay, the Canadian High Arctic, northern Foxe Basin,  
276 and northwestern Hudson Bay. Wintering occurs in areas of unconsolidated pack ice such as  
277 northern Hudson Bay, Hudson Strait, central Davis Strait, southern Baffin Bay, and off West  
278 Greenland. Historically, bowhead whales were common further south along the Labrador and  
279 northern Newfoundland coasts, where they were hunted by Basque whalers (Cumbaa, 1986).  
280 Although severely depleted by commercial whaling in the early 20<sup>th</sup> century, this population  
281 appears to be increasing and was estimated to number 6,446 (CV=0.26) whales in 2013 (Doniol-  
282 Valcroze et al., 2015b).

283         As in other areas, common minke, fin, humpback and blue whales migrate to NWA  
284 waters each spring, as part of their annual feeding migration. The northward extent of this  
285 migration varies, but as ice extent declines, all species appear to be moving farther into arctic  
286 regions (Higdon and Ferguson 2011). Based upon an aerial survey carried out in 2007, Heide-  
287 Jørgensen et al (2010a) estimated abundance of the West Greenland stock of minke whales to be  
288 16,609 (95% CI 7,172-38,461) which was much larger than any previous estimate. However,  
289 analysis of data from a similar survey conducted in 2015 resulted in a much lower estimate of  
290 5,241 whales offshore West Greenland (95% CI 2,114-12,992; IWC 2018). It is unknown if the

291 difference in estimates represents a decline in overall abundance, a change in distribution among  
292 the feeding areas, inconsistent or biased survey methods, or some combination of both. In  
293 Canadian waters of the NWA, Lawson and Gosselin (2018) estimated 4,020 (CV 0.43) minke  
294 whales in 2007 after correcting for perception and availability bias. In 2016, an estimated 13,008  
295 (CV 0.459) minke whales were present in the same area (Lawson and Gosselin 2018). More  
296 whales were seen in the northern portion of the survey area, indicating that this increase in  
297 estimated number was likely due to the movement of whales further north in 2016, possibly in  
298 response to the earlier timing of ice retreat, rather than a three-fold increase in population size.

299         Fin whale abundance in West Greenland was estimated to be 4,468 (95%CI 1,343-  
300 14,871) from aerial surveys conducted in 2007 (Heide-Jørgensen et al., 2010b). This estimate  
301 was considered to be negatively biased as it was not corrected for submerged whales and likely  
302 missed whales to the west of the survey lines. Even as a minimum estimate, however, it was  
303 much larger than previous studies suggesting that abundance of fin whales in West Greenland  
304 had increased, perhaps due to increased food availability (Heide-Jørgensen et al., 2010b). A  
305 more recent survey (2015) resulted in a much lower estimate (465, 95% CI 233-929; NAMMCO,  
306 2016). Like minke whales, the reason for the order-of- magnitude difference in fin whale  
307 estimates between 2007 and 2015 surveys is unknown; it could not be accounted for by harvest  
308 and may be a result of inconsistent or biased survey methods, whale responses to large scale  
309 ecosystem changes (NAMMCO, 2016), or some combination of these factors. Correcting for  
310 submerged whales and perception bias, Lawson and Gosselin (2018) estimated 2,177 (CV 0.465)  
311 fin whales between the Grand Banks and Hudson Strait in 2016. Unlike minke whales, this  
312 estimate is similar to the estimate obtained in 2007 of 1,795 (CV 0.40) fin whales. An additional  
313 1,967 (CV 0.36) fin whales were estimated for the Gulf of St. Lawrence and Scotian Shelf. Of

314 note, fin whale calls were recorded in Davis Strait from June through January 2006-2008, with  
315 peak calling in November-December, suggesting that whales remain there through early winter  
316 (Simon et al., 2010). A negative correlation between advancing sea ice and whale calling  
317 suggests that fin whales may extend their stay even longer in a future with further sea ice loss  
318 due to global warming.

319 Humpback whale numbers in the NWA appear to be far lower than in the NEA. Based  
320 upon an aerial survey along West Greenland in 2007, Heide-Jørgensen and Laidre (2015)  
321 estimated humpback whale abundance to be 4,090 (95% CI=1,620-10,324) using mark-recapture  
322 distance sampling analysis (MRDS), while a strip-census method for analysing the data resulted  
323 in a lower, but more precise estimate (2,704, 95% CI = 1,402-5,215). Comparing surveys carried  
324 out between 1984 and 2007, Heide-Jørgensen et al. (2012a) estimated that the population had  
325 increased at a rate of 9.4% yr<sup>-1</sup>. However, a similar survey in 2015, analysed using MRDS  
326 methods, resulted in a lower, but not significantly different estimate of 1,321 (95% CI 578-  
327 3,022) humpback whales off West Greenland (NAMMCO, 2016). In Canadian waters, Lawson  
328 and Gosselin (2018) reported 2,214 (CV 0.36) humpback whales during their comprehensive  
329 survey of the Labrador shelf and Grand Banks in 2007. The estimate obtained during 2016  
330 survey was higher (8,439; CV 0.49) although both estimates had fairly large variance.

331 Blue whales in the NWA are designated as Endangered in Canada, with the current  
332 population thought to contain less than 200 mature individuals (Beauchamp et al., 2009).  
333 Although protected from hunting since the 1960s, the population does not appear to be  
334 recovering. During the summer, this population ranges from Davis Strait off West Greenland, to  
335 Newfoundland, the Gulf of St. Lawrence and New England. Gomes et al. (2017) identified  
336 potential habitat for blue whales in Canadian waters using a model that incorporated available

337 sighting data, physical features and primary productive as indicated by persistent chlorophyll.  
338 They predicted that priority areas for blue whales were primarily located along the outer margins  
339 of the eastern and western Scotian shelf and southern portions of the Newfoundland Shelf. Areas  
340 of low priority for blue whales were in northern Labrador and off eastern Newfoundland. The  
341 winter distribution of blue whales in the North Atlantic is poorly understood, but some whales  
342 remain in waters south of Iceland and near Newfoundland and Nova Scotia (Stenson et al., 2003;  
343 Beauchamp et al., 2009). Blue whales have been observed along the southwest coast of  
344 Newfoundland during the early spring where they feed along the ice edge at the mouth of the  
345 Gulf of St. Lawrence. Unfortunately, because of currents and the nature of the coastline, they can  
346 be trapped during heavy ice years and pushed onto shore resulting in high mortality in some  
347 years (Stenson et al., 2003).

### 348 3.3 *Pacific sector*

349 In the Pacific sector, the Bering-Chukchi-Beaufort (BCB) bowhead population was  
350 estimated to number 16,820 (95% CI = 15,176-18,643) whales from an ice-based census  
351 conducted in 2011 (Givens et al., 2016). This population has been the focus of intense study  
352 since the late 1970s, due both to their importance as a subsistence resource and potential  
353 vulnerability to impacts from offshore commercial activities (Burns et al., 1993). These whales  
354 undertake a predictable seasonal migration, leaving overwintering areas in the northern Bering  
355 Sea in March-April to arrive feeding areas in the Beaufort Sea in May-June. After summer  
356 feeding, the whales reverse their route in August-September, arriving in Chukchi and northern  
357 Bering waters from October-December (see George et al., 2015: Fig.1). Passive acoustic  
358 sampling suggests that some whales deviate from this pattern, however, with bowhead calls  
359 recorded near the Chukchi Plateau from March through August (Moore et al., 2012). During the

360 August-October migration period, bowheads typically occupy shallow continental shelf habitats  
361 in the Beaufort and Chukchi seas (**Figure 3D**), selecting these waters over those of the deeper  
362 slope and basin (Moore et al., 2000). Satellite telemetry studies have identified six core-use  
363 habitats within this range (Citta et al., 2015) and noted contrasting patterns of occurrence during  
364 the autumn migration across the northern Chukchi Sea that correspond to the presence (or  
365 absence) of Bering Sea water, which often contains krill (Citta et al., 2017). Further, with the  
366 delay in sea ice formation now common in the Pacific sector, tagged bowheads sometimes linger  
367 in the northern Chukchi Sea through December, with two whales overwintering there in 2017-  
368 2018.

369 BCB bowheads commonly feed on copepods and krill in the Chukchi and Beaufort seas,  
370 with winter feeding in the northern Bering Sea inferred from dive patterns (Citta et al., 2015).  
371 The reduction in summer sea ice in the Pacific sector has been accompanied by evidence of  
372 improved body condition, especially for juvenile whales, in this population (George et al., 2015).  
373 Specifically, improved body condition was significantly correlated with the duration of the open  
374 water season, later date of freeze up, and upwelling conditions. Furthermore, bowhead whale  
375 use of the western Beaufort Sea increased substantially for the period 1997-2014 compared to  
376 1982-1986, coincident with a dramatic reduction of sea ice there (Druckenmiller et al., 2017);  
377 conditions which would enhance the upwelling conditions described in the krill trap model  
378 (Ashjian et al., 2010). In sum, these results support the suggestion that bowheads are benefitting  
379 both from (i) the availability of more arctic-endemic copepods from increased primary and  
380 secondary production, and (ii) more krill available due to stronger transport through Bering Strait  
381 and increased upwelling events along the Beaufort slope (Moore, 2016: fig. 1). This improved  
382 feeding scenario also finds support in the dramatic increase in the number of bowhead calves



383 seen on aerial surveys in recent years (Clarke et al., 2017). Females must be in good body  
384 condition to carry calves to term, so the increase in calf numbers implies plentiful food in recent  
385 years.

386         The Eastern North Pacific (ENP) population of gray whales numbers roughly 20,000  
387 animals (Table 2), with some exchange with the Western North Pacific stock recognized in  
388 recent years (Mate et al., 2015). Gray whales are seasonally-resident in the Pacific Arctic sector  
389 from April through October, undertaking a migration to and from waters offshore Mexico from  
390 November through March (Rugh et al., 2001). Their range extends from the Bering Sea through  
391 the Chukchi and into the western Beaufort, with occasional sightings as far east as the Canadian  
392 Beaufort Sea. Gray whales select shallow coastal and shoal habitats throughout this area, where  
393 they feed primarily on benthic infaunal amphipods, but they also take epifauna and pelagic prey  
394 when available (Brower et al., 2017; Moore et al., 2000). Aerial surveys and satellite telemetry  
395 studies indicate gray whales remain in localized areas while feeding, with slow movements and  
396 strong site fidelity described for foraging on amphipods in nearshore waters of the Chukotka  
397 peninsula (Heide-Jørgensen et al., 2012b). Responses of the ENP population of gray whales to  
398 climate signals resulted in one of the first attempts to consider baleen whales ecosystem sentinels  
399 (Moore, 2008). Six observations provided supporting evidence, including: (i) a one-week delay  
400 in the southbound migration associated with a regime shift in the North Pacific; (ii) an increase  
401 in calf production associated with early ice retreat from a northern Bering Sea feeding area  
402 (Chirikov Basin); (iii) reduction in calf numbers and changes in occupancy of breeding lagoons  
403 in Mexico associated with 1997-98 El Niño event; (iv) reduction of gray whale feeding in the  
404 Chirikov Basin and increase in the southern Chukchi, associated with shifts in prey density; (v)  
405 gray whales feeding year-round near Kodiak Island in the northern Gulf of Alaska in response to

406 localized prey availability; and (vi) gray whale calls detected year-round in the western Beaufort  
407 Sea, associated with a reduction and thinning of sea ice providing breathing opportunities along  
408 cracks in winter. Like bowheads, gray whale calf counts during aerial surveys have been  
409 especially high in recent years (Clarke et al., 2017), associated with extreme losses of sea ice in  
410 the Pacific sector.

411 Humpback, fin and minke whales are now commonly seen during summer in the southern  
412 Chukchi Sea (**Figure 3D**), although their numbers are low (Table 2) and stock identity remains  
413 unknown (Brower et al., 2018). Specifically, these three species were seen in the eastern  
414 Chukchi Sea (mostly between and 67<sup>0</sup>-69 N latitude) during aerial surveys conducted from July  
415 through September 2009-2012, where none were seen during surveys conducted from 1982 to  
416 1991 (Brower et al., 2018). The cluster of sightings in the southeastern Chukchi Sea is  
417 associated with a well-known biological ‘hotspot’ where benthic and pelagic prey densities are  
418 high (Grebmeier et al., 2015; Nishino et al., 2016). Annual counts in these waters remain low  
419 (10s of whales/species) compared to 100s-1,000s of humpback, fin and minke whales estimated  
420 for the southeastern Bering Sea (Friday et al., 2013). These subarctic species appear to have  
421 expanded their range in late summer to join the arctic endemic bowhead whale and the  
422 seasonally-resident gray whale in the rapidly changing marine ecosystem of the Pacific sector  
423 (Moore, 2016). Detections of whale calls at an autonomous recorder deployed from 2009-2012  
424 revealed that humpback and fin whales remain in southern Chukchi waters through October and  
425 in some years into November (Woodgate et al., 2015; Tsujii et al., 2016). Of note, detections of  
426 humpback and fin whale calls ceased near the onset of sea-ice formation each year, coincident  
427 with the onset of bowhead whale call detections (Woodgate et al., 2015). In other words, the  
428 subarctic species departed as the arctic endemic species arrived, along with seasonal sea ice.

#### 429        **4. Baleen whale prey**

430            Subarctic baleen whales generally feed on macro-zooplankton (e.g., copepods,  
431 euphausiids/krill, mysids), squid and forage fishes such as herring (*Clupea haerengus*), capelin  
432 (*Mallotus villosus*) and sand eel (*Ammodytidae* spp.; Bowen and Siniff, 2000; Christensen *et al.*,  
433 1992; Haug *et al.*, 2002; Víkingsson *et al.*, 2014, 2015; Windsland *et al.*, 2007). Blue whales are  
434 the exception, feeding almost solely on euphausiids. Bowhead whales forage primarily on  
435 macro-zooplankton (e.g., copepods, mysids and euphausiids), with small fish occasionally  
436 reported (Lowry, 1993). Gray whales are the only species capable of feeding on benthic infauna,  
437 using suction to extract prey and sediment, then pushing the muds out through their course  
438 baleen and retaining amphipods. This species may be the ultimate ‘generalist’ in that they can  
439 also feed on epi-benthic and pelagic prey, including krill. Understanding the ecology of baleen  
440 whale prey species is often a focus of research that accompanies commercial fishery  
441 management. As there has been extensive commercial fishing in the Atlantic sector, but none in  
442 the Pacific sector, the amount and level of information on macro-zooplankton and forage fishes  
443 between sectors contrasts sharply. Still, there are a number of recent reviews and comparative  
444 papers of both baleen whale diet and high-latitude marine ecosystems responses to global  
445 warming (e.g., Hunt *et al.*, 2013; Fossheim *et al.*, 2015; Haug *et al.*, 2017; Eriksen *et al.* 2017)  
446 and we draw from these and others in the regional reviews below.

#### 447        4.1 *NEA and CNA*

448            In the NEA, the pelagic biomass, dominated by krill and forage fishes, increased from 6  
449 to 30 million tons during the last three decades, with some of the pelagic species shifting their  
450 distribution to the northeast (Eriksen *et al.*, 2017). The inflow of zooplankton biomass through  
451 Fram Strait far exceeds that through Bering Strait, with high abundances of copepods observed

452 in all months (Basedow et al, 2018). Results from the joint Russian – Norwegian ecosystem  
453 surveys in September-August 2003-2012 showed that both fin and humpback whales inhabit  
454 both Arctic and Atlantic waters, with highest densities in arctic waters north of the polar front  
455 (Skern-Mauritzen et al. 2011, Ressler et al., 2015). In the north, the baleen whale distributions  
456 were restricted to a narrow zone along the northern rim of the capelin migration front, in areas  
457 with abundant krill. Modelling exercises with whale distributions and available prey have shown  
458 positive associations between krill and both fin and humpback whales, suggesting that both these  
459 whale species aggregate in areas where krill is abundant (Ressler et al., 2015). The large baleen  
460 whales did not occupy areas with high capelin or polar cod densities. These results suggest, at  
461 least for years with low capelin abundance, that: i) large baleen whales in northern arctic waters  
462 target zooplankton rather than pelagic fish, and ii) the whales forage ahead of the capelin  
463 migration front as a response to prey depletion in areas occupied by capelin. In that case, pelagic  
464 fish and baleen whales compete for the same resource, and this competition may structure the  
465 baleen whales' northern distributions. In the southern N-Atlantic waters, both fin and minke  
466 whales aggregated at high herring and blue whiting densities, suggesting that pelagic fish are  
467 preyed upon in this area. Nevertheless, the low density of baleen whales in southern Barents Sea  
468 suggests that the abundant pelagic fish stocks in the south experienced relatively low predation  
469 pressure by baleen whales in this season.

470           Substantial changes have occurred in the Barents Sea ecosystem, the most conspicuous  
471 being related to the cyclical nature of stocks of the two dominant pelagic shoaling fish species,  
472 capelin and herring. Following a collapse in the capelin stock in 1992-1993, minke whales  
473 foraging in the northern Barents Sea switched from a capelin-dominated diet to a diet almost  
474 completely comprised of krill (Haug et al., 2002). The southern region of the Barents Sea

475 represents important nursery areas for the Norwegian spring spawning herring. Good recruitment  
476 to this stock provides strong cohorts and large numbers of young, immature herring (0-3 years  
477 old) that serve as the main food for minke whales feeding in the area. Recruitment failure with  
478 subsequent weak cohorts seems to reduce the availability of immature herring to such an extent  
479 that minke whales switch to other prey items such as krill, capelin and gadoid fish. Minke  
480 whales, particularly immatures and adult females, show improved body condition in years when  
481 the abundance of immature herring is high (Haug et al., 2002). The considerable size range of  
482 consumed prey (0.2 – 78 cm) suggest that minke whales are not particularly size selective and  
483 consumption appears to be determined by the availability of different size classes (Windsland et  
484 al., 2007).

485 In the CNA, significant changes in distribution of several fish species have also been  
486 reported in recent decades. Several southern species e.g. haddock, monkfish, mackerel) have  
487 extended farther north and a dominant northern pelagic species (capelin) has retreated towards  
488 the colder east Greenland waters. (Astthorsson et al., 2007, Valdimarsson et al., 2012). In the  
489 NEA and CNA, fin whales feed on krill (*Meganycitphanes norvegica* and *Thysanoessa sp.*) and  
490 forage fish such as capelin, blue whiting (*Micromesistius poutassou*) and herring (Heide-  
491 Jørgensen et al., 2010). In the Irminger Sea (between Iceland and East Greenland), stomach  
492 analyses have shown fin whales to feed almost exclusively (>95%) on euphausiids (primarily *M.*  
493 *norvegica*; Víkingsson 1997, 2004a).

494 In Icelandic waters, common minke whales feed on a wide variety of prey with 14  
495 species identified in a 2003-2007 study (Víkingsson et al., 2014). Sand eel was the most  
496 important prey found in more than 50% of the whales. Other frequently occurring prey types  
497 include, herring, capelin, haddock (*Melanogrammus aeglefinus*, cod (*Gadus morhua*) and krill.

498 The only previous investigation on minke whale diet in this area (1977-1984) had shown much  
499 higher proportions of capelin and krill (Sigurjónsson et al., 2000), indicating a significant shift in  
500 diet between these periods. During the course of the more recent study (2003-2007) there were  
501 also appreciable changes in diet composition with decreasing prevalence of sandeel (94% (2003)  
502 to 18% (2007)), coincident with a near-collapse of the sandeel stock around 2005 with severe  
503 consequences for breeding success of seabirds in South and Southwest Iceland and feeding  
504 conditions for common minke whales (Lilliendahl et al., 2013, Víkingsson et al., 2015). The  
505 decreased proportion of sandeel was compensated with increased predation on herring and  
506 gadoids (Víkingsson et al. 2014). These changes in diet composition are consistent with recent  
507 changes in the Icelandic continental shelf ecosystem, including increased sea surface and bottom  
508 temperatures and changes in distribution and abundance. Overall, in terms of whale prey, the  
509 “invasion” of the mackerel stock from the south into Icelandic waters (Astthorsson et al., 2012)  
510 and the shift in summer distribution of capelin away from Icelandic waters (Pálsson et al., 2012)  
511 may be of particular importance. Warming of 1–2°C in the waters south and west of Iceland  
512 during the past 20 years appears to be the most obvious explanation for these changes  
513 (Valdimarsson et al., 2012).

#### 514 4.2 NWA

515 Subarctic baleen whales offshore West Greenland feed primarily on capelin, sand eel and  
516 krill, with integrated krill abundance the most important parameter in predicting whale presence  
517 (Laidre et al., 2010). In Canadian waters, baleen whales appear to feed on a mixture of these  
518 same species, as well as herring, squid and pre-recruit cod (Mitchell, 1973, 1975; Bundy et al.,  
519 2000). While quantitative data on the current diet of any of the baleen whales in the NWA are  
520 not available, capelin appear to be the predominant prey of minke whales in Greenland coastal

521 waters, whereas sand eel and krill are often consumed in more offshore areas (Neve, 2000).  
522 Bowhead whales feed primarily on epibenthic copepods in Disko Bay, West Greenland from  
523 February through May, with unprecedented densities of *Calanus finmarchicus* reported there in  
524 2006 (Laidre et al., 2007). Bowheads depart Disko Bay in late May and June, with data from  
525 satellite-tagged whales showing that whales left 15d later in 2008-2010 compared to 2001-2006.  
526 This later departure may be a response to an extended spring bloom fostered by reduced sea ice  
527 cover, providing whales longer access to their copepod prey (Laidre and Heide-Jorgensen,2012).  
528 Isotopic evidence suggests bowheads feed on both copepods and krill in the NWA, although  
529 where they do this is unclear (Pomerleau et al., 2014).

530         The Newfoundland and Labrador shelves of the western NWA are at the intersection of  
531 several major oceanographic domains that result in the formation and persistence of spatially  
532 well-defined zooplankton communities (Pepin et al., 2015). These provide important food  
533 sources for species such as blue and sei whales that specialize on zooplankton or other species  
534 that may use them to supplement capelin. Monitoring of oceanographic conditions on the  
535 Newfoundland and Labrador shelves has indicated that in recent years there has been a general  
536 decline in productivity (with declining levels of nitrates and phytoplankton), as well as declines  
537 in the magnitude and duration of the spring bloom (DFO, 2017). As a result, total copepod  
538 abundance in the Labrador Sea has been below normal since ~2013 although different groups  
539 varied considerably; the abundance of the *Calanus finmarchicus*, the primary copepod in the  
540 region, has been below normal since 2013, while the small, less energy rich copepod  
541 *Pseudocalanus spp.* has been more abundant. The abundance of non-copepod mesozooplankton  
542 were also above normal compared to the previous decade (DFO, 2017). These changes in  
543 zooplankton abundance are likely to impact the health and distribution of zooplankton feeding

544 baleen whales in a manner similar to the changes in distribution observed among North Atlantic  
545 Right Whales who have moved northward into the Gulf of St. Lawrence and encountered new  
546 threats in response to lower *Calanus* abundance in their historic summer feeding areas (Meyer-  
547 Gutbrod et al 2018).

548         In the 1970s and 1980s, capelin were the dominant prey in the diets of minke, humpback  
549 and fin whales in the Newfoundland area (Sergeant, 1963; Mitchell, 1975; Piatte et al., 1989).  
550 However, dramatic changes have occurred in the Labrador Sea ecosystems over the past 3  
551 decades attributed to a regime shift (Buren et al., 2014a). In the late 1980s and early 1990s,  
552 populations of Atlantic cod and capelin collapsed (Buren et al., 2014a, b; Rice, 2002). Although  
553 populations of both species have shown some signs of recovering, they still remain low in  
554 comparison to their pre-collapse abundance. Buren et al (2014a) found that changes in capelin  
555 biomass were influenced by changes in the timing of ice retreat which, in turn resulted in the  
556 changes in the timing of the primary productivity bloom. These changes also included a  
557 mismatch between the timing of the spring bloom and the emergence of *Calanus spp.* from  
558 diapause. This in turn, resulted in reduced *Calanus* which are the main prey of capelin.  
559 Unfortunately, the impact of the collapse in capelin on baleen whales in the area are not known  
560 due to uncertainty about population trends and a lack of concomitant assessment of whale diets  
561 or body condition. However, capelin are also the major prey of a variety of predators who have  
562 been impacted by declines capelin abundance. For example, the presence of capelin in the diets  
563 of seabirds off Labrador declined (e.g. Baillie and Jones 2004) while reduced reproductive rates  
564 and increased occurrence of late term abortions in harp seals have been shown to be influenced  
565 by low capelin biomass (Stenson et al 2016).

566



567 4.3 *Pacific sector*

568           There is less known about the distribution and abundance of macrozooplankton and  
569 forage fishes in the Pacific sector, due to the lack of commercial fishing north of 60<sup>0</sup>N latitude.  
570 Routine surveys of marine fish communities have been conducted only since the mid-2000s, as  
571 interest in the Pacific Arctic increased due to climate change and the potential for resource  
572 extraction. The northern Bering and Chukchi seas are benthic dominated shelf-systems  
573 (Grebmeier et al., 2015), with very few fishes (or crabs) of commercial size. Logerwell et al.  
574 (2015) examined available fish survey data across a spectrum of habitats in the northeastern  
575 Chukchi and western Beaufort Seas and found: (i) Arctic cod (*Boreogadus saida*) dominated  
576 mid-water and benthic habitats in both seas, (ii) forage fishes (sand lance, herring, capelin,  
577 rainbow smelt) preferred lagoon and nearshore habitats, and (iii) salmon (*Oncorhynchus* spp.),  
578 which may be expanding their range north with warmer seas, were most prevalent in Beaufort  
579 Sea lagoons and surface waters in the Chukchi Sea.

580           Macrozooplankton that bowhead whales rely upon in the Pacific sector include copepods,  
581 euphausiids/krill (*Thysanoessa* spp.), mysids and amphipods. The analysis of stomach contents  
582 from whales taken by Inuit hunters indicate that copepods are the most common prey in the  
583 eastern Beaufort Sea, while krill often dominate in the western Beaufort (Lowry et al., 2004).  
584 Observational and stomach-content data confirm that, in late summer, bowheads feed on  
585 euphausiids along the Chukotka coast (Moore et al., 1995), near Utqiagvik (formerly known as  
586 Barrow), Alaska (Moore et al., 2010) and as far east as Kaktovik, Alaska (Lowry et al., 2004).  
587 These krill are likely transported into the Pacific sector through Bering Strait (Berline et al.,  
588 2008) and carried eastward in the Beaufort shelf break jet possibly as far as the Mackenzie Shelf  
589 (Lin et al., 2016). The 50% increase in inflow through Bering Strait between 2000 and 2015

590 (Woodgate, 2018) may have advected more krill into the Pacific sector than in earlier years, with  
591 large wash-ups now commonly reported along barrier island beaches in the western Beaufort Sea  
592 (**Figure 4 A,B**). Near Utqiagvik, a mechanistic model called the ‘krill trap’ describes how  
593 alternating wind patterns serve to aggregate krill in nearshore waters, resulting in large numbers  
594 of feeding bowheads (**Figure 4C**) which are a boon for local Inuit subsistence hunters (Ashjian  
595 et al., 2010). Gray whales, often considered benthic-only foragers, are also commonly seen  
596 feeding in these dense krill swarms (**Figure 4D**).

597

## 598 **5. Discussion**

599 We have presented the first-ever review of baleen whale ecology in northern high-latitudes,  
600 to provide both a circumpolar baseline of population estimates and habitats for these species and  
601 to assess their capacity as ecosystem sentinels in an era of rapid habitat alteration. Atlantic and  
602 Pacific sector arctic and subarctic seas offer contrasting habitats for baleen whales. The Atlantic  
603 sector is comprised of three regions, which provides diverse habitats that support 100,000s of  
604 seasonally-migrant baleen whales, but only 100-1000s of arctic-endemic bowhead whales. In  
605 part, the comparatively low numbers of bowhead whales in the Atlantic sector is likely due to  
606 slow recovery from commercial harvests in earlier centuries. In contrast, the Pacific sector,  
607 which is comparatively small and less diverse in habitats, currently supports a robust population  
608 of bowhead whales as well as large seasonally-migrant gray whale population, but only 10s to  
609 low 100s of humpback, fin and minke whales. Forage fishes are many and varied throughout the  
610 Atlantic sector, but few and localized in the Pacific sector. While krill are recognized as key  
611 prey for forage fishes and baleen whales in the Atlantic Arctic sector, their role in Pacific Arctic  
612 food webs is poorly understood. Right now, the migratory cycles of the arctic-endemic

613 bowhead whale and the subarctic baleen whale species restricts overlap in habitat use. This was  
614 especially evident via acoustic sampling at Bering Strait, and in satellite tagging results near  
615 Davis Strait; in both cases bowhead whales departed/arrived, as humpback whales  
616 arrived/departed (Woodgate et al. 2015; Laidre and Heide-Jørgensen, 2012).

617 The Arctic is warming over twice as fast as anywhere else on the planet, with a state-change  
618 in climate now recognized in both terrestrial and marine ecosystems (Richter-Menge et al.,  
619 2017). In the future, arctic and subarctic seas likely will be warmer, fresher and seasonally ice-  
620 free. Regional differences in primary production will depend on the vagaries of seasonal sea ice  
621 cover and ocean mixing, stratification and advection; specifically, in how those dynamic  
622 processes impact nutrient replenishment to near-surface waters. Based on trends over the past  
623 *ca.* 30 years, it seems likely that future arctic and subarctic seas will be more productive overall,  
624 marked by strong regional variability that will impact marine ecosystems at each rung of the  
625 trophic ladder from bacteria to whales. In this context, we examine the idea of baleen whales as  
626 sentinels to ecosystem variability and reorganization.

### 627 *5.1 Baleen whales as ecosystem sentinels*

628 As upper trophic level predators, baleen whales are important components of ocean  
629 ecosystems (Roman et al., 2014) that can serve as sentinels to habitat alteration through changes  
630 in their distribution, abundance, phenology and body condition (Figure 5; Moore 2018). The  
631 highly mobile nature of many species allows them to shift distribution to reflect variability in  
632 prey availability and/or environmental conditions. For example, the increase in humpback and  
633 fin whales, and decreases in minke whales, in the waters around Iceland between 1987 and 2007  
634 was associated with a decrease in abundance of euphausiids and sand eels, and a local increase in  
635 herring and other potential prey species associated with warming and salinification of Icelandic

636 waters (Víkingsson et al., 2014, 2015). Similarly, the large differences in abundance estimates  
637 obtained from successive surveys in the NWA suggests a distinct shift in distribution, likely in  
638 related to alterations in prey availability. Despite the mobility and flexibility in feeding, changes  
639 in prey availability have been shown to affect body condition and fecundity in baleen whale  
640 species (Haug et al., 2002; Williams et al., 2013; George et al., 2015; Solvang et al., 2017). In  
641 the NEA, minke whales and harp seals (*Pagophilus groenlandicus*) are the primary marine  
642 mammal predators, and over the period 1992-2013 a negative trend in body condition was  
643 observed in both species (Bogstad et al., 2015). This occurred during a period of record high cod  
644 abundance, also a top predator (and commercially important fish) in the area, and Bogstad et al.  
645 (2015) suggested that cod may simply have outperformed the whales (and seals) in competition  
646 for common food resources. In this context, it is important to recognize that in terms of biomass,  
647 top predators are minor components of most ocean ecosystems. For example, an analysis of  
648 carbon flux in the food web of the entire Barents Sea found that that less than 1% of the  
649 harvestable production is channeled through the dominant higher trophic species such as cod,  
650 harp seals, minke whales and sea birds (Wassmann et al. 2006).

651 In sum, we have presented examples of both ecological (extrinsic) and physiological  
652 (intrinsic) responses of baleen whale populations to biophysical forcing in four high latitude  
653 habitats. In so doing, we have demonstrated that baleen whales are highly mobile predators  
654 capable of shifts in distribution and phenology, and that most display a degree of foraging  
655 plasticity exemplified by variable diets and changes in body condition. In short, baleen whales  
656 can act as sentinels to the state of the marine ecosystem, integrated to the trophic-level of  
657 macrozooplankton, macrobenthos and forage fishes (Haug et al., 2017).

658 *5.2 Baleen whale ecology and ecosystem models*

659           We then ask, how can the signal that baleen whales are providing contribute to ecosystem  
660 models and our capability to forecast future states? The first modelling attempts to include  
661 baleen whales in the NEA and CNA aimed to assess the relations and interaction between whales  
662 and fish species that were important both as whale prey and for commercial fisheries. The  
663 conclusions were that baleen whale species, such as minke, fin and humpback whales, may have  
664 significant effects on the long-term yield of fish stocks such as capelin and cod (Stefansson et al,  
665 1997; Schweder et al., 2000) although the authors stressed the large uncertainty in the results.  
666 Similar conclusions were drawn from runs with MULTSPEC, an area, age and length structured  
667 multispecies model for the species capelin, herring, cod, harp seal and minke whales (Bogstad et  
668 al., 1997). In a later study, Lindstrøm et al. (2009) used another age-length structured multi-  
669 species model (Gadget: Globally applicable Area-Disaggregated General Ecosystem Toolbox) to  
670 analyze the historic population dynamics of key fish and marine mammal species in the Barents  
671 Sea. The results suggest that changes in cod mortality from fishing or cod cannibalism have the  
672 largest effect on the ecosystem. Alternate whale migration scenarios had only a moderate impact  
673 on the modelled ecosystem. Recently, Storrie et al. (2018) described northward shifts by  
674 seasonally-resident baleen whale species in the Svalbard Archipelago, based upon kernel density  
675 and Maxent modelling of a 13 year (2002-2013) ‘citizen science’ data base. These range  
676 expansions were likely due to loss of sea ice and warming seas causing shifts in prey abundance  
677 and availability.

678           In the NWA, the only ecosystem model that includes baleen whales is the Ecopath  
679 trophic mass-balance model (Bundy et al., 2000; Bundy 2001). Cetaceans were identified as  
680 major consumers in these models but conclusions were limited because of the lack of good  
681 estimates of abundance for most of the baleen whales at the time. This is changing with

682 improved data from recent surveys and a new Ecopath model is anticipated that will incorporate  
683 these new estimates. However, the newer model will focus only on the Labrador Sea area and  
684 not Baffin Bay, and it will include only the subarctic baleen whale species and not bowheads. A  
685 parallel model is being constructed for the Barents Sea which will allow comparisons between  
686 the two systems to identify how the key factors influencing the ecosystems may vary and  
687 therefore, how climate change may affect the two regions differently. In the Pacific sector,  
688 Ecopath has been applied only to the eastern Chukchi Sea (Whitehouse et al., 2014). Bowhead  
689 and gray whales were included in the analysis, along with beluga, polar bears, walrus and ice  
690 seals. The model found extreme benthic dominance in food web structure and associated mass  
691 flows, which did not provide strong vectors to the baleen whale components of the ecosystem.

692         The concepts of resource waves and tipping points underlie two modeling approaches  
693 that may be useful in interpreting baleen whale responses rapid habitat alteration. The resource  
694 waves concept suggests that the ecosystem ‘signal’ that baleen whales can provide will depend  
695 on how they modify their seasonal distribution and phenology in response to oceanographic  
696 changes that impact resources in high latitudes. Armstrong et al. (2016) note that “*Time is*  
697 *particularly limiting for consumers in seasonal environments where phenology may have a*  
698 *strong effect on trophic interactions*”. In short, baleen whales must find and process large  
699 amounts of ephemeral prey over seasonal time frames. The concept of resource waves extends  
700 the more narrowly focused idea of trophic match-mismatch to seasonal time frames wherein  
701 whales can reflect phenological diversity of the ecosystem throughout their range. In model  
702 simulations of resource waves, phenological diversity was often more important to consumer  
703 energy gain than prey abundance per se. To apply the resource wave model to baleen whale  
704 seasonal distribution and phenology, the next step would be to develop case studies to quantify

705 whale movements in response to seasonal waves of ocean productivity and prey in the Pacific  
706 Arctic and in sub-regions of the Atlantic sector. Sufficient data for such an exercise seem  
707 available for bowhead whales in the NWA region and Pacific sector, and for humpback, fin and  
708 minke whales in the CNA and NWA regions. An analysis of this type would provide a clearer  
709 understanding of the type and strength of signal that baleen whales can provide as ecosystem  
710 sentinels. Specifically, this approach could provide a dynamic means to compare the importance  
711 of krill in baleen whale diets among the three Atlantic sub-regions and the Pacific sector. The  
712 results of such work could support the inclusion of baleen whales in models of climate change  
713 impacts on population dynamics, as has been done for other migratory marine species (e.g.,  
714 Anderson et al., 2013; Abrahms et al., 2019).

715         Tipping points, whereby small perturbations trigger large responses, is another concept  
716 often applied in evaluation of the impacts of climate change on ecosystems (Lenton, 2013).  
717 With regard to baleen whale habitats at high latitudes, perturbations both large and small are now  
718 common and varied by region. For example, the impacts of climate change seem to be greater  
719 in the NEA and CNA than in the NWA where changes do not seem to be as rapid. This is likely  
720 due to the fact that the NEA and CNA are heavily influenced by the amount of Atlantic water  
721 inflow, while the NWA (especially the western side) is strongly influenced by the cold Labrador  
722 Current. Future developments in two large-scale ocean processes that could essentially ‘change  
723 everything’ are: (1) the recently described Arctic Atlantification, whereby inflow of Atlantic  
724 water is making the NEA Arctic sector structurally similar to the Eurasian Basin (Polyakov et al.,  
725 2017), and (2) the potential for a ‘breakdown’ of the Beaufort Gyre resulting in a large pulse of  
726 cold-freshwater outflow in the North Atlantic (Krishfield et al., 2014; Håkkinen, 1993). There is  
727 already evidence of both processes in the “Atlantification” of the western Eurasian Basin from

728 observations in 2013-2015, and in the export of *ca.* 320 km<sup>3</sup> of fresh water to the North Atlantic  
729 in 2010-2012. The potential impact of such perturbations to baleen whale habitats is difficult to  
730 predict, but the spatial scale of such processes suggest a large step-change alteration to high  
731 latitude marine habitats.

732           In the Pacific sector, the Arctic Marine Pulses (AMP) conceptual model depicts seasonal  
733 ‘pulses’ in the ecosystem by linking biophysical processes in four previously-defined contiguous  
734 ecological domains, including the: (i) Pacific Arctic domain; (ii) Seasonal Ice Zone domain; (iii)  
735 the Marginal domain (i.e., the shelf break and slope); and (iv) Riverine Coastal domain (Moore  
736 et al., 2016). Some of the biophysical processes included in the AMP model, such as pelagic-  
737 benthic coupling on the broad shelves of the northern Bering and Chukchi seas and advection  
738 and upwelling of zooplankton along the western Beaufort shelf (i.e. the krill trap), have been the  
739 focus of long-term studies, which could provide data germane to analysis of baleen whale  
740 habitats with regard to resource waves and tipping points. An overarching goal of the AMP  
741 model is to provide a foundation for the development of predictive human-inclusive ecosystem  
742 models for the Pacific Arctic region. Further, with its focus on phenology and signals provided  
743 by UTL species, the AMP model might also facilitate communication between conventional  
744 science approaches to marine research and seasonal-cycle-based Indigenous Knowledge of  
745 marine ecosystems.

### 746 *5.3 Future directions and recommendations*

747           We have presented the first pan-Arctic review of baleen whale distribution, phenology,  
748 body condition and diet for populations that rely on arctic and subarctic habitats. Incorporating  
749 aspects of these data into ecosystem models at a regional scale is an essential step towards  
750 applying the sentinel capability these whales offer to improve our understanding of ocean



751 habitats (Moore and Gulland, 2014; Moore and Reeves, 2018). This capacity is germane not  
752 only to high latitude systems, but to all ocean regions. Notably, the Global Ocean Observing  
753 System (GOOS) is now advancing the goal of including data products from research on marine  
754 turtles, birds, and mammals as Essential Ocean Variables (EOVs) in the global system of ocean  
755 observatories (Miloslavich et al., 2018; [www.goosocean.org/eov](http://www.goosocean.org/eov)). Work on this goal is in the  
756 early stages, which makes this an opportune time to consider how research on baleen whales  
757 might contribute to this global ocean observation enterprise and inform future ecosystem models  
758 (Moore and Reeves, 2018).

759         There is no single path toward improving our capacity to integrate aspects of baleen  
760 ecology to ocean observatories, but a focus on attempting to do so for high northern latitude  
761 habitats may benefit from the very strong climate warming signal now evident there. In addition,  
762 there are comparatively long-term data on several species of baleen whales in each of the four  
763 ocean regions reviewed here. With those caveats in mind, we recommend four steps towards the  
764 goal of the routine integration of indices derived from baleen whale ecology in pan-Arctic ocean  
765 observatories: (1) routinely include visual and passive acoustic surveys for baleen whales in  
766 multidisciplinary ocean research enterprises, as done during development of the Distributed  
767 Biological Observatory in the Pacific Arctic sector (Moore and Grebmeier 2018) and the Joint  
768 Norwegian-Russian Ecosystem Survey in the Barents Sea (Michaelsen et al. 2013); (2) working  
769 with the IUCN Cetacean Specialist Group, the IWC Scientific Committee, NAMMCO,  
770 governmental agencies and other whale research and management organizations, promote the  
771 development of a common meta-data portal to collate extant information on baleen whale  
772 ecology and body condition for populations that depend on northern hemisphere polar habitats;  
773 (3) promote the inclusion of extant data on baleen whale ecology and body condition in next-

774 generation ecosystem models for each of the four ocean regions reviewed here; and (4) undertake  
775 an evaluation of how inclusion of parameters of baleen whale ecology have contributed to  
776 improved understanding of regional ecosystem dynamics.

777         Baleen whales are resilient species, capable of adapting to ecosystem shifts as well as  
778 recovering from the severe commercial hunting pressure of previous centuries. However, we are  
779 now in an age of rapid ecosystem alteration driven primarily by planetary warming. Including  
780 baleen whales in future assessments of marine ecosystems can provide information not only on  
781 their capacity to adapt, but also serve as a guide to ecosystem shifts that might otherwise go  
782 unnoticed. Given the pace of environmental change, it seems time we take better advantage of  
783 the capacity of whales and other upper trophic level species to tell us what is going on in their  
784 ocean world.

## 785 **AUTHOR CONTRIBUTIONS**

786 Moore and Haug conceived and outlined this review paper, and all authors contributed to the  
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1334 **FIGURE CAPTIONS**

1335 **Figure 1.** Regional maps depicting bathymetry and currents in the Northeast Atlantic (A: NEA,  
1336 Eriksen et al., 2017), Central North Atlantic (B: CNA, Víkingsson et al., 2015), Norwest Atlantic  
1337 (C: NWA, Curry et al., 2014) sub-regions, and the Pacific sector (D, Moore and Stabeno et al.,  
1338 2015).

1339 **Figure 2.** Schematic representation of fundamental differences in baleen whale fauna and  
1340 numbers between the Atlantic and Pacific sectors.

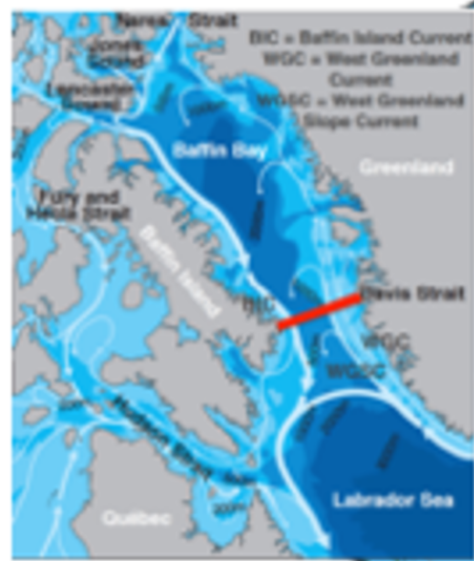
1341 **Figure 3.** Regional examples of baleen whale distribution showing species variability in the  
1342 Northeast Atlantic (A: NEA, Norwegian ecosystem survey, 2017), Central North Atlantic (B:  
1343 CNA, Pike et al., 2018), Northwest Atlantic (C: NWA, C, Lawson and Gosselin, 2018) sub-  
1344 regions, and the Pacific sector (D, Clarke et al., 2017).

1345 **Figure 4.** Photo examples of krill wash-ups on beaches near Point Barrow, Alaska (A, B), a  
1346 bowhead whale feeding assemblage (C) and a gray whale skim-feeding krill near Barrow (D),  
1347 September 2009.

1348 **Figure 5.** As upper-trophic level (UTL) predators, marine mammals can act as sentinels to  
1349 ecosystem alterations caused by climate change through shifts in habitat use (extrinsic responses)  
1350 and body condition (intrinsic responses); from Moore et al. (2018).

1351

1 C: NWA



1 B: CNA

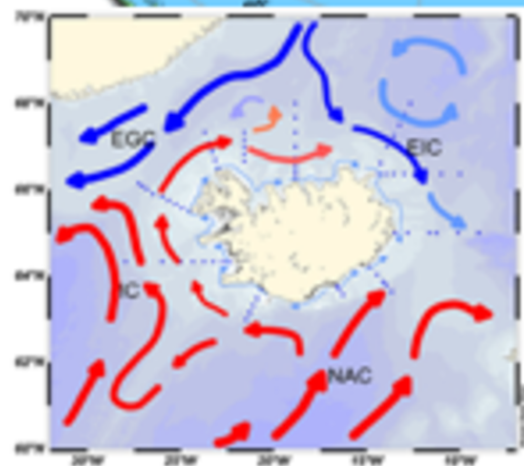
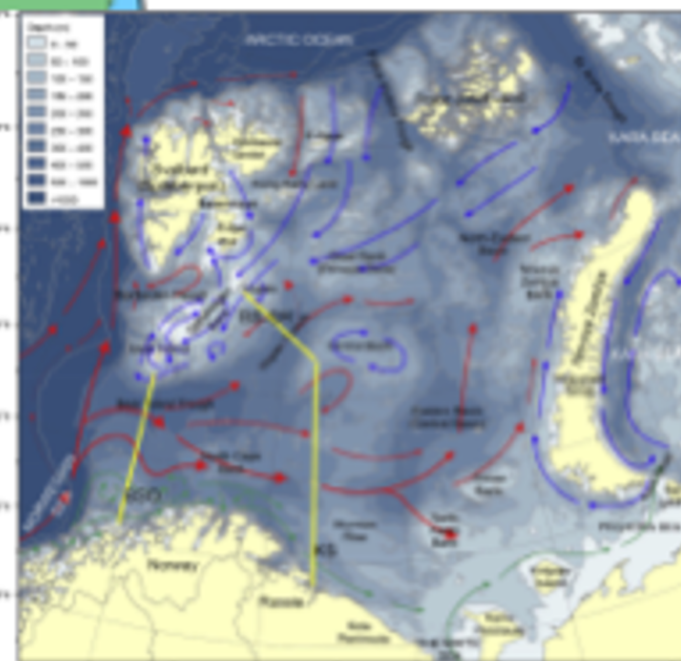


Figure 1



1 D: Pacific



1 A: NEA

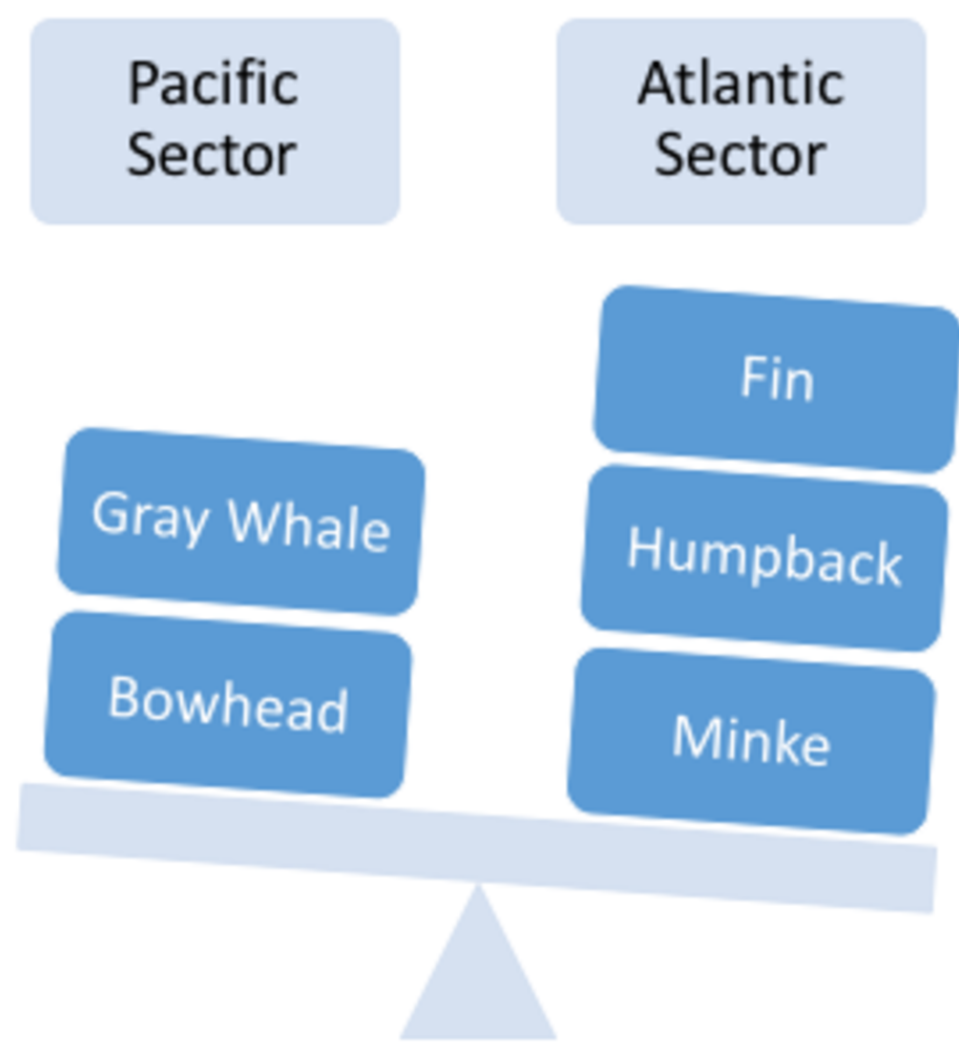


Figure 2

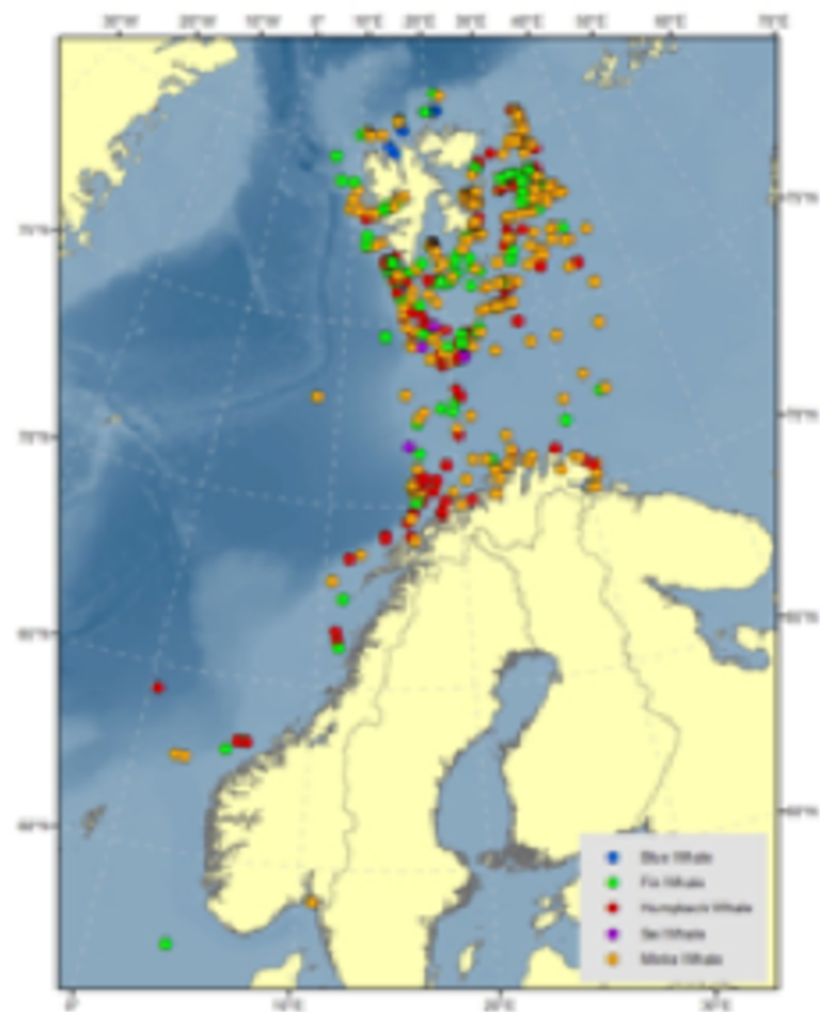


Figure 3A

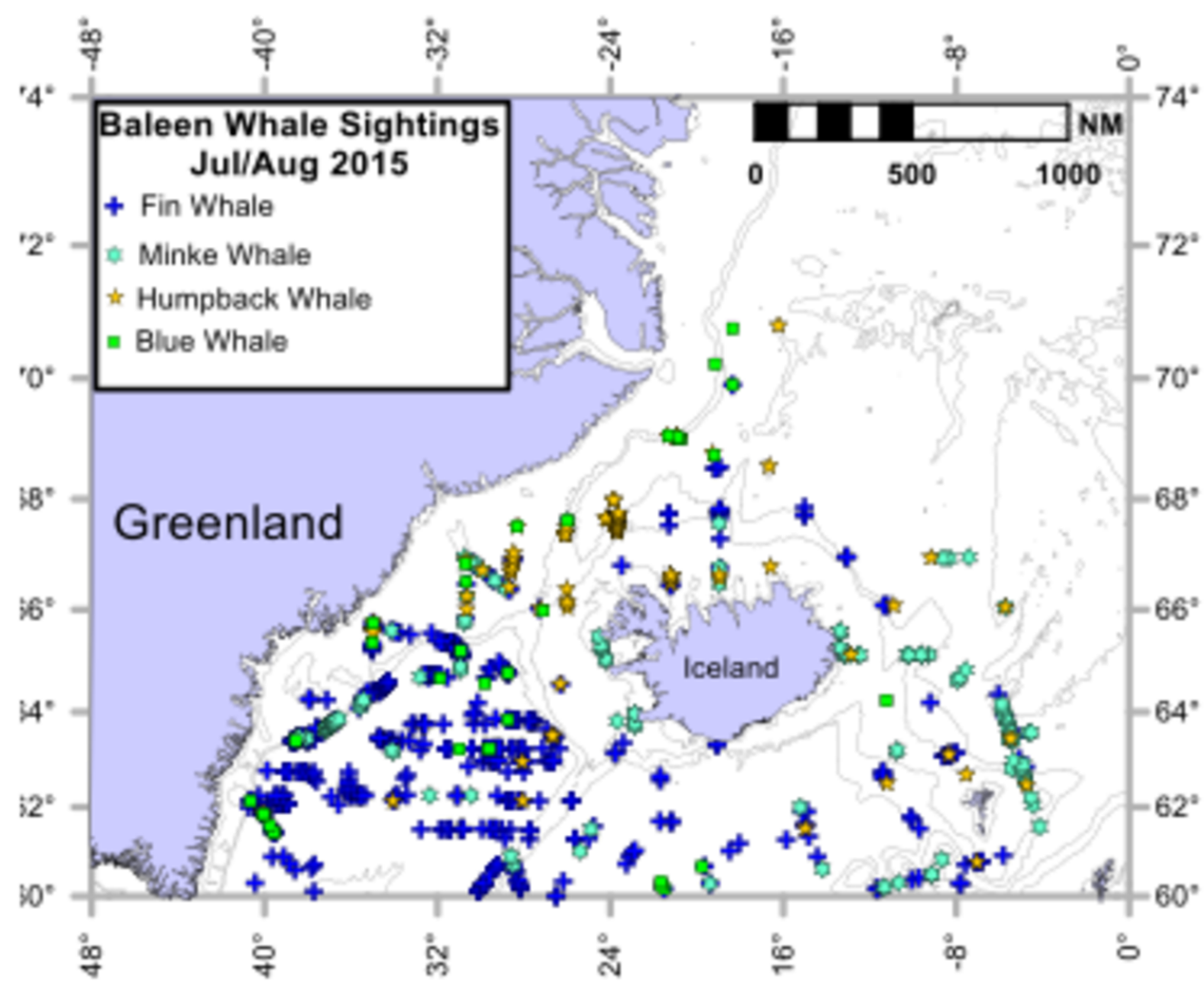


Figure 3B

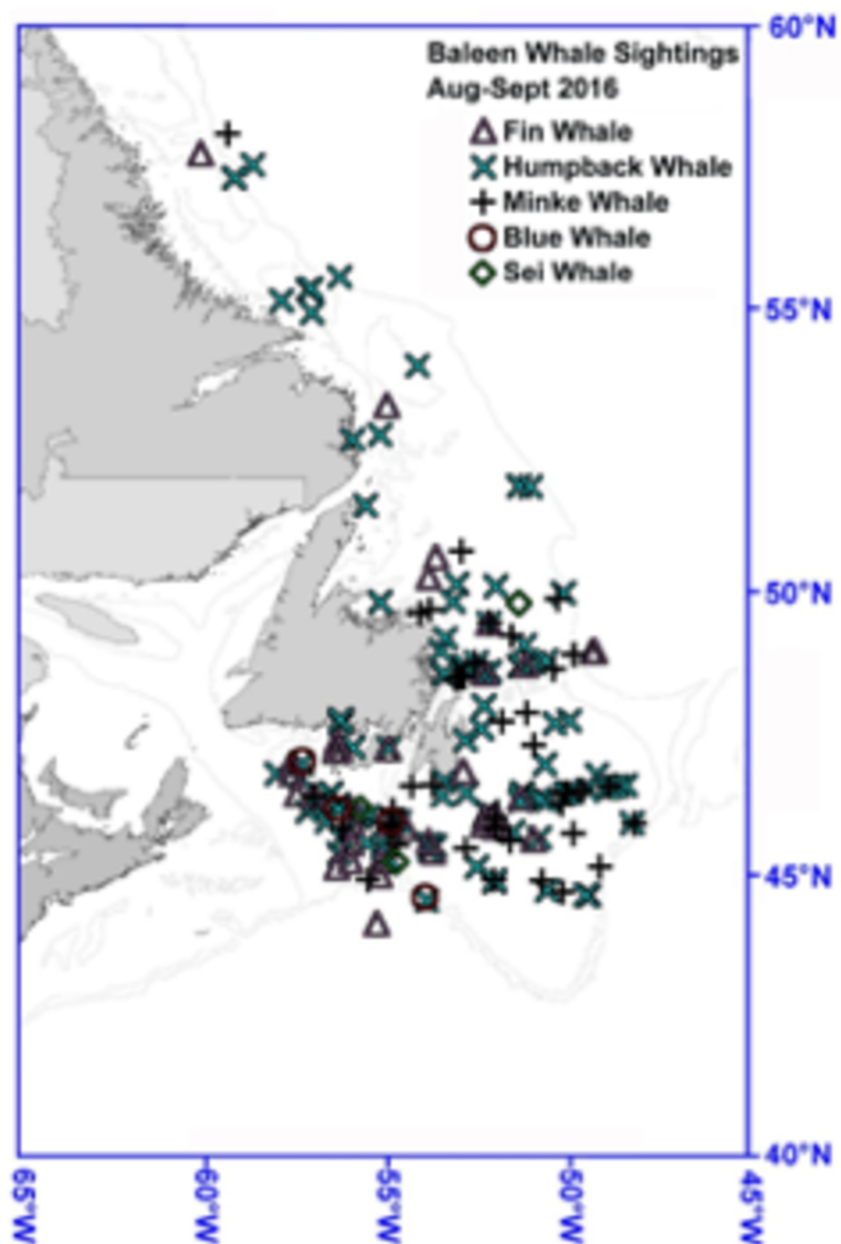


Figure 3C

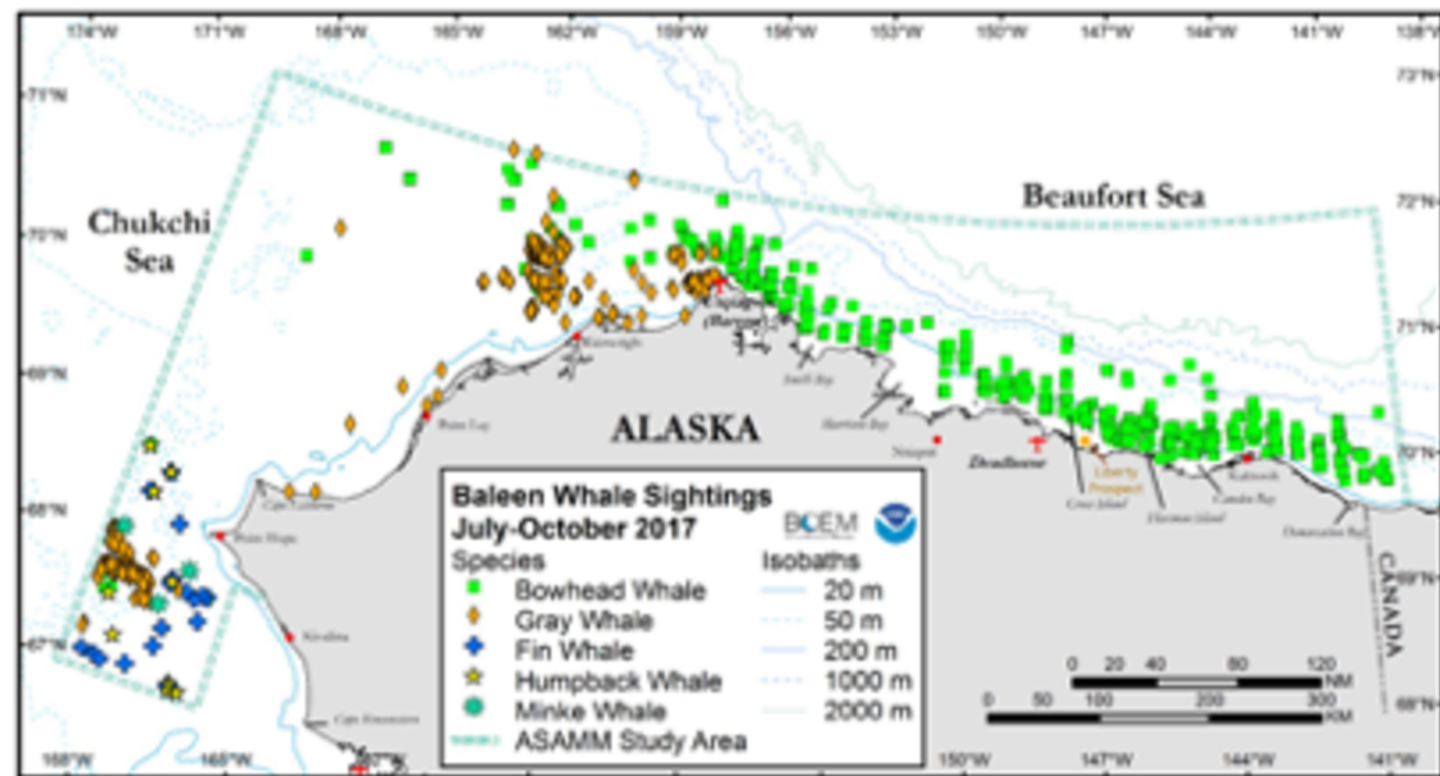


Figure 3D



Figure 4 A,B



Photo: NOAA/Marine Mammal Laboratory



Photo: Kate Stafford, UW/APL

**Figure 4 C,D**

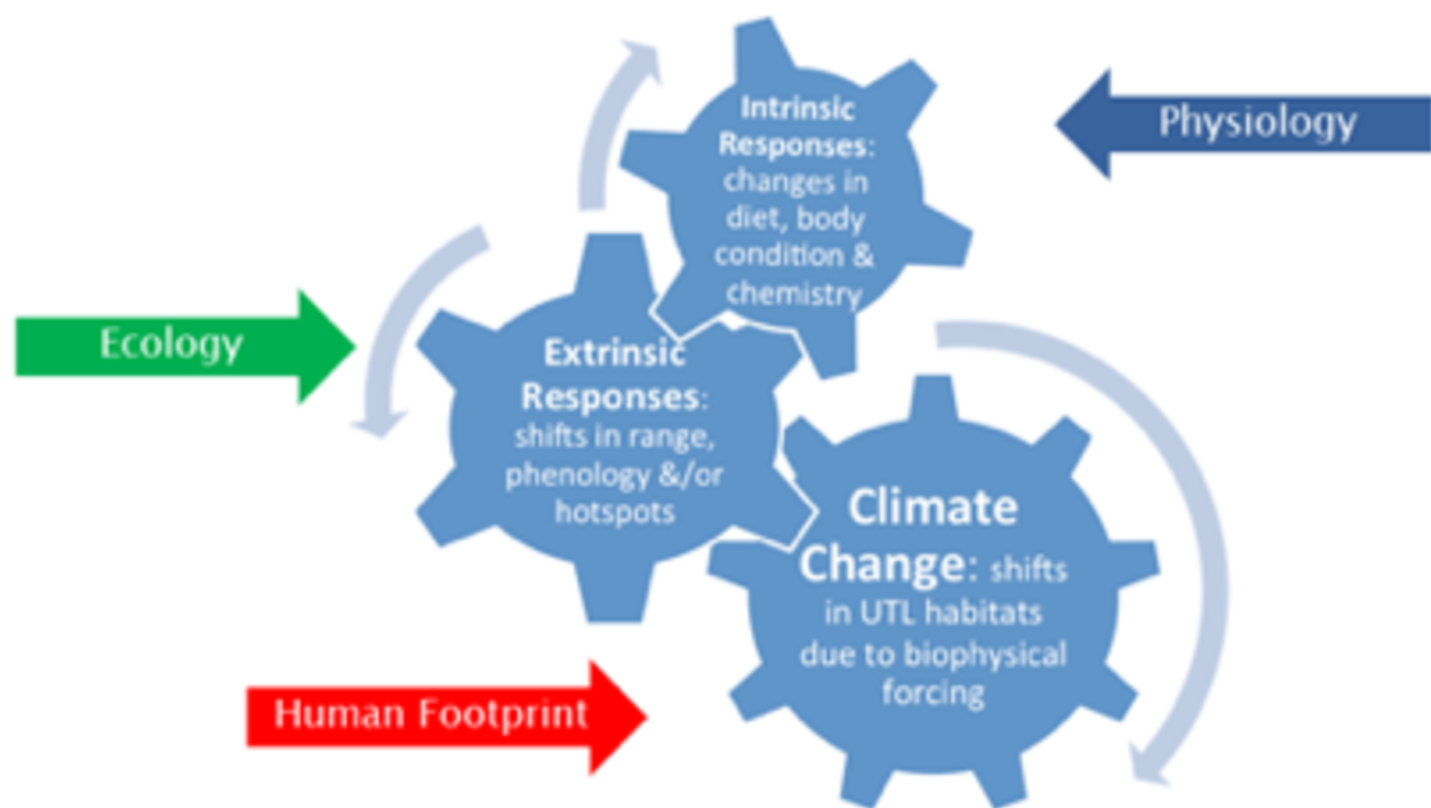


Figure 5



**Table 1**

Summary of reported changes in sea ice and measures of net primary productivity (NPP) in Atlantic and Pacific sectors of the Arctic. Laidre et al. (2015: fig. 3)<sup>1</sup> and Arrigo and van Dijken (2015; tables 1 & 2)<sup>2</sup>. Note different periods/reference; **bold** = statistically significant trend or % change.

Sub-region	Trend in ice-free season <sup>1</sup> (1979-2013)	Trend in maximum open water area (1998-2012) <sup>2</sup>	Mean NPP and ( % ) change (1998-2012) <sup>2</sup>
<b>NE Atlantic</b> Barents Sea	<b>&gt;20 days/decade</b>	+ 4062 km <sup>2</sup> /year	126.6 ( <b>28.3</b> )
<b>CN Atlantic</b> NE Greenland/Iceland	<b>+10-12 days/decade</b>	- 3455 km <sup>2</sup> /year	136.3 ( <b>-15.2</b> )
<b>NW Atlantic</b> Labrador Sea Baffin Bay	<b>+16-20 days/decade</b> <b>+10-12 days/decade</b>	+ 2733 km <sup>2</sup> /year	30.7 (8.3)
<b>Pacific</b> Chukchi Beaufort	<b>+ 13-15 days/decade</b> <b>+ 13-15 days/decade</b>	<b>+ 17,650 km<sup>2</sup>/year</b> <b>+ 30,264 km<sup>2</sup>/year</b>	32.1 ( <b>42.1</b> ) 34.0 ( <b>53.1</b> )

**Table 2.**

Population size estimates for baleen whales common to Atlantic and Pacific sub-arctic and arctic waters. Bowhead whales are endemic to arctic waters, all other species are seasonal migrants. Blue whales occur only in the Atlantic sector and gray whales only in the Pacific sector. In NWA: **WG** = West Greenland, **NF/L** = Newfoundland/Labrador, **GSL/SS** = Gulf of St. Lawrence/Scotian Shelf, **GB-HS** = Grand Banks to Hudson Strait. N/A = not available.

<b>Species</b>	<b>NE &amp; CN Atlantic</b>	<b>NW Atlantic</b>	<b>Pacific</b>
Bowhead whale	343 (CV = 0.488) <sup>1</sup>	6,446; CV=0.26 <sup>6</sup>	16,820 <sup>13</sup>  95% CI = 15,176-18,643
Common Minke whale	<b>NEA:</b> 89,623 (in 2008-2013) (CV = 0.18). Thereof <i>ca</i> 84,458 north of 60°N <sup>3</sup>  <b>CNA:</b> 42,515 (in 2015) 95% CI = 22,896-78,942, (CV = 0.31). Thereof, <i>ca</i> 37,443 north of 60°N. <sup>2</sup>	<b>WG:</b> 16,609 (in 2007) <sup>7</sup> 95% CI =7,172-38,461;  <b>WG:</b> 5,241 (in 2015) <sup>8</sup> 95% CI 2,114-12,992  <b>NF/L:</b> 13,008 (in 2016) CV=0.46 <sup>11</sup>	N/; 10s of whales <sup>14</sup>
Fin whale	<b>NEA:</b> 1,746 (in 2015); 95% CI = 859-3,552 <sup>4</sup>  <b>CNA::</b> 36,773 (in 2015) 95% CI 25,811-52,392733. Thereof <i>ca</i> 21,668 north of 60°N <sup>5</sup>	<b>WG:</b> 4,468 (in 2007) <sup>7</sup> 95%CI =1,343-14,871  <b>WG:</b> 465 (in 2015) <sup>8</sup> 95% CI = 233-929  <b>NF/L:</b> 2,177 (in 2016) (CV = 0.46) <sup>11</sup>	N/A; 10s of whales <sup>14</sup>

Humpback whale	<b>NEA:</b> 1,034 (in 2015) 95% CI = 487-2,194 <sup>4</sup>  <b>CNA:</b> 9,867 (in 2015) 95% CI 4,830-20,300.  Thereof <i>ca</i> 8,808 north of 60°N <sup>5</sup>	<b>WG:</b> 2,704, 95% CI=1,402-5,215 <sup>9</sup>  <b>WG:</b> 1,321, 95% CI= 578-3,022 <sup>8</sup>  <b>NF/L:</b> 8,439 (in 2016) (CV=0.49) <sup>11</sup>	N/A; 10s <sup>14</sup> of whales
Blue whale	<b>CNA:</b> 3,000 (In 2015)  95% CI 1,377-6,534 (cv 0.40) Thereof <i>ca</i> 2,456 north of 60°N <sup>5</sup>	<i>ca.</i> 250 <sup>10</sup>	
Gray whale			19,126, CV=0.07) <sup>15</sup>

<sup>1</sup> Vacquié-Garcia et al., 2017: estimate from survey of a portion of the Norwegian High Arctic.

<sup>2</sup> Pike 2018 (preliminary unpublished numbers)

<sup>3</sup> IWC 2016).

<sup>4</sup> Leonard and Øien, 2018 (preliminary unpublished numbers)

<sup>5</sup> Pike et al., 2018 (preliminary unpublished numbers)

<sup>6</sup> Doniol-Valcroze *et al.*, 2015b

<sup>7</sup> Heide-Jørgensen et al., 2010

<sup>8</sup> IWC, 2018

<sup>9</sup> Heide-Jørgensen and Laidre 2015

<sup>10</sup> Beauchamp et al., 2009

<sup>11</sup> Lawson and Gosselin, 2018

<sup>13</sup> Givens et al., 2016

<sup>14</sup> Brower et al., 2018

<sup>15</sup> Laake et al., 2012