Change in the Beaufort Sea ecosystem: Diverging trends in body condition and/or production in five marine vertebrate species

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Change in the Beaufort Sea ecosystem: Diverging trends in body condition and/or production in five marine vertebrate species

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ABSTRACT

Studies of the body condition of five marine vertebrate predators in the Beaufort Sea, conducted independently during the past 2–4 decades, suggest each has been affected by biophysical changes in the marine ecosystem. We summarize a temporal trend of increasing body condition in two species (bowhead whale subadults, Arctic char), in both cases influenced by the extent and persistence of annual sea ice. Three other species (ringed seal, beluga, black guillemot chicks), consumers with a dietary preference for Arctic cod, experienced declines in condition, growth and/or production during the same time period. The proximate causes of these observed changes remain unknown, but may reflect an upward trend in secondary productivity, and a concurrent downward trend in the availability of forage fishes, such as the preferred Arctic cod. To further our understanding of these apparent ecosystem shifts, we urge the use of multiple marine vertebrate species in the design of biophysical sampling studies to identify causes of these changes. Continued long-term, standardized monitoring of vertebrate body condition should be paired with concurrent direct (stomach contents) or indirect (isotopes, fatty acids) monitoring of diet, detailed study of movements and seasonal ranges to establish and refine baselines, and identification of critical habitats of the marine vertebrates being monitored. This would be coordinated with biophysical and oceanographic sampling, at spatial and temporal scales, and geographic locations, that are relevant to the home range, critical habitats and prey of the vertebrate indicator species showing changes in condition and related parameters.

1. Introduction

Marine fish, seabirds and mammals provide a means to examine shifts in marine ecosystems from the top down, being tractable links to oceanography and acting as 'sentinels' of marine ecosystems through their responses to environmental variability (Moore et al., 2014). In turn, studies monitoring changes in biophysical parameters of the marine ecosystem can identify the proximate causal factors and possibly predict the magnitude and direction of changes being measured in these marine vertebrates. As long-lived predators, marine mammals and birds are particularly useful indicators of the state of the ecosystem (Montevecchi and Myers, 1996; Boyd, 2002; Moore, 2008; Gunnlaugsson et al., 2013; Williams et al., 2013), because they provide evidence of changes to the food web and trophic structure of the ecosystem accumulated throughout their longer lifespans. In this paper, we summarize and compare emerging trends in body condition and related biological parameters in five marine vertebrate predators (bowhead whale, *Balaena mysticetus*; Arctic char, *Salvelinus alpinus*; ringed seal, *Pusa hispida*; beluga whale, *Delphinapterus leucas*; black guillemot, *Cepphus grylle*) in the Beaufort Sea (Fig. 1). Our objective is to provide a multi-species synthesis which can be used to inform the design of future studies to interpret factors influencing ecosystem shifts, specifically those which are linked to changing sea ice and climate (Tynan and DeMaster, 1997; Melling et al., 2005; Serreze et al., 2007; Comiso et al., 2008; Walsh, 2008; Tivy et al., 2011).

Marine vertebrates respond to ecosystem variability both intrinsically (body condition, reproduction, health) or extrinsically through shifts in their prey choices and their distribution (Moore et al., 2014; Moore and Gulland, 2014). Changes in body condition influence reproduction, growth rates and survival of individuals

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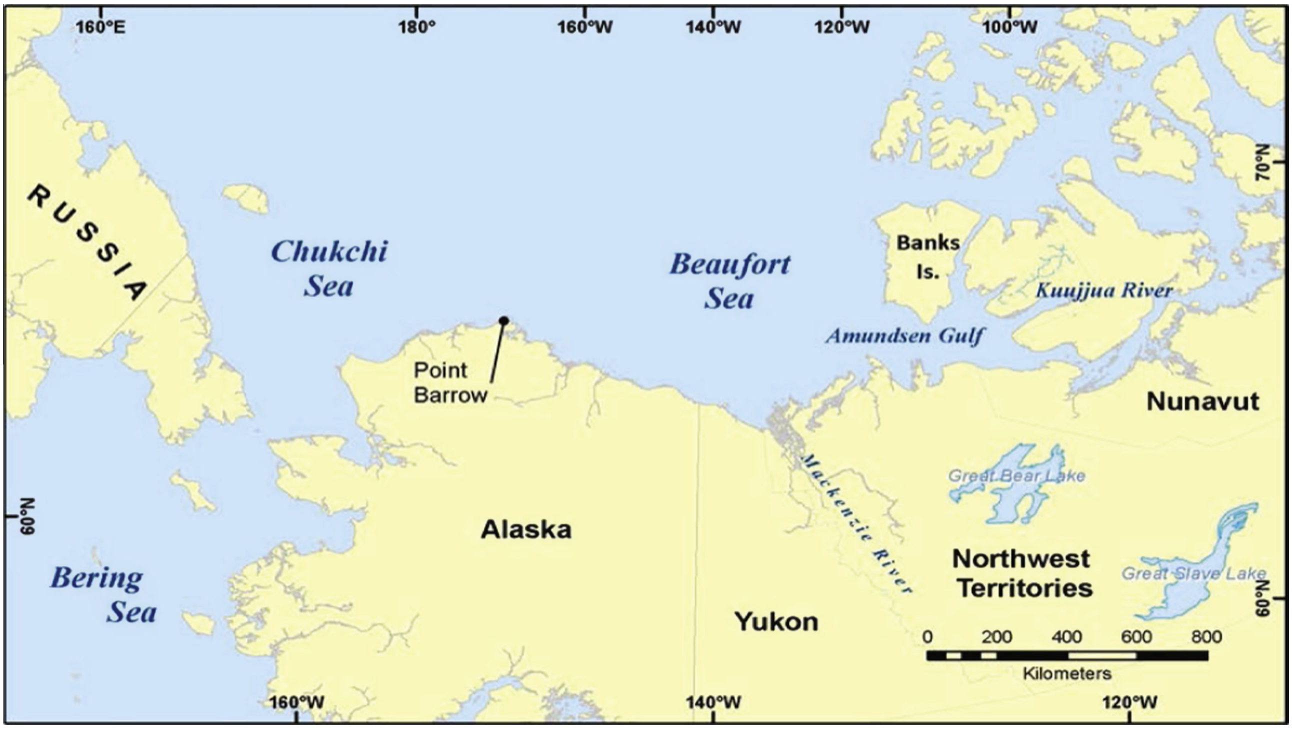

Fig. 1. Study area and locations mentioned in text. Cooper Island is 40 km southeast of Point Barrow.

(i.e., fin whales, Williams et al., 2013; gray whales, Moore, 2008; ringed seals, Smith, 1987; Harwood et al., 2012a; bowhead whales, George et al., this issue; black guillemots, Divoky et al., this issue). Among other factors, the body condition of marine vertebrates is directly linked to the total annual availability and quality of their prey, with nutritional stress ultimately linked to health of individuals and populations (Moore and Gulland, 2014).

Herein we provide a compendium of observed trends in condition and/or production of several marine species during a span of two or more decades, to deliver a multi-species evaluation of the utility of assessing environmental variability. We follow with examples of coordinated monitoring and biophysical sampling, and recommendations for future studies using current technologies. We discuss the importance of continued monitoring of body condition, collaboration among disciplines, and alignment of ecological and biophysical sampling scales, to improve linkages between body condition and ecosystem shifts. We also suggest alternative approaches, which would be the method of choice in situations where in situ biophysical sampling is not feasible.

2. Observed trends in body condition of five marine vertebrates in the Beaufort Sea and Amundsen Gulf

Long-term monitoring of harvested specimens, dating back in some cases to the 1970s, revealed changes in body condition in various marine vertebrates of the Beaufort Sea and Amundsen Gulf (Table 1). Since the 1990s, some monitored species have shown a trend of increasing body condition and related parameters, while others have shown the opposite, with declining body condition, growth rates and/or production (details and references, see Table 1). By studying species that are specialists at various trophic levels, we can take advantage of their ability to locate dense patches of marine resources and zones of high productivity (e.g., Kuletz et al., this issue; Citta et al., this issue).

2.1. Bowhead whale

George et al. (this issue) examined the effects of summer sea ice conditions and upwelling-favorable wind in the Beaufort Sea on the body condition of Bering-Chukchi-Beaufort (BCB) Sea bowhead whales. Using a subset of a long-term (40-year) dataset collected from whales harvested by the Inupiat, they determined that the strongest seasonal differences in body condition occurred in the subadult bowhead whales. Subadult bowheads, the most sensitive age class to environmental change, showed a detectable response, with a significant temporal trend of increasing body condition between 1989 and 2011 (Fig. 2).

The increase in subadult condition has been associated with an overall reduction of summer sea ice extent, including increased duration of open water, changes in upwelling potential (wind stress), and possibly higher primary production in the marine ecosystem favouring herbivorous zooplankters that are targeted by bowheads (LGL, 1988; Lowry et al., 1978; Walkusz et al., 2012). Significant correlations between body condition, and both upwelling favorable winds and late summer open water fraction, were found for the eastern Beaufort Sea as well as off the Mackenzie Delta and the west coast of Banks Island (George et al., this issue). Climate change models are consistent with observations to date, having predicted accelerated break-up of the fast ice in spring, longer open water periods, enhanced upwelling of nutrients along the Beaufort slope, and increases in pelagic primary productivity followed by enhanced production up the food chain (Carmack and Wassmann, 2006; Wu et al., 2007; Barber et al., 2008; Lavoie et al., 2010). Also, Moore and Laidre (2006) provided an analysis of trends in sea ice cover at local scales within the range of BCB bowhead whales, in an attempt to describe how this environmental feature has changed in feeding and migration areas. Their conceptual model also suggests that reductions in sea ice cover will increase prey availability for bowheads, by both secondary production and advective processes.

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Table 1
Observed trends in body condition and/or production that have been revealed through long-term monitoring and recorded for five species of marine vertebrates in the Beaufort Sea region.

Species, stock	Changes in body condition and/or production that have been observed to date	Direction of change, trend	Main prey	Monitoring time frame during which change was detected	Trend relevant to what feeding season	Trend relevant to what feeding location	References
Bowhead Whale, Bering, Beaufort, Chukchi	(1) Increased stock size and increased numbers using offshore Beaufort Sea for summer feeding, (2) arrive earlier to Beaufort in August, (3) increased body condition in subadults, and (4) increased abundance of calves	Temporal increase, moderated by ice conditions	Zooplankton (copepods, amphipods)	1980–1986 vs. 2007–2010 for (1), (2) and (4); 1989–2011 for (3)	August–September	Beaufort Sea, Amundsen Gulf	Harwood et al. (2010), Clarke et al. (2013, 2014), George et al. (this issue), and Givens et al. (2013)
Arctic char, Kuujjua River	(1) Enhanced somatic condition and fitness in years when spring break up is early; (2) overall trend toward increasing growth rates over time, and (3) local reports of increased size of fish and increased abundance of fish	Temporal increases, moderated by ice conditions	Forage fish (arctic cod, capelin, sand lance) and zooplankton	1991–2009	July–August	Amundsen Gulf east (nearshore waters)	Harwood et al. (2013); and local observations (J. Alikamik, pers. comm.)
Ringed seal, Western Arctic, Amundsen Gulf	(1) Temporal decline in body condition, adults and subadults; (2) decreased body condition and reproduction in years with late break up of the sea ice in spring; vice versa in years with early break up	Temporal decreases, moderated by ice conditions	Arctic cod main winter prey; zooplankton opportunistically, esp. in open water	1971–1979 and 1992–2014	Winter and spring	Amundsen Gulf east and west Prince Albert Sound	Smith (1987) and Harwood et al. (2012a)
Beluga Whale, Beaufort Sea	Weak, temporal decline in size-at-age beginning 2000 (growth rate)	Temporal decrease	Mainly arctic cod; other forage fishes, squid, char	1980–2009	Lifetime	Bering, Chukchi, Beaufort Seas	Harwood et al. (2014) and Ulukhaktok HTC (unpubl. data)
Black Guillemot, Cooper Island Alaska	Decrease in Arctic cod in the chicks' diet resulted in (1) lower growth rates, (2) decreased fledging weights and (3) increased nestling mortality when 1975–1984 compared with 2003–2012	Temporal decrease, moderated by ice conditions	Arctic cod-shifts to provisioning chicks with demersal prey in July	1975–2012	July	20 km radius of Cooper Island, Western Beaufort Seas	Divoky et al. (this issue)

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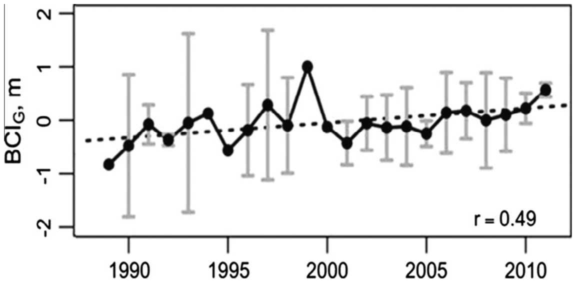

Fig. 2. Trend in BCI (body condition index based on axillary girth only) for fall subadult bowhead whales (1989–2011, $n = 100$). Data point for each year is the mean for all whales landed for that given fall season. Error bars represent the 95% confidence interval for the whales sampled that year (adapted from George et al. (this issue)).

Possibly related to increased body condition, George et al. (this issue) also noted that the size of BCB bowhead population has increased in the last decade (Givens et al., 2013). They speculated that an increase in marine production might improve rates of survival and reproduction, because body condition of adult females may be increasing. The apparent increase in BCB bowhead whale population size corresponds to observed changes in migration phenology and productivity. First, observations made during the spring ice-based bowhead whale census at Barrow, indicate bowheads are initiating spring migration earlier than 30 years ago (George et al., 2013). Earlier arrival times have also been observed in the Canadian Beaufort Sea (Harwood et al., 2010). Calving rates in the western Beaufort Sea appear to have recently increased, with the ratio of calves to total number of bowheads higher in 2012–2013 surveys than in the preceding 30 years (Clarke et al., 2013, 2014). Collectively, these observations suggest that the bowhead whale population has undergone a degree of improved fitness and productivity in recent years; however, George et al. (2013) caution that future trajectories for bowhead population size and body condition are uncertain.

2.2. Arctic char

In the western Arctic, anadromous Arctic char of the Kuujjua River stock have been the subject of a long-term (1992–present), harvest-based monitoring study at Tatik Lake, Victoria Island, NT (Harwood et al., 2013). Anadromous Arctic char migrate to the ocean in summer, where they access rich marine resources for 2–3 months (Dempson and Kristofferson, 1987), building condition before migrating upstream to lakes for overwintering (Johnson, 1980; Boivin and Power, 1990; Gyselman, 1994). With two decades of fall sampling conducted at the same location and time of year, soon after the fish returned from summer feeding, annual measures of char condition reflect the annual quality/quantity of marine prey available in nearshore waters of the eastern Amundsen Gulf (Harwood et al., 2013).

Harwood et al. (2013) reported that mean annual condition indices of the char were variable among the years of study, with annual condition indices being significantly correlated with timing of sea ice retreat in spring (Fig. 3). Earlier retreat of the fast ice in spring was linked with increased char condition, while late retreat was linked with poor condition (Table 1, Harwood et al., 2013). Observations of local fishers, and long-term, standardized measures of fish size and catch-per-unit-effort also show that the char have increasing growth rates, are becoming larger, and are more abundant than a decade ago (Knopp, 2010; Harwood et al., 2013). Similar to the BCB bowhead whales, the Kuujjua River Arctic char stock appears to be gaining some degree of improved fitness related to changes in environmental productivity and sea ice, although subject to annual variation. For example, in recent years, there has been a noticeable reduction in the number of younger, smaller Arctic char in the community's late summer subsistence fishery (H. Wright, Ulukhaktok, NT, personal communication, 2014), and future trajectories for stock size and fitness are uncertain.

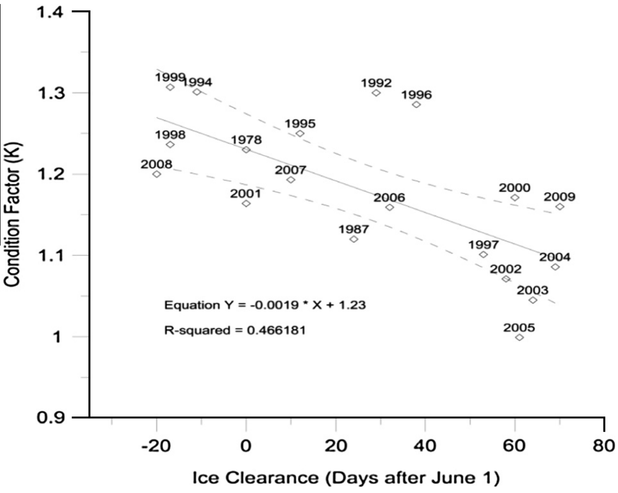

Fig. 3. Scatterplot of ice clearance date in East Amundsen Gulf and condition factor of Arctic Char caught in the under-ice subsistence fishery at Tatik Lake, 1987 and 1989 (data for 1978 and 1987 from Lewis et al. (1989)) and 1992–2009 (this study) (adapted from Harwood et al. (2013)).

The annual development of fast ice, and the timing of ice retreat in spring are driven by meteorological events that vary in intensity and timing from year to year. They reflect oceanographic and atmospheric conditions, and collectively, influence the strength and persistence of the plankton bloom in spring (Wu et al., 2007; Brown and Belt, 2012). From 1970 to 2010, there has been an overall trend toward earlier retreat of sea ice in spring, 7.4 days per decade in east Amundsen Gulf, statistically significant at the 90% level (Harwood et al., 2012a). Early retreat of sea ice promotes the growth of pelagic plankton communities, which in Amundsen Gulf in 2008, showed an 80% increase in primary production compared to the average ice year in 2004 (review in Barber et al., 2008; Forest et al., 2011; Sallon et al., 2011).

There is a paucity of data about the marine prey available to and selected by Kuujjua char in summer in nearshore eastern Amundsen Gulf. The only scientific collection of Arctic char stomach contents from this area was done in July–August 1977 and 1978 ($n = 220$, authors unpublished data), where Arctic cod (*Boregadus saida*) predominated (91% by weight, $n = 220$ stomachs), along with 9% mysids (*Mysis oculata*) and amphipods (*Onisimus glacialis*). In 2013 and 2014, subsistence fishers (John Alikamik, personal communication, 2014) report summering Kuujjua River Arctic char with stomach contents consisting mainly of sand lance (*Ammodytes* spp.), and reported to us that Arctic cod were now 'scarce' in the nearshore areas during spring and summer. This may reflect annual differences or a shift in the Arctic char's prey choice or availability from Arctic cod/invertebrates in the 1970s, to forage fish such as sand lance or capelin (*Mallotus villosus*) in recent years. Similar shifts in diet have been observed in Arctic char stocks in other areas, such as Northern Labrador (Dempson et al., 2002).

Studies are now becoming available that address Arctic cod distribution, abundance and life history in the Beaufort (Logerwell et al., this issue; Walkusz et al., 2013), but these have limited capacity to detect or assess temporal or annual ecosystem change as it relates to the vast, distant and variable habitats used by Arctic

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cod annually and over their life cycle. In eastern Amundsen Gulf, environmental change may be facilitating an influx of different forage fishes, as has been documented in the North Atlantic following the collapse of the Atlantic cod stocks (Frank et al., 2011). This is now occurring in Cumberland Sound, where Arctic Char have shifted from an invertebrate-based diet to capelin (Imrie and Tallman, 2013). Capelin is an important summer prey of Arctic char in nearshore marine areas of Amundsen Gulf, only 300 km to the southwest of the Kuujjua River (Harwood and Babaluk, 2014). In August 2014, sand lance was the prey of choice of Arctic char sampled in eastern Amundsen Gulf, sampled coincidently with unprecedented numbers of beluga whales (*Delphinapterus leucas*) which had entered the nearshore areas (John Alikamik, personal communication, 2014) and were also purported to have been feeding on sand lance.

2.3. Ringed seal

Ringed seal adults and subadults in eastern Amundsen Gulf exhibited a significant, sustained temporal decline in spring body condition that was measured over two decades, based on samples from a single location and collected by a single monitor (1992–2011, $n \geqslant 2300$; Table 1; Fig. 4; Harwood et al., 2012a). These results from eastern Amundsen Gulf suggested there has been a shift in the quality, quantity and/or distribution of the seal's main prey, Arctic cod (Smith, 1987; Smith and Harwood, 2001). Further, it was found that ovulation failed and reproduction was reduced in years with particularly late retreat of the sea ice in spring (1974, 2005) (Smith, 1987; Harwood et al., 2012a). Extreme ice years coincided with the years of poorest seal condition, also in 1974 and 2005 (Smith, 1987; Harwood et al., 2012a). The year 2005 was also the year with the lowest somatic condition in Arctic char (Harwood et al., 2013), thinnest blubber measured in belugas (Harwood et al., 2014), and when there was nutritional stress (Stirling et al., 2008) and a 25–50% decline in abundance in the Beaufort Sea polar bear population (Bromaghin et al., 2015).

The samples that were used to examine ringed seal body condition in eastern Amundsen Gulf were collected during the months of June and July, so variation in seal condition reflects the quality/quantity and/or availability of prey during the preceding winter and spring. The results of a concurrent satellite tagging study (Harwood et al., 2015) revealed that seals in this area forage in winter habitats that are located mainly in eastern Amundsen Gulf and western Prince Albert Sound. From spatial and temporal linkages between these two studies we can infer that changes may be occurring in the winter and spring prey base of ringed seals in eastern Amundsen Gulf and west Prince Albert Sound (Harwood et al., 2012a).

The consequences of this downturn in condition, and fluctuations in productivity associated with ice conditions, could be far-reaching for the eastern Beaufort/Amundsen ecosystem. In 2012, 2013 and 2014, the proportion of ringed seal pups in the summer harvests were among the lowest measured since the start of the study in 1992, and coincident with failed (2012) and low (2013, 2014) ovulation rates during the same years (L. Harwood, unpublished data). This may be related to declining body condition that has been observed since 1994. Monitoring is expected to continue, and is being augmented with studies of diet (FJMC, 2014). We note that a ringed seal monitoring study in the Chukchi Sea found evidence of a contemporary dietary shift in ringed seals, but report that the prey changes did not appear to have had a detectable influence on condition, growth or production of seals in that particular region (Crawford et al., this issue).

Temporary declines in seal productivity in the southeast Beaufort Sea have been documented in the past, coincidentally with declines in body condition and reproductive output of polar bears in the 1970s (Kingsley, 1979; Stirling, 2002). In 2004–2006, the underlying causes of observed changes in polar bear body condition and foraging behavior were unknown, but the most likely explanation was major changes in the sea ice and marine environment (Stirling et al., 2008). Linkages to downturns in the seal population were also suggested as a possible explanation.

2.4. Beluga whale

There has been a subtle but sustained decline in the growth rate of adult beluga whales in the southeastern Beaufort Sea, beginning in 1994 (Harwood et al., 2014). Whales were sampled over a 21-year period (1988–2008), as part of a standardized, long-term monitoring effort involving subsistence-harvested belugas ($n = 1059$; Fig. 5). Sampling took place in July, the main time of the annual harvest and immediately following the beluga's arrival from wintering areas in the Bering Sea and spring migration through the Chukchi Sea and western Beaufort Sea.

The vast annual range occupied annually by Beaufort Sea belugas includes the Bering, Chukchi and Beaufort Seas, and beyond, and is gradually becoming understood through satellite telemetry (Richard et al., 2001; Hauser et al., 2014). While they do not appear to feed extensively when in the Mackenzie River estuary (Day, 2002; Harwood et al., 2002), they feed during spring migration through the western Beaufort Sea (Quakenbush et al., in press), in east Amundsen Gulf (John Alikamik, Ulukhaktok, NT, personal

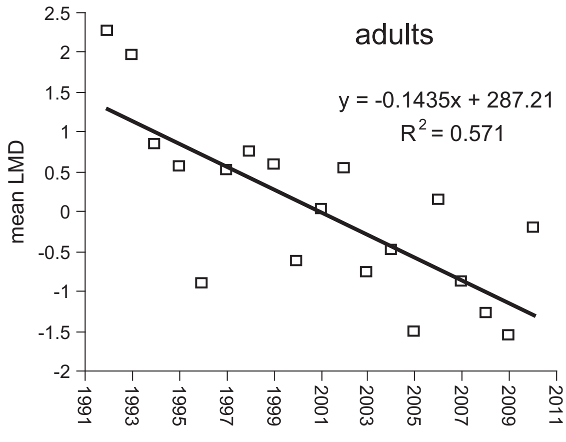

Fig. 4. Temporal trend in mean annual body condition indices of adult ringed seals sampled near Ulukhaktok, NT, June–July, 1992–2010 (adapted from Harwood et al. (2012a)).

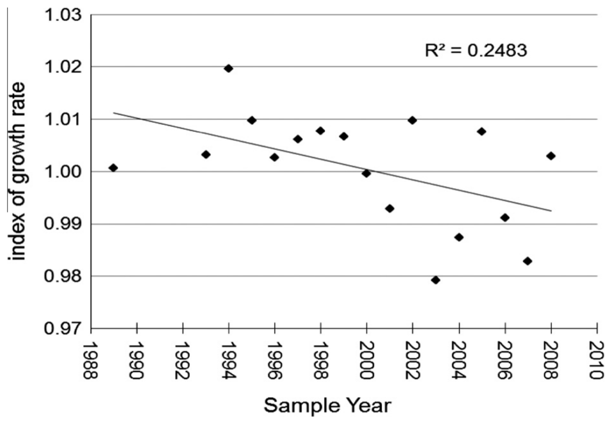

Fig. 5. Temporal trend in size-at-age (growth rate) of belugas landed in Delta and Paulatuk subsistence harvests, 1989, and 1993–2008 (adapted from Harwood et al. (2014)).

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communication, 2014), and offshore of the Tuktoyaktuk Peninsula in fall (Orr and Harwood, 1998), where Arctic cod, sand lance and Arctic cisco (*Coregonus autumnalis*) respectively, predominated in the stomach contents examined. Further sampling and measuring of harvested belugas, in conjunction with isotopic and fatty acid profiling, are needed to substantiate the observed declines in growth rate, and to determine the causative factors. A concurrent decline in the mercury concentrations in the liver of the harvested belugas in the last decade (Loseto et al., 2015) also provides evidence to corroborate that there have been dietary shifts.

2.5. Black guillemot

The black guillemot has been the subject of an ongoing monitoring study since 1975 on Cooper Island in the Alaskan Beaufort Sea. Like belugas and ringed seals, guillemots focus their foraging efforts on Arctic cod. During the nesting season, parents provisioning their chicks fly up to 20 km from the island to find prey for their young, and from 1975 to 2002, Arctic cod were the primary prey items returned to the nestlings. Beginning in 2003, however, near-shore demersal fish, such as four-horned sculpin (*Myoxocephalus quadricornis*), began to comprise a larger portion of the diet coincident with decreasing sea ice and increasing sea surface temperatures (SST) in the waters directly north of the island (Divoky et al., this issue).

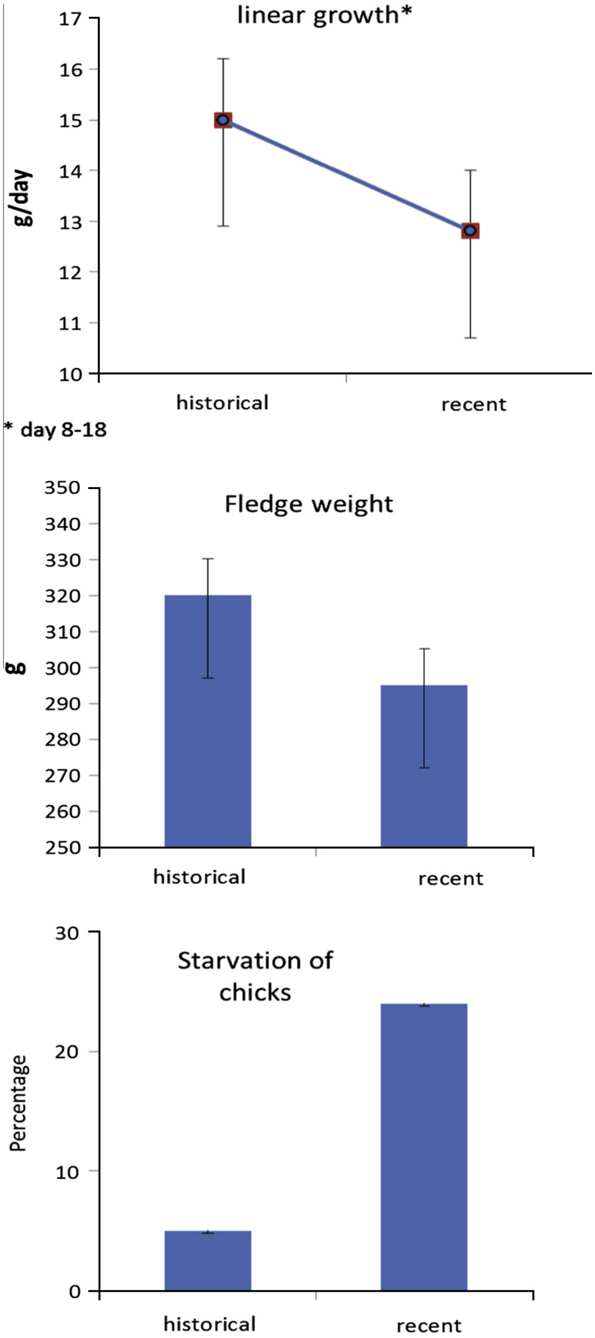

Fig. 6. Black guillemot chick condition for historical (1976–1984) and recent (2003–2012) (adapted from Divoky et al. (this issue)).

A comparison of the first decade of the study (1975–1984) with a recent decade (2003–2012) found that the decrease in Arctic cod in the chicks' diet was linked with lower growth rates in the chicks, decreased fledging weights and increased nestling mortality. Analysis of annual oceanographic conditions north of the colony from 1975 to 2012, for the time of year when parents provision their young (mid-July to early September), revealed no major regime shifts in ice or SST until the early 2000s (Divoky et al., this issue). While Arctic cod comprised over 95% of the prey provided to nestlings in 1975–1984, in 2003–2012, 80% of the years had seasonal decreases, and frequent disappearance, of Arctic cod from the diet of nestlings. Nearshore demersals comprised the majority of the diet in recent years, and associated with this shift from Arctic cod, were reductions in nestling growth and fledging mass. Nestling starvation rates were five times higher (Fig. 6). Adult survival during the nonbreeding season (September–May) showed no significant difference between the historical and recent periods, suggesting no major change in the availability of Arctic cod or other forage fishes at the ice edge in the Beaufort, Chukchi and Bering seas. These findings of a substantial decrease in Arctic cod availability in response to decreased ice extent and increasing SST near the colony have implications for the entire Arctic, given the ongoing and predicted basin-wide reductions in sea ice.

In the Canadian Beaufort Sea, there is also a small colony of black guillemots which nest at Herschel Island offshore of the Yukon coast. This colony has been monitored since the mid-1980s, with Arctic cod also being the preferred prey of Herschel Island guillemots. The 2014 nesting season was the poorest since 2004, with adults provisioning chicks mainly with small sculpins (*Myoxocephalus* sp.), a bony fish that is difficult for the guillemot chicks to swallow (Cameron Eckert, Yukon Territorial Government, personal communication, 2014). In 2014, there were increases in the number of failed nests, and clutch sizes were smaller and there were fewer surviving chicks than in previous years of the study.

3. How can increasing or decreasing trends in body condition in marine vertebrates inform and direct biophysical sampling in the Beaufort Sea?

In Section 2, we summarize incidences of increasing body condition in two species (bowhead whale subadults, Arctic Char), and an opposing trend in the corresponding period in condition, growth and/or production in three other species (ringed seals, belugas, black guillemot chicks). The proximate causes of these apparent shifts remain unknown, but may be a reflection of a trend of increasing secondary productivity and a downward trend in the availability of forage fishes such as Arctic cod. The apparent changes in the prey bases appear to be having cascading effects on a range of species, which has also been documented for other marine vertebrates in other ecosystems (Fauchald, 2009; Furness and Camphuysen, 1997; Montevecchi and Myers, 1996; Kowalczyk et al., 2014; Frank et al., 2011; Gavrilchuk et al., 2014).

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Trends in body condition of marine vertebrates can inform and direct biophysical sampling in the Beaufort Sea. The great advantage of using marine vertebrate species to direct biophysical sampling efforts is that they are specialists in feeding at various trophic levels, having the ability to locate and feed on dense patches of marine resources. Once the range, critical habitats, and main prey types of these key species are identified, biophysical sampling can be designed to obtain an understanding of the oceanographic features which influence the distribution and abundance of their prey. To date, attempts to understand species responses have often been constrained by a lack of comparability in the spatial and temporal sampling regimes used to study the species, and those used to describe the critical habitats and resources upon which they depend (Moore and Laidre, 2006).

Continuation of monitoring is essential. There have been at least two decades of monitoring for each of the species reviewed in Section 2, and in some cases four, providing a robust database against which trends in body condition and productivity can be continually evaluated in the years ahead. It is fundamental for the continued success of studies of this type to be standardized, long-term and well-funded (Bell and Harwood, 2012), and ensure statistical power through adequate sample size (VanGerwen-Toyne et al., 2014). For the five species reviewed here, there are varying amounts of published literature available regarding important feeding areas, times and preferred prey choices. The location and timing of their movements have been obtained through telemetry, passive acoustics and visual surveys, but interannual variability is poorly understood. Incomplete information is largely due to the cost and logistical challenges of conducting such studies at intervals and frequencies where year-to-year variation can be assessed.

3.1. Biophysical sampling in localized and/or nearshore feeding areas: When sampling in situ is practical

Ship-based oceanographic studies of zooplankton have long confirmed the aggregated distribution of forage fish and zooplankton (LGL, 1988). Aggregations have been related to biophysical parameters such as bottom topography, currents (upwelling) and other features promoting dense prey occurrence, such as was done for bowhead whale feeding patches (Walkusz et al., 2012).

Bowhead whales use a range of nearshore and offshore feeding areas in the Beaufort Sea and Amundsen Gulf in summer (ADFG, 2014; Citta et al., this issue). Sampling lower trophic levels, and the oceanographic features which influence their distribution and abundance concurrently within the vast, remote and numerous feeding areas (ADFG, 2014; Citta et al., this issue) would not be practical. However, it is possible to sample within specific patches or aggregation areas used regularly by feeding bowhead whales in the Beaufort Sea. There are two examples of multi-disciplinary studies of prey and BCB bowhead whale feeding in the southeast Beaufort Sea (Walkusz et al., 2012) and the western Beaufort Sea near Point Barrow (Okkonen et al., 2011). The studies involved prey sampling, either directly or inferred from satellite imagery, oceanographic and meteorological sampling in areas and at scales relevant to the bowhead's feeding behavior. Both studies were coupled with coincident aerial surveys, telemetry information describing residence times of bowheads in feeding areas (ADFG, 2014), and the descriptions of the oceanographic features which drive the development and variability of the prey that the bowheads were selecting. These are important examples where the coordination of studies within and among disciplines can contribute to the eventual elucidation of factors influencing bowhead condition (George et al., this issue). More and expanded studies of this kind are warranted.

Biophysical sampling in nearshore feeding habitats used by anadromous Arctic char feeding in summer in eastern Amundsen Gulf has never been investigated, but the results reviewed here suggest that this may be an ideal candidate for studying ecosystem shifts through in situ biophysical sampling. The observed relationship between Arctic char condition and the timing of breakup of the fast ice, and the possibilities of a recent prey shift, are similar in timing and trend as the trends observed in subadult bowhead whales, but at a much smaller scale. These results could be used to frame a well-matched sampling effort of Arctic char condition, with Arctic char prey and the biophysical factors which influence them, in the nearshore waters of eastern Amundsen Gulf.

Local knowledge and tag returns, obtained through the local subsistence fisheries, provide a clear picture of where and when Kuujjua River Arctic char feed in summer. Future research efforts could focus on sampling forage fish and zooplankton during summer in these areas. This would involve using a combination of shore and ship-based prey and oceanographic sampling in the relatively localized and accessible locations where the Arctic char feed in summer. Such studies could be designed to collect data on the types of prey that the Arctic char select throughout the late June–mid August feeding period, and other types of prey that are present. This would address such aspects as variation within and among years, and the relationship of nearshore productivity with the extent and persistence of annual sea ice. This is a practical opportunity to study changes in marine productivity in an area that is both accessible and localized, with the added advantage of two decades of data on Arctic char condition and associated ice conditions.

3.2. Biophysical sampling in vast and distant feeding areas: Using marine mammals and seabirds as sampling platforms

Three species, the beluga, ringed seal and black guillemot, show an opposing trend to that observed in subadult bowhead whales and Arctic char. Decades of monitoring revealed that these three species, each with a preference for a diet of Arctic cod, have shown sustained temporal declines in body condition, growth and/or production since the early 1990s.

The overall downward temporal trend observed in ringed seals relates to winter and spring feeding areas, which for this stock includes mainly eastern Amundsen Gulf (Harwood et al., 2015). In the case of beluga, their annual range is huge, including vast, distant overwintering areas in the Bering Sea (Richard et al., 2001), migration routes through the western Beaufort Sea, and summering areas in the Beaufort Sea, Amundsen Gulf and beyond. The effects on black guillemot chicks, reflecting a similar downward trend, are from a localized area, approximately 20 km surrounding the seabird colony. Together, results from these two species suggest that declines or changes may be occurring in forage fish stocks (Logerwell et al., this issue), in a wide range of areas, at a range of scales and in different seasons in the Beaufort Sea, Amundsen Gulf and beyond.

Predicted and contemporary oceanographic and sea ice changes in the Arctic will influence the structuring of the region's marine food web (Tynan and DeMaster, 1997; Serreze et al., 2007; Comiso et al., 2008; Bluhm and Gradinger, 2008; Walsh, 2008; Laidre et al., 2008; Kovacs et al., 2010). Major reductions in the extent and thickness of sea ice, and resulting increases in ocean temperature and salinity during this century could be the explanation for the apparent downward trend or change in forage fishes in the Beaufort Sea and Amundsen Gulf. Sea ice changes would modify the distribution and availability of forage fishes, such as Arctic cod, which are found under sea ice or cold waters (<4 °C) adjacent to sea ice (Bradstreet, 1982; Bradstreet et al., 1986; Bluhm and Gradinger, 2008; Crawford et al., 2012). Arctic cod

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use the ice as a feeding habitat where they consume crustaceans associated with the ice undersurface and from the adjacent water column (Crawford and Jorgenson, 1993), and young-of-the-year cod seek refuge in spring under the nearshore ice in Amundsen Gulf (Harold Wright, Ulukhaktok, NT, personal communication, 2014). Arctic cod is considered to be the most important trophic link from lower trophic levels (copepods and under-ice amphipods) to other fish, birds, seals and whales (Bradstreet, 1982; Tynan and DeMaster, 1997). In offshore trawls in the Beaufort Sea in 2002 and 2012, no other forage fish were as abundant or of as high energetic value as Arctic cod (Crawford et al., 2012; Reist, 2014). However, the large aggregations of cod that were observed in 2012 were not relocated during surveys in 2013, these being conducted in the same area and at the same time of year (Reist, 2014). Although the temporal and spatial scale of sampling were not sufficient either year to confirm, refute or describe an ecosystem shift, however the contrast in presence/absence of Arctic cod among years warrants further study.

We have as yet only limited information about the distribution and abundance of forage fishes, including Arctic cod, in the Beaufort Sea and Amundsen Gulf, or the controlling factors. Arctic cod are known to use a variety of habitats that occur in a range of conditions, areas, and seasons (Logerwell et al., this issue). Most of these habitats are inaccessible using ship-based surveys, limiting the conduct of studies with the intent of understanding environmental change. It would be impractical and inordinately expensive to directly collect field data in the feeding locations used by marine vertebrate predators, with the objective of examining changes in the prey base, diet and food web structure used by belugas (Richard et al., 2001) or ringed seals in winter (Harwood et al., 2015). The opportunity now exists, however, using satellite tags or data loggers deployed on seabirds and marine mammals to study water masses which influence the distribution of lower trophic levels and forage fish such as Arctic cod. Well-funded, long-term research programs, using marine mammals and seabirds as “educated oceanographic sampling platforms” could be key to understanding the changes that are occurring in the Arctic marine ecosystem (Smith, 2001; Lydersen et al., 2002, 2004; Fedak, 2004).

Studies have been done and others underway using marine mammals and seabirds to direct biophysical sampling efforts to areas of productivity. Lydersen et al. (2002) report results from satellite-linked conductivity–temperature–depth (CTD) loggers deployed on belugas to examine the oceanographic structure of an Arctic fjord on Svalbard. The whales dove to the bottom of the fjord routinely, occupying areas with up to 90% ice-cover, where the use of conventional ship-based CTD-casts would have been difficult. Their study confirmed that marine-mammal-based CTDs have enormous potential for cost-effective, future oceanographic studies.

A second example, using a behavioral state model (D. Yurkowski, unpublished data; methods described in Harwood et al., 2015) was applied to satellite tracking data from subadult ringed seals tagged in Amundsen Gulf in 2001 and 2002, and subsequently tracked to the Chukchi Sea (reported in Harwood et al. (2012b). It is possible to differentiate between locations where the tagged ringed seals made sustained, directional movements indicative of migration, vs. areas where the tagged seals lingered

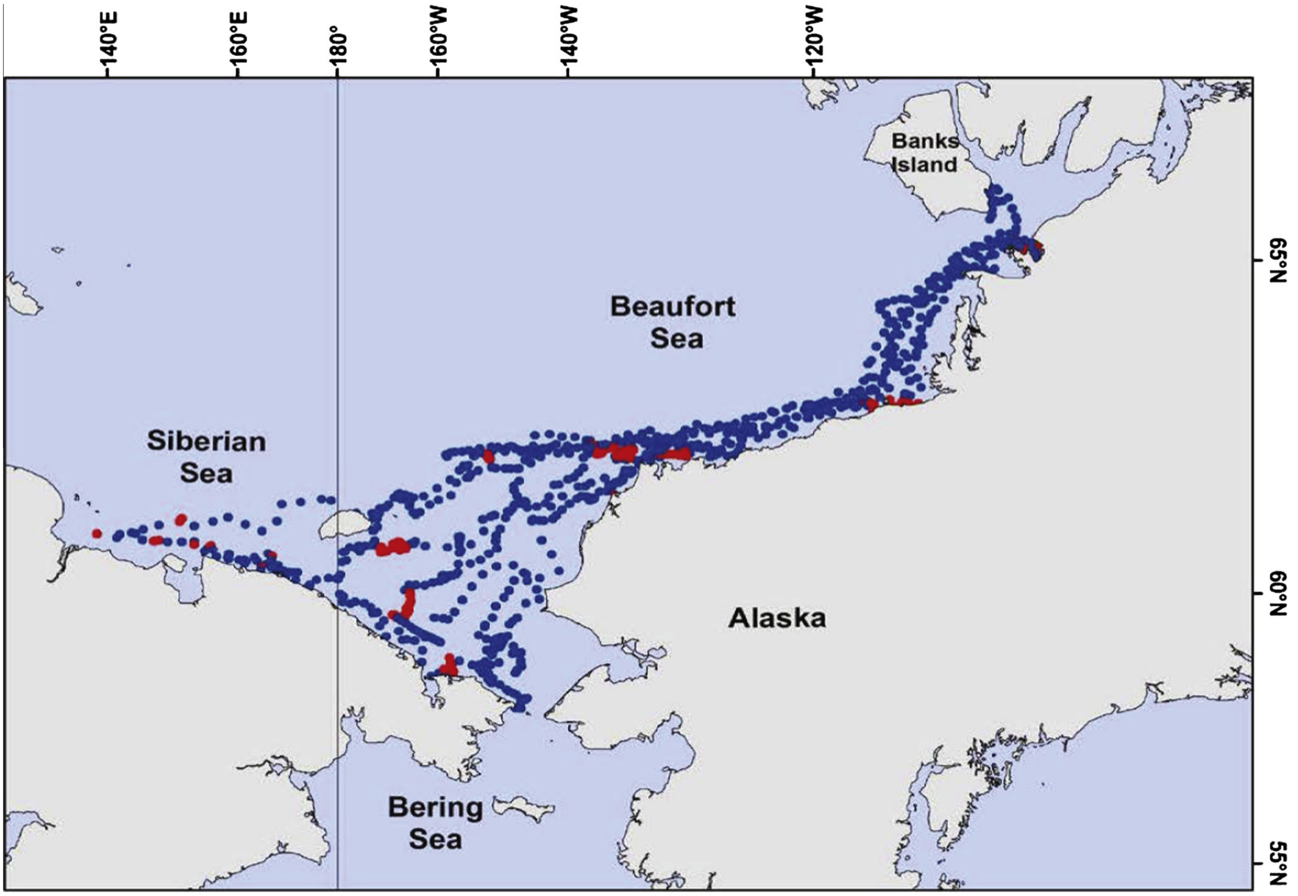

Fig. 7. Location estimates for eight ringed seals during the fall (September to January) that were tagged at Cape Parry in Amundsen Gulf, Northwest Territories, Canada in September 2001 and September 2002. Each location represents a 12-h time-step and is associated with a behavior state estimate (blue = traveling, red = resident/foraging; (methods as in Harwood et al. (2015)).

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and were likely foraging (Fig. 7). Models could be prepared for multiple species tracked concurrently, to reveal areas which are the most productive and provide clues as to what types of prey are available there. Results to date contribute to an emerging picture of distant, offshore foraging habitats favoured by belugas, bowheads and ringed seals (Richard et al., 2001; Citta et al., this issue; Harwood et al., 2015).

There is also one study underway in the western Beaufort Sea using instrumented black guillemots (Divoky, unpublished data). Data loggers that monitor water temperature and pressure (depth) have been deployed on parent guillemots during the June–August breeding season and record water temperature and depth every 2 s during a dive. Preliminary analysis of the data shows that in June, guillemots take adult Arctic cod from the water column adjacent to sea ice, but as ice retreats and water temperatures warm, the birds switch to foraging over benthic habitats in shallower waters where first-year Arctic cod are taken. The data loggers and concurrent observations of prey returned to nestlings demonstrate a switch to demersal prey when water temperatures are >4 °C.

In the case of certain species, such as the philopatric ringed seal or breeding seabirds, there also exists the added opportunity of recapturing tagged individuals to recover the tag. In the case of the seal, this could open new avenues for gaining more detailed information, such as using head-mount cameras for recording food ingested and food selection methods (kinds, size, and frequency), particularly during periods when ice precludes *in situ* sampling effort.

4. Overarching considerations: Scale and collaboration

While changes in body condition of marine vertebrates provide clues as to the nature and direction of environmental change, the scale of biophysical sampling needs to be matched with the ecological scale of the marine vertebrate species showing the trend (Moore et al., 2014). We note that for the Beaufort Sea species listed in Table 1, core seasonal habitats and feeding areas occur at a wide range of spatial scales: from 10s of km (Arctic char and black guillemots in summer) to 100s of km (ringed seals in winter), to 1000s of km (belugas, bowhead whales). Once ecological scale is known, studies aimed at sampling the food chain and the factors controlling prey availability or quality need to be done at temporal and spatial scales that are matched with, and relevant to, the marine vertebrate consumer.

The considerable knowledge already extant about the life histories, distribution and behavior of the marine vertebrates points to the specific areas, times and at what scale biophysical sampling would be relevant, but this needs to be refined in all cases. The vast and remote nature of multiple, prime feeding areas make it difficult or impossible for conventional ship-based biophysical sampling to be conducted at intervals and scales that would detect changes in food web structure, and illuminate our understanding of the ecosystem changes. In other cases, food web structure in core feeding areas, such as nearshore feeding areas used by Kuujjua River Arctic char in summer, and also visited opportunistically by beluga in August 2014, could be sampled and monitored, given their more localized and accessible geographic extent.

Finally, there is much to be gained through collaboration among disciplines studying environmental changes relevant to the marine vertebrate species. We urge scientists studying marine vertebrate species to join with scientists studying physical, chemical, and other biological aspects of the environment to work collaboratively. It will be most productive to select well-studied vertebrate species, perhaps starting with the five listed in Table 1, where there is a high probability of obtaining a continuing, long-term sample size (e.g., harvested species). This is essential to improve interpretation of top-down responses to shifts in the marine ecosystem, and will be greatly advanced by building well-planned collaborations among sampling teams from different disciplines.

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