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Killer whale (*Orcinus orca*) predation in a multi-prey system

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Abstract Predation can regulate prey numbers but predator behaviour in multiple-prey systems can complicate understanding of control mechanisms. We investigate killer whale (*Orcinus orca*) predation in an ocean system where multiple marine mammal prey coexist. Using stochastic models with Monte-Carlo simulations, we test the most likely outcome of predator selection and compare scenarios where killer whales: (1) focus predation on larger prey which presumably offer more energy per effort, (2) generalize by feeding on prey as encountered during searches, or (3) follow a mixed foraging strategy based on a combination of encounter rate and prey size selection. We test alternative relationships within the Hudson Bay geographic region, where evidence suggests killer whales seasonally concentrate feeding activities on the large-bodied bowhead whale (*Balaena mysticetus*). However, model results indicate that killer whales do not show strong prey specialization and instead alternatively feed on narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*) whales early and late in the ice-free season. Evidence does support the conjecture that during the peak of the open water season, killer whale predation can differ regionally and feeding techniques can focus on bowhead whale prey. The mixed foraging strategy used by killer whales includes seasonal predator specialization and has management and conservation significance since killer whale predation may not be constrained by a regulatory functional response.

Keywords Bowhead whale · Commercial whaling · Functional response · Inuit traditional ecological knowledge · Marine mammals · Monte Carlo model

Introduction

Predation is one of the driving forces behind evolution. Most predators have the opportunity to switch among prey types of varying energy per unit effort, thereby resulting in a sigmoidal functional response owing to bioenergetic optimization in selecting prey (Oaten and Murdoch 1975). But how predator behaviour relates to population processes has been difficult to disentangle, particularly in field situations when multiple prey species are involved (Srinivasan et al. 2010). Since predators are capable of regulating their prey, selection of prey types must have critical implications for prey population dynamics. Killer whales (*Orcinus orca*) are ubiquitous top marine predators and feed on various prey from 6-ounce herrings (*Clupea harengus*) to 60-ton bowhead whales (*Balaena mysticetus*) depending on geographic location and learned predator behaviour. Some sympatric killer whale groups specialize on narrowly defined prey groups, for example on marine mammals or certain kinds of fish to the exclusion of other available, prey (Baird and Dill 1995; Ford et al. 2000, 2005). In various regions killer whales have learned to specialize on small fish as the major food (Similä et al. 1996) or a mixed

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diet of fish and seals (Foote et al. 2009), and in the Antarctic region four distinct groups of killer whales show different foraging specializations (Pitman and Ensor 2003; Pitman et al. 2007).

Killer whales visiting polar waters in summer have been observed successfully attacking other marine mammals in the Antarctic (Condy et al. 1978) and Arctic (Reeves and Mitchell 1988) including pinnipeds, mysticetes and odontocetes. In the eastern Canadian Arctic, prey include a number of seal species, bowheads, narwhals (*Monodon monoceros*), and belugas (*Delphinapterus leucas*) (Higdon et al. 2011). During the Arctic ice free season, typically July–October, killer whale groups of various sizes and compositions travel extensively throughout the eastern Canadian Arctic searching for prey. Ice-adapted marine mammals tend to use sea ice to hide from killer whales, both for concealment and because prey are better at navigating in ice than killer whales (Ferguson et al. 2010a). Groups of marine-mammal-eating killer whales typically move quietly through large regions until prey is detected. They then stalk the prey until it is caught or until the chase enters shallow water. Killer whales will often pause after unsuccessful chases before continuing new searches (Srinivasan and Markowitz 2009). Marine mammals are evidently very frightened of killer whales and behave defensively when they are nearby. Ringed seals (*Pusa hispida*), for example, haul out on land, which they otherwise seldom do (Kovacs and Lydersen 2008). Narwhals, which usually prefer deep water, cling to shorelines or ice edges, or crowd tightly packed into narrow bays (Campbell et al. 1988; Laidre et al. 2006). Delays and threats to the recovery of the eastern Canadian stock of bowhead whales have been attributed to killer whale predation (Reeves and Mitchell 1988; Finley 1990; Moshenko et al. 2003). The killer whale may now be present increasingly often, and in greater numbers, in the Hudson Bay region of the eastern Canadian Arctic (Higdon and Ferguson 2009; Ferguson et al. 2010b) raising concerns over the effect of predation on stocks of marine mammals that are hunted by local Inuit.

Killer whales are known to be an important factor in predation of marine mammals (Jefferson et al. 1991; Springer et al. 2003) raising the possibility of limiting population rate of increase of prey species. Predation is considered limiting if mortality of prey is additive, at least partially (sensu Messier 1991). In contrast, a regulating factor keeps prey numbers within a given range and therefore requires a density-dependent feedback mechanism. For regulation, the limiting effect must increase when prey numbers increase and conversely decrease when prey numbers decline. Understanding limiting and regulating factors is fundamental to understanding predator–prey relationships. Wildlife managers need to know the regions of prey density where killer whales have a regulating influence on prey to determine goals for human harvest. Knowledge of how killer whale predation is limiting or regulating dictates the behaviour of models predicting the effects of expansion of killer whale distribution into environments such as the Hudson Bay region.

We examine empirical data on killer whale predation in a multiple prey system in Hudson Bay, Canada, where killer whales prey on more than one marine mammal species (Ferguson et al. 2010b). Highly mobile predators like killer whales utilize an active (vs. an ambush) style of hunting and typically have a varied diet that differs regionally (Rosenheim et al. 2004; Dahlheim et al. 2009). Other studies have noted a strong seasonality to high-latitude killer whale groups specializing on a specific prey item during spring and summer (Hoelzel 1991; George and Suydam 1998; Ford and Ellis 2006; Barrett-Lennard et al. 2011; Matthews et al. 2011). In such cases, presumably that specific prey species alone would support killer whale population energetic needs. We investigate marine-mammal-eating killer whales of the Canadian Arctic to understand possible regulatory effects in a multiple-prey system. We describe a model of the summer predation of killer whales on three types of marine mammals in Hudson Bay and adjacent waters, where a group of killer whales seems to spend about 3 months in summer (Ferguson et al. 2010b). Using information derived from a sighting database (Higdon 2007; Higdon et al. 2011) that includes traditional ecological knowledge (TEK) (or *Inuit Qaujimajatuqangit*, IQ) surveys of the Hudson Bay region, we model killer whale predation on three types of prey: bowhead whales, belugas and narwhals (monodontids), and seals. Using killer whales as the model, we consider the effects of three types of predator foraging behaviour on a multiple prey system: (1) predators focus on the largest prey type; (2) predators are non-adaptive generalists and feed on all alternative prey types as encountered during searches; and (3) predators are adaptive generalists behaving as optimal foragers that switch prey seasonally and regionally.

Materials and methods

Sighting database

Marine mammal systems are difficult models to test predator–prey ecology due to the inaccessibility and unpredictability of observing predation events. We collected anecdotal occurrence data of killer whale sightings ($n = 207$) from diverse sources, including peer-reviewed literature, consulting reports, newspapers, and government documents, as well as information solicited from northern residents, tourists and researchers (see Higdon 2007).

Information on additional killer whale sightings was acquired from 55 semi-directed interviews (Huntington 1998) with Inuit hunters and elders conducted in five Hudson Bay communities from 2007 to 2009 (Ferguson et al. 2010b). The database included information on killer whale sighting date, behaviour, location, estimated group size, observer or information source, observations of predation events including predator–prey behaviour, associations with other species, and an indication of group composition or sex. Anecdotal records of obscure animals are vulnerable to inaccuracy due to possible reporting error and bias (McKelvey et al. 2008). However we are confident of the data accuracy following a quantitative evaluation for spatial and temporal reliability and/or quality before analysis (see Higdon et al. 2011).

Prey species were grouped as 'monodontid' for beluga or narwhal predation events because of similarity in size and behaviour and as 'phocid' for harp seal (*Pagophilus groenlandicus*), ringed seal, bearded seal (*Erignathus barbatus*), harbour seal (*Phoca vitulina*), or unidentified seal predation events.

Model construction

The model used quantitative assumptions about the size, composition and total numbers of the killer whale group, with estimates of the average weight of each size class, the proportional daily ration, and the proportion of the annual ration taken in summer to estimate the weight of food that the group consumes in the course of a summer in Hudson Bay, Canada (see the Electronic Supplementary Material). Key assumptions include a median of 25 killer whales (0–0.20 whales per 100 km^2) structured according to observed age/sex/size (0.27 adult males, 0.58 females and juvenile males, and 0.15 calves). The prey weight consumed in an average attack was calculated from the proportions of predatory attacks on each prey type, prey weights, the number killed in an attack, and the fractions of body weight consumed for the different kinds of prey. We assumed for the purposes of this model that the killer whales summering in Hudson Bay feed exclusively on marine mammals; the possibility that they prey, for example, on Arctic char (*Salvelinus alpinus*) was not considered likely according to TEK survey results. The standing stock of marine mammals totals about 120,000 tons (Hoover 2010), excluding walrus (*Odobenus rosmarus rosmarus*), which are not observed as killer whale prey in this region.

Marine mammal species that killer whales prey upon can be either solitary or gregarious, and attacks on the latter typically result in multiple kills (Laidre et al. 2006). The number killed in an attack was sampled from (the number of failures in) a negative binomial distribution with 1 added. Although there is one possibly questionable report of several bowhead whales being killed in a single attack (Higdon et al. 2011), the number likely to be killed during an attack was kept to one because the animals themselves are so large (e.g., Barrett-Lennard et al. 2011). In contrast, narwhal and beluga are gregarious species (Kingsley et al. 1994; Smith and Martin 1994; Richard et al. 2010) which often associate in quite large groups, and there are several reliable reports (both species) of several being killed in a single attack. The number of monodontids killed in a killer whale attack was therefore allowed to range up to about 12. Ringed and bearded seals, the two most numerous marine mammal species in these waters, are relatively solitary (Reidman 1990). Therefore, we considered that each killer whale attack would only take one seal. The ratio of total consumption to weight per attack gave an estimate of the number of attacks in Hudson Bay in the course of a summer. The number of attacks on each type of prey, and the number of animals killed, was calculated by allocating the estimated number of attacks back to prey types in the given proportions. The ratios of these numbers to the estimates of population size provided an estimate of the annual mortality due to killer whale predation for each prey type.

Prey population size was from published estimates of beluga (57,300; Richard 2005), seals (774,000; Hoover 2010), and narwhal (5,100; DFO 2008). For bowheads we used the population estimate agreed by the Scientific Committee of the International Whaling Commission, i.e., a fully corrected strip-transect estimate of 1,525 (333–6,990) whales for Hudson Bay–Foxe Basin in 2004 (IWC 2009). An additional detail considered in the discussion is that the bowheads in Foxe Basin and Hudson Bay region are actually only part of the larger Eastern Canada-West Greenland bowhead population (COSEWIC 2009).

There are reasons not to expect that all species are preyed upon equally—some may be easier to find, easier to catch, or simply preferred. The sighting data provides estimates as to the relative frequency with which different prey types are attacked by killer whales. However, we considered that observation numbers incorporate some observational bias, bowhead whales being large, gregarious, obvious, and their whereabouts often known, while seals are small, discreet, ubiquitous, and often solitary, and predation on them less likely to be observed. Since observed relative frequencies influence prey mortality; we ran the model with attacks distributed among prey types according to several different predation scenarios. First, (1) we ran the model with the assumption that killer whales specialize on prey that provided the greatest potential amount of food for a given effort. Here, the model assumed attacks occurred in proportion to biomass (i.e., selection for large-bodied species). Second, (2) we ran the model assuming killer whales are non-adaptive generalists and predatory attacks were distributed among prey types in proportion to numbers available/encountered. The model was run assuming (3) killer whales are adaptive generalists and attacked and ate prey in proportion to that observed by humans (i.e., according to the sighting database). Observations of predatory attacks on different kinds of marine mammals in the Hudson Bay region have been compiled ($n = 56$, Ferguson et al. 2010b). The distribution of these observations provided preliminary estimates of 34% of observed attacks on bowhead whales, 29% each on narwhals and belugas, and the remaining 8% on seals.

Sensitivity analysis

A version of the model was also constructed in which, instead of starting with initial input of the distribution of attacks on different prey types and working through to the possible diet composition, the input was the diet composition and the calculations worked back to the likely distribution of attacks. In both cases the likely number of attacks in the course of the summer was also produced, as killer whales have to budget not only energy, but also time.

Model solution

The model was constructed and run using the WinBUGS platform v. 1.4.3. (Lunn et al. 2000), developed for fitting statistical models using Bayesian methods, but here used as a means of running Monte Carlo sampling of a stochastic model. The model contained no prior estimates of killer-whale-related mortality (or of any of the other data which could be included as a likelihood function) and was characterised by a number of uncertainty parameters. Many of the functions were multiplications or divisions, and (approximately) the error coefficient of variance (e.c.v., the estimated standard error divided by the estimated mean) of the result of such an operation is the sum of the e.c.v.s of the terms, and therefore the relative contributions of the different errors could be detailed.

Functional response

Regulation can fall into two general categories: functional and numerical responses (Solomon 1949). Numerical responses describe changes in predator densities in response to changes in prey densities and can affect predator–prey relationships (Mech 1970). Functional responses describe relationships between kill rate per predator and prey abundance (Messier 1991) and can also influence predation behaviour (Sinclair 1991). Predator behaviour can be quantified by kill rate, or the number of prey killed per predator per unit time. A Type I functional response assumes a linear increase in predation rate with prey density, i.e., that the time needed by the predator to process a food item is negligible, or that consuming food does not interfere with searching for additional prey. A Type II functional response is characterized by a decelerating predation rate that assumes the predator is limited by its capacity to process food. For example, as the number of bowhead, monodontids, and seals increases the number of kills per killer whale also increases, however, at higher densities of prey, killer whales need very little time to find prey and spend almost all their time handling prey and very little time searching (i.e., are then saturated; see Dahlheim and White 2010). A Type III functional response is similar to type II in that at high levels of prey density, saturation occurs. But now, at low prey density levels, the graphical relationship of number of prey consumed and the density of the prey population is a more than linearly increasing function of prey consumed by predators. This accelerating function is caused by learning time, prey switching, or a combination of both phenomena. Prey switching involves two or more prey species and one predator species. When prey species are at unequal prey densities, the predator will discriminate between prey species. If individuals or groups of predators respond to an increase in prey by killing a higher proportion of the prey population, the functional response is considered to result in regulation. Kill rate will plateau at some level resulting in a sigmoidal curve (i.e., a type III functional response; Holling 1966).

We graphed all calculated combinations of predation rates (kills per day) from the six models (see above) relative to the number of prey of each type killed in the diet to define the form of predation by killer whales on prey groups: bowhead, narwhal, beluga, and seals. The described relationships provide an understanding of predator behaviour relevant to a discussion of possible regulation (Lima 1998).

Results

The estimated summer feeding of killer whales in Hudson Bay totals about 1/3 of a million kilograms (Table 1). If killer whales could be assumed to eat all they killed, the overall average mortality due to killer whales would be about 0.275% a year of the total number of marine mammal prey. Results are presented for three different possible scenarios for the distribution of killer whale attacks to different prey types.

Specialists on prey biomass

If killer whale attacks are distributed according to prey biomass available, predation focuses on seals over bowheads and narwhals (Table 2a). Under these model assumptions, the proportion of attacks targeting seals is over 50%. However, bowheads provide over 50% of the diet biomass, while seals provide about 3% of the diet. The monodontids provide about 40% of the diet, but the more numerous belugas provide most of it, while narwhals only provide about 4% of the total. The number of attacks on prey is high, indicating about four successful predation events per day for the group of killer whales. Seals are the target of most attacks, while only providing the smallest proportion of the diet in biomass. The proportion of diet provided by bowheads is similar to that in other scenarios described below, and accordingly bowhead whales experience high mortality from killer-whale attacks (49/year). However, mortality of both monodontids is low, and for seals, although they are the target of the majority of the attacks, mortality is still negligible relative to overall population size ($n = 774{,}000$).

Table 1 Biomass summary statistics of marine mammal prey species in Hudson Bay region

Prey type or species	Median prey		Observed attacks (%)	Negative binomial parameters (n, P)
	Number	Biomass (t)		
Bowhead whale[a]	990	13,450	34	
Narwhal	5,100	2,817	29	4, 0.60
Beluga	57,330	27,370	29	4, 0.60
Seals (mixed)	774,000	47,200	08	

[a] Killer whales are only considered to prey on calf and subadult bowhead whales, but can take any beluga, narwhal, or seal

Non-adaptive generalists on prey numbers

When killer whale attacks are considered to be distributed according to prey numbers, seals receive over 90% of the attacks and contribute >30% of the diet (Table 2b). Most (>50%) of the rest of the diet is provided by belugas, which are relatively heavy and much more numerous than either of the other whale prey. Narwhals are about three times as numerous as bowheads and provide a correspondingly larger proportion of the diet. Bowheads contribute less than 1% to the diet. If attacks are allocated on this basis, all prey mortality levels are low. Narwhals and belugas have higher mortality than bowheads because the average number killed in an attack is expected to be greater for these two gregarious species. However, if attacks are proportional to availability, killer whales must make a very large number of attacks in the course of a summer—25 per day. A high proportion of these attacks are on individual seals.

Adaptive generalists (observed attacks)

If killer whale attacks are considered to be distributed between the prey types according to the available

Table 2 Statistics for summer predation by killer whales on marine mammals of the Hudson Bay region

	Attacks a year	Bowheads	Narwhals	Belugas	Seals
(a) Attacks distributed by prey biomass	335.2 (131.8, 48.7)				
Distribution of attacks (%)		14.7 (3.6, 33.3)	2.9 (1.4, 60.7)	30.0 (5.3, 23.9)	51.8 (6.0, 15.7)
Distribution of diet (%)		53.3 (15.0, 41.4)	4.2 (2.6, 80.9)	38.7 (14.1, 53.7)	2.9 (1.2, 50.8)
Mortality (%/year)		3.2 (1.2, 49.5)	0.6 (0.4, 82.5)	0.6 (0.2, 59.0)	0.0 (0.0, 52.6)
No. killed (/year)		49.4 (18.2, 49.1)	30.7 (21.2, 85.2)	326 (142, 59.7)	173 (80.0, 56.1)
(b) Attacks distributed by numbers of prey	2,237 (1,087, 64.6)				
Distribution of attacks (%)		0.0 (0.2, 650.5)	0.5 (0.6, 143.0)	6.8 (2.3, 44.6)	92.5 (2.4, 3.4)
Distribution of diet (%)		0.4 (5.2, 648.7)	4.2 (5.1, 143.3)	56.3 (15.2, 38.9)	34.7 (14.9, 60.4)
Mortality (%/year)		0.0 (0.3, 640.0)	0.6 (0.8, 144.2)	0.8 (0.3, 48.7)	0.3 (0.1, 64.6)
No. killed (/year)		0.4 (5.1, 645.6)	31.0 (40.3, 147)	471 (167, 47.6)	2,068 (1030, 65.9)
(c) Attacks distributed by observations	161.6 (56.4, 44.1)				
Distribution of attacks (%)		35.1 (6.7, 25.9)	28.2 (6.3, 30.7)	28.2 (6.3, 30.5)	7.3 (3.8, 68.0)
Distribution of diet (%)		61.5 (14.8, 35.3)	20.0 (8.9, 63.3)	17.2 (7.8, 63.4)	0.2 (0.1, 82.2)
Mortality (%/year)		3.7 (1.4, 49.6)	2.9 (1.6, 72.2)	0.3 (0.1, 72.1)	0.0 (0.0, 89.4)
No. killed (/year)		56.9 (19.4, 44.9)	146 (75.4, 68.9)	146 (76.2, 68.9)	11.5 (8.8, 87.1)

Attack-priority models included: (a) according to prey biomass (size specialists); (b) according to encounters (non-adaptive generalists); and (c) according to sighting database (adaptive generalists)

Statistics tabulated are medians of probability distributions. In parentheses, the standard deviation and the ratio (%) of interquartile range to median. Results are from 100,000 samplings of each model

Table 3 Statistics for summer predation by killer whales on marine mammals of the Hudson Bay region according to a diet-priority model

	Attacks a year	Bowheads	Narwhals	Belugas	Seals
Diet percentage: large whale preference	138.5 (93.3, 61.1)	95	2	2	1
Percentage of attacks		67.7 (21.6, 51.5)	2.2 (5.0, 192.3)	2.6 (5.6, 190.8)	21.4 (23.2, 180.9)
Percent in diet		95.6 (3.1, 4.1)	1.4 (2.0, 156.8)	1.4 (2.0, 156.7)	0.5 (1.4, 265.7)
Mortality (%/year)		5.9 (1.7, 38.0)	0.2 (0.3, 161.9)	0.0 (0.0, 162.4)	0.0 (0.0, 269.9)
Kills (/year)		89.9 (21.9, 31.8)	10.4 (15.5, 158.9)	12.0 (18.0, 161.0)	27.7 (87.9, 269.3)
Diet percentage: whale preference	231.2 (140.7, 69.8)	76	11	11	2
Percentage of attacks		31.4 (15.0, 68.4)	10.9 (8.6, 99.6)	12.6 (9.8, 99.8)	38.1 (22.2, 95.4)
Percent in diet		76.4 (6.0, 10.7)	10.5 (4.4, 56.2)	10.5 (4.4, 56.1)	1.4 (2.0, 157.0)
Mortality (%/year)		4.7 (1.4, 39.4)	1.5 (0.8, 66.0)	0.2 (0.1, 66.1)	0.0 (0.0, 161.5)
Kills (/year)		71.8 (18.4, 33.5)	77.4 (38.1, 62.8)	89.2 (43.8, 62.7)	83.3 (124.9, 160.4)
Diet percentage: according to observations	281.1 (173.2, 74.8)	50	24	24	2
Percentage of attacks		16.8 (9.6, 75.4)	21.2 (10.3, 69.5)	24.6 (11.7, 69.2)	31.5 (21.4, 109.4)
Percent in diet		50.0 (7.0, 19.2)	23.7 (6.0, 34.2)	23.7 (6.0, 34.4)	1.4 (2.0, 156.3)
Mortality (%/year)		3.1 (1.0, 42.4)	3.4 (1.3, 48.8)	0.4 (0.1, 49.0)	0.0 (0.0, 161.3)
Kills (/year)		46.8 (13.4, 37.1)	174.5 (59.5, 44.3)	201.7 (68.8, 44.4)	83.4 (124.9, 159.7)
Diet percentage: monodontid preference	551.7 (273., 63.7)	30	32	32	6
Percentage of attacks		5.1 (3.2, 71.8)	14.4 (8.7, 81.1)	16.8 (9.9, 80.9)	62.0 (17.7, 41.7)
Percent in diet		29.7 (6.4, 29.6)	31.8 (6.5, 28.0)	31.8 (6.6, 28.3)	5.4 (3.3, 79.5)
Mortality (%/year)		1.8 (0.7, 48.0)	4.6 (1.6, 44.9)	0.5 (0.2, 44.7)	0.0 (0.0, 87.4)
Kills (/year)		27.9 (9.4, 43.4)	234.4 (71.2, 39.8)	271.3 (82.3, 39.5)	322.3 (219.8, 84.7)

Diet headings are input proportions of diet obtained from bowhead whale, narwhal, beluga, and seal. Statistics tabulated are posterior medians with the ratio (%) of interquartile range to median in parentheses. Results are from 100,000 samplings of the model

observations, which are over one-third on bowheads and over one-quarter each on narwhals and belugas, bowheads make the largest contribution to the diet at over 60% (Table 2c). Belugas and narwhals contribute about 20% each, and the contribution by seals is negligible. Mortality is highest on bowheads at nearly 4%/year. Narwhals also suffer high mortality at 2.9%/year, but for belugas which are ten times as numerous, mortality is low. Because attacks are concentrated to such an extent on large prey, the number of attacks is less than 2 per day over the 90-day summer season.

Model performance

As a test of model results, we ran the model from diet back to the distribution of attacks. The results were consistent with those obtained by working from attacks to diet (Table 3). Mortality of any prey type tended to be roughly proportional to its contribution to the diet. With the diet compositions considered, neither belugas nor seals suffered significant mortality as a result of killer whale predation. If killer whales preyed almost exclusively on monodontids, the median estimate of narwhal and beluga mortality was estimated at 4.6 and 0.5%/year, respectively, and the number of attacks at 506. If seals composed any significant fraction of the diet, the number of attacks increased considerably. The combined uncertainties of the different assumptions meant that results were associated with large uncertainties.

Functional response

Combining scenarios and model runs produced a predator response graph (Fig. 1). The number of bowheads in the killer whale diet decreased linearly with kills/day (Fig. 1) suggesting that the proportion of bowhead prey eaten does not approach a maximum or show density-dependent regulation. In contrast, the monodontid and seal prey proportions in the killer whale diet increases linearly to an asymptote of 30% for either beluga or narwhal and 10% for seals (Table 2). Killer whale kill rate increases positively with seal and small whale mortality indicating that density-dependent feedback mechanisms are possible for these prey populations.

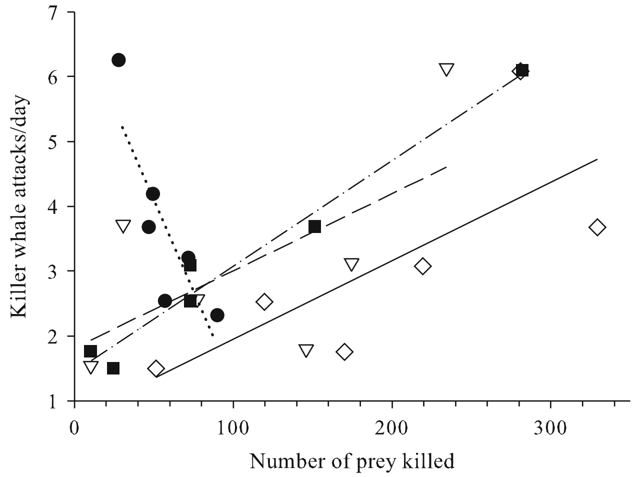

Fig. 1 Killer whale predation rate (attacks/day) relative to number of prey killed for three prey groups (*black circle/dotted line* bowhead, *white triangle/dashed line* narwhal, *white diamond/solid line* beluga, *black square/dash-dot line* seals) in the Hudson Bay region

Discussion

Functional response has rarely been estimated for large mammalian predators, despite the need to understand predator–prey dynamics and limiting and regulating factors in the context of management and conservation (Sinclair and Pech 1996). Large mammalian predators such as wolves (*Canis lupus*) (Lidicker 1978) and killer whales (Estes et al. 1998) can have anti-regulatory effects on prey populations, particularly in multiple-prey ecosystems. Results suggest killer whales feeding in the greater Hudson Bay region have developed regionally unique prey-specific specializations to their largest prey species, bowhead whales, during the peak period of sea ice retraction of the ice-free summer. Bowhead distribution is relatively predictable, in summer, in areas where mysid and copepod blooms occur (Reeves et al. 1983; Higdon and Ferguson 2010; Ferguson et al. 2010a) which may provide predictable prey availability for killer whales. The functional response observed indicates high kill rates at relatively low bowhead whale densities. The timing of killer whale predation events in the Canadian Arctic region describe a pattern of killer whales attacking belugas and narwhals during migration to and from sea-ice refugia with feeding specialization on bowhead whales during the peak summer period (August–September; Higdon et al. 2011). As a result the observed functional response varied with prey whereby density-dependent changes in prey vulnerability (circa Holling 1966) occurred for monodontids whales but was not evident for the larger bowhead whales. Functional response curves can be anti-regulatory if predation is largely non-compensatory (Oaten and Murdoch 1975; Taylor 1984). Management implications include the possibility of a density-dependent response by killer whales to reduced monodontid prey, such as the relatively small Northern Hudson Bay narwhal population.

Our modelling described an asymptotic relationship between killer whale predators and ice-adapted whales as prey in Hudson Bay. Learning by predators can create a regulatory functional response (Tinbergen 1960; Holt 1977). For example, we assume variable prey-handling techniques by killer whales depending on prey being targeted since we found evidence of seasonal prey specialization (see also Dahlheim and White 2010). Ecological reasons for why a predator changes predatory activity in response to changes in prey availability include: optimization of search effort by predators (Sih 1984), existence of prey refugia (Taylor 1984; Ferguson et al. 2010a), behavioural changes associated with risk assessment by prey (Abrams 1982), and changes in prey vulnerability (Holling 1965). The often clumped spatial distribution of large mammal prey may be anti-regulatory because of the swamping effects of high densities (Bergerud 1975; Skogland 1991). Thus a clumped spatial distribution exacerbates the anti-regulatory shape of the predation response curve. Shifts in seasonal range use of highly mobile prey can also reduce the numerical response of a predator.

Killer whales are highly specialized and efficient predators. However, there are many unknowns about prey selection. We speculate that foraging behaviour is under constant selection pressure to adapt to changing prey numbers and accessibility. Large whale abundance in the North Atlantic was severely reduced by centuries of European and North American commercial whaling (Mitchell and Reeves 1982; Roman and Palumbi 2003; Higdon 2010), although the pattern of harvesting varied over time according to technological advancement and market conditions (Clark and Lamberson 1982). Prey selection by predators may have changed during the commercial whaling era with reductions in prey numbers and availability of carcasses for scavenging (Whitehead and Reeves 2005; Reeves et al. 2006). In addition, killer whales have been harvested in low (almost non-existent) subsistence takes by Inuit in Baffin Bay for centuries (Mitchell and Reeves 1988; Heide-Jørgensen 1988; Higdon 2007). Harvesting of killer whales by Greenlanders continues and likely affects killer whale numbers in Eastern Canadian Arctic (Higdon 2007). The commercial whale harvest of killer whales by Greenland and Norway may have limited the ability of killer whales to regulate the bowhead prey population. During the past 100 years, since the cessation of commercial whaling, bowhead whale numbers have increased and continue to increase (Heide-Jørgensen and Laidre 2006; Higdon and Ferguson 2010). The killer whale population has likely already adapted and specialized to accommodate a return to similar prey diversity and abundance as occurred many centuries ago.

Partial preferences for alternative prey types occur due to interplay between behavioural ecology and population dynamics (Křivan 1996). Predators that have the ability to switch among alternative prey are more likely to produce sigmoidal functional responses (Hassell et al. 1977; Post et al. 2000). In addition, if the predator is at or near satiation then optimal foraging behaviour predicts decreasing predation effort with increasing prey density even when prey-switching can occur (Sih 1984; Křivan and Sikder 1999). During the open-water season, killer whales in polar environments with multiple marine mammal prey may often be near food satiation. Model results suggest that a functional response exists for monodontid whale predation whereby predation increases with prey abundance. Variation in food availability likely results in numerical responses by killer whales through immigration, changes in migration behaviour, and reproduction. The presence of multiple prey species may reduce the potential for killer whale predators to regulate the Eastern Canada-West Greenland bowhead whale population.

Generally, killer whale predation at higher latitudes shows a strong seasonal pattern (George and Suydam 1998; Ford and Ellis 2006; Barrett-Lennard et al. 2011). For the eastern Canadian Arctic, the proportion of predation on each cetacean species by season remained relatively constant with the possible exception of bowhead whales where a greater frequency of predation events were observed during the summer season relative to the spring season (Higdon et al. 2011). For the Hudson Bay region, this seasonal pattern may be explained by the cycle of bowhead movements associated with birth and lactation. Parturition occurs between April and early June (Nerini et al. 1984) in heavy ice concentration (Ferguson et al. 2010a). Nursing calves move from Hudson Bay to the floe edge in northern Foxe Basin by late June (NWMB 2000). Bowhead calves and juveniles are vulnerable to killer whale predation (Mehta et al. 2007). Thus, a nursery ground of cow-calf pairs and juvenile whales (NWMB 2000; Cosens and Blouw 2003) occurs in July in an open water polynya located in northern Foxe Basin. The Foxe Basin region may serve as a refuge from predation during spring (Higdon and Ferguson 2010; Ferguson et al. 2010a). However, it may be an important feeding area for killer whales during the summer following the sea ice melt. Another line of evidence supporting bowhead being a focal prey species for killer whales was provided by δ^{15} Nitrogen stable isotope analysis of muscle, skin, and tooth tissue of a 30+ year old female killer whale found dead near Repulse Bay, Hudson Bay in November 2009. Results were consistent with the assertion that the killer whale fed primarily on mysticete whales relative to odontocete or pinniped prey prior to its death and likely throughout its life (C. Matthews, unpublished data).

In single predator–prey systems (e.g., wolf–moose *Alces alces*), regulation follows the classical density-dependent feedback pattern (Messier 1985). However, in multiple prey systems some prey are more at risk than others due to species-specific characteristics and predator behaviour. For example, when the abundance of primary prey increases, predators may increase and severely deplete secondary prey species, as reductions in secondary prey do not cause corresponding reductions in predator abundance (Jones 2003). As with most predators, killer whales are adapted to take advantage of changing prey availability and accessibility, whereas their prey are likely less adaptable. In the case of Hudson Bay marine mammals, it is unlikely that the observed functional response would result in regulation of Hudson Bay beluga populations because killer whales currently cannot access the belugas that use shallow estuaries in summer. For killer whales, narwhals may be more profitable (energy/effort) prey than beluga because they are: (1) somewhat larger and provide more blubber, (2) are generally in deeper waters particularly in summer, and (3) overlap in summer range with bowhead whales, hypothesized as the preferred prey (whereas beluga largely do not). In contrast, for bowheads the numerical response may be reduced and the potential for regulation lessened due to high mobility and their ability to change movement patterns over long time periods (Dyke et al. 1996; Polyak et al. 2010).

Our analyses are based on the assumption of a generic killer whale with standard foraging responses and efficiencies; both assumptions are oversimplification given the diversity of predator behaviour (Bolnick et al. 2003). Social structure of killer whale communities likely influence predation behaviour as related groups may operate in various group size units according to learned prey behaviour (Barrett-Lennard et al. 2011). Predators with a high population growth rate relative to prey populations have the potential to regulate prey (Sinclair et al. 1990) and one mechanism of population regulation is variability in predator group sizes (e.g., fragmentation of wolf packs; Bergerud 1980). Similarly, killer whale social organization is characteristically ‘fission–fusion’ with loose associations among related animals (Ford and Ellis 1999; Baird and Whitehead 2000) so that clusters may collapse into smaller groups while hunting or re-establish as larger groups depending on prey (TEK observations on file). For example, optimal group size for Pacific killer whales preying on harbour seals is three (Baird and Dill 1996). In the eastern Canadian Arctic median group size for predation observations was lowest for bowhead whale (4) and phocid predation events (2) and highest for monodontid (7) predation events (Higdon et al. 2011).

In conclusion, the best strategy supported by our modelling is for killer whales to stay with the nursing segment of the Eastern Canada-West Greenland bowhead population, where the return from an attack is much higher than for other kinds of prey. If attacks on prey are allocated with biases toward the large-bodied prey species, the number of attacks that killer whales must make in the course of the summer is manageable, but cetacean mortality may be on the margin of what is sustainable for the preferred prey population. If killer whales attack prey in proportion to their numbers (non-adaptive generalists), the resulting concentration on numerous, but small, prey requires killer whales to make very many attacks over the course of the summer. If the model was run with an assumed diet composition derived from sighting observations (adaptive generalists), the number of attacks a summer varied seasonally and predation pressure was distributed across prey groups. Results for the adaptive generalists foraging scenario calculated consumption rates more similar to reports of transient killer whales eating every day (Baird and Dill 1995, 1996; Williams et al. 2004; Dahlheim et al. 2009; Barrett-Lennard et al. 2011). Optimal foraging theory predicts that the more profitable prey is always included in the predator diet while the alternative, less profitable prey, is included only if the density of the more profitable prey decreases below a critical threshold (Charnov 1976; Chesson 1978). However, experimental and field studies (Stephens and Krebs 1986), including our results, indicate that the inclusion of less profitable prey type in the predator diet is more common than predicted by optimal foraging theory. The management and conservation implications of these results are largely unspecific due to the complexity of regulatory effects of predation in a multiple-prey system (Jefferson et al. 1991). Therefore, more research is necessary to predict changes in Arctic ecosystems with continued loss of sea ice including a need for understanding the effects of increasing killer whale predation in orchestrating distributional shifts of prey populations.

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