



Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions

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A central theme in ecology is the search for pattern in the response of a species to changing environmental conditions. Natural resource management and endangered species conservation require an understanding of density-dependent and density-independent factors that regulate populations. Marine mammal populations are expected to express density dependence in the same way as terrestrial mammals, but logistical difficulties in data acquisition for many large whale species have hindered attempts to identify population-regulation mechanisms. We explored relationships between body condition (inferred from patterns in blubber thickness) and *per capita* prey abundance, and between pregnancy rate and body condition in North Atlantic fin whales as environmental conditions and population size varied between 1967 and 2010. Blubber thickness in both males and females declined at low *per capita* prey availability, and in breeding-age females, pregnancy rate declined at low blubber thickness, demonstrating a density-dependent response of pregnancy to prey limitation mediated through body condition. To the best of our knowledge, this is the first time a quantitative relationship among *per capita* prey abundance, body condition, and pregnancy rate has been documented for whales. As long-lived predators, marine mammals can act as indicators of the state of marine ecosystems. Improving our understanding of the relationships that link prey, body condition, and population parameters such as pregnancy rate and survival will become increasingly useful as these systems are affected by natural and anthropogenic change. Quantifying linkages among prey, fitness and vital rates will improve our ability to predict population consequences of subtle, sublethal impacts of ocean noise and other anthropogenic stressors.

Keywords: cetacean, demography, density dependence, energetics, fecundity, marine mammal.

Introduction

The search for pattern in the responses of species to changing environmental conditions is a central task in ecology, natural

resource management, and endangered species conservation (Walther *et al.*, 2002). A key element of this task is to understand how population size may be regulated by density-dependent

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responses to available resources (Neubert and Caswell, 2000). Many studies have examined population regulation in large mammals using model species that are chosen in part for their ease of study (Saether, 1997; Pettorelli et al., 2002). Mammals are important predators in shaping marine ecosystems (Bowen, 1997). A better understanding of how marine mammal populations respond to a changing environment could allow us to use marine mammals as indicators of what is happening to the rest of the ecosystem (Moore, 2008). Human activities can alter the prey available to marine mammals through fishing, habitat degradation, climate-mediated changes in production, and by generating ocean noise that can mask the acoustic cues that whales may use to find prey (Clark et al., 2009; Williams et al., 2011). Changes in prey resources can be natural and anthropogenic, direct and indirect, and there are a number of research and management applications that would benefit from improved understanding of species responses to changing prey availability.

There are limited data for investigating density dependence in marine mammals compared to invertebrates, fish, small mammals, and ungulates (Fowler, 1981; Pettorelli et al., 2002). A very few well-studied cetacean populations suggest that density dependence exists (Fowler, 1984; Olesiuk et al., 1990), but the data are inadequate to suggest the shape of the underlying relationship (Taylor and DeMaster, 1993). Marine mammal populations are expected to express density dependence in the same way as terrestrial mammals; the failure to detect it may be a reflection of the difficulty in data acquisition for marine mammals (Fowler, 1981).

It is not entirely clear which aspect of marine mammal life history should demonstrate an effect of density dependence when availability of resources varies (Clutton-Brock et al., 1997). Drawing from the terrestrial literature, one study of wild reindeer (*Rangifer tarandus*) revealed a density-dependent response in juvenile survival, and resource limitation resulted in a delay in the time of calving (Skogland, 1985). A density-dependent effect on pregnancy rate has been shown in elk (*Cervus elaphus*), such that good summer feeding conditions were critical to accumulate sufficient body stores to buffer winter conditions (Stewart et al., 2005). No evidence was found for changes in Southern Hemisphere fin whale pregnancy rate as abundance declined due to whaling (Mizroch and York, 1985). Periods of reduced abundance of preferred prey were correlated with periods of reduced survivorship and fecundity in killer whales (*Orcinus orca*) (Ward et al., 2009; Ford et al., 2010). In field research on whales, logistical constraints generally require a definition of fecundity to incorporate both pregnancy rate and calf survival to a period (e.g. 6 months) when the calf is available for photo-identification.

As well as improving understanding of population regulation, knowledge of how marine mammals respond to a changing environment is essential for providing robust scientific advice for conservation and management of species that are threatened by human activities (Taylor and DeMaster, 1993). Marine environmental conditions are changing due to broad-scale impacts of natural and anthropogenic processes, and large whales will experience changes in *per capita* prey abundance as depleted populations recover from historical exploitation (Clapham et al., 1999). So far, the evidence for intra- or interspecific competition for prey in baleen whales is equivocal (Clapham, 1996).

Data available for North Atlantic fin whales (*Balaenoptera physalus*) offer a rare opportunity to investigate the density-dependent response of a large, long-lived marine mammal to changing environmental conditions. Fin whales are migratory, spending the

summers at high-latitude feeding grounds where they deposit energy reserves before leaving in autumn for breeding grounds at lower latitudes (Lockyer, 1987a; Vikingsson, 1995; Aguilar and Borrell, 1990). In Icelandic waters, fin whales are most common during May–September (Stefansson et al., 1997). Fin whales can live more than 90 years, but they feed on short-lived species. In Icelandic waters, they prey primarily on swarming euphausiids (especially northern krill, *Meganyctiphanes norvegica*) that display relatively volatile population dynamics (Vikingsson, 1997). Fin whale abundance in this region has been estimated from regular surveys since 1987 (Vikingsson et al., 2009). Previous work examining body condition of carcasses of whales hunted off Iceland from 1976–1988 has shown that the body fat stores of adult females increases as the summer feeding season progresses, and qualitative relationships have been shown between environment, body condition, and pregnancy rate of fin whales (Lockyer, 1987b; Vikingsson, 1995). A significant correlation was found between krill availability (from Continuous Plankton Recorder data) and age at attainment of sexual maturity for fin whales off west Iceland, but the underlying mechanisms for this relationship could not be explained (Sigurjonsson and Vikingsson, 1992).

We revisit and expand on previously described relationships using: (i) an additional 20 years of whale records; (ii) time-series of data on zooplankton biomass from the North Atlantic; and (iii) data on fin whale abundance as it recovers toward historical pre-whaling population size. Our objectives were to quantify relationships between body condition and *per capita* prey abundance, and between pregnancy rate and body condition as environmental conditions and population size (i.e. inferred from population trajectories informed by survey-derived estimates and catch statistics) varied between 1967 and 2010. We hypothesized that body condition would worsen as *per capita* prey abundance decreased, and that pregnancy rate may decline as body condition became poorer.

Material and methods

Whale data

Body condition

Anatomical measurements have been made in conjunction with whaling operations off southwestern Iceland since 1967 (Lockyer, 1986), and all data are stored at the Marine Research Institute, Iceland. Blubber thickness (in millimetres) has been measured at several places along the body of whales examined during this period, but the most consistently measured blubber thickness (recorded as “m4”) was taken around the middle of the body along the dorsal–ventral axis, and in line with the anterior edge of the dorsal fin along the anterior–posterior axis (Lockyer, 1987b) (Table 1). All measurements relating to body condition were highly correlated. We used the medial measurement of blubber thickness “m4” as a measure of body condition because it was measured most often, although as a check we repeated the analysis using the next most commonly recorded measurement, ventral blubber thickness (recorded as “v4”). Models attempting to explain variation in girth generally failed to converge, no doubt due to insufficient data. Only measurements taken on adult animals (male and female) were used.

Reproduction

Only measurements from adult, reproductive-age females were included in the reproduction analyses. For the purposes of this paper, whales were scored as either pregnant or not pregnant. Non-pregnant females (i.e. mature but not pregnant) included

those scored as resting, lactating, or ovulating. Non-lactating adult females were scored as pregnant if post-mortem examination recorded the presence of an embryo or foetus, a *corpus luteum* of pregnancy in the ovaries, or in some cases as a result of histological examination of the uterine mucosa (Lockyer and Smellie, 1985). This use of multiple lines of evidence minimizes the possibility that pregnancy became more detectable as the season progressed.

Zooplankton data

Three time-series of zooplankton data were available: (i) two transects surveyed north (Siglunes, 1967–2010) and southwest (Selvogsbanki, 1972–2010) of Iceland; and (ii) a broader-scale survey conducted under the Continuous Plankton Recorder programme (CPR, 1967–1986 and 2006–2010; courtesy D. Johns; see Data Reference). The Selvogsbanki transect samples zooplankton at a location close to the feeding grounds where Icelandic whaling takes place (Vikingsson, 1997). The Icelandic surveys were conducted in May–June with fine meshed (200- μ) Hensen nets (1967–1991) or WP2 nets (1992–present) towed through the upper 50 m at eight (Siglunes) or five (Selvogsbanki) sampling stations. After having measured the displacement volumes of the samples, they were either stored in 4% formalin or frozen until analysed in the laboratory ashore. For the present analysis, we used dry weight values derived from these samples (Matthews and Heimdal, 1980; Postel *et al.*, 2000), standardized per cubic metre of water filtered. The average biomass of total zooplankton sampled at each transect in grams (dry weight) per square metre was calculated by multiplying the per cubic metre values by the sampled depth (usually 50 m).

Although the CPR, Hensen, or WP2 nets are not very efficient for sampling adult euphausiids (Sameoto *et al.*, 2000; Wiebe and Benfield, 2003), the eggs and youngest larval stages are caught effectively by these gears. These three time-series do, therefore, provide information on relative, interannual variability in zooplankton density, including early-stage euphausiid recruits, available to feeding fin whales. We assumed that underestimation of large size classes of northern krill has remained relatively constant over time in all three datasets (Clutter and Anraku, 1968).

Although fin whales feed primarily on euphausiids in Icelandic waters (Vikingsson, 1997), copepods also appear in the diet. Previous studies have not attempted to quantify differences in the ability of total zooplankton or euphausiid biomass to predict fin whale body condition (Lockyer, 1987b). Since 1990, some of the zooplankton samples have been identified to species level. However, the aggregated biomass data are available since 1971, so the decision was made to use only the aggregated biomass data in this long-term analysis. An analysis of the species-specific data within the total zooplankton biomass counts off Selvogsbanki showed a good correlation ($r^2 = 0.5$) between log transformed number of krill [eggs and larvae (nauplii, calyptopis, furcilia)] and total biomass of zooplankton (A. Gislason, pers. comm.). Therefore, we consider total zooplankton biomass to provide a relevant proxy for prey abundance.

The Continuous Plankton Recorder (CPR) programme has used consistent sampling methods since 1946 to quantify relative abundance of zooplankton, including euphausiids, in the upper 10 m of the North Atlantic (Batten *et al.*, 2003; Letessier *et al.*, 2011). We extracted data on total euphausiid counts (mean number of individuals per sample, which equates to $\sim 3 \text{ m}^3$ of filtered seawater, towed over 10 nautical miles) from the region 59–

63°N 31–43°W (i.e. the same region sampled in Lockyer, 1987b). We used the summer (April–September) average euphausiid counts (Letessier *et al.*, 2011) as a proxy for euphausiids available to the North Atlantic fin whale population during the boreal summer feeding season at a large spatial scale.

Data from all three zooplankton time-series were converted to *per capita* prey abundance by dividing by fin whale abundance in each year. Fin whale abundance was obtained from modelled population trajectories from the International Whaling Commission (IWC) baseline implementation simulation trials for North Atlantic fin whales in the West Iceland and East Greenland subareas (International Whaling Commission, 2009). Results of the simulations differ depending on the assumed stock structure hypothesis and maximum sustainable yield (MSY) rate. We used results from simulations for the stock structure model called “hypothesis 1” and a MSY rate = 4%, which were considered by the Scientific Committee of the IWC to be the most plausible (International Whaling Commission, 2009).

Analytical methods

We adopted a two-stage modelling process. First day-of-year (Julian day), *per capita* prey abundance, fin whale body length, and reproductive category (male, pregnant female, non-pregnant female) were used to predict body condition (i.e. medial blubber thickness). Second medial blubber thickness of females was used to predict probability of pregnancy. We used data from both sexes in the first analysis because this allowed us to account for any differences between sexes or pregnancy status in blubber thickness—without doing this, any relationship between blubber thickness and *per capita* prey abundance could be due to changes in proportion pregnant (National Research Council, 2003). We used generalized additive models (GAMs) (Wood, 2006), using package *mgcv* in R version 2.15.2 (R Development Core Team, 2012) to allow for non-linear relationships between continuous covariates and response. Non-linear relationships were modelled using thin plate regression splines, with the amount of smoothness chosen using generalized cross validation (Wood, 2006); the gamma parameter within *mgcv* was set to 1.4 to prevent under-smoothing, as recommended by Wood, (2006).

For the body condition model, we initially used the subset of years for which prey abundance data were available for three prey abundance datasets. We regressed the natural log of medial blubber thickness (assumed normally distributed) on five candidate continuous covariates (day-of-year, body length, and *per capita* prey abundance at Siglunes, Selvogsbanki, and from the CPR programme), with reproductive category of whale as an additional factor covariate, using an identity link function. The log of blubber thickness was used because model diagnostics showed that this produced a more satisfactory distribution of residuals than untransformed blubber thickness. The three prey abundance variables were treated as alternatives in the modelling—i.e. at most one of them was entered into a model. A total of 53 candidate models were fit, ranging from simple models containing only a single covariate, through models with two, three, and four covariates, and finally to models where the effect of the continuous covariates were allowed to vary by reproductive category of whale (see Supplementary material for a full list of models). In the most complex model, day, body length, and *per capita* prey on blubber thickness were all allowed to differ between males, pregnant females, and non-pregnant females. For each model, we calculated the Akaike Information Criterion, adjusted for small

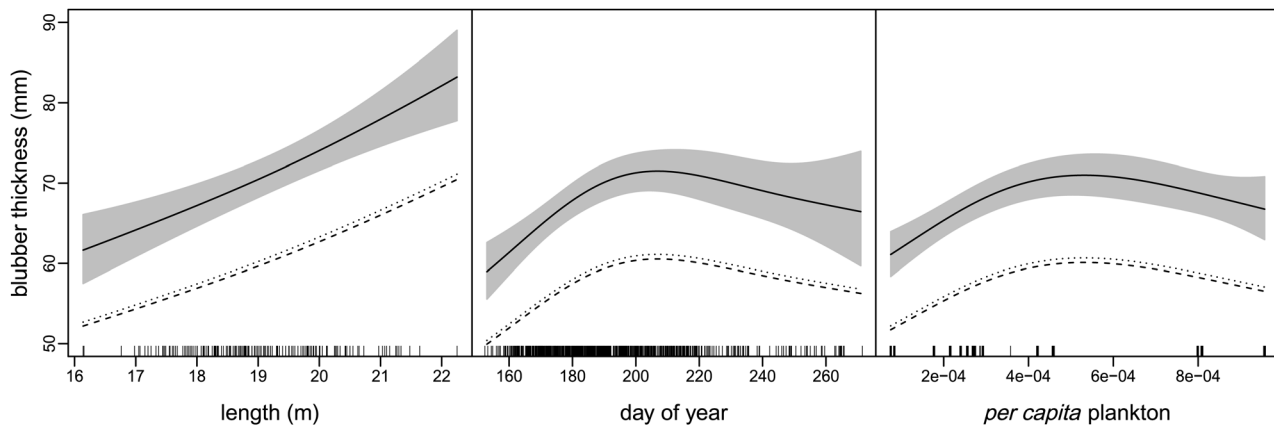


Figure 1. Component smooth functions from the selected body condition model (backtransformed from the logarithmic scale) to show the estimated relationship between medial blubber thickness (mm) and body length (m), day of year, and mean *per capita* plankton abundance on the Selvgosbanki transects (mean biomass of total zooplankton sampled along Selvgosbanki transects in grams (dry weight) per square metre, normalized by modelled abundance of whales in the population in that year). Solid, dashed, and dotted lines show the estimates for pregnant females, non-pregnant females, and males, respectively. Shading indicates the pointwise 95% confidence interval for the pregnant female estimate; confidence intervals for the other reproductive categories are omitted for clarity, but are of similar width. Short vertical lines along the bottom of each plot show the location of datapoints; for day of year and *per capita* plankton, these have been jittered slightly.

sample size (AICc), and we selected for inference the model with the smallest AICc value (Wood, 2006).

The selected model included *per capita* prey abundance sampled at Selvgosbanki (PC_Sel); this gave us the opportunity to refit the model using more data, since this was measured in three years when prey abundance at Siglunes was not. We, therefore, refit the best model, and other competitive models (those with AICc of < 3 higher than the best model), using the expanded dataset (see Supplementary data).

The pregnancy rate model regressed probability of pregnancy (assumed binomially distributed, with a logit link) against blubber thickness.

Results

Body condition

The initial model selection took place on 646 animals sampled in years for which all three prey abundance measures were available. The best model (according to AICc) included the covariates day-of-year, body length, *per capita* prey abundance sampled at Selvgosbanki and reproductive category, but did not include any interactions between type and the other covariates. The next most parsimonious model, with an AICc difference of 0.8, included the same covariates, but allowed the relationship between blubber thickness and body length to vary by animal type. Two other models were within 3 AICc points of the best model. A full list of the models and AICc statistics is given in the Supplementary data. None of these models included *per capita* prey abundance at Siglunes, so we were able to refit them using the additional three years for which data were available at Selvgosbanki, but not Siglunes, giving 771 animals for analysis. The same model was second best (see Supplementary material), but the AICc difference increased to 2.9. We selected the best model according to AICc fit to the extended dataset.

The estimated relationship between blubber thickness and the covariates in the final model is shown in Figure 1 (partial residual plots are given in the Supplementary data). Blubber thickness

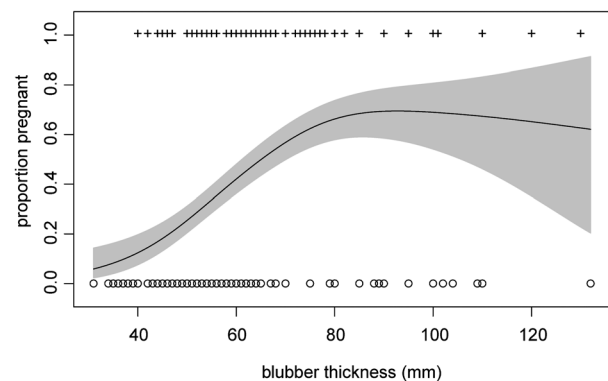


Figure 2. Estimated pregnancy rate as a function of medial blubber thickness (line), with 95% pointwise confidence interval (shading). Crosses and circles show data values for pregnant and non-pregnant females, respectively.

increased with day-of-year up to approximately day 210, thereafter levelling off or even possibly decreasing. Blubber thickness increased linearly with body length. Blubber thickness was lower during years with low *per capita* prey abundance, higher during years with medium *per capita* prey abundance, and similar or slightly lower during years with high *per capita* prey abundance. Finally, blubber thickness was higher in pregnant females than in non-pregnant females and males (Figure 1). Goodness-of-fit of the model was satisfactory (see Supplementary data), and the model had an adjusted r^2 of 0.24.

Analysis using ventral, rather than medial, blubber thickness (“v4”) showed very similar patterns, with an even stronger positive relationship between blubber thickness and *per capita* prey abundance (see Supplementary data).

Pregnancy rate

Whales with medial blubber < 50 mm thick had low probability of being pregnant (Figure 2). Whales with blubber thickness greater

Table 1. Sample size (number of individual whales in the database), by sex, for which each of eight morphometric measurements are available.

| | m4 | v4 | g3 | g5 | m3 | v3 | m5 | v5 |
|--------|-----|-----|-----|-----|-----|-----|-----|-----|
| Male | 848 | 774 | 238 | 243 | 141 | 176 | 237 | 237 |
| Female | 976 | 892 | 292 | 305 | 155 | 214 | 295 | 296 |

Sample size is shown for blubber thickness measurements taken in three well-defined locations along the anterior–posterior axis (i.e. 3–5 from anterior to posterior) and dorso–ventral axis (m = medial; v = ventral). In addition, sample size for girth (g) measurements is shown at two locations.

than ~75 mm had a high probability of being pregnant. At blubber thickness greater than ~100 mm, there was no obvious relationship between pregnancy rate and blubber thickness, likely due to small sample size at extreme values of blubber thickness and the constraint of this relationship being bound between 0 and 1.

Discussion

We show that body condition in fin whales off western Iceland increased with *per capita* prey availability measured near local feeding grounds, but reached an asymptote around the middle of the range of measured prey densities (Figure 1). This relationship takes into account that longer, and generally older, animals had thicker blubber, and that blubber thickness increased overall as the feeding season progressed from June–October (Figure 1). This was true for all reproductive categories (males, and pregnant and non-pregnant females), but blubber thickness was highest in pregnant females. This relationship is confounded, which serves as an important reminder that reproductive state itself affects body condition, with females needing to store energy when pregnant to cover the energetic cost of lactation. Superimposed on this physiological link, our new evidence suggests that nutritional status also influences pregnancy rate. Variation in fin whale body condition in response to these factors has been previously described qualitatively (Lockyer, 1987b), but not in relation to whale abundance. This is also the first time that an asymptotic relationship between body condition and *per capita* prey availability has been shown, such that below an apparent threshold body condition declines as prey availability declines, but above which surplus prey are not utilized to increase blubber thickness and thus improve body condition. We show that pregnancy rate is asymptotically related to blubber thickness in North Atlantic fin whales. Whales with thin blubber had a significantly lower probability of being pregnant than those with average blubber thickness, but extremely thick blubber had little effect on pregnancy rate (Figure 2). Many of the individual components of this suite of factors have been examined previously, e.g. by Lockyer (1986), and Miller *et al.* (2011). Considering *per capita* prey available to individuals in a population allows us to quantify a density-dependent response, and treating both steps (prey to condition, and condition to vital rate) in a unified statistical framework provides new parameter estimates to feed into subsequent population models to predict consequences of human perturbations of the environment. To the best of our knowledge, this is the first time relationships among the entire suite of these variables have been shown quantitatively for a large whale species.

The combination of the relationship between pregnancy rate and body condition and between body condition and *per capita* prey abundance is consistent with a density-dependent response in North Atlantic fin whale pregnancy rate. It is noteworthy that such a signal was detectable despite relatively small sample size,

substantial variability in the data and resulting low explanatory power of the fitted models, together with the well-known problems of tractability in studying marine mammals (Fowler, 1987). This finding is important because changes in body condition can show responses to changing ecological conditions long before demographic changes become apparent (Boyd, 2002; Moore, 2008). In red deer (*Cervus elaphus*), bioenergetic modelling has shown that, at high densities, females that had a calf in one year were unable to replenish energy reserves sufficiently to conceive the following year (Saether, 1997). Fin whales have a natural biennial reproductive cycle because of a long gestation (Lockyer, 1987b), but a similar mechanism may be causing the reduction in pregnancy rate at the low *per capita* prey abundance shown in our analysis. Investigation of atypically long calving intervals in North Atlantic right whales (*Eubalaena glacialis*) led Knowlton *et al.* (1994) to suggest that one mechanism in years of poor prey abundance could be early-term abortion, which would save the energetic cost of gestation as well as lactation. Bioenergetic modelling may help to improve our understanding of whether this is a likely mechanism for reduced pregnancy rate when prey is scarce for North Atlantic fin whales. Alternatives could include failure to conceive or ovulate, but presumably these mechanisms would have lent support for models with a one-year time lag. Physiological hormone monitoring offers a powerful tool to detect hormones associated with pregnancy using material collected from exhaled breath or faeces (Wasser *et al.*, 2000; Rolland *et al.*, 2012). Hormone studies offer the potential to detect pregnancies that are later lost, which makes them a powerful complement to studies of known individual animals, and we encourage future research to explore these powerful new tools.

Variation in body condition was best predicted by the time-series of zooplankton (including euphausiids and other zooplankton) counts sampled at Selvogsbanki, which is comparatively close to the location where whales were sampled. Oceanographically, it makes sense that the Selvogsbanki site better explains patterns of body condition in the whales sampled in this study. Our working hypothesis is that zooplankton found off the south coast would drift in currents westward along the south coast and northward along the west coast, and some may even be advected into the Irminger Sea (the main feeding area of the fin whales). Thus, the relationship with Selvogsbanki seems reasonable. In contrast, zooplankton sampled at the northern site (Siglunes) are likely to drift eastwards according to the prevailing current pattern, which would take those plankton away from the main feeding ground of the whales sampled in this study. In hindsight, it seems reasonable that we do not find a relationship for that series. The fact that euphausiid counts in the CPR data were not more informative is somewhat surprising. That said, none of the zooplankton time-series available is an ideal measure of the size class that the whales are actually targeting. Despite our use of proxies, the zooplankton data still provide meaningful relationships between body condition and prey. Better measures of prey density might improve them, and future work could seek better ways to quantify absolute abundance of krill in the whales' feeding grounds. Similar attempts to link variability in prey abundance to body condition and reproductive success in harbour porpoise (*Phocoena phocoena*) have been hindered by the use of fishery stock assessment data that do not reflect the quantity or quality of prey available to porpoises (Read, 2001).

In these analyses, body condition was measured from fin whales killed during whaling operations, but using lethal methods for

research is atypical and, for many researchers, impossible. However, even for difficult-to-study cetaceans, a number of emerging techniques allow us to measure the body condition of live animals. Photo- and laser-grammetric methods are being developed to generate length–girth relationships for right (Pettis *et al.*, 2004; Miller *et al.*, 2012), gray (Perryman and Lynn, 2002; Bradford *et al.*, 2012), and killer whales (Fearnbach *et al.*, 2011). An ultrasound method has been developed to measure blubber thickness in free-ranging North Atlantic right whales (Moore *et al.*, 2001). Linking these measurements to a long-term database of individuals with known reproductive histories allows studies of how environmental conditions can influence population dynamics through changes in body condition (Miller *et al.*, 2012). Telemetry methods have allowed measurements of body condition to be made during drift dives in foraging elephant seals (*Mirounga leonina*) (Biuw *et al.*, 2007), and further advances may make these tools available for cetaceans in the near future. Long-term photo-identification studies on humpback whales in the Gulf of Maine reveal that periods of relatively low calf survival were correlated with periods of relatively low prey [sand lance (*Ammodytes americanus*)] abundance in the year following weaning, although no information was available on body condition to develop mechanistic models (Robbins, 2007). Adding a photogrammetric body condition component to ongoing photo-ID studies will allow us to understand how individual health can translate to demographic effects in many other cetaceans (Fearnbach *et al.*, 2011).

It should be noted that we are drawing inference about body condition from blubber thickness. This is a defensible position, given the importance of blubber as a mechanism for energy storage in cetaceans (Lockyer, 2007), but blubber thickness is by no means the only or best metric of body condition. Lipid content can vary dramatically in blubber strata and through time (Aguilar and Borrell, 1990), which is why it is important that this dataset measured blubber thickness at the same anatomical location over time. Emerging techniques may allow us to infer cost of living and condition from other tissues and other indicators from blubber (e.g. mitochondrial density or lipid content in muscle, (Spitz *et al.*, 2012). Depending on logistical constraints imposed by the study animal, other body condition indices could include mass (as it varies by age, sex, and season), girth, blubber thickness and lipid content, and many measures of blood chemistry, haematology, or immunocompetency (Wells *et al.*, 2004).

One of the most important tasks we face in ecology and conservation biology is to predict how populations will respond to natural and environmental variation so that the additional impact of anthropogenic activities can be assessed (Coulson *et al.*, 2000; Benton *et al.*, 2006). A major unknown in marine ecology is the likely response of zooplankton communities, including krill, to an increasingly warm and acidic sea (Hays *et al.*, 2005; Kawaguchi *et al.*, 2011). As we try to predict how large whales and other marine mammals will respond to changing prey availability—due to both natural and anthropogenic processes—it is essential to improve our understanding of the relationships that link prey, body condition, and population parameters such as pregnancy rate and survival.

Supplementary data

Supplementary material is available at *ICES Journal of Marine Science* online, giving analysis, expanded methods, and results.

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