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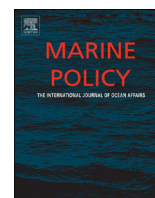
Gauging allowable harm limits to cumulative, sub-lethal effects of human activities on wildlife: A case-study approach using two whale populations

Rob Williams [a,*], Len Thomas [b], Erin Ashe [a], Christopher W. Clark [c], Philip S. Hammond [a]

[a] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews KY16 8LB, Scotland, UK
[b] Centre for Research into Ecological & Environmental Modelling, The Observatory, University of St Andrews, St Andrews KY16 9LZ, Scotland, UK
[c] Bioacoustics Research Program, Cornell Lab of Ornithology, 159 Sapsucker Woods Rd., Ithaca, NY 14850, USA

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ABSTRACT

As sublethal human pressures on marine wildlife and their habitats increase and interact in complex ways, there is a pressing need for methods to quantify cumulative impacts of these stressors on populations, and policy decisions about allowable harm limits. Few studies quantify population consequences of individual stressors, and fewer quantify synergistic effects. Incorporating all sources of uncertainty can cause predictions to span the range from negligible to catastrophic. Two places were identified to bound this problem through energetic mechanisms that reduce prey available to individuals. First, the US Marine Mammal Protection Act's Potential Biological Removal (PBR) equation was used as a placeholder allowable harm limit to represent the number of animals that can be removed annually without depleting a population below agreed-upon management targets. That rephrased the research question from, "How big could cumulative impacts be?" to "How big would cumulative impacts have to be to exceed an agreed-upon threshold?" Secondly, two data-rich case studies, namely Gulf of Maine humpback and northeast Pacific resident killer whales, were used as examples to parameterize the weakest link, namely between prey availability and demography. Given no additional information, the model predicted that human activities need only reduce prey available to the killer whale population by ~10% to cause a population-level take, through reduced fecundity and/or survival, equivalent to PBR. By contrast, in the humpback population, reduction in prey availability of ~50% was needed to cause a similar, PBR-sized effect. The paper describes an approach – results are merely illustrative. The two case studies differ in prey specialization, life history, and, no doubt, proximity to carrying capacity. This method of inverting the problem refocuses discussions around what the level of prey depletion – via competition with commercial fisheries, displacement from feeding areas through noise-generating activities, or acoustic masking of signals used to detect prey – would have to occur to exceed allowable harm limits set for lethal takes in fisheries or other, more easily quantifiable, human activities.

1. Introduction

Pressing challenges in wildlife conservation and natural resource management include the need for research methods to quantify cumulative impacts of both lethal and sub-lethal stressors on impacted populations, and policy decisions about allowable harm limits [1]. As direct and indirect human impacts on animal populations grow (e.g., via habitat degradation; displacement from important habitats; competition with fishing for prey species; bycatch in fisheries; or pollution, including chemical and noise pollution), guidance is needed to identify reference points and prioritize mitigation measures before declines become irreversible [2,3]. Previous attempts to quantify cumulative impacts of anthropogenic activities have faced a common set of problems [4,5]. Few studies quantify population consequences of individual stressors, and fewer still quantify synergistic effects [6]. Incorporating all sources of uncertainty can cause predictions with such large confidence intervals as to become practically useless in real-world decision-making. Given these difficulties, it is no surprise that cumulative impacts are poorly handled in environmental assessments and impact assessments [7].

Much progress has been made in fundamental research to develop tools that can ultimately predict population consequences of

* Corresponding author.
  E-mail address: rmcw@st-andrews.ac.uk (R. Williams).

cumulative impacts of multiple sublethal stressors, but current policies set standards that science is poorly equipped to reach. Consider exposure of marine mammals to ocean noise. The US National Environmental Policy Act requires that a judgement call be made regarding whether a proposed project will cause a "negligible" effect [8], which implies an ability to relate the number of marine mammal "takes" relative to population size. Conceptually, this standard is similar to the way other statutes (e.g., US Marine Mammal Protection Act) assess sustainability of bycatch of marine mammals in fisheries [9], except that (a) the term "negligible" has a clearly defined meaning in the context of bycatch under MMPA, and (b) numbers are vastly harder to estimate when dealing with many cryptic, sublethal stressors than counting by-caught animals in well-monitored fisheries. Given the rapid growth of human populations and economies, and resulting industrialization, simple decision-support tools and guidance are needed urgently [5].

To date, efforts to quantify cumulative impacts of multiple sublethal stressors on marine mammal populations fall short of estimating population consequences in absolute terms. This is not a criticism of the science. The task at hand is extremely complex; it may be unreasonable to set policies that hinge on an ability to quantify whether cumulative human impacts on a population, let alone an ecosystem, are negligible. Emerging techniques are heading in that direction, but so far, cumulative human impacts models tend to stop at the point of conceptual frameworks [10] or decision-support tools to prioritize which stressors may be most important in a system [11]. Newer methods are combining quantitative, qualitative and expert-driven models to consider relative magnitude and direction of various anthropogenic threats [12], and a number of studies have used spatially explicit methods to map how various threats are superimposed [13,14].

Recent progress made in understanding how multiple sublethal stressors interact is impressive, but in order to make that progress, some important simplifying assumptions have had to be made, including *inter alia*: the assumption that all stressor layers are of roughly equal importance; subjective decisions in how to put different kinds of stressors in the same currency (i.e., how to normalize them); an untenable or untested assumption that stressors combine in a linear way; an untenable or untested assumption that species or ecosystems respond to individual and cumulative stressors in a linear way; and reliance on expert judgement in how to weight vulnerability of species or ecosystems to various stressors [15]. Simplifying assumptions about how to combine multiple stressors are particularly important. Cumulative impacts can be additive, synergistic or antagonistic (i.e., compensatory) [16]. In the absence of methods to quantify effects one expects to be synergistic (i.e., that the whole should be greater than the sum of its parts), many methods simply sum individual stressors in an additive way [15].

As marine ecologists and statisticians develop increasingly sophisticated methods to estimate absolute numbers of individuals in a population that may be harmed or killed by the cumulative effect of sublethal injuries (e.g., [17]), a number of applied methods are underway to elide some of the more data-sparse steps in that process to generate rules of thumb about whether a particular activity or development is likely to cause greater than negligible effects. One such rule of thumb relates to the time it takes a marine community to recover from a given perturbation [18], which was used to gauge retrospectively the cumulative impacts arising from two alternative fishing methods. Although simplification necessitates loss of detail, it may be logistically impossible (or ethically unacceptable) to measure whether every pairwise combination of effects combine in a linear or nonlinear way [19] and it may never be possible to predict synergistic effects of all possible combinations of multiple stressors. Even if such an exercise were possible, the low precision on any prediction means that a subjective decision may still need to be made about how precautionary a regulator wants to be when comparing a statistical distribution of predicted effect sizes to an allowable harm level.

This paper inverted the problem by starting at the "allowable harm" side of the equation, which reflects a policy decision that may differ from one jurisdiction to another. Two places were identified to bound this problem for activities that may affect wildlife through energetic mechanisms that reduce prey available to individuals. First, allowable harm was quantified relative to a pre-defined and quantitative limit, namely to the mathematically equivalent mortality levels that would be deemed unacceptable for bycatch in well-monitored fisheries. The US Marine Mammal Protection Act's Potential Biological Removal (PBR) equation [9] was used as a placeholder allowable harm limit to represent the maximum number of animals that can be removed annually without compromising a population's recovery to agreed-upon management targets of optimum population size. That rephrased the research question from, "*How big could cumulative impacts be?*" to "*How big would cumulative impacts have to be to exceed this agreed-upon threshold?*" The primary objective was to introduce a new conceptual approach that makes incremental progress on an important topic in marine policy and management. There are specific policies guiding the implementation of PBR for managing fisheries bycatch [9]. The intent here was not to replicate exactly how PBR is implemented, and no attempt was made to reproduce how managers in the USA might respond when a population warrants listing under the Endangered Species Act. On the contrary, the overarching objective was to describe a flexible approach, starting with any given allowable harm limit, based on a stochastic simulation. The computer code used to illustrate the approach is freely available [20]; this code can readily be modified to replace PBR with any quantitative population-level reference point or management objective, such as the New Zealand MAL-FIRM limit, an IWC rule of thumb that any mortalities exceeding 1% of population size warrant closer attention, or fisheries bycatch limits agreed upon under ASCOBANS (reviewed in [21]). Secondly, long-term studies of northern and southern resident killer whales (northeast Pacific) and Gulf of Maine (northwest Atlantic) humpback whales were used to illustrate the approach by parameterizing the weakest link, namely the one between prey availability and demography (calf and/or adult survival, and/or fecundity). The code can also be adapted to any marine or terrestrial species for which a prey-demography link exists, and an allowable harm limit can be specified.

Inverting the problem permits more tractable future research questions that assess whether all human activities in a region could conceivably reduce prey in the environment or available to wildlife. The intent is not to advocate use of these models in decision-making directly when assessing the risks associated with a single proposed industrial development application. Instead, this approach is intended to help focus discussions about the magnitude of the cumulative risks of all industrial activities in a region, and the plausibility that cumulative sublethal impacts (i.e., reduced fecundity and survival) could cause population-level effects that regulators would not tolerate if they were caused by direct mortality in fisheries.

2. Methods

Matrix-based population models were constructed that incorporated annual stochasticity in prey availability in the environment, demographic parameters, and an index representing proportional reduction of the amount of prey in the environment made available to animals. Ideally, one would construct fully

parameterized, mechanistic models linking each step between stressor and population dynamics [1]. In practice, such linkages are difficult to parameterize for most species, and synergistic effects may take many years to quantify. Published prey-demography links were used to allow these steps to be elided, solve for the effect size it would take to reach pre-determined allowable harm limits, and work backward from there. The following section first describes the simulation approach, and then describes its illustrative application to two hypothetical whale populations. Although the underlying demographic parameters and prey-demography relationships were drawn from three specific populations (northern and southern resident killer whales, and Gulf of Maine humpback whales), the method was illustrated with hypothetical populations of humpback and killer whales similar in number to those reported off British Columbia, Canada [22]. The choice of geography for the case studies was driven by the number of large industrial development applications (e.g., port expansions, liquefied natural gas terminals, and oil pipelines and associated tanker traffic) proposed for the region [23]. The decision to use a hypothetical killer whale population intermediate in size between northern and southern resident killer whales was driven by the desire to avoid having to reconstruct separate prey-demography relationships for the two populations and because some prey-demography linkages are a decade out of date. Because the models report risk in relative terms, initial population size is somewhat irrelevant when illustrating the approach. That said, the underlying prey-demography links come from populations in particular states, including being at specific fractions of carrying capacity, and one would not want to substitute prey-demography links from populations at very different states.

2.1. Simulation approach

Species were identified where estimates of age- and sex-specific demographic parameters were available from the literature, as well as quantified relationships between one or more demographic parameters and environmental indices related to prey availability. For each species, 1000 simulation runs were performed. Each run consisted of the following steps (Fig. 1).

First, an initial population of animals were simulated, using a fixed total population size and assigning animals randomly to sex and age classes by drawing from a multinomial distribution, with probabilities taken from the stable sex and age structure given the mean of the environment indices for each species. This stable age structure was calculated empirically by simulating the population stochastically in time under the mean environment for 200 years from an arbitrary start point that assumed equal numbers in each age and sex class, and taking the sex and age ratio at the end of the simulation. An alternative would be a deterministic approach, namely taking the dominant eigenvector of the Leslie matrix corresponding to the mean value of environmental indices (see, e.g., [24]).

Second, the population was projected forward one year, assuming no prey reduction. To do this, a random year was sampled from the environment indices and, given this, random binomial quantiles were drawn for survival in each sex and age class and for fecundity in each female age class.

Third, the population was projected forward again from the same start point, but this time assuming ten different values of prey reduction ranging from 0.1 to 1.0 (with 0.1 corresponding to a 10% reduction in prey availability; and 1.0 corresponding to all prey in the environment being made inaccessible to the whale, via masking, habitat displacement or behavioural disruption). In doing this projection, the same environmental index and binomial quantiles were used, thereby removing the "noise" caused by environmental and demographic stochasticity so that differences in
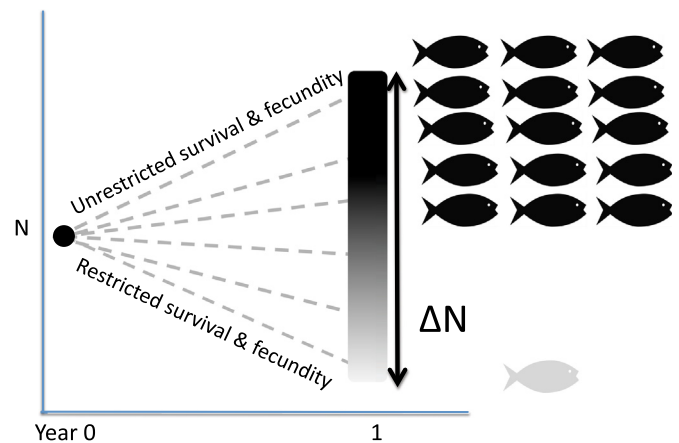

Fig. 1. Conceptual diagram of statistical approach to reverse-engineering allowable harm limits, taking into account demographic and environmental (illustrated by fish) stochasticity, and cumulative anthropogenic impact (illustrated by dashed lines effectively reducing fish in the environment made available to whales). Populations are projected forward by one year under some random value of prey abundance, which is incrementally reduced by 10% intervals. At each step, the differences in total population size between the undisturbed scenario and each of the prey reduction scenarios were calculated, referred to subsequently as ∆N. Each of these differences were then divided by the value of Potential Biological Removal (PBR) for the species, to yield a set of scaled differences normalized to the abundance of each species, called the "population-level effect", in units of multiples of the allowable harm limit. The process is repeated 1000 times for each species.

projected population sizes between projections were caused solely by prey reduction.

Fourth, the differences in total population size between the undisturbed scenario and each of the prey reduction scenarios were calculated, referred to subsequently as ∆N. Each of these differences were then divided by the value of Potential Biological Removal (PBR) for the species, to yield a set of scaled differences normalized to the abundance of each species, called the "population-level effect". If the value is more than 1, then anthropogenic impacts were predicted to remove more than the equivalent of PBR (i.e., more than the population can withstand, according to the allowable harm definition specified in the model), via reduced survivorship, fecundity or both. PBR was calculated according to the standard formula [9]:

$$PBR = N_{min} * 0.5(R_{max}) * F_r, \tag{1}$$

where N_{min} is the 20th percentile of the lognormal population estimate; $0.5(R_{max})$ is one-half the maximum theoretical growth rate of the population at small population size; and a recovery factor (F, ranging from 0.1 to 1.0) is set to be more precautionary for endangered populations than healthy ones. To obtain values of N_{min}, a coefficient of variation on each population size estimate was set to 20%, and true population sizes were assumed to be equal to the initial population sizes.

2.2. Illustrative example: killer whales

Two fish-eating, "resident" populations of killer whales in the northeastern Pacific Ocean show extreme specialization on salmon, especially the largest species, Chinook salmon [25]. Chinook numbers were found to affect both survival and fecundity of killer whales based on prey-demography relationships measured on northern resident killer whales between 1973 and 2005 [26] and southern resident killer whales between 1981 and 2007 [27]. These two papers used slightly different indices of Chinook abundance (based on catch-per-unit-effort statistics); a simple linear least-squares regression was used to derive a relationship between them (adjusted R^2 of the fit 0.99) and to convert the

Chinook indices used in the fecundity study [27] to estimates of the Chinook indices used in the survival study [26]. Age- and sex-specific survival values were given for years with good and bad environmental conditions [26]. Good conditions occurred in 2002 and 2003 and had a mean Chinook index of 1.32; bad conditions occurred in 1995–2000 inclusive and had a mean Chinook index of 0.65. Linear interpolation/extrapolation was used to forecast survival probability under other Chinook index values. Although linear extrapolation could, in theory, produce negative values for survival, the lowest value observed in practice was for 22–26 year old males, which were assigned survival probabilities of 0.68 under full prey reduction (survival was 0.81 and 0.96 under Chinook indices of 0.65 and 1.32, respectively, with no prey reduction). In any case, results for large prey reduction are based on extrapolation and should therefore be treated with caution. To forecast fecundity rate, the nonlinear relationship between logit-transformed age-specific fecundity and Chinook index (i.e., Table 1 and Fig. 2 in Ward et al.) was used; again this involved extrapolation at high levels of prey reduction, although because of the logit transform there was no danger of predicting a fecundity less than 0.

The simulation assumed a starting population size of 200 (loosely based on [22]), which meant that N_{min} was 169 and the PBR 1.69. Following [26], the simulation used 51 age classes. Environmental conditions (Chinook index) were simulated for each year by drawing at random from the observed values.

2.3. Illustrative example: humpback whales

For humpback whales, a variety of models was considered but the only significant prey-demography relationship found in a long-term (1988–2003) study of Gulf of Maine humpback whales was between sand lance abundance and calf survival [28]. Interannual variability in sand lance abundance was quantified using data from stratified bottom trawl resource surveys conducted twice annually by Northeast Fisheries Science Center (Woods Hole, MA), from the Gulf of Maine to North Carolina [28]. The sand lance index is reported in units of the mean number of individuals caught per standard tow. Robbins found no support from the data for a model linking heterogeneity in adult survival to abundance of prey, which may reflect the diverse diet of the Gulf of Maine humpback whale rather than a lack of a relationship *per se*. At extremely low values of prey abundance, one would expect to see effects of prey depletion on both calf and adult survival. The highest sand lance abundance index (3138 sand lance per tow) was in 1988 and the lowest (19 sand lance per tow) was in 1990; calf survival was assumed to vary linearly between these bounds, from 1.0 to 0.63, while adult survival was fixed at 0.96. For the simulation, values for the environment index were drawn from a uniform value between these bounds. Since the lowest sand lance index was close to 0, very little extrapolation of calf survival was required even for the high prey reduction scenarios.

An arbitrary starting population size of 2000 animals was used, giving an N_{min} for humpback whales of 1693 and the PBR 16.9. The humpback model used 7 age classes, with age at first breeding of 6 and an inter-birth interval of 2.36 years [28].

3. Results

Models were constructed using demographic parameters drawn from two well studied marine mammal species, in order to mimic the dynamics of a hypothetical killer whale and humpback whale population. Before presenting results, some caveats must be made. Taken at face value, the models predict a larger population-level consequence of prey depletion in killer whales than in
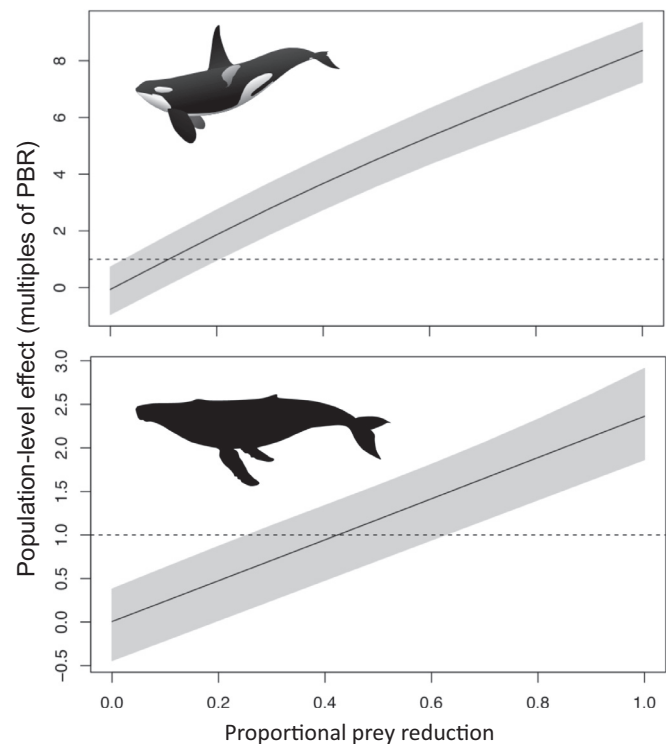

Fig. 2. Model outputs (i.e., tentative results and 95% confidence intervals in the shaded polygon around the regression) are shown for a killer whale (top) and humpback whale (bottom) population, at varying levels of proportional prey reduction over historical averages. In the two whale case studies, horizontal dashed lines are shown at a placeholder allowable harm level (y=1 represents default values of the Potential Biological Removal, or "PBR", equation under the US Marine Mammal Protection Act), and the y axis is plotted in multiples of 1 for ease of visual interpretation. In practice, managers would set lower values of PBR as stocks were depleted and listed under relevant statutes (e.g., Endangered Species Act), and managers in other jurisdictions or managing other taxa may set higher or lower allowable harm limits. Negative values on the y axis indicate that in some stochastic simulations, the population did better in the prey reduction scenario than the undisturbed scenario, particularly when there were very low levels of prey reduction. Values > 1 mean that the population reduction under the prey reduction scenario was larger than the PBR.

humpback whales (Fig. 2). These results are illustrative, not conclusive. This apparent difference is a function of available data on prey-demography relationships, given the status of the population at the time of study (e.g., population size relative to carrying capacity), and the volatility of the prey base during the period of study. While the knowledge base grows to quantify ecological (prey-demography) relationships on a larger number of demographic parameters and taxa, it is presently possible to model prey-demography relationships with only a handful of long-running cetacean studies, which began in earnest in the 1980s [29]. Consequently, empirical data on whale population dynamics are available only across the ranges of population size relative to carrying capacity and prey abundance observed during the years of those studies. Because many whale populations were hunted to extremely low levels, there is a lack of information on whale population dynamics near carrying capacity. The primary objective was to introduce this conceptual approach, and there is no intention to imply a robust result that would allow inter-specific comparisons to be made at the present time.

Given no additional information, models predicted that human activities need only reduce prey available to killer whales by ~10% to cause a population-level take (i.e., through reduced fecundity and/or survival) equivalent to PBR. If human activities reduced killer whale prey intake by 50%, this would cause the net

population-level effect on killer whales of removals four times as high as the PBR limit.

For humpback whales, removing ∼50% of sand lance was predicted to cause sufficient reduction in calf survival to reach the equivalent of a PBR-sized effect. A 10% reduction in sand lance would cause effective removals of ∼0.25 of PBR, whereas a 90% reduction in sand lance was predicted to cause PBR to be exceeded by a factor of 2 (Fig. 2).

4. Discussion

The logistical and statistical problems inherent in quantifying population-level impacts of multiple, sublethal stressors on wildlife has caused many agencies to give superficial treatment to cumulative human impacts in environmental impact statements and other conservation, management and policy actions [5]. The current study offers a new way for managers and policy-makers to contextualize any discussion of cumulative impacts to marine mammal populations. By inverting the problem, the relevant scientific question becomes more tractable, namely from "How big could the cumulative impacts of a proposed project be?" to "How big would the cumulative impacts of a proposed project have to be to exceed a threshold already agreed-upon in other policy arenas?" There are important issues to be resolved before this approach is taken from a conceptual approach to implementation, but we believe that the case studies illustrate reasonable starting points for discussion. Importantly, the results of the case studies are based on empirical measurements from species that have been studied for decades. The tentative estimates of population consequences of anthropogenic reduction in average prey base should apply to other populations of the species at a similar state of N/K as the case study populations were during the time the prey-demography links were quantified. Clearly, the further away in time between measurement and application in a risk assessment framework, the less reliable the inference becomes. An important caveat is that our predictions rely on relatively large extrapolations in cases of large prey reduction scenarios. These are linear extrapolations and should not be considered reliable. Although fairly large fluctuations in prey density have been observed over time, we lack information on behaviour of either population at extremely low densities of prey, which may become important for human activities predicted to have large impacts of prey available to wildlife populations. Parameterizing the extremely low end of prey-demography links for other scenarios may require a focused review of cases where large die-offs of mammalian populations have been attributed conclusively to starvation [30,31].

Raw time-series data exist that would allow us to answer the latter question for many marine mammal and seabird populations (e.g., [32], but those datasets may require reanalyses [33–38]). Generating a rough estimate of allowable harm limits is a useful placeholder value to have as ecological and statistical studies improve the ability to predict the population consequences of multiple stressors [5,15]. There is a need for active dialogue at the science-policy-stakeholder interface to assess (a) a population's ability to sustain a given level of cumulative impacts of multiple stressors; and (b) how likely it is that human activities are exceeding that threshold. This problem touches on both policy decisions and natural sciences, and progress on this topic will inherently involve interdisciplinary work.

The approach used in this paper deliberately elides certain steps where data are lacking, but this shortcoming is intended to be resolved in an iterative fashion as new information becomes available. Perhaps the most serious limitation of these methods is the fact that density dependence affects demographic parameters, so the prey-demography relationships used were measured on populations that may be undergoing density dependent regulation and therefore just apply to the population levels during those three long-term studies [26–28]. The methods in this paper only predict forward for a short time interval (one year); longer-term predictions will require information on how other populations behave at various fractions of carrying capacity. The method presented here is intended to gauge allowable harm limits roughly that can be articulated in the following way: based on past behaviour of the population in question, it is predicted that, say, a 5, 10 or 50% reduction in prey intake would cause a population-level effect that would be deemed unsustainable in the context of fisheries bycatch management. Note that these limits only include reduction in prey, and do not include other impacts, such as physiological stress [39], effects of contaminants on reproduction or survival [40], or a reduction in survival or fecundity caused by physiologically induced immunosuppression [41]. These models are designed to complement ongoing efforts to assess how big cumulative human impacts could be relative to population size, via reduction in prey intake via habitat displacement from key feeding grounds [42,43], masking acoustic cues used in finding prey [44], increased energetic cost of avoiding human activities [45], behavioural disruption of feeding [46,47] or reduced pregnancy rates via prey-mediated effects in foraging and body condition [35]. The models are meant to place the above-mentioned cumulative impacts assessment efforts in the context of an allowable harm limit framework, by focusing future empirical research efforts or expert elicitation to gauge whether it is conceivable that human activities could be causing a reduction in prey intake large enough to cause a population-level effect that policy-makers have called unsustainable in some other policy arena.

In our view, the paucity of robust prey-demography links may be the biggest barrier to implementing this approach. It is hoped that this approach will encourage colleagues to re-examine evidence for prey-demography relationships in long-term datasets on marine predators, given the ease of incorporating prey as a covariate in mark-recapture models [48] and the increasing number of time series of prey species (e.g., RAM Legacy Stock Assessment Database [49] or the Sir Alister Hardy Foundation for Ocean Science's Continuous Plankton Recorder database). We hope that this conceptual approach may provide impetus to re-examine valuable time-series data on well studied populations where quantitative, explicit prey-demography links could be derived (e.g., Antarctic fur seals and penguins [50]; Arctic marine mammals and seabirds [51]; eastern North Pacific gray whales [52]; or northern and southern right whales [53]).

There are several practical benefits to inverting the problem to estimate the effect size needed for cumulative impacts to exceed an agreed-upon threshold, as long as the limitations, assumptions and caveats are specified clearly. On the scientific side, there are many emerging techniques to quantify the effects of reduction in prey biomass on predator fitness or productivity [17,38]. On the policy side, once a limit of acceptable change has been estimated (e.g., using the statistical method presented here), many well-established policy instruments and market-based initiatives are available to allocate those lethal or sublethal takes across sectors or among players operating within a system [54]. Taken together, the scientific development presented here, in a progressive policy arena, would collectively offer a constructive way to improve the evidence base for identifying sustainable limits to cumulative, sublethal human impacts on wildlife species. This philosophy is well established in many environmental markets for pollutants. For example, the US Environmental Protection Agency sets a Total Maximum Daily Load to restore the Chesapeake Bay, which populates a "pollution diet" (of aquatic nitrogen, phosphorus and sediment discharges) to be allocated among states or watersheds. In future, model outputs from an approach like the one presented

here could be used to set caps analogous to those used in ensuring good air quality or markets in carbon, nitrogen, sulfur or other gaseous emissions [55,56]. Fisheries management already uses similar methods to set total allowable catch and a variety of methods to allocate quotas for target and non-target species, as well as rights-based management and incentives for responsible fishing. If a regulator were to set total allowable harm limits to marine mammals from industry-wide oil and gas exploration and extraction activities in the Arctic or the Atlantic, for example, one could imagine the sector learning from fisheries management experience in (1) risk pools, which allow access to resources without trading quotas on the open market, and (2) buffer quotas, if a particularly vulnerable species ("choke species") becomes an impediment. When managers set industry-wide allowable harm limits, industry players have proven remarkably inventive at modifying activities in mixed fisheries if the consequence is closing a fishery prematurely when target or bycatch quotas are exceeded [57–59].

All of the above-mentioned common-pool resource management and allocation examples require policy-makers to specify quantitative limits to unintended harm to species. When it comes to cumulative impacts of multiple human stressors, the focus thus far has been on the difficulty in calculating effect size [14]. Starting with a population-level effect that policy-makers have already articulated as a limit offers a tractable way forward to design future studies to assess whether human activities are exceeding those limits, and offers a strong incentive for stakeholders operating in a common-pool resource framework to innovate and share information on best practices. If this approach were adopted for marine mammals, there are already opportunities to work within existing management cycle frameworks [5]. Bureau of Ocean Energy Management (BOEM) recently issued a programmatic environmental impact statement (PEIS) listing risks associated with all outer continental shelf oil and gas exploration and extraction lease sales over the 5-year period, 2012–2017 [60]. A similarly large-scale review was conducted by the U. S. National Marine Fisheries Service to evaluate the aggregate risk of all proposed scientific research on endangered Steller sea lions, in order to avoid the underestimation of cumulative impacts that could arise by evaluating each individual permit application in isolation [61]. The approach presented here could introduce a quantitative element to many similar exercises that are currently qualitative. As offshore renewable energy developments evolve from planning to build-out stage throughout European waters, this paper's approach would facilitate an effort to gauge whether the cumulative effect of multiple sublethal threats on harbour porpoise [43] or a chronic loss of acoustic communication space [62] could lead to reduced prey acquisition that would cause unacceptable population-level changes. The approach might be helpful for placing the risk of proposed industrial developments in the Arctic in the broader context of climate-mediated changes that some species, such as polar bears, are already facing [63].

5. Conclusion

Many human activities can interact to reduce the prey available to marine wildlife populations, via competition with commercial fisheries, displacement from feeding areas through noise-generating activities, or acoustic masking of signals used to detect prey. Predicting population consequences arising from multiple anthropogenic activities has suffered from lack of empirical data and resulting measures of uncertainty that make predictions of limited value to management. Inverting the problem refocuses discussions around the level of sublethal impacts, via prey depletion, it would take to exceed allowable harm limits that have

been set for lethal takes in fisheries or other, more easily quantifiable, human activities. The goal is not to lead managers to a go/no-go decision, but rather to help researchers, managers and stakeholders focus conversations and dedicate targeted research efforts to gauge whether cryptic, sublethal stressors could collectively add up to levels that policy-makers have already articulated as being large enough to warrant management or mitigation.

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