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A metapopulation model for whale-fall specialists: The largest whales are essential to prevent species extinctions

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ABSTRACT

The sunken carcasses of great whales (i.e., whale falls) provide an important deep-sea habitat for more than 100 species that may be considered whale-fall specialists. Commercial whaling has reduced the abundance and size of whales, and thus whale-fall habitats, as great whales were hunted and removed from the oceans, often to near extinction. In this article, we use a metapopulation modeling approach to explore the consequences of whaling to the abundance and persistence of whale-fall habitats in the deep sea and to the potential for extinction of whale-fall specialists. Our modeling indicates that the persistence of metapopulations of whale-fall specialists is linearly related to the abundance of whales, and extremely sensitive (to the fourth power) to the mean size of whales. Thus, whaling-induced declines in the mean size of whales are likely to have been as important as declines in whale abundance to extinction pressure on whale-fall specialists. Our modeling also indicates that commercial whaling, even under proposed sustainable yield scenarios, has the potential to yield substantial extinction of whale-fall specialists. The loss of whale-fall habitat is likely to have had the greatest impact on the diversity of whale-fall specialists in areas where whales have been hunted for centuries, allowing extinctions to proceed to completion. The North Atlantic experienced dramatic declines, and even extirpation, of many whale species before the 20th century; thus, extinctions of whale-fall specialists are likely to have already occurred in this region. Whale depletions have occurred more recently in the Southern Hemisphere and across most of the North Pacific; thus, these regions may still have substantial "extinction debts," and many extant whale-fall specialists may be destined for extinction if whale populations do not recover in abundance and mean size over the next few decades. Prior to the resumption of commercial whaling, or the loosening of protections to reduce incidental take, the impacts of hunting on deep-sea whale-fall ecosystems, as well as differential protection of the largest whales within and across species, should be carefully considered.

Keywords: Whaling, whale fall, whale-fall specialist, metapopulation model, habitat loss, extinction

1. Introduction

The bodies of great whales (baleen and sperm whales) form the largest detrital parcels in the ocean, and their sunken carcasses (i.e., "whale falls") can create organic-rich habitat

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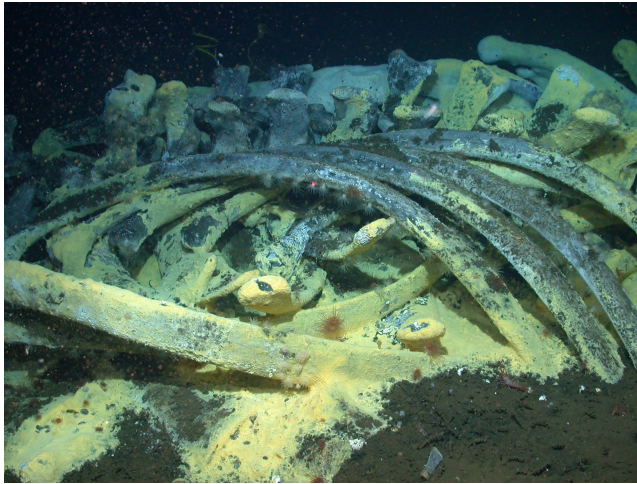
Figure 1. Carcass of a 30-ton gray whale that has been on the seafloor at 1674 m for 6.8 y in Santa Cruz Basin, off the coast of California, USA. This whale fall is in the sulfophilic stage, as indicated by the mats of yellow and white sulfur bacteria covering bones and nearby sediments, and the white shells of vesicomyid bivalves visible in adjacent sediments. The carcass hosts many species considered to be whale-fall specialists, including polychaete worms and molluscs that have been found in abundance on whale falls and not in any other habitat.

islands at the seafloor (Smith 2006; Smith et al. 2015). In the food-poor deep sea, whale-fall communities pass through a series of overlapping successional stages characterized in turn by mobile scavengers, enrichment opportunists, and sulfophilic (chemoautotrophic) assemblages (Baco and Smith 2003). The latter two stages are supported, at least in part, by the large, persistent reservoirs of energy-rich lipids in the whale skeleton (Baco and Smith 2003; Smith et al. 2014, 2015). The enrichment-opportunist and sulfophilic stages combined provide distinct "island" habitats for >100 faunal species found in abundance on deep-sea whale falls and, thus far, in no other habitat (Smith et al. 2015). These species are likely to be whale-fall specialists, requiring a sunken whale carcass (Figure 1) to complete their life cycles and maintain their populations (Smith et al. 2015). Potential whale-fall specialists include multiple species with chemoautotrophic endosymbionts such as bathymodiolin mussels; a diversity of dorvilleid polychaete worms and gastropod limpets that graze mats of sulfur bacteria (Wiklund et al. 2012; Smith et al. 2015); and heterotrophic species that directly utilize lipids and collagen from the bones such as bone-eating polychaetes in the genus *Osedax* and sipunculan worms.

Whaling by humans has depleted the abundance of great whales by 66%–90% compared with prehistoric periods (Roman et al. 2014). Industrial whaling during the 20th century led to even steeper declines of the largest whales, the blues and fins, which were the focus of intense hunting in the Southern Hemisphere (Tulloch et al. 2018).

A necessary consequence of the reduction of great-whale populations is a decrease in the frequency of whale falls arriving at the deep-sea floor, resulting in habitat loss for species dependent on whale falls (Smith 2006). Habitat loss is a major cause of species extinctions across a broad range of ecosystems (Pimm et al. 1995); we thus expect loss of whale-fall habitat to apply extinction pressure on species dependent on whale falls.

There are at least two major consequences of whaling for whale-fall specialists and their habitat: (1) a vast reduction in the abundance of live whales and hence the potential for whales to die and sink to the deep-sea floor to provide whale-fall habitats; and (2) a reduction in the mean size of great-whale species by removing the largest species (e.g., blue whales) and the largest individuals within species. In this article, we use a variation of the Levins (1969) metapopulation model to explore how changes in abundance and size of whales could influence the likelihood of persistence of whale-fall specialists, in particular species dispersing as planktonic larvae and living as adults on lipid-rich whale skeletons.

In brief, we find that the decline in the average size of great whales could be as important as the decline in whale abundance in endangering whale-fall specialists. Extinctions of whale-fall specialists because of whaling are likely to be most advanced (with extinction debts realized) in regions such as the North Atlantic, where great-whale populations (e.g., those of gray, right, and bowhead whales) have been depleted or extinct for >100 years (Notarbartolo di Sciara et al., 1998; Allen and Keay 2006).

a. Goal of the article

We use a metapopulation modeling approach to explore the consequences of whaling to the abundance and persistence of whale-fall habitats, and thus to habitat loss and potential extinction of whale-fall specialists. We focus on the sulfophilic stage of whale-fall succession, when reduced inorganic chemicals (e.g., sulfide) emanating from the whale bones support diverse macrofaunal assemblages sustained by chemoautotrophy.

b. Metapopulation context for whale-fall communities

Deep-sea whale falls provide a classic metapopulation framework, with distinct habitat islands supporting populations of specialized species linked by dispersal to other island populations. Whale falls, particularly during the sulfophilic stage, are seafloor oases rich in organic matter and reduced inorganic chemicals distributed across a vast deep-ocean floor where organic matter and reduced chemicals are very limited (Baco and Smith 2003; Smith et al. 2015). Whale-fall habitats are created abruptly after a carcass sinks to the seafloor. The sulfophilic stage, during which reduced chemicals from anaerobic decomposition of whale-bone lipids support a chemoautotrophically dependent fauna (Figure 1), can persist on deep-sea whale skeletons for decades (Schuller, Kadko, and Smith 2004; Smith et al. 2015). Whale falls are widely dispersed, typically separated by >10 km, and provide seafloor habitat patches of approximately 10–100 m^2 in area (Smith et al. 2014). Whale-fall

communities contain a diversity of macrofaunal species, including many apparent whale-fall specialists, with limited adult mobility (Baco and Smith 2003; Smith et al. 2015); these species require larval dispersal to colonize new whale falls. The lipids and collagen in whale skeletons become depleted over time as they are consumed by sulfate-reducing microbes and by metazoans such as *Osedax* (Treude et al. 2009; Smith et al. 2015). The sulfophilic assemblage on the whale skeleton persists as long as bone lipids and other tissue are available; once these resources are depleted, the sulfophilic habitat island disappears (Smith et al. 2015). The persistence time of the sulfophilic stage has been shown to vary with carcass size, and it may also vary with water depth and other environmental parameters (Smith et al. 2015). Populations of whale-fall specialists can disappear from individual carcasses because of declining resources related to bone lipids, but also from Allee effects, species interactions such as predation and competition, and pathogen outbreaks. These characteristics lead to a system of island habitats of finite duration, connected by larval dispersal, and subject to population extinctions, making whale-fall populations well suited to study with metapopulation and metacommunity models (Hanski and Gilpin 1997; Roman et al. 2014). Such characteristics are also broadly analogous to hydrothermal vent communities in the deep sea (Mullineaux et al. 2018).

2. A metapopulation model and extinction criterion

To analyze the criteria for global extinction of a whale-fall specialist, let us consider a model that takes into account a number of related factors. The basic equation governing our model is a variation of the classic Levins metapopulation equation (Levins 1969, 1970). Our equation is

$$\frac{dO}{dt} = q(S - O) - \varphi F. \tag{1}$$

where t represents time in years; O is the number of whale-fall sites occupied by our species; q is the probability that a given unoccupied site will become occupied in a given year; S represents the total available number of nondepleted whale-fall sites (i.e., skeletons containing sufficient lipids to support the sulfophilic stage); φ represents the probability that a site that is T years old is occupied by our particular species, where T denotes the mean persistence time of an active (i.e., lipid-containing) whale fall as a habitat; and F is the annual number of new whale falls, which at equilibrium is also the number of whale-fall sites that become lipid-depleted annually.

For future reference, note that at equilibrium the total number of whale-fall sites satisfies $S = F \cdot T$.

The last term of the differential equation has been modified from the standard model to account for the fact that, because whale-fall habitats last for a relatively long period of time, an older site that is becoming lipid-depleted is much more likely to be occupied than an average site. On the other hand, we have omitted the term for habitat extinction resulting from causes other than resource depletion. The main contributor to this term for whale-fall

specialists would probably be predation or possibly pathogens (e.g., Van Dover et al. 2007), and random habitat extinctions seem unlikely because of large population sizes in whale-fall specialists (Baco and Smith 2003; Smith et al. 2015). An analysis of the model including both terms (habitat loss attributable to resource exhaustion and other causes) is given in the Appendix. The analysis is only slightly more complicated, and the results are qualitatively similar.

For our metapopulation model, $P = O/S$ is the fraction of whale-fall sites occupied by a particular whale-fall species.

One goal is to describe the proportion of available sites that should be occupied by a particular species prior to whaling to ensure survival after whaling, in terms of the population of living whales and their mean length. To this end, we introduce those variables: N is the number of living (nonjuvenile) whales, and L denotes the mean length of a whale sinking to the seafloor.

There are three parameters, whose roles will be explained subsequently: m is the annual mortality rate for (nonjuvenile) whales, so that $F = m \cdot N$; a is a constant such that $T = a \cdot L$; and d is a parameter for the colonization rate, used in equation (2).

Our analysis will consider potential equilibrium situations, pertaining to either prewhaling or postwhaling. For that reason, we suppress the possible time dependence of some of these variables.

There is an implicit assumption that bone-lipid depletion in adult whale skeletons ultimately results from microbial processes deep within the bone matrix (Treude et al. 2009; Smith et al. 2015); thus, whale-fall persistence time does not depend on whether the site is occupied by a particular macrofaunal species. We also assume that interactions between macrofaunal species at a whale fall do not cause local population extinctions; this assumption may not apply to some members of the genus *Osedax* with overlapping niches and thus a potential for competitive exclusion (Higgs et al. 2014). Because whale-bone resources (lipids, collagen) are consumed by bacteria and bone borers such as *Osedax*, which degrade the bone from the surface area inward (Schuller et al. 2004; Treude et al. 2009; Smith et al. 2015), we assume that the rate of bone degradation is proportional to bone surface area (i.e., L^2). The amount of degradable bone resource is proportional to bone volume (i.e., L^3) (Schuller et al. 2004; Higgs, Little, and Glover 2010), so we assume that the persistence time T of a mature whale skeleton harboring whale-fall specialists is proportional to $L^3/L^2 = L$. Thus, for some constant a, we obtain $T = aL$.

Populations of whale-skeleton colonists are concentrated on the skeleton surface, so we assume that the number of individuals on an occupied site is proportional to skeleton surface area, and hence to L^2. The total population size of a whale-skeleton specialist is proportional to the number O of occupied sites and to the number of individuals per site.

Let us further assume that $q(t)$, the probability that an unoccupied whale-fall site will become colonized within a given year, is proportional to the size of the larval pool produced by the existing colonies. The number of larvae produced in turn depends on the total population on all occupied sites, and hence on the product of O and L^2. As $q(t)$ is a probability,

it has a maximum value of 1. Introducing a proportionality constant d, we can write

$$q = \min(dL^2O, 1). \tag{2}$$

The constant d depends on the rate of production of larvae per unit area of colony, but also on the spacing of the occupied whale falls (wider spacing yields greater larval wastage), which will vary with basin size and the number of active whale-fall habitats. The constant d may be hard to estimate, but as long as we are comparing prewhaling and postwhaling situations from the same basin, we do not need to know its value. Moreover, equation (2) implicitly assumes that larvae produced by whale falls are instantaneously mixed so as to be homogeneous (equally available) across the modeled region. This may not be fully realistic, but it is necessary to assume in a model without spatial structure.

The crucial term φ can be determined by considering the probability $\psi(t)$ that a given whale fall is occupied by our modeled species after t years. This satisfies the differential equation

$$\frac{d\psi}{dt} = q(1 - \psi), \tag{3}$$

$$\psi(0) = 0. \tag{4}$$

Regarding q as a constant (at equilibrium), the solution is

$$\psi(t) = 1 - e^{-qt}, \tag{5}$$

so that

$$\varphi = \psi(T) = 1 - e^{-qT}. \tag{6}$$

Now we rewrite the original differential equation (1):

$$\frac{dO}{dt} = q(S - O) - \varphi\frac{S}{T}. \tag{7}$$

At equilibrium, we set dO/dt to zero, divide by S, and solve to obtain

$$P = \frac{O}{S} = 1 - \frac{\varphi}{q \cdot T}. \tag{8}$$

This is interesting, but φ depends on q, and q depends on O, so the variables are not independent. In principle, we would like to rewrite equation (8) using only the variables O, L, and N and then solve for O to obtain an expression of the form $O = f(L, N)$ for the steady-state occupancy as a function of length and the number of whales. This is not practical, so we take a different tack.

Substituting the expression for φ into the right side of equation (8) yields

$$P = 1 - \frac{1 - e^{-qT}}{qT} \tag{9}$$

$$= \frac{e^{-qT} - 1 + qT}{qT}. \tag{10}$$

Let us assume that $q < 1$, so that $q = dL^2O$. Then, substituting for O and S in the left side,

$$\frac{q}{dL^2 \cdot F \cdot T} = \frac{qT}{dL^2FT^2} = \frac{qT}{ma^2dL^4N} = \frac{e^{-qT} - 1 + qT}{qT}, \tag{11}$$

whence

$$\frac{1}{ma^2d} = L^4N \left(\frac{e^{-qT} - 1 + qT}{(qT)^2} \right). \tag{12}$$

Because $qT = adL^3O$, equation (12) implicitly gives the relation between O, L, and N, but in a form that cannot be solved for O; moreover, it involves parameters m, a, and d, which we can only roughly estimate. However, there is another way to use equation (12).

Let us use q_0, L_0, N_0, and so on, for the prewhaling values, and q_1, L_1, N_1, and so on, for the postwhaling values. Because the left side $(1/ma^2d)$ of equation (12) is a constant, we have that

$$L_0^4N_0 \left(\frac{e^{-q_0T_0} - 1 + q_0T_0}{(q_0T_0)^2} \right) = L_1^4N_1 \left(\frac{e^{-q_1T_1} - 1 + q_1T_1}{(q_1T_1)^2} \right). \tag{13}$$

To get the extinction criterion, we set $q_1 = 0$, which involves taking a straightforward calculus limit for the expression in parentheses:

$$L_0^4N_0 \left(\frac{e^{-q_0T_0} - 1 + q_0T}{(q_0T_0)^2} \right) = L_1^4N_1 \cdot \frac{1}{2} \tag{14}$$

or

$$\frac{e^{-q_0T_0} - 1 + q_0T_0}{(q_0T_0)^2} = \frac{1}{2} \left(\frac{L_1}{L_0} \right)^4 \left(\frac{N_1}{N_0} \right) \tag{15}$$

at the threshold for extinction.

Given the values of L_1/L_0 and N_1/N_0, equation (15) can be solved for q_0T_0 numerically. Comparing the left side of equation (15) with the formula for P_0,

$$P_0 = \frac{e^{-q_0T_0} - 1 + q_0T_0}{q_0T_0}. \tag{16}$$

Table 1. Prewhaling occupancy rate of whale falls (P_0) required for the postwhaling survival by a whale-fall specialist in terms of abundance of live whales before (N_0) and after (N_1) whaling and the mean length of whales before (L_0) and after (L_1) whaling.

		N_1/N_0									
		0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
	0.1	1	1	1	1	1	1	1	1	1	1
	0.2	1	1	1	1	1	1	1	1	1	1
	0.3	1	1	1	1	1	1	1	1	1	1
	0.4	1	1	1	1	0.99	0.99	0.99	0.99	0.99	0.99
L_1/L_0	0.5	1	0.99	0.99	0.99	0.98	0.98	0.98	0.97	0.97	0.97
	0.6	0.99	0.99	0.98	0.97	0.97	0.96	0.95	0.95	0.94	0.93
	0.7	0.99	0.98	0.96	0.95	0.94	0.92	0.91	0.89	0.88	0.86
	0.8	0.98	0.96	0.93	0.91	0.89	0.86	0.83	0.80	0.76	0.73
	0.9	0.97	0.93	0.89	0.85	0.80	0.74	0.68	0.61	0.54	0.47
	1.0	0.95	0.89	0.82	0.74	0.64	0.53	0.41	0.28	0.15	*

We multiply the right side of equation (15) by $q_0 T_0$ to obtain the value of the prewhaling occupancy ratio P_0 needed for survival; that is,

$$P_0 > \frac{q_0 T_0}{2} \left(\frac{L_1}{L_0}\right)^4 \left(\frac{N_1}{N_0}\right). \tag{17}$$

Thus, we can use P_0 as a surrogate for the unknown colonization parameter d to determine the prewhaling occupancy ratio that would be needed for the species to survive after whaling. In the next section, we will apply this criterion to data for various ocean basins and globally.

3. Applications of the survival criterion

Table 1 uses the inequality (17) to estimate, for various values of L_1/L_0 and N_1/N_0, the minimum proportion of whale-fall habitats that a species must have occupied prior to whaling to allow metapopulation survival after postwhaling reductions in whale abundance and mean body size. Figure 2 shows the level curves for the function in Table 1.

Our model indicates that the long-term persistence of whale-fall species after whaling, and hence the chances of whale-specialist extinctions, is (a) sensitive (linearly related) to reductions in the number of living whales, and (b) extremely sensitive (to the fourth power) to reductions in the mean size of whales.

If whale populations were reduced by only 10% (to 90% of prewhaling levels) but the mean size of whales were reduced by 30% (i.e., $L_1/L_0 = 0.7$) through removal of the largest species and the largest individuals within a species, a prewhaling occupancy rate of nearly 90% would be required for long-term survival of a whale-fall specialist in the aftermath of whaling. In fact, the largest individuals, as well as the largest species, of great whales were typically the targets of commercial whaling. The mean body size of blue, fin, and
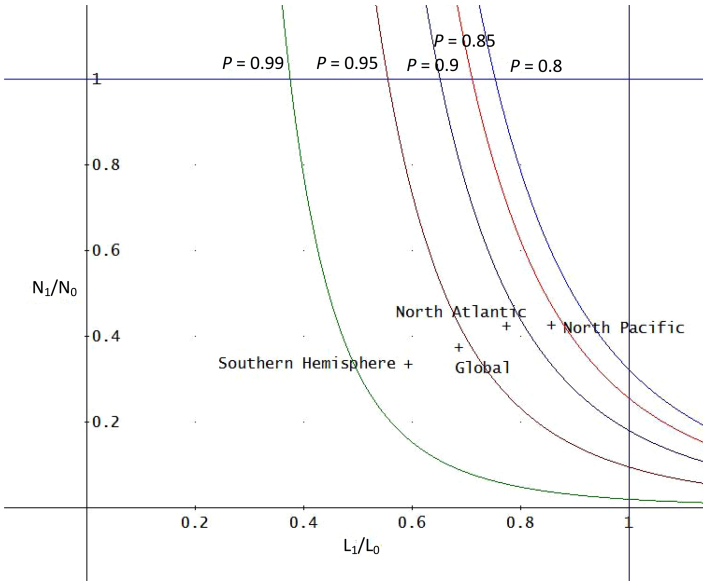
Figure 2. Level curves for the function P_0, showing the pre-whaling occupancy rate of whale falls required for the post-whaling survival by a whale-fall specialist. P_0 is plotted in terms of the relative decline in mean whale length (L_1/L_0) versus the relative decline in whale abundance (N_1/N_0) resulting from whaling. For example, if a L_1/L_0 versus N_1/N_0 point falls on the green curve marked $P_0 = 0.99$, then a whale-fall specialist would need to have occupied at least 99% of the available whale-fall sites prior to whaling to avoid extinction. The "+" signs mark our estimates for the various ocean regions, based on Table 2. Note that P_0 is initially much more sensitive to changes in whale length than to changes in whale abundance. The calculations and graph were done using Derive 6 (Texas Instruments).

sei whales caught during the 20th century declined dramatically during industrial whaling, with L_1/L_0 apparently falling to 0.8–0.9 over a 70-year period (Clements et al. 2017). The reduction in mean body size within species, plus the dramatic reductions in the abundance of the largest species of whales, very likely reduced L_1/L_0 across all great whale species to well below 0.8. Considering that the largest species of whales, the blue whale, remains heavily depleted, and that widespread commercial whaling was halted in the 1970s and 1980s, which is less than one life span ago for many whales (Bannister, 2018), the mean body size of great whales likely remains substantially below prewhaling levels.

According to our metapopulation model, the drastic reduction in the number and size of whales sinking to the deep-sea floor is likely to cause, or to already have caused, numerous species extinctions of whale-fall specialists. Even maintaining great whale populations at the International Whaling Commission sustainable yield level of 54% of prewhaling population sizes may put whale specialists at risk of extinction, requiring prewhaling occupancy rates of more than 90% of lipid-rich skeletons at the seafloor at the current length ratio $L_1/L_0 \approx 0.7$ (and more than 75% for $L_1/L_0 = 0.9$).

It is important to note, however, that whale-specialist extinctions resulting from reductions in the abundance and size of whale carcasses would not occur instantaneously. Rather, they would lag behind the reductions in whale populations as whale-fall habitats and associated populations of specialists die out, causing an "extinction debt" (Kuussaari et al. 2009). The duration of such a debt, or the length of time it will take for species richness on whale falls to relax to a lower postwhaling equilibrium, is related to the persistence times of the sulfophilic whale-fall habitats and to the life spans and recruitment dynamics of the whale-fall specialists destined for extinction (Smith 2006; Kuussaari et al. 2009). Because these whale-fall habitats can last for decades, the abundance of sulfophilic communities should respond with a time lag of at least 30–40 years to whale depletion (Smith 2006), and long-lived or self-recruiting whale specialists may persist even longer on large whale falls that last for 70–80 years (Schuller et al. 2004). If great-whale populations are allowed to recover in numbers and body size before extinction debts are fully paid, biodiversity losses in whale-fall specialists could be mitigated (cf. Kuussaari et al. 2009). Because of this time lag, the temporal and spatial patterns of whale-population decline and recovery are likely to influence the realized levels of whale-specialist extinctions in different ocean basins. In the North Atlantic, for example, some great-whale species or populations have long been extinct; the North Atlantic gray whale and the eastern population of the North Atlantic right whale were likely extirpated more than 150 years ago (Notarbartolo di Sciara et al. 1998; Smith 2006). Ongoing commercial whaling for fin and minke whales, and incidental mortality from shipping and fishing-gear entanglements, could continue to apply extinction pressure to these whale-fall communities. In the North Pacific, the removal of many great whales occurred as recently as the 1960s and 1970s, and some populations (e.g., the northeast Pacific gray whale) have substantially recovered in abundance (Smith 2006), so extinctions might have been avoided. Declines in the diversity of whale-fall specialists resulting from whaling may be relatively advanced in areas of the North Atlantic, but they could be mitigated by whale-population recoveries in parts of the northeast Pacific. There is reason to be concerned about the Southern Hemisphere, which suffered the world's largest removals of great whales from 1920 to 1960 (Smith 2006). Even with 100 years of future protection from whaling, the Antarctic blue, fin, and southern right whales will likely remain at <50% of preexploitation numbers because of slow population growth rates (Tulloch et al. 2018), yielding ample time for extinction debts to be realized.

Because the extinction effects of whaling are likely to be region specific, we now turn to projections for particular ocean regions. For these projections, data from Doughty et al. (2016) and Clements et al. (2017) were used to estimate the number of whales and their mean length, respectively, for various ocean regions and for the global ocean (see the Appendix). The whale species used for these calculations are blue, bowhead, Bryde's, fin, gray, humpback, minke, right, sei, and sperm whales. The column labeled P_0 in Table 2 is derived according to the condition set in equation (17).

An obvious conclusion from these projections is that extinction pressure is more extreme in the Southern Ocean, even without considering extinction debt, than in the northern oceans.

Table 2. Prewhaling occupancy rate of whale falls (P_0) needed to ensure long-term survival of a whale-fall specialist after whaling for different ocean regions. Lengths before (L_0) and after (L_1) whaling are given in meters, and population sizes before (N_0) and after (N_1) whaling are in thousands.

Basin	L_0	L_1	N_0	N_1	P_0
North Atlantic	15.9	12.3	875	369	0.91
North Pacific	17.5	14.9	712	296	0.87
Southern Hemisphere	17.0	10.1	2,461	819	0.98
Global	16.8	11.6	4,049	1,484	0.96

This is because the largest species of whales remain at very low abundances in the Southern Hemisphere; that is, Southern Ocean blue and fin whales are still at a few percent of estimated prewhaling levels (https://iwc.int/status). These two species were also among the first to reach commercial extinction in the Southern Hemisphere, as whalers focused on the largest individuals and species first, before depleting the smaller humpback and sperm whales, and eventually resorting to the diminutive minke whale (Rocha, Clapham, and Ivaschenko 2015). To make matters worse for deep-sea communities, many whale carcasses were completely removed from the ocean during the 20th century, when they were processed aboard factory ships rather than being flensed alongside wooden ships, where skeletons and organs would often be left to sink (Smith 2006). Given that most blue and fin whales were removed from the Southern Ocean between 1920 and 1960 (i.e., more than 60 years ago), it is likely that whale-specialist extinction debts are well on their way to being paid, with extinctions likely to reach completion before blue and fin whale populations recover to prewhaling levels. The situation in the North Pacific is not as dire because P_0 is lower (i.e., 0.87 vs. 0.98 in the Southern Hemisphere), whale removal was more recent (occurring after 1955; Smith 2006), and some whale populations (e.g., gray and humpback whales) are recovering. The diversity of whale specialists may thus be substantially closer to prewhaling levels in the northeast Pacific, especially within the gray whale's range.

Our global results should be interpreted with caution, as they combine basins that may have distinct species and metapopulations of whale-fall specialists (e.g., Sumida et al. 2016). They also do not consider the geographic and temporal variation of commercial whaling. Whale species along the European coast, such as the North Atlantic right whale, were extirpated centuries ago, and whale-fall specialists in that area are likely to have disappeared along with their habitat. This habitat loss might have had a particular effect on whale-fall species in the Mediterranean, which has a high degree of endemism (Coll et al. 2010). Despite these potential limitations, our results emphasize that whaling may have severe consequences on the survival prospects for whale-fall specialists globally, as well as in major ocean regions.

4. Conclusions and insights

Our metapopulation model for whale-fall specialists suggests that occupancy rates of deep-sea carcasses prior to whaling would have to have been extremely high (0.87 to 0.98)

for these specialists to persist in many parts of our whale-depleted oceans. Our modeling also indicates, surprisingly, that the extinction potential for whale specialists may be more sensitive to reductions in the mean size of whales than to declines in population abundance. Some parts of the oceans, especially the Southern Hemisphere, are predicted to be especially vulnerable to whale-specialist extinctions because very large populations of the biggest whales were heavily depleted and remain at extremely low abundance levels; furthermore, these depletions occurred more than 60 years ago, so extinction debts may be well on their way to being paid. For other regions, such as the North Pacific, extinction pressure on whale-fall specialists does not appear be as large or as long-standing because some whale populations are in advanced stages of recovery.

The model yields some new and intriguing insights. First, in regions where whale abundance and mean size have long been reduced, such as the North Atlantic and very likely the Southern Ocean, the diversity of whale-fall specialists is expected to be low relative to prewhaling conditions. Whale-fall occupancy rates by specialists may also be relatively low in these regions because of reduced connectivity caused by lower larval production and higher carcass spacing. Second, as the abundance and mean size of great whales return to prewhaling levels, occupancy rates of whale falls by specialists should eventually be high (>80%); otherwise, these species would be unlikely to have survived the prolonged bottleneck in whale-fall habitat availability. Unfortunately, we cannot test these predictions because whale falls are too poorly sampled to generate reliable estimates of whale-fall occupancy rates (Smith et al. 2017). A third insight is that the evolution and persistence of whale-fall specialists are likely to have been highly dependent on the evolution and widespread occurrence of very large whales; thus, regions with an abundance of very large whale species over evolutionary timescales, such as the Southern Ocean, are likely to have developed the greatest diversity of whale-fall specialists. Finally, conservation of whale-fall specialists is likely to be highly dependent on conservation of the largest whales, both within and across species, because of nonlinear effects of whale length on whale-fall habitat persistence times and larval production. By inference, the carcasses of juvenile whales may be relatively unimportant in preventing extinctions from whaling because of this nonlinear scaling with whale size. The observed absence or very short duration of the sulfophilic stage on juvenile whale falls (Baco and Smith 2003; Smith et al. 2015) is consistent with this inference. Thus, as whale populations recover, any discussion of the resumption of commercial whaling should address the impact of hunting on deep-sea whale-fall ecosystems and especially consider differential protection of the largest whales within and across species.

APPENDIX

In the model presented in Section 2, site extinction was assumed to be attributable to depletion of resources, and the usual term corresponding to random site extinction was omitted from the metapopulation equation. The first part of the Appendix considers the

case when both terms are included. As we shall see, the adjustments required are relatively minor, and the results are qualitatively the same.

The calculations for Table 2 are based on estimates for historical and current whale populations and lengths. The second part of the Appendix reproduces the spreadsheet we used for those calculations and gives the sources for those estimates.

a. A generalized model and extinction criterion

For a metapopulation model that allows site extinction attributable to both resource depletion and random other factors, we replace equation (1) with

$$\frac{dO}{dt} = q(S - O) - \varepsilon O - \varphi F, \tag{A1}$$

where ε represents the annual probability that an occupied site will cease to be occupied for reasons other than resource depletion, and the other variables are the same as in Section 2. The three terms on the right side of equation (A1) represent (i) the site colonization rate $q(S - O)$, (ii) the random site extinction rate $-\varepsilon O$, and (iii) the rate for site extinction attributable to resource depletion $-\varphi F$.

The standard Levins model contains the first two terms. The model in Section 2 assumes the second term is negligible and contains only the first and third terms. Now we consider equation (A1) with all three terms on the right side.

Again note that at equilibrium the total number of whale-fall sites satisfies $S = F \cdot T$, and let $P = O/S$ be the fraction of the nondepleted sites occupied by our particular species. As before, N is the number of living (nonjuvenile) whales, and L denotes the mean length of a whale carcass. Likewise, the parameters m, a, and d are used as previously, and the probability q satisfies

$$q = \min(dL^2O, 1). \tag{A2}$$

The crucial term φ in equation (A1) is determined by considering the probability $\psi(t)$ that a given whale-fall is occupied by our species after t years. The differential equation for $d\psi/dt$ must be modified to include a term for random site extinction:

$$\frac{d\psi}{dt} = q(1 - \psi) - \varepsilon\psi, \tag{A3}$$

$$\psi(0) = 0. \tag{A4}$$

Regarding q as a constant (at equilibrium), the solution is

$$\psi(t) = \frac{q}{q + \varepsilon}(1 - e^{-(q+\varepsilon)t}), \tag{A5}$$

so that

$$\varphi = \psi(T) = \frac{q}{q + \varepsilon}(1 - e^{-(q+\varepsilon)T}). \tag{A6}$$

Now we rewrite the original differential equation (A1):

$$\frac{dO}{dt} = q(S - O) - \varepsilon O - \varphi\frac{S}{T}. \tag{A7}$$

At equilibrium, we set dO/dt to zero, divide by S, and solve to obtain

$$P = \frac{O}{S} = \frac{1}{q + \varepsilon}\left(q - \frac{\varphi}{T}\right). \tag{A8}$$

Substituting the expression for φ into the right side of equation (A8), and simplifying yields

$$P = \frac{1}{(q + \varepsilon)T}\left(qT - \frac{q}{q + \varepsilon}(1 - e^{-(q+\varepsilon)T})\right) \tag{A9}$$

$$= \frac{q}{(q + \varepsilon)^2 T}\left(e^{-(q+\varepsilon)T} - 1 + (q + \varepsilon)T\right). \tag{A10}$$

Still mimicking Section 2, let us assume that $q < 1$, so that $q = dL^2 O$, then substitute for O and S in the left side:

$$\frac{q}{dL^2 \cdot FT} = \frac{qT}{dL^2 FT^2} = \frac{qT}{ma^2 dL^4 N} = \frac{q}{(q + \varepsilon)^2 T}\left(e^{-(q+\varepsilon)T} - 1 + (q + \varepsilon)T\right), \tag{A11}$$

whence

$$\frac{1}{ma^2 d} = L^4 N\left(\frac{e^{-(q+\varepsilon)T} - 1 + (q + \varepsilon)T}{(q + \varepsilon)^2 T^2}\right). \tag{A12}$$

This is the same as equation (12) in the main text, with q replaced by $q + \varepsilon$. Note, however, that the equations (A9) and (A10) for P are different by a factor of $q/q + \varepsilon$.

Again we use q_0, L_0, N_0, and so on, for the prewhaling values, and q_1, L_1, N_1, and so on, for the postwhaling values. Because the left side $(1/ma^2 d)$ of equation (A12) is a constant, we have that

$$L_0^4 N_0\left(\frac{e^{-(q_0+\varepsilon)T_0} - 1 + (q_0 + \varepsilon)T_0}{(q_0 + \varepsilon)^2 T_0^2}\right) = L_1^4 N_1\left(\frac{e^{-(q_1+\varepsilon)T_1} - 1 + (q_1 + \varepsilon)T_1}{(q_1 + \varepsilon)^2 T_1^2}\right). \tag{A13}$$

To get the extinction criterion, set $q_1 = 0$, which gives

$$L_0^4 N_0\left(\frac{e^{-(q_0+\varepsilon)T_0} - 1 + (q_0 + \varepsilon)T_0}{(q_0 + \varepsilon)^2 T_0^2}\right) = L_1^4 N_1\left(\frac{e^{-\varepsilon T_1} - 1 + \varepsilon T_1}{\varepsilon^2 T_1^2}\right) \tag{A14}$$

or

$$\frac{e^{-(q_0+\varepsilon)T_0} - 1 + (q_0 + \varepsilon)T_0}{(q_0 + \varepsilon)^2 T_0^2} = \left(\frac{L_1}{L_0}\right)^4\left(\frac{N_1}{N_0}\right)\left(\frac{e^{-\varepsilon T_1} - 1 + \varepsilon T_1}{\varepsilon^2 T_1^2}\right) \tag{A15}$$

at the threshold for extinction.

In order to use equation (A15), we need estimates for the values for L_1/L_0, N_1/N_0, ε, and T_1. The value of T_0 can then be obtained from the assumption $T_1/T_0 = L_1/L_0$. Next, we evaluate the right side of equation (A15); note that the third term is a function of εT_1, which has a limit of $1/2$ when $\varepsilon T_1 = 0$ and decreases slowly toward 0 as $\varepsilon T_1 \to \infty$. If the right side evaluates to R, then numerically solve

$$\frac{e^{-x} - 1 + x}{x^2} = R \tag{A16}$$

for $x = (q_0 + \varepsilon)T_0$. Because ε and T_0 are known, this determines q_0. Comparing equations (A10) and (A15), we see that

$$P_0 = q_0 T_0 R \tag{A17}$$

at the point of extinction. Thus, the criterion for survival becomes

$$P_0 > q_0 T_0 R. \tag{A18}$$

Again, P_0 is the prewhaling occupancy ratio that would be needed in order for the species to survive postwhaling.

Let us work through an example of the calculations. Consider the case $L_1/L_0 = 0.85$, $N_1/N_0 = 0.40$, $\varepsilon = 0.10$, and $T_1 = 30$, with the first two corresponding roughly to the global figures. From $T_1/T_0 = L_1/L_0$, we obtain $T_0 \doteq 35$. Plugging these numbers into the right side of equation (A15) gives $R = 0.0474$. Solving equation (A16) numerically, we get $x = (q_0 + \varepsilon)T_0 = 20$, whence $q_0 T_0 = 16.5$. The extinction criterion then becomes

$$P_0 > 16.5 \times 0.0474 \doteq 0.78. \tag{A19}$$

Note that this is somewhat lower than the global extinction criterion $P_0 > 0.96$ given in Table 2, mainly by the factor $\dfrac{q_0}{q_0 + \varepsilon} \doteq \dfrac{0.471}{0.571} \doteq 0.82$. This may seem paradoxical at first, but random site extinctions also have a large effect on prewhaling occupancy. Indeed, by equation (A8), the maximum possible occupancy (with $q = \varphi = 1$) is

$$P_{\max} = \frac{1}{1 + \varepsilon}\left(1 - \frac{1}{T}\right). \tag{A20}$$

b. Populations and mean lengths of great whales

The calculations for Table 2 in the article are based on estimates for historical and current whale populations and lengths. Table 3 reproduces the spreadsheet we used for those calculations. Present and historical population sizes are from Doughty et al. (2016) with several updates.

Population sizes for the Antarctic minke whale are from Ruegg et al. (2010) and the International Whaling Commission (2013a). Population sizes for the southern right whale

Table 3. Estimates for historical and current whale populations and lengths. Lengths are given in meters, and populations in thousands.

Basin	Species	L_0	L_1	N_0	N_1
North Atlantic					
	Blue	27	22	7.5	0.4
	(*Balaenoptera musculus*)				
	Bowhead	20	20	80	8
	(*Balaena mysticetus*)				
	Common minke	7	7	211	157
	(*Balaenoptera acutorostrata*)				
	Fin	23	20	73	56
	(*Balaenoptera physalus*)				
	Humpback	16	16	112	20
	(*Megaptera novaeangliae*)				
	Right	16	16	14	0.5
	(*Eubalaena glacialis*)				
	Sei	16	14	10.6	7
	(*Balaenoptera borealis*)				
	Sperm	18.5	14.5	367	120
	(*Physeter microcephalus*)				
	Means/totals	15.9	12.3	875.1	368.9
		$L_1/L_0 = 0.775$		$N_1/N_0 = 0.422$	
North Pacific					
	Blue	27	22	6	3
	(*Balaenoptera musculus*)				
	Bowhead	20	20	30	18
	(*Balaena mysticetus*)				
	Bryde's	15	15	52	41
	(*Balaenoptera brydei*)				
	Common minke	7	7	47	32
	(*Balaenoptera acutorostrata*)				
	Fin	23	20	65	31
	(*Balaenoptera physalus*)				
	Gray	15	15	25	16
	(*Eschrichtius robustus*)				
	Humpback	16	16	20	20
	(*Megaptera novaeangliae*)				
	Right	16	16	32	0.4
	(*Eubalaena japonica*)				

Table 3. Continued

Basin	Species	L_0	L_1	N_0	N_1
	Sei	16	14	68.4	14.7
	(*Balaenoptera borealis*)				
	Sperm	18.5	14.5	367	120
	(*Physeter microcephalus*)				
	Means/totals	17.5	14.9	712.4	296.1
		$L_1/L_0 = 0.851$		$N_1/N_0 = 0.416$	
Southern Hemisphere					
	Antarctic minke	7	7	670	515
	(*Balaenoptera bonaerensis*)				
	Blue	27	22	290	2
	(*Balaenoptera musculus*)				
	Bryde's	15	15	94	91
	(*Balaenoptera brydei*)				
	Fin	23	20	625	23
	(*Balaenoptera physalus*)				
	Humpback	16	16	170	30
	(*Megaptera novaeangliae*)				
	Right	16	16	78	13.6
	(*Eubalaena australis*)				
	Sei	16	14	167	27.4
	(*Balaenoptera borealis*)				
	Sperm	18.5	14.5	367	120
	(*Physeter microcephalus*)				
		17.0	10.1	2,461	822
		$L_1/L_0 = 0.595$		$N_1/N_0 = 0.334$	
Global					
		L_0	L_1	N_0	N_1
		16.8	11.6	4,048.5	1,487
		$L_1/L_0 = 0.689$		$N_1/N_0 = 0.367$	

are from the International Whaling Commission (2013b). Population sizes for bowhead whales in the North Atlantic are from Allen and Keay (2006), Cooke and Reeves (2018), and Vacquié-Garcia et al. (2017). Population sizes for bowhead whales in the North Pacific are from Cooke and Reeves (2018), Givens et al. (2016), and Shpak et al. (2017). Population sizes for blue whales in the Southern Hemisphere are from Branch, Matsuoka, and Miyashita (2004) and Branch et al. (2007).

The global distribution of sperm whales is based on Whitehead (2002). He estimated that 33% of the global population would be found in the North Atlantic, and we assumed a 50% split of the remainder between the North Pacific and Southern Hemisphere.

The mean lengths of blue, fin, sei and sperm whales before and after whaling are based on Clements et al. (2017).

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