POPULATION DYNAMICS

Boom-bust cycles in gray whales associated with dynamic and changing Arctic conditions

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Climate change is affecting a wide range of global systems, with polar ecosystems experiencing the most rapid change. Although climate impacts affect lower-trophic-level and short-lived species most directly, it is less clear how long-lived and mobile species will respond to rapid polar warming because they may have the short-term ability to accommodate ecological disruptions while adapting to new conditions. We found that the population dynamics of an iconic and highly mobile polar-associated species are tightly coupled to Arctic prey availability and access to feeding areas. When low prey biomass coincided with high ice cover, gray whales experienced major mortality events, each reducing the population by 15 to 25%. This suggests that even mobile, long-lived species are sensitive to dynamic and changing conditions as the Arctic warms.

The Bering and Chukchi seas in the Pacific Arctic are extremely productive shallow basins (*1*–*3*) that support seasonal foraging opportunities for a wide variety of migratory and Arctic-associated taxa (*4*). The Pacific Arctic food web is characterized by ice-associated algal growth during spring and early summer, which is transported to the benthos through decay and sinking of particulate organic carbon (*3*). This tight pelagic-benthic coupling historically resulted in some of the most productive nearshore benthic systems in the world (*3*), attracting migrants from throughout the Pacific and supporting large populations of marine species (*4*, *5*).

As the Arctic has rapidly warmed, sea ice retreat has occurred progressively earlier in the spring, and the Bering and Chukchi seas have remained ice free for longer in the autumn (*6*). This has resulted in increased water-column productivity (*7*, *8*) but has reduced the amount of particulate organic carbon that reaches the sea floor through pelagic-benthic coupling that is dependent on sinking ice-associated algae (*5*). In addition, decreased sea ice cover allows stronger current-driven flow over the shallow basins of the Pacific Arctic, reducing the quantity of finer-sediment grain size within the benthos that support habitat for tube-building amphipods, which have some of the highest lipid content of benthic crustaceans (*9*, *10*). Collectively, these impacts have driven changes to the structure of Arctic benthic communities, which may translate into impacts on higher-trophic-level species that migrate seasonally to access these foraging hotspots (*5*, *9*, *10*).

Eastern North Pacific gray whales (*Eschrichtius robustus*) undertake one of the longest mammalian migrations between wintering areas in Baja California, Mexico, and summer feeding areas in the Bering and Chukchi seas to take advantage of these highly concentrated benthic prey resources (*11*). Gray whales have specialized baleen plates adapted to suction feeding in soft sediments and are the only baleen whale to feed primarily on benthic prey (*11*). Although they are capable of feeding on pelagic zooplankton, the diet of gray whales feeding in the Arctic is dominated by benthic crustaceans—in particular, ampeliscid amphipods—that are found in abundance in shallow Arctic basins (*12*).

Estimates of pre-whaling population sizes range from 15,000 to 30,000 individuals for the eastern North Pacific gray whale population, based on population models fitted to estimates from abundance surveys combined with commercial and aboriginal harvest data (*13*). Genetic estimates of prehistoric abundance are much higher, ranging from ~75,000 to 120,000 individuals (*14*), although this likely included the now endangered western North Pacific population and may reflect a larger carrying capacity supported by increased benthic habitat availability during the Last Glacial Minimum (*15*). Commercial whaling in the lagoons of Baja California and throughout the North Pacific depleted the eastern North Pacific gray whale population to fewer than 5000 individuals by the early 1900s (*13*). A rapid and sustained post-whaling increase in abundance led to the delisting of the population from the Endangered Species Act in and is widely viewed as an iconic example of successful conservation and species recovery (*16*).

The status and stability of eastern North Pacific gray whales has come into question as the population experienced two major documented mortality events in 1999–2000 and 2019–2022 (*17*, *18*). In response to the first mortality event in 1999, there was speculation that the population may have reached its carrying capacity and was suffering from density-dependent effects on survival (*19*). In light of fluctuations in reproductive output and a second major mortality event two decades later, many studies have proposed that variable and changing Arctic conditions may be drivers of eastern North Pacific gray whale population dynamics (*12*, *20*–*22*).

Arctic sea ice extent has been proposed as a contributor to gray whale vital rates—especially reproduction—by physically restricting access to summer feeding areas (*20*, *22*, *23*). However, in recent years previously identified relationships between gray whale reproduction and Arctic sea ice extent have begun to decouple (*22*, *23*), and variability in sea ice has been insufficient to explain mortality rates (*20*). Eastern North Pacific gray whales have the most complete long-term abundance and demographic data available for any large whale species, and we leveraged these extensive datasets to examine environmental drivers of population dynamics not possible in other species. We combined time series of gray whale abundance, reproduction, nutritive condition, and strandings spanning more than half a century into a population dynamics model to estimate annual carrying capacity for the population. We show that this annual carrying capacity is well explained by ice-mediated access to the population's primary foraging grounds in the Arctic and biomass of benthic crustaceans. The observed boom-bust cycles in gray whale abundance and vital rates suggest that as large whales recover from post-whaling depletion, their populations may become increasingly governed by environmental constraints and climate variability.

Results and discussion

We combined 31 estimates of eastern North Pacific gray whale abundance over 54 years (1968 to 2022) (*24*), 30 estimates of calf production over 42 years (1980 to 2022) (*22*, *25*), 1391 records of stranded gray whales on the United States coastline over 48 years (1974 to 2022), and 1334 body condition measurements over 32 years (1987 to 2019) (*26*) into an integrated population dynamics model that estimates annual abundance, birth rates, and mortality rates. The model uses evidence of human interactions in stranded gray whales to estimate proportional hazards of anthropogenic and natural contributions to mortality.

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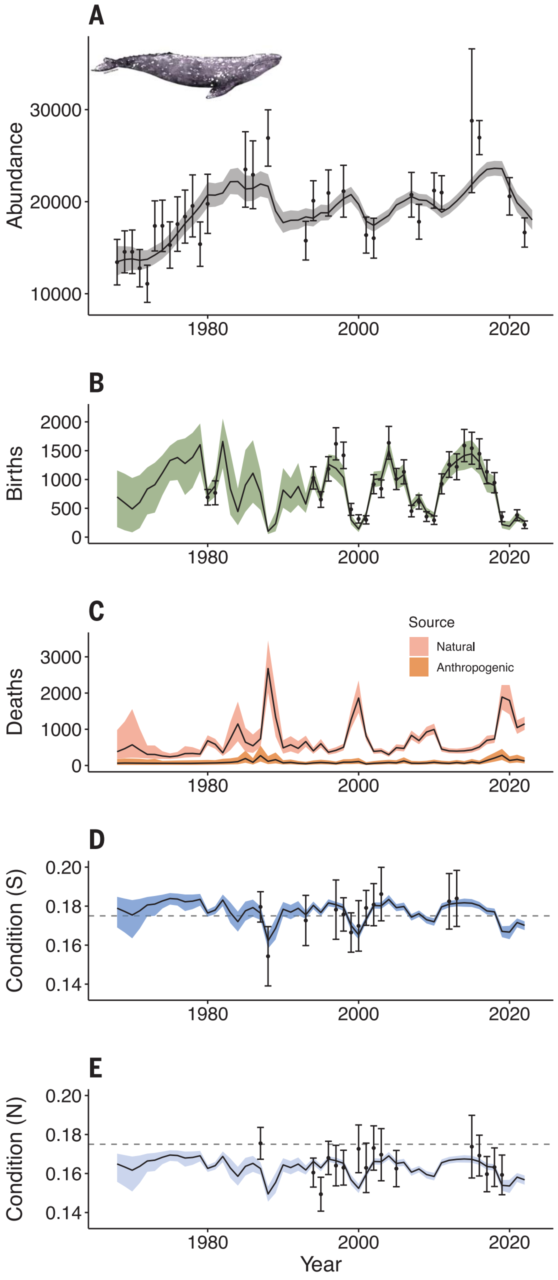
Fig. 1. Population dynamics of eastern North Pacific gray whales. (**A**) Gray whales have experienced major fluctuations in abundance after an initial post-whaling recovery, including three major declines beginning in 1987, 1999, and 2019. (**B** to **E**) These declines and subsequent recoveries in the 1990s and 2000s were associated with synchronous changes in (B) births and (C) mortality, as well as changes in nutritive condition in (D) southbound and (E) northbound migrating whales. Black points in (A) and (B) indicate the median estimated abundance and calf production from visual surveys, with standard errors of model estimates (vertical bars). Black points in (D) and (E) indicate the mean values of body condition measurements from each survey year and the standard deviation of observations (vertical bars). In (A) to (E), the black lines indicate the median of the posterior distribution of model-estimated values, and the shaded regions indicate the 95% posterior credible intervals.



In addition, the model estimates both the long-term carrying capacity (K), as well as an annually varying carrying capacity (K_t) that reflects year-to-year variation in the strength of negative density dependence as determined by environmental covariates and stochastic effects. We considered three Arctic time series as candidate covariates for annual gray whale carrying capacity: (i) access to feeding grounds, defined as the number of days with <50% sea ice cover on the historic gray whale foraging grounds in the Chirikov basin and southern Chukchi Sea (1979 to 2021) (*23*, *27*); (ii) benthic infaunal crustacean biomass, averaged over the same foraging hotspots as sea ice access (1971 to 2019) (*28*); and (iii) zooplankton density estimated by using a global ocean ecosystem model that includes the entire Arctic Ocean ecosystem, averaged over gray whale foraging hotspots (1992 to 2020) (*29*). The data and population model are described in detail in the Data sources and Integrated population model sections of the supplementary materials.

The eastern North Pacific gray whale population has experienced three major mortality events, each resulting in reductions of 15 to 25% of total abundance within the half-century of nearly continuous monitoring, representing extraordinarily high periodic mortality rates for a long-lived vertebrate (Fig. 1). These mortality events were associated with peaks in reported strandings during the 1999–2000 and 2019–2022 periods. The 1987–1989 abundance decline is the largest in magnitude but was not associated with an increase in strandings, likely because reporting structures and survey effort to detect strandings were expanded and improved substantially beginning in 1990. However, this major impact to the population is also reflected in the poorest recorded body condition of the survey history in 1988, falling rapidly from very good condition in 1987 (Fig. 1D). The population dynamics model estimated low annual carrying capacities (K_t) of approximately 10,000 individuals during each of these die-offs (Fig. 2A), indicating that Arctic foraging grounds periodically experience major disruptions, limiting the number of whales that they can support. These fluctuations in annual carrying capacity were represented in mortality rates, body condition, and most strongly in birth rates, which had the greatest proportional change with varying carrying capacity (fig. S5). On the basis of anthropogenic injury rates in stranded whales, model-estimated anthropogenic mortality rates remained low and stable, whereas natural mortality rates varied substantially and peaked during major die-offs, suggesting direct human impacts such as vessel strikes and entanglements in fishing gear are not the primary drivers of mortality in this population.

The maximum birth rate estimated by the model was 0.111 (95% credible intervals 0.108 to 0.114). The realized annual birth rate ranged from a low of 0.0046 in 1998 (0.0024 to 0.0076) to a high of 0.085 in 1975 (0.062 to 0.102). Within the span of calf production observations (1994–2022), the minimum birth rate was 0.007 in 2000 (0.004 to 0.01), and the maximum was 0.082 in 2004 (0.069 to 0.09). The minimum estimated mortality rate was 0.011 (0.009 to 0.014). The realized annual mortality rate ranged from a low of 0.019 in 1975 (0.014 to 0.027) to a high of 0.13 in 1988 (0.099 to 0.162). During the three major mortality events, median estimated mortality rates were 0.13 and 0.079 (in 1988 and 1989); 0.065 and 0.099 (in 1999 and 2000); and 0.092, 0.089, 0.061, and 0.067 (from 2019 to 2022).

Model-estimated mean body condition was lowest in 1988 [median 0.162, 95% confidence interval (CI) 0.158 to 0.166], 2000 (0.165, 0.163 to 0.168), and 2020 (0.167, 0.163 to 0.170). The highest estimated body condition was in 1975 (0.184, 0.181 to 0.187), although there were no photogrammetric measurements before 1987. The 3 years with highest estimated body condition and corresponding condition measurements were 2013 (0.181, 0.180 to 0.183), 2012 (0.181, 0.179 to 0.183), and 1997 (0.181, 0.179 to 0.182). The estimated northbound body

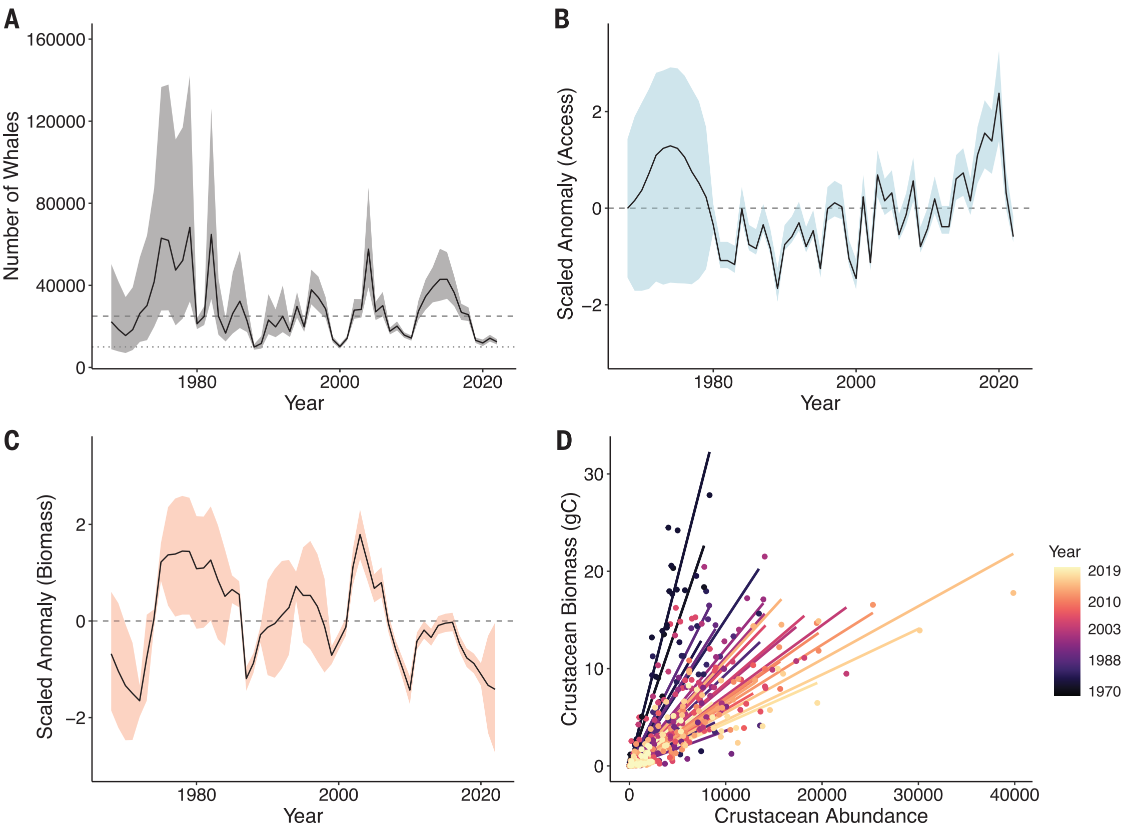


Fig. 2. Drivers of eastern North Pacific gray whale carrying capacity. (**A**) Estimated annual carrying capacity (K_t) from the population dynamics model, with reference lines at 25,000 (dashed line) and 10,000 (dotted line). (**B**) Estimated ice access anomaly, which is the *Z*-scored number of days with 50% or lower ice cover on gray whale feeding grounds. (**C**) Estimated crustacean biomass anomaly, which is the *Z*-scored mean grams of carbon of benthic crustaceans on key gray whale feeding grounds. (**D**) Decline in benthic crustacean per capita biomass from 1970 to 2019, showing the relationship each sampling year between benthic crustacean abundance and biomass in grams of carbon (gC). In (A) to (C), the black lines indicate the median of the posterior distribution of estimates, and the shaded regions indicate the 95% posterior credible intervals.

condition scaling factor was 0.922 (0.913 to 0.930), indicating an ~8% decline in body condition between southbound and northbound measurements.

The estimated long-term average *K* was 22,062 (18,967 to 24,725). This long-term average is lower than the median of annual K_t values (24,500, 95% CI 21,771 to 27,797), which is to be expected given that it is the arithmetic mean outcome of a stochastic process and thus reflects the effects of environmental variability on expected abundance (*30*).

We found a significant positive relationship between benthic crustacean biomass and carrying capacity (99.9% probability slope > 0), no relationship with zooplankton density (39.2% > 0), and a high probability of a positive relationship with sea ice access (93.5% > 0). With the zooplankton density covariate eliminated from the model, both crustacean biomass (100% > 0) and sea ice access (96.2% > 0) had significant positive relationships with carrying capacity. This suggests that the ability of the eastern North Pacific gray whale population to physically access key feeding areas, in combination with in situ prey availability, explains fluctuations in body condition, reproduction, and mortality. The three major mortality events occurred during periods of simultaneous low crustacean biomass and restricted access to feeding areas (Fig. 2). In 2010, a rapid decrease in crustacean biomass but a period of average ice access led to a depression in birth rates and a modest decrease in abundance but not a major mortality event. The onset of the 2019 mortality event appears to have been driven initially by low crustacean biomass and exacerbated by a steep reduction in access to feeding areas over the following 2 years.

The decision to model gray whale population dynamics by applying annual covariate effects to carrying capacity (*K*), rather than the population's intrinsic growth rate (*r*), is uncommon. Although in theory either model formulation could be used to explain fluctuations in abundance and vital rates, we believe that applying covariate effects to carrying capacity better reflects biological reality. The Bering and Chukchi seas are the primary feeding area for virtually all eastern North Pacific gray whales, suggesting that the quality and quantity of prey in these areas will have a greater impact on vital rates when there is high intraspecific competition at higher levels of gray whale abundance. This is supported empirically by our estimates of population growth rate relative to abundance. Mean population growth rates were significantly higher at low than at high abundance levels, and major busts (annual declines of >9 to 10%) only occurred when the gray whale population was at high abundance (fig. S9), which supports the existence of density-dependent controls on vital rates. By applying covariate effects to carrying capacity, we simultaneously account for environmental conditions and the effects of negative density dependence (*31*). In addition, this avoids a scenario in which, in a model that applies covariate effects to *r* instead of *K*, the population exceeds a stationary carrying capacity but continues to grow because of positive covariate effects on growth rate. Instead, our estimated annual carrying capacity (K_t) captures short-term fluctuations in the strength of density dependence and can be interpreted as an abstract parameter corresponding to the expected equilibrium abundance if environmental conditions remained fixed at the values recorded during that year (*32*).

Over the past 50 years, the per capita biomass of benthic infaunal crustaceans has declined precipitously (Fig. 2D and fig. S3), and the three major gray whale mortality events coincided with periods of low per capita biomass, which translated into low total crustacean biomass. This decline in per capita biomass is most likely associated with species distribution shifts of benthic amphipods and other crustaceans. As ice cover decreases in response to rapid Arctic warming, current speed in the Chirikov basin has increased, leading to larger sediment grain size and reduced particulate organic carbon reaching the seafloor (*5*). These conditions favor smaller amphipods with lower lipid content over the lipid-rich, tube-building ampeliscid amphipods that historically dominated the shallow basins of the Bering and Chukchi seas (*10*). This regime shift has likely contributed to declining per capita biomass of gray whale prey, which despite steady or increasing prey abundance has resulted in lower overall available biomass (fig. S3).

The combined effect of sea ice cover and benthic productivity on gray whale population dynamics has driven major boom-bust cycles, including two modern booms in abundance that may have exceeded preexploitation levels (*13*). High benthic biomass and prey quality in the late 1970s and early 1980s supported almost 25,000 gray whales, contributing to their delisting from the US Endangered Species Act. More recently, rapid Arctic warming in response to climate change increased access to feeding areas (Fig. 2B), supporting a sustained increase in gray whale abundance over the past decade (Fig. 1A). Although recent Arctic warming may have provided sufficient benefit to the population to counteract decreasing benthic biomass over the short term, the outlook for benthic prey quality is not favorable. Rising water column and bottom water temperatures and projected decoupling of pelagic and benthic productivity caused by retreating sea ice will likely lead to continued declines in Arctic benthic crustacean biomass (*5*). Access to feeding areas reached a peak of 266 days in 2019, which is presumably approaching a point of diminishing returns given that the species migrates to Mexico each winter. Poleward shifts in gray whale feeding locations have already been documented, which likely reflect the declining quality and shifting distribution of their preferred prey (*12*). Future declines in benthic biomass will likely drive decreases in gray whale carrying capacity that cannot be offset by continued increases in ice access. Reports of gray whales shifting their Arctic feeding distribution and targeting pelagic prey (*12*) suggest that they may have the ability to compensate for these changing conditions to some extent, but our results suggest that any ongoing behavioral adaptations have thus far been insufficient to prevent major mortality events.

Eastern North Pacific gray whales are the most closely monitored large whale species, with records of abundance, reproduction, mortality, and condition spanning more than half a century. The abundance of most large whale species remains far below pre-whaling levels (*33*, *34*), which limits our understanding of the dynamics and behavior of whale populations as they approach carrying capacity and become increasingly governed by density-dependent processes. By contrast, gray whales have recovered rapidly from post-whaling lows to numbers that may approach or exceed pre-whaling levels and have low rates of direct human mortality, providing a rare window into the possible natural fluctuations of large whale populations. The periodic mortality events and major population swings that we report are surprising for a long-lived vertebrate that must by definition have high average survival rates to facilitate longevity. However, whales achieve their immense body sizes by feeding on large quantities of low-trophic-level prey (*35*), which may make them sensitive to oceanographic and environmental fluctuations. The feeding-fasting cycles associated with migratory baleen whales may also increase their susceptibility to environmental perturbations. Gray whales migrate more than 15,000 km each year and rely on a 4- to 5-month feeding season to support a majority of their energetic requirements for the year. This strategy may place them at a physiological threshold at which disruptions to their food supply translate into major impacts to vital rates—a pattern that may be widespread across migratory whales and may become more pronounced as species and populations recover to their pre-whaling abundances. Climate-driven ocean warming is expected to have profound impacts on ocean circulation, upwelling strength, and primary production (*36*, *37*), which may in turn have major implications for large whale population dynamics and viability through predator-prey interactions (*34*).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S9
References (*39–55*)
MDAR Reproducibility Checklist

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Editor’s summary
Environments are responding to human-induced climate warming in a variety of ways, not all of them expected. Such changes can have large impacts on species and ecosystems. Responses to such changes may be most obvious in shorter-lived species, but Stewart *et al*. show that even some of the largest animals on the planet are susceptible to relatively minor changes (see the Perspective by Read). Specifically, they looked across a 50-year database on gray whale population estimates and found clear evidence of rapid population increases and declines in response to changing prey biomass and ice cover. —Sacha Vignieri

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