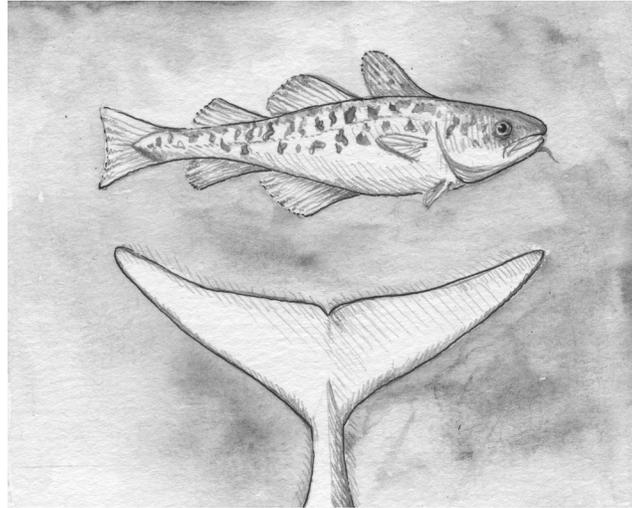


Ecosystem Effects of Fishing and Whaling in the North Pacific and Atlantic Oceans

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Human alterations of marine ecosystems have occurred throughout history, but only over the last century have these reached global proportions. Three major types of changes have been described: (1) the changing of nutrient cycles and climate, which may affect ecosystem structure from the bottom up, (2) fishing, which may affect ecosystems from the top down, and (3) habitat alteration and pollution, which affect all trophic levels and therefore were recently termed side-in impacts (Lotze and Milewski 2004). Although the large-scale consequences of these changes for marine food webs and ecosystems are only beginning to be understood (Pauly et al. 1998; Micheli 1999; Jackson et al. 2001; Beaugrand et al. 2002; Worm et al. 2002; Worm and Myers 2003; Lotze and Milewski 2004), the implications for management are often profound (Lotze 2004).

Fishing and whaling were arguably the first massive human-induced alteration of the marine environment, preceding other impacts such as pollution and climate change (Jackson et al. 2001). What were the ecosystem impacts of removing millions of large whales from the ocean (Katona and Whitehead 1988)? Because much of the changes occurred in past centuries (Reeves and Smith, Chapter 8 in this volume), we may never know with absolute certainty, but we can formulate hypotheses based on (1) what we know

about the role of whales in the food web and (2) what has been observed in other species playing a similar role. Then we may explore whether the available evidence supports these hypotheses. Experiments and detailed observations in lakes, streams, and coastal and shelf ecosystems have shown that the removal of large predatory fishes or marine mammals almost always causes release of prey populations, which often set off ecological chain reactions such as trophic cascades (Estes and Duggins 1995; Micheli 1999; Pace et al. 1999; Shurin et al. 2002; Worm and Myers 2003). Another important interaction is competitive release, in which formerly suppressed species replace formerly dominant ones that were reduced by fishing (Fogarty and Murawski 1998; Myers and Worm 2003). Although both prey release and competitive release appear to be general ecosystem effects of fishing, it is unclear how these processes apply to whales and whaling.

In this paper we use time-series analysis to explore whether prey release and competitive release have occurred during or shortly after the period of industrial whaling (from 1950 to 1980) in the Northwest Atlantic and Northeast Pacific Oceans, respectively. We focus on these two regions because they are well known, food webs are relatively simple, and there are data available on whale abundance, diets, and the abundance of prey and competitor populations. Unfortunately, time-series

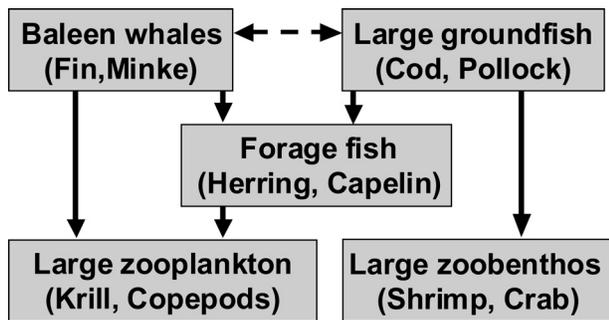


FIGURE 26.1. Predator-prey (solid arrows) and potential competitive (broken arrows) relationships between whales, groundfish, forage fish, benthic and pelagic invertebrates. Species names represent the focal species discussed in this chapter.

abundance data predating the 1950s are very scarce. Therefore, at this point, we were not able to explore the long-term (century-scale) effects of whaling, which began as early as the eleventh century in the Atlantic (Clapham and Link, Chapter 24 in this volume). Also, we caution that short time series such as those that are available to us bear a number of statistical problems, such as low sample size and temporal autocorrelation.

The focal species of this chapter and their interactions are shown in Figure 26.1. Diet data indicate that baleen whales feed primarily on small schooling fish (often called forage fish), such as herring (*Clupea* spp.), capelin (*Mallotus villosus*), or sand lance (*Ammodytes* spp.), and on zooplankton such as krill or calanoid copepods (Kawamura 1980). Forage fish and benthic invertebrates (such as northern shrimp, *Pandalus borealis*, or snow crab, *Chionoecetes opilio*) represent the primary diet of large groundfish such as Atlantic cod (*Gadus morhua*) and walleye pollock (*Theragra chalcogramma*) (Lilly 1984; Dwyer et al. 1987; Link and Garrison 2002). Because of diet overlap with respect to forage fish, groundfish and baleen whales may potentially compete for food in regions where both reach high abundance (Figure 26.1). Exploitation competition for food could be exacerbated by interference competition, in which whales (for example, minke whales; Lindstrøm et al. 1998) feed on groundfish. This may be particularly important in the Bering Sea, where school-forming juvenile walleye pollock represent an important forage fish species for marine mammals (Brodeur et al. 1996; Merrick 1997).

Recent studies have shown that the biomasses of groundfish and their prey generally show countervailing abundance trends and strong negative correlations in the Northwest Atlantic and Northeast Pacific, respectively (Figure 26.2). This was true particularly for the Northern shrimp (Figure 26.2A, B), which is an important prey species of groundfish such as cod, but trends were also evident for other crustaceans such as snow crab (Figure 26.2D) and forage fishes such as herring and capelin (Figure 26.2C). Strong predation or top-down effects should result in such a negative correlation between predator and prey, because predators suppress prey abundance (McQueen et al. 1989). Most predator-prey models, other than

donor-controlled models (Pimm 1991), predict such a negative relationship if strong predator-prey linkages are assumed. Although trends in the North Atlantic were clearly indicative of a predation effect (Worm and Myers 2003; R. A. Myers, B. Worm, and W. Blanchard, *Canadian Journal of Fisheries and Aquatic Sciences*, in review), large concurrent changes in climate in the North Pacific may render the situation there more complex (Anderson and Piatt 1999). Note, however, that community changes shown in Figure 26.2 were already well under way when the main climate shift occurred in 1977. An interesting contrast between the two regions is that groundfish abundance has increased and reached high levels in the North Pacific, whereas it has collapsed to low levels in most of the North Atlantic due to overfishing (Myers et al. 1996). In both cases, prey species such as benthic invertebrates and forage fishes showed the opposite pattern to groundfish, which supports the hypothesis of a general top-down linkage (Figure 26.2).

Based on this top-down hypothesis, we predict that there may be negative correlations between whale and forage fish abundance (prey release), between groundfish and forage fish abundance (prey release), and possibly between whale and groundfish abundance (competitive release) during or shortly after the period of industrial whaling in the Northwest Atlantic and Northeast Pacific.

Methods

We assembled time-series data of selected forage fish, groundfish, and baleen whale species abundances for the Southern Grand Banks (NW Atlantic, NAFO region 3 NO) and the Bering Sea (NE Pacific, PICES region BSC) from 1950 to 1980, when industrial whaling for large baleen whales occurred (Table 26.1). Inclusion of the period before 1950 would be desirable but would require a different approach, because time-series data are not readily available.

For whales, we focused on fin (*Balaenoptera physalus*) and minke whales (*B. acutorostrata*) because fin and minke whales represented the majority of catches between 1950 and 1975 in the NW Atlantic, and fin whales dominated the catch of baleen whales in the NE Pacific. In contrast to other baleen whales that were harvested concurrently (such as blue and sei whales), fin and minke are considered important consumers of forage fishes in these regions (Kenney et al. 1997; Lindstrøm et al. 1998). We used current fin and minke whale abundances for the Bering Sea/Aleutian region as given by Pfister and DeMaster (Chapter 10 in this volume). These estimates are preliminary but the best available data at this point (see Pfister and DeMaster, Chapter 10 in this volume, for a detailed discussion of caveats). Minke whale abundance was assumed stable over time in the Pacific (Pfister and DeMaster, Chapter 10 in this volume), and fin whale abundance was assumed to have declined substantially as a result of whaling (Danner et al., Chapter 11 in this volume). For the Atlantic, we used the published estimates for the NW Atlantic fin and Canadian East Coast

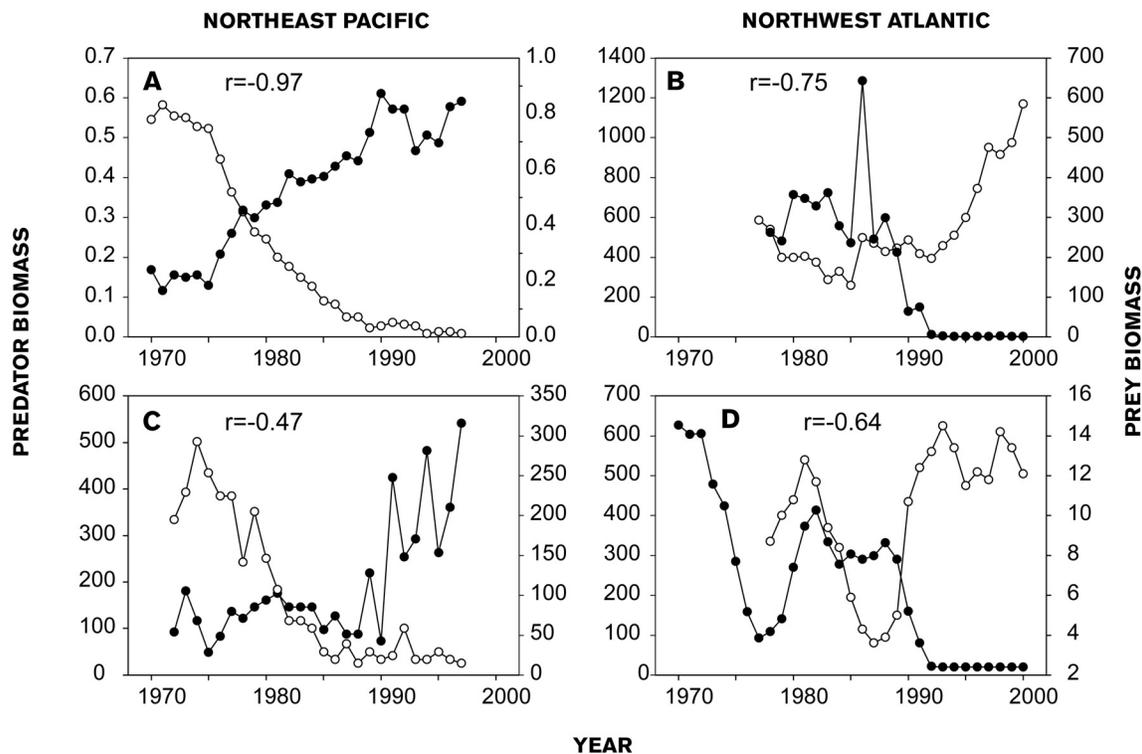


FIGURE 26.2. Strongly inverse abundance trends of predator (black circles) and prey populations (white circles) in the North Atlantic (Newfoundland Shelf) and North Pacific (Gulf of Alaska). Time series represent biomass estimates for total groundfish and Northern shrimp (*Pandalus borealis*) (A), Atlantic cod (*Gadus morhua*) and Northern shrimp (B), total groundfish and forage fish (herring, *Clupea pallasii*, and capelin, *Mallotus villosus*) (C) and groundfish and snow crab (*Chionoecetes opilio*) (D), respectively. Strong negative correlations may be interpreted as evidence for general top-down effects of large groundfish on prey populations. All data except for snow crab are based on research surveys. Units are: survey biomass as kg per tow (A, C), total biomass in thousands of metric tons (B, D: groundfish), and catch per unit of effort (CPUE; catch per trap) (D: snow crab). Modified after data from Anderson and Piatt (1999), Worm and Myers (2003), and R. A. Myers, B. Worm, and W. Blanchard (*Canadian Journal of Fisheries and Aquatic Sciences*, in review).

TABLE 26.1
Data Used for Analysis

Species		Method	Unit	Source
NE Pacific				
Whales	<i>Balaenoptera physalus</i> , <i>B. acutorostrata</i>	Reconstruction from catches	Individuals	IWC
Groundfish	<i>Theragra chalcogramma</i>	Biomass (SPA)	1000 mt	Myers et al. 1995
Forage fish	<i>Clupea pallasii</i>	Biomass (SPA)	1000 mt	Myers et al. 1995
NW Atlantic				
Whales	<i>Balaenoptera physalus</i> , <i>B. acutorostrata</i>	Reconstruction from catches	Individuals	IWC
Groundfish	<i>Gadus morhua</i> , <i>Melanogrammus aeglefinus</i> ^a	Biomass (Survey)	1000 mt	Casey 2000
Forage Fish	<i>Ammodytes</i> sp., <i>Mallotus villosus</i>	Biomass (Survey)	Proportion of tows	Casey 2000

^aNW Atlantic groundfish also included several other Gadidae, Pleuronectidae, Rajidae, Scorpaenidae, and Anarhichadidae.

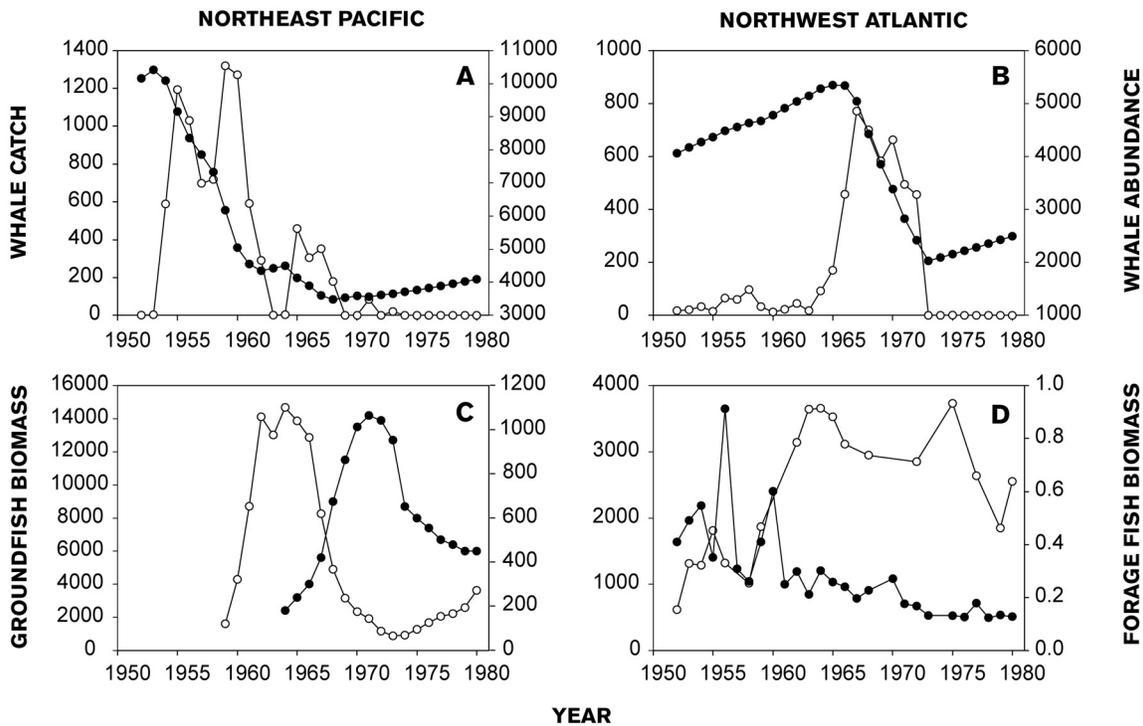


FIGURE 26.3. Trajectories of reconstructed fin and minke whale abundance (A, B, black circles), and catches (A, B, white circles), groundfish abundance (C: walleye pollock, D: Atlantic cod and haddock, black circles) and forage fish abundance (C: Pacific herring, D: capelin and sand lance, white circles) in the Bering Sea, Northeast Pacific and the Newfoundland shelf, Northwest Atlantic, 1950–1980. For data description refer to Table 26.1; for analysis, refer to Table 26.2. Units are numbers of whales (A, B), total biomass as thousands of metric tons (C, D: groundfish, herring), and survey catch per unit effort (CPUE) as proportions of tows (D: capelin and sand lance).

minke whale populations (Waring et al. 2001). These estimates are mostly based on direct ship and flight transect survey counts and should also be considered preliminary. Because no time-series abundance data were available for large whales in these regions, we back-calculated probable trends in whale numbers from current abundances and catches using minimal assumptions. Whale abundance X at time t was reconstructed from recent estimates using

$$X_t = (X_{t+1} + C_t)(1-r), \quad (26.1)$$

where we assumed that the catch C was known without error, and the specific rate of population growth r was derived from published values for Northern Hemisphere baleen whales, as compiled by the IWC (<http://www.iwcoffice.org/estimate.htm>). We assumed that the population was sufficiently low during this period that density dependence was not important. This assumption is consistent with the strong convexity hypothesis: that density dependence for cetaceans occurs only at or close to carrying capacity (Fowler 1981; Best 1993). Catches were compiled from the International Whaling Commission (IWC) database for the Bering Sea (Japanese whaling operations) and the East Canadian Shelf (Newfoundland and Nova Scotian operations) regions, respectively. The resulting time series likely underestimate total declines, at least

in the Bering Sea, as only Japanese catch data are available at this point, but other nations are known to have operated there as well. The resulting time series are not meant to represent accurate representations of historic trajectories but rather a simple representation of how catches may have affected trends in whale abundance over the period of industrial whaling.

For selected forage and groundfish species, abundance time series were compiled from published sources (Table 26.1). For the Grand Banks, data on the abundance of large groundfish (mostly Atlantic cod and haddock), and forage fish (capelin, sand lance) from standardized research trawl surveys were used (Casey 2000). For the Bering Sea, abundance estimates from published stock assessments for walleye pollock and Pacific herring were used. These stock assessments used sequential population analysis (SPA) of catch and survey data to estimate changes in abundance over time. Data and assessment details are available from Ransom Myers's global fish population database (Myers et al. 1995), which is available online at <http://fish.dal.ca>.

Relationships between time series were analyzed using standard techniques for partial correlation. We used partial correlation in order to control for the confounding effects of changes in groundfish abundance when testing effects of whales on forage fish and vice versa. All time series data were log-transformed. Time series showed intermediate to strong

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TABLE 26.2
Partial Correlation Analysis

	Slope	<i>r</i>	<i>t</i>	<i>P</i>	<i>P</i> ^a	Model <i>r</i>	Adjusted <i>r</i> ²
NE Pacific							
Dependent: Forage fish biomass							
Whales	-0.694	-0.577	-2.55	0.0243	0.4430	0.862	0.704
Groundfish	-1.379	-0.815	-5.07	0.0002	0.1850		
Dependent: Groundfish biomass							
Whales	-0.622	-0.876	-6.55	<0.0001	0.3201	0.954	0.897
Forage fish	-0.481	-0.815	-5.06	0.0002	0.1850		
NW Atlantic							
Dependent: Forage fish biomass							
Whales	0.421	0.416	1.71	0.1090	0.7269	0.675	0.378
Groundfish	-0.837	-0.673	-3.40	0.0043	0.3280		
Dependent: Groundfish biomass							
Whales	0.555	0.682	3.49	0.0036	0.3180	0.805	0.598
Forage fish	-0.541	-0.673	-3.40	0.0043	0.3280		

^aNote that *P* values were corrected for autocorrelation.

autocorrelation ($r=0.6-0.96$ at 1-year lag) and correction for autocorrelation was performed using the modified Chelton method as described by Pyper and Peterman (1998).

Results

Whale catches increased sharply through the 1950s and 1960s in the Bering Sea (Figure 26.3A) and NW Atlantic (Figure 26.3B) but then ended abruptly in 1972 and 1975, respectively, because of legal protection from commercial whaling. While catches were high, whale abundance likely declined steeply in the 1950s and 1960s and may have started to recover in the 1970s, after commercial whaling had ceased (Figure 26.3A, B). Total reported removals of fin and minke whales were 9,114 whales from the Bering Sea (Japanese whaling) and 5,768 whales from the East Canadian Shelf (Newfoundland and Nova Scotia whaling).

While catches were high and whale abundance declined in the Bering Sea, first herring and then walleye pollock abundance increased by an order of magnitude (Figure 26.3C). As pollock spawning stock biomass reached its historic peak of 14 million metric tons, herring declined to low levels but started to recover when pollock biomass declined again in the 1970s. Partial correlations revealed strong negative relationships between whales and herring ($r_{\text{partial}} = -0.58$), pollock and herring ($r_{\text{partial}} = -0.82$), and whales and pollock ($r_{\text{partial}} = -0.88$), respectively (Table 26.2). These relationships were statistically significant ($P < 0.05$) only if autocorrelation of time series was ignored. If we corrected for autocorrelation,

true sample sizes declined to $n \approx 4$, and significance levels increased to $P > 0.05$ (Table 26.2).

In the NW Atlantic, groundfish biomass was high in the 1950s but then declined gradually from 1950 to 1980, while capelin and sand lance abundance showed an inverse pattern in abundance (Figure 26.3D). Forage fish abundance was weakly positively correlated with whale abundance ($r_{\text{partial}} = 0.42$) and strongly negatively correlated with groundfish biomass ($r_{\text{partial}} = -0.68$). Groundfish abundance was positively related to whale abundance ($r_{\text{partial}} = -0.68$). Again, formal significance of the latter two relationships broke down when temporal autocorrelation was accounted for (Table 26.2).

Overall, partial correlations among whales, groundfish, and forage fish could explain 83%–91% of total variance in the NE Pacific but only 38%–60% of variance in the NW Atlantic. A sensitivity analysis revealed that negative correlations in both data sets remained stable or became stronger when only years with whale removals (1952–1973) were analyzed. Positive correlations between whales and groundfish in the NW Atlantic weakened considerably in this alternative analysis ($r_{\text{partial}} = 0.45$).

Discussion

The evidence discussed in this chapter is in accordance with a general top-down effect of groundfish on forage species (schooling fish and benthic invertebrates), but the effects of whales on forage species appeared more ambiguous and

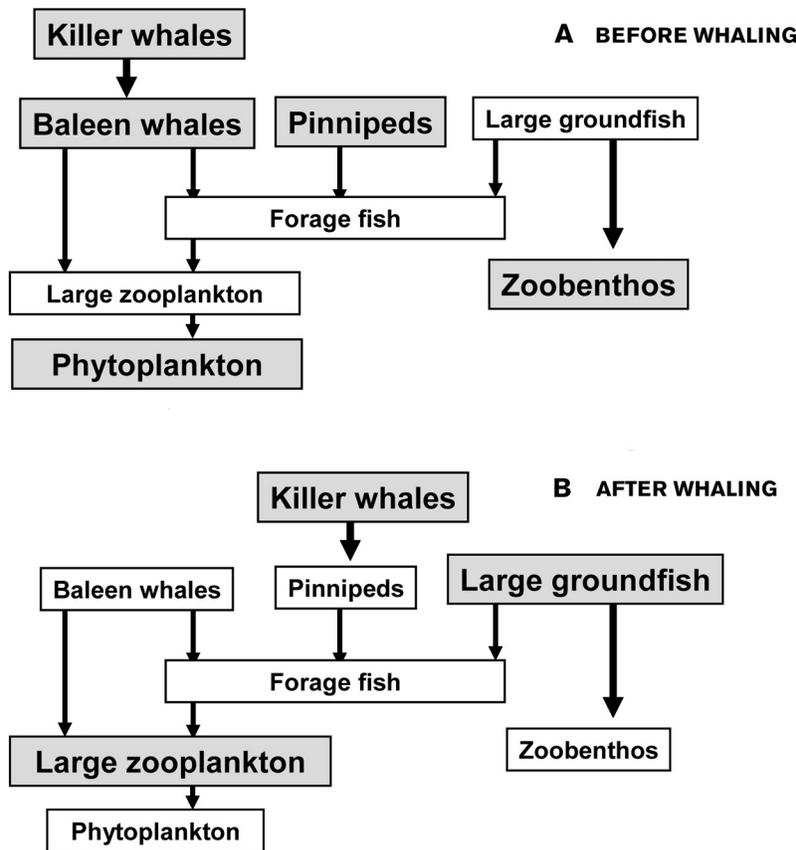


FIGURE 26.4. Hypothetical effects of industrial whaling on some major components of the Bering Sea ecosystem. Functionally dominant groups are shaded. Prewhaling (before 1950) the ecosystem is dominated by marine mammals; post-whaling (after 1972) it is dominated by groundfish.

differed markedly between the NW Atlantic and NE Pacific. This difference is likely explained by the contrasting exploitation history of the two regions: Massive whaling operations had occurred before 1950 in the NW Atlantic but not to the same extent in the NE Pacific.

In the NE Pacific, the available data indicate large declines of whale biomass in the 1960s, which may have triggered subsequent increases in herring and walleye pollock, the latter reducing herring again to low levels. Pollock increased more slowly than herring, possibly because of its lower intrinsic rate of increase and higher age at maturity. All species showed strong negative correlations, the whale-pollock relationship being the strongest, explaining 77% of the variance in pollock abundance. Thus, whaling may have contributed to a long-term shift from marine mammal to groundfish dominance in this ecosystem (Figure 26.4). It is important to note that the removal of whales coincided with massive removals of pinnipeds such as fur seals and Steller sea lions from the same region, which may have accentuated the shift from marine mammals to fish in this ecosystem (Merrick 1997). Killer whales, switching from whales to

alternative prey species (Figure 26.4), may have further escalated the decline of pinnipeds and, later, sea otters in this region (Estes et al. 1998; Springer et al. 2003). Finally, if top-down effects were general, we hypothesize that the decline of whales may have increased large-zooplankton biomass, possibly causing phytoplankton abundance to decline, and the increase in groundfish may have reduced zoobenthic biomass (Figure 26.4).

In the NW Atlantic a gradual depletion of both whales and groundfish occurred from the 1950 to the 1970s, and no dominance shift was observed. Capelin and sand lance increased in the 1960s, but the partial correlation analysis suggested that these increases were explained by release from groundfish (not whale) predation (Table 26.2). Indeed, whales showed weak positive correlations with forage fish and groundfish, which does not support the top-down hypothesis. Positive linkages could indicate a weak bottom-up effect (such as similar response to climate variation) or that humans exploited all groups at the same time, and trajectories co-vary for that reason. Ultimately, the striking differences observed between the two regions (NE Pacific,

NW Atlantic) may be explained by their different exploitation history. The NW Atlantic has been exploited heavily for many decades, and intense industrial whaling and a large-scale groundfishery were in place there long before 1950 (Lear 1997). In contrast, the Bering Sea experienced fewer removals of baleen whales before 1950 (but note that right, bowhead, and humpback whales were hunted before 1950), and an industrial-scale fishery for walleye pollock emerged only in the 1960s and 1970s. Moreover, this latter fishery was managed relatively conservatively, avoiding the depletion seen in the NW Atlantic and its associated ecosystem effects.

Of course, a correlative historical analysis like this has many caveats. First, reconstructions of past whale abundances rely heavily on simplifying assumptions and can most likely only reproduce broad trends. There are also unresolved questions with respect to current abundance estimates and the completeness of whaling records, among others (Danner et al., Chapter 11 in this volume; Pfister and DeMaster, Chapter 10 in this volume). Secondly, correlations are one way to summarize patterns in nature, but we cannot use them to infer causality. Third, short time series offer only limited information, particularly if they are heavily autocorrelated. Still, they may allow us to examine trends and to formulate interesting hypotheses, such as the dominance shift hypothesis outlined in Figure 26.4. Finally, we are presenting data from only two regions, which represent an effective sample size of $n = 2$. A broader analysis would combine results from a larger set of species from many regions, allowing for a proper meta-analysis of species interactions, as presented by Micheli (1999) and Worm and Myers (2003). Unfortunately, long-term time-series data are not readily available for forage fish and whales in particular. Carefully constructing such data sets from historical records represents an important challenge (Reeves and Smith, Chapter 8 in this volume).

A largely open question is how the effects of fishing and whaling propagate further through the food web. Increases in forage fishes due to removal of whales (NE Pacific) and groundfish (NW Atlantic) could have had strong effects on zooplankton and phytoplankton. Evidence for such pelagic trophic cascades, for example in the NW Atlantic (Carscadden et al. 2001) and NE Pacific (Shiomoto et al. 1997) is accumulating, but arguments are often based on weak evidence. In a comprehensive meta-analysis of 20 pelagic food webs, Micheli (1999) found strong evidence for a fish-zooplankton link but no general effect on phytoplankton. Another potential effect of the increased forage fish biomass could be that humans switched from whales to forage fish, as the whales become scarce. Indeed, large purse-seine fisheries for herring and capelin developed in the NW Atlantic and NE Pacific in the 1960s and 1970s, partly replacing the role of whales as consumers of forage fishes. This pattern of serial depletion of predators and their prey has been documented as a general pathology of global fisheries (Pauly et al. 1998).

Conclusions

This paper is about hypotheses. Although we will likely never know for sure what the precise ecosystem effects of past fishing and whaling were, a careful exploration of the topic may teach us some important rules about managing marine ecosystems. Here, we suggest that exploitation can cause trophic cascades from humans to fish and invertebrates and that evidence for strong top-down linkages is often seen, where data exist and where they are carefully analyzed. Although many of the underlying data sets undoubtedly have serious problems, it is the collective weight of the evidence that points toward a more general phenomenon. Marine ecosystems can change rapidly in response to perturbations and may shift to new stable states, as seen in the Bering Sea example. They also may completely reorganize, leading to outbreaks of some species and near-extirpation of others (Scheffer et al. 2001). These shifts could be due to whaling, fishing, climate change, or a combination of these factors, all of which are partly or entirely anthropogenic and therefore within our responsibility. From the present analysis it appears at least conceivable that industrial whaling in the Bering Sea, 1950–1975, has contributed to, and possibly initiated, a shift in food web structure from marine mammals to groundfish, which may have been further emphasized by fisheries management and climate instability, as suggested by Merrick (1997). The lack of such clear responses during the same time period in the NW Atlantic could be interpreted as an indication that baleen whales were ecologically less important in this ecosystem. However, the North Atlantic has the longest whaling record of any ocean, going back to the eleventh century (Clapham and Link, Chapter 24 in this volume). At that point in time, whales may have well been dominant, and perhaps only their decline over the following centuries gave rise to the great abundance of fish that made this region world-famous. However, industrial fishing again transformed that situation. The recent collapses of cod and other gadoids in the NW Atlantic had clear ecosystem effects, such as massive increases in forage species (Fogarty and Murawski 1998; Worm and Myers 2003; R. Myers, B. Worm, and W. Blanchard, *Canadian Journal of Fisheries and Aquatic Sciences*, in review) and possible shifts to new stable states (Swain and Sinclair 2000). The lesson may be that the effects of whaling can be understood only as part of a bigger, emerging picture: the destabilizing effects of removing most large predators, such as whales, seals, turtles, bony fishes, sharks, and rays, effectively terminating their roles as key functional components of marine ecosystems.

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[AUQ1] (Methods, 3rd paragraph) Do you mean the Stock Recruitment Database?