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Kenneth T. Frank, *et al.*

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Kenneth T. Frank,[1]* Brian Petrie,[1] Jae S. Choi,[1,2] William C. Leggett[2]

Removal of top predators from ecosystems can result in cascading effects through the trophic levels below, completely restructuring the food web. Cascades have been observed in small-scale or simple food webs, but not in large, complex, open-ocean ecosystems. Using data spanning many decades from a once cod-dominated northwest Atlantic ecosystem, we demonstrate a trophic cascade in a large marine ecosystem. Several cod stocks in other geographic areas have also collapsed without recovery, suggesting the existence of trophic cascades in these systems.

Trophic cascades, defined by (i) top-down control of community structure by predators and (ii) conspicuous indirect effects two or more links distant from the primary one, have been intensively researched and controversial for decades (*1*, *2*). The existence of top-down control of ecosystem structure (implied by trophic cascades) creates opportunities for the understanding and manipulation/management of exploited ecosystems, because exploitation is generally focused on top predators (*3*, *4*). From a theoretical perspective, the spatiotemporal balance between the "top-down" (predator dominated) and "bottom-up" (nutrient driven) regulation of ecosystems provides a foundation for understanding their structure, function, and evolution (*5*).

Most ecosystems for which trophic cascades have been shown feature one or more of the following: low species diversity, simple food webs, and small geographic size (*6*, *7*); examples from more complex ecosystems exist (*8*, *9*). This restricted subset of ecological types characterizes many freshwater ecosystems, which constitute most aquatic-based examples of trophic cascades (*6*). Marine continental shelf ecosystems, which generally have large spatial scales, high species diversity, and food web complexity, have not yet revealed unequivocal evidence of trophic cascades. Steele and Collie (*10*) reasoned that continental shelf ecosystems, with their massive changes in predatory fish populations

because of exploitation, should provide the most definitive tests of the trophic cascade hypothesis, yet none were found. Reid *et al.* (*5*) found no evidence of trophic cascades in the heavily exploited North Sea, nor did Micheli's (*11*) meta-analysis of 20 open marine systems. However, Worm and Myers's (*12*) meta-analysis of nine continental shelf ecosystems revealed large increases in macroinvertebrate populations following declines in cod (*Gadus morhua*) stocks. Although their findings do not provide evidence of a trophic cascade, they suggest the potential for predation-induced top-down effects in large marine ecosystems. Estes *et al.* (*9*) found evidence of a four-level cascade consisting of killer whales, sea otters, sea urchins, and kelp. However, their time series were limited and the changes in killer whale abundance were unknown. Thus, the evidence for trophic cascades in open ocean systems is equivocal.

Here we provide evidence of a trophic cascade in the large eastern Scotian Shelf ecosystem off Nova Scotia, Canada (Fig. 1) (*13*). The cascade involved four trophic levels and nutrients and was driven by changes in the abundance of large predators (primarily cod) of fish and macroinvertebrates, thereby meeting the requirements of top-down control and indirect effects with multiple links (*1*). Moreover, the cascading effects involved the entire community, rather than only a subset of the species that occupy each of the affected trophic levels.

Consistent with the first criterion of trophic cascades, the system changes were driven by the collapse of the benthic fish community (Fig. 1A). In addition to cod, several other commercially exploited species declined, including haddock (*Melanogrammus aeglefinus*), white hake (*Urophycis tenuis*), silver hake

(*Merluccius bilinearis*), pollock (*Pollachius virens*), cusk (*Brosme brosme*), redfish (*Sebastes* sp.), American plaice (*Hippoglossoides platessoides*), yellowtail flounder (*Limanda ferruginea*), thorny skate (*Raja radiata*), and winter skate (*Raja ocellata*). The transition occurred during the mid-1980s and early 1990s and resulted in the virtual elimination of the ecosystem-structuring role of the large-bodied predators that had dominated for centuries (*14*). The abundance of small pelagic fishes and benthic macroinvertebrates [predominantly northern snow crab (*Chionoecetes opilio*) and northern shrimp (*Pandalus borealis*)], once among the primary prey of the benthic fish community (supporting text), increased markedly following the benthic fish collapse (Fig. 1B). The correlations between the benthic fish biomass and small pelagic fishes ($r = -0.61$, $n = 33$ years), snow crab ($r = -0.70$, $n = 24$), and shrimp abundances ($r = -0.76$, $n = 24$) were negative.

Consistent with the second criterion of trophic cascades, there were conspicuous indirect effects resulting from removal of the top predator. As predicted, the correlation between the time series of the benthic fish community (landings) and large (>2 mm), herbivorous zooplankton was positive ($r = 0.45$, $n = 23$), and that for phytoplankton was negative ($r = -0.72$, $n = 24$). These relationships remained equally strong when survey estimates of groundfish biomass were used in place of landings (*13*).

The herbivorous zooplankton abundance series revealed strong evidence of a transition from high to low abundance of large-bodied species from the 1960s and 1970s to the 1990s and beyond (Fig. 1C). This finding is consistent with the enhanced role of size-selective predation on zooplankton by pelagic fishes and early-life stages of shrimp and crab. The abundance of small-bodied (<2 mm) zooplankton remained similar throughout the study period (Fig. 1C). The phytoplankton record (Fig. 1D) revealed a reciprocal pattern: Abundances were low in the 1960s and 1970s and high in the 1990s and beyond. Plankton data ancillary to the continuous plankton recorder data (*13*) revealed a 45% greater abundance of large zooplankton during the early 1980s relative to the late 1990s (Fig. 1C). In contrast, chlorophyll levels were higher in the 1990s relative to the 1980s, but the differences were slight (Fig. 1D). Finally, nitrate concentrations, a major limiting factor in marine systems, showed the expected reciprocal re-

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1621

sponse to changes in phytoplankton abundance (Fig. 1D).

The predatory impact of the expanding grey seal (*Halichoerus grypus*) population (*13*) on the resident cod stock was minor (Fig. 1A) (*15*). Seals appear to have benefited from the cod collapse, which released their forage base (small pelagic fish and benthic invertebrates) from predation. A strong positive correlation between the abundances of small pelagics and grey seals ($r = 0.70$, $n = 33$) and the ongoing exponential rate of increase in the seal population (*16*) support this claim.

Principal component analysis of the series that we used (Fig. 1) and of other biotic, abiotic, and human variables conducted by Choi *et al.* (*17*) has provided statistical evidence and a concise assessment of the change in ecosystem structure. Principal component 1 explained 33% of the variance; its amplitude

was positive and nearly constant from 1970 to the mid-1980s, featured a linear transition from the mid-1980s to negative values in the early 1990s, and remained negative and nearly constant since then. Initially (1970 to 1986), benthic fish, possessing good physiological condition, high growth rates, and supporting a >100 × 10³ metric tons (kt) commercial fishery, dominated; the current period (post-1990) is a pelagic fish/macroinvertebrate–dominated system characterized by poor benthic fish productivity, a <50-kt benthic fish fishery, and a small (<50 kt), but increasing, macroinvertebrate fishery directed at shrimp and snow crab. Several management measures designed to reverse the trend and restore the system to its earlier state have failed. The actions taken included establishment of a fishing closure on two major offshore banks in 1987 that encompass about 15% of the management unit area (*18*), establishment of a moratorium on

directed fishing of the dominant benthic fish species (cod, haddock, and pollock) in 1993, and development of new fisheries designed to divert fishing mortality away from the remaining benthic fish species. In 1995, sentinel surveys, supplementing existing scientific surveys, were instituted to monitor and document the anticipated recovery.

Whether the recent ecosystem changes are reversible is an open question. Other factors, both intrinsic and extrinsic, were associated with the ecosystem changes. For example, the expected inverse and reversible relationship between fishing mortality and cod biomass (*13*) that characterized the 1960 to early 1990 period does not hold after 1993 despite the near-elimination of exploitation (Fig. 2A). Physical environmental changes may have contributed to the restructuring of the food web. During the mid-1980s, the average deep-water temperatures declined by ~1°C. This decline started about 4 years before the collapse of cod and other benthic fishes. Recently, temperatures have been normal or above normal without a corresponding increase in benthic fish abundance (Fig. 2B). Vertical stratification of the water column intensified after the collapse and is therefore unlikely to have been a meaningful driver of the changes observed. Stratification has continued to intensify (Fig. 2B), however, and may be contributing to diminished energy flux to the benthic fish community, as revealed by reduced physiological condition and reproductive output (*19*).

Fig. 1. Illustration of a trophic cascade on the eastern Scotian Shelf across four levels and nutrients. (**A**) Commercial landings of benthic fish species, fishery-independent survey estimates of benthic fish, and population biomass estimates of grey seals. (**B**) The forage base of benthic fish species (and seals), including small pelagic fish species and benthic macroinvertebrates. (**C**) Large (>2 mm) zooplankton, combined abundance of copepodite and adult stages of *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreous*; small zooplankton, represented by the combined abundance of Calanoid copepods (28 species) other than *Calanus* sp. with body lengths < 2 mm, and large *Calanus* sp. (average number per m³) from two ancillary sampling programs shown as horizontal lines. (**D**) Phytoplankton color, 0 to 50 m average in situ chlorophyll (mg chlorophyll/m³), shown as horizontal lines, and 0 to 100 m integrated, dissolved nitrate.
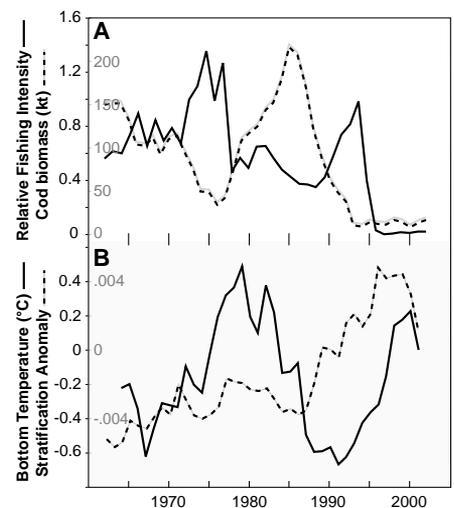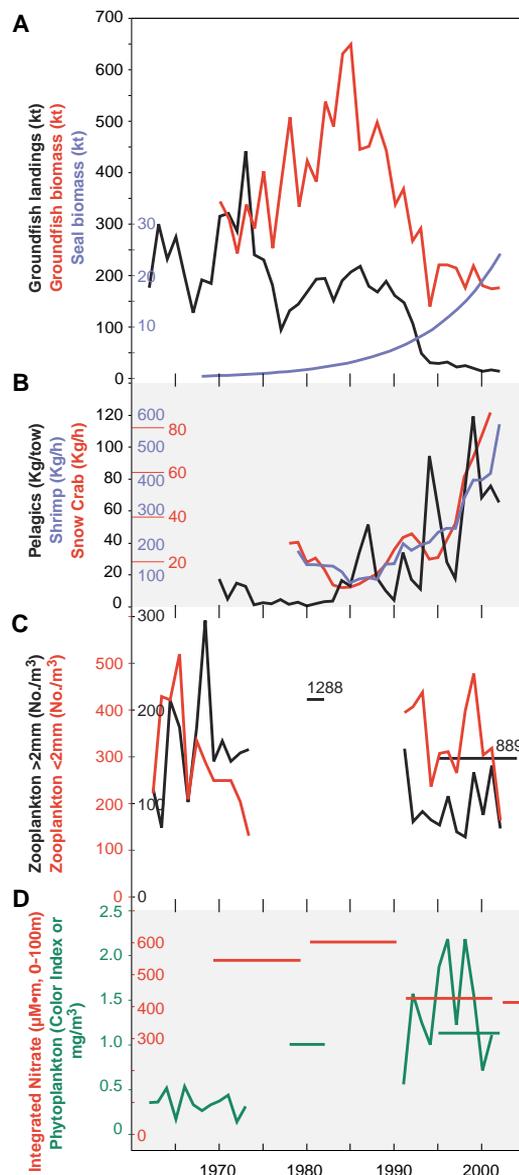
Fig. 2. Intrinsic and extrinsic factors influencing the trophic cascade. (**A**) Time series of cod spawning stock biomass and an index of directed exploitation on the eastern Scotian Shelf. The expected increase in biomass following the reduction of fishing intensity in 1993, as occurred in the late 1970s, is not seen. (**B**) Changes in bottom-water temperatures and vertical stratification [kg/(m³·m)] of the water column (both shown as 5-year, center-weighted running means) on the eastern Scotian Shelf.

We suspect that this system is not unique. Several cod stocks, inhabiting similar oceanographic regimes (north of 44°N latitude) in the northwest Atlantic where they were the dominant predators, collapsed in the early 1990s (decline by >95% of maximum historical biomass) and failed to respond to complete cessation of fishing [there was one exceptional stock (table S1)]. For example, the current biomass of these stocks has increased only slightly, ranging from 0.4 to 7.0% during the past 10+ years (table S1). Reciprocal relationships between macroinvertebrate biomass and cod abundance in these areas (*12*) suggest that the processes that we document for the Scotian Shelf may have occurred there. On the other hand, the three major cod stocks resident south of 44° N, though reaching historical minimum levels at about the same time as the northerly stocks and experiencing similar intensive fishing pressure, declined by only 50 to 70%; current biomass has increased from 10 to 44% of historical minimum levels. These stocks inhabit different oceanographic regimes with respect to temperature and stratification and do not show the inverse relationship between the biomass of macroinvertebrates and cod found by Worm and Myers (*12*). These geographic differences in cod population dynamics merit additional study.

The changes in top-predator abundance and the cascading effects on lower trophic levels that we report reflect a major perturbation of the eastern Scotian Shelf ecosystem. This perturbation has produced a new fishery regime in which the inflation-adjusted, monetary value of the combined shrimp and crab landings alone now far exceed that of the groundfish fishery it replaced (*13*). From an economic perspective, this may be a more attractive situation. However, one cannot ignore the fundamental importance of biological and functional diversity as a stabilizing force in ecosystems, and indeed in individual populations (*20*), in the face of possible future perturbations (whether natural or human-made). One must acknowledge the ecological risks inherent in "fishing down the food web" (*21*), as is currently occurring on the Scotian Shelf, or the ramifications associated with indirect effects reverberating across levels throughout the food web, such as altered primary production and nutrient cycling.

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22. We thank the Department of Fisheries and Oceans staff who collected and maintained the data with care and thoroughness, and M. Pace, N. L. Shackell, J. E. Carscadden, and two anonymous reviewers for helpful criticisms. This research was supported by Fisheries and Oceans Canada and a grant from the Natural Sciences and Engineering Research Council of Canada Discovery (to K.T.F. and W.C.L.).

Inferences of Competence from Faces Predict Election Outcomes

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We show that inferences of competence based solely on facial appearance predicted the outcomes of U.S. congressional elections better than chance (e.g., 68.8% of the Senate races in 2004) and also were linearly related to the margin of victory. These inferences were specific to competence and occurred within a 1-second exposure to the faces of the candidates. The findings suggest that rapid, unreflective trait inferences can contribute to voting choices, which are widely assumed to be based primarily on rational and deliberative considerations.

Faces are a major source of information about other people. The rapid recognition of familiar individuals and communication cues (such as expressions of emotion) is critical for successful social interaction (*1*). However, people go beyond the inferences afforded by a person's facial appearance to make inferences about personal dispositions (*2*, *3*). Here, we argue that rapid, unreflective trait inferences from faces influence consequential decisions. Specifically, we show that inferences of competence, based solely on the facial appearance of political candidates and with no prior knowledge about the person, predict the outcomes of elections for the U.S. Congress.

In each election cycle, millions of dollars are spent on campaigns to disseminate information about candidates for the U.S. House of Representatives and Senate and to convince citizens to vote for these candidates. Is it possible that quick, unreflective judgments based solely on facial appearance can predict the outcomes of these elections? There are many reasons why inferences from facial appearance should not play an important role in voting decisions. From a rational perspective, information about the candidates should override any fleeting initial impressions. From an ideological perspective, party affiliation should sway such impressions. Party affiliation is one of the most important predictors of voting decisions in congressional elections (*4*). From a voter's subjective perspective, voting decisions are justified not in terms of the candidate's looks but in terms of the candidate's position on issues important to the voter.

Yet, from a psychological perspective, rapid automatic inferences from the facial appearance of political candidates can influence processing of subsequent information about these candidates. Recent models of social cognition and decision-making (*5*, *6*) posit a qualitative distinction between fast, unreflective, effortless "system 1" processes and slow, deliberate, effortful "system 2" processes. Many inferences about other people, including inferences from facial appearance,

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1623