

# Accelerating Trophic-level Dysfunction in Kelp Forest Ecosystems of the Western North Atlantic

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## ABSTRACT

We use archaeological, historical, ecological, and fisheries data to identify three distinct and sequential phases in the trophic structure of kelp forests in the western North Atlantic's Gulf of Maine. Phase 1 is characterized by vertebrate apex predators such as Atlantic cod, haddock, and wolffish and persisted for more than 4,000 years. Phase 2 is characterized by herbivorous sea urchins and lasted from the 1970s to the 1990s. Phase 3 is dominated by invertebrate predators such as large crabs and has developed since 1995. Each phase change resulted directly or indirectly from fisheries-induced "trophic-level dysfunction," in which populations of functionally important species at higher trophic levels fell below the densities necessary to limit prey populations at lower trophic levels. By using fractional trophic-level analysis, we found that phase changes occurred rapidly (over a few years to a few decades) as well as relatively recently (over the past

half-century). Interphase durations have declined as fishing effects have accelerated in recent years. The naturally low species diversity of the kelp forest ecosystem we studied may facilitate rapid changes because the redundancy within each trophic level is low. If the biodiversity within controlling trophic levels is a buffer against trophic-level dysfunction, then our observations from Maine may be predictive of the fate of other, more diverse systems. If fishing successively targets most, or all, strong interactors at higher trophic levels, then as those population densities decline, the potential for trophic-level dysfunction and associated instabilities will increase.

**Key words:** apex predators; ecosystem stability; fisheries effects; food webs; fractional trophic-level analysis; gulf of Maine; phase changes; trophic cascades.

## INTRODUCTION

Food webs define the structure and function of coastal marine ecosystems (Paine 1980). Often, predators at high trophic levels have a disproportionate influence on the distribution, abundance, dominance, and diversity of organisms at lower trophic levels ( Hairston and others 1960; Paine 1966, Paine 1980). Such trophic cascades corre-

spond to both the high per capita interaction strength and the population density of the consumers (Sala and Graham 2002).

Trophic cascades result from the functional removal of higher trophic levels, shifting the dominance and effects of consumers to lower levels (Paine 1980; Sala and others 1998). Although species may become rare, at any trophic level, they are unlikely to go locally or biologically extinct. Reductions in the population density of strongly interacting species, functional groups, or trophic levels will reduce their functional role as consumers in the system (Estes and others 1989). Sufficient reduc-

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tions of strong interactors within a trophic level, or *trophic-level dysfunction*, can destabilize the community by releasing prey populations that had been suppressed by consumers at higher trophic levels.

Fishing is one of the oldest and most conspicuous human disturbances to marine ecosystems (Jackson and others 2001). Often, highest-order, or “apex,” predators are targeted because they are large and conspicuous, or simply because they have the greatest food and commercial value. If fishing pressure reduces the population density of the apex predators to the point where they become rare or economically unprofitable, the fishery target will shift to lower trophic levels. Fishing of lower trophic levels may become profitable if economic markets develop for the invertebrates at these levels and if those species become more abundant due to their release from predation by the former apex predators. This sequential reduction of highest-order trophic levels is known as “fishing down marine food webs” (Pauly and others 1998, 2001).

Most published accounts of fishing down food webs cover this phenomenon on an oceanic scale and document events occurring over the past several decades to a century (see, for example, Pauly and others 2001). In this paper, we review and analyze studies and fishing records to describe the trophodynamics of coastal zones in the western North Atlantic over the past several thousand years. We used several categories of information, including long-term archaeological and historical records, commercial fisheries data, and in situ ecological studies.

Our results suggest that there have been three distinct phases of trophic dominance in this system over the past 4,500 years; these three phases were characterized by the dominance of predatory finfish, herbivorous sea urchins, and predatory invertebrates, respectively. We consider these phases to be alternate stable states because each persists beyond the life span of the dominant organisms (Sousa and Connell 1985), is followed by a rapid shift to the next phase once a threshold is reached (Knowlton 1992), and is maintained by positive feedbacks (Petraitis and Latham 1999).

## RECONSTRUCTING FOOD WEBS OF THE WESTERN NORTH ATLANTIC

The normally species-diverse shallow rocky subtidal zones are species-depauperate in the western North Atlantic (Steneck and others 2002). This is because the North Atlantic is relatively young, the assembly of its biota from the North Pacific is relatively recent (that is, 3.5 Mya) (Vermeij 1991), and its rocky

shores have been frequently glaciated, causing localized extinctions at approximately 20,000-year cycles (Adey and Steneck 2001). Western North Atlantic food webs generally have four trophic levels; diversity is low within each level because the species pool is low throughout the region.

Determining the original prehuman composition of food webs is a challenging task. Marine macrofossils from the Holocene are rare; thus, it is impossible to estimate food web structure prior to the human colonization of coastal zones in the Gulf of Maine. The best evidence of what existed in the past is derived from archaeological sites in the region. Using archaeological evidence and early historical accounts, we reconstructed the “pristine” food web of coastal Maine. Contemporary ecological studies and fisheries landings data provide much better resolution of the structure and function of more recent food webs. Below we describe three distinctly different phases in the trophic structure of shallow subtidal zones of Maine.

### Phase 1: Predatory Fishes Dominate

By all accounts, cod and other large predatory fish were stable components of coastal zones throughout the western North Atlantic in phase 1 (Table 1 and Figure 1). These predatory fishes were abundant in the Gulf of Maine, as evident from the bones excavated by archaeologists from Indian middens dating from 200 to over 4,000 years ago (Carlson 1986; Bourque 1995; Steneck 1997). Indigenous hook-and-line fishers subsisted on a varied diet of marine organisms such as cod, other fish, oysters, and clams, as well as terrestrial animals such as deer and sea mink (now extinct) (Bourque 1995). When the first Europeans explored the Gulf of Maine, the abundance of large fish impressed them (Rosier 1605). On his 1526 map of the New World, Vespucci labeled the western North Atlantic coast *Bacallaos*, which is Portuguese for “land of the codfish.” In 1602, Bartholomew Gosnold named Cape Cod for the myriad fish that “vexed” his ship. Extensive fishing grounds for cod and other predatory fishes were mapped for coastal zones in Maine first in the 1880s (Collins and Rathbun 1887) and then again in the 1920s (Rich 1929), with remarkably little change in areal extent or location (Steneck 1997).

Predatory fishes consume and control the distribution and abundance of large benthic invertebrates (Keats and others 1986; Witman and Sebens 1992; Vadas and Steneck 1995) (Figure 1). Significantly, in Maine no large decapod crabs or lobsters have been found in Native American middens dating between 5,000 and 400 years before present

**Table 1.** Functional Groups Species, and Trophic Levels of Benthic Marine Communities in Coastal Maine at Three Time Periods and Phases

Species	TL	Phase 1 (before 1940)	Phase 2 1970–1990	Phase 3 (after 1995)
Crustose coralline algae (e.g., <i>Clathromorphum</i> spp., <i>Lithothamnion</i> spp., <i>Phymatolithon</i> )	1	Rare? <sup>a</sup>	Abundant <sup>a</sup>	Rare <sup>a, b</sup>
Understory algae (e.g., <i>Chondrus crispus</i> , <i>Desmarestia</i> spp., <i>Ceramium</i> spp., <i>Corallina officinalis</i> , <i>Bonnemaisonia hamifera</i> , <i>Enteromorpha</i> sp., <i>Phycodrus rubens</i> , <i>Ptilota serrata</i> )	1	Abundant? <sup>a</sup>	Rare <sup>a, c</sup>	Abundant <sup>b</sup>
Kelps (e.g., <i>Laminaria</i> sp., <i>Alaria esculenta</i> , <i>Agarum clathratum</i> , <i>Desmarestia</i> sp.)	1	Abundant <sup>a</sup>	Rare <sup>a, c</sup>	Abundant <sup>a, b</sup>
Gastropods (e.g. <i>Crepidula</i> sp.) Sea cucumber ( <i>Cucumaria</i> )	2.1	?	?	?
Mussels ( <i>Mytilus edulis</i> , <i>Modiolus modiolus</i> )	2.1	Rare <sup>d</sup>	Rare <sup>e</sup>	Rare <sup>b</sup>
Green sea urchin ( <i>Strongylocentrotus droebachiensis</i> )	2	Rare <sup>d</sup>	Abundant <sup>a, c</sup>	Rare <sup>a, b</sup>
Gastropods (e.g., <i>Tectura testudinalis</i> <i>Tonicella</i> sp., <i>Lacuna vincta</i> )	2.4	Rare? <sup>d</sup>	Common? <sup>c, f</sup>	Rare? <sup>g</sup>
Amphipods (e.g., <i>Gammarus</i> sp.)	2.3	Common? <sup>h</sup>	Rare <sup>a, b</sup>	Common <sup>a, h</sup>
Crabs ( <i>Cancer</i> spp., <i>Libinia</i> sp., <i>Hyas</i> sp.)	2.5	Rare to common <sup>d, i, w</sup>	Common <sup>g, j</sup>	Abundant <sup>i</sup>
Gastropods (e.g., <i>Buccinum undatum</i> )	2.6	?	?	?
Sea stars ( <i>Asterias</i> sp.)	3.1	?	?	?
American lobster ( <i>Homarus americanus</i> )	3.2	Rare to common <sup>d, k, l, w</sup>	Abundant <sup>k</sup>	Abundant <sup>k</sup>
Hake ( <i>Urophycis</i> sp., <i>Merluccius</i> sp.)	3.6–4.2	Abundant? <sup>d</sup>	Common <sup>k, m</sup>	Rare <sup>g, m</sup>
Atlantic wolffish ( <i>Anarhichas lupus</i> )	3.2	Abundant? <sup>n</sup>	Rare <sup>k, m</sup>	Rare <sup>k, m</sup>
Flounder ( <i>Pleuronectes</i> sp.)	3.2	Abundant <sup>o</sup>	Common <sup>a</sup>	Rare <sup>g</sup>
Tomcod ( <i>Microgadus tomcod</i> )	3.3	Common <sup>d, o</sup>	?	?
Sturgeon ( <i>Acipenser oxyrinchus</i> )	3.4	Common <sup>d, o</sup>	Rare <sup>g</sup>	Rare <sup>g</sup>
Cunner ( <i>Tautoglabrus adspersus</i> )	3.5	Rare <sup>d</sup>	Common <sup>p, q</sup>	Common <sup>o</sup>
Rock gunnel ( <i>Pholis gunnellus</i> )	3.5	?	Common <sup>p, q</sup>	Common <sup>g</sup>
Haddock ( <i>Melanogrammus aeglefinus</i> )	3.6	Abundant <sup>l, q, r, s, t</sup>	Rare <sup>g, k, q</sup>	Rare <sup>g</sup>
Sculpin ( <i>Myoxocephalus</i> spp.)	3.6	Common <sup>o</sup>	Common <sup>q</sup>	Common <sup>q</sup>
American plaice ( <i>Hippoglossoides platessoides</i> )	3.7	?	Common <sup>g, m</sup>	Rare <sup>m</sup>
Skates ( <i>Raja</i> sp., <i>Torpedo</i> , <i>Dasyatis</i> sp.)	3.7	Rare <sup>d, l</sup>	Rare <sup>g</sup>	Rare <sup>g</sup>
Cusk ( <i>Brosme brosme</i> )	4	Common <sup>l</sup>	Rare <sup>m</sup>	Rare <sup>m, r</sup>
Seals ( <i>Phoca</i> sp., <i>Halichoerus grypus</i> )	4	Rare? <sup>d</sup>	?	Common <sup>u</sup>
Dogfish ( <i>Squalus acanthias</i> )	4.3	Common <sup>s</sup>	Rare <sup>g</sup>	Rare <sup>g</sup>
Atlantic cod ( <i>Gadus morhua</i> )	4.4	Very Abundant <sup>d, l</sup>	Rare <sup>k, r</sup>	Rare <sup>g</sup>
Radiated shanty ( <i>Ulvaria subbifurcata</i> )	4.4	?	Common <sup>k</sup>	Common <sup>g</sup>
Pollock ( <i>Palladius virens</i> )	4.5	Abundant <sup>l, s, t</sup>	Rare <sup>g</sup>	Common <sup>g</sup>
Bluefish ( <i>Pomatomus saltatrix</i> )	4.5	Rare <sup>d, l, s</sup>	Common?	Common?

**Table 1.** Continued

Species	TL	Phase 1 (before 1940)	Phase 2 1970–1990	Phase 3 (after 1995)
Atlantic halibut ( <i>Hippoglossus hippoglossus</i> )	4.6	Common <sup>l</sup>	Rare <sup>g</sup>	Very rare <sup>g</sup>
White shark ( <i>Carcharodon carcharias</i> )	4.6	Rare <sup>v</sup>	Very rare	Absent

TL, trophic level (from Froese and Pauly 2002)

The earliest record for phase 1 is based on archaeological data for 4,300 to 400 years ago (Carlson 1986; Spiess and Lewis 2001), whereas later historical records are from Rosier (1605) and Collins and Rathbun (1887) and (other studies are reviewed in Steneck 1997; Steneck and others 2003). Food webs during phases 2 and 3 are based on in situ ecological studies and other studies, as follows:

<sup>a</sup>Steneck and others (2002)

<sup>b</sup>Vavrinec (2003)

<sup>c</sup>Steneck and Dethier (1994)

<sup>d</sup>Spiess and Lewis (2001)

<sup>e</sup>Witman (1985)

<sup>f</sup>Steneck (1982)

<sup>g</sup>Steneck (1997)

<sup>h</sup>Hacker and Steneck (1990)

<sup>i</sup>Smith (1879)

<sup>j</sup>Leland (2002)

<sup>k</sup>R. S. Steneck (unpublished)

<sup>l</sup>Collins and Rathbun (1887)

<sup>m</sup>DMR (1971–2000)

<sup>n</sup>Verrill (1871)

<sup>o</sup>Carlson (1986)

<sup>p</sup>Levin (1994)

<sup>q</sup>Malpass (1992)

<sup>r</sup>Witman and Sebens (1992)

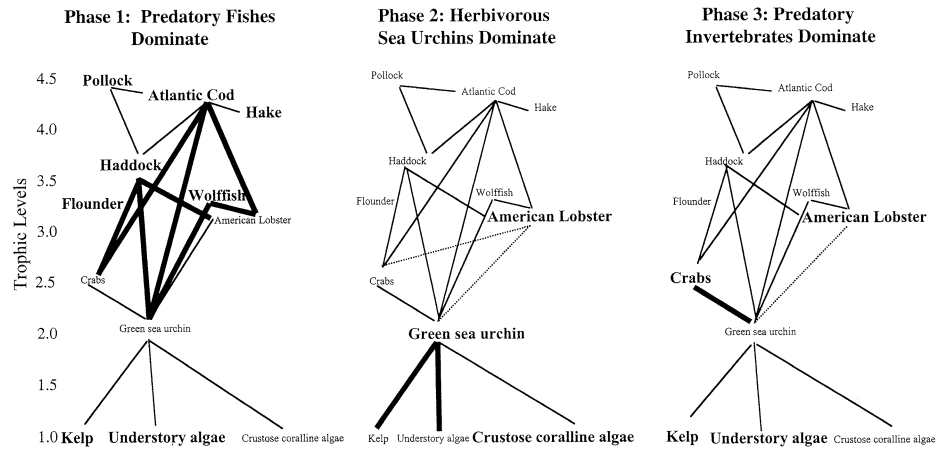
<sup>s</sup>Rosier (1605)

<sup>t</sup>Rich (1929)

<sup>u</sup>Gilbert and Guldager (1998)

<sup>v</sup>Bigelow and Schroeder (1953)

<sup>w</sup>No crabs or lobsters have been reported in Native American middens in Maine, but by the 1600s they were reported on the coast (Rosier 1605) and by the 1800s they were common (Smith 1879; Collins and Rathbun 1887).



**Figure 1.** Food webs of coastal zones of Maine. All species determined to have been abundant at one time were plotted with their assigned trophic level (see Table 1). Abundant species are shown in bold face; rare or low-abundance species are shown in smaller regular type. Most trophic linkages (*lines connecting species*) have been demonstrated with ecological studies. Apex fish predators (all above TL 3.2) feed on invertebrates (TL less than 3). Predatory invertebrates (TL 2.5–3.0) feed on the herbivorous sea urchin (TL 2), which feeds on algae (all TL 1). Interaction strengths correspond to the width of trophic linkage lines. Note that some species are weak interactors in this system. Flounder have no identifiable trophic linkage with other species in this system. Lobster's trophic linkages are weak despite their abundance in recent years because they feed primarily on lobster bait (R.S. Steneck unpublished).

(ybp) (Carlson 1986; Bourque 1995; Spiess and Lewis 2001). It is possible that these decapods simply were not preserved in the middens, although mussel shells and sea urchin tests were found at these sites. However, early historical records do document the existence of lobsters (Rosier 1605; Smith 1616; Collins and Rathbun 1887) and crabs (Smith 1879); so it is possible that even while predators were still dominating the system, some invertebrate populations may have begun to expand as coastal populations of predatory finfish declined.

Sea urchins, the only functional herbivores in the system (Steneck and Dethier 1994), were probably uncommon (Spiess and Lewis 2001) and cryptic (Lowery and Pearse 1973; Harrold and Reed 1985) (Figure 1). In the few offshore habitats where large predatory fishes still persist, urchins and decapods are rare and kelps are abundant (Vadas and Steneck 1988, Vadas and Steneck 1995; Witman and Sebens 1992) and attack rates on tethered sea urchins are high (Vadas and Steneck 1995). Significantly, very small urchins (a few millimeters in diameter) were found at this site, suggesting that they can settle but do not recruit, probably due to high rates of fish predation (Vadas and Steneck 1995).

Through at least the 1930s, kelp forests dominated the benthos, while predatory finfish were abundant in coastal zones (Steneck 1997; Steneck and others 2002). Hervey (1881) described all three dominant kelp species (Table 1) as being "very abundant from Greenland to Cape Cod" and re-

ported that they often "washed ashore in great numbers." Windrows of kelp detritus have been shown to be a good indication that adjacent subtidal zones are kelp-forested (Novaczek and McLachlan 1986). There was no mention of deforested patches at that time. The earliest scientific study in the region (Johnson and Skutch 1928) reported that kelps were the "most characteristic plant in the midlevels of the sublittoral zone." Similarly, Nova Scotia was described as kelp-dominated in the early 1950s (MacFarlane 1952).

Tests of stability often require proof that the dominant components of the ecosystem can persist for more than one generation (Connell and Sousa 1983). By all accounts, this first phase, which was dominated by predatory finfish, lasted from at least 4000 ybp to the mid 1960s. Because the average life span of the resident groundfish is 1–2 decades (Bigelow and Schroeder 1953) and *Laminaria* live 2–4 years (Chapman 1984, Chapman 1986), phase 1 can be considered stable.

### Phase 2: Herbivorous Sea Urchins Dominate

Stocks of cod and other groundfish persisted until more sophisticated fishing practices were implemented. Mechanized fishing technology and on-board refrigeration enabled the targeting of spawning aggregations of cod in the 1930s (Conkling and Ames 1996). This led to a rapid decline in the numbers and body size of coastal cod in the Gulf of Maine (Steneck 1997; Jackson and others 2001). Dominant

fish predators in the coastal zone were replaced by small, commercially less important species, such as sculpins (Malpass 1992). By the 1940s, the extirpation of coastal cod and other fishes in the Gulf of Maine resulted in the functional loss of apex predators, which fundamentally altered coastal food webs.

As fish populations were exploited, predation pressure on lower trophic levels decreased, probably fostering the increase of urchins and other mobile benthic invertebrates within the kelp beds. As localized coastal fish predation dropped to low levels urchins were able to aggregate into feeding fronts and denude the benthos of fleshy macroalgae at an estimated rate of  $4 \text{ m mo}^{-1}$  (for a review, see Scheibling and Hatcher 2001). Locally this transition could happen rapidly, but regionally it probably took decades. By the mid-1960s, there was a mosaic of kelp beds and urchin "barrens" (Lamb and Zimmerman 1964; W. Adey personal communication). Similar patches were described a decade later in Nova Scotia (Breen and Mann 1976). Deforested areas continued to expand and coalesce, and by the mid-1970s to the early 1980s kelp forests reached an all-time low in their distribution and abundance throughout the region (Steneck 1997; Steneck and others 2002).

Phase 2 was characterized by expansive sea urchin barrens, with kelp beds only in urchin-free shallow turbulent zones (Steneck and Dethier 1994) (Table 1). High urchin densities led to high grazing pressure, which prevented the establishment of young algal sporophytes (Chapman 1981) (Figure 1). Grazing-resistant coralline algae dominated the benthos (90%–100% cover in places) (Steneck 1982; Steneck and Dethier 1994), but they lacked the spatial complexity of kelp forests and other erect macroalgae that create habitat for animals, such as amphipods (Hacker and Steneck 1990) and some predatory fish (Levin 1994). Thus, the coastal benthos had become a good nursery ground for sea urchins (McNaught 1999) but a poor nursery habitat for their predators (Levin 1994). Although this phase did not persist as long as phase 1, it appears to have been stable along much of the coast for at least 2 decades, which is more than the average 15-year life span of the green sea urchin (Vadas and Beal 1999).

### Phase 3: Predatory Invertebrates Dominate

Fishing of the green sea urchin began in 1987 (Steneck and Carlton 2001) and quickly depleted populations from vast areas along the coast of Maine, thus destabilizing phase 2. When the population of urchins dropped below a threshold biomass (McNaught 1999; Vavrinc 2003), their graz-

ing pressure could no longer control macroalgal recruitment. Local reestablishment of macroalgal beds usually occurred in 1–3 years (McNaught 1999), but fish predators remained functionally absent (Table 1). Most phase shifts to macroalgal dominance occurred in the mid-1990s (McNaught 1999).

Phase 3 also appears to be stable, but it is maintained by different predatory mechanisms (Figure 1). Parts of the coast that are closed to urchin fishing have remained algal beds for at least 6 years (Vavrinc 2003). Predation by crustaceans living in the complex algal habitat probably maintains phase 3 by preventing repopulation by urchins. Small crab (*Cancer* and *Hyas* spp.) and gammarid amphipods appear to eat newly settling sea urchins, so the annual survival rate in these algal beds is reported to be less than 1% (McNaught 1999). A study conducted in 2000–1 showed that large crabs (especially *Cancer borealis*) prey on and eliminate dense populations of reintroduced adult sea urchins (Leland 2002). This effectively keeps vast regions free of sea urchins, thus maintaining stable algal communities. Functionally, crabs are now the region's apex predator because there is no higher-order predator to limit their population density (Leland 2002).

Macroalgae may also prevent the reestablishment of sea urchin populations. Whiplash (*sensu* Dayton 1975) or the sweeping of the benthos by frondose algae may dislodge encroaching populations of sea urchins (Kennelly 1989; Konar 2000; Konar and Estes 2003). In many parts of the southern Gulf of Maine, kelp beds are giving way to diverse native understory assemblages (Vavrinc 2003) or to monocultures of the nonnative bushy green alga *Codium fragile* (Levin and others 2002). These understory assemblages are much denser than kelp beds (as in phase 1), occupy more of the substrate, and may further exclude urchins (Levin and others 2002).

## TROPHIC-LEVEL DYSFUNCTION AND FOOD WEB INSTABILITY

In all phases, stability was lost when population densities within a structuring trophic level were reduced below a controlling threshold. Although each species was extant within each trophic level, their individual or collective population densities could no longer demographically limit lower trophic levels (trophic-level dysfunction had occurred). Thus, the decline in the abundance of predatory finfishes in coastal waters destabilized phase 1, releasing sea urchin and other invertebrate

populations (phase 2). Likewise, declines in sea urchin abundance and the grazing rate led to the reestablishment of algal beds (phase 3).

The rapidity of recent phase shifts may have resulted from the inherently low species diversity in this system. Decreased diversity, especially within functional groups or trophic levels (for example, Naeem and others 1994; Tillman 1996; McGrady-Steed and Morin 2000, but see Hairston and others 1968; Austin and Cook 1974), and strong interactions of species between trophic levels (Polis and Strong 1996; Nuetal and others 2002) can destabilize ecosystems. Most trophic levels in the Gulf of Maine consist of only one or a few strongly interacting species (Figure 1). Declines in those species can result in trophic-level dysfunction, with cascading effects to lower trophic levels. Such naturally low-diversity ecosystems may presage the fate of more diverse systems in which anthropogenic reductions in biodiversity are contributing to the growing frequency of "catastrophic" phase shifts (*sensu* Scheffer and others 2001).

### Temporal Trends in Trophic Levels: The Fisheries Signal

Several recent studies offered a global perspective on the effects of fisheries. From those studies, there emerged the concept of "fishing down marine food webs" (Pauly and others 1998). In the preceding sections, we qualitatively reconstructed the food webs of the western North Atlantic using both fisheries-dependent and independent evidence. Below we revisit the Gulf of Maine ecosystem looking for quantitative evidence of fished-down trophic levels and using only fisheries-dependent data. For this analysis, we will apply the fractional trophic-level approach pioneered by Pauly and others (Pauly and others 1998, Pauly and others 2001, Pauly and others 2002).

Trophic-level (TL) analysis assigns numbers to species that indicate where on a trophic pyramid the organism feeds, based on studies of its diet. Thus, autotrophs, such as the algae at the bottom of the food web, are assigned a TL of 1; herbivorous sea urchins feeding on algae are TL 2; fishes or invertebrates such as lobsters and sea stars feeding on sea urchins are around TL 3; and higher-order carnivorous fish whose food is a mixture of herbivores and small carnivores range from TL 3.5 to TL 4.6. Fractional trophic levels for the dominant species of coastal Maine were obtained from published studies (Froese and Pauly 2002) and are listed in Table 1.

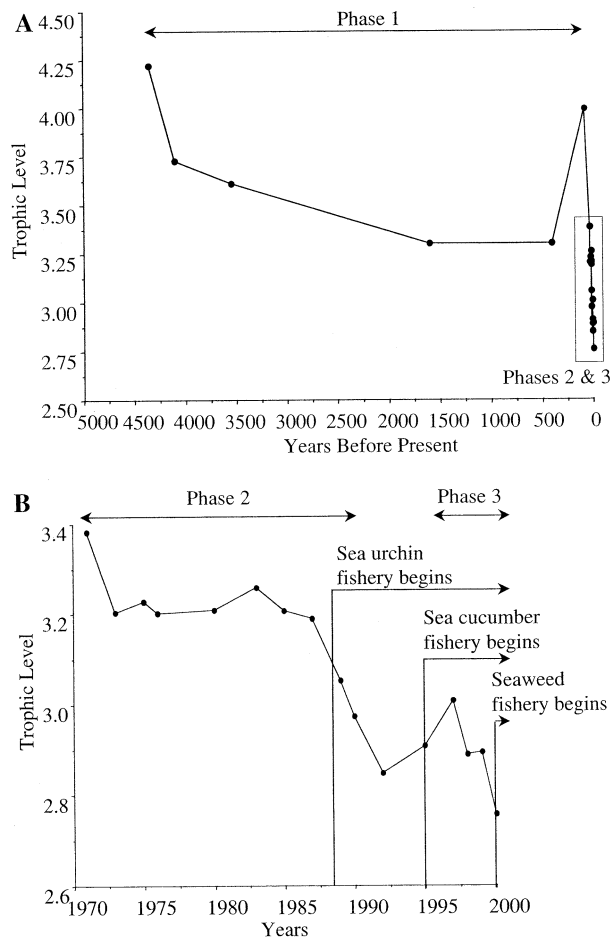
We applied fractional trophic-level analysis to archaeological studies to characterize the patterns of

consumption of prehistoric people. Studies of Native American middens indicate that the first coastal populations to live on the Maine coast, dating back to 4500 ybp, ate primarily marine organisms (Spiess and Lewis 2001; Carlson 1986; Bourque 1995, Bourque 2001). Fish bones dominate some coastal middens, with as much as 70%–85% of the bone mass comprised of cod bones (Carlson 1986; Spiess and Lewis 2001). In addition, isotope analyses of nitrogen and carbon from human bones reveal "a high intake of marine protein (flesh) in their diets" (Bourque 2001).

Fisheries landings for each species, estimated from bone and shell fragments and weighted by fractional trophic level (see Figure 2 for methods), reveal that predatory fishes, especially Atlantic cod, dominated landings for thousands of years (Figure 2A and Table 1). During phase 1, the mean TL ranged between 3.25 and 4.25 (Figure 2A). The highest TL was estimated in the oldest portion of the midden, which dates to more than 4000 ybp and then declines marginally, indicating that even indigenous people were affecting coastal food webs. Other studies in North Pacific coastal ecosystems have shown early human-induced phase shifts occurring 8,000 to 10,000 years ago (Simenstad and others 1978; Erlandson and others 2004).

In 1927, the mean TL, based on published fisheries reports, was 3.99 (Rich 1929) (Figure 2A). Unquestionably, large predatory fishes were still abundant in coastal systems, as evident in mapped fishing areas for each species (quantified in Steneck 1997). In fact, the five species harvested in greatest number in coastal zones at that time were cod, haddock, hake, cusk, and pollock (Rich 1929). This deviation from the previous decline in TL may have been due to improvements in fishing practices (for example, trawlers) rather than a change in ecosystem structure.

In recent decades, the mean TL, as derived from inshore commercial fisheries landings, has declined (Figure 2). During most of phase 2 the mean harvested TL remained relatively high (around 3.2), but it dropped precipitously toward the end of this period (Figure 2B). Between phase 2 and phase 3, landings for 23 of the 28 species fished in coastal zones declined (DMR 1971–2000; NMFS 1971–2000). Most of the harvested stocks (that is, 22 of the 28 species) declined 50% or more. Declines were reported for all of the important predatory fishes, such as cod, wolffish, hake, and flounder, which were already at low levels during phase 2. During this phase shift, landings increased only for lobsters, sea urchins, sea cucumbers, mussels, and skates. Of these, only the lobster had been



**Figure 2.** Temporal trends in trophic levels (TL) of harvested species over the past 4,300 years showing the duration of the three phases. **A** Entire record of TL analysis from archaeological studies to the recent period. Area within the box on the right includes phases 2 and 3. **B** Expanded recent temporal scale shows phases 2 and 3, with the rapid decline in TL since 1970. The trophic levels of fished species from inshore waters of Maine (0–3 mil) were determined from published studies (Pauly and others 2001). The abundances of harvested species prior to record keeping were estimated as the percent of total bone and shell fragments of each subtidal marine species excavated from Native American middens (Spiess and Lewis 2001). In 1927, landings data were integrated with detailed maps of fishing grounds in coastal Maine (Rich 1929). Landings of each species were calculated as the percent of all coastal fishing grounds. Standardized state of Maine landings data were used from 1971 to 2000 (DMR 1971–2000). Total landings caught in inshore waters for each species was estimated using a ratio of inshore to total landings generated from federal landings statistics (NMFS 1971–2000). When a fished species was not listed in the federal landings data (NMFS 1971–2000), it was considered to be caught inshore.

targeted as a prime fishery species throughout phase 2. The emergence of the sea urchin fishery in the latter part of phase 2 is reflected in the decreasing TL (Figure 2B) and ultimately resulted in the termination of phase 2. In phase 3, the TL has ranged from 3.0 to 2.7, probably due to the collapse of the urchin fishery and a shift in fishing pressure toward other herbivores (for example, sea cucumbers) and primary producers. Significantly, in 2001, marine algae were included by Maine's Department of Marine Resources in the "fisheries" landings.

The overall TL decline we report for coastal Maine over the past 3 decades is similar to that published for Canada (Pauly and others 2001). The TL decline from 3.4 in 1970 to 2.7 in 2000 (Figure 2B) for Maine is about the same as that for the east coast of Canada, which decline experienced a TL from 3.4 to 2.9 over roughly the same time period (Pauly and others 2001). Such cross-regional trends, derived from entirely different data sets, imply that these reductions in TL are not artifacts of the fisheries data.

## CONCLUSIONS

Based on data from a number of sources, we conclude that fishers in the Gulf of Maine have fished down the food web for millennia. Serial targeting and depletion of abundant top consumers has repeatedly led to trophic-level dysfunction (that is, functional loss of a trophic level), creating trophic cascades that changed the structure and function of the ecosystem. Each new phase shift appears to be constant until fishing pressure again destabilizes the controlling trophic level. The phase shifts may occur due to the inherently low diversity in the region, which renders food webs into food chains. If so, our observations in Maine may be predictive of the fate of other, more diverse systems in which fishing successively targets most or all of the strong interactors within upper trophic levels. Therefore, the changes occurring in the Gulf of Maine may be instructive for managers seeking to understand what effects reductions in biodiversity may have in their own systems.

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