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The ups and downs of trophic control in continental shelf ecosystems

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Traditionally, marine ecosystem structure was thought to be determined by phytoplankton dynamics. However, an integrated view on the relative roles of top-down (consumer-driven) and bottom-up (resource-driven) forcing in large-scale, exploited marine ecosystems is emerging. Long time series of scientific survey data, underpinning the management of commercially exploited species such as cod, are being used to diagnose mechanisms that could affect the composition and relative abundance of species in marine food webs. By assembling published data from studies in exploited North Atlantic ecosystems, we found pronounced geographical variation in top-down and bottom-up trophic forcing. The data suggest that ecosystem susceptibility to top-down control and their resiliency to exploitation are related to species richness and oceanic temperature conditions. Such knowledge could be used to produce ecosystem guidelines to regulate and manage fisheries in a sustainable fashion.

The structure of marine ecosystems

The traditional view of how marine ecosystems are structured is based on resource control, where phytoplankton dynamics determines the production and biomass variability of the upper trophic level [1–5]. The alternative viewpoint of consumer or top-down control, where predation determines the abundance and composition of prey, was considered limited to nearshore or intertidal communities involving one or two dominant predator and prey species [6,7]. Until recently, continental shelf ecosystems were thought immune to top-down control, because of their relatively large spatial scales, high species diversity and food-web complexity. Steele [8] contended that he knew of no cases where large changes in predatory marine fish stocks had affected their food supplies, in other words no top-down control.

Here, our viewpoint is based on recent studies of heavily exploited ecosystems in the North Atlantic Ocean whose type of trophic forcing was assessed from correlations between time series of the relative abundances of successive trophic levels (or species). The response (correlation) varies temporally and spatially, with a geographical distribution that is statistically related to species richness and ocean temperature. We suggest that species-rich, warmer water areas are more resilient to exploitation than are relatively species-poor, colder regions. It also appears that undisturbed areas are structured from the bottom up, as

were areas before the onset of significant commercial exploitation. The accumulation of knowledge on trophic dynamics could be used to formulate ecosystem guidelines to regulate and manage fisheries in a sustainable fashion.

Support for top-down dynamics

During the early 1990s, Parsons *et al.* [9] drew attention to the effects of top predator removal by marine fisheries, using examples from the Atlantic, Pacific and Antarctic Oceans. The effects ranged from replacement by alternate predators, increased production at lower trophic levels, and/or long-term ecosystem-level change. More recently, Reid *et al.* [10] concluded that, although there were few convincing examples of top-down control, particularly in the well-studied North Sea, the Barents Sea ecosystem provided a clear example of top-down and size-selective predation by fish on zooplankton.

The Barents Sea is a relatively simple, low-diversity arctic system in contrast to the species-rich, temperate North Sea. By analyzing time series of cod *Gadus morhua* (predator) and shrimp *Pandalus borealis* (prey) abundances from several North Atlantic continental shelf locations, Worm and Myers [11] revealed precipitous declines in cod stocks followed by large increases in shrimp populations in most areas examined. The authors concluded that predation was a strong structuring force in the North Atlantic, with a few exceptional areas mainly near the southern limit of the species where bottom-up processes dominated [11].

Unexpected impacts of overfishing

The slow recovery (in several instances, their failure to recover [12,13]) of several collapsed North Atlantic cod populations has also fueled an interest in trophic forcing, particularly as it relates to the formation of alternate ecosystem states [14,15]. Top-down forcing can lead to a 'quasi-permanent' ecosystem change (i.e. a regime shift typified by fundamentally different structural and functional attributes from the one preceding it). Strong [16] maintains that top-down structuring is not the norm for ecosystems but instead represents a form of biological instability. When larger predator species are depleted through overfishing, the balance between predator and prey populations is disrupted. The imbalance can impede the recovery of predators by increased predation and/or competition for food from their prey during the early life stages of the predators [17,18]. This predator–prey role reversal has been implicated for cod and herring in the lack of recovery of cod in the southern Gulf of St Lawrence [19].

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In the North Sea, populations of grey gurnard *Eutrigla gurnardus* (an early maturing benthic fish species of no commercial value) have increased dramatically and occupy an ecological niche similar to that filled by the once dominant cod. The habit of gurnards of feeding on juveniles of commercially exploited species and their greatly expanded spatial distribution have also been implicated in the lack of recovery of North Sea cod and whiting stocks [20].

Cury and Shannon [21] discussed how overfishing has initiated and maintained a regime shift within the Benguela upwelling system off South Africa through tightly coupled predation processes, including predator–prey role reversals. This suggests that top-down processes are cascading to lower trophic levels, resulting in conspicuous indirect effects that lead to a reorganization of the entire food-web. Such a condition (i.e. a trophic cascade) has been repeatedly documented for several freshwater systems [22], although infrequently for large marine ecosystems.

An examination of trophic forcing was made within a single geographical area, the eastern half of the continental shelf off Nova Scotia, Canada, where the resident cod population, which had been subject to ongoing heavy exploitation, collapsed during the early 1990s and has failed to recover, despite the cessation of fishing for over a decade [23]. Analysis of time series spanning several decades revealed top-down control and a trophic cascade emanating from the top predator level, resulting in alternating changes (i.e. negative correlations between adjacent trophic levels) in abundance from planktivorous fish species to herbivorous zooplankton and then to phytoplankton (Figure 1 [23]). The cascade further penetrated to the basal nutrient level, as nitrate concentrations were negatively correlated with phytoplankton abundance. This study clearly demonstrated that strong, possibly irreversible, cascading effects can occur in marine systems.

The bottom-up versus top-down controversy

Hunt and McKinnell [24] discuss the complexity of unraveling the effects of trophic forcing within ecosystems and contend that the necessary data to test hypotheses about predator effects on trophic structuring in marine systems are generally lacking. Other investigators have lamented that studies involving exploited marine ecosystems have reached no consensus on how animal abundances and productivities are controlled, with apparent demonstrations of both top-down and bottom-up controls [25]. Still others believe that the tendency for interpreting all marine pelagic food webs from a resource perspective alone has resulted in limited understanding and poor predictability of the processes influencing the structure and function of these ecosystems [26]. Unfortunately, studies that have given balanced attention to top-down and bottom-up processes are rare, owing in part to the lack of data sets that include time series of multiple trophic levels within and among years [27]. A previous study of a relatively data-rich region (the western North Atlantic) has addressed the spatial and temporal aspects of these processes [28].

The importance of context (where and when)

Where

Frank *et al.* [28] examined abundance time series of several species of predators and prey from nine heavily exploited regions in the western North Atlantic. The data were derived from fishery-independent surveys that collect all fish species at all life stages (except eggs and larvae). The resultant estimates of numerical abundances are generally reliable from age 1 onward and diminish the need to introduce time lags into the correlation analysis because the expression of change in abundance of the components species making up a trophic level occurs relatively rapidly.

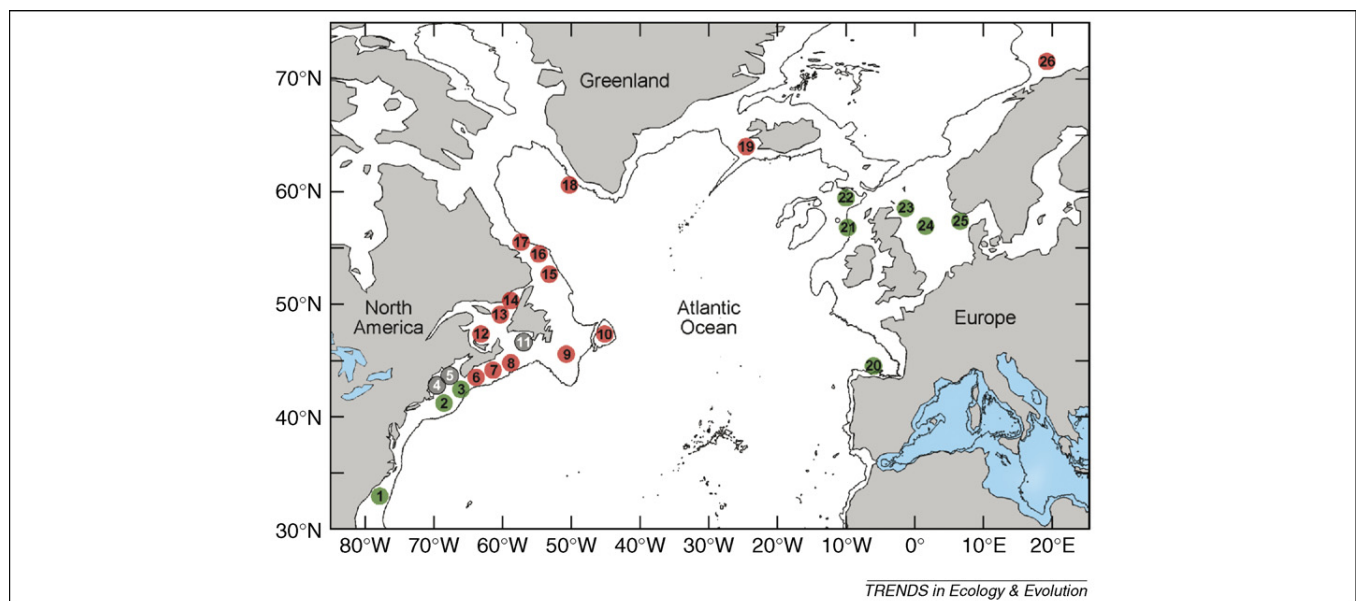


Figure 1. Geographical location of the assembled data on trophic forcing. Dot colour refers to the type of trophic forcing and the number on the dot refers to the data source (Table 1). Green dots represent correlation coefficients (r) between predator and prey >0.2 ; red < -0.2 ; and grey $-0.2 < r < 0.2$. No correlation is available for Area 1 but the information [36] suggests the existence of a positive correlation. There are some large gaps in the availability of published studies on trophic forcing, particularly south of 40° N.

Pronounced spatial variance of trophic control was revealed, a result that is consistent with that of Worm and Myers [11], whose analysis was for a single predator (cod) and prey (shrimp) species. Top-down control, based on negative correlations between predator and prey [28], was found to dominate in northern areas that were typified by low species richness and colder temperatures (Table 1). Bottom-up control (i.e. positive correlations between predator and prey) governed the predator–prey dynamics in the southern areas, where species richness was relatively high and water temperatures were warmer. The authors argued that species diversity, acting through compensation of the overfished predators by nontarget species, and temperature, which influences the demographic rates of the component species, provide a robust explanation for the resilience to overfishing effects in the southern areas and the manifestation of negative effects in the northern ones.

In contrast to the western Atlantic, fish production on the continental margin of the eastern Pacific has been argued to be uniformly controlled from the bottom up for 11 contiguous areas from southern California to western Alaska based on long-term averages of fishery landings and an index of primary production [29]. A study in the subarctic North Pacific (latitudes 55–60° N, six-year data series) suggested a cascading predation effect based on alternating yearly abundances of pink salmon *Oncorhynchus gorboscha*, zooplankton and chlorophyll [30]. Strong negative correlations were reported between time series of functional groupings of piscivores and their prey

in the Kodiak Island region, Gulf of Alaska at 58°N [31]; a similar pattern was seen in the eastern Bering Sea (56° N) involving the predators Pacific cod *Gadus macrocephalus* and yellow fin sole *Pleuronectes asper* and their prey, red king crab *Paralithodes camtschatica* [32]. At an unfished, deep water (>4000 m) location off southern California (35° N), positive correlations were observed between eight benthic macro-invertebrate species and resident fish abundance [25]. Collectively, these studies suggest a geographical gradient in the type of trophic forcing in the North Pacific.

When

Temporal changes in trophic dynamics were also observed in three of the nine continental shelf areas studied in Ref. [28]. For example, on the eastern half of the Scotian Shelf, a major groundfish fishery flourished throughout the 1970s and 1980s, when trophic forcing was persistently bottom up. A weakening of bottom-up forcing eventually developed as overfishing depleted the top predators, with the transition from bottom-up to top-down control probably occurring between 1982 and 1990. Conversely, in the relatively warmer, species-rich waters of the Gulf of Maine, the system responded to a reduction in fishing pressure by transforming from top-down to bottom-up control, suggesting the effects of overfishing were reversible in this area. The correlation analysis points to a time between 1982 and 1990 when the trophic dynamics changed. The studies [20,25,30–32] suggest that it is necessary to examine the temporal variability of the predator–prey

Table 1. Type of trophic forcing based on correlation analysis of interacting trophic levels or species within areas of the western and eastern North Atlantic

Location	Area (number) ^a	Trophic level ^b	Western (WA) or eastern Atlantic (EA)	Decimal latitude (°)	Correlation coefficient (r)	Species richness ^c	Temperature (°C) ^c	Refs
Southeast US Shelf	1	1–2	WA	32.00	–	–	–	[36]
Georges Bank	2	3–4	WA	41.00	0.44	162	8.74	[28]
Browns Bank	3	3–4	WA	42.00	0.70	108	6.55	[28]
Gulf of Maine	4	3–4	WA	43.00	–0.02	97	7.12	[28]
	5	3–4	WA	43.50	–0.13	113	7.12	[11]
East Scotian Shelf	6	3–4	WA	44.83	–0.23	107	4.85	[28]
	7	3–4	WA	44.83	–0.86	109	4.85	[11]
	8	3–4	WA	44.83	–0.61	107	4.85	[23]
Southeast Shoal	9	3–4	WA	45.00	–0.49	77	2.37	[28]
Flemish Cap	10	3–4	WA	47.50	–0.53	96	3.81	[11]
St Pierre Bank	11	3–4	WA	46.00	0.20	86	2.96	[28]
Southern Gulf of St Lawrence	12	3–4	WA	47.00	–0.52	65	1.88	[28]
Northern Gulf of St Lawrence	13	3–4	WA	49.00	–0.52	74	3.18	[28]
	14	3–4	WA	49.83	–0.71	86	3.18	[11]
Northern Newfoundland	15	3–4	WA	52.50	–0.91	75	0.31	[11]
Newfoundland/Labrador	16	3–4	WA	51.00	–0.75	69	1.17	[28]
Labrador Shelf	17	3–4	WA	55.00	–0.75	64	0.56	[11]
West Greenland	18	3–4	WA	62.00	–0.79	34	4.35	[37]
Iceland	19	3–4	EA	66.50	–0.46	122	4.57	[11]
Bay of Biscay	20	3–4	EA	43.60	0.38	186	12.60	[42]
Several areas	21	1–2	EA	56.00	0.27	162	7.50	[39]
Faroe Shelf	22	1–4	EA	62.00	0.76	133	6.67	[40]
Southeast Scotland	23	1–2–3–4	EA	57.00	0.80	144	7.56	[41]
North Sea	24	2–3	EA	56.50	0.36	146	7.93	[38]
	24	3–4	EA	56.50	0.44	146	7.93	[38]
Skagerrak	25	3–4	EA	57.67	0.79	143	6.99	[11]
Barents Sea	26	3–4	EA	74.00	–0.41	104	2.3	[11]

^aSee Figure 1.

^b1, phytoplankton; 2, zooplankton; 3, forage fish or macroinvertebrates; 4, top predators (piscivores).

^cSpecies richness estimates in the nine areas examined in Ref. [28] are based on survey data alone; other estimates are derived from Ref. [44]. Temperature data were obtained from the references or the data used to construct Figure 2b.

interaction to conclude which type of trophic dynamics applies.

Temporal variability of trophic forcing was also suggested by Hunt *et al.* [33], who proposed that the pelagic ecosystem of the southeastern Bering Sea has alternated between bottom-up and top-down control during warm and cold water regimes. Cury and Shannon report a similar finding for the northern and southern Benguela upwelling regions [21], as does Tang *et al.* for the Bohai Sea [34]. Although these studies give emphasis to environmental changes that are responsible for ecosystem variability, fishing pressure alone or in concert with environmental variability requires as much attention as a probable cause.

Generality of recent findings

How general are these findings? Do they reconcile the inconsistencies previously noted [25,35] that no general consensus exists of how animal abundances and productivities are controlled in marine systems? We believe that the body of research conducted thus far in the exploited ecosystems of the western North Atlantic has provided important clues as to when and where top-down forcing effects occur.

Several published studies from other continental shelf and/or shallow sea ecosystems in the North Atlantic deal with trophic structuring (Table 1). These enable us to extend the more spatially limited results of Frank *et al.* [28] and to examine the relationship of trophic response to natural gradients in biophysical variables (species richness and temperature). Such gradients provide an important tool for exploring the forces that influence variation in food-chain dynamics. The predator–prey correlations reported from these studies spanned 30 degrees of latitude and usually involved the two upper trophic levels (piscivores and forage fish) from areas that have been subjected to intense fishing pressure. A few studies were based on lower trophic levels involving zooplankton and phytoplankton. Collectively, this body of information enabled us to determine the degree to which the type of trophic forcing was associated with and possibly influenced by species richness and temperature. However, because temperature and species richness are strongly correlated, the roles of these two variables could not be separated.

Geographical variation of trophic control

Mapping the assembled data revealed a systematic latitudinal variation in the type of trophic control (Figure 1). In the western Atlantic, bottom-up forcing was prevalent in southern areas associated with the Gulf of Maine and the southeastern continental shelf [36]. Top-down forcing prevailed in most of the other areas, from the eastern Scotian Shelf to West Greenland [37]. In the eastern Atlantic, the North Sea [38,39], Faroe Shelf [40], southeast Scotland [41] and Bay of Biscay [42] were regulated from the bottom up. Iceland [11] and the Barents Sea [11,43], the most northern areas, were top down. At similar latitudes, the type of trophic control differed between the western and eastern Atlantic. Although many of these correlations are not statistically significant because the series tend to be strongly auto-correlated and short relative to the dominant temporal variability

[28], the consistency of the pattern is compelling and suggests that large-scale ocean forcing and/or biological properties are significantly affecting trophic control.

Geographical variation of species richness

A community can respond to the depletion or loss of a dominant species through compensatory increases in other species, which in turn depends on species richness, an ecosystem characteristic worthy of further examination. Marine fish species richness generally decreases from the tropics to the poles in both hemispheres [44] (Figure 2a). The data for Atlantic Ocean fish species were derived from taxonomic references, species checklists and biological atlases. Species lists derived from annual scientific surveys conducted during 25 years in the western Atlantic, spanning 25° latitude [45], correspond well with those from Ref. [44] (Figure 2a).

Species richness varied systematically with latitude on both sides of the North Atlantic, but declined at a lesser rate with increasing latitude in the eastern Atlantic. In addition, species richness was generally two to three times greater at all latitudes of the eastern Atlantic, starting at 45°N and higher, compared with the western Atlantic. Although the causes of the latitudinal gradients are continually discussed [46], our primary interest is their possible effects on resilience to overfishing. By comparing Figures 1 and 2a, one might conclude that bottom-up (top-down) trophic dynamics are more prevalent in areas with higher (lower) species richness.

Geographical variation of ocean temperature

The capacity of a species to withstand and/or recover from overexploitation can depend, in part, on temperature effects that influence growth and maturation rates [47]. The North Atlantic ocean temperatures exhibit a pronounced pattern of poleward, declining values with a steeper gradient in the western Atlantic than in the eastern Atlantic (Figure 2b). The temperature isotherms also generally slant upward from west to east, reflecting the long-held view of the water circulation in the North Atlantic [48] (Box 1). Given the similarity in the latitudinal patterns in temperature and species richness, it was not surprising that the two variables are strongly correlated ($r = 0.79$, $n = 25$, $p < 0.001$); however, without a plausible mechanism connecting the two variables, the high correlation does not necessarily indicate cause and effect; it does however complicate the interpretation of the pattern of trophic response.

Box 1. Temperature distribution and North Atlantic circulation

The eastern coast of the USA is dominated by the poleward-flowing Gulf Stream, which subsequently turns east and north, becoming the North Atlantic Current (NAC) near the Tail of Grand Bank. It transports heat to western Europe and into the Arctic Ocean via the Barents Sea, leading to relatively warm waters in those areas.

The Canadian coast is largely governed by the equator-ward advection by the Labrador Current (LC) of colder waters compared with those of the NAC. The influence of the NAC on European shelf waters and the LC on Canadian waters gives rise to a difference in the ocean temperature climates at similar latitudes of the eastern and western North Atlantic.

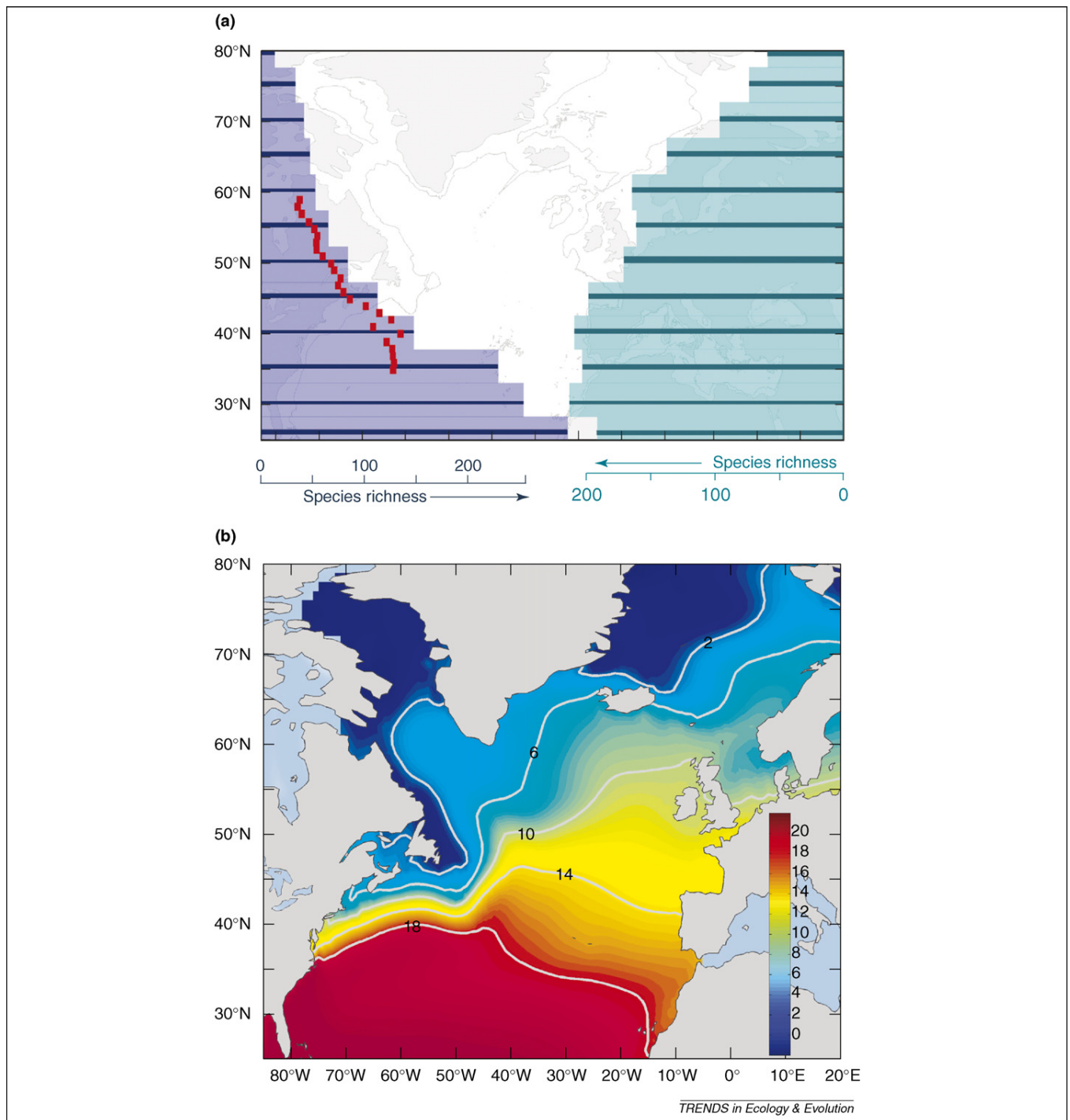


Figure 2. Large-scale gradients in species richness and temperature. **(a)** Latitudinal variation in marine fish species richness based on data obtained from Ref. [44] for the western (blue bars) and eastern (green bars) Atlantic at 5° latitude intervals. The additional data source for the western Atlantic, resolved to 1° of latitude and based on scientific surveys conducted from 1970 to 1994, is shown as red squares. For the eastern and western Atlantic, the number of species increases southward, with a larger gradient on the western side. **(b)** The annual average water column (0–200 m) temperature for the North Atlantic Ocean, from temperature fields obtained from the World Ocean Atlas 2005 (http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html). Isotherms are shown as lines and are labeled (°C). The southward (northward) extent of colder (warmer) water on the western (eastern) side of the ocean reflects the influence of the Labrador (North Atlantic) Current.

Linking species richness and temperature to trophic forcing

The pattern of association between species richness and trophic forcing among nine Northwest Atlantic areas [28] was also evident within the assembled data across the North Atlantic. Areas with fewer species tended to be characterized by top-down forcing, whereas species-rich

areas tended to be forced from the bottom up (Figure 3). However, a strong relationship was also evident between water temperature and trophic forcing as expected, given the positive correlation between temperature and species richness. Summarizing, northern areas, which have fewer species and colder water temperatures, had negative predator–prey correlations through time, suggesting strong

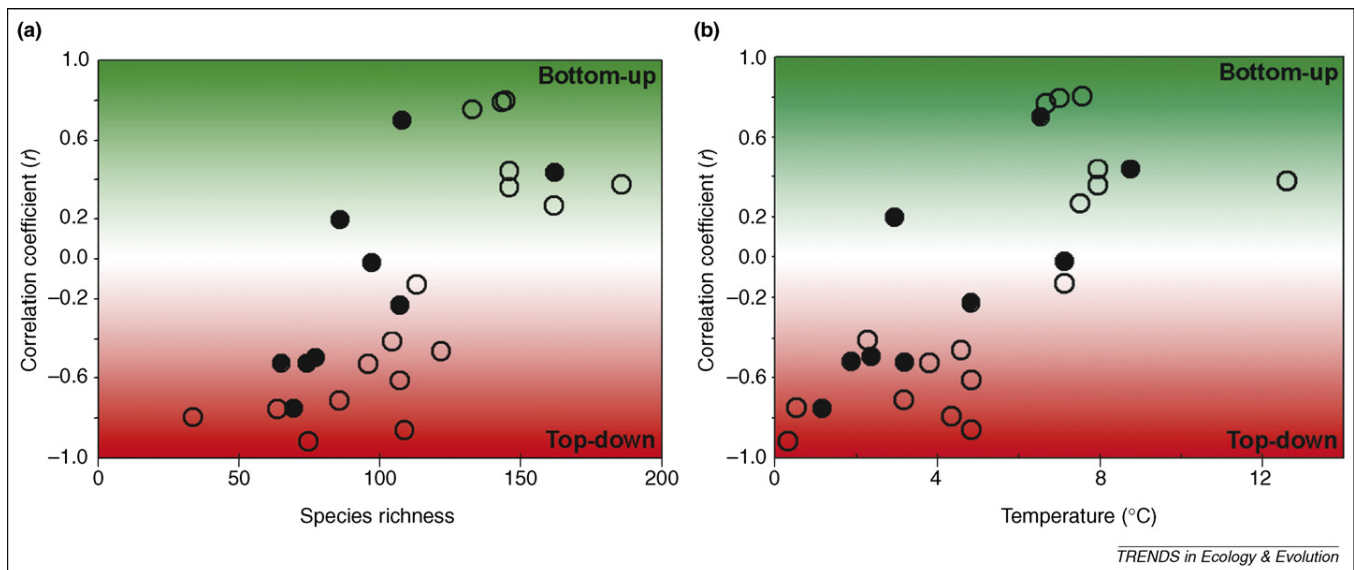


Figure 3. The relationship of the type of trophic forcing with (a) species richness and (b) temperature. Trophic forcing is based on the sign of the correlation between predator and prey abundance. The species richness–trophic forcing relationship has a significant correlation ($r=0.75$, $n=26$, $p<0.001$) as does the temperature–trophic forcing relationship ($r=0.74$, $p<0.001$). All available data (Table 1, main text) are shown, including the original study (closed circles) by Frank *et al.* [28].

impacts of piscivores on their prey. Warmer, southern areas, which are more species rich showed positive predator–prey associations, suggesting that resources limit predator abundance.

Temporal dynamics of trophic forcing

Temporal dynamics in the type of trophic forcing was a prominent feature in some of the geographical areas investigated in Ref. [28]. There are few published studies that have investigated this phenomenon in the North Atlantic. However, it has been suggested that, during the warmer-than-normal 1920s and 1930s in the North Atlantic, high latitude areas (north of 60° N) such as West Greenland, Iceland and the Barents Sea were driven primarily by bottom-up processes [49]. At this time, productivity at all trophic levels was high and had given rise to the development of expanding fisheries for cod, herring and other species. These areas, which apparently benefited from a combination of relatively warmer waters and low exploitation, are now distinctly driven by top-down processes. Temporal variability of trophic forcing also typified the pelagic ecosystem of the southeastern Bering Sea [33].

Conclusions and future directions

Most large marine ecosystems were previously considered to be resource controlled. Throughout the past decade, however, evidence of predator control in exploited marine systems began to accrue as commercial exploitation severely depleted cod and other top predators. Some fisheries collapsed without recovery and others persisted, albeit at low levels. Geographical variation of trophic forcing in formerly cod-dominated ecosystems, owing to variation in species richness and temperature, was established [28]. Warmer areas with greater species richness were able to withstand excessive exploitation through higher demographic rates and a potentially greater pool of compensatory species.

Using data from 26 studies in 18 exploited North Atlantic ecosystems, we have shown that the type of trophic forcing is strongly correlated with species richness and temperature. We suggested that this ocean-scale relationship translates directly to variation in the resilience to exploitation. Whereas very cold and species-poor areas might readily succumb to top-down control and recover slowly (if ever), warmer areas with more species might oscillate between top-down and bottom-up control, depending on exploitation rates and, possibly, changing temperature regimes. Other studies from the eastern north Pacific, off South Africa and in the Bohai Sea (SE Asia) indicate that these findings might be more broadly applicable.

The existence of top-down control in exploited ecosystems does not necessarily lead to trophic cascades or even alternate states (regime shifts). It is, however, the initial step and leads to an obvious question. How much can we deplete apex predators before a system becomes top down? At this time, our results offer a qualitative assessment, suggesting that fishing effort on top predators should be relatively low in colder, species-poor areas. Although many have derided the term ‘ecosystem-based management’ because it has become jargon and non-operational, we believe that this developing body of knowledge on trophic forcing could be used to create ecosystem-level guidelines for sustainable fisheries.

Given that top-down or bottom-up control reflects not only resilience to fishing, but also the underlying level of exploitation, there is a need to develop quantitative relationships linking exploitation, species richness and ocean climate variability. Such an analysis would provide a direct measure of the limits to fishing that are necessary to prevent top-down forcing in different marine systems.

We believe that the expansive backdrop presented for the North Atlantic can be developed for other oceanic systems, and that data consolidation and synthesis in

these geographical areas would further advance our knowledge of trophic forcing on a global scale. Such an initiative will serve to increase our understanding of resilience and trophic control in large marine ecosystems.

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