

REVIEW

Cascading top-down effects of changing oceanic predator abundances

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Summary

1. Top-down control can be an important determinant of ecosystem structure and function, but in oceanic ecosystems, where cascading effects of predator depletions, recoveries, and invasions could be significant, such effects had rarely been demonstrated until recently.
2. Here we synthesize the evidence for oceanic top-down control that has emerged over the last decade, focusing on large, high trophic-level predators inhabiting continental shelves, seas, and the open ocean.
3. In these ecosystems, where controlled manipulations are largely infeasible, 'pseudo-experimental' analyses of predator–prey interactions that treat independent predator populations as 'replicates', and temporal or spatial contrasts in predator populations and climate as 'treatments', are increasingly employed to help disentangle predator effects from environmental variation and noise.
4. Substantial reductions in marine mammals, sharks, and piscivorous fishes have led to meso-predator and invertebrate predator increases. Conversely, abundant oceanic predators have suppressed prey abundances. Predation has also inhibited recovery of depleted species, sometimes through predator–prey role reversals. Trophic cascades have been initiated by oceanic predators linking to neritic food webs, but seem inconsistent in the pelagic realm with effects often attenuating at plankton.
5. Top-down control is not uniformly strong in the ocean, and appears contingent on the intensity and nature of perturbations to predator abundances. Predator diversity may dampen cascading effects except where nonselective fisheries deplete entire predator functional groups. In other cases, simultaneous exploitation of predator and prey can inhibit prey responses. Explicit consideration of anthropogenic modifications to oceanic foodwebs should help inform predictions about trophic control.
6. *Synthesis and applications.* Oceanic top-down control can have important socio-economic, conservation, and management implications as mesopredators and invertebrates assume dominance, and recovery of overexploited predators is impaired. Continued research aimed at integrating across trophic levels is needed to understand and forecast the ecosystem effects of changing oceanic predator abundances, the relative strength of top-down and bottom-up control, and interactions with intensifying anthropogenic stressors such as climate change.

Key-words: apex predator, indirect effects of fishing, macro-ecology, meta-analysis

Introduction

Anthropogenic changes have greatly altered the abundance of oceanic species, especially large predators at high trophic levels (Hutchings & Baum 2005). While there are few known oceanic predator extinctions, exploitation has extirpated many marine mammal and seabird populations (Dulvy, Sadovy & Reynolds 2003) and routinely depletes marine fish populations by 50% to 70% (Hilborn *et al.* 2003; FAO 2007) with

losses exceeding 90% increasingly common (Myers & Worm 2005). Conversely, species invasions and reductions in exploitation levels have led to substantial increases of some predators. Although the magnitude and prevalence of these predator changes have raised important questions about their potential for indirect ecological consequences (May *et al.* 1979; Dayton *et al.* 1995; Botsford, Castilla & Peterson 1997), understanding and forecasting outcomes of altered species interactions has proven challenging (McCann 2007).

Decades of ecological research have shown that changes in predator abundance can have far-reaching consequences for

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ecosystem structure, functioning, and resilience (Paine 1969; Duffy 2002). While recognizing that predators engage in various biotic interactions, we focus here on predator–prey relationships and top-down control of prey abundance or biomass (Paine 1980) through their direct consumption. Top-down control may be exerted directly across one trophic link, or indirectly across multiple trophic links. Trophic cascades, are among the best-known examples, and involve strong predator effects propagating downwards through food webs resulting in inverse patterns in abundance across two or more trophic links (Pace *et al.* 1999). Although trophic cascades may be present in stationary food webs, their effects are often seen most clearly after a perturbation. For example, sea otter (*Enhydra lutris*) overexploitation in Alaska led to population explosions of their sea urchin prey and kelp forest overgrazing (Estes & Palmisano 1974). This ecosystem transformation altered productivity, species assemblages, and coastal erosion, and reversed only once sea otters recovered (Estes & Duggins 1995). Trophic cascades have been repeatedly demonstrated in kelp forests (Estes & Palmisano 1974), lakes (Carpenter & Kitchell 1993), streams (Power 1990), and rocky intertidal ecosystems (Menge 2000).

In contrast, empirical evidence for top-down control in oceanic ecosystems (continental shelves, seas, and the open ocean) has been sparse. Two previous reviews related to this topic (Botsford *et al.* 1997; Pace *et al.* 1999) focused on a single example: a putative trophic cascade in the Bering Sea involving pink salmon (*Oncorhynchus gorbuscha*; Shiomoto *et al.* 1997). Abundance of this planktivore has fluctuated by an order of magnitude on a 2-year cycle, and in summers when it was plentiful its macrozooplankton prey biomass was low and phytoplankton biomass high. In alternate years, the pattern reversed. This cascading pattern was, however, evident only in half the 10-year time series and statistically significant only for the link between salmon and macrozooplankton (Shiomoto *et al.* 1997).

Why has the evidence been so limited? One possibility, in accordance with a predominant view of oceanographers, is that these ecosystems are structured from the bottom-up (resource limitation) and top-down control by oceanic predators is truly rare (Cushing 1975; Aebischer, Coulson & Colebrook 1990; Verity & Smetacek 1996). Large-scale empirical demonstrations of bottom-up control in the ocean have reinforced this view (Chavez *et al.* 2003; Ware & Thompson 2005; Chassot *et al.* 2007). Furthermore, the high degree of connectance among species, the prevalence of omnivory, dietary breadth and ontogenetic diet shifts led others to concur that oceanic food webs might be little altered by predator removals (Larkin 1979; Jennings & Kaiser 1998; Steele 1998; Link 2002). An alternative hypothesis, articulated by some ecologists, is that we have lacked examples of top-down control only because oceanic ecosystems are ‘broken’ (*sensu* Ainley *et al.* 2007), with predator losses largely preceding ecological data collection (Dayton *et al.* 1995; Steneck & Sala 2005; Ainley & Blight 2008).

Mounting evidence over the past decade suggests a simpler explanation: top-down control is not absent from the ocean,

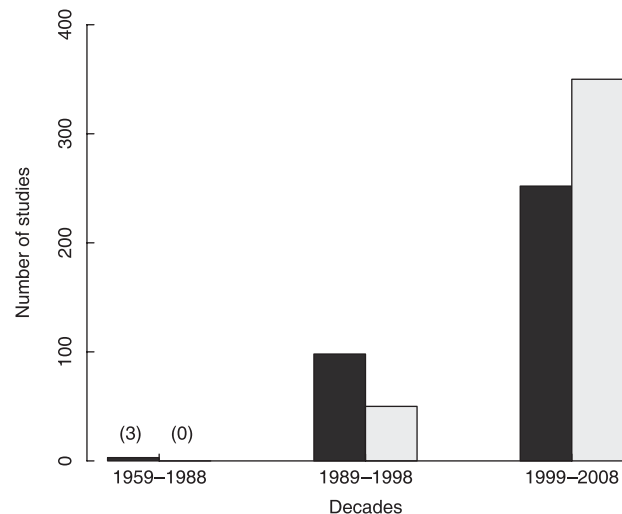


Fig. 1. Number of studies examining bottom-up control (black bars) or top-down control (grey bars) in the ocean from the past decade (1999–2008), the decade prior (1989–1998), and the three decades before that (1959–1988), as indicated by an ISI Web of Science search for trophic cascade, trophic control, top-down control, top-down forcing, trophic forcing, cascading effect, or bottom-up control, and at least one of ocean, sea, or continental shelf. Note this search overestimates the number of cases of either form of oceanic trophic control because it includes reviews, experiments, and coastal ocean studies (as well as studies solely of planktonic organisms not included herein). The number of top-down studies increased sevenfold in this period, almost three times as fast as studies focused on bottom-up control in the ocean.

but had been little studied (Fig. 1). This is not surprising given the methodological challenges of assessing ecosystem-scale processes occurring over large scales, and the need to coordinate data and expertise from marine ecology, fisheries science, and oceanography; disparate research disciplines with different foci and tools. However, a shift in research attention occurred in the late 1990s in the wake of realization that marine ecosystems were increasingly dominated by human influences (Botsford *et al.* 1997) and the ecosystem effects of fishing may well be large, yet were unaccounted for by a predominant single-species focus in fisheries (Jennings & Kaiser 1998). The increasing availability of long-term ecological and climatic time-series data, and a growing appreciation of the relevance of macro-ecological scale studies for examining human impacts on natural ecosystems (Kerr, Kharouba & Currie 2007) have also facilitated research in this area.

Evidence of cascading effects of predator alterations, with their associated conservation and economic implications, has heightened the need to better understand the drivers of oceanic ecosystem processes. Our emphasis herein on top-down control is not meant to imply its predominance, but rather that we believe further progress towards this goal can be made by synthesizing what has been learned over the past decade about these cascading effects and the factors that drive them. To begin, we conducted a systematic literature review in ISI Web of Science for 1998 to 2008, searching for ocean, sea, or continental shelf in combination with any of the following

terms: top-down control, top-down forcing, trophic cascade, trophic forcing, trophic control, cascading effects, ecosystem effects of fishing, indirect effects of fishing. This search returned 401 citations. Whereas some of these examined oceanic top-down control only in planktonic organisms, here we explicitly consider higher trophic-level predators. In addition, the many studies focusing on nearshore coastal ecosystems (e.g. kelp forests, coral reefs, rocky intertidal) have been reviewed elsewhere in detail (e.g. Menge 2000; Pinnegar *et al.* 2000; Steneck & Sala 2005; Heck & Valentine 2007). We included studies from these ecosystems only where oceanic predators spatially linked to nearshore processes via their trophic interactions. We located additional studies through the references of relevant papers from the literature search and papers that have since cited them, in total finding 29 case studies of oceanic top-down control (Table 1).

In this paper, we first discuss the methodological challenges to studying oceanic top-down control, and outline a framework for a 'pseudo-experimental' approach (*sensu* Kerr *et al.* 2007) to robust ecosystem-scale analyses. We then review recent evidence for ecological changes associated with oceanic predator removals and recoveries, highlighting potential ecological and anthropogenic factors that may determine the presence and strength of oceanic top-down control. Next, we discuss implications for the management of oceanic resources and ecosystems. We finish by suggesting future research directions to help resolve open questions about trophic control in oceanic ecosystems.

Challenges and advances in assessing top-down effects

METHODOLOGICAL AND DATA CHALLENGES

Controlled, manipulative experiments are the hallmark of modern ecological research, yet have limited applicability for evaluating oceanic top-down control. Experimental tests involving large, highly mobile, and long-lived predators are typically infeasible for logistical, ethical, and financial reasons. It is also unclear to what extent lessons from experimental manipulations of other ecosystems or studies involving only small planktonic organisms scale up to high trophic-level oceanic predators (Walters & Holling 1990; Carpenter 1996; Rice 2001; Hewitt *et al.* 2007). Moreover, small-scale experiments seldom capture the complex nature of anthropogenic perturbations to oceanic ecosystems, nor can they document actual ecosystem changes resulting from these perturbations.

Instead, evidence of top-down control in the ocean is typically deduced from phenomenological analyses of ecosystem-scale observational data in which the underlying mechanisms are inferred. This approach represents a fundamental departure from the experimental method, and involves trading-off control in order to attain the appropriate scale of study. For example, in the absence of direct predator manipulation, wild predator populations must be observed at different abundances to discern if their prey populations have contrasting responses. While anthropogenic alterations of predator

abundances provide ample opportunity to test for top-down effects, their detection is still a data-intensive endeavour requiring species abundance or biomass data from multiple trophic levels over long time-spans (decades) and large spatial scales (10^2 – 10^6 km²), ideally complemented by environmental data.

These prohibitive requirements have long limited analyses and subsequent inference about oceanic trophic control. For example, fisheries catches, which provide data for many species at the appropriate spatial and temporal scales, have sometimes shown a pattern suggestive of top-down control, where declining catches of large predatory fishes were followed by rising catches of small fishes or invertebrates (detailed in Parsons 1992). Yet these patterns may also reflect variation in fishing effort, gear, seasons, locations, and economic factors. Other studies have drawn upon standardized catch rates, fisheries-independent research surveys, and population dynamics models (Pauly 1988; Shiomoto *et al.* 1997), which more accurately reflect species abundances. These time series may, however, still be of limited use for distinguishing among competing hypotheses, as they tend to be short and highly variable and thus yield low statistical power (see Myers & Mertz 1998). Finally, few studies have included sufficient environmental data to adequately assess alternative mechanisms, such as bottom-up control through variation in climate and nutrient supply.

PROGRESS TOWARDS STRONGER INFERENCE IN ECOSYSTEM-SCALE STUDIES

'Pseudo-experimental' approaches

Increasingly, observational studies are borrowing principles from manipulative experiments to examine the repeatability of patterns and disentangle predator effects from other processes, with the aim of making more reliable inferences about the underlying causes of observed ecosystem changes. Studies can treat predator populations either as replicates (if predator abundances changed similarly) or treatment levels (if they differed), with environmental variables as additional treatments. In this context, exploitation may be regarded as a predator-removal experiment and conversely, fisheries closures, no-take marine reserves, and species invasions as predator-addition experiments. Such analyses retain the fundamental weakness that the causation of observed ecosystem changes cannot be proven, and thus it is imperative that they are robust, transparent, and reproducible. Although data for most oceanic food webs remain incomplete, accumulating long-term ecological and climatic time series and large-scale field studies are enabling researchers to apply these 'pseudo-experimental' methods in some systems.

The generality of trophic forcing patterns can, for example, be examined using independent predator–prey 'replicates'. Recent studies have employed this approach using time series to compare correlations among predator–prey pairs across regions, and meta-analysis to formally combine the correlations (Table 1). For instance, Worm & Myers (2003) showed that cod (*Gadus morhua*) declines in seven of nine Atlantic

Table 1. Examples of recent (1998–2008) studies identifying top-down control by oceanic predators, including the predator and prey species, evidence used to identify top-down control, the change (\uparrow = increase, \downarrow = decrease) in predator abundance that triggered the top-down effect, and the inferred ecosystem effect (e.g. prey release: MR = mesopredator release or IR = invertebrate prey release; TC = trophic cascade; PD = prey (mesopredator and/or invertebrate) decline)

Ecosystem	Region	Predator–prey	Evidence	Change in predator abundance and driver	Inferred effect of top-down control	Refs
Open ocean	Central N Pacific	Sperm whales, swordfish, blue shark – large squid	Dynamic model (Ecosim), pre-exploitation food web reconstruction based on fisheries stock assessments	\downarrow – Exploitation	MR: Dominance shift in apex predator guild to large squid	1
	Central N Pacific	Billfish, sharks, yellowfin tuna – mahi-mahi, smaller tunas and other pelagic fishes	Dynamic model (Ecosim); same base EcoPath model as above; simulations of (i) increased fishing, and (ii) no fishing	(i) \downarrow – Exploitation (ii) \uparrow – cessation of exploitation produces eightfold blue marlin increase, two fourfold tuna and shark increase	(i) MR: Increases in mesopredators; (ii) PD: Small pelagic fishes decline; some predators decline after initial increases, due to their role as blue marlin prey	2
	Central Pacific	Tunas, billfish, sharks – pelagic stingray, pomfret, skipjack tuna, snake mackerel	Comparison of 1950s survey with 1990s fishery catch rates	\downarrow – Exploitation	MR: Increase in mesopredatory pelagic fishes	3
Seamount	Central Pacific: Northwestern Hawaiian Islands	Hawaiian monk seal – subphotic (300–500 m) fish assemblage	Fish surveys using submersibles and ROVs at 11 seamounts between 1998–2003	\uparrow/\downarrow – Spatial variation across island	MR: Fish biomass density correlated with distance to seal colony and colony size, not with oceanic productivity, depth or substrate	4
Open ocean to coast	NW Atlantic: US E coast	Apex and near-apex predatory sharks – smaller elasmobranchs (skates, rays, sharks)	Meta-analysis of research surveys and fisheries catch rates (1970–2005), diet data	\downarrow – Exploitation	MR: Four- to 10-fold increases in slope, shelf, coastal elasmobranchs	5
	NW Atlantic: North Carolina	Apex and near-apex predatory sharks – cownose ray – bay scallop	As above; long-term field sampling; controlled, replicated cownose ray enclosure experiments	\downarrow – Exploitation	TC: Eightfold increase in cownose ray \rightarrow bay scallop crash	5
	N Pacific: Aleutian Islands	Killer whale – sea otter – sea urchin – kelp	Long-term field observations (1970–1996), behavioural data, spatial contrast, consumption rates	\downarrow – Killer whale predation reverses sea otter recovery from hunting	TC: Urchin overgrazing \rightarrow up to ten times less kelp	6,7
Continental shelf	NE Pacific: Gulf of Alaska	Pacific cod – capelin and shrimp	Research survey and landings (1972–2005) pre- and post-1976/77 regime shift	\uparrow – Climate-induced oscillation from bottom-up to top-down control	PD: Shift in community to groundfish dominance; prey poor state	8,9
	Gulf of Alaska	Groundfish – shrimp	Smallmesh trawl survey (1972–1997)	\uparrow – Climate-induced	PD: Shrimp decline 95%	10
	NE Pacific: Central California	Humboldt squid – Pacific hake	Monthly deep-water videos (1989–2005), pre- and post-squid invasion	\uparrow – Range expansion after predators/competitor (tuna billfish) depletion, & climate change	PD: Prey abundance suppressed when squid present	11
	N Pacific: Chirikov Basin, Bering Sea	Gray whales – ampeliscid amphipods	Gray whale trends, amphipod biomass (1986–88, 2002–03), oceanographic and oceanographic data	\uparrow Recovery from hunting	PD: almost 50% prey biomass decline, mainly due to loss of largest size classes	12
	N Pacific: Bristol Bay, Bering Sea	Pacific cod & yellowfin sole – red king crab	Research survey (1972–2004), diet data	\uparrow – Strong year classes	PD: reduction in red king crab; Five other crab species not linked to predators; climate forcing important	13

Table 1. *Continued*

Ecosystem	Region	Predator–prey	Evidence	Change in predator abundance and driver	Inferred effect of top-down control	Refs
Continental shelf (cont'd)	NW Atlantic: E Scotian Shelf	Cod & other benthic fishes – snow crab, shrimp, small pelagic fish – zooplankton – phytoplankton	Research survey & landings (1965–2002), patchy plankton data, oceanographic data	↓ – Exploitation	TC: dominance shift from piscivores to macroinvertebrates, small pelagic fishes → plankton shift	14,15
	NW Atlantic: W Scotian Shelf & Georges Bank	Cod and other groundfish – silver hake, redfish, yellowtail & winter flounder	Research surveys & landings (1970–2005), diet data	↓ – Exploitation	MR: prey increases (also competitive release)	16,17
	NW Atlantic: Newfoundland	Cod (& other benthic fishes, harp seals) – capelin – zooplankton – phytoplankton	Research survey & landings (1967–1998), oceanographic and patchy plankton data	↓ – Exploitation	MR: increase in capelin biomass; possible TC involving plankton	18
	NW Atlantic	Cod – snow crab	Meta-analysis of research surveys (~1970–2000) from 10 regions	↓ – Exploitation	IR: general increase in crab biomass	19
	NW Atlantic: Gulf of Mexico	Great sharks – smaller elasmobranchs (Atlantic angel shark, spreadfin skate, smooth dogfish)	Research surveys (1972–2002)	↓ – Exploitation	MR: increase in deepwater prey; fishing inhibits response of coastal prey	20
	N Atlantic	Cod and other benthic fishes – small pelagic fishes	Meta-analysis of research surveys (1970–1994) from nine regions; landings, chlorophyll, & temperature data	↓ – Exploitation	MR: in northern regions; bottom-up control in southern regions	21
	N Atlantic	Cod – shrimp	Meta-analysis of research survey, fisheries assessment and standardized catch rate data (1970–2000) from nine regions, temperature data	↓ – Exploitation	IR: general increase in shrimp biomass, weaker at southern range limits	22
	NE Atlantic: Celtic Sea	Largest size classes of fish – smallest size classes of fish	Size structure analysis of research survey data (1987–2003)	↓ – Size-selective exploitation of large fishes	MR: increased abundance of smallest size classes of fish	23
	NE Atlantic: North Sea	Largest size classes of fish – smallest size classes of fish	Size structure analysis of survey data (1977–2000)	↓ – Size-selective exploitation of large fishes	MR: increased abundance of smallest size classes of fish	24
Arctic Ocean: Barents Sea	Fishery, cod, herring – capelin	Mechanistic models of capelin abundance based on acoustic surveys (capelin, herring), VPA model (cod), harvest for 1973–2001; simulations	↑/↓ – Fluctuations over time	PD: Harvest, herring competition and larval predation cause capelin to collapse (95%) twice; Cod inhibits recovery by depensation	25	
Continental shelf to coast	Antarctica: W Ross Sea	Adélie penguins, minke & killer whales – Antarctic silverfish, krill – diatoms	Long-term (1996–2005) field observations, ‘natural experiments’	↑ – High seasonal abundance of mobile top predators	TC: seasonal decrease in prey → phytoplankton ungrazed	26
	S Atlantic: South Georgia	Leopard seal – fur seal	Long-term census & field observations (9 years), spatial contrast, demographic model	Presence vs. absence of apex predator	MR: fur seal population recovery only where apex predator is absent	27
Continental shelf, offshore or upwelling	N Atlantic and NE Pacific	Small pelagic fish – zooplankton – phytoplankton	Meta-analysis of fish, zooplankton, phytoplankton, nutrients using time series ($n = 7–45$ years) from 20 areas	↑/↓ – Varied by area	PD: zooplankton decline when fish abundant, little response in phytoplankton	28
	South Africa, Ghana, Japan, Black Sea	Small pelagic fish – zooplankton	Time series ($n = 24–45$ years) of pelagic fish catch data, zooplankton biomass or abundance	↑	PD: top-down effects in these areas; not in California Current; bottom-up control of planktivores	29

Table 1. Continued

Ecosystem	Region	Predator–prey	Evidence	Change in predator abundance and driver	Inferred effect of top-down control	Refs
Semi-enclosed sea	Baltic Sea	Cod – sprat – copepod	Time series (1974–2005) modelling using multispecies virtual population analyses (MSVPA) for cod, sprat; plankton samples and proxies; hydrographic and climatic data	↓ – Low salinity & exploitation	TC: increase in sprat depletes one copepod species, shifting dominance to another copepod. Temperature and salinity driving forces	30
		Seals (and other marine mammals) – cod – clupeids (herring, sprat)	Dynamic model (Ecosim) for 1900–2000 based on biomass estimates and hindcasts	↓ – 1. Hunting, pollution nearly eliminate marine mammals 2. Cod exploitation and low recruitment due to low salinity and oxygen	MR: cod increase follows seal depletion; four-fold sprat increase follows subsequent cod overfishing. Eutrophication also important.	31
		Cod – clupeids (herring, sprat)	Dynamic model (Ecosim) for 1974–2000 based on MSVPAs	↓ – Exploitation	MR: Cod top-down control on sprat, but not herring	32
Enclosed sea	Black Sea	Bonito, mackerel, bluefish – horse mackerel, sprat, anchovy, jelly- fish – zooplankton– phytoplankton	Research survey and landings (late 1950s–~2001), hydrographic and climate data; dynamic model (Ecosim)	↓ – Exploitation	TC: Mesopredator release and jellyfish invasion → twofold decline in zooplankton, doubling of phytoplankton biomass; Eutrophication and climate important	33–35

References: 1, Essington 2007b; 2, Kitchell *et al.* 2006; 3, Ward & Myers 2005; 4, Parrish 2008; 5, Myers *et al.* 2007; 6, Springer *et al.* 2003; 7, Estes *et al.* 1998; 8, Litzow & Ciannelli 2007; 9, Mueter & Norcross 2000; 10, Anderson & Piatt 1999; 11, Zeidberg & Robison 2007; 12, Coyle *et al.* 2007; 13, Zheng & Kruse 2006; 14, Frank *et al.* 2005; 15, Choi *et al.* 2004; 16, Shackell *et al.* 2007; 17, Fogarty & Murawski 1998; 18, Carscadden *et al.* 2001; 19, Myers *et al.* unpublished; 20, Shepherd & Myers 2005; 21, Frank *et al.* 2006; 22, Worm & Myers 2003; 23, Blanchard *et al.* 2005; 24, Daan *et al.* 2005; 25, Hjermann *et al.* 2004; 26, Ainley *et al.* 2006; 27, Boveng *et al.* 1998; 28, Micheli 1999; 29, Cury *et al.* 2000; 30, Möllmann *et al.* 2008; 31, Österblom *et al.* 2007; 32, Harvey *et al.* 2003; 33, Oguz & Gilbert 2007; 34, Daskalov *et al.* 2007; 35, Daskalov 2002.

regions were accompanied by increases in northern shrimp (*Pandalus borealis*), an important benthic prey species (Fig. 2a,d). Once corrected for temporal autocorrelation and measurement error, negative predator–prey correlations (suggestive of top-down control) were statistically significant in only three regions, although the overall meta-analytic mean was significantly negative (Worm & Myers 2003; Fig. 2d). The meta-analysis also revealed a broad-scale spatial pattern that previously had not been evident: weakly negative or positive (suggestive of bottom-up control) correlations occurred only at the southern range limit of these species, where temperatures were higher. Similar spatial variation in trophic control was found in a subsequent study relating benthic predators and their pelagic prey across the Northwest Atlantic (Frank *et al.* 2006). Combining these ‘replicate’ correlations meta-analytically reveals a striking north–south gradient, from strongly negative to either positive or weak negative correlations (Fig. 2b,e).

Observed patterns should also be consistent across ‘replicate’ predator–prey data sources from within the same region. For example, to assess changes in apex predatory sharks and their elasmobranch (shark, skate, ray) prey on the US east coast, Myers *et al.* (2007) analysed 17 independent research surveys and two fisheries-dependent data sets, meta-analytically combining the estimates for each species. If robustness is not tested in this manner, or when different data sets lead to contradictory conclusions, inferred ecological processes remain open to alternative explanations.

Temporal and spatial contrasts in predator abundance may serve as ‘treatment levels’ to evaluate predator–prey interactions. Time series that include both increases and decreases in predator abundance should show corresponding opposite temporal changes in prey abundance if the predator is the determinant of prey abundance (assuming a linear predation relationship). A paucity of data with sufficient contrasts in predator abundances (and without confounding environmental changes) has limited this approach. One recent study, however, used this approach to show an alternating pattern of high–low–high abundance of a predator (Humboldt squid, *Dosidicus gigas*) invading the central California coast, that coincided with a low–high–low abundance pattern of its Pacific hake (*Merluccius productus*) prey, suggestive of top-down forcing (Table 1; Zeidberg & Robison 2007). Estes & Palmisano (1974) pioneered the use of spatial gradients by contrasting islands with and without sea otters to document a coastal trophic cascade. More recently, a comparison of fur seal (*Arctocephalus gazella*) abundance and productivity between areas with (South Shetland Islands) and without (South Georgia) leopard seals (*Hydrurga leptonyx*) implicated this oceanic predator as the factor limiting fur seal recovery from overhunting (Table 1; Boveng *et al.* 1998). Although spatial comparisons of predator and prey communities inside and outside no-take reserves are now common in coastal waters, this approach has not yet, to our knowledge, been applied to oceanic predators except in model simulations (Martell *et al.* 2005). This reflects the current mismatch between the small size and coastal placement of most reserves and the highly mobile nature of

most oceanic predators. If implemented, large-scale oceanic reserves could provide spatial ‘experiments’ to examine trophic interactions.

Combining physical ‘treatments’, such as resource availability and climatic measures, with predator abundance ‘treatments’ is an important additional step to help assess competing hypotheses about causative agents of prey population changes. Such analyses are analogous to a factorial experiment, and with sufficient data for a balanced design, should allow otherwise confounding effects to be disentangled (e.g. Litzow & Cianelli 2007; Möllmann *et al.* 2008). For example, comparing deepwater fish communities across eleven Hawaiian seamounts, Parrish (2008) showed that their biomass was strongly correlated with predation pressure, but not with oceanic productivity, depth, or habitat type (Table 1). This factorial approach could also allow interactions between predator and climate effects to be tested (Stenseth *et al.* 2002), highlighting potential ecosystem effects of climate change.

Opportunistic ‘natural experiments’ also can cause contrasting ecological conditions that help diagnose mechanisms of trophic control. At Ross Island, Antarctica, Ainley, Ballard & Dugger (2006) documented an apparent seasonal trophic cascade extending from apex predators to krill, silverfish, and diatoms that was triggered in each of nine ‘replicate’ years with the summer influx of penguins and whales (Table 1; Fig. 3). Two natural experiments helped confirm predation as the most likely cause of these changes: first, the predators’ effect of reducing their prey was accentuated when a short-term polynya concentrated them in a confined area; second, prey switching from krill to silverfish occurred even when grounded icebergs inhibited the regular mid-season dispersal of krill from the area (Ainley *et al.* 2006; Ainley 2007).

Finally, a growing body of research employs ecosystem models to simulate food web responses to various fisheries manipulations. Most widely used are Ecopath with Ecosim mass-balance models (Pauly, Christensen & Walters 2000), which have been applied now to over 100 ecosystems around the world (see www.ecopath.org). Models built on the Atlantis framework are also increasingly applied (Fulton, Smith & Punt 2005). The major drawbacks of these virtual experiments are that they are very data intensive, and the reliability of any given model is constrained by the quality and quantity of data used in its development (Essington 2007a). Results also may be strongly affected by the choice of model assumptions (for more detail see Plaganyi & Butterworth 2004; Kitchell *et al.* 2006). For example, Ecosim’s vulnerability parameter, which can be estimated or assumed, determines how available prey is to its predator(s) and hence the strength of top-down control. Although while detailed model predictions are not yet reliable, ecosystem models that closely reconstruct observed trajectories for major species can provide useful insights into the type of trophic control underlying observed dynamics.

Biological basis for ecosystem-scale studies

Even with these ‘pseudo-experimental’ advances, strong inference about trophic control still requires a solid biological

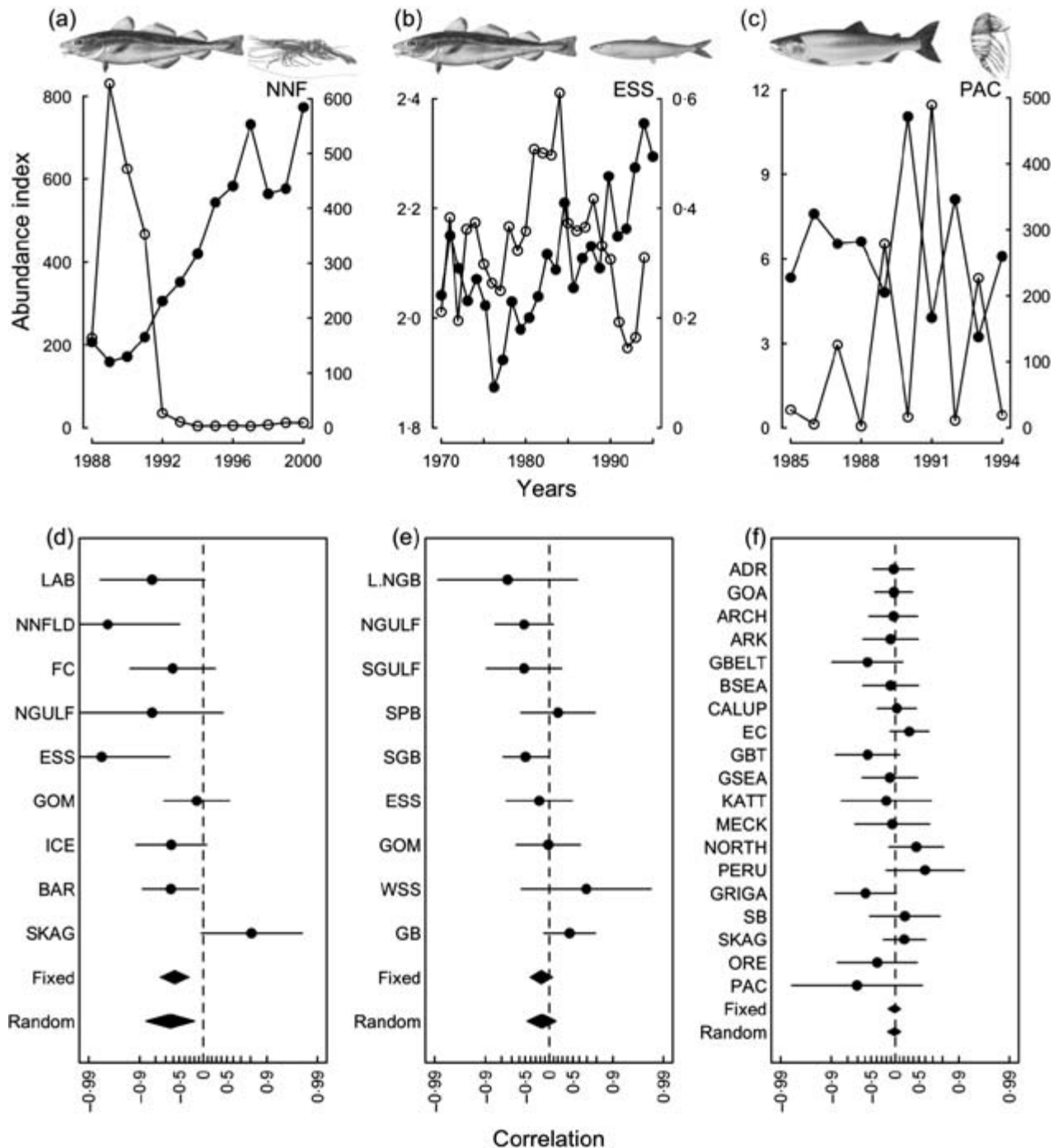


Fig. 2. Meta-analyses of predator–prey interactions from time series data based on Worm & Myers' (2003) methods. Shown are (a–c) example time series of predator (○) and prey (●) abundances, and (d–f) corresponding meta-analyses of the effects of (a,d) cod on shrimp (data from Worm & Myers 2003), (b,e) cod and other benthic piscivores on pelagic fishes (data from Frank *et al.* 2006), (c,f) pelagic fishes on zooplankton (data from Micheli 1999), including Pearson correlation coefficients (circles, with 95% confidence intervals), and weighted mean correlations (diamonds, with 95% CIs) calculated using fixed-effects (fixed) and random-effects (random) models; all data plotted on a Fisher's z scale. Study regions are as follows: (d) LAB, Labrador; NNFLD, northern Newfoundland; FC, Flemish Cap; NGULF, northern Gulf of St. Lawrence; ESS, eastern Scotian Shelf; GOM, Gulf of Maine; ICE, Iceland; BAR, Barents Sea; SKAG, Skagerrak; (e) LNGB, Labrador and northern Grand Bank; SGL, southern Gulf of St. Lawrence; SPB, St. Pierre Bank; SGB, southern Grand Bank; WSS, western Scotian Shelf; GB, Georges Bank; (f) ADR, Adriatic Sea; GOA, Gulf of Alaska; ARCH, Archipelago Sea; ARK, Arkona Sea; GBELT, Great Belt; BSEA, Bornholm Sea; CALUP, California upwelling system; EC, English Channel; GBT, German Bight; GSEA, Gotland Sea; KATT, Kattegat; MECK, Mecklenburg Bay; NORTH, Northumberland coast; PERU, Peruvian upwelling; GRIGA, Gulf of Riga; SB, Southern Bight; ORE, Oresund; PAC, subarctic Pacific.

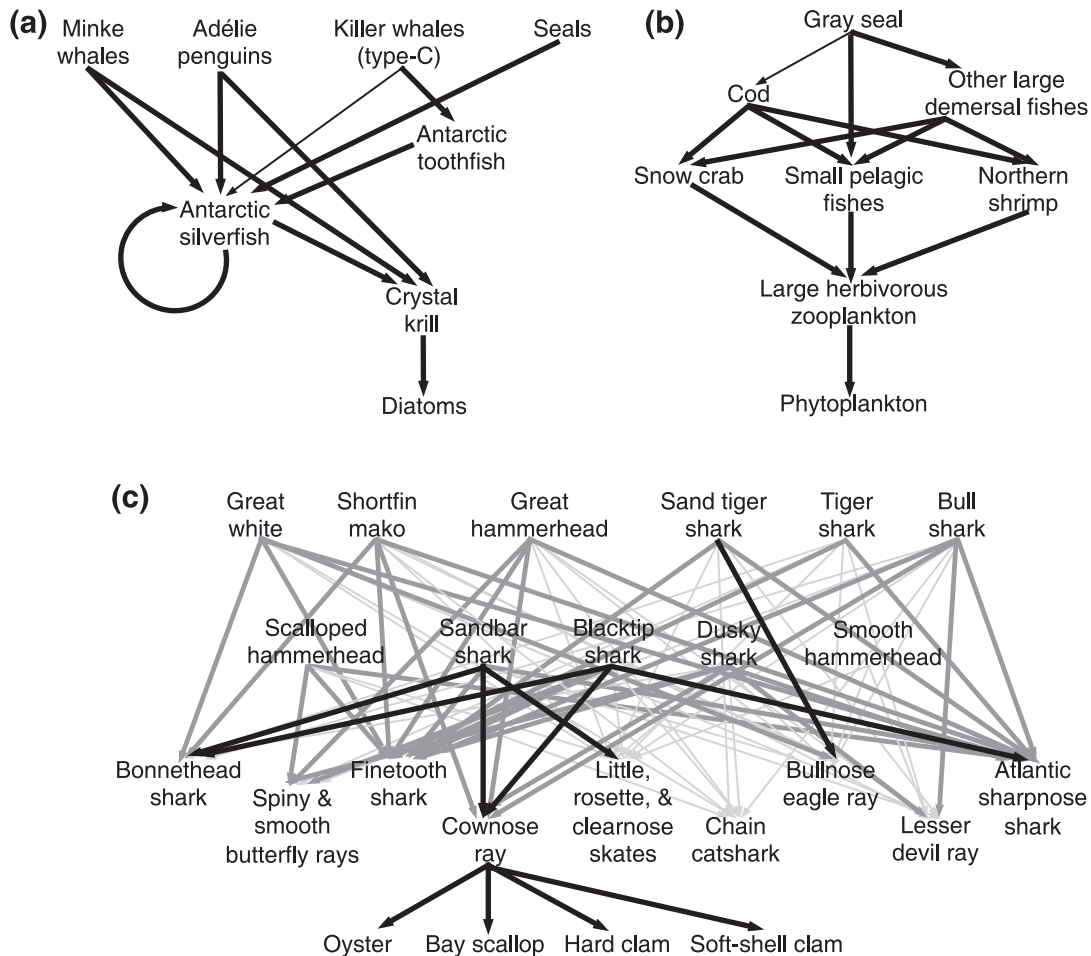


Fig. 3. Simplified oceanic food webs showing the species and direct species interactions involved in the documented trophic cascades: significant predator (thick black arrow), minor predator (thin black arrow); for sharks diet data are often known only at taxonomic levels above species: predator on species within genus (medium grey arrow), predator on species within family (thin pale grey arrow). (a) Polar sea: seasonal trophic cascade occurs as migratory apex predators deplete prey (Ainley *et al.* 2006); (b) temperate continental shelf: trophic cascade due to overfishing of cod and other benthic fishes (Frank *et al.* 2005); (c) temperate coastal, continental shelf and pelagic waters: overfishing great sharks (top two rows) leads to mesopredator release, and a trophic cascade through cownose ray to bay scallops (Myers *et al.* 2007).

foundation. The challenge lies in documenting significant predator–prey relationships in topologically complex food webs with scores of possible interactions. Here, good knowledge of species’ natural histories and diets is critical (Dayton 2003); bioenergetics and demographic models can also play a role in evaluating the plausibility of hypothesized trophic interactions (Williams *et al.* 2004). For teleost fish and plankton communities, where predator–prey relationships are strongly size structured (Verity & Smetacek 1996), trends in community size structure also may be appropriate metrics of community-wide cascading effects (e.g. Blanchard *et al.* 2005), particularly when details about specific predator–prey relationships are poorly known. Once large data sets are assembled, the temptation to examine correlations among numerous species combinations without hypotheses should be resisted (e.g. Reid *et al.* 2000), since such tactics will almost certainly produce spurious results.

Emerging patterns and factors moderating top-down effects

CASCADING EFFECTS OF CHANGES IN PREDATOR ABUNDANCE

Mesopredator release

For temperate continental shelves, evidence of mesopredator release (increases in medium-sized vertebrate predator populations following removal of their predators) continues to accumulate (Table 1). In the Northwest Atlantic, herring (*Chupea harengus*), capelin (*Mallotus villosus*), and sand lance (*Ammodytes dubius*) increased substantially on the Scotian Shelf after the collapse of cod and other large benthic fishes in the late 1980s (Table 1; Fig. 3); prey biomass was negatively correlated with predators over a 33-year time series (Choi

et al. 2004; Frank *et al.* 2005). The Newfoundland cod collapse evoked similar changes (Carscadden, Frank & Leggett 2001). In the Northeast Atlantic, a decrease in predatory fishes (100–169 g) in the Celtic Sea was associated with a significant increase in smaller species (4–25 g) (Blanchard *et al.* 2005). This size-structured analysis accounted for environmental forcing (related to the North Atlantic Oscillation), but indicated the effect of fishing on community size structure had dominated. Likewise, trawl surveys showed significant increases in small fish (< 40 cm) abundance across much of the North Sea over the past 30 years, coinciding with declines in larger predators (Daan *et al.* 2005). In the Baltic Sea, Österblom *et al.* (2007) documented successive mesopredatory releases over the twentieth century: marine mammal depletions first led to greater numbers of cod, which when depleted decades later by fishing and poor environmental conditions, led to increases in small pelagic fish. Combining trophic control studies from across the North Atlantic, Frank *et al.* (2006) and Frank, Petrie & Shackell (2007) found proliferations of mesopredatory fishes only in these and other cold, low-diversity regions.

Yet, evidence of mesopredator release also has emerged in tropical food webs, namely the open ocean (Table 1) where apex predatory tunas, billfishes, and sharks have declined significantly. In the tropical Pacific, a comparison of the early 1950s and late 1990s pelagic fish community indicated that during this time biomass of 12 apex predators plummeted while abundances of smaller fishes were either stable or increased (Ward & Myers 2005). In particular, the data suggest up to 100-fold increases in pelagic stingray (*Dasyatis violacea*) and pomfret (Bramidae) abundance, or expansion into habitats previously dominated by their predators (Ward & Myers 2005). Studies simulating changes to apex predatory fishes in the central North Pacific using Ecosim models found qualitatively similar results (reviewed by Kitchell *et al.* 2006): doubling fishing mortality further reduced apex predators with accompanying pelagic mesopredator increases. Food web responses to simulated removals of single apex predators depended on their overall predation rates and degree of dietary overlap with other predators: removal of blue shark (*Prionace glauca*), for example, had minimal effect since reduced predation by this species could be compensated for by highly productive yellowfin tuna (*Thunnus albacares*) (Schindler *et al.* 2002).

In contrast, multiple data sets show removal of large sharks from the US east coast was accompanied by significant compensatory increases in 12 elasmobranch prey species (Table 1), likely because large sharks together comprised their only significant source of predation (Myers *et al.* 2007). A similar study demonstrated, however, that simultaneous exploitation of predator and prey species could override this mesopredator release. In the northern Gulf of Mexico, where shrimp trawling yields much benthic elasmobranch bycatch, mesopredator release followed depletion of large sharks only for those deepwater mesopredators whose habitat provided a refuge from trawling (Table 1; Shepherd & Myers 2005). Shallow-water mesopredators such as cownose ray (*Rhinoptera bonasus*), smooth butterfly ray (*Gymnura micrura*), and Atlantic

sharpnose shark (*Rhizoprionodon terraenovae*) all declined along with their predators (Shepherd & Myers 2005). The same species showed large increases on the US east coast, where their predators likewise declined, but shrimp trawling is uncommon (Myers *et al.* 2007).

Invertebrate release

Rapid increases in benthic macro-invertebrates following predator depletions also appear to be common in oceanic regions, as they are in nearshore ecosystems. For example, large increases in the abundance of shrimp, crabs, and possibly lobster have followed cod depletions in continental shelf ecosystems on both sides of the Atlantic Ocean (Worm & Myers 2003; Frank *et al.* 2005; R. A. Myers, B. Worm & W. Blanchard, unpublished).

For most pelagic invertebrates, however, the underlying causes of increases are difficult to examine rigorously due to highly variable, spatially and temporally limited data. Caddy & Rodhouse (1998) speculated that the global rise in cephalopod landings between 1974 and 1994 might reflect increases in abundance due to diminished predation pressure, while observed jellyfish population explosions have been variously attributed to climatic changes (Brodeur *et al.* 1999; Attrill, Wright & Edwards 2007), competitive release (Brodeur, Sugisaki & Hunt 2002), and reduced predation (Daskalov 2002; Lynam *et al.* 2006). A central North Pacific Ecosim model supports a top-down hypothesis for squid increases, with the most perceptible ecosystem changes being marked declines in apex predators and associated increases in large squid and epipelagic fishes (Table 1; Essington 2007b). Increases in large squid, which are themselves high trophic level (> 4) predators, were linked primarily to reduced predation by sperm whales (*Physeter catodon*; trophic level = 4.7). According to this model, the apex predator guild's total biomass may have declined only slightly, but with cephalopods now constituting three-quarters of it, the composition is shifted from long-lived species to short-lived ones (Essington 2007b).

Mesopredator and invertebrate declines

Not all examples of top-down effects involve declining predator populations (Table 1). Recent papers note top-down effects involving invasive predators (Zeidberg & Robison 2007), recovering predators (Coyle *et al.* 2007), and high seasonal convergences of predators (Ainley *et al.* 2006). These predatory effects can have negative consequences for fisheries, as demonstrated for capelin in the Barents Sea. This important commercial fish has experienced two population collapses since the early 1970s, which are in part attributed to herring predation on larval capelin and competition (Hjermann, Ottersen & Stenseth 2004). Post-collapse, predation by Atlantic cod was invoked with delaying capelin recovery (Hjermann *et al.* 2004). Declines in commercial forage species also have been noted in the North Pacific: increasing groundfish stocks are thought to have contributed to declines in small pelagic fishes, shrimp, and some crab populations, in accordance with

a top-down hypothesis, but corresponding climatic changes there have also played a role (see Anderson & Piatt 1999; Zheng & Kruse 2006).

Trophic cascades

In some cases top-down control of mesopredators and invertebrates cascades to lower trophic levels. It is currently unclear how general these results are since the scarcity of standardized data covering three or more trophic levels in oceanic food webs has prevented most studies from examining this question.

Within pelagic food webs, top-down effects have seemed often to be cut short at zooplankton. Micheli (1999) performed the only meta-analytic test of oceanic trophic cascades, assembling primary data for the three lowest trophic levels and nutrient availability across 20 areas (Table 1). While a negative effect of planktivorous fish on herbivorous zooplankton abundance was found, these effects did not cascade to phytoplankton, which instead was influenced by bottom-up control of nutrients (Micheli 1999). Upon re-analysis to account for autocorrelation, even the effects on zooplankton appear nonsignificant (Fig. 2 c,f), suggesting predatory marine fishes do not generally affect plankton.

However, more recent studies paint a different picture, with some trophic cascades spanning from piscivores to plankton (Table 1). In the Black Sea, pronounced declines in dolphins and piscivorous fishes by the early 1970s led to increased abundance of planktivorous fishes, reduced zooplankton biomass, and a doubling of phytoplankton (Daskalov 2002; Daskalov *et al.* 2007). Following planktivore overexploitation, gelatinous carnivores filled their trophic niche (Oguz & Gilbert 2007). Time-series data from ~1960–1990 showed significant inverse trends in abundance across these four trophic levels; an Ecosim model reproduced the observed cascading patterns over these 30 years best when intense exploitation was combined with known increases in productivity via eutrophication (Daskalov 2002). In the Baltic, cascading effects of cod declines involved increasing sprat (*Sprattus sprattus*) and decreasing copepods *Pseudocalanus acuspes* (Möllmann *et al.* 2008). These events were probably precipitated both by cod overfishing and climate-induced shifts in salinity and temperature, which limited cod reproduction and shifted zooplankton dominance patterns. A similar cascade may have followed the Scotian Shelf cod collapse (Frank *et al.* 2005); cod and other benthic fishes showed the predicted correlations with large herbivorous zooplankton and phytoplankton, but the plankton data were patchy (time series were unavailable from the early 1970s to early 1990s), precluding their comparison with mesopredators and macro-invertebrates.

While the previous examples played out entirely in oceanic food webs, there is also evidence for mobile predators linking dynamics of oceanic and nearshore ecosystems (McCann, Rasmussen & Umbanhowar 2005). Altered predation by transient killer whales, for example, recently increased sea otter mortality in the Aleutians, Alaska, reversing the classic sea otter – urchin – kelp trophic cascade (Table 1; Estes *et al.* 1998; Springer *et al.* 2003). Notwithstanding controversy about

the cause of shifting killer whale predation (e.g. DeMaster *et al.* 2006), multiple lines of evidence point to this predation as the cause of the declines. Bioenergetics modelling suggests predation by even a few killer whales would have been sufficient to drive observed otter declines (Estes *et al.* 1998; Williams *et al.* 2004). Similarly, following depletion of large sharks on the US east coast, mesopredator release of cownose ray led to depletion of its nearshore bay scallop prey: ray-exclusion experiments reveal them as the cause of near-total scallop mortality each fall (Myers *et al.* 2007; Table 1; Fig. 3).

FACTORS PROMOTING OR INHIBITING TOP-DOWN EFFECTS

Although top-down effects are not uniformly strong in the ocean, the emerging body of literature allows for some insight as to when and where they might be expected. It is, for instance, now clear that top-down control is not limited to simple freshwater and nearshore aquatic ecosystems as previously hypothesized (Strong 1992). There is evidence of top-down control in many oceanic habitats (Table 1), a notable exception being upwelling regions, where trophic control may be dominated by pelagic planktivores (whose populations are typically large and strongly fluctuating) that seem to control the abundance of their predators, rather than vice versa (e.g. Cury *et al.* 2000). In other oceanic ecosystems, there are a growing number of examples of top-down control between trophic levels of predators, but still little evidence of these effects extending down to zooplankton (Fig. 2f; but see Daskalov 2002; Möllmann *et al.* 2008). A similar dampening of top-down control has been found in marine pelagic food web experiments ($n = 47$, Micheli 1999; $n = 9$, Shurin *et al.* 2002), but one trophic level lower, at the zooplankton–phytoplankton link. It has been suggested that this may reflect weak coupling at this link, as seen in lakes (Brett & Goldman 1997). However, more recent experiments with finer-scale taxonomic resolution suggested trophic cascades do reach the base of these food webs, but along two parallel food chains of contrasting length in which copepods reduce large algae but simultaneously promote small algae by feeding on ciliates, such that top-down effects on total algal biomass cancel out (Stibor *et al.* 2004). Although this finding still requires testing on large scales, it is clear from field observations that the edibility of algae, and the composition of the grazer community can affect the balance of top-down and bottom-up control (e.g. Ainley 2007).

A related hypothesis states that predator diversity may dampen cascading top-down effects due to increased species compensation. Recent experiments show, however, that this is not necessarily so, but that outcomes are influenced by predator and prey traits and the specific predator–prey interactions that predominate. While predator diversity can enhance trophic cascades through complementarity of diets, interspecific facilitation (Sih *et al.* 1998; Duffy 2002), increased likelihood of keystone predators, or different behavioural responses by prey (Byrnes *et al.* 2006), impacts on prey may be reduced if predators engage in cannibalism, omnivory (Bruno

& O'Connor 2005), or intraguild predation (Sih, Englund & Wooster 1998; Finke & Denno 2005). In the ocean, this question has been explored by Frank *et al.* (2006, 2007), who documented declining strength of top-down control on continental shelf ecosystems with increasing diversity along a latitudinal gradient. It is currently unresolved to what extent temperature, which strongly co-varies with diversity, may also be important in affecting the strength of top-down control, for example by influencing maximum population growth rates and predator vulnerability to overexploitation (Frank *et al.* 2007).

In addition to these ecological factors, there is evidence of climate-induced oscillations in trophic control. For instance, the Gulf of Alaska's transition from decapod crustacean and small pelagic fish dominance to Pacific cod (*Gadus macrocephalus*) dominance during the 1976/1977 shift to a warmer regime was apparently facilitated by a climate-induced temporary switch from bottom-up to top-down control (Table 1; Litzow & Ciannelli 2007). Thus, while climate forcing is typically regarded as a driver of bottom-up control, rapid climate shifts may also reorganize a system's trophic control. The generality of this mechanism remains to be seen.

Overlaid on these dynamics is the role of humans as top predators, and the question of whether top-down effects arise in these ecosystems only as 'aberration[s] imposed by man' (Strong 1992). We note that perturbations to predator populations are no longer aberrations, but the norm in all fished oceanic ecosystems, and submit that these perturbations have increased the likelihood of both occurrence and detection of cascading effects in the ocean. Three properties of exploitation appear particularly important in this regard. First, exploitation is sufficiently intense to significantly reduce the abundance of oceanic predators. Second, by targeting top predators, exploitation removes species likely to be strong interactors (Bascompte, Melia & Sala 2005). Third, even in ecosystems with high diversity and connectance, in which prey populations are controlled diffusely by multiple predators, the nonselective nature of most industrial fishing gear renders many operations de facto multispecies fisheries such that the abundance of whole predator functional groups, and overall predation, is reduced. In essence, the impact of exploitation may be to simplify oceanic ecosystems, rendering them more like those aquatic food webs in which cascading effects appear common. Explicit consideration of anthropogenic modifications to oceanic food webs thus should help inform predictions about trophic control, and may yield results not necessarily predicted by small-scale experiments.

Management implications of top-down control in the ocean

Oceanic top-down control implies that species cannot be managed in isolation, and predator-prey interactions must be understood and accounted for. Cascading effects documented to date generally involve few species rather than whole communities, but whereas the significance of such 'limited' effects has been questioned for other ecosystems (Polis *et al.* 2000), the stakes for fisheries and oceanic ecosystems are high. For

example, the socioeconomic consequences of such changes can be significant: the Northwest Atlantic cod collapse was devastating, particularly for coastal fishing communities, but also led to the boom in commercially valuable invertebrates that fuelled new fisheries for shrimp and snow crab. Such economic benefits have, however, sometimes been short lived as fisheries tracked cascading changes and reversed the trajectory of increased populations (Österblom *et al.* 2007).

Top-down control also can have important conservation implications by preventing depleted predator populations from rebuilding. Sharks may be impeding population growth both of endangered monk seals (*Monachus schauinslandi*) in the Northwest Hawaiian Islands (Bertilsson-Friedman 2006) and harbour seals (*Phoca vitulina*) on Sable Island, Nova Scotia (Lucas & Stobo 2000), while killer whales and leopard seals have apparently inhibited or reversed recovery of some marine mammals (Boveng *et al.* 1998; Estes *et al.* 1998). Predation by marine mammals also may affect commercially valuable fishes: grey seal (*Halichoerus grypus*) predation has been suggested as a factor contributing to the failed recovery of Atlantic cod. On the eastern Scotian Shelf, where seals have been increasing exponentially until recently, there is some support for this mechanism (Fig. 3; Trzcinski, Mohn & Bowen 2007). These interactions highlight potential conflicts between the full protection of marine mammals and commercial fisheries, and have led to calls for managed reductions in seal numbers despite a lack of evidence that past culls have benefited fisheries (Yodzis 2001). Predator control programmes appear much less predictable in the ocean than in lakes (Persson *et al.* 2007). Direct positive effects of reducing seal predation on cod could, for example, be overridden by indirect negative effects of reduced predation on other seal prey species, which compete with and predate on the larval stages of these fishes (Swain & Sinclair 2000).

Indeed, predation by former prey species also is implicated in the limited recovery of some piscivorous fishes, especially collapsed Atlantic cod populations. In the southern Gulf of St. Lawrence, increased predation of cod eggs and larvae by now abundant herring and mackerel may critically limit cod recruitment (Swain & Sinclair 2000). Similar interactions have been observed in the Baltic Sea (Köster & Möllmann 2000) and Georges Bank (Garrison *et al.* 2000). This is generalized in the 'cultivation-depensation' hypothesis (Walters & Kitchell 2001; or 'predator to prey loop', Bakun & Weeks 2006), where a dominant predator 'cultivates' favourable conditions for the survival of its own offspring by 'cropping down' larval predators or competitors. If the predator population declines to a critical level, however, increasing abundance of its prey can cause depensatory decreases in its own larval or juvenile survivorship. Such predator-prey role reversals are probably common in oceanic food webs, where substantial ontogenetic diet shifts mean predators attain higher trophic levels over their lifetime.

These cascading effects present considerable challenges to fisheries managers, as they may impose (i) increased variability in the system, and (ii) abrupt transitions between 'stable' states and subsequent hysteresis (Scheffer *et al.* 2001). Communities

characterized by dominant prey and depleted predators are inherently more variable both because prey are typically shorter lived (and thus more sensitive to environmental fluctuations; Jennings & Blanchard 2004) and have higher population growth rates, and because predator populations at low abundance may experience large increases in juvenile survival variability (Minto, Myers & Blanchard 2008). A likely consequence is decreased stability of fisheries catches. The failure of many depleted predator populations to recover has also challenged the traditional assumption of constant single-species stock-recruitment relationships, showing instead that these trajectories can be nonstationary, and leaving the path to recovery unclear. In some areas, top-down effects have contributed to major ecosystem changes (e.g. Baltic Sea, Black Sea, Scotian Shelf), which do not seem easily reversible. Whether managers should attempt to revert these ecosystems to their former states is debatable, but even if they wanted to, how they would do so, barring large-scale adaptive management experiments that have proven socially unacceptable to date, is generally unclear (Walters & Holling 1990). Increased variability and uncertainty as well as limited recovery rates and shifts to alternative states all should expedite the need to understand trophic control on large spatial scales.

Conclusions and future directions

We have attempted to synthesize the evidence from ecosystem-scale studies conducted in the past decade about top-down control in the ocean. There is evidence of top-down control being exerted by most taxa of high-trophic level oceanic predators (marine mammals, elasmobranchs, large teleost fishes), and of these effects playing out in many geographical regions and almost all oceanic ecosystem types (Table 1). Still, top-down control is not ubiquitous: most evidence to date involves top-down control only between predators at two adjacent trophic levels, rather than between first order predators–herbivores–plants. There is also little evidence of it being exerted by seabirds (other than penguins), or occurring in upwelling ecosystems or outside north temperate waters. We suspect this geographical gap in evidence partly reflects biases in data availability, whereas the taxonomic and ecosystem gaps may reflect real ecological differences, between the feeding ecology and dietary breadth of seabirds and other oceanic predators, and between nutrient availability and advection of upwelling and other ecosystems, respectively (Essington, in press).

Knowledge about oceanic top-down control is important as jurisdictions around the world are adopting ecosystem approaches to marine resource management and require some capacity to anticipate these effects (Pikitch *et al.* 2004). Yet while our retrospective understanding has improved, predictive capacities are still lacking. Future research should focus on identifying general rules and mechanisms that can serve as informative priors for management decisions, or engaging in experimental or adaptive management. We hope this review helps stimulate this research, and suggest the following questions as key to advancing understanding in this arena:

1. *Are there thresholds beyond which cascading changes occur, and if so what determines them?* It is uncertain how much predator abundances can be altered before cascading effects occur, and whether there are clear thresholds for large-scale ecosystem transformation. While observed cascading effects have usually followed order-of-magnitude declines in predator populations (e.g. Frank *et al.* 2005, Myers *et al.* 2007), it is unclear if this is a smooth process or if there are thresholds that we can anticipate? Carpenter and colleagues (2008) recently investigated leading indicators of trophic cascades in a modelling study of lakes, suggesting that signals of cascading regime shifts can be detected well in advance, as substantial changes in time series standard deviations, return rates after a perturbation, and variance spectra. An empirical test of such indicators in the ocean would be an important contribution.
2. *How important are non-consumptive effects of predators to oceanic top-down control?* Almost all empirical evidence for oceanic top-down control to date is based on density-mediated (i.e. consumptive) predator effects; yet a growing body of literature shows that non-consumptive effects (also known as ‘trait-mediated’ or ‘risk’ effects), which induce changes in prey behaviour, growth, or development can play an important role in predator–prey dynamics (e.g. see Peckarsky *et al.* 2008; Wirsing *et al.* 2008). We suspect that nonconsumptive effects have often been underestimated and that an improved understanding could shed much light on the mechanisms by which oceanic top-down control operates.
3. *To what extent do cascading effects propagate through ecosystems?* The ‘species-level’ cascades documented herein might truly attenuate as the number of trophic links from the originating predator(s) increases, or ‘community-level’ cascades (*sensu* Polis *et al.* 2000) may be occurring but going undetected because of data limitations or long time lags. This applies both to the questions of how broadly top-down effects extend laterally in oceanic food webs, and whether they typically propagate down through, or attenuate in, plankton communities.
4. *Interactions between top-down control, bottom-up control, and other anthropogenic stressors.* Top-down effects do not act in isolation; there is also much evidence for the importance of nutrient supply, temperature, climatic variations, and habitat. Addressing these factors together to understand their relative strengths and interdependencies (e.g. Stenseth *et al.* 2002) is still a pressing research frontier in oceanic environments where oceanographers and fisheries scientists have historically tended to focus on opposite ends of the food web and data limitations have hindered progress. Analyses that include predator abundance and biophysical ‘treatments’ with enough contrast to run the equivalent to ‘factorial experiments’ should allow researchers to start disentangling these processes and determine the factors driving spatial and temporal variation in their dominance (Hunt & McKinnell 2006; Frank *et al.* 2006). ‘End-to-end’ ecosystem models that link physical and plankton models with those focusing on higher trophic levels (Fulton *et al.* 2005; Cury *et al.* 2008) also hold great promise in this regard. A better understanding of these interactions is

needed, particularly as climate change, overexploitation, species invasions, and eutrophication are simultaneously impacting many oceanic ecosystems.

The study of oceanic top-down control is maturing from one based on correlations of single predator–prey populations, which were generally open to alternative explanations, to more robust ‘pseudo-experimental’ approaches, which emphasize replication and examination of competing hypotheses. Future studies would benefit from the growth of collaborations between oceanographers, fisheries scientists, and marine ecologists, the development of global databases that integrate oceanographic data with ecological data for oceanic species from all trophic levels, and the continuation of long-term monitoring programmes. Collaborative studies that can integrate comprehensive data into this ‘pseudo-experimental’ framework should lead to robust inferences about the operation of oceanic top-down control, and its interactions with bottom-up control and intensifying anthropogenic stresses such as climate change. Advances of this nature would enable ecosystem effects of changing oceanic predator abundances to be mitigated and better forecasted, both of which are essential for the successful long-term management of oceanic resources.

Acknowledgements

The authors express their gratitude to the late R.A. Myers for guidance and inspiration. We thank K. Frank and F. Micheli for sharing data and helpful discussions, C. Minto for insightful comments and discussion, J. Estes and D. Ainley and one anonymous reviewer for constructive comments, and the Lenfest Ocean Program, David H. Smith Research Fellows program, and NSERC for funding.

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Received 18 November 2008; accepted 19 January 2009
Handling editor: Graeme Hays